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THE LOTKA-VOLTERRA MODELS WITH NON-LOCAL REACTION TERMS

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ABSTRACT. In this paper we consider a diffusive Lotka-Volterra system including nonlocal terms in the reaction functions. We analyze the main types of interactions between species: competition, predator-prey and cooperation. We provide existence and non-existence of positive solutions results. For that, we employ mainly bifurcation method and a priori bounds.

1. Introduction. Since the paper of Furter and Grinfeld [8] (1989) is admitted that there is no real justification for assuming that the interactions between species are local. Hence, they proposed to include non-local terms in space to consider the interactions between species giving more reasonable and more realistic models, see also Britton [1] where a population model is proposed including an intraspecific competition term that depends not simply on the population density at that point but on the average population density near the point.

In this paper we consider two species inhabiting in Ω , a regular and bounded domain in \mathbb{R}^N , whose population densities are denoted by $u(x)$ and $v(x)$. Specifically, we deal with the following system

$$\begin{cases} -\Delta u = u \left(\lambda - u - \int_{\Omega} a(x)u(x)dx + b_1v + b_2 \int_{\Omega} b(x)v(x)dx \right) & \text{in } \Omega, \\ -\Delta v = v \left(\mu - v - \int_{\Omega} d(x)v(x)dx + c_1u + c_2 \int_{\Omega} c(x)u(x)dx \right) & \text{in } \Omega, \\ u = v = 0 & \text{on } \partial\Omega, \end{cases} \quad (1)$$

where $\lambda, \mu \in \mathbb{R}$ denote the growth rates of the species u and v , respectively, b_1 and c_1 are the local interaction coefficients, both negative or positive imply a competition or

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symbiosis interaction, respectively, and one of them positive and the other negative represent a prey-predator interaction.

Observe that in (1) we have included two types of non-local terms. The first one appears when one species is not present, that is, in the absence of one species, the other follows a non-local logistic equation of the form

$$\begin{cases} -\Delta w = w \left(\gamma - w - \int_{\Omega} e(x)w(x)dx \right) & \text{in } \Omega, \\ w = 0 & \text{on } \partial\Omega, \end{cases} \quad (2)$$

where $\gamma \in \mathbb{R}$ and the term $-\int_{\Omega} e(x)w(x)dx$ represents the intraspecific nonlocal competition. Hence, in (1) the species take into account two negative crowding effects caused by the intraspecific competition, one local, $-u$ and $-v$, and other nonlocal, $-\int_{\Omega} a(x)u(x)dx$ and $-\int_{\Omega} d(x)v(x)dx$, with positive weights $a, d \in C(\bar{\Omega})$, $a, d \geq 0$, $a, d \not\equiv 0$.

The second non-local term is related with the interspecific non-local interactions. Indeed, b_2 and c_2 stand for the strength of nonlocal interspecific coefficients, being the nonlocal terms $\int_{\Omega} b(x)v(x)dx$ and $\int_{\Omega} c(x)u(x)dx$ with $b, c \in C(\bar{\Omega})$, $b, c \geq 0$, $b, c \not\equiv 0$. Of course, due to the biological interpretation, b_2 and c_2 have the same signs than b_1 and c_1 , respectively, that is, $b_1 \cdot b_2 \geq 0$, $c_1 \cdot c_2 \geq 0$ and $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$.

When $b_2 = c_2 = 0$ and the intraspecific nonlocal competition is not present, that is $a \equiv d \equiv 0$, then (1) is the classical Lotka-Volterra system which has been extensively analyzed, see for instance the monograph [2].

System (1) has been studied in [12] in the competition case (that is $b_i < 0$, $c_i < 0$, $i = 1, 2$). In this work, the nonlocal competition term is determined by a diffusion kernel function to model the movement pattern of the biological species. This allows to convert the nonlocal problem (1) into an equivalent local system with three variables.

