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EXTINCTION OR COEXISTENCE IN PERIODIC KOLMOGOROV SYSTEMS OF COMPETITIVE TYPE

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Abstract. We study a periodic Kolmogorov system describing two species nonlinear competition. We discuss coexistence and extinction of one or both species, and describe the domain of attraction of nontrivial periodic solutions in the axes, under conditions that generalise Gopalsamy conditions. Finally, we apply our results to a model of microbial growth and to a model of phytoplankton competition under the effect of toxins.

1. **Introduction.**

Consider the competition system

$$\begin{cases} x_1' = x_1 f_1(t, x_1, x_2), \\ x_2' = x_2 f_2(t, x_1, x_2) \end{cases} \tag{$\mathcal{S}$}$$

where x_1, x_2 represent the densities of two species and $f_1, f_2 \colon \mathbb{R} \times \mathbb{R}^2_{+0} \to \mathbb{R}$ are respectively the per capita growth rate of the first and the second species, which we suppose to be continuous, (x_1, x_2)-continuously differentiable, T-periodic in the first variable functions and satisfying for all $(t, x_1, x_2) \in [0, T] \times \mathbb{R}^2_{+0}$, $\dfrac{\partial f_i}{\partial x_i}(t, x_i \mathbf{e}_i) < 0$, for $i = 1, 2$, and $\dfrac{\partial f_i}{\partial x_j}(t, x_1, x_2) \leq 0$, for $i, j = 1, 2$ and $i \neq j$. (If necessary, check the notation in use at the end of this section.) In the literature, system $\mathcal{S}$ is

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called a *Kolmogorov system* and it models the interaction of two competing species experiencing seasonally fluctuating environments. From the ecological point of view, to know if there is extinction of one or both species or the convergence to a positive periodic solution, which gives rise to an oscillatory regime, is of course of great importance.

In the seminal paper [5], the authors consider the system

$$\begin{cases} x_1' = x_1\big(A_1(t) - a_{11}(t)x_1 - a_{12}(t)x_2\big), \\ x_2' = x_2\big(A_2(t) - a_{21}(t)x_1 - a_{22}(t)x_2\big) \end{cases} \tag{$\mathcal{S}_0$}$$

where the coefficients $A_i(t)$ and $a_{ij}(t)$ are T-periodic continuous functions. This system describes the dynamics of two species under linear competition, the $a_{ii}(t)$ reflect the intra-specific competition and the $a_{ij}(t)$, $i \neq j$, the inter-specific competition. The authors prove that all the orbits converge to a periodic one. This important result is a consequence of the monotonicity of the Poincaré-map associated to a competitive system. Through a detailed analysis of the behaviour of the Poincaré-map the authors obtain results on the domain of attraction of its fixed points and give an example of existence of a positive periodic orbit even when for the corresponding averaged system no periodic orbits exist. In a subsequent paper [7] the author assumes

$$(A_i)_L > 0, i = 1, 2 \text{ and } \frac{(a_{21})_M}{(a_{11})_L} < \frac{(A_2)_L}{(A_1)_M} \leq \frac{(A_2)_M}{(A_1)_L} \leq \frac{(a_{22})_L}{(a_{12})_M}$$

where $(.)_M$ and $(.)_L$ represent, respectively, the maximum and minimum in $[0, T]$, and proves the existence of a positive periodic solution. These conditions and their improved version in [8] for the n-dimensional case are known as *Gopalsamy conditions*. Then in [1] the global stability of the positive periodic solution was proved under these conditions and this result was refined in [21] both in the case of competitive systems and prey-predator ones. In [3] the authors prove the global stability in a more general setting for the case of the prey-predator system.

Some years later, in [20] the authors analyze the case of extinction of both or one of the species for system $\mathcal{S}_0$. They prove the extinction of one species under conditions on the coefficients which imply that all hypothetical positive periodic solutions are asymptotically stable or asymptotically unstable, arriving then to a contradiction when assuming that one of such orbits exists. These conditions generalise the Gopalsamy conditions and hence the results of Gopalsamy were obtained under the assumption that all the possible positive periodic orbits have the same stability.

As mentioned in [6] (see also the references therein) to assume the per capita growth rate of each species a linear function is not always adequate. In this paper a variant of the classical Lotka-Volterra model motivated by experiments was given in which the linear functions are replaced by nonlinear ones. The models proposed here and their variants were used in many situations. We refer a recent paper about microbial growth [14] which presents a competitive model which we will analyze in section 6. Also several papers about two species competition under the effect of toxins consider nonlinear per capita growth rates [4, 19, 10, 23].

Taking into account the importance of modelling competition in a more general way, we considered system $\mathcal{S}$. For this system we were able to give conditions for the extinction of both species (Theorem 4.1), for the extinction of one species when there exists only one nontrivial periodic orbit on the axis (Theorem 4.2), for the extinction of one species when there exists one nontrivial periodic orbit on each axis (Theorem 4.3 and Theorem 4.4) and for coexistence (Theorems 4.5 and Theorem 4.6). We can deal with the case in which for an interval of time the intra-specific or the inter-specific competition are zero which is natural in periods of time in which there is more abundance of resources.

In the case of extinction of exactly one species, when both axis have nontrivial periodic solutions, our results assume a condition analogous to the one in [20] and hence assume that all possible positive periodic orbits have the same stability. In order to tackle cases which do not satisfy these assumptions we obtained results (Theorem 5.3 and Corollary 4) in the line of a previous in [5] which describe the attraction domain of the periodic orbits in the axis. These results help doing numerical simulations as they give hints about initial conditions of solutions which can converge to coexistence orbits.

We end the paper with two applications.

Notation. Here, we list a few notations that will be used throughout this paper. For any continuous functions $z, w\colon I\times Q\subset\mathbb{R}^{1+n}\to\mathbb{R}$, we write $z\prec w$ if $z(t,x)\le w(t,x)$ for all $(t,x)\in I\times Q$ and there exists $t^*\in I$ such that $z(t^*,x)<w(t^*,x)$ for all $x\in Q$. Likewise, we write $z\prec w$ if $z,w\colon I\subset\mathbb{R}\to\mathbb{R}$ with $z(t)\le w(t)$ for all $t\in I$ and $z\not\equiv w$. We may also write $w\succ z$ whenever $z\prec w$. Given $f\colon Q\subset\mathbb{R}\to\mathbb{R}$, $Graf_f$ represents the graph of f. For any $P\in\mathbb{R}^2$, we call its first coordinate P_{x_1} and its second P_{x_2}. We denote $\mathbb{R}_+=\,]0,+\infty[$ and $\mathbb{R}_{+0}=[0,+\infty[$. Finally, $(\mathbf{e}_1,\mathbf{e}_2)$ stands for the canonical basis of $\mathbb{R}^2$.

2. **Basic properties of system $\mathcal{S}$.**

In this section, we establish the first properties of system $\mathcal{S}$ and some tools that will be useful in our future analysis.

For the convenience of the reader, we start by reproducing a classical result on existence and uniqueness of nonnegative T-periodic solutions for the one-dimensional problem

$$x' = xH(t,x). \tag{1}$$

Lemma 2.1. *Assume*

(H_0) *$H\colon\mathbb{R}\times\mathbb{R}_{+0}\to\mathbb{R}$ is a continuous function such that $H(\cdot,x)$ is T-periodic for all $x\ge 0$ and $H(t,\cdot)$ is continuously differentiable for all $t\in\mathbb{R}$,*

(H_1) $\dfrac{\partial H}{\partial x}(t,x)\prec 0,$

(H_2) *there exists $R>0$ such that* $\displaystyle\int_0^T H(t,R)\,\mathrm{d}t<0,$

(H_3) $\displaystyle\int_0^T H(t,0)\,\mathrm{d}t>0.$

Then problem 1 has a unique positive T-periodic solution $\tilde{x}(t)$. This solution is defined in $\mathbb{R}$ and is a global attractor of 1 in $]0,+\infty[$, that is, if $x(t)$ is a positive solution of 1, then

$$\lim_{t\to+\infty}\big(x(t)-\tilde{x}(t)\big)=0.$$

This result, which is a direct consequence of [25, Proposition 5] and [12, Theorem 1.1] — see also [13, 24, 22] — will often be useful when considering the evolution of each species in the absence of the other. This situation corresponds to the restriction of system $\mathcal{S}$ to each positive coordinate axis and is described by the decoupled equations

$$x_1' = x_1 f_1(t, x_1, 0) \tag{2}$$

and

$$x_2' = x_2 f_2(t, 0, x_2). \tag{3}$$

Remark 1. Assume (H_0), (H_1) and

(H_3^*) $\displaystyle\int_0^T H(t,0)\,\mathrm{d}t \leq 0.$

Then the same conclusion as in Lemma 2.1 holds with $\tilde{x} \equiv 0$.

Note that in this case, (H_2) follows from (H_1) and (H_3^*), and hence all nonnegative solutions are bounded. Also, the assumptions imply that there are no positive periodic orbits. Thus, the remark follows from [13, Theorem 2].

Now, we turn our attention to some preliminary results on the qualitative analysis of system $\mathcal{S}$.

