



# A simple geometrical condition for the existence of periodic solutions of planar periodic systems. Applications to some biological models



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## ABSTRACT

Using invariant regions for proving the existence of periodic solutions of periodic ordinary differential equations is a common tool. However, describing such a region is, in general, far from trivial. In this paper we provide sufficient conditions for the existence of an invariant region for certain planar systems. Our method locates the solution, in the sense that the region we determine evolves with time around the solution in the phase plane. Also, unlike other approaches, the construction does not depend on upper or lower bounds with respect to time of the functions involved in the system. The criterion is formulated for a general planar periodic ODEs system, and therefore it can be applied in very different contexts. In particular, we use the criterion to improve on previously known results on Holling's type II predator–prey periodic model, and on the classic periodic competition model.

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## 1. Introduction

Non-autonomous ordinary differential systems are widely used for modeling natural phenomena. In particular, in that context, periodic functions are commonly involved and periodic solutions of the system are of interest. This is the case whenever one addresses problems in ecology, biology, epidemiology, geology, etc. In all these cases, environmental conditions that are often periodic, like light, temperature, humidity, rain, etc., highly influence the problem, and as a consequence periodic solutions are expected.

In this paper we present an original approach to the problem of detecting the existence of  $T$ -periodic solutions of planar periodic ordinary differential equation systems of the form:

$$\begin{cases} n' = f(t, n, p), \\ p' = g(t, n, p), \end{cases} \quad (1)$$

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where  $'$  stands for the derivative  $d/dt$ , and  $f, g \in C^1(\mathbb{R} \times \mathbb{R}^2)$  are periodic functions of  $t$  with the same period  $T$ . Our main result is a sufficient condition for the existence of at least one periodic solution of the system (1), which holds under certain hypotheses on the system (see the beginning of Section 2, but also Remark 2.3). Hence, we add a new approach to the variety of already available techniques for solving problems of this kind.

Our result has been motivated by the study of some models in population dynamics [25]; in fact, the result and the ideas behind are applicable, in concrete, to several predator–prey models, as well as to classical competition periodic models. Nevertheless, our ideas do not need to be formulated in a biological context.

A typical approach to prove the existence of periodic solutions is to determine an invariant region for the system (1) under study, where Brouwer’s fixed point theorem can be applied to the induced Poincaré map. See, for instance, Section 4.4 in [12] for an application to a two competing species periodic system. However, there is no general method for building such a region, and finding it is in fact a hard question. Typically (as in [12]) the construction of the invariant region is based on upper and lower bounds with respect to time of the functions  $f$  and  $g$ . In contrast, here we do not need or use these bounds (since we work locally).

A different approach is based on bifurcation techniques (e.g. [7]) and perturbation techniques (e.g. [26]). In [7] Cushing deals with a general  $n$ -dimensional periodic Kolmogorov system (see also the comments at the end of Section 2 herein) and derives the existence of a continuum of non-trivial solutions as a bifurcation phenomenon from a branch of trivial solutions. The underlying tool is a classical result due to Rabinowitz [28]. Compared to this approach, our main result here does not require the existence of a continuum of trivial solutions from where non-trivial ones bifurcate. Bifurcation appears again in [26], where the authors prove the existence of periodic solutions for small enough periodic perturbations by using techniques based on [16].

Also, another alternative is Mawhin’s continuation theorem [13] (see, for instance, [11]). In this case, the existence result is stated in terms of the average value of the periodic parameters of the model. Compared to this, our method does not require any consideration on the average values of these parameters.

The paper is organized as follows. In Section 2 we prove our main result. We apply it in Section 3 to study a predator–prey model with Holling’s II type functional response. To our knowledge, the results in this section are the first ones considering a periodic “closure term” [22,21]. In Section 4 we show how the ideas leading to the main result in Section 2 can be adapted to different settings, or even yield non-existence of positive periodic solution results. To this end, we revisit the standard competition periodic model [15] which still receives certain attention [1,23], and we provide new coexistence/species exclusion conditions. Finally, Section 5 contains some conclusions and observations about on-going research.