In [14] a very general reaction-diffusion system depending on the spatial average is studied. It is shown that for the two-species model, Hopf bifurcation from the constant equilibrium can occur. A nonlocal cooperative Lotka-Volterra model and a nonlocal Rosenzweig-MacArthur predator-prey model are used to demonstrate the bifurcation of spatially non-homogeneous patterns.

In [17] the local terms do not appear and it is assumed that $\lambda = \mu$. Under some conditions on the coefficients and in the competition case, the authors obtain the existence of positive solutions using bifurcation arguments.

Different nonlocal reactions terms appear in [3], [13], [16] and references therein.

In this paper, the main goal is to give existence and non-existence of positive solution results. Specifically, we are interested in determining coexistence regions, that is, subsets $\mathcal{D} \subset \mathbb{R}^2$ such that if $(\lambda, \mu) \in \mathcal{D}$ then (1) possesses at least a *coexistence state*. A coexistence state is a solution (u, v) of (1) such that $u(x), v(x) > 0$ for all $x \in \Omega$. On the contrary, we also provide non-existence regions $\mathcal{N} \subset \mathbb{R}^2$, namely if $(\lambda, \mu) \in \mathcal{N}$ then (1) does not admit positive solutions. Surely, these regions depend on the type of interactions between the species. To obtain these results, the nonlocal terms cause difficulties, mainly because classical comparison arguments do not work in general. To overcome this difficulty we have used the bifurcation arguments. In order to do it, we study in details the semitrivial solutions, $(u, 0)$ and $(0, v)$, and then we prove the existence of a continuum of coexistence states

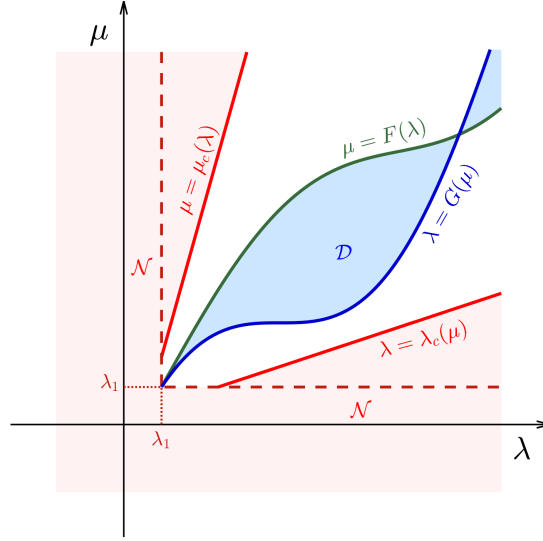


FIGURE 1. Coexistence (\mathcal{D}) and non-existence (\mathcal{N}) regions of (1) in the competition case.

emanating from them. Again, the behaviour of this continuum depends strongly on the interactions of the species.

Now, we state our main results. For that, we need to introduce some notation. Denote by λ_1 the principal eigenvalue of $-\Delta$ under homogenous Dirichlet boundary conditions. Moreover, there exist two continuous functions $F, G : [\lambda_1, \infty) \rightarrow \mathbf{R}$, which will be provided later, and that satisfy the following properties:

1. $F(\lambda)$ is increasing (resp. decreasing) if $c_1, c_2 \leq 0$ (resp. $c_1, c_2 \geq 0$), $(c_1, c_2) \neq (0, 0)$ and

$$\lim_{\lambda \rightarrow +\infty} F(\lambda) = +\infty \quad (\text{resp. } -\infty).$$

2. $G(\mu)$ is increasing (resp. decreasing) if $b_1, b_2 \leq 0$ (resp. $b_1, b_2 \geq 0$), $(b_1, b_2) \neq (0, 0)$ and

$$\lim_{\mu \rightarrow +\infty} G(\mu) = +\infty \quad (\text{resp. } -\infty).$$

Our first result is concerning to the competition case. We show a competitive exclusion principle: fixed the growth rate of a species, the two species can not coexist if the growth rate of the other species is small or large. Also, we show a coexistence result (see Figure 1).