Lemma 2.2. *Assume*

(h_0) $f_i \colon \mathbb{R} \times \mathbb{R}^2_{+0} \to \mathbb{R}$ *is a continuous function such that* $f_i(\cdot, x_1, x_2)$ *is* T*-periodic for all* $(x_1, x_2) \in \mathbb{R}^2_{+0}$ *and* $f_i(t, \cdot)$ *is continuously differentiable for all* $t \in \mathbb{R}$, *for* $i = 1, 2$,

(h_1) $\dfrac{\partial f_i}{\partial x_i}(t, x_i \mathbf{e}_i) \prec 0$, *for* $i = 1, 2$, *and* $\dfrac{\partial f_i}{\partial x_j}(t, x_1, x_2) \prec 0$, *for* $i, j = 1, 2$ *and* $i \neq j$,

(h_2) *there exists* $R > 0$ *such that* $\displaystyle\int_0^T f_1(t, R, 0)\,\mathrm{d}t < 0$ *and* $\displaystyle\int_0^T f_2(t, 0, R)\,\mathrm{d}t < 0.$

Then system $\mathcal{S}$ *is dissipative, that is, there exists* $r > 0$ *such that any solution* $(x_1(t), x_2(t))$ *of* $\mathcal{S}$ *in* $\mathbb{R}^2_{+0}$ *satisfies*

$$\limsup_{t \to +\infty} \| \, (x_1(t), x_2(t)) \, \|_\infty \leq r. \tag{4}$$

Proof. Let $(x_1(t), x_2(t)) \in \mathbb{R}^2_{+0}$ be a solution of system $\mathcal{S}$. Then, for all $i = 1, 2$, $x_i(t)$ satisfies

$$x_i' \leq x_i f_i(t, x_i \mathbf{e}_i) \quad \text{ for all } t \in \mathbb{R} \text{ and } \; x_i \geq 0.$$

By the comparison theorem for first order ordinary differential equations,

$$x_i(t) \leq x_i^*(t), \qquad \text{for all } t \in \mathbb{R}$$

where $x_i^*(t)$ is the solution of the Cauchy problem for

$$x' = x f_i(t, x \mathbf{e}_i) \tag{5}$$

with initial condition $x(0) = x_i(0)$. From Lemma 2.1 and Remark 1, $\lim\limits_{t \to +\infty} (x_i^*(t) - \tilde{x}_i(t)) = 0$, where $\tilde{x}_i(t)$ is the unique nonnegative T-periodic solution of equation 5. Therefore, there is $r > 0$ such that for all $i = 1, 2$,

$$\limsup_{t \to +\infty} x_i(t) \leq \limsup_{t \to +\infty} x_i^*(t) \leq r.$$

□

Remark 2. Under our assumptions, any Cauchy problem for $\mathcal{S}$ has a unique solution defined for each $t \geq t_0$ for each initial data $(x_1(t_0), x_2(t_0)) = (x_{10}, x_{20}) \in \mathbb{R}^2_{+0}$. An easy consequence of the uniqueness of solution of Cauchy problems associated to $\mathcal{S}$ is that the first quadrant $\mathbb{R}^2_+$ is *invariant* for the flow of system $\mathcal{S}$. The same happens with the positive axes $]0, +\infty[\times \{0\}$ and $\{0\} \times]0, +\infty[$.

As the solution of any Cauchy problem for $\mathcal{S}$ in $\mathbb{R}^2_{+0}$ is defined in $[0,+\infty[$, we may introduce the *Poincaré-map*

$$\Phi\colon \mathbb{R}^2_{+0} \to \mathbb{R}^2_{+0}, \tag{6}$$

which is the function that associates to any $(x_{10}, x_{20}) \in \mathbb{R}^2_{+0}$ the point

$$\Phi(x_{10}, x_{20}) := (x_1(T), x_2(T)),$$

where $(x_1(t), x_2(t))$ is the solution of system $\mathcal{S}$ satisfying $(x_1(0), x_2(0)) = (x_{10}, x_{20})$.

As usual, fixed points of Φ are in a one-to-one correspondence with T-periodic solutions of $\mathcal{S}$. Moreover, any such solution has the same asymptotical stability as its corresponding fixed point of Φ relative to the discrete dynamical system $\mathbb{N} \times \mathbb{R}^2_{+0} \ni (n, P) \mapsto \Phi^n(P) \in \mathbb{R}^2_{+0}$. See [11] for more details.

Lemma 2.3. *Assume (h_0), (h_1) and (h_2). Then there exists $\bar{R} \geq R$, with R defined in (h_2), such that $\mathfrak{S}_1 = [0, \bar{R}] \times [0, \bar{R}]$ is invariant under Φ. That is, $\Phi(\mathfrak{S}_1) \subseteq \mathfrak{S}_1$.*

Proof. Indeed, notice that the map $t \mapsto \int_t^T f_1(s, R, 0)\,\mathrm{d}s$ is continuous on $[0, T]$. Thus, we can define $t_1 \in [0, T]$ such that

$$M_1 := \int_{t_1}^T f_1(s, R, 0)\,\mathrm{d}s \geq \int_t^T f_1(s, R, 0)\,\mathrm{d}s, \quad \text{for every } t \in [0, T].$$

By the same argument, there exists $t_2 \in [0, T]$ such that

$$M_2 := \int_{t_2}^T f_2(s, 0, R)\,\mathrm{d}s \geq \int_t^T f_2(s, 0, R)\,\mathrm{d}s, \quad \text{for every } t \in [0, T].$$

Now, let $\bar{M} := \max\{M_1, M_2\} \geq 0$ and $\bar{R} := Re^{\bar{M}}$.

By contradiction, let us suppose that there exists $(x_0, y_0) \in \mathfrak{S}_1$ such that $\Phi(x_0, y_0) \notin \mathfrak{S}_1$. Without loss of generality, we may assume that $x_1(T) > \bar{R}$. If $x_1(t) > R$ for all $t \in [0, T]$, then assumptions (h_1) and (h_2) imply that

$$x_1(T) = x_1(0)e^{\int_0^T f_1(t, x_1(t), x_2(t))\,\mathrm{d}t} < x_1(0)e^{\int_0^T f_1(t, R, 0)\,\mathrm{d}t} < x_1(0) \leq \bar{R}.$$

Otherwise, by the continuity of $x_1(t)$, there exists

$$\bar{t} := \max\{t \in [0, T] \colon x_1(t) \leq R\}.$$

Then we have

$$\begin{aligned} x_1(T) &= x_1(\bar{t})e^{\int_{\bar{t}}^T f_1(t, x_1(t), x_2(t))\,\mathrm{d}t} \\ &\leq x_1(\bar{t})e^{\int_{\bar{t}}^T f_1(t, R, 0)\,\mathrm{d}t} \leq x_1(\bar{t})e^{\int_{t_1}^T f_1(t, R, 0)\,\mathrm{d}t} = Re^{M_1} \leq Re^{\bar{M}} = \bar{R}. \end{aligned}$$

In both cases, we obtain a contradiction. □

Corollary 1. *Assume (h_0), (h_1) and (h_2). Then there exists $\bar{R} > 0$ such that the set $\mathfrak{S}_1$, defined in Lemma 2.3, is both* Φ-invariant *and* attractive.

Proof. Indeed, in the proof of Lemma 2.3, we may consider $\bar{R} = \max\{Re^{\bar{M}}, r\}$, with r given in Lemma 2.2. By doing so, the claim is proved. □

Also, note that the Poincaré-map Φ is a particular case of the *solution operator* defined for any $t \geq t_0$ as the map

$$G(t, t_0) \colon \mathbb{R}^2_{+0} \to \mathbb{R}^2_{+0}$$

that associates any point $(x_{10}, x_{20}) \in \mathbb{R}^2_{+0}$ to the point

$$G(t, t_0)(x_{10}, x_{20}) := (x_1(t), x_2(t)),$$

where $(x_1(\cdot), x_2(\cdot))$ is the solution of $\mathcal{S}$ satisfying $(x_1(t_0), x_2(t_0)) = (x_{10}, x_{20})$.

The map G is continuous, t-differentiable for $t \geq t_0$, $\mathbb{R}^2_+$ and the positive coordinate axes are invariant under G, and $G(t, r)G(r, t_0) = G(t, t_0)$ for all $t \geq r \geq t_0$. In what follows we will always consider $t_0 = 0$.

For any $\hat{P} = (\hat{x}_1, \hat{x}_2) \in \mathbb{R}^2_+$, we define the *relative open quadrants of* $\hat{P}$ as

$$\begin{aligned}
\big[\hat{P}\big]_1 &= \big\{(x_1, x_2) \in \mathbb{R}^2_+ \colon x_1 > \hat{x}_1 \,,\, x_2 > \hat{x}_2\big\},\\
\big[\hat{P}\big]_2 &= \big\{(x_1, x_2) \in \mathbb{R}^2_+ \colon x_1 < \hat{x}_1 \,,\, x_2 > \hat{x}_2\big\},\\
\big[\hat{P}\big]_3 &= \big\{(x_1, x_2) \in \mathbb{R}^2_+ \colon x_1 < \hat{x}_1 \,,\, x_2 < \hat{x}_2\big\},\\
\big[\hat{P}\big]_4 &= \big\{(x_1, x_2) \in \mathbb{R}^2_+ \colon x_1 > \hat{x}_1 \,,\, x_2 < \hat{x}_2\big\}.
\end{aligned}$$

In the remaining of this section, we shall prove some useful results concerning the evolution of the relative open quadrants through the solution operator $G(t, 0)$.

Lemma 2.4. *Assume* (h_0) *and*

(h_1^-) *for all* $(t, x_1, x_2) \in [0, T] \times \mathbb{R}^2_{+0}$, $\dfrac{\partial f_i}{\partial x_j}(t, x_1, x_2) \leq 0$, *for* $i, j = 1, 2$ *and* $i \neq j$.

Take $P \in \mathbb{R}^2_+$ *and* $Q \in \overline{\big[P\big]_i} \setminus \{P\}$, *with* $i = 2, 4$. *Then the following inclusion holds*

$$G(t, 0)Q \in \overline{\big[G(t, 0)P\big]_i} \setminus \{G(t, 0)P\}, \qquad \textit{for all } t > 0.$$

Proof. The claim for $i = 4$ follows from Lemma 2 in [18].

On the other hand, if $P \in \mathbb{R}^2_+$ and $Q \in \overline{\big[P\big]_2} \setminus \{P\}$, then obviously $P \in \overline{\big[Q\big]_4} \setminus \{Q\}$. By the previous statement,

$$G(t, 0)P \in \overline{\big[G(t, 0)Q\big]_4} \setminus \{G(t, 0)Q\}, \qquad \text{for all } t > 0,$$

and therefore

$$G(t, 0)Q \in \overline{\big[G(t, 0)P\big]_2} \setminus \{G(t, 0)P\}, \qquad \text{for all } t > 0.$$

$\square$

Lemma 2.5. *Assume* (h_0) *and* (h_1^-). *Let* $P \in \mathbb{R}^2_+$ *and* $Q \in \big[P\big]_i$, *with* $i = 1, 3$. *Then one of the following alternatives holds*

(S_1) $G(t, 0)Q \in \big[G(t, 0)P\big]_i$ *for all* $t \geq 0$,

(S_2) *there exists* $t' > 0$ *such that*

$$G(t', 0)Q \in \overline{\big[G(t', 0)P\big]_j} \setminus \{G(t', 0)P\} \qquad \textit{for } j = 2 \textit{ or } j = 4,$$

and for all $t > t'$,

$$G(t, 0)Q \in \overline{\big[G(t, 0)P\big]_j} \setminus \{G(t, 0)P\} \qquad \textit{with } j = 2 \textit{ or } j = 4, \textit{ respectively.}$$

Proof. Without loss of generality, we may take $i = 1$. Let us write

$G(t, 0)P = \big(x_1(t), x_2(t)\big)$ and $G(t, 0)Q = \big(x_1(t) + h_1(t), x_2(t) + h_2(t)\big)$, for all $t \geq 0$,

where $h_i(t)$ is continuous for $t \geq 0$ and $i = 1, 2$. Note that $h_1(0), h_2(0) > 0$. Then there are only three possibilities.