## 2. Main results

Our results are essentially of local nature and can be adapted to many different situations. However, in order to emphasize the main ideas and to make the reading as clear as possible, we will formulate some of the hypotheses required on the system (1) in a general fashion on the positive cone (see remarks after the main Theorem 2.1). One may observe that in fact our reasoning works the same in any appropriate region homeomorphic to the positive cone. The hypotheses that we require are:

- (H1) Every equation of the auxiliary system, obtained from (1) by setting  $p' = 0$  and  $n' = 0$ , can be solved for  $p$ . That is, there exist unique functions  $\varphi$  and  $\psi$  such that  $f(t, n, \varphi(t, n)) = 0$ ,  $g(t, n, \psi(t, n)) = 0$ .
- (H2) For each  $t \in \mathbb{R}$  the curves  $p = \varphi(t, n)$  and  $p = \psi(t, n)$  meet just once in the positive cone. We denote the intersection point by  $(\bar{n}(t), \bar{p}(t))$ . Because of the periodicity on  $t$  of functions  $f$  and  $g$  (and, therefore, of  $\varphi$  and  $\psi$ ) we have that  $(\bar{n}(t), \bar{p}(t)) = (\bar{n}(t + T), \bar{p}(t + T))$ ,  $\forall t \in \mathbb{R}$ .
- (H3) As  $n$  increases and regardless the value of  $t$ , the function  $\psi(t, n)$  is strictly increasing, while  $\varphi(t, n)$  is strictly decreasing.

In particular, any solution  $(n(t), p(t))$  of (1) fulfilling that  $p = \varphi(t, n)$  satisfies that  $n'(t) = 0$ . Similarly, if  $(n(t), p(t))$  fulfills  $p = \psi(t, n)$  then  $n'(t) = 0$ . In other words, for each  $t$  the curves  $p = \varphi(t, n)$  and  $p = \psi(t, n)$  divide the positive cone of the  $np$ -plane into regions where the sign of the derivatives of  $n(t)$  and  $p(t)$  is constant. We denote these regions by  $n_+(t)$ ,  $n_-(t)$  and  $p_+(t)$ ,  $p_-(t)$ , respectively, where the subindex stands for the sign of the corresponding derivative. Such regions vary with  $t$ ; hence, in the sequel we also assume that the following property holds:

(H4) The regions  $n_-(t)$  and  $p_-(t)$  are

$$\begin{aligned} n_-(t) &:= \{n > 0, p > 0; p > \varphi(t, n)\} \\ p_-(t) &:= \{n > 0, p > 0; p > \psi(t, n)\}. \end{aligned}$$

Next we present our main result. It is based on the fact that, for each  $t$ , we can find a compact non-empty convex region  $\mathcal{R}(t)$  in the positive  $np$  cone satisfying that:

- (P1)  $\mathcal{R}(t) = \mathcal{R}(t + T) \forall t \in \mathbb{R}$  and the boundary of  $\mathcal{R}(t)$  varies continuously with  $t$ .
- (P2) The derivatives at any  $t \in \mathbb{R}$  of any solution of system (1) starting at  $\partial\mathcal{R}(t)$ , the boundary of  $\mathcal{R}(t)$ , point towards the interior of  $\mathcal{R}(t)$ .

The following theorem provides the sufficient condition alluded to in the Introduction. Here, we denote the partial derivative of a function  $\Phi(t, \bar{n}(t))$  with respect to  $n$  at  $n = \bar{n}(t)$ , as  $\Phi'_n(t, \bar{n}(t))$ .

**Theorem 2.1.** *Assume that the hypotheses (H1), (H2), (H3), (H4) are satisfied. If for each  $t \in [t_*, t_* + T]$  it holds that  $\bar{p}(t) > 0$ , and*

$$\varphi'_n(t, \bar{n}(t)) + \psi'_n(t, \bar{n}(t)) < 0, \tag{2}$$

where  $T$  is the period of the system and  $t_* \in \mathbb{R}$ , then the system (1) has at least one positive periodic solution.

**Proof.** The proof proceeds first in a constructive way by building a convex compact region  $\mathcal{R}(t_*)$  fulfilling (P1) and (P2) (see Fig. 1); in a second step we show that any solution of the system (1) with initial value in  $\mathcal{R}(t_*)$  at  $t = t_*$  reaches  $\mathcal{R}(t_*)$  again at time  $t = t_* + T$ . Finally, Brouwer’s Fixed Point Theorem [5] comes into play to derive the conclusion.

