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Topological degree in the generalized Gause prey–predator model

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ABSTRACT

We consider a generalized Gause prey–predator model with T-periodic continuous coefficients. In the case where the Poincaré map $\mathcal{P}$ over time T is well defined, the result of the paper can be explained as follows: we locate a subset U of $\mathbb{R}^2$ such that the topological degree $d(I-\mathcal{P},U)$ equals to $+1$. The novelty of the paper is that the later is done under only continuity and (some) monotonicity assumptions for the coefficients of the model. A suitable integral operator is used in place of the Poincaré map to cope with possible nonuniqueness of solutions. The paper, therefore, provides a new framework for studying the generalized Gause model with functional differential perturbations and multi-valued ingredients.

1. Introduction

The generalized Gause prey–predator model with time-dependent coefficients reads as

$$\begin{aligned}\dot{x} &= xa(t,x) - yb(t,x),\\ \dot{y} &= y\big(c(t,x) - d(t)\big),\end{aligned} \tag{1}$$

where $a(t,x)$ is the specific growth rate of the prey in the absence of any predators, $b(t,x)$ is the predator response function, $c(t,x)$ is the proportion as to how the presence of prey enhances the growth of predator, $d(t)$ is the rate of how the predator population declines in the absence of prey. The generalized autonomous Gause model has been introduced by Freedman in [10, Ch. 4] and system (1) comes from accounting for periodic changes of the environment in that autonomous model. A fundamental dynamical property of prey–predator models, known as *permanence*, is that their solutions are often trapped within a positive rectangular region R_∞.[1] Sufficient conditions for system (1) to be permanent are proposed in Teng, Li and Jiang [35] and Luo [23], where the interested reader can also learn the biological relevance of this property. One of the consequences of permanence is the existence of a periodic solution in R which persists under functional differential perturbations of system (1), useful for incorporating delays, neutral and impulsive terms into (1). In this paper we are interested in a weaker (as proved in Zanolin [37]) property of system (1) which still ensures the presence of a periodic solution with the same stability properties, but requires just basic assumptions for the coefficients. Specifically, let W be the set of all continuous functions acting from $[0,T]$ to the interior of a rectangular subset R of R_∞ that contains all positive T-periodic solutions of (1) and let $d(I-\Phi,W_R)$ be the topological degree (see [20]) of the integral operator

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[1] We say "rectangular region" when refer to a set of the form $\{(x,y)\colon\ x_1<x<x_2,\ y_1<y<y_2\}$.

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$$\big(\Phi(x,y)\big)(t)=\begin{pmatrix}x(T)\\ y(T)\end{pmatrix}+\int_0^t\begin{pmatrix}x(\tau)a(\tau,x(\tau))-y(\tau)b(\tau,x(\tau))\\ y(\tau)(c(\tau,x(\tau))-d(\tau))\end{pmatrix}d\tau$$

with respect to W_R. We prove that R is bounded and that

$$d(I-\Phi,W_R)=1 \tag{2}$$

under the following assumptions:

(A) $a(t,0)>0$ for all $t\in[0,T]$, for every $t\in[0,T]$ there exists a unique $x_a(t)$ such that $a(t,x_a(t))=0$ and $a(t,x)<0$ for all $x>x_a(t)$.
(B) $b(t,x)>0$ for all $t\in[0,T]$ and $x>0$, $b(t,0)\equiv 0$, for any $x_0>0$ there exists $B(x_0)>0$ such that $b(t,x)\geqslant B(x_0)$ for all $x\geqslant x_0$ and $t\in[0,T]$, $\underline{\lim}_{x\to 0}\frac{x}{b(t,x)}>0$ for any $t\in[0,T]$.
(C) $c(t,x)>0$, $d(t)>0$ for all $t\in[0,T]$ and $x>0$, $c(t,0)\equiv 0$, $c(t,x)$ doesn't decrease in $x\geqslant 0$ for each fixed $t\in[0,T]$, given any $t\in[0,T]$ there exists a unique $x_c(t)$ such that $c(t,x_c(t))=d(t)$.
(X) $\sup_{t\in[0,T]}x_c(t)<\inf_{t\in[0,T]}x_a(t)$, $\sup_{t\in[0,T]}x_a(t)<\infty$.

Assumptions (A), (B), (C) are weaker than those currently available in the literature on permanence of (1) (that would imply (2)) and the existence of positive periodic solutions to (1) (that (2) implies). As the amount of references is huge we review only those whose assumptions do not contradict (A), (B), (C), which can be deemed standard according to Freedman [10, Ch. 4]. While studying a particular form of (1) the paper by Hu, Liu and Yan [16] requires that the partial derivative b'_x exists and is strictly positive everywhere and that $\lim_{x\to\infty}b(t,x)$ exists and is finite. Applying the result of Teng, Li and Jiang [35] one would need to assume that the y component of all positive solutions of (1) are uniformly bounded as $t\to\infty$. A sufficient condition that this paper provides requires that a certain time-integral of $c(t,x)-d(t)$ is negative for large x, which is not the case for (1). The paper Wolkowicz and Zhao [36] considers a particular form of (1) while still requires $b(t,x)$ to be strictly increasing in x. A Gause model of similar to (1) (but with a particular form of $a(t,x)$) is considered in Moghadas and Alexander [28] and Liu and Lou [21] where $b'_x(t,x)>0$ and $b''_{xx}(t,x)<0$ for all $x>0$, $t\in\mathbb{R}$. The paper Luo [23] considers a more general form of (1), but requires that $a'_x(t,x)\leqslant 0$ for all $x\geqslant 0$, $t\in\mathbb{R}$ and assumes boundedness of $b(t,x)$ and $c(t,x)$ when applied to (1). The fundamental assumptions in Ding, Su and Hao [5] and Ding and Jiang [6] are comparable with ours, however these authors assume $x\mapsto b(t,x)$ sub-linear for all $x\geqslant 0$ and we need the later at $x=0$ only. The condition (X) plays a similar role as the requirements for time-integrals of the coefficients of (1), that literally all of the papers [16,5,36,28,21,23,6,35] assume (paper [28] doesn't impose any conditions for time-integrals because it deals with nearly constant T-periodic solutions only). Detailed comparison of (X) with the respective assumptions in these papers is outside the scope of this introduction.

Somewhat stronger assumptions in the above mentioned papers are often used to get stronger results compared to the goal (2) of this paper. We understand that the assumptions of some of these papers can be relaxed (in particular, the proofs in Ding, Su and Hao [5] and Ding and Jiang [6] obtained for more complex versions of (1) can possibly be adjusted to our settings). Our introduction doesn't aim to document that we got stronger results, but rather wants to emphasize that our new technique leads to the assumptions, which are different from those used in the relevant literature. Moreover, our technique may appear simpler (for some readers) than those used in papers [16,5,36,28,21,23,6,35].

We stress that assumptions (A), (B), (C) do not assume any differentiability or Lipschitz continuity for the coefficients of (1). This is important if we were to implement the group defense phenomenon (see Freedman and Wolkowicz [11]) or to incorporate complicate variants of the Rosenzweig law of the growth of the prey population in the absence of predators (see Bravo, Fernandez, Gamez, Granados and Tineo [2]). In particular, in contrast with the mentioned papers, we neither need $c'_x(t,x)>0$, nor $c'_x(t,x)\geqslant 0$ for any of $x>0$. Relaxed regularity is also a necessary step towards considering switch-like interactions between the species, that would lead to Filippov-type differential inclusions versus ordinary differential equations in (1) (see Gouze and Sari [13]). Along similar lines, our approach may provide useful information in studying stochastic versions of model (1) where the known conditions (see Lv and Wang [24] and references therein) for stochastic permanence do not hold.

As for the monotonicity assumption in (C), it is not vital for the proofs. However, it is important for the proof of Lemma 2.1 that $c(t,x)>d(t)$ for large values of $x>0$. In particular, our result cannot be immediately extended to Gause models with non-monotonic functional responses from Hu [16], Ding and Jiang [4], or Fan and Wang [8]. At the same time the results can be extended to account for more complex functional responses, where the coefficients b and c depend on y. In this way our ideas may complement the existence results in Liu and Yan [22], Fan, Li and Wang [9] and Dai, Su and Hu [3].