Theorem 1.1. (Competition) *Assume that $b_i, c_i \leq 0$ with $i = 1, 2$, $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$.*

1. (1) does not admit coexistence states if $\lambda \leq \lambda_1$ or $\mu \leq \lambda_1$.
2. Fix $\lambda > \lambda_1$ (resp. $\mu > \lambda_1$), there exists $\mu_c(\lambda) > 0$ (resp. $\lambda_c(\mu) > 0$) such that (1) does not admit coexistence states if $\mu > \mu_c(\lambda)$ (resp. $\lambda > \lambda_c(\mu)$).
3. (1) possesses at least a coexistence state if

$$(\mu - F(\lambda))(\lambda - G(\mu)) > 0.$$

With respect to the prey-predator case, we have (Figure 2):

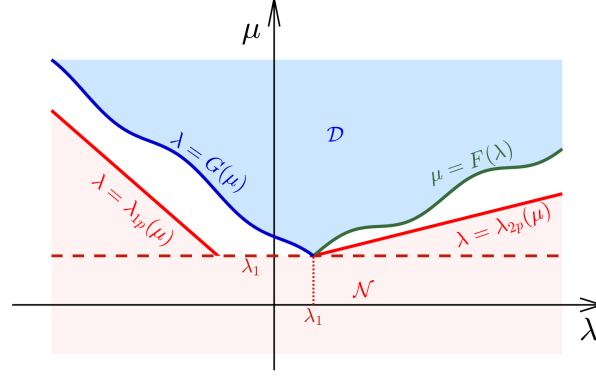


FIGURE 2. Coexistence (\mathcal{D}) and non-existence (\mathcal{N}) regions of (1) in the predator-prey case.

Theorem 1.2. (Predator-prey) *Assume that $c_i \leq 0 \leq b_i$ with $i = 1, 2$ and $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$.*

1. (1) does not admit coexistence states if $\mu \leq \lambda_1$.
2. Fix $\mu > \lambda_1$, there exist $\lambda_{1p}(\mu) < 0 < \lambda_{2p}(\mu)$ such that (1) does not admit coexistence states if $\lambda < \lambda_{1p}(\mu)$ or $\lambda > \lambda_{2p}(\mu)$.
3. (1) possesses at least a coexistence state if

$$\mu > F(\lambda) \quad \text{and} \quad \lambda > G(\mu).$$

The cooperation case is more involved. We assume in this case that $b_1 c_1 < 1$, that is a weak local cooperation. Now, we can find two different regimes. The first one assumes that all the cooperation coefficients are small. In the second one, the nonlocal interspecific cooperation coefficients can be large.

Theorem 1.3. (Symbiosis) *Assume $b_i, c_i \geq 0$ for $i = 1, 2$, $(b_1, b_2) \neq 0 \neq (c_1, c_2)$.*

1. (Weak nonlocal cooperation) Assume

$$(H_w) \quad (b_1 + b_2 \|b\|_1)(c_1 + c_2 \|c\|_1) < 1.$$

- (a) (1) does not admit coexistence states if $\lambda \leq \lambda_1$ and $\mu \leq \lambda_1$.
- (b) Fix $\lambda > \lambda_1$ (resp. $\mu > \lambda_1$), there exists $\mu_{ws}(\lambda) \in \mathbf{R}$ (resp. $\lambda_{ws}(\mu) \in \mathbf{R}$) such that (1) does not admit coexistence states if $\mu < \mu_{ws}(\lambda)$ (resp. $\lambda < \lambda_{ws}(\mu)$).
- (c) (1) possesses at least a coexistence state if