**Step 1.** We first claim that

$$\psi(t, \bar{n}(t) - \xi) > \varphi(t, \bar{n}(t) + \xi) \tag{3}$$

and

$$\psi(t, \bar{n}(t) + \xi) < \varphi(t, \bar{n}(t) - \xi) \tag{4}$$

for  $\xi$  close enough to zero and for all  $t \in [t_*, t_* + T]$ . Indeed, recall that  $\psi(t, \bar{n}(t)) = \varphi(t, \bar{n}(t))$ , and consider the following chain of equalities:

$$\begin{aligned} &\lim_{\xi \rightarrow 0} \frac{\psi(t, \bar{n}(t) - \xi) - \varphi(t, \bar{n}(t) + \xi)}{\xi} \\ &= \lim_{\xi \rightarrow 0} \frac{\psi(t, \bar{n}(t) - \xi) - \psi(t, \bar{n}(t)) + \varphi(t, \bar{n}(t)) - \varphi(t, \bar{n}(t) + \xi)}{\xi} \end{aligned}$$

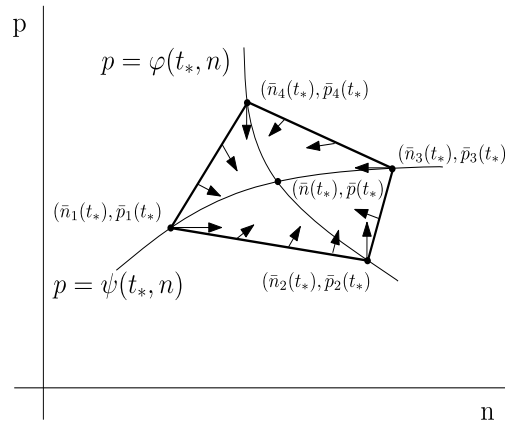


Fig. 1. Region  $\mathcal{R}(t_*)$ .

$$\begin{aligned}
 &= \lim_{\xi \rightarrow 0} \frac{\psi(t, \bar{n}(t) - \xi) - \psi(t, \bar{n}(t))}{\xi} + \lim_{\xi \rightarrow 0} \frac{\varphi(t, \bar{n}(t) - \xi) - \varphi(t, \bar{n}(t) + \xi)}{\xi} \\
 &= -\psi'_n(t, \bar{n}(t)) - \varphi'_n(t, \bar{n}(t))
 \end{aligned}$$

From the statement of the theorem we have that the above number is positive, and therefore (3) holds. Similar considerations lead to condition (4).

Now, let us fix  $t_* \in \mathbb{R}$ . Taking into account the above reasonings, we deduce that there exists  $\xi_* > 0$  such that for all  $\xi \in (0, \xi_*)$  conditions (3) and (4) hold simultaneously. Let us choose  $\xi_1 \in (0, \xi_*)$  and let us define

$$\begin{aligned}
 n_1(t_*) &:= \bar{n}(t_*) - \xi_1, & p_1(t_*) &:= \psi(n_1(t_*)) \\
 n_2(t_*) &:= \bar{n}(t_*) + \xi_1, & p_2(t_*) &:= \varphi(n_2(t_*)).
 \end{aligned}$$

On the other hand, from condition (4) and the continuity of the functions  $\varphi$  and  $\psi$  we derive the existence of  $\delta_1 > 0$  such that for any  $\xi \in (\xi_1 - \delta_1, \xi_1 + \delta_1)$ ,

$$\varphi(t_*, \bar{n}(t_*) - \xi) > \psi(t_*, \bar{n}(t_*) + \xi_1)$$

which, in particular, holds for  $\xi_2 \in (\xi_1 - \delta_1, \xi_1)$ . The same argument guarantees the existence of  $\delta_2 > 0$  and  $\xi_3 \in (\xi_1, \xi_1 + \delta_2)$  satisfying that

$$\varphi(t_*, \bar{n}(t_*) - \xi_2) > \psi(t_*, \bar{n}(t_*) + \xi_3).$$

Then, we define

$$\begin{aligned}
 n_3(t_*) &:= \bar{n}(t_*) + \xi_3, & p_3(t_*) &:= \psi(n_3(t_*)) \\
 n_4(t_*) &:= \bar{n}(t_*) - \xi_2, & p_4(t_*) &:= \phi(n_4(t_*)),
 \end{aligned}$$

and, because of the construction, it follows that

$$n_1(t_*) < n_4(t_*) < n_2(t_*) < n_3(t_*), \quad p_2(t_*) < p_1(t_*) < p_3(t_*) < p_4(t_*). \tag{5}$$

Then, we denote as  $\mathcal{R}(t_*)$  the convex quadrilateral defined by the following vertexes (see Fig. 1), that we spell anticlockwise

$$(n_1(t_*), p_1(t_*)), (n_2(t_*), p_2(t_*)), (n_3(t_*), p_3(t_*)), (n_4(t_*), p_4(t_*)). \tag{6}$$

The above construction can be made for any  $t \in \mathbb{R}$  and in such a way that the vertexes in (6) are continuous  $T$ -periodic function of  $t \in \mathbb{R}$ . Therefore,  $\mathcal{R}(t_*) = \mathcal{R}(t_* + T)$ ; so,  $\mathcal{R}(t_*)$  fulfills (P1) and (P2). Notice that this construction can be done for any  $t_* \in \mathbb{R}$ .