Let us now briefly look through the idea and the layout of the paper. The most initial consideration is that (2) holds, if we were successful to locate a region $R\subset\mathbb{R}^2$ such that the vector field of (1) is pointed towards the interior of R on the boundary of R at any time. Rectangular regions R are most convenient to verify this property. Fig. 1(left) suggests little chances to locate such a rectangular region for the vector field of (1), however in Section 2 we propose an ε-perturbation (3) of (1) that raises bifurcation of a rectangular region R_ε with the required properties from infinity (see Lemma 2.1). The rest of Section 2 (Lemma 2.3) is devoted to showing that the T-periodic solutions of the perturbed system (3) lie in a

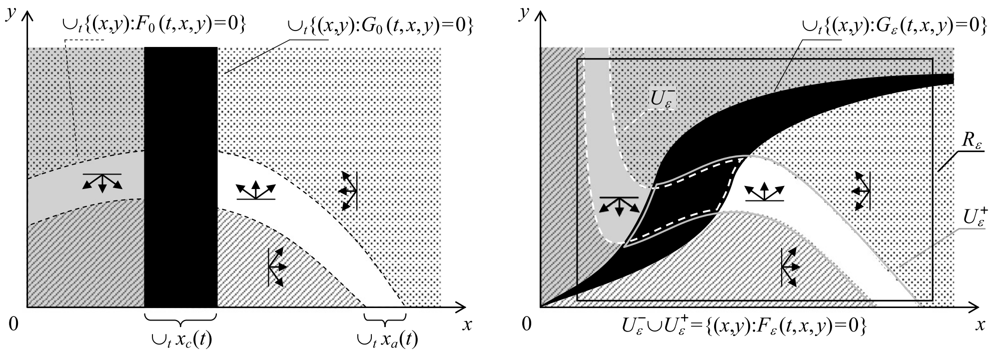

Fig. 1. Schematic picture of isoclines and the respective directions of the vector field of the Gause model (1) (left figure) and its perturbation (3) (right figure). The set where $F_\varepsilon(t,x,y)<0$ (dotted white and dotted dark fillings) is separated from the set where $F_\varepsilon(t,x,y)>0$ (diagonal white and diagonal dark fillings) by a curved strip (not black one) where $F_\varepsilon(t,x,y)=0$ for some $t\in[0,T]$. Similarly, the set where $G_\varepsilon(t,x,y)<0$ (dark dotted and dark diagonal fillings) is separated from the set where $G_\varepsilon(t,x,y)>0$ (white dotted and white diagonal filling) by a black strip where $G_\varepsilon(t,x,y)=0$ for some $t\in[0,T]$. The figure also illustrates the crucial difference between the original and the perturbed models: the right figure admits a rectangular region R_ε that is strictly invariant under the flow of (3) with $\varepsilon>0$.

smaller rectangle R that doesn't depend on ε. This property is used in Section 3 to prove the coincidence of $d(I-\Phi_\varepsilon, W_{R_\varepsilon})$ and $d(I-\Phi_0, W_R)$ in Theorem 3.1, which is the main result of the paper in the case where the uniqueness of solutions of (1) holds. For Guase models (1) with negative divergence (see (21) for the definition) our result implies the existence of an asymptotically stable T-periodic solution in R provided that the period T is not too big. This result is proved in Theorem 4.1 of Section 4. Theorem 4.1 is then applied in Section 5 to derive conditions for the existence of an asymptotically stable T-periodic solution to the Lotka–Volterra model with Holling type-II predator response function. A short introduction precedes the statement of the main result (Theorem 5.1) there. The requirement for the uniqueness of solutions of (1) is removed in Section 6 (Theorem 6.1) by providing a relevant version (Lemma 6.1) of the Krasnoselskii's T-irreversibility lemma. Theorem 6.1 is the main result of this paper, it proves (2) under assumptions (A), (B), (C) and (X) only. A formulation of Theorem 6.1 in terms of the Mawhin's coincidence degree (typical for the literature on prey–predator models) appears as Theorem 6.2. An acknowledgments section concludes the paper.

2. A perturbation that unfolds a rectangular trapping region

As outlined in the introduction, the presence of a set R such that the vector field of (1) is pointed to the interior of R on the boundary ∂R of R would be sufficient to prove the property (2). The reason for this paper is that we cannot locate such a set for the original system (1) (see Fig. 1(left) for the phase portrait), but can do that for the following perturbation

$$\begin{aligned}\dot{x} &= xa(t,x) - yb(t,x) + \varepsilon =: F_\varepsilon(t,x,y),\\ \dot{y} &= y\big(c(t,x) - d(t)y^\varepsilon\big) =: G_\varepsilon(t,x,y),\end{aligned} \tag{3}$$

that we discovered. Specifically, we can prove that rectangular strictly invariant regions $R_\varepsilon\subset\mathbb{R}^2$ bifurcate in system (3) from infinity as ε crosses zero (see Fig. 1). The whole text of the paper is basically a proof of the convergence of T-periodic solutions of (3) that strict invariance of R_ε implies (Brouwer theorem, see [19, Theorem 3.1]) to a T-periodic solution of (1). The focus on the topological degree doesn't make proofs longer, but opens a potential room for further applications and generalizations, thus our topological settings.

A simple intuition as for why the perturbation in (3) helps us so much can be gained from studying x- and y isoclines of (3), i.e. the curves of the phase plane where the vector fields $(x,y)\mapsto F_\varepsilon(t,x,y)$ and $(x,y)\mapsto G_\varepsilon(t,x,y)$ take zero values. For $\varepsilon>0$ these isoclines are found as

$$\begin{aligned}&F_\varepsilon\big(t,x,f_\varepsilon(t,x)\big)=0, \quad \text{where } f_\varepsilon(t,x)=\frac{xa(t,x)}{b(t,x)}+\frac{\varepsilon}{b(t,x)},\ x>0,\\ &G_\varepsilon\big(t,x,g_\varepsilon(t,x)\big)=0, \quad \text{where } g_\varepsilon(t,\varepsilon)=\left(\frac{c(t,x)}{d(t)}\right)^{1/\varepsilon},\ x>0\end{aligned}$$

and we have

$$F_\varepsilon(t,x,y)<0 \qquad \big(F_\varepsilon(t,x,y)>0\big), \quad \text{if } y>f_\varepsilon(t,x)\ \big(0<y<f_\varepsilon(t,x)\big), \tag{4}$$

$$G_\varepsilon(t,x,y)<0 \qquad \big(G_\varepsilon(t,x,y)>0\big), \quad \text{if } y>g_\varepsilon(t,x)\ \big(0<y<g_\varepsilon(t,x)\big). \tag{5}$$

Fig. 1(right) explains how the strictly invariant rectangular region R_ε of (3) needs to be built. Next lemma is the proof of this pictorial observation.

Lemma 2.1. *Let a, b, c, d be continuous functions satisfying* (A), (B), (C) *and* (X). *Fix an arbitrary* $\Delta > 0$. *Then there exists* $\varepsilon_0 > 0$ *such that given any* $\varepsilon \in (0, \varepsilon_0]$ *and* $M > 0$ *there exist*

$$\underline{x}_\varepsilon \in (0, \varepsilon), \qquad \underline{y}_\varepsilon \in (0, \varepsilon), \qquad \bar{y}_\varepsilon > M$$

such that the vector field $(x, y) \mapsto \binom{F_\varepsilon(t,x,y)}{G_\varepsilon(t,x,y)}$ *points strictly inward the set*

$$R_\varepsilon = \left\{(x, y) \in \mathbb{R}^2:\ \underline{x}_\varepsilon < x < \sup_{t\in[0,T]} x_a(t) + \Delta,\ \underline{y}_\varepsilon < y < \bar{y}_\varepsilon\right\}$$

on its boundary ∂R_ε *at any* $t \in [0, T]$.

Proof. Put $\bar{x} = \sup_{t\in[0,T]} x_a(t) + \Delta$ and choose such an $\varepsilon_0 > 0$ that $F_\varepsilon(t, \bar{x}, y) < 0$ for all $t \in [0, T]$, $y > 0$. Fix $\varepsilon \in (0, \varepsilon_0]$ and $M > 0$. We define $\bar{y}_\varepsilon$, $\underline{x}_\varepsilon$, $\underline{y}_\varepsilon$ one by one as any constants that satisfy the respective condition:

$$\begin{aligned}
&\bar{y}_\varepsilon: && \bar{y}_\varepsilon > M \text{ and } y_\varepsilon > \max\nolimits_{t\in[0,T]} g_\varepsilon(t, \bar{x}),\\
&\underline{x}_\varepsilon: && \underline{x}_\varepsilon \in (0, \varepsilon) \text{ and } \min\nolimits_{t\in[0,T]} f_\varepsilon(t, \underline{x}_\varepsilon) > \bar{y}_\varepsilon\\
& && (\text{such a choice is possible because } f_\varepsilon(t, x) \geqslant \tfrac{\varepsilon}{b(t,x)} \geqslant l_2 \tfrac{\varepsilon}{x} \text{ and } b(t, 0) = 0),\\
&\underline{y}_\varepsilon: && \underline{y}_\varepsilon \in (0, \varepsilon) \text{ and } \underline{y}_\varepsilon < \min\nolimits_{t\in[0,T]} g_\varepsilon(t, \underline{x}_\varepsilon).
\end{aligned}$$