If $h_1(t) > 0$ and $h_2(t) > 0$, for all $t \geq 0$, then situation (S_1) holds.

If there is some $t' > 0$ such that either $h_1(t') = 0$ and $h_2(t') > 0$, or $h_1(t') > 0$ and $h_2(t') = 0$, then

$G(t', 0)Q \in \overline{\big[G(t', 0)P\big]_j}$ for $j = 2$ or $j = 4$, respectively, and $G(t', 0)Q \neq G(t', 0)P$.

Then the statement of situation (S_2) follows from Lemma 2.4.

Finally, if there is $t'' > 0$ such that $h_1(t'') = h_2(t'') = 0$, then $G(t'', 0)Q = G(t'', 0)P$. Note that this contradicts the uniqueness of solution for Cauchy problems associated with $\mathcal{S}$, and therefore this situation will not occur. $\square$

In the next corollaries we see that a stronger assumption on the partial derivatives allows to sharpen the previous results.

Corollary 2. *Assume* (h_0) *and*

(h_1^+) *for all* $(t, x_1, x_2) \in [0, T] \times \mathbb{R}^2_{+0}$, $\dfrac{\partial f_i}{\partial x_j}(t, x_1, x_2) < 0$, *for* $i, j = 1, 2$ *and* $i \neq j$.

Take $P \in \mathbb{R}^2_+$ *and* $Q \in \overline{\left[P\right]_i} \setminus \{P\}$, *with* $i = 2, 4$. *Then the following inclusion holds*

$$G(t, 0)Q \in \left[G(t, 0)P\right]_i, \quad \text{for all } t > 0.$$

Corollary 3. *Assume* (h_0) *and* (h_1^+). *Let* $P \in \mathbb{R}^2_+$ *and* $Q \in \left[P\right]_i$, *with* $i = 1, 3$. *Then one of the following alternatives holds*

(S_1) $G(t, 0)Q \in \left[G(t, 0)P\right]_i$ *for all* $t \geq 0$,

(S_2^*) *there exists* $t' > 0$ *such that*

$$G(t', 0)Q \in \overline{\left[G(t', 0)P\right]_j} \setminus \{G(t', 0)P\} \quad \text{for } j = 2 \text{ or } j = 4,$$

and for all $t > t'$,

$$G(t, 0)Q \in \left[G(t, 0)P\right]_j \quad \text{with } j = 2 \text{ or } j = 4, \text{ respectively.}$$

We will only demonstrate Corollary 2, as the proof of Corollary 3 is identical to the one of Lemma 2.5.

Proof of Corollary 2. It follows closely the proof of Lemma 3.2 in [5].

Without loss of generality, let us assume that $i = 2$. Take $Q \in \overline{\left[P\right]_2}$ and $Q \neq P$. We will show that

$$G(t, 0)Q \in \left[G(t, 0)P\right]_2.$$

To do so, let us denote

$G(t, 0)P = \big(x_1(t), x_2(t)\big)$ and $G(t, 0)Q = \big(x_1(t) + h_1(t), x_2(t) + h_2(t)\big)$, for all $t \geq 0$,

where $h_i(t)$ is continuous for $t \geq 0$ and $i = 1, 2$. By assumption,

$$h_1(0) \leq 0, \quad h_2(0) \geq 0, \quad -h_1(0) + h_2(0) > 0,$$

and we would like to prove that

$$h_1(t) < 0 \text{ and } h_2(t) > 0, \quad \text{for all } t > 0.$$

The pair $(h_1(t), h_2(t))$ satisfies

$$\begin{cases} h_1' = x_1\big(f_1(t, x_1 + h_1, x_2 + h_2) - f_1(t, x_1, x_2)\big) + h_1 f_1(t, x_1 + h_1, x_2 + h_2) \\ h_2' = x_2\big(f_2(t, x_1 + h_1, x_2 + h_2) - f_2(t, x_1, x_2)\big) + h_2 f_2(t, x_1 + h_1, x_2 + h_2) \end{cases}.$$

If $h_1(0) = 0$, then $h_2(0) > 0$ and, from assumption (h_1^+), we have

$$h_1'(0) = x_1\big(f_1(0, x_1, x_2 + h_2) - f_1(0, x_1, x_2)\big) < 0.$$

The same way, if $h_2(0) = 0$, we see that

$$h_1(0) < 0 \quad \text{and} \quad h_2'(0) = x_2\big(f_2(0, x_1 + h_1, x_2) - f_2(0, x_1, x_2)\big) > 0.$$

Then, there exists $\tau > 0$ such that

$$h_1(t) < 0 \text{ and } h_2(t) > 0, \qquad \text{for all } t \in \,]0, \tau[.$$

Now, let us suppose that $h_1(\tau) = 0$. By the uniqueness of solution for Cauchy problems associated with $\mathcal{S}$, we see that $h_2(\tau) > 0$. So, arguing as above, we obtain

$$h_1'(\tau) = x_1\big(f_1(t, x_1, x_2 + h_2) - f_1(t, x_1, x_2)\big) < 0,$$

which is impossible. Analogously, we would obtain a contradiction if we considered $h_2(\tau) = 0$. □

Finally, we conclude this section with an important result on the limit of all nonnegative solutions of system $\mathcal{S}$, which follows from [18, Theorem 4]. Its proof is included for completeness.

Theorem 2.6. *Assume (h_0), (h_1) and (h_2). Then for any $P \in \mathbb{R}^2_{+0}$, the sequence $\big(\Phi^n(P)\big)_n$ converges to a fixed point of Φ. In other words, any nonnegative solution of $\mathcal{S}$ converges to a T-periodic solution as $t \to +\infty$.*

Proof. Notice that if $P \in [0, +\infty[\, \times \{0\}$ or $P \in \{0\} \times [0, +\infty[$, then the claim is a direct result of the application of Lemma 2.1 and Remark 1 to systems 2 or 3, respectively.

If $P \in \mathbb{R}^2_+$, we may follow the lines of [5, Theorem 4.1].

If $\Phi(P) = P$, the claim is proved. If not, there is some $i = 1, 2, 3, 4$, such that $\Phi(P) \in \overline{[P]_i} \setminus \{P\}$. From Lemmas 2.4 and 2.5 and Corollary 1, there exist $j = 1, 2, 3, 4$ and $n_0 > 0$ such that for all $n > n_0$ we have

$$\Phi^n(P) \in \overline{[\Phi^{n-1}(P)]_j} \quad \text{and} \quad \Phi^n(P) \in \mathfrak{S}_1.$$

Then both coordinates of $\big(\Phi^n(P)\big)_{n>n_0}$ are monotone and bounded. Therefore the sequence $\big(\Phi^n(P)\big)_n$ converges to a fixed point of Φ. □

3. **Auxiliary Lemmas.** Here, we collect some useful results on the stability of the trivial solution of linear T-periodic systems with continuous coefficients of the form

$$\begin{bmatrix} u_1' \\ u_2' \end{bmatrix} = \begin{bmatrix} a_{11}(t) & a_{12}(t) \\ a_{21}(t) & a_{22}(t) \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = A(t) \begin{bmatrix} u_1 \\ u_2 \end{bmatrix}. \tag{7}$$

Our results generalise Lemmas 3 and 4 in [20], as we allow the coefficients $a_{ij}(t)$, with $i \neq j$, to take the value zero.

Until the end of this section, let $V(t)$ be the fundamental matrix of system 7 with $V(0) = I_2 = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$.

Lemma 3.1. *Assume*

(A_0) *$a_{ij} \colon \mathbb{R} \to \mathbb{R}$ is a continuous T-periodic function for all $i, j = 1, 2$,*

(A_1) *$a_{ij}(t) \succ 0$ for all $i, j = 1, 2$ and $i \neq j$.*

Then $\mathbb{R}^2_{+0}$ is invariant under the flow of system 7. In addition, for any nontrivial solution in $\mathbb{R}^2_{+0}$ with $u_i(0) = 0$, for some $i = 1, 2$, there exists $t' \in [0, T]$ such that $u_i(t) > 0$ for all $t > t'$.

Proof. We may assume, without loss of generality, that $a_{ii} > 0$ for $i = 1, 2$. Indeed, if it were not the case, let $\eta_0 > 0$ be such that $a_{ii}(t) + \eta_0 > 0$ for all $t \in \mathbb{R}$ and $i = 1, 2$. Set $W(t) = V(t) \exp(\eta_0 t)$. Notice that $W(t)$ satisfies

$$W'(t) = (A(t) + \eta_0 I_2)\, W(t) = \tilde{A}(t) W(t) \quad \text{and} \quad W(0) = I_2,$$

where $\tilde{A}(t)$ is a T-periodic matrix satisfying all our positivity assumptions, and that $V_{ij}(t)$ as the same sign as $W_{ij}(t)$ for all $t \in \mathbb{R}$.

It is easily seen that $\mathbb{R}^2_+$ is invariant under the flow of system 7.

If without loss of generality, we suppose that $u_1(0) = 0$ and $u_2(0) > 0$, then we get

$$u_2'(0) = a_{22}(0)u_2(0) > 0.$$

So, there exists $\delta > 0$ such that $u_2(t) > 0$ for all $t \in [0, \delta[$. This implies that $u_2(t) > 0$ for all $t \geq 0$. In fact, if that was not the case, let

$$t^* := \inf\{t > 0 \colon u_2(t) = 0\}.$$

Then there exists $s \in]0, t^*[$ such that $u_2'(s) < 0$.

On the other hand, notice that writing $\varphi(t) := a_{12}(t)u_2(t)$, we have

$$u_1'(t) = a_{11}(t)u_1(t) + \varphi(t).$$

Then, given the initial condition $u_1(0) = 0$, we see that

$$u_1(t) = e^{\int_0^t a_{11}(s)\,\mathrm{d}s} \int_0^t \varphi(s) e^{\int_0^t -a_{11}(\xi)\,\mathrm{d}\xi}\,\mathrm{d}s \geq 0 \quad \text{for all } t \in [0, t^*]. \tag{8}$$

Therefore, we obtain the contradiction

$$u_2'(s) = a_{21}(s)u_1(s) + a_{22}(s)u_2(s) > 0$$

and verify that $u_2(t) > 0$ for all $t \geq 0$.