**Step 2.** Next, we prove that any solution of the system (1) starting in  $\mathcal{R}(t_*)$  at  $t = t_*$  reaches  $\mathcal{R}(t_*)$  again at time  $t = t_* + T$ . For this purpose, let  $z(t, t_0, z_0)$  represent the solution of the system (1) fulfilling that  $z(t_0) = z_0$ ; we also define the set

$$\Gamma = \bigcup_{t \in [t_*, t_* + T]} \mathcal{R}(t),$$

where  $\mathcal{R}(t)$  is the section of  $\Gamma$  by any value of  $t \in [t_*, t_* + T]$ . Since any section  $\mathcal{R}(t)$  of  $\Gamma$  fulfills (P2), no solution  $z(t, t_*, z_*)$  of system (1) with  $z_* \in \mathcal{R}(t_*)$  can leave the set  $\Gamma$ . Now since  $\mathcal{R}(t_* + T) = \mathcal{R}(t_*)$ , the statement holds.

**Step 3.** Finally, consider the Poincare operator  $\phi_T : \mathcal{R}(t_*) \rightarrow \mathcal{R}(t_* + T) = \mathcal{R}(t_*)$  defined by

$$\phi_T(z_*) = z(t_* + T, t_*, z_*)$$

This operator maps each initial value  $z_*$  in  $\mathcal{R}(t_*)$  into the value at time  $t = t_* + T$  of the solution of the problem (1) starting at  $z_*$  in  $t = t_*$ . This is a continuous map and  $\mathcal{R}(t_*)$  is convex. Hence, by Brouwer’s Fixed Point Theorem, this operator has a fixed point, which means that there exists a solution  $z^*(t, t_*, \bar{z})$  of the problem (1) such that

$$z^*(t_*, t_*, \bar{z}) = z^*(t_* + T, t_*, \bar{z}).$$

Then, due to the uniqueness of the solutions of the system (1),  $z^*(t, t_*, \bar{z})$  is a periodic solution.  $\square$

**Remark 2.2.** A region  $\mathcal{R}(t)$  cannot be arbitrarily small. Indeed, each of the quantities  $\xi, \xi^*, \xi_k, k = 1, 2, 3$ , involved in the size of  $\mathcal{R}(t)$  is positive and can be chosen to depend continuously on time  $t$ , that is  $\xi(t), \xi^*(t), \xi_k(t), k = 1, 2, 3$ , on a compact set  $[t_*, t_* + T]$ . Therefore, each of them achieves a strictly positive minimum, which prevents  $\mathcal{R}(t)$  from being arbitrarily small (or collapsing into  $(\bar{n}(t), \bar{p}(t))$ ).

**Remark 2.3.**

1. The construction used in the proof of Theorem 2.1 is essentially of local nature; so, it suffices that the hypotheses hold locally.
2. The underlying geometrical reasoning works the same under less (local) restrictive conditions. For instance, function  $\psi$  could be constant or even strictly decreasing, as shown in Section 4.
3. The geometrical ideas used in Theorem 2.1 can be adapted to produce non-existence results.

We finish this section with some comments on the two dimensional Kolmogorov system

$$\begin{cases} n' = nf(t, n, p), \\ p' = pg(t, n, p), \end{cases} \tag{7}$$

which has deserved great attention, in particular, in the context of predator–prey Kolmogorov models (see, for instance, [32,20] and references therein). A usual assumption on system (7) (see [32] or [20]) is that

the function  $g(t, n, p)$  is continuous for all  $t \geq 0$ ,  $n > 0$  and  $p \geq 0$ . This assumption precludes introducing periodic forcing terms in system (7) as in the following system

$$\begin{cases} n' = n, f(t, n, p) + h(t), \\ p' = pg(t, n, p) + s(t), \end{cases} \tag{8}$$

since the function  $g(t, n, p) + s(t)/p$  does not fulfill the aforementioned hypotheses. Our results, in contrast, can certainly deal with a system like (8), whenever the hypotheses required by Theorem 2.1 hold (see also Remark 2.3).