From (4)–(5) we conclude that

$$\begin{aligned}
&F_\varepsilon(t, \underline{x}_\varepsilon, y) > 0, \quad \text{for any } y \in [\underline{y}_\varepsilon, \bar{y}_\varepsilon],\\
&F_\varepsilon(t, \bar{x}, y) < 0, \quad \text{for any } y \in [\underline{y}_\varepsilon, \bar{y}_\varepsilon], \quad (\text{provided that } \varepsilon_0 > 0 \text{ is small enough})\\
&G_\varepsilon(t, x, \underline{y}_\varepsilon) > 0, \quad \text{for any } x \in [\underline{x}_\varepsilon, \bar{x}],\\
&G_\varepsilon(t, x, \bar{y}_\varepsilon) < 0, \quad \text{for any } x \in [\underline{x}_\varepsilon, \bar{x}]
\end{aligned}$$

by construction, which is the statement of the lemma. □

The isoclines for system (3) with $\varepsilon = 0$ are given in Fig. 1(left) and the interested reader can check that the trick of Lemma 2.1 cannot be applied for the unperturbed Gause model. As we will prove in Theorem 6.1, Lemma 2.1 implies that $d(I - \Phi_\varepsilon, W_{R_\varepsilon}) = 1$, whose disadvantage is that R_ε blows up as ε converges to 0, so that we cannot yet pass to the limit as $\varepsilon \to 0$. However, next lemma allows to see that we don't miss any T-periodic solutions, if transform sets R_ε to a smaller rectangular region R that doesn't depend on ε. This will allow us making the above mentioned passage to the limit. Introduce

$$x_{max} = \sup_{s\in[0,T]} x_a(s), \qquad y_{max} = \max_{t\in[0,T],\ x\in[0,x_{max}]} \frac{x \cdot \max\{0, a(t, x)\}}{b(t, x)} \exp\left(\int_0^T c(s, x_{max})\, ds\right). \tag{6}$$

Lemma 2.2. *Let a, b, c, d be continuous functions satisfying* (A), (B), (C) *and* (X). *Fix* $\Delta > 0$. *Then there exists* $\varepsilon_0 > 0$ *such that given any* $\varepsilon \in [0, \varepsilon_0]$ *system* (3) *does not have T-periodic solutions* (x, y) *with initial conditions* $(x(0), y(0))$ *in* $\bigcup_{\mu\in(0,\varepsilon_0]} \partial R^0_\mu$, *where* ∂R^0_μ *is the boundary of the set*

$$R^0_\mu = \left\{(x, y):\ \mu < x < x_{max} + \Delta,\ \mu < y < (y_{max} + \Delta)\frac{\varepsilon_0}{\mu}\right\}.$$

The following lemma is a part of the proof of Lemma 2.2, but it may also be of independent interest as an estimate for the location of T-periodic solutions in the original model (1).

Lemma 2.3. *Let a, b, c and d be continuous functions satisfying* (A), (B) *and* (C). *Assume that*

$$x_{max} < \infty$$

and consider $\Delta > 0$. *Then there exist* $\varepsilon_0 > 0$ *and* $L \in (0, \Delta]$ *such that given any* $\varepsilon \in [0, \varepsilon_0]$ *the following properties hold for any solution* (x, y) *of* (3) *that has a point in* $(0, \infty) \times (0, \infty)$ *and verifies* $(x(0), y(0)) = (x(T), y(T))$:

1) *positiveness of x and y*: $0 < x(t)$ *and* $0 < y(t)$, *for all* $t \in [0, T]$, *boundedness of x from above*: $x(t) < x_{max} + \Delta$, *for all* $t \in [0, T]$,
2) *an estimate for the lowermost points of x*: $x([0, T]) \cap (0, \sup_{t\in[0,T]} x_c(t) + \Delta) \neq \emptyset$,
3) *an estimate for the uppermost points of x*: $x([0, T]) \cap [L, \infty) \neq \emptyset$,
4) *boundedness of y from above*: $y(t) < y_{max} + \Delta$, $t \in [0, T]$.

The solutions (x, y) of (3) that satisfy $(x(0), y(0)) = (x(T), y(T))$ will be loosely called T-periodic solutions. Next brief result on the uniqueness of solution of a specific Cauchy problem associated to the equations of (1) is required for the proof of Lemma 2.3.

Lemma 2.4. *Assume that $\phi \in C^0(\mathbb{R}\times\mathbb{R},\mathbb{R})$. Then the Cauchy problem*

$$\dot{x} = x\phi(t, x),$$
$$x(t_0) = 0$$

has a unique solution for any $t_0 \in \mathbb{R}$. This solution is given by $x(t) \equiv 0$.

Proof. Let x_* be any solution of the Cauchy problem under consideration. Then x_* is a solution to the Cauchy problem

$$\dot{x} = x\phi\big(t, x_*(t)\big),$$
$$x(t_0) = 0,$$

which is given by the formula $x(t) = x(t_0)\exp(\int_{t_0}^t \phi(\tau, x_*(\tau))\,d\tau) \equiv 0$. Thus the assertion. $\square$

Proof of Lemma 2.3. In what follows we prove the 4 statements of the lemma one by one.

1) The estimate $0 < x(t)$ holds for $\varepsilon > 0$ because $F_\varepsilon(t, 0, y) > 0$ for any $\varepsilon > 0$ and $y \geqslant 0$. To justify this estimate for $\varepsilon = 0$ one has to notice that due to Lemma 2.4 the equation $\dot{x} = F_0(t, x, y(t))$ cannot have non-trivial T-periodic solutions that touch $x = 0$. If the estimate for y doesn't hold for some $\varepsilon \in (0, \varepsilon_0]$ then we have the existence of $\tau \in \mathbb{R}$ and $\delta > 0$ such that

$$y(\tau) = 0, \qquad 0 < y(t) < \min_{s\in[0,T]} g_\varepsilon\big(s, x(t)\big), \quad t \in [\tau - \delta, \tau).$$

But according to (5) this implies that $t \mapsto y(t)$ increases on $[\tau - \delta, \tau]$ and cannot reach 0 at $t = \tau$. We have $y(t) > 0$ in the case where $\varepsilon = 0$ too. Indeed, similar to the arguments for $x(t)$ the later statement follows from Lemma 2.4, i.e. from the fact that $\dot{y} = G_0(t, x(t), y)$ cannot have non-trivial T-periodic solutions that touch $y = 0$. The upper estimate for x now follows from the fact that $F_0(t, x, y) < 0$ for all $x > \sup_{t\in[0,T]} x_a(t)$ and $y \geqslant 0$.

2) Introduce

$$U_\varepsilon^- = \bigcup_{t\in[0,T]} \big\{(x, y) \in (0,\infty)\times(0,\infty)\colon F_\varepsilon(t, x, y) = 0,\ G_\varepsilon(t, x, y) \leqslant 0\big\},$$

see Fig. 1(right). One always has the existence of $t^- \in [0, T]$ such that $(x(t^-), y(t^-)) \in U_\varepsilon$. This follows from the fact that either $(\dot{x}(t), \dot{y}(t)) = 0$ at some $t \in [0, T]$ or the vector $\frac{(\dot{x}(t),\dot{y}(t))}{\|(\dot{x}(t),\dot{y}(t))\|}$ fills in a complete unit circle when t varies from 0 to T. Therefore, to achieve the statement of part 2 it is sufficient to show that there exists $\varepsilon_0 > 0$ such that for any $\varepsilon \in [0, \varepsilon_0]$ one has

$$x < \sup_{t\in[0,T]} x_c(t) + \Delta, \quad \text{for all } (x, y) \in U_\varepsilon^-. \tag{7}$$

Since $G_0(t, x, y) \leqslant 0$ for any $x \leqslant x_c(t)$ and any $y > 0$, property (7) holds for $\varepsilon = 0$ automatically. We, therefore, focus on considering $\varepsilon > 0$. In this case

$$U_\varepsilon^- = \bigcup_{(t,x)\in[0,T]\times[0,\infty)\colon f_\varepsilon(t,x)\geqslant g_\varepsilon(t,x),\ f_\varepsilon(t,x)>0} \big\{\big(x, f_\varepsilon(t, x)\big)\big\}.$$

If $\sup_{t\in[0,T]} x_c(t) = \infty$ the estimate (7) holds straight away and we need to focus on the case $\sup_{t\in[0,T]} x_c(t) < \infty$ only. Observe that there exists $l > 0$ such that

$$\frac{c(t, x)}{d(t)} \geqslant 1 + l, \quad \text{for all } x \geqslant \sup_{t\in[0,T]} x_c(t) + \Delta,\ t \in [0, T]. \tag{8}$$

Indeed, assume that (8) doesn't hold, i.e. for any $l > 0$ one can find $t_* \in [0, T]$ and $x_* \geqslant \sup_{t\in[0,T]} x_c(t) + \Delta$ such that

$$\frac{c(t_*, \sup_{t\in[0,T]} x_c(t) + \Delta)}{d(t_*)} \leqslant \frac{c(t_*, x_*)}{d(t_*)} < 1 + l$$

(where non-decreasing of c has been used). By passing to the limit as $l \to 0$ one gets the existence of $t_* \in [0, T]$ such that $\frac{c(t_*,\sup_{t\in[0,T]} x_c(t)+L)}{d(t_*)} \leqslant 1$. But $\frac{c(t_*,x_c(t_*))}{d(t_*)} = 1$ by the definition of x_c and one can conclude that $\frac{c(t_*,\sup_{t\in[0,T]} x_c(t)+L)}{d(t_*)} < 1$ by the uniqueness property of x_c, see (C). This contradicts non-decreasing of $x \mapsto c(t_*, x)$ on $[x_c(t_*), \sup_{t\in[0,T]} x_c(t) + \Delta]$ and completes the proof of (8).