$$\mu > F(\lambda) \quad \text{and} \quad \lambda > G(\mu).$$

2. (Strong nonlocal cooperation) Assume that $b_1 c_1 < 1$, $b(x), c(x) > 0$ for all $x \in \overline{\Omega}$ and $b_2 > C b_1$, for some $C > 0$. There exists a continuous and nonincreasing function $H : \mathbf{R}_+ \mapsto \mathbf{R}_+$ such that if

$$(H_s) \quad c_2 > H(b_2),$$

then,

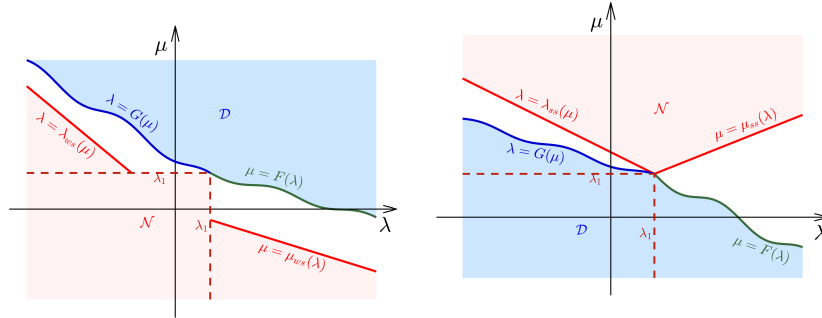


FIGURE 3. Coexistence (\mathcal{D}) and non-existence (\mathcal{N}) regions of (1) in the symbiosis case: weak (on left) and strong (on right)

- (a) Fix $\lambda \in \mathbb{R}$ (resp. $\mu \in \mathbb{R}$), there exists $\mu_{ss}(\lambda) \in \mathbb{R}$ (resp. $\lambda_{ss}(\mu) \in \mathbb{R}$) such that (1) does not admit coexistence states if $\mu > \mu_{ss}(\lambda)$ (resp. $\lambda > \lambda_{ss}(\mu)$).
- (b) (1) possesses at least a coexistence state if

$$\mu < F(\lambda) \quad \text{or} \quad \lambda < G(\mu). \quad (3)$$

Let us compare our results with the classical local Lotka-Volterra model. The obtained results in the competition, predator-prey and weak cooperation cases are rather similar to the those in the Lotka-Volterra model, although mainly due to loss of monotony results, our techniques differ from those used to obtain the results in the local case. However, the strong cooperation case is completely different to the local case. Indeed, in the local case when the cooperation is strong ($b_1 c_1 > 1$) it is necessary to impose some restrictions in the dimension of the space, specifically, $N < 5$, to obtain existence of coexistence states for λ and μ verifying (3), see [6] and [11]. In this case, when the cooperation is strong in the non-local term (b_2 or c_2 large) we obtain existence of coexistence states for λ and μ verifying (3) without any restriction in the spatial dimension.

An outline of the paper is as follows: In Section 2 we present some results useful throughout the paper. Section 3 is devoted to nonlocal logistic equation. In Section 4 we give some general bifurcations results. These results are applied in the last section to prove the main results.

2. Preliminaries. In this section we collect some results which will be used along the paper.

We start by fixing some notations. Given $m \in L^\infty(\Omega)$ we denote by $\lambda_1[-\Delta + m]$ the principal eigenvalue of the problem

$$\begin{cases} -\Delta u + m(x)u = \lambda u & \text{in } \Omega, \\ u = 0 & \text{on } \partial\Omega. \end{cases} \quad (4)$$

It is well-known that the map

$$m \in L^\infty(\Omega) \mapsto \lambda_1[-\Delta + m] \in \mathbb{R} \quad \text{is continuous and increasing.} \quad (5)$$

We denote by

$$\lambda_1 := \lambda_1[-\Delta]$$

and φ_1 its principal positive eigenfunction associated such that $\|\varphi_1\|_\infty = 1$.