### 3. Predator–prey model with Holling’s II functional response

Since the pioneer papers by Lotka and Volterra and up today, predator–prey models have inspired an amazing amount of research and ideas, some of which are cited in Section 1. As we have already said, the results in Section 2 were also motivated by the study of the predator–prey model.

The functional response in a predator–prey model corresponds to the amount of prey eaten per unit of predator and per unit of time. This important concept has been introduced in Solomon [30], see also [4]. The functional response plays a crucial role in predator–prey dynamics, that is at the community level, since it is based on individuals properties (metabolism, behavior, etc.). A wide variety of functional responses can be found in the literature, see for instance [14] for a review. In [19], the author proposes a classification of functional responses in three types according to the general shape of their graph as a function of prey density. Type I corresponds to linear pieces functions (positive slope for low prey density and constant after a threshold of prey density). Type II corresponds to increasing concave functions. Type III concerns sigmoidal shapes for low prey densities. The Holling type II “disc-equation” [19] is famous among ecologists and is used in this paper assuming that the coefficients are periodic. Let us denote preys and predators populations at time  $t$  by  $n(t)$  and  $p(t)$ , respectively. The periodic “disc-equation” reads as

$$g(t, n) = \frac{a(t)n}{b(t) + n}$$

where  $a(t)$  is the maximum ingestion rate of prey per unit of predator at time  $t$  and  $b(t)$  is the half saturation constant at time  $t$ , which is inversely proportional to the “handling time” defined by Holling in [19].

In order to complete the model, we assume that in absence of predators, preys evolve according to the periodic logistic growth equation with net growth rate  $r(t)$ , and carrying capacity  $k(t)$ . Regarding predators, we consider density dependent mortality rate given by  $\mu(t) + e(t)p$  [21,27]. We consider that all the coefficients are periodic functions of time with the same period  $T$ , so that the complete model is:

$$\begin{cases} n' = \lambda(t)n \left( 1 - \frac{n}{k(t)} \right) - \frac{a(t)np}{b(t) + n}, \\ p' = -(\mu(t) + e(t)p)p + \frac{\alpha a(t)np}{b(t) + n}, \end{cases} \tag{9}$$

where  $\alpha \in (0, 1)$  is the conversion efficiency. Though rare, the term  $e(t)p$  is nothing but part of the density dependent predator population mortality rate. It may represent intra-specific competition between predators for food that is scarce at high-predator densities, as well as an elementary description of cannibalism; see [27] and references therein. The term  $e(t)p^2$  is called a “closure term” when it represents the mortality induced by super-predators (predators predating on predators); e.g. see [10,21] and references therein. To our knowledge, ours is the first paper dealing with a periodic predator–prey model with Holling type II functional response including the term  $e(t)y^2$ .

**Theorem 3.1.** *If it holds that:*

- (i)  $\frac{k(t)}{2} < \frac{\mu(t)b(t)}{\alpha a(t) - \mu(t)} < k(t)$ ,
- (ii)  $\alpha k(t)a^2(t) < \lambda(t)e(t)b^2(t)$ ,

*then the corresponding Holling system (9) has at least one periodic solution.*

**Proof.** One may see that when we set  $n' = p' = 0$  in Holling’s system, we can solve the equations for  $p$ ; so, (H1) holds. More precisely, we get  $\varphi(t, n) = \lambda(k - n)(b + n)/ak$  (here  $k, b, a$  depend on  $t$ , although we do not spell it to simplify the notation; similarly for  $\psi(t, n)$ ). Besides, we get  $\psi(t, n) = \frac{1}{e} \cdot [\frac{\alpha a n}{b + n} - \mu]$ . Notice also that from hypothesis (i), and taking into account that  $b$  is non-negative, it follows that  $\alpha a - \mu > 0$ . Now we see that for a fixed  $t$ :

- (a)  $\varphi(t, n)$  is a concave parabola, intersecting the non-negative  $n$ -semi-axis at  $n = k$ .
- (b)  $\psi(t, n)$  is a hyperbola which, whenever  $\alpha a - \mu > 0$ , intersects the positive  $n$ -semi-axis at  $n = \frac{\mu b}{\alpha a - \mu}$ . Besides, it is positive and concave for  $n \in (\frac{\mu b}{\alpha a - \mu}, \infty)$ .