We use (8) to show the existence of $\varepsilon_0 > 0$ such that (7) holds for $\varepsilon \in (0, \varepsilon_0]$. Indeed, arguing by contradiction we obtain the existence of $\varepsilon_n \to 0$ as $n \to \infty$ and $(x_n, y_n) \in U^-_{\varepsilon_n}$, $n \in \mathbb{N}$, such that $x_n \geqslant \sup_{t\in[0,T]} x_c(t) + \Delta$. We conclude from (8) that

$$\frac{c(t,x_n)}{d(t)} \geqslant 1 + l, \quad \text{for all } t \in [0,T],\ n \in \mathbb{N},$$

and, therefore,

$$g_{\varepsilon_n}(t,x_n) = \left(\frac{c(t,x_n)}{d(t)}\right)^{1/\varepsilon_n} \to \infty \quad \text{as } n \to \infty.$$

By using the definition of U^-_ε we now have

$$f_{\varepsilon_n}(t,x_n) \to \infty \quad \text{as } n \to \infty \text{ uniformly in } t \in [0,T].$$

But since $x \leqslant \sup_{t\in[0,T]} x_a(t) + \Delta$ for any $(x,y) \in U^-_\varepsilon$, we have

$$f_{\varepsilon_n}(t,x) \leqslant \frac{\max_{t\in[0,T],x\in[0,\sup_{t\in[0,T]} x_a(t)+\Delta]} xa(t,x) + \varepsilon}{B(\sup_{t\in[0,T]} x_c(t) + \Delta)}, \quad \text{for all } x \geqslant \sup_t x_c(t) + \Delta.$$

This contradiction completes the proof of part 2.

3) Similar to part 2, each T-periodic solution that is addresses in the statement of the lemma must pass through the region

$$U^+_\varepsilon = \bigcup_{t\in[0,T]} \big\{(x,y) \in (0,\infty)\times(0,\infty)\colon\ F_\varepsilon(t,x,y) = 0,\ G_\varepsilon(t,x,y) \geqslant 0\big\},$$

see Fig. 1(right). The goal of part 3 is to show that $L > 0$ and $\varepsilon_0 > 0$ can be diminished in such a way that

$$L \leqslant x, \quad \text{for any } (x,y) \in U^+_\varepsilon \text{ and } \varepsilon \in [0,\varepsilon_0]. \tag{9}$$

Observe that there exists $l > 0$ such that $\frac{c(t,0)}{d(t)} < 1 - l$ for all $t \in \mathbb{R}$ (one would have $\frac{c(t_0,0)}{d(t_0)} \geqslant 1$ for some $t_0 \in [0,T]$ otherwise, that contradicts (C)). We now take a sufficiently small $L > 0$ (and within $[0,\Delta]$ as lemma requires) to have

$$\frac{c(t,x)}{d(t)} < 1 - \frac{l}{2}, \quad \text{for all } x \in [0,L],\ t \in [0,T].$$

This property, in particular, implies that $G_0(t,x,y) < 0$ for any $t \in [0,T]$, $x \in [0,L]$ and $y > 0$. Therefore, (9) holds for $\varepsilon = 0$ and it remains to prove that (9) holds for $\varepsilon \in (0,\varepsilon_0]$, where $\varepsilon_0 > 0$ is sufficiently small. Assuming the contrary, we get the existence of ε_n and $(x_n,y_n) \in U_{\varepsilon_n}$, such that $L \leqslant x_n$ for $n \in \mathbb{N}$. Therefore,

$$\frac{c(t,x_n)}{d(t)} < 1 - \frac{l}{2}, \quad \text{for all } t \in [0,T],\ n \in \mathbb{N},$$

and

$$g_{\varepsilon_n}(t,x_n) = \left(\frac{c(t,x_n)}{d(t)}\right)^{1/\varepsilon_n} \to 0 \quad \text{as } n \to \infty.$$

As in the proof of part 2, we observe, that for $\varepsilon > 0$ the set U^+_ε takes the form

$$U^+_\varepsilon = \bigcup_{(t,x)\in[0,T]\times[0,\infty)\colon\ 0<f_\varepsilon(t,x)<g_\varepsilon(t,x)} \big\{\big(x, f_\varepsilon(t,x)\big)\big\},$$

and, therefore,

$$f_{\varepsilon_n}(t,x_n) \to 0 \quad \text{as } n \to \infty \text{ uniformly in } t \in [0,T].$$

At the same time assumption (B) implies that $L > 0$ can be diminished so that

$$f_{\varepsilon_n}(t,x) \geqslant \delta a_{min}, \quad \text{where } \delta > 0 \text{ is a suitable constant, } a_{min} = \min_{t\in[0,T],\ x\in[0,L]} a(t,x).$$

We now diminish $L > 0$ again and achieve $a_{min} > 0$, which is possible because of (A). This raises a contradiction with the convergence of $f_{\varepsilon_n}(t,x_n)$ and completes the proof of (9).

4) To achieve the statement of part 4 we first use part 1 to sharp the estimate for the set U^+_ε that we obtained earlier. By combining (9) with part 1 we conclude that $\varepsilon_0 > 0$ can be diminished so that

$$L \leqslant x < \sup_{t\in[0,T]} x_a(t) + \Delta, \quad \text{for any } (x,y) \in U^+_\varepsilon \text{ and } \varepsilon \in [0,\varepsilon_0].$$

Secondly, letting $f_{max} = \max_{t\in[0,T], x\in[L, \sup_{t\in[0,T]} x_a(t)+\Delta]} \max\{0, f_0(t,x)\}$ we diminish $\varepsilon_0 > 0$ further, so that

$$L \leqslant x < \sup_{t\in[0,T]} x_a(t) + \Delta \quad \text{and} \quad 0 < y < f_{max} + \Delta \quad \text{for any } (x,y) \in U_\varepsilon^+ \text{ and } \varepsilon \in [0, \varepsilon_0]. \tag{10}$$

The estimate (10) along with monotonicity of c allow to use the differential inequalities techniques (see [19, §1.4]) to prove the boundedness of y from above. Let $\varepsilon \in [0, \varepsilon_0]$ and let (x,y) be a T-periodic solution to (3) that has a point in $(0,\infty)\times(0,\infty)$. As in the proof of part 3 we utilize the existence of $t^+ \in [0,T]$ such that $(x(t^+), y(t^+)) \in U_\varepsilon^+$. Since $y(c(t,x) - d(t)y^\varepsilon) < yc(t, \sup_{t\in[0,T]} x_a(t) + \Delta)$ for all $t \in [0,T]$, $0 \leqslant x \leqslant \sup_{t\in[0,T]} x_a(t) + \Delta$, and $y > 0$ we have that

$$y(t) \leqslant y_m(t),$$

where y_m is the solution of the Cauchy problem

$$\begin{aligned} &\dot y_* = y_* c\Big(t, \sup_{t\in[0,T]} x_a(t) + \Delta\Big), \\ &y_*(t^+) = f_{max} + \Delta. \end{aligned} \tag{11}$$

Since the general solution of the scalar differential equation $\dot y = A(t)y$ is given by $y(t) = y(\tau)\exp(\int_\tau^t A(s)\,ds)$, then any solution y_* of (11) whose initial condition doesn't exceed $f_{max} + \Delta$ must satisfy

$$y_*(t) < y_{max} + M(\Delta), \quad t \in [0,T],$$

for the constant $y_{max} > 0$ given by (6) and for some $M(\Delta) \to 0$ as $\Delta \to 0$, which doesn't depend on the choice of ε and y_*. Since the whole analysis can be carried out for some $\tilde\Delta \in (0,\Delta)$ playing the role of Δ and such that $M_1(\tilde\Delta) < \Delta$, we can formulate the lemma with $M(\Delta)$ replaced by Δ.