From 8, we now conclude that $u_1(t) \geq 0$ for all $t \geq 0$. Moreover, since there exists $t' \in [0, T]$ such that $a_{12}(t') > 0$, then $u_1(t) > 0$ for all $t > t'$, which proves the claim. □

Lemma 3.2. *Assume* (A_0), (A_1) *and*

(B_S) *there exist* $\alpha_1, \alpha_2 > 0$ *such that for all* $t \in [0, T]$

$$B_1(t) = \alpha_1 a_{11}(t) + \alpha_2 a_{21}(t) \leq 0, \quad B_2(t) = \alpha_1 a_{12}(t) + \alpha_2 a_{22}(t) \leq 0,$$

and $B_1(t) + B_2(t) \prec 0$.

Then the eigenvalues λ_1, λ_2 *of* $V(T)$ *satisfy* $0 < \lambda_1 < \lambda_2 < 1$, *and hence, the zero solution of system 7 is asymptotically stable.*

Proof. From Lemma 3.1, it follows in particular that the fundamental matrix $V(t)$ satisfies $V(t) \geq 0$ for all $t \geq 0$. More precisely, $V_{ii}(t) > 0$ for all $t \geq 0$, for $i = 1, 2$, and there exists $t'' \in [0, T[$ such that $V_{ij}(t) > 0$ for all $t > t''$, for $i, j = 1, 2$ and $i \neq j$.

Therefore, we have $V_{ij}(T) > 0$ for all $i, j = 1, 2$. Then Perron-Frobenius Theorem (see for example [9]) implies that the eigenvalues λ_1, λ_2 of $V(T)$ satisfy

i) $\lambda_1, \lambda_2 \in \mathbb{R}$, $\lambda_2 > 0$ and $|\lambda_1| < \lambda_2$,

ii) there exists an eigenvector $v_0 = (v_{10}, v_{20})$ such that $v_{i0} > 0$, for $i = 1, 2$, and $V(T)v_0 = \lambda_2 v_0$.

Let

$$v(t) = \begin{bmatrix} v_1(t) \\ v_2(t) \end{bmatrix} = V(t)v_0 = \begin{bmatrix} V_{11}(t)v_{10} + V_{12}(t)v_{20} \\ V_{21}(t)v_{10} + V_{22}(t)v_{20} \end{bmatrix}.$$

Clearly, $v_i(t) > 0$ for all $t \geq 0$ and $i = 1, 2$ and $v(T) = \lambda_2 v_0$. Now, let us consider $S(t) := \alpha_1 v_1(t) + \alpha_2 v_2(t)$, where α_1 and α_2 are the constants in assumption (B_S). Taking the derivative, we obtain

$$\frac{\mathrm{d}S}{\mathrm{d}t} = B_1(t)v_1(t) + B_2(t)v_2(t) \quad \text{for all } t \geq 0$$

and thus

$$S(T) - S(0) = \int_0^T B_1(t)v_1(t) + B_2(t)v_2(t)\,\mathrm{d}t < 0.$$

Hence, we get

$$\lambda_2(\alpha_1 v_{10} + \alpha_2 v_{20}) < \alpha_1 v_{10} + \alpha_2 v_{20}$$

and, since v_0 is an eigenvector,

$$\lambda_2 < 1.$$

From Liouville's formula we see that

$$\lambda_1\lambda_2 = \det V(T) = e^{\int_0^T a_{11}(t)+a_{22}(t)\,\mathrm{d}t} > 0.$$

Then

$$0 < \lambda_1 < \lambda_2 < 1.$$

Finally, the Floquet theory for periodic linear systems yields the asymptotical stability of the zero solution of 7. □

Lemma 3.3. *Assume* (A_0), (A_1) *and*

(A_2) $\displaystyle\int_0^T \big(a_{11}(t) + a_{22}(t)\big)\,\mathrm{d}t \le 0,$

(B_U) *there exist* $\alpha_1, \alpha_2 > 0$ *such that for all* $t \in [0, T]$

$$B_1(t) = \alpha_1 a_{11}(t) + \alpha_2 a_{21}(t) \ge 0, \quad B_2(t) = \alpha_1 a_{12}(t) + \alpha_2 a_{22}(t) \ge 0,$$

and $B_1(t) + B_2(t) \succ 0$.

Then the eigenvalues λ_1, λ_2 *of* $V(T)$ *satisfy* $0 < \lambda_1 < 1 < \lambda_2$, *and hence, the zero solution of system 7 is a saddle point.*

Proof. Arguing as in the Proof of Lemma 3.2, we see that

$$S(T) - S(0) = \int_0^T B_1(t)v_1(t) + B_2(t)v_2(t)\,\mathrm{d}t > 0.$$

Therefore,

$$\lambda_2(\alpha_1 v_{10} + \alpha_2 v_{20}) > \alpha_1 v_{10} + \alpha_2 v_{20},$$

which yields

$$\lambda_2 > 1.$$

On the other hand, from Liouville's formula and assumption (A_2) it follows that

$$0 < \lambda_1\lambda_2 = \det V(T) = e^{\int_0^T a_{11}(t)+a_{22}(t)\,\mathrm{d}t} \le 1.$$

Hence,

$$0 < \lambda_1 < 1.$$

Then the Floquet theory for periodic linear systems implies that the zero solution of system 7 is a saddle point. □

Remark 3. Notice that assumption (B_S) in Lemma 3.2 implies that $a_{ii} \prec 0$, for $i = 1, 2$, which is a stronger condition than assumption (A_2).

4. **Extinction and coexistence results.** In this section, we study the dynamics of system $\mathcal{S}$. Under our assumptions, system $\mathcal{S}$ has a trivial solution $(0,0)$ and at most two semi-trivial T-periodic solutions $(\tilde{x}_1, 0)$ and $(0, \tilde{x}_2)$, with $\tilde{x}_i(t) > 0$, for all $t \in \mathbb{R}$ and $i = 1, 2$. Our results will correspond to different dynamics of $\mathcal{S}$: extinction of one or both species or coexistence. We mention that in [16] there are results in the line of the ones in this section for discrete systems. In particular, permanence is proved under analogous conditions of the ones in Theorem 4.6.

We will first consider a situation where there are no positive T-periodic solutions on the axes. As one may expect, in this case both species will go extinct.

Theorem 4.1. *Assume* (h_0), (h_1), (h_2), *and*

(h_{3a}) $\displaystyle\int_0^T f_i(t,0,0)\,\mathrm{d}t \le 0$, *for* $i = 1, 2$.

Then any nonnegative solution $(x_1(t), x_2(t))$ *of problem* $\mathcal{S}$ *with* $x_1(0) \ge 0$ *and* $x_2(0) \ge 0$ *satisfies*

$$\lim_{t\to+\infty} x_1(t) = \lim_{t\to+\infty} x_2(t) = 0.$$

Proof. From (h_1), we have

$$x_1' = x_1 f_1(t, x_1, x_2) \le x_1 f_1(t, x_1, 0)$$

for all $t \ge 0$ and all $(x_1, x_2) \in \mathbb{R}^2_{+0}$. Let us consider the solution $u_1(t)$ of the initial value problem

$$\begin{cases} u' = u\, f_1(t, u, 0), \\ u(0) = x_1(0). \end{cases}$$

The comparison theorem for first order differential equations implies that

$$0 \le x_1(t) \le u_1(t) \qquad \text{for all } t \ge 0.$$

Under our assumptions, Remark 1 yields $\lim_{t\to+\infty} u_1(t) = 0$, and therefore $\lim_{t\to+\infty} x_1(t) = 0$.

In a similar way, one can see that $\lim_{t\to+\infty} x_2(t) = 0$. □

Next, we discuss a situation where there exists a positive T-periodic solution on one axis, and none on the other.

Theorem 4.2. *Assume* (h_0), (h_1), (h_2),

(h_1^{++}) *for all* $(t, x_1) \in [0,T] \times \mathbb{R}_{+0}$, $\quad \dfrac{\partial f_1}{\partial x_1}(t, x_1, 0) < 0$,

(h_{3b}) $\displaystyle\int_0^T f_1(t,0,0)\,\mathrm{d}t > 0$ *and* $\displaystyle\int_0^T f_2(t,0,0)\,\mathrm{d}t \le 0$.

Then any nonnegative solution $(x_1(t), x_2(t))$ *of problem* $\mathcal{S}$ *with* $x_1(0) > 0$ *and* $x_2(0) \ge 0$ *satisfies*

$$\lim_{t\to+\infty} \big(x_1(t) - \tilde{x}_1(t)\big) = 0 \quad \textit{and} \quad \lim_{t\to+\infty} x_2(t) = 0,$$

where $\tilde{x}_1(t)$ *is the unique positive* T*-periodic solution of* 2.

Proof. The same argument as in Theorem 4.1 shows that

$$\lim_{t\to+\infty} x_2(t) = 0. \tag{9}$$

Also as before, we have

$$x_1' = x_1 f_1(t, x_1, x_2(t)) \le x_1 f_1(t, x_1, 0),$$

for all $t \ge 0$ and all $x_1 \ge 0$. By Lemma 2.1, equation 2 has a unique positive T-periodic solution $\tilde{x}_1(t)$ which is globally asymptotically stable in $]0, +\infty[\times\{0\}$. Then the comparison theorem implies that for every $\varepsilon > 0$ there exists $t_0 > 0$ such that

$$x_1(t) \le \tilde{x}_1(t) + \varepsilon \quad \text{ for all } t \ge t_0. \tag{10}$$

We will now show that there exists $t' \ge t_0$ such that

$$\tilde{x}_1(t) - \varepsilon \le x_1(t) \quad \text{ for all } t \ge t'. \tag{11}$$

From the assumptions on f_1, we infer that there exists $\eta_0 > 0$ such that for all $\eta \in [0, \eta_0]$ we have

$$\frac{\partial f_1}{\partial x_1}(t, x_1, \eta) < 0, \quad \text{ for all } t \ge 0 \text{ and } 0 \le x_1 \le \bar{R},$$

$$\int_0^T f_1(t, 0, \eta)\,\mathrm{d}t > 0 \quad \text{ and } \quad \int_0^T f_1(t, R, \eta)\,\mathrm{d}t < 0,$$

with R and $\bar{R} > 0$ given in (h_2) and in Corollary 1, respectively. Moreover, from 9, we see that for all $\eta \in]0, \eta_0[$ there exists $t_1(\eta) > 0$ such that

$$x_1' = x_1 f_1(t, x_1, x_2(t)) \ge x_1 f_1(t, x_1, \eta)$$

for all $t \ge t_1(\eta)$ and all $x_1 \ge 0$. Note that, by Lemma 2.1, the auxiliary equation

$$u' = u\, f_1(t, u, \eta)$$

has a unique positive T-periodic globally asymptotically stable solution, which we will represent by $u_\eta(t)$. Then, the comparison theorem implies that there is some $t_2(\eta) > t_1(\eta)$ such that

$$x_1(t) \ge u_\eta(t) - \eta \quad \text{ for all } t \ge t_2(\eta).$$

By the theorem on the continuous dependence on parameters, we see that

$$u_\eta(t) \to u_0(t) \quad \text{ uniformly in } [0, T] \text{ as } \eta \to 0$$

and this convergence is indeed in $\mathbb{R}$ as the solutions are T-periodic. Note that $u_0(t) = \tilde{x}_1(t)$, by the uniqueness of the positive T-periodic solution of equation 2. Then, for all $\varepsilon > 0$ there exists $\eta_\varepsilon > 0$ such that

$$x_1(t) \ge u_{\eta_\varepsilon}(t) - \eta_\varepsilon \ge \tilde{x}_1(t) - \varepsilon \quad \text{ for all } t \ge t_2(\eta_\varepsilon),$$

so that 11 is indeed true. Finally, from 10 and 11 we conclude that

$$\lim_{t \to +\infty} \big(x_1(t) - \tilde{x}_1(t)\big) = 0.$$

□

The situations that interest us the most are the ones where both species survive when isolated. Motivated by [20], we will discuss situations where all positive T-periodic solutions of $\mathcal{S}$ have the same stability. We will see that the stability of the semi-trivial solutions plays a fundamental role in the dynamics of $\mathcal{S}$.