From the geometry of  $\varphi(t, n)$  and  $\psi(t, n)$  one may see that (H3) holds. In addition, it is clear that for a fixed  $t_*$ , assuming that  $\frac{\mu b}{\alpha a - \mu} < k$  we get that both functions intersect just once in the first quadrant at a point  $\bar{n} \in (\frac{\mu b}{\alpha a - \mu}, k)$ . Hence, (H2) holds. One can also easily check that (H4) holds too. Now the maximum of  $\varphi(t, n)$  is reached at a point  $n \leq k/2$ . So, assuming  $k/2 < \frac{\mu b}{\alpha a - \mu}$  we deduce that the intersection  $\bar{n}$  satisfies that  $\bar{n} > k/2$ ; furthermore, at that point  $\varphi(t, n)$  is decreasing and  $\psi(t, n)$  is increasing. Under our assumptions  $\varphi(t, n)$  and  $\psi(t, n)$  are both concave for  $n > 0$ ; thus,  $\varphi'(t, n), \psi'(t, n)$  are decreasing for  $n > 0$ . Since  $\bar{n} > k/2$ , we deduce that

$$\varphi'(t_*, \bar{n}) + \psi'(t_*, \bar{n}) < \varphi'(t_*, k/2) + \psi'(t_*, k/2) = \frac{-\lambda b}{ka} + \frac{\alpha ab}{e(b + k)^2}$$

Multiplying and dividing by  $b$  in the second term, we can bound the above sum by  $\frac{-\lambda b}{ka} + \frac{\alpha a}{eb}$ , and therefore we get that

$$\varphi'(t_*, \bar{n}) + \psi'(t_*, \bar{n}) < \frac{-\lambda eb^2 + \alpha ka^2}{bka}$$

So, if  $\lambda eb^2 > \alpha ka^2$  the result follows from [Theorem 2.1](#), as the previous discussion does not depend on  $t_*$ . □

**Remark 3.2.** Notice that predator–prey systems without a closure term do not fulfill hypotheses (H1) and (H3). Examples of this are the Gause-type predator–prey model [26] and its generalized version [24] (see also references therein). Therefore, [Theorem 2.1](#) does not apply in these cases, since new hypotheses replacing (H1) and (H3) would be needed. Nevertheless, even though our techniques cannot be applied to these models, the basic ideas can be kept and, combined with the construction done in [24], they can be used to improve on known results related to the existence of periodic solutions.

#### 4. The classic periodic competition model revisited

This section is aimed to illustrate how the construction described in Section 2 can be adapted to the case when the function  $\varphi(t, n)$  is decreasing in  $n$  (see hypothesis (H3)). In fact, in this case the underlying geometrical ideas also allow to state the non-existence of periodic solutions, under certain hypotheses.

To this end we revisit the classic two species periodic competition model. Denoting the competing species by  $n$  and  $p$ , respectively, we consider the system

$$\begin{cases} n' = n(a(t) - b(t)n - c(t)p), \\ p' = p(d(t) - e(t)n - f(t)p). \end{cases} \tag{10}$$

Each equation consists of a logistic term, which describes the dynamics in the absence of the other species, plus a competition term. In this scenario the main issue is to find coexistence/exclusion conditions. The classical results [15,12] hold upon the existence of upper and lower bounds of the coefficients of the system (10). Although more recent papers include delays and other settings [31], the periodic system (10) still attracts great attention. For instance, the results in [1] or [23] (and references therein) relate species coexistence/exclusion to the stability of the semi-trivial solutions (those with just one zero component) of the system (10) by making use of the average values of the coefficients and the semi-trivial solution of system (10).

Compared to this, the results we present in Theorem 4.1 provide with: (i) a natural extension of the classic coexistence conditions (see Remark 4.2) and (ii) exclusion conditions that do not require either the average value of the coefficients of the system or the explicit computation of the semi-trivial solutions of the system. Even though our conditions are not, at a first glance, comparable with those in [1] or [23], ours are quite general, easier to check than those in [23] and complementary to those in [1].

**Theorem 4.1.** *System (10) has at least one positive solution if the conditions*

$$a(t)/c(t) > d(t)/f(t) \quad \text{and} \quad d(t)/e(t) > a(t)/b(t) \tag{11}$$

*hold. Instead, species  $p$  is driven to extinction if the following hold:*

$$a(t)/c(t) > d(t)/f(t) \quad \text{and} \quad d(t)/e(t) < a(t)/b(t). \tag{12}$$

**Proof.** Let us consider a fixed  $t$  and let us set the right hand-side of each equation in the system (10) equal to zero. By performing easy calculations, we get that

$$p = \varphi(t, n) := \frac{a(t) - b(t)n}{c(t)} \quad \text{and} \quad p = \psi(t, n) := \frac{d(t) - e(t)n}{f(t)} \tag{13}$$

divide the plane into regions where the sign of  $n'$  and  $p'$  is constant.