The proof of the lemma is complete. □

Proof of Lemma 2.2. The proof is by assuming the contrary. We therefore have a sequence $\{(x_n, y_n)\}_{n=1}^\infty$ of T-periodic functions and sequences $(\varepsilon_n, \mu_n) \to 0$ as $n \to \infty$ such that (x_n, y_n) solves (3) with $\varepsilon = \varepsilon_n$ and $(x_n(0), y_n(0)) \in \partial R^0_{\mu_n}$ for all $n \in \mathbb{N}$. Uniform boundedness of $\{(x_n, y_n)\}_{n=1}^\infty$ given by Lemma 2.3 allows us to consider this sequence convergent. Let

$$(x_0, y_0) = \lim_{n\to\infty} (x_n, y_n).$$

The choice of the rectangles $R^0_{\mu_n}$ is such that Lemma 2.3 (parts 1 and 4) ensures that (x_n, y_n) neither touches the right $(x = \sup_{t\in[0,T]} x_a(t) + \Delta)$ nor touches the top $(y = (y_{max} + \Delta)\frac{\varepsilon_0}{\mu_n})$ sides of $R^0_{\mu_n}$. This implies that either $x_0(t) \equiv 0$ or $y_0(t) \equiv 0$. The first case is impossible because of part 3 of Lemma 2.3 and we must conclude that x_0 is a T-periodic solution of the equation

$$\dot x = xg(t,x). \tag{12}$$

Part 3 of Lemma 2.3 ensures that x_0 is non-trivial. At the same time assumption (X) allows us to consider $\Delta > 0$ such that $\sup_{t\in[0,T]} x_c(t) + \Delta < \inf_{t\in[0,T]} x_a(t)$, so that

$$xg(t,x) > 0 \quad \text{for any } t \in [0,T],\ x \in \Big(0, \sup_{t\in[0,T]} x_c(t) + \Delta\Big).$$

Therefore, none of the elements of $(0, \sup_{t\in[0,T]} x_c(t) + \Delta)$ can be initial conditions of T-periodic solutions to (12), that contradicts part 2 of Lemma 2.3. The proof of the lemma is complete. □

3. Evaluation of the topological degree in the case of smooth coefficients

In this section we prove our main result for the class of smooth systems (3). Such an assumption allows to consider the Poincaré map $\mathcal{P}_\varepsilon$ (over the period T) of (3), which may be more familiar to some readers than the integral operator Φ_ε we use in Section 6.2 (where the uniqueness of solutions is not required).

Remark 3.1. In order for $\mathcal{P}_\varepsilon$ to be defined we also use the continuability of each solution of the unperturbed model (1) originating at $t = 0$ in $(0,\infty)\times(0,\infty)$ on the whole $[0,T]$. Let us briefly verify that the later is granted under the conditions (A), (B) and (C). Consider $(x_0, y_0) \in (0,\infty)\times(0,\infty)$ and the solution (x,y) of (1) with the initial condition $(x,y)(0) = (x_0, y_0)$. Consider the set

$$\widehat{R} = \big\{(x,y) \in \mathbb{R}^2\colon\ 0 < x < r_1,\ 0 < y < r_2\big\},$$

such that

$$r_1 > \max\Big\{x_0, \sup_{t\in[0,T]} x_a(t)\Big\}, \quad r_2 > y_*(T),$$

where y_* is the solution of

$$\dot{y}_* = y_* c(t, r_1),$$
$$y_*(0) = y_0.$$

We have that $r_2 > y_0$. According to the solutions extension theorem (see Hartman [14, Theorem 3.1]) the solution (x, y) must leave $\widehat{R}$ through the boundary $\partial\widehat{R}$, if this solution doesn't stay in $\widehat{R}$ for the whole time-interval $[0, T]$. But (x, y) cannot cross ∂R and leave R due to our choice of r_1 and r_2 (x doesn't reach r_1 because $F_0(t, r_1, y) < 0$ for all $t \in [0, T]$, $y > 0$ (see the proof of Lemma 2.1) and y doesn't reach r_2 since $y(t) \leqslant y_*(t)$ due to the differential inequalities lemma (see the proof of Lemma 2.3, part 3)).

We briefly recall that if the uniqueness and continuability (from $t = 0$ to $t = T$) of solutions hold, then the Poincaré map $\mathcal{P}_\varepsilon$ is defined as

$$\mathcal{P}_\varepsilon\big((x_0, y_0)\big) = \big(x(T), y(T)\big),$$

where (x, y) is the solution of (3) with the initial condition $(x(0), y(0)) = (x_0, y_0)$. We are now in the position to prove the analogue of (2) for the Gause model (1) with smooth coefficients.

Theorem 3.1. *Let a, b, c, d be C^1-functions that satisfy (A), (B), (C) and (X). Then given any $\Delta > 0$ there exists $\varepsilon_0 > 0$ such that*

$$d(I - \mathcal{P}_0, R) = 1,$$

where

$$R = \big\{(x, y) \in \mathbb{R}^2\colon\ \varepsilon_0 < x < x_{max} + \Delta,\ \varepsilon_0 < y < y_{max} + \Delta\big\}$$

and x_{max}, y_{max} are the constants given by (6).

Proof. Let $\varepsilon_0 > 0$ and $\{R_\varepsilon\}_{\varepsilon\in(0,\varepsilon_0]}$ be those given by Lemma 2.1. The conclusion of Lemma 2.1 implies that, for $\varepsilon \in (0, \varepsilon_0]$,

1) each solution (x, y) of (3) that starts at $t = 0$ at ∂R_ε doesn't pass through $(x(0), y(0))$ during $(0, T]$ (the property termed *T-irreversibility* in [19]);
2) $d(\binom{F_\varepsilon}{G_\varepsilon}, R_\varepsilon) = 1$.

Therefore, by Krasnoselskii's T-irreversibility lemma (see [19, Lemma 6.1]) one gets

$$d(I - \mathcal{P}_\varepsilon, R_\varepsilon) = 1, \quad \text{for any } \varepsilon \in (0, \varepsilon_0]. \tag{13}$$

Let us now diminish $\varepsilon_0 > 0$ so that the conclusion of Lemma 2.2 holds, thus ensuring that

$$\mathcal{P}_\varepsilon x \neq x \quad \text{for any } x \in \overline{R}_\varepsilon \backslash R \text{ and any } \varepsilon \in (0, \varepsilon_0]. \tag{14}$$

This allows to apply the additivity (excision) property of the topological degree to conclude that

$$d(I - \mathcal{P}_\varepsilon, R) = d(I - \mathcal{P}_\varepsilon, R_\varepsilon) = 1, \quad \text{for any } \varepsilon \in (0, \varepsilon_0],$$

while using that $d(I - \mathcal{P}_\varepsilon, R_\varepsilon \backslash \overline{R}) = 0$, which comes from (14). Lemma 2.2 implies that $d(I - \mathcal{P}_0, R)$ is defined and so $d(I - \mathcal{P}_0, R) = d(I - \mathcal{P}_\varepsilon, R)$ for $\varepsilon > 0$ sufficiently small, that completes the proof. □

4. The Gause model with negative divergence

In this section we show that property (2) of the topological degree implies the existence of an asymptotically stable periodic solution to real-analytic Gause models (1) provided that the divergence of (1) is strictly negative in $(0, \infty) \times (0, \infty)$ and that a suitable estimate holds for the period of the right-hand side of (1). The later condition is used to ensure that the Floquet multiplicators of any T-periodic solution of (1) are real and positive. The sign of the divergence further restricts the value of one of these multiplicators and the topological degree restricts the value of the another one. The real analyticity of a time-periodic function $(t, \xi) \mapsto \psi(t, \xi)$ of period T here means the following: for each $\xi_* \in (0, \infty)$ there exists $r > 0$ such that

$$\psi(t, \xi) = \sum_{\alpha\in\mathbb{N}} \psi_\alpha(t)(\xi - \xi_*)^\alpha, \quad t \in \mathbb{R}, \big\|\xi - \xi_*\big\| < r,$$

where the coefficients ψ_α are continuous and T-periodic in t and the convergence of the series is uniform in t. Real-analyticity is assumed in order to have isolateness of T-periodic solutions of (1).

The results of this section, Lemma 4.1 and Theorem 4.1, have several common points with the work of Amine and Ortega [1] and Ortega and Tineo [32], who investigated the finiteness of the number of T-periodic solutions and the connection of the topological degree and asymptotic stability in prey–predator models of Lotka–Volterra type. In particular, to not allow negative multipliers of T-periodic solutions of (1) to exist we use assumption (18) (see below) earlier discovered in [1]. The presentation in this section is split in two parts. We first establish asymptotic stability for a general planar system in Lemma 4.1 and then apply Lemma 4.1 to the Gause model (1) in Theorem 4.1. Some remarks towards alternative ways of avoiding negative multipliers (i.e. towards relaxing (18)) that we attempted to pursue conclude the section.