Theorem 4.3. *Assume* (h_0), (h_1), (h_2),

(h_3) $\displaystyle\int_0^T f_i(t, 0, 0)\,\mathrm{d}t > 0$, *for* $i = 1, 2$,

(h_3) $\int_0^T f_1(t,0,\tilde{x}_2(t))\,\mathrm{d}t > 0$ *and* $\int_0^T f_2(t,\tilde{x}_1(t),0)\,\mathrm{d}t < 0$, *where* $\tilde{x}_1(t)$ *and* $\tilde{x}_2(t)$ *are the unique positive T-periodic solutions of equations 2 and 3, respectively,*

(h_{5S}) *there exist* $\alpha_1, \alpha_2 > 0$ *such that for all* $(t,x_1,x_2) \in [0,T] \times \mathfrak{S}_1$

$$A_1(t,x_1,x_2) = \alpha_1 \frac{\partial f_1}{\partial x_1}(t,x_1,x_2) - \alpha_2 \frac{\partial f_2}{\partial x_1}(t,x_1,x_2) \leq 0,$$
$$A_2(t,x_1,x_2) = -\alpha_1 \frac{\partial f_1}{\partial x_2}(t,x_1,x_2) + \alpha_2 \frac{\partial f_2}{\partial x_2}(t,x_1,x_2) \leq 0,$$

and $A_1(t,x_1,x_2) + A_2(t,x_1,x_2) \prec 0$.

Then any nonnegative solution $(x_1(t),x_2(t))$ *of problem* $\mathcal{S}$ *with* $x_1(0) > 0$ *and* $x_2(0) \geq 0$ *satisfies*

$$\lim_{t\to+\infty} \big(x_1(t) - \tilde{x}_1(t)\big) = 0 \quad \textit{and} \quad \lim_{t\to+\infty} x_2(t) = 0. \tag{12}$$

Proof. First, we notice that $\mathcal{S}$ has a trivial solution $(0,0)$ and two semi-trivial solutions $(\tilde{x}_1,0)$ and $(0,\tilde{x}_2)$, where, according to Lemma 2.1, $\tilde{x}_1$ and $\tilde{x}_2$ are the unique positive T-periodic solutions of the decoupled equations 2 and 3, respectively. We will prove that under our assumptions $(\tilde{x}_1,0)$ is a global attractor. To do so, we divide the proof in five steps.

Step 1: Stability analysis of the trivial and semi-trivial solutions of $\mathcal{S}$. For the trivial solution, the linearization of $\mathcal{S}$ at $(0,0)$ is

$$\begin{cases} u_1' = u_1 f_1(t,0,0), \\ u_2' = u_2 f_2(t,0,0). \end{cases}$$

Then, by assumption (h_3), the Floquet multipliers are

$$e^{\int_0^T f_1(t,0,0)\,\mathrm{d}t} > 1 \quad \text{and} \quad e^{\int_0^T f_2(t,0,0)\,\mathrm{d}t} > 1.$$

Hence, $(0,0)$ is linearly unstable.

The linearization of $\mathcal{S}$ at $(\tilde{x}_1,0)$ is

$$\begin{cases} u_1' = u_1 f_1(t,\tilde{x}_1,0) + u_1\tilde{x}_1 \dfrac{\partial f_1}{\partial x_1}(t,\tilde{x}_1,0) + u_2\tilde{x}_1 \dfrac{\partial f_1}{\partial x_2}(t,\tilde{x}_1,0), \\ u_2' = u_2 f_2(t,\tilde{x}_1,0). \end{cases}$$

Since $\int_0^T f_1(t,\tilde{x}_1,0)\,\mathrm{d}t = 0$, assumptions (h_1) and (h_4) guarantee that the Floquet multipliers are

$$e^{\int_0^T f_2(t,\tilde{x}_1(t),0)\,\mathrm{d}t} < 1 \quad \text{and} \quad e^{\int_0^T \tilde{x}_1(t)\frac{\partial f_1}{\partial x_1}(t,\tilde{x}_1(t),0)\,\mathrm{d}t} < 1,$$

and so $(\tilde{x}_1,0)$ is linearly asymptotically stable.

Analogously, the linearization of $\mathcal{S}$ at $(0,\tilde{x}_2)$ is

$$\begin{cases} u_1' = u_1 f_1(t,0,\tilde{x}_2), \\ u_2' = u_1\tilde{x}_2 \dfrac{\partial f_2}{\partial x_1}(t,0,\tilde{x}_2) + u_2 f_2(t,0,\tilde{x}_2) + u_2\tilde{x}_2 \dfrac{\partial f_2}{\partial x_2}(t,0,\tilde{x}_2). \end{cases}$$

The Floquet multipliers are

$$e^{\int_0^T f_1(t,0,\tilde{x}_2(t))\,\mathrm{d}t} > 1 \quad \text{and} \quad e^{\int_0^T \tilde{x}_2(t)\frac{\partial f_2}{\partial x_2}(t,0,\tilde{x}_2(t))\,\mathrm{d}t} < 1,$$

and therefore $(0,\tilde{x}_2)$ is a saddle point.

Step 2: Stability analysis of any positive T-periodic solution of $\mathcal{S}$. Let us assume that $(x_1^*(t), x_2^*(t)) \in \mathbb{R}^2_+$ is a T-periodic solution of $\mathcal{S}$. Introducing the change of variables

$$u_1 = \frac{x_1}{x_1^*} - 1 \quad \text{and} \quad u_2 = 1 - \frac{x_2}{x_2^*},$$

the linearization of system $\mathcal{S}$ at $(u_1, u_2) = (0,0)$ becomes

$$\begin{cases} u_1' = \dfrac{\partial f_1}{\partial x_1}(t, x_1^*, x_2^*)x_1^* u_1 - \dfrac{\partial f_1}{\partial x_2}(t, x_1^*, x_2^*)x_2^* u_2, \\ u_2' = -\dfrac{\partial f_2}{\partial x_1}(t, x_1^*, x_2^*)x_1^* u_1 + \dfrac{\partial f_2}{\partial x_2}(t, x_1^*, x_2^*)x_2^* u_2. \end{cases} \tag{13}$$

Notice that system 13 satisfies all the assumptions of Lemma 3.2. Then the zero solution of system 13 is asymptotically stable. This in turn implies that any positive T-periodic solution $(x_1^*(t), x_2^*(t))$ of $\mathcal{S}$ is also asymptotically stable.

Step 3: Finiteness of the number of positive T-periodic solutions of $\mathcal{S}$. By contradiction, let us suppose that there exists a sequence $\big((x_{1,n}(t), x_{2,n}(t))\big)_n$ of positive T-periodic solutions of $\mathcal{S}$ such that $(x_{1,n}(t), x_{2,n}(t)) \neq (x_{1,m}(t), x_{2,m}(t))$ for every $n \neq m$. From Lemma 2.2 it follows that any T-periodic solution of $\mathcal{S}$ belongs to $\Omega = \{(x_1, x_2) \in \mathbb{R}^2_{+0} \colon \|(x_1, x_2)\|_\infty \leq r\}$. We notice that

$$|x_{i,n}'(t)| \leq r\|f_i\|_{L^\infty([0,T]\times\Omega)} \quad \text{for every } t \in \mathbb{R},\ i = 1, 2,$$

and so the sequence $\big((x_{1,n}(t), x_{2,n}(t))\big)_n$ is equicontinuous and uniformly bounded in $\mathbb{R}$. Then Ascoli-Arzelà Theorem guarantees the existence of a subsequence $\big((x_{1,n_k}(t), x_{2,n_k}(t))\big)_k$, that we will still denote by $\big((x_{1,n}(t), x_{2,n}(t))\big)_n$, and a continuous T-periodic function $(z_1(t), z_2(t)) \in \Omega$ such that $\big((x_{1,n}(t), x_{2,n}(t))\big)_n$ converges to $(z_1(t), z_2(t))$ uniformly in $\mathbb{R}$.

From Steps 1 and 2, it follows that any T-periodic solution of $\mathcal{S}$ in $\mathbb{R}^2_{+0}$ is isolated. Thus, we conclude that $(z_1(t), z_2(t))$ is an isolated T-periodic solution of $\mathcal{S}$, contradicting the fact that it is the limit of a sequence of T-periodic functions.

Step 4: Non-existence of positive T-periodic solutions of $\mathcal{S}$. Let us consider the Poincaré-map Φ defined in 6.