Regarding the first assertion, condition (11) implies that for each  $t$ ,  $\varphi(t, n)$  and  $\psi(t, n)$  meet once in the first quadrant. So, it is straightforward to define the invariant region as we did in Theorem 2.1.

Regarding the second assertion, conditions (12) imply that  $\varphi(t, n)$  and  $\psi(t, n)$  do not meet at any values of  $t$  nor  $n$ . Let us define, for each value of  $t$ , the segment lines  $\mathcal{L}_\psi(t) = [0, \infty) \times [0, \infty) \cap \{p = \psi(t, n)\}$ ; similarly for  $\mathcal{L}_\varphi(t)$  (see Fig. 2). The segment  $\mathcal{L}_\psi(t)$  divides the positive cone into two disjunct regions  $\mathcal{A}_1(t)$ ,  $\mathcal{A}_2(t)$ , where  $p' > 0$  and  $p' < 0$ , respectively. Notice that even though the regions  $\mathcal{A}_i(t)$  vary with time, the fact that  $p' = 0$  and  $n' > 0$  on  $\mathcal{L}_\psi(t)$  holds for any  $t$ . For each  $\delta > 0$  and  $\psi_\delta(t, n) = \psi(t, n) + \delta$ , we also define the region  $\mathcal{B}_\delta(t) := \{(n, p); \leq (d(t) + \delta)/e(t) \leq n, \psi_\delta(t, n) \leq p\}$  and  $\mathcal{L}_{\psi_\delta}(t)$ .

The key idea is to show that, for an appropriate  $\delta > 0$  and regardless of the value of  $t$ , the region  $\mathcal{B}_\delta(t)$  fulfills that: (i)  $p'$  is negative and bounded by a strictly negative number in  $\mathcal{B}_\delta(t)$ ; (ii) any solution with positive initial values not in  $\mathcal{B}_\delta(t)$  will reach  $\mathcal{B}_\delta(t)$  after a transient time; (iii) any solution with initial values in  $\mathcal{B}_\delta(t)$  cannot leave  $\mathcal{B}_\delta(t)$ . These three conditions imply that  $p(t) \rightarrow 0$  as  $t \rightarrow \infty$ .

Condition (i) follows in a straightforward way from the definition of  $\mathcal{B}_\delta(t)$ .

Let us prove condition (ii). We note  $z(t, t_0, z_0) = (n(t, t_0, n_0), p(t, t_0, p_0))$  as in the proof of Theorem 2.1, but related to the system (10). Furthermore, let  $z_0 = (p_0, n_0) \in \mathcal{A}_1(t_0)$ . We claim that



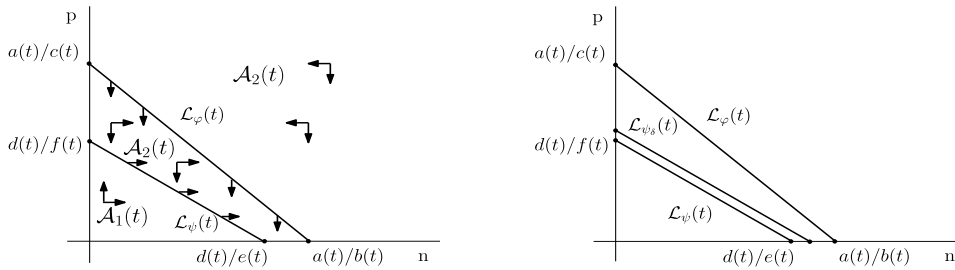


Fig. 2. Left: the intersection  $\mathcal{L}_\varphi(t)$  and  $\mathcal{L}_\psi(t)$  of the nullclines  $p = \varphi(t, n)$  and  $p = \psi(t, n)$  of the system (10) with the non-negative cone under conditions (11) and the flow direction in regions  $\mathcal{A}_i$ ,  $i = 1, 2$ . Right: The segment lines  $\mathcal{L}_\varphi(t)$ ,  $\mathcal{L}_\psi(t)$  and  $\mathcal{L}_{\psi_\delta}(t)$ .