4.1. Topological index and the existence of asymptotically stable periodic solutions in planar differential equations with negative divergence

Consider a planar system of T-periodic in time C^1-smooth differential equations

$$\dot{u} = \psi(t, u), \tag{15}$$

whose solutions are continuable on $[0, T]$, and denote by $\mathcal{P}$ the respective Poincaré map over period T. In this subsection we discuss the asymptotic stability of a T-periodic solution u_0 of (15) under the assumption $\operatorname{ind}(u_0(0), \mathcal{P}) = 1$. Here $\operatorname{ind}(v, \mathcal{P})$ stays for the topological index of a fixed point v of map $\mathcal{P}$, i.e. for the value of $d(I - \mathcal{P}, V)$ where V is any neighborhood of v that don't have other fixed points of $\mathcal{P}$. The fundamental result that we are going to utilize follows from Ortega [31] and Kolesov [18]: *if the eigenvalues ρ_1 and ρ_2 of $\mathcal{P}'(u_0(0))$ satisfy $\rho_1 \geqslant 0$ and $\rho_2 \in (0, 1)$ then u_0 is asymptotically stable.* Negative divergence assumption often ensures $\rho_1 \geqslant 0$ and $\rho_2 \in (0, 1)$ for systems (15) where the time-dependent part is small (see Makarenkov and Ortega [26], Makarenkov and Martynova [25]), but an additional hypothesis is needed otherwise. The condition (18) that we use below can be viewed as a restriction of the influence of the time-dependent part too.

Lemma 4.1. *Let $(t, u) \mapsto \psi(t, u)$, $u \in \mathbb{R}^2$, be a real-analytic T-periodic in time function. Assume that the following conditions are satisfied for a T-periodic solution u_0 of (15):*

$$\operatorname{ind}\big(u_0(0), \mathcal{P}\big) = 1, \tag{16}$$

$$\textit{negative divergence}: \quad \operatorname{Sp} \psi_u'\big(t, u_0(t)\big) = \big[\psi_u'\big(t, u_0(t)\big)\big]_{11} + \big[\psi_u'\big(t, u_0(t)\big)\big]_{22} < 0, \quad t \in [0, T], \tag{17}$$

$$T < \pi \Big/ \left(\max\big\{\big|\big[\psi_u'\big(t, u_0(t)\big)\big]_{12}\big|, \big|\big[\psi_u'\big(t, u_0(t)\big)\big]_{21}\big|\big\} + \frac{1}{2}\big|\big[\psi_u'\big(t, u_0(t)\big)\big]_{11} - \big[\psi_u'\big(t, u_0(t)\big)\big]_{22}\big| \right), \quad t \in [0, T]. \tag{18}$$

Then u_0 is asymptotically stable.

For a 2×2-matrix A, we write $[A]_{ij}$ to denote the element of the i-th raw and j-th column.

Proof. Let ρ_1, ρ_2 be the eigenvalues of $\mathcal{P}'(u_0(0))$. By using the Lioville formula [14, Theorem 1.2] and negative divergence assumption (17) one obtains

$$\rho_1 \rho_2 = \det\big\|(\mathcal{P})'\big(u_0(0)\big)\big\| = \exp \int_0^T \operatorname{Sp} \psi_u'\big(\tau, u_0(\tau)\big)\, d\tau \in (0, 1).$$

The statement of the lemma is, therefore, immediate, if ρ_1 and ρ_2 are complex conjugated. We assume that $\rho_1 < \rho_2$ are real from now on. Since $\rho_1 \rho_2 \in (0, 1)$, one of the following two situations must take place:

a) $\rho_1 \in (0, 1)$, $\rho_2 > 0$,
b) $\rho_1 < 0$, $\rho_2 < 0$.

Asymptotic stability of u_0 that satisfies (16) and a) follows from Ortega result [31]. It turns out that assumption (18) rules out option b). This statement is proved in Amine and Ortega [1, §4], but we give an independent proof for the purpose of completeness. It is sufficient to prove that the linearized system

$$\dot{v} = \psi_u'\big(t, u_0(t)\big) v \tag{19}$$

cannot have non-trivial solutions v such that

$$\operatorname{sign} v_1(T) = -\operatorname{sign} v_1(0), \qquad \operatorname{sign} v_2(T) = -\operatorname{sign} v_2(0). \tag{20}$$

Indeed, let $\tilde{v}$ be a solution of (19) that satisfies (20). Consider $\tilde{r}, \tilde{\phi} \in C^1(\mathbb{R}, \mathbb{R})$ verifying

$$\tilde{v}_1(t) = \tilde{r}(t)\cos\tilde{\phi}(t), \qquad \tilde{v}_2(t) = \tilde{r}(t)\sin\tilde{\phi}(t).$$

Then $\tilde{\phi}$ is a solution to

$$\dot{\phi} = (\psi_{21})'_u\big(t, u_0(t)\big)\cos^2\phi + \frac{1}{2}\big[(\psi_{22})'_u\big(t, u_0(t)\big) - (\psi_{11})'_u\big(t, u_0(t)\big)\big]\sin 2\phi - (\psi_{12})'_u\big(t, u_0(t)\big)\sin^2\phi.$$

Assumption (18) ensures that $|\tilde{\phi}(t) - \tilde{\phi}(0)|$ doesn't reach π whenever $t \in [0, T]$, i.e. (20) cannot occur to $\tilde{v}$. This contradiction completes the proof. □

Remark 4.1. The ideas of Amine and Ortega [1, §4] can be used in order to relax (18) based on introducing an auxiliary parameter. The relaxed assumption takes form (18) for the value 1 of the auxiliary parameter.

4.2. Application to the Gause model with negative divergence

We are now in the position to state the main result of this section, some remarks will follow afterwards.

Theorem 4.1. *Let a, b, c, d be real-analytic T-periodic in time functions and let the assumptions (A), (B), (C), (X) be satisfied. If the negative divergence condition*

$$a(t,x) + xa'_x(t,x) - yb'_x(t,x) + c(t,x) - d(t) < 0, \quad \text{for any } t \in \mathbb{R},\ x > 0,\ y > 0 \tag{21}$$

holds, then (1) has at most a finite number of strictly positive T-periodic solutions and all these solutions are located in $(0, x_{max}] \times (0, y_{max}]$, where x_{max}, y_{max} are the constants given by (6). If, in addition,

$$T < \pi \Big/ \Bigg[\max_{t\in[0,T],\ x\in[0,x_{max}],\ y\in[0,y_{max}]} \bigg(\max\big\{c'_x(t,x)y_{max}, b(t,x)\big\} + \frac{1}{2}\big(a(t,x) + xa'_x(t,x) - yb'_x(t,x) - c(t,x) + d(t)\big)\bigg)\Bigg] \tag{22}$$

then (1) has at least one asymptotically stable T-periodic solution lying in $(0, x_{max}] \times (0, y_{max}]$.

Proof. From Lemma 2.3 we have that each strictly positive T-periodic solution of (1) belongs to $(0, x_{max}] \times (0, y_{max}]$. The finiteness of the number of T-periodic solutions follows from the Nakajima–Seifert theorem [30] upon the following observation. The result [30, Theorem, p. 431] formally assumes that the system under consideration is dissipative, that is not granted in our case. However, the only fact that is used in the proof in [30] out of dissipativity is that the set of T-periodic solutions is bounded.[2]

Following Section 3 we denote by $\mathcal{P}_0$ the Poincaré map over period T of the Gause model (1). Let $\{v_i\}_{i=1}^n$ be the set of all fixed points of the Poincaré map $\mathcal{P}_0$ in R. By the additivity of the topological degree

$$\sum_{i=1}^n \operatorname{ind}(v_i, \mathcal{P}_0) = d(I - \mathcal{P}_0, R) = 1.$$

Therefore, $\mathcal{P}_0$ has a fixed point $v_* \in R$ with

$$\operatorname{ind}(v_*, \mathcal{P}_0) = 1 \tag{23}$$

and the conclusion follows from Lemma 4.1. □

Remark 4.2. A possible way to avoid requirement (22) is by proving the existence of $v_* \in R$ such that

$$\operatorname{ind}(v_*, \mathcal{P}_0\mathcal{P}_0) = 1 \quad \text{and} \quad v_* = \mathcal{P}(v_*). \tag{24}$$

This would imply that both the eigenvalues of $(\mathcal{P}_0)'(v_*)$ are positive. Unfortunately,

$$\operatorname{ind}(v_*, \mathcal{P}_0\mathcal{P}_0) \neq \operatorname{ind}(v_*, \mathcal{P}_0) \tag{25}$$

[2] Indeed, the top line at p. 438 of [30] says: "Since system (2) is dissipative, $0(F)$ is bounded". And $0(F)$ in [30] is the set of fixed points of the Poincaré map over the period.

in general (see [20, Theorem 31.1] for the respective result) and (24) doesn't follow from (23). However, a v_* satisfying (24) can be found for the Gause model (1), if we a priory know that each $2T$-periodic solution of (1) is T-periodic. Such a property is known as *nonexistence of second-order subharmonic solutions*, see Amine and Ortega [1]. Assumption (22) is a simplest way to avoid the existence of second-order subharmonic solutions. In particular, a more general criterion is offered in [1], see Remark 4.1. There is a wide class of prey–predator models, known as *monotone systems*, whose Poincaré map respects a partial order on the cone $\mathbb{R}^2_+$ and where second-order subharmonic solutions do not exist, see Mottoni and Schiaffino [29] for a study of a particular class of monotone competitive systems and Hirsch and Smith [15] for a general theory of monotone systems. As a matter of fact, Gause model (1) is never monotone under assumptions (A), (B) and (C), even if all the coefficients are assumed monotone. Another way to avoid the existence of second-order subharmonic solutions is by assuming that the dynamics of (1) is one-dimensional, see Smith [34] and references therein for the respective conditions. This way of linking topological degree and asymptotic stability is pursued in Ortega [33] and is applied to a second-order differential equation of pendulum type. We don't know whether or not this approach carries over to the Gause model (1).