Lemma 2.3, together with the invariance of Φ in $\{0\} \times [0, \bar{R}]$ and in $[0, \bar{R}] \times \{0\}$, allows us to extend the map Φ by reflection on the axes to the set $\mathfrak{S} = [-\bar{R}, \bar{R}] \times [-\bar{R}, \bar{R}]$. We will still denote this extension by Φ. This way, the map Φ is continuous on $\mathfrak{S}$ and $\Phi(\mathfrak{S}) \subseteq \mathfrak{S}$. Since there are no fixed points on the boundary of $\mathfrak{S}$, the Leray-Schauder degree is well defined and satisfies

$$\deg(I - \Phi, \mathfrak{S}, 0) = 1. \tag{14}$$

On the other hand, from [11] we infer that $i[\Phi, (0,0)] = 1$, $i[\Phi, (\tilde{x}_1, 0)] = 1$, $i[\Phi, (0, \tilde{x}_2)] = -1$, and $i[\Phi, (x_1^*, x_2^*)] = 1$ for any positive T-periodic solution (x_1^*, x_2^*) of $\mathcal{S}$. Let us assume that there exist n T-periodic solutions of $\mathcal{S}$ in $\mathbb{R}^2_+$. By the symmetry of Φ, there are exactly $4n + 5$ fixed points of Φ in $\mathfrak{S}$ and each has the same index value as its reflection in $\mathfrak{S}_1$. Thus, we have

$$\begin{aligned} \deg(I - \Phi, \mathfrak{S}, 0) &= 4n(i[\Phi, (x_1^*, x_2^*)]) + i[\Phi, (0,0)] + 2(i[\Phi, (\tilde{x}_1, 0)]) + 2(i[\Phi, (0, \tilde{x}_2)]) \\ &= 4n + 1. \end{aligned} \tag{15}$$

From 14 and 15, it follows that $n = 0$, and therefore $\mathcal{S}$ has no positive T-periodic solutions.

Step 5: Extinction of the species x_2. Theorem 2.6 guarantees that any nonnegative solution of $\mathcal{S}$ converges to a T-periodic solution. Since $(0,0)$ is a repeller, $(0,\tilde{x}_2)$ repels solutions in $\mathbb{R}^2_+$ and $(\tilde{x}_1,0)$ is asymptotically stable, we conclude that $(\tilde{x}_1,0)$ is a global attractor of $\mathcal{S}$ in $\mathbb{R}^2_+ \cup]0,+\infty[\times \{0\}$. □

In the next theorem, we discuss a situation where all positive T-periodic orbits are unstable. The conclusion will be identical to the one of the previous theorem.

Theorem 4.4. *Assume (h_0), (h_1), (h_2), (h_3), (h_4),*

(h_{5U}) *there exist $\alpha_1,\alpha_2>0$ such that for all $(t,x_1,x_2)\in[0,T]\times\mathfrak{S}_1$*

$$A_1(t,x_1,x_2)=\alpha_1\frac{\partial f_1}{\partial x_1}(t,x_1,x_2)-\alpha_2\frac{\partial f_2}{\partial x_1}(t,x_1,x_2)\geq 0,$$
$$A_2(t,x_1,x_2)=-\alpha_1\frac{\partial f_1}{\partial x_2}(t,x_1,x_2)+\alpha_2\frac{\partial f_2}{\partial x_2}(t,x_1,x_2)\geq 0,$$

and $A_1(t,x_1,x_2)+A_2(t,x_1,x_2)\succ 0$,

(h_6) $\displaystyle\int_0^T\left(\frac{\partial f_1}{\partial x_1}(t,x_1,x_2)+\frac{\partial f_2}{\partial x_2}(t,x_1,x_2)\right)\mathrm{d}t\leq 0$, *for all $(x_1,x_2)\in\mathfrak{S}_1$.*

Then any nonnegative solution $(x_1(t),x_2(t))$ of problem $\mathcal{S}$ with $x_1(0)>0$ and $x_2(0)\geq 0$ satisfies

$$\lim_{t\to+\infty}\big(x_1(t)-\tilde{x}_1(t)\big)=0 \quad \textit{and} \quad \lim_{t\to+\infty}x_2(t)=0. \tag{16}$$

Proof. Analogous to the proof of Theorem 4.3 and makes use of Lemma 3.3. □

We now discuss situations where the T-periodic solutions on the axes have the same asymptotical stability. We begin with the case where both $(\tilde{x}_1,0)$ and $(0,\tilde{x}_2)$ are asymptotically stable.

Theorem 4.5. *Assume (h_0), (h_1), (h_2), (h_3), and*

(h_{4S}) $\displaystyle\int_0^T f_1(t,0,\tilde{x}_2(t))\,\mathrm{d}t<0$ *and* $\displaystyle\int_0^T f_2(t,\tilde{x}_1(t),0)\,\mathrm{d}t<0$, *where $\tilde{x}_1(t)$ and $\tilde{x}_2(t)$ are the unique positive T-periodic solutions of equations 2 and 3, respectively.*

Then there exists at least one positive T-periodic solution $(x_1^*(t),x_2^*(t))$ of $\mathcal{S}$ which is not asymptotically stable.

Moreover, if assumptions (h_{5U}) and (h_6) hold, then there exists exactly one positive T-periodic solution $(x_1^*(t),x_2^*(t))$ of $\mathcal{S}$ and it is a saddle point.

Proof. Arguing as in the proof of Theorem 4.4, we see that

$$\deg(I-\Phi,\mathfrak{S},0)=4\sum i[\Phi,(x_1^*,x_2^*)]+i[\Phi,(0,0)]+2(i[\Phi,(\tilde{x}_1,0)])+2(i[\Phi,(0,\tilde{x}_2)]). \tag{17}$$

Let K be the sum of the indices of all positive T-periodic solutions $(x_1^*(t),x_2^*(t))$ of $\mathcal{S}$. Then

$$4K+5=1$$
$$K=-1$$

Then there exists at least one positive T-periodic solution $(x_1^*(t),x_2^*(t))$ of $\mathcal{S}$. If all such solutions were asymptotically stable, then

$$i[\Phi,(x_1^*,x_2^*)]=1 \quad \text{for all } (x_1^*,x_2^*)\in\mathbb{R}^2_+.$$

Then $K = 4n$, where $n > 0$ is the number of positive T-periodic solutions of $\mathcal{S}$, and 17 would yield a contradiction.

Finally, under assumptions (h_{5U}) and (h_6), any positive T-periodic solution $(x_1^*(t), x_2^*(t))$ of $\mathcal{S}$ is linearly unstable and its index is

$$i[\Phi, (x_1^*, x_2^*)] = -1.$$

Therefore, we obtain

$$\deg(I-\Phi, \mathfrak{S}, 0) = 4n(i[\Phi, (x_1^*, x_2^*)]) + i[\Phi, (0,0)] + 2(i[\Phi, (\tilde{x}_1, 0)]) + 2(i[\Phi, (0, \tilde{x}_2)]) = 1$$
$$-4n + 5 = 1$$
$$n = 1$$

which proves that there exists exactly one positive T-periodic solution $(x_1^*(t), x_2^*(t))$ of $\mathcal{S}$. □

An analogous conclusion follows when both $(\tilde{x}_1, 0)$ and $(0, \tilde{x}_2)$ are saddle points.

Theorem 4.6. *Assume (h_0), (h_1), (h_2), (h_3), and*

(h_{4U}) $\int_0^T f_1(t, 0, \tilde{x}_2(t))\,\mathrm{d}t > 0$ *and* $\int_0^T f_2(t, \tilde{x}_1(t), 0)\,\mathrm{d}t > 0$, *where $\tilde{x}_1(t)$ and $\tilde{x}_2(t)$ are the unique positive T-periodic solutions of equations 2 and 3, respectively.*

Then there exists at least one positive T-periodic solution $(x_1^*(t), x_2^*(t))$ of $\mathcal{S}$ which is not a saddle point.

Moreover, if (h_{5S}) holds, then there exists exactly one positive T-periodic solution $(x_1^*(t), x_2^*(t))$ of $\mathcal{S}$ which is a global attractor in $\mathbb{R}^2_+$.

5. **Domains of attraction.** As mentioned in section 2, the fixed points of the Poincaré-map Φ, defined in 6, are in a one-to-one correspondence with the T-periodic solutions of system $\mathcal{S}$. In particular, the trivial solution $(0,0)$ and the semi-trivial solutions $(\tilde{x}_1, 0)$ and $(0, \tilde{x}_2)$ of $\mathcal{S}$, when they exist, correspond to three distinct fixed points of Φ. Moreover, given Corollary 1, all fixed points of the Poincaré-map Φ lie in the set $\mathfrak{S}_1$.

Inspired by [5], the aim of the present section is to characterise further the domains of attraction of the fixed points of the Poincaré-map Φ in the positive axes.

We start by introducing some notation. Let $P \in \mathbb{R}^2_{+0}$ be a fixed point of Φ. We denote by $\mathcal{A}(P)$ the *domain of attraction of* P, that is, the set

$$\mathcal{A}(P) = \left\{ Q \in \mathbb{R}^2_{+0} \colon \Phi^n(Q) \to P \right\}.$$

The next result is a straightforward consequence of Lemma 2.4.

Lemma 5.1. *Assume (h_0) and (h_1^-). Let $P \in \mathbb{R}^2_+$ be a fixed point of Φ. Then for any $R, S \in \mathcal{A}(P)$, we have $\overline{[R]_2} \cap \overline{[S]_4} \subset \mathcal{A}(P)$.*

Proof. Let $Q \in \overline{[R]_2} \cap \overline{[S]_4}$. From Lemma 2.4, we see that $\Phi^n(Q) \in \overline{[\Phi^n(R)]_2} \cap \overline{[\Phi^n(S)]_4}$, for all $n > 0$, that is, the coordinates of the three points satisfy

$$\Phi^n(S)_{x_1} \le \Phi^n(Q)_{x_1} \le \Phi^n(R)_{x_1} \quad \text{and} \quad \Phi^n(R)_{x_2} \le \Phi^n(Q)_{x_2} \le \Phi^n(S)_{x_2}.$$

Since $R, S \in \mathcal{A}(P)$, we conclude that $\Phi^n(Q) \to P$, as $n \to +\infty$. □

From now on, we centre our attention in the domains of attraction of the semi-trivial solutions $(\tilde{x}_1, 0)$ and $(0, \tilde{x}_2)$, and the corresponding fixed points of Φ, $(\tilde{x}_1(0), 0)$ and $\big(0, \tilde{x}_2(0)\big)$, respectively.

Lemma 5.2. *Assume (h_0), (h_1), (h_2) and (h_3). Let $\tilde{x}_1(t)$ and $\tilde{x}_2(t)$ be the unique positive T-periodic solutions of equations 2 and 3, respectively.*

Then for any $P \in \mathcal{A}\big(\tilde{x}_1(0), 0\big)$, we have $\overline{\big[P\big]_4} \subset \mathcal{A}\big(\tilde{x}_1(0), 0\big)$, and for any $P \in \mathcal{A}\big(0, \tilde{x}_2(0)\big)$, we have $\overline{\big[P\big]_2} \subset \mathcal{A}\big(0, \tilde{x}_2(0)\big)$.

Proof. Let $P \in \mathcal{A}\big(\tilde{x}_1(0), 0\big)$ and $Q \in \overline{\big[P\big]_4}$.