$z(t, t_0, n_0)$  must reach  $\mathcal{L}_\psi(t)$  at certain  $t$ . Indeed, consider the sequences  $\{t_k = t_0 + k\}$  and  $z(t_k, t_0, z_0) = (n(t_k, t_0, k_0), p(t_k, t_0, p_0))$ ; notice that if  $z(t_k, n_0, p_0)$  is in  $\mathcal{A}_1(t)$ , then  $n(t_k, n_0, p_0)$  is strictly increasing while  $p(t_k, n_0, p_0)$  is non-decreasing. If  $z(t_k, n_0, p_0)$  leaves  $\mathcal{A}_1(t)$ , then there exists  $t_*$  such that  $z(t_*, n_0, p_0) \in \mathcal{L}_\psi(t)$ . Otherwise there exists  $\lim_{k \rightarrow \infty} z(t_k, n_0, p_0) = z_* \in \mathcal{A}_1(t)$ , so that  $z_*$  is an interior equilibrium point of the system (10), which is not possible. Therefore any solution starting in  $\mathcal{A}_1(t)$  will reach  $\mathcal{L}_\psi(t)$ , where the flow of the system points strictly outwards  $\mathcal{A}_1(t)$  for every  $t$ . The same argument proves that any solution of system (10) with initial values on  $\mathcal{L}_\psi(t)$  will reach  $\mathcal{L}_{\psi_\delta}(t)$  for a certain  $t$ .

Note that for each  $t$  and  $\delta > 0$  the slope of the segment  $\mathcal{L}_{\psi_\delta}(t)$  is  $-e(t)/f(t)$ . Furthermore, there exists  $\gamma > 0$  such that  $-\gamma > -\max\{e(t)/f(t), t\}$ . Since  $p'(t) = 0$  and  $n'(t) > 0$  on  $\mathcal{L}_\varphi(t)$ , we can choose  $0 < \delta < \gamma$  small enough so that

$$\min \left\{ \frac{p'(t, t_0, p_0)}{n'(t, t_0, n_0)}, (n_0, p_0) \in \mathcal{L}_{\phi_\delta}(t), t \right\} > -\delta,$$

it means that the flow on  $\mathcal{L}_{\phi_\delta}(t)$  points strictly inward  $\mathcal{B}_\delta(t)$ , regardless of  $t$ , which completes the proof of (ii) and also implies (iii).  $\square$

**Remark 4.2.** Let us denote by  $h_L$  and  $h_M$ , respectively, the minimum and the maximum values achieved by a periodic function  $h(t)$ . The classical results on existence of positive periodic solutions to the system (10) replace conditions (11) by

$$a_L/c_M > d_M/f_L \quad \text{and} \quad d_L/e_M > a_M/b_L.$$

### 5. Conclusions and on-going work

We have presented (Theorem 2.1) a sufficient condition for a system of the form (1) to have at least one periodic solution. From the previous sections, one may see that the technique described herein is somehow new and provides an alternative approach to available techniques, like bifurcation or perturbation methods and continuation theory. Besides, the construction of the invariant region can be seen as a sort of specialization of the classical technique based on the existence of upper and lower bounds for the periodic terms. Furthermore, because of the geometric foundations of the construction and its local nature, the technique can be modified to handle a variety of models.

As far as predation relations are concerned, the construction presented herein can be used to deal with the class of periodic predator–prey models with predator interference in the functional response. This family of models has been shown to fit much better field data than those without predator interference [29]. We refer, in particular, to the periodic Crowley–Martin model [6], the Hassell–Varley model [18] or the Beddington–DeAngelis model [3,8], which has recently received much attention (see [17] for the autonomous version, and [11] for the non-autonomous version). We are currently trying to apply the ideas and results in this paper to obtain new or improved results on the periodic versions of the models.

As shown in Section 4, the construction of the invariant region presented in Section 2 can be easily adapted to study competition models. We may distinguish between exploitative competition and interference competition (system (10) corresponds to the latter). As noted in [2], although interference competition is almost everywhere (see [22] and [9]), most theories in interspecific competition focus on exploitative competition. Our results are applicable to two species interference competition models, but not to exploitative models. Given species  $x_i$  with  $i = 1, 2$ , typical applications consider competition terms of the form  $x_i f_i(x_j)$  with  $i \neq j$ . More general and realistic models should include competition terms of the form  $x_i f_i(x_i, x_j)$  and, for managed communities, analyzing systems of the form (8) is of full interest.

Furthermore, similar considerations hold for cooperative models; so, there is a wide range of models where the results achieved in this paper can be applied.

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