Remark 4.3. It is possible to prove the following alternative, provided that R is positively invariant under the flow of (1): either there exist $v_* \in R$ and $m \in \mathbb{N}$ such that

$$\operatorname{ind}\big(v_*, (\mathcal{P}_0)^{2^m}\big) = 1 \quad \text{and} \quad v_* = (\mathcal{P}_0)^{2^{m-1}}(v_*) \tag{26}$$

or there exists $v_{**} \in R$ that accumulates initial conditions of periodic solutions of arbitrary large least periods. Property (26) would imply the existence of an asymptotically stable solution of period mT, if the existence of v_{**} is ruled out. Unfortunately, we didn't succeed to design conditions that prevent accumulation of periodic solutions of arbitrary large periods in the Gause model (1). An example of Gause model (1) whose flow keeps R positively invariant is studied in Wolkowicz and Zhao [36].

5. The Lotka–Volterra model with Holling type-II predator response function

Theorem 4.1 suggests conditions for the existence of asymptotically stable T-periodic solutions in Lotka–Volterra models with Holling type-II predator response function:

$$\dot{x} = x\big(a_1(t) - a_2(t)x\big) - y\frac{b_1(t)x}{b_2(t)+x}, \tag{27}$$

$$\dot{y} = y\left(\frac{c_1(t)x}{c_2(t)+x} - d(t)\right). \tag{28}$$

The global asymptotic stability of a periodic solution in a model of form (27)–(28) with ratio-dependent Holling type-II predator response, i.e. with $b_2(t)$ and $c_2(t)$ multiplied by y, is established in Fan, Wang and Zou [7]. However, the ratio-dependence in the above mentioned result seems to be vital (if one goes through the lines of the proof in [7]). We are not aware of any paper that leads to the existence of a stable periodic solution in the ratio-independent system under consideration. The particular form of the coefficients $a(t,x)$, $b(t,x)$ and $c(t,x)$ of (1) that is implemented in (27)–(28) implies that

- a'_x, b'_x, b''_{xx}, c'_x exist and $a'_x(t,x) \leqslant 0$, $b'_x(t,x) > 0$, $b''_{xx}(t,x) < 0$, $c'_x(t,x) > 0$ for all $t \in \mathbb{R}$, $x > 0$,
- $\lim_{t\to\infty} b(t,x)$ and $\lim_{t\to\infty} c(t,x)$ exist and are finite,

i.e. the settings of the results [16,35,36,28,21,23] mentioned in the introduction hold (it can be noticed that the result of [16] makes [35] applicable). However, none of these results mention anything about asymptotic stability with the exception of Moghadas and Alexander [28] which deals with nearly constant periodic solutions only. We refer the reader to the paper [12] by Garulli, Mocenni, Vicino and Tesi for numerical results (received with LOCBIF and WINPP software) about stable periodic solutions to (27)–(28) with $a_1(t) = M + N\sin(2\pi t/12 + 1)$ and constant other coefficients. To summarize, the following corollary of Theorem 4.1 might be a useful addition within the literature on periodic solutions of (27)–(28).

Theorem 5.1. *Assume that $a_1, a_2, b_1, b_2, c_1, c_2, d$ are continuous, T-periodic and strictly positive functions. Define*

$$x_{max} = \max_{t\in[0,T]} \frac{a_1(t)}{a_2(t)}, \qquad y_{max} = \max_{t\in[0,T]} \frac{a_1(t)(b_2(t)+x_{max})}{b_1(t)}.$$

If

1) $a_1(t) < d(t) < c_1(t) < 2a_2(t)c_2(t)$, *for any* $t \in [0,T]$,

2) $\displaystyle\max_{t\in[0,T]} \frac{d(t)c_2(t)}{c_1(t)-d(t)} < \min_{t\in[0,T]} \frac{a_1(t)}{a_2(t)}$,

$$3)\ T < \pi \Big/ \left[\max_{t\in[0,T],\ x\in[0,x_{max}],\ y\in[0,y_{max}]} \left(\max\left\{ \frac{c_1(t)}{c_2(t)} y_{max}, \frac{b_1(t)}{b_2(t)} x_{max} \right\} + \frac{1}{2}\left(a_1(t) - 2a_2(t)x - \frac{b_1(t)b_2(t)y}{(b_2(t)+x)^2} - \frac{c_1(t)x}{c_2(t)+x} + d(t) \right) \right) \right]$$

then system (27)–(28) has at least one asymptotically stable T-periodic solution in $(0, x_{max}] \times (0, y_{max}]$.

Proof. The negative divergence condition (21) takes the form

$$a_1(t) - 2a_2(t)x - \frac{b_1(t)b_2(t)y}{(b_2(t)+x)^2} + \frac{c_1(t)x}{c_2(t)+x} - d(t) < 0, \quad t \in [0, T],$$

that uses the first and the last inequalities in 1) in order to hold. Furthermore, we have

$$x_a(t) = \frac{a_1(t)}{a_2(t)}, \qquad x_c(t) = \frac{d(t)c_2(t)}{c_1(t) - d(t)},$$

that leads to the middle inequality in 1) (that ensures that x_c is strictly positive) and to 2) (that ensures that (X) holds). Strict positivity of each of the coefficients in (27)–(28) is required to have the positivity assumptions in (A), (B) and (C) fulfilled. The statement is, therefore, a direct consequence of Theorem 4.1. □

Remark 5.1. The paper Wolkowicz and Zhao [36] discovers a class of systems (27)–(28) that possesses a rectangular trapping region in $\mathbb{R}^2_+$, but these authors don't evaluate the bounds of this region explicitly. Making the later step could help deriving conditions for the existence of a globally stable periodic solution to (27)–(28) along the lines of Fan, Wang and Zou [7].

6. Evaluation of the topological degree in the general case

This section is devoted to the proof of the main result of this paper in the most general settings, the formula (2). In combination with the continuity of the topological degree, formula (2) allows to incorporate delays (see Krasnoselskii [19, Appendix II, §3], Krasnoselskii and Zabreyko [20, §41.5]) and other functionals (see [20]) into Gause model (1), with potential bearings towards complementing the results in [16,5,21,6] (see introduction). Formula (2) also allows incorporating time-periodic impulses that can be viewed as perturbations of the integral operator Φ. In this way formula (2) may, for instance, extend the results of Ding, Su and Hao [5].

Though formula (2) can be received as a consequence of Theorem 3.1 over the duality principle between Poincaré map $\mathcal{P}_0$ and integral operator Φ (see [19, Appendix II.2]), we suggest a proof that doesn't employ uniqueness of solutions. The reasons for that are twofold. Firstly, allowing nonuniqueness creates a wider room to account for the phenomenon of group defence. An autonomous Gause model with group defense has been analysed by Freedman in [11], where nonuniqueness took place along the x-axis only. A modification of this phenomenon may shift nonsmoothness to the $(0,\infty) \times (0,\infty)$ region. Secondly, our level of generality enables a simple extension of the main result to Gause models with multi-valued terms, e.g. to account for switch-like interactions between species (see Gouze and Sari [13]). The functions x_a and x_c will naturally be multi-valued in such a case, that can be accommodated by all the proofs.

As the main tool of the proof in Theorem 3.1 is the T-irreversibility lemma by Krasnoselski, we need its version that doesn't employ uniqueness of solutions. Such a lemma is proposed in the next subsection of the paper.

6.1. *T-irreversibility lemma for periodic differential equations with continuous right-hand terms*

Consider a differential equation

$$\dot{u} = \psi(t, u), \tag{29}$$

where $\psi \in C^0(\mathbb{R} \times \mathbb{R}^n, \mathbb{R}^n)$, and introduce the integral operator

$$(\Psi u)(t) = u(T) + \int_0^t \psi\big(\tau, u(\tau)\big)\, d\tau,$$

associated to the T-periodic problem. Our result will assume the following stronger version of the Krasnoselskii's T-irreversibility condition.