From Lemma 2.4, it follows that $\Phi^n(Q) \in \overline{\big[\Phi^n(P)\big]_4}$, for all $n > 0$, that is, the second coordinates of these points satisfy

$$0 \leq \Phi^n(Q)_{x_2} \leq \Phi^n(P)_{x_2} \quad \text{for all } n > 0.$$

Since $P \in \mathcal{A}\big(\tilde{x}_1(0), 0\big)$, Theorem 2.6 and the inequalities above imply that the sequence $\big(\Phi^n(Q)\big)_n$ converges to a fixed point of Φ of the form $(X, 0)$, with $X \geq 0$. But from Lemma 2.1, we see that the only fixed points of Φ in the nonnegative x_1-axis are $(0, 0)$, which is repulsive, and $\big(\tilde{x}_1(0), 0\big)$. Therefore we conclude that $\Phi^n(Q) \to \big(\tilde{x}_1(0), 0\big)$, as $n \to +\infty$.

An analogous argument holds for $\big(0, \tilde{x}_2(0)\big)$. ∎

Theorem 5.3. *Assume (h_0), (h_1), (h_2) and*

(h_3^-) $\displaystyle\int_0^T f_1(t, 0, 0)\,\mathrm{d}t > 0,$

(h_4^-) $\displaystyle\int_0^T f_2(t, \tilde{x}_1(t), 0)\,\mathrm{d}t < 0,$ *where $\tilde{x}_1(t)$ is the unique positive T-periodic solution of equation 2.*

Then either $\mathcal{A}\big(\tilde{x}_1(0), 0\big) = \mathbb{R}^2_+ \cup \,]0, +\infty[\, \times \{0\}$, or there exist $z_1 \in \,]0, +\infty]$ and a nondecreasing function $\psi_1 \colon]0, z_1[\, \to [0, +\infty[$ such that

$$\mathcal{A}\big(\tilde{x}_1(0), 0\big) = \big\{(x_1, x_2) \in \mathbb{R}^2_{+0} \colon 0 < x_1 < z_1 \,,\, 0 \leq x_2 < \psi_1(x_1)\big\} \\ \cup\ \big\{(x_1, x_2) \in \mathbb{R}^2_{+0} \colon x_1 \geq z_1 \,,\, x_2 \geq 0\big\}.$$

If $z_1 = +\infty$, then the second set is empty.

Proof. Notice that under our assumptions $\big(\tilde{x}_1(0), 0\big)$ is locally asymptotically stable. By [2, Remark 17.5], its domain of attraction $\mathcal{A}\big(\tilde{x}_1(0), 0\big)$ is a nonempty open set.

Fix $\hat{u}_1 > 0$.

If $P = (\hat{u}_1, \hat{u}_2) \in \mathcal{A}\big(\tilde{x}_1(0), 0\big)$, for some $\hat{u}_2 \geq 0$, then all points of the form $Q = (\hat{u}_1, x_2)$, with $0 \leq x_2 \leq \hat{u}_2$, belong to $\mathcal{A}\big(\tilde{x}_1(0), 0\big)$, by Lemma 5.2. Therefore,

$$\mathcal{A}\big(\tilde{x}_1(0), 0\big) \cap \big\{(x_1, x_2) \in \mathbb{R}^2_{+0} \colon x_1 = \hat{u}_1\big\} = \\ = \big\{(x_1, x_2) \in \mathbb{R}^2_{+0} \colon x_1 = \hat{u}_1 \,,\, 0 \leq x_2 < \psi(\hat{u}_1)\big\},$$

where the map $\psi \colon]0, +\infty[\, \to [0, +\infty]$ is defined as

$$\psi(\hat{u}_1) = \sup\big\{x_2 \geq 0 \colon (\hat{u}_1, x_2) \in \mathcal{A}\big(\tilde{x}_1(0), 0\big)\big\}.$$

Notice that ψ is a nondecreasing map. Indeed, given $0 < x_1 < x_1'$, with $\psi(x_1) > 0$, take $0 \leq x_2 < \psi(x_1)$ and consider the points $P = (x_1, x_2) \in \mathcal{A}\big(\tilde{x}_1(0), 0\big)$ and $Q = (x_1', x_2')$, with $0 \leq x_2' \leq x_2$. Clearly, $Q \in \overline{\big[P\big]_4}$. Thus, Lemma 5.2 implies that $Q \in \mathcal{A}\big(\tilde{x}_1(0),0\big)$. Therefore, $\psi(x_1') \geq x_2$, for all $x_2 < \psi(x_1)$, and hence $\psi(x_1') \geq \psi(x_1)$. Finally, notice that if $\psi(x_1) = 0$, the conclusion is obviously true, by the definition of ψ.

Finally, if $\psi(0^+) < +\infty$, let

$$z_1 = \sup\big\{x_1 > 0 \colon \psi(x_1) < +\infty\big\}.$$

It is easily seen that the map $\psi_1 \colon]0, z_1[\to [0,+\infty[$ defined as the restriction of ψ to $]0, z_1[$ satisfies all the claims in the theorem. $\square$

Theorem 5.4. *Assume (h_0), (h_1), (h_2), (h_3^-) and (h_4^-). The map ψ_1, defined in Theorem 5.3, has at most a countable set of jump discontinuities. Moreover, the boundary of $\mathcal{A}\big(\tilde{x}_1(0),0\big)$ in $\mathbb{R}^2_{+0}$ is a Φ-invariant set given by*

$$\begin{aligned}
&\mathrm{fr}\ \mathcal{A}\big(\tilde{x}_1(0),0\big) = Graf_{\psi_1}\\
&\cup \big\{(x_1,x_2) \in]0,z_1[\times \mathbb{R}_{+0} \colon \psi_1 \textit{ is discontinuous at } x_1\,,\ \psi_1(x_1^-) \leq x_2 \leq \psi_1(x_1^+)\big\}\\
&\qquad \cup \big\{(0,x_2) \in \mathbb{R}^2_{+0} \colon 0 \leq x_2 \leq \psi_1(0^+)\big\} \cup \big\{(z_1,x_2) \in \mathbb{R}^2_{+0} \colon x_2 \geq \psi_1(z_1^-)\big\},
\end{aligned}$$

where the last set is empty, if either $z_1 = +\infty$ or $\psi_1(z_1^-) = +\infty$.

Proof. The first claim follows from Darboux-Froda's Theorem (see [15]) while the characterisation of the boundary of $\mathcal{A}\big(\tilde{x}_1(0),0\big)$ is due to the definition of ψ_1.

It remains to prove that fr $\mathcal{A}\big(\tilde{x}_1(0),0\big)$ is a Φ-invariant set. Let $P = (P_{x_1}, P_{x_2}) \in$ fr $\mathcal{A}\big(\tilde{x}_1(0),0\big)$. Then there exist sequences $(P_k)_k \subset \mathcal{A}\big(\tilde{x}_1(0),0\big)$ and $(Q_k)_k \subset \mathbb{R}^2_{+0} \setminus \mathcal{A}\big(\tilde{x}_1(0),0\big)$ such that

$$P_k \xrightarrow{k} P \quad \text{and} \quad Q_k \xrightarrow{k} P, \quad \text{as } k \to +\infty,$$

and, for all $k > 0$,

$$\Phi^n(P_k) \xrightarrow{n} \big(\tilde{x}_1(0),0\big) \quad \text{and} \quad \Phi^n(Q_k) \not\xrightarrow{n} \big(\tilde{x}_1(0),0\big) \quad \text{as } n \to +\infty.$$

As the Poincaré-map Φ is continuous,

$$\Phi(P_k) \xrightarrow{k} \Phi(P) \quad \text{and} \quad \Phi(Q_k) \xrightarrow{k} \Phi(P), \quad \text{as } k \to +\infty,$$

and obviously, for all $k > 0$,

$$\begin{aligned}
\Phi^n(\Phi(P_k)) = \Phi^{n+1}(P_k) \xrightarrow{n} \big(\tilde{x}_1(0),0\big) \quad &\text{and}\\
&\Phi^n(\Phi(Q_k)) = \Phi^{n+1}(Q_k) \not\xrightarrow{n} \big(\tilde{x}_1(0),0\big) \quad \text{as } n \to +\infty,
\end{aligned}$$

which proves that $\Phi(P) \in$ fr $\mathcal{A}\big(\tilde{x}_1(0),0\big)$. We then conclude that fr $\mathcal{A}\big(\tilde{x}_1(0),0\big)$ is Φ-invariant. $\square$

Remark 4. Note that, as no point of the x_2-axis is the image by Φ of a point $P = (P_{x_1}, P_{x_2})$ with $P_{x_1} > 0$, the set

$$\Gamma = \mathrm{fr}\ \mathcal{A}\big(\tilde{x}_1(0),0\big) \setminus \big\{(0,x_2) \in \mathbb{R}^2_{+0} \colon 0 \leq x_2 \leq \psi_1(0^+)\big\}$$

is also Φ-invariant.

Under the stronger assumption (h_1^+) on the inter-species competition terms, we may generalise the characterisation given in [5].

Lemma 5.5. *Assume* (h_0) *and* (h_1^+)*. Let* $\Sigma \subset \mathbb{R}^2_+$ *be a* Φ*-invariant curve such that for all* $(x_1, x_2), (x_1', x_2') \in \Sigma$*, we have*

$$x_1 \le x_1' \quad \textit{if and only if} \quad x_2 \le x_2'.$$

Then Σ *does not contain any horizontal or vertical segment, that is, for all* (x_1, x_2)*,* $(x_1', x_2') \in \Sigma$*, we have*

$$x_1 < x_1' \quad \textit{if and only if} \quad x_2 < x_2'.$$

Proof. Suppose without loss of generality that $P = (x_1, x_2), P' = (x_1', x_2') \in \Sigma$ are such that

$$x_1 < x_1' \quad \text{and} \quad x_2 = x_2'.$$

Then

$$P' \in \overline{[P]_4} \setminus \{P\}.$$

Let $\Phi(P) = (v_1, v_2)$ and $\Phi(P') = (v_1', v_2')$. Either $v_1 \le v_1'$ or $v_1 > v_1'$. As Σ is Φ-invariant, $\Phi(P), \Phi(P') \in \Sigma$. Therefore, either $v_2 \le v_2'$ or $v_2 \ge v_2'$.

In both cases,

$$\Phi(P') \notin \big[\Phi(P)\big]_4,$$

which contradicts Corollary 2. $\square$

Corollary 4. *Assume* (h_0)*,* (h_1^+)*,* (h_1^{++})*,* (h_2)*,* (h_3^-) *and* (h_4^-)*. Then the function* ψ_1*, defined in Theorem 5.3, is a continuous increasing map such that* $\psi_1(0^+) = Y_0$*, with* $Y_0 \ge 0$ *such that* $(0, Y_0)$ *is a fixed point of* Φ*, and if* $z_1 < +\infty$*,* $\psi_1(z_1^-) = +\infty$*. Moreover,*

$$\operatorname{fr} \mathcal{A}\big(\tilde{x}_1(0), 0\big) = Graf_{\psi_1} \ \cup \ \big\{(0, x_2) \in \mathbb{R}^2_{+0} \colon 0 \le x_2 \le Y_0\big\}.$$

Proof. By Lemma 5.5, ψ_1 is a continuous and increasing function, as the set Γ, defined in Remark 4, cannot contain any vertical or horizontal segment. Moreover, if $z_1 < +\infty$, then $\psi_1(z_1^-) = +\infty$.

As ψ_1 is increasing and bounded from below by zero, $\psi_1(0^+) \in [0, +\infty[$. Let us denote it by Y_0. Let $x_n \to 0$, then $\psi_1(x_n) \to Y_0$ and $\Phi(x_n, \psi_1(x_n)) \to \Phi(0, Y_0)$.

By Remark 4, the graph of ψ_1, $Graf_{\psi_1} = \Gamma$ is Φ-invariant. As $(x_n, \psi_1(x_n)) \in \overline{Graf_{\psi_1}}$, then $\Phi(x_n, \psi_1(x_n)) \in Graf_{\psi_1}$. Hence, we have that $\Phi(0, Y_0)$ is both in $\overline{Graf_{\psi_1}}$ and in the x_2-axis. We conclude that $\Phi(0, Y_0) = (0, Y_0)$. $\square$

Remark 5. If also (h_1) holds and $Y_0 \ne 0$, that is if $Y_0 = \tilde{x}_2(0)$ we conclude that there must exist a fixed point of Φ in $Graf_{\psi_1}$ as in this case $(0, \tilde{x}_2(0))$ cannot be attractive. If we assume that $\frac{\partial f_i}{\partial x_i}$, $i = 1, 2$ are negative in the first quadrant, by [17, Proposition 3.7] and [12, Theorem 2.2], the fixed points of Φ lie in a decreasing curve connecting the fixed point in the x_2-axis to the one in the x_1-axis. This is in contradiction with the fact that ψ_1 is increasing. Hence, under this extra condition, $\psi_1(0^+) = 0$.

When the characterisation of the dynamics of system $\mathcal{S}$ is not fully understood and one would like to run numerical simulations, Theorem 5.3 gives some suggestion as where to look for initial conditions of solutions which converge to hypothetical T-periodic solutions. If, for instance, the semi-trivial solution $(\tilde{x}_1, 0)$ is asymptotically stable, but the number of positive T-periodic solutions is unknown, or the stability of all positive T-periodic solutions is not known, then it seems a good idea to investigate the asymptotical behaviour of solutions with initial conditions in the upper left corner of the invariant set $\mathfrak{S}_1$ defined in Lemma 2.3 and near the positive x_2-coordinate axis.

6. **Applications.** We consider two models with nonlinear competition that have been studied in the literature. The first model was considered only in its autonomous version.

In the examples, we opted to study the case in which in the axes we have one stable and one unstable solution, as this is the case for which the behaviour of the averaged system can be completely different.

A model for microbial growth in a mixed culture

In [14] the authors studied the model

$$\begin{cases} x_1' = r_1(t)\alpha_1(t)x_1\left(1 - \dfrac{x_1^{\nu_1}}{K_1(t)^{\nu_1}} - c_2(t)\dfrac{x_2^{\nu_2}}{K_1(t)^{\nu_1}}\right), \\ \\ x_2' = r_2(t)\alpha_2(t)x_2\left(1 - c_1(t)\dfrac{x_1^{\nu_1}}{K_2(t)^{\nu_2}} - \dfrac{x_2^{\nu_2}}{K_2(t)^{\nu_2}}\right), \end{cases} \tag{$\mathcal{R}$}$$

which describes the competition between two microbial genotypes. This model is deduced in [14] from a model of two genotypes of virus which compete for a nutrient. The authors explain the importance of a mathematical model in order to give insight, as opposed to competition experiments, which have many counterparts (require distinct markers, require competition strains to growth in the same environment, among others). For $i = 1, 2$, x_i represents the density of each strain, r_i is the specific growth rate at low density, K_i is the maximum cell density, ν_i is a deceleration parameter, $\alpha_i(t)$ is the adjustment function, which describes the fraction of the population that has adjusted to the new growth conditions by time t, and c_i is a competition coefficient, more precisely, the ratio between interstrain and intrastrain competitive effects. In [14], r_i, K_i, c_i and ν_i are positive constants and $\alpha_i(t)$ can be a constant or a non-periodic function, and some results were obtained numerically. The aim in that paper was to find estimates for the competition coefficients and then predicting the values for the cell densities.

Here, we assume that,

(C_1) $R_i = r_i\alpha_i \geq 0,\ c_i \geq 0,\ K_i > 0,$ are continuous T-periodic functions, for $i = 1, 2$.

We have the following result.

Proposition 1. *Assume* (C_1),

(C_2) $\nu_i > 1$, *for* $i = 1, 2$,

(C_3) $\exists\, t_i, i = 1, 2,$ *such that* $R_1(t_1)c_2(t_1) > 0$ *and* $R_2(t_2)c_1(t_2) > 0$,

(C_4) $\displaystyle\int_0^T R_1(t)\left(1 - \frac{c_2(t)\tilde{x}_2^{\nu_2}(t)}{K_1^{\nu_1}(t)}\right)\mathrm{d}t > 0$ *and* $\displaystyle\int_0^T R_2(t)\left(1 - \frac{c_1(t)\tilde{x}_1^{\nu_1}(t)}{K_2^{\nu_1}(t)}\right)\mathrm{d}t < 0$, *where, for* $i = 1, 2$, $\tilde{x}_i(t)$ *is the non-zero component of the unique* T*-periodic solution of* $\mathcal{R}$ *in the* x_i*-axis,*

(C_5) $\displaystyle\min_{[0,T]} c_1(t) \min_{[0,T]} c_2(t) > 1$ *or* $\displaystyle\max_{[0,T]} c_1(t) \max_{[0,T]} c_2(t) < 1$.

Then any nonnegative solution $(x_1(t), x_2(t))$ *of problem* $\mathcal{R}$ *with* $x_1(0) > 0$ *and* $x_2(0) \geq 0$ *satisfies*

$$\lim_{t\to+\infty}\big(x_1(t) - \tilde{x}_1(t)\big) = 0 \quad \text{and} \quad \lim_{t\to+\infty} x_2(t) = 0. \tag{18}$$

Proof. The result follows from Theorems 4.3 or 4.4. In fact, (h_0), (h_1), (h_2), (h_3), (h_4) and (h_6) hold. In what concerns (h_{5S}) and (h_{5U}), they follow from the assumptions on $c_i,\ i = 1, 2$. $\square$

A model for two competing phytoplankton species with the production of a toxin

As a second application, we consider a two phytoplankton species competitive system with nonlinear inter-inhibition terms and the production of a toxin proposed in [23]. More precisely, we consider the system

$$\begin{cases} x_1' = x_1\left(r_1(t) - a_1(t)x_1 - \dfrac{b_1(t)x_2}{1+x_2} - c_1(t)x_1x_2\right), \\ x_2' = x_2\left(r_2(t) - \dfrac{b_2(t)x_1}{1+x_1} - a_2(t)x_2\right), \end{cases} \tag{$\mathcal{P}$}$$

where, for $i = 1, 2$, x_i represents the population density of each species, r_i is the intrinsic growth rate, a_i is the intraspecific competition rate, b_i is the interspecific competition rate, and c_1 is the toxin production rate. Note that only the second species can produce toxins affecting the other species.

We assume that,

(D_1) $c_1 \geq 0$, $r_i \succ 0$, $a_i \succ 0$, and $b_i \succ 0$ are continuous T-periodic functions, for $i = 1, 2$.

We have the following result.

Proposition 2. *Assume* (D_1)*,*

(D_2) $\displaystyle\int_0^T r_1(t) - \frac{b_1(t)\tilde{x}_2(t)}{1+\tilde{x}_2(t)}\,\mathrm{d}t > 0$ *and* $\displaystyle\int_0^T r_2(t) - \frac{b_2(t)\tilde{x}_1(t)}{1+\tilde{x}_1(t)}\,\mathrm{d}t < 0$*, where, for* $i = 1, 2$*,* $\tilde{x}_i(t)$ *is the non-zero component of the unique* T*-periodic solution of* $\mathcal{P}$ *in the* x_i*-axis,*

(D_3) *for all* $t \in [0, T]$*,* $\quad a_2(t) > 0$ *and* $b_2(t) > 0$*,*

and one of the following assumptions

(D_{4S}) $\displaystyle\max_{[0,T]} \frac{b_1(t) + c_1(t)\bar{R}}{a_2(t)} < \min_{[0,T]} \frac{a_1(t)}{b_2(t)}$,

(D_{4U}) $\displaystyle\min_{[0,T]} \frac{b_1(t)}{a_2(t)\big(1+\bar{R}\big)^2} > \max_{[0,T]} \frac{\big(a_1(t) + c_1(t)\bar{R}\big)\big(1+\bar{R}\big)^2}{b_2(t)}$,

where $\bar{R} > 0$ *is defined in Lemma 2.3.*

Then any nonnegative solution $(x_1(t), x_2(t))$ *of problem* $\mathcal{P}$ *with* $x_1(0) > 0$ *and* $x_2(0) \geq 0$ *satisfies*

$$\lim_{t\to+\infty} \big(x_1(t) - \tilde{x}_1(t)\big) = 0 \quad \textit{and} \quad \lim_{t\to+\infty} x_2(t) = 0.$$

Proof. The result follows from Theorems 4.3 or 4.4. It is easily seen that (h_0), (h_1), (h_2), (h_3), (h_4) and (h_6) hold. From (D_{4S}), there exist $\alpha_1, \alpha_2 > 0$ such that for all $(t, x_1, x_2) \in [0, T] \times \mathfrak{S}_1$, we have that

$$\alpha_2 \frac{b_2(t)}{\left(1+x_1\right)^2} < \alpha_1\big(a_1(t) + c_1(t)x_2\big).$$

Then (h_{5S}) holds. Similarly, if we assume (D_{4U}), then (h_{5U}) is satisfied. $\square$

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