Definition 6.1. We call a point $\xi \in \mathbb{R}^n$ a *point of strong T-irreversibility* of the solutions of (29), if given any $t_0 \in [0, T]$ and any solution u of (29) with the initial condition $u(t_0) = \xi$, the trajectory $t \mapsto u(t)$ doesn't have self-interactions on any interval $t_0 \in [s_1, s_2] \subset [0, T]$ where this trajectory is defined.

Lemma 6.1. *Consider $\psi \in C^0(\mathbb{R}\times\mathbb{R}^n,\mathbb{R}^n)$ and let $U \subset \mathbb{R}^n$ be an open bounded set. Assume that $\psi(0,\cdot)$ doesn't vanish on ∂U. Assume that all points of ∂U are points of strong T-irreversibility of the solutions of (29). Then $d(I-\Psi, W_U)$ is defined and*

$$d(I-\Psi, W_U) = d\big(-\psi(0,\cdot), U\big). \tag{30}$$

Proof. Observe that the integral operator

$$(\Psi_\lambda u)(t) = u(T) + \lambda \int_0^t \psi\big(\lambda\tau, u(\tau)\big)\,d\tau$$

doesn't have fixed points on ∂W for any $\lambda \in (0,1]$. Indeed, if $\Psi_\lambda u = u$ then $v(t) = u(t/\lambda)$ is a solution of (29) with $v(0) = v(\lambda T)$ and $v([0,\lambda T]) \cap \partial U \neq \emptyset$, that contradicts the strong T-irreversibility assumption. We claim that for $\lambda > 0$ sufficiently small Ψ_λ is homotopic to

$$(\overline{\Psi}_\lambda u)(t) = u(T) + \lambda \int_0^T \psi\big(0, u(\tau)\big)\,d\tau$$

on W_U. To show this we prove that the deformation

$$(\Psi_{\lambda,\alpha} u)(t) = u(T) + \lambda \int_0^{\alpha t + (1-\alpha)T} \psi\big(\lambda\alpha\tau, u(\tau)\big)\,d\tau, \quad \alpha \in [0,1]$$

doesn't have fixed points on ∂W for all $\lambda > 0$ sufficiently small. We prove by contradiction, i.e. we assume the existence of $\lambda_k \to 0$, $\alpha_k \to \alpha_0$, $u_k \to u_0$, $u_k \in \partial W_U$, as $k \to \infty$, such that

$$u_k(t) = u_k(T) + \lambda_k \int_0^{\alpha_k t + (1-\alpha_k)T} \psi\big(\lambda_k\alpha_k\tau, u_k(\tau)\big)\,d\tau. \tag{31}$$

Since $\dot u_k \to 0$ as $k \to \infty$ we conclude that $u_0(t) = u_*$, where $u_* \in \partial U$. By plugging $t = T$ in (31), dividing by λ_k and passing to the limit as $k \to \infty$ we obtain

$$\int_0^T \psi(0, u_*)\,d\tau = T\psi(0,u_*) = 0$$

which contradicts nonsingularity of $\psi(0,\cdot)$ on ∂U. Therefore

$$d(I-\Psi_1, W_U) = d(I-\overline{\Psi}_\lambda, W_U)$$

for $\lambda > 0$ sufficiently small. Since $\overline{\Psi}_\lambda C([0,T],\mathbb{R}^n) \subset C([0,T],\mathbb{R}^n) \cap \mathbb{R}^n$, the reduction theorem [20, Theorem 27.1] implies that

$$d(I-\overline{\Psi}_\lambda, W_U) = d\big(I-\overline{\Psi}_\lambda, W_U \cap \mathbb{R}^n\big) = d_{\mathbb{R}^n}(I-\overline{\psi}_\lambda, U),$$

where $\overline{\psi}_\lambda(\xi) = \xi + \lambda\int_0^T \psi(0,\xi)\,d\tau = \xi + \lambda T\psi(0,\xi)$, $\xi \in \mathbb{R}^n$. Since the linear deformation between $I-\overline{\psi}_\lambda$ and $I-\overline{\psi}_{1/T}$ is nonsingular on ∂U, we finally conclude

$$d(I-\Psi_1, W_U) = d(I-\overline{\psi}_\lambda, U) = d(I-\overline{\psi}_{1/T}, U) = d\big(-\psi(0,\cdot), U\big). \qquad \square$$

Remark 6.1. Our definition of strong T-irreversibility takes the form of the T-irreversibility by Krasnoselskii (see the proof of Theorem 3.1 for the Krasnoselskii's definition), if t_0 is set as 0. That could be possible to prove Lemma 6.1 under the later T-irreversibility assumption. However, that won't be the set W_U in (30) in such a case, but the integral funnel of (29) emanating from U over time T. We note that is the set W_U which is considered in Zanolin [37].

6.2. The main result

We are finally ready to prove formula (2).

Theorem 6.1. *Let a, b, c, d be continuous functions that satisfy (A), (B), (C) and (X). Then given any $\Delta > 0$ there exists $\varepsilon_0 > 0$ such that*

$$d(I - \Phi, W_R) = 1,$$

where

$$W_R = \left\{(x, y) \in C^0\left([0, T], \mathbb{R}^2\right):\ \varepsilon_0 < x(t) < x_{max} + \Delta,\ \varepsilon_0 < y(t) < y_{max} + \Delta,\ t \in [0, T]\right\} \tag{32}$$

and x_{max}, y_{max} are the constants given by (6).

The proof just follows the lines of the proof of Theorem 3.1 with the following natural amendments:

1) The integral operator

$$\Phi_\varepsilon \begin{pmatrix} x \\ y \end{pmatrix}(t) = x(T) + \int_0^t \begin{pmatrix} F_\varepsilon(\tau, x(\tau), y(\tau)) \\ G_\varepsilon(\tau, x(\tau), y(\tau)) \end{pmatrix} d\tau$$

will replace the Poincaré map $\mathcal{P}_\varepsilon$ and the set

$$W_{R_\varepsilon} = \left\{(x, y) \in C^0\left([0, T], \mathbb{R}^2\right):\ \left(x(t), y(t)\right) \in R_\varepsilon,\ t \in [0, T]\right\}$$

will replace R_ε.

2) Lemma 6.1 has to be used instead of the T-irreversibility lemma by Krasnoselskii (one needs to observe that Lemma 2.1 implies not only T-irreversibility of solutions, but also the strong T-irreversibility), to have $d(I - \Phi_\varepsilon, W_{R_\varepsilon}) = 1$ in analogy with (13).

Because a considerable part of the literature on the competitive biological model has been achieved over the so-called coincidence degree (see Mawhin [27, p. 19]), we express our main result in terms of this degree too. We wish this makes our work useful for a wider audience.

6.3. A corollary for the coincidence degree

Let $Z = \{(x, y) \in C([0, T], \mathbb{R}^2):\ x(0) = x(T),\ \ y(0) = y(T)\}$ and let $L : \operatorname{dom} L \subset Z \to L^1([0, T], \mathbb{R}^n)$ be the linear operator defined by $(L(x, y))(\cdot) = (\dot{x}(\cdot), \dot{y}(\cdot))$ with $\operatorname{dom} L = \{(x, y) \in Z:\ x \text{ and } y \text{ are absolutely continuous}\}$. The operator L is a Fredholm operator of index zero, see e.g. Mawhin [27]. Let $N : Z \to L^1([0, T], \mathbb{R}^2)$ be the Nemitcky operator defined by the right-hand sides of Gause model (1) as follows

$$\left(N(x, y)\right)(t) = \begin{pmatrix} F_0(t, x(t), y(t)) \\ G_0(t, x(t), y(t)) \end{pmatrix}.$$

Thus the existence of T-periodic solutions for system (2) is equivalent to the solvability of the equation

$$L(x, y) = N(x, y), \quad (x, y) \in \operatorname{dom} L. \tag{33}$$

The next theorem is a version of formula (2) in terms of the coincidence degree $D_L(L - N, W \cap Z)$ of L and N (see [27, p. 19] for a detailed definition).

Theorem 6.2. *Let a, b, c, d be continuous functions that satisfy (A), (B), (C) and (X). Then given $\Delta > 0$ there exist $\varepsilon_0, M > 0$ such that*

$$D_L(L - N, W_{\Delta, \varepsilon_0, M} \cap Z) = 1,$$

where $W_{\Delta, \varepsilon_0, M}$ is given by (32).

The proof follows from the duality principle (see Mawhin [27, Ch. 3]) between the coincidence degree and the one we used in (2) (Leray–Schauder degree). We refer the reader to [17, Corollary 2.6] for details.

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