Finally, given $g \in C(\overline{\Omega})$ we denote by

$$g_L := \min_{x \in \overline{\Omega}} g(x), \quad g_M := \max_{x \in \overline{\Omega}} g(x).$$

We also need to study the classical local logistic equation

$$\begin{cases} -\Delta w = w(\gamma - w) & \text{in } \Omega, \\ w = 0 & \text{on } \partial\Omega, \end{cases} \quad (6)$$

where $\gamma \in \mathbb{R}$.

In what follows, we summarize some well-known results concerning to (6), see for instance [2] and [6].

Proposition 1. *There exists a classical positive solution of (6) if and only if $\gamma > \lambda_1$. In such case, it is unique and we denote it by ω_γ . Moreover:*

1. *Defining $\omega_{\lambda_1} \equiv 0$, the map $\gamma \in [\lambda_1, +\infty) \mapsto \omega_\gamma \in C_0^2(\overline{\Omega})$ is continuous and increasing.*
2. *It holds that*

$$(\gamma - \lambda_1)\varphi_1 \leq \omega_\gamma \leq \gamma \quad \text{in } \Omega. \quad (7)$$

3. *If \bar{w} is a positive supersolution of (6), then*

$$(\gamma - \lambda_1)\varphi_1 \leq \omega_\gamma \leq \bar{w} \quad \text{in } \Omega.$$

4. *If \underline{w} is a positive subsolution of (6), then*

$$\underline{w} \leq \omega_\gamma \leq \gamma \quad \text{in } \Omega.$$

3. The nonlocal equation of one species. In this Section, we obtain results for the nonlocal logistic equation, that is, what happens when one of the species is not present, specifically of the equation

$$\begin{cases} -\Delta w = w \left(\gamma - w - \int_{\Omega} e(x)w(x)dx \right) & \text{in } \Omega, \\ w = 0 & \text{on } \partial\Omega, \end{cases} \quad (8)$$

where $\gamma \in \mathbb{R}$ and $e \in C(\overline{\Omega})$, $e \geq 0$, $e \not\equiv 0$ in Ω .

Before giving the main results, we will study an auxiliary linear non-local problem.

Lemma 3.1. *Let $m \in L^\infty(\Omega)$, $n \in L^\infty(\Omega)$, such that $\lambda_1[-\Delta + m] > 0$ and $n \geq 0$ in Ω . Thus, for each $f \in L^2(\Omega)$, there exists a unique solution $u \in W^{2,2}(\Omega)$ of*

$$\begin{cases} -\Delta u + m(x)u + n(x) \int_{\Omega} e(x)u(x)dx = f(x) & \text{in } \Omega, \\ u = 0 & \text{on } \partial\Omega. \end{cases} \quad (9)$$

Moreover, if $f \in L^p(\Omega)$, $p > 1$, then $u \in W^{2,p}(\Omega)$.

Proof. Since $\lambda_1[-\Delta + m] > 0$, by the characterization of the maximum principle, there exists a unique positive solution $h \in W^{2,\infty}(\Omega)$ of

$$\begin{cases} -\Delta h + m(x)h = e(x) & \text{in } \Omega, \\ h = 0 & \text{on } \partial\Omega. \end{cases} \quad (10)$$

Similarly, let $w \in W^{2,2}(\Omega)$ be the unique solution of

$$\begin{cases} -\Delta w + m(x)w = f(x) - \frac{\int_{\Omega} f(x)h(x)dx}{1 + \int_{\Omega} h(x)n(x)dx}n(x) & \text{in } \Omega, \\ w = 0 & \text{on } \partial\Omega. \end{cases} \quad (11)$$

We claim that w is the unique solution of (9). To prove that, it is sufficient to show

$$\int_{\Omega} e(x)w(x)dx = \frac{\int_{\Omega} f(x)h(x)dx}{1 + \int_{\Omega} h(x)n(x)dx}.$$

Taking h as test function in (11) yields

$$\int_{\Omega} e(x)w(x)dx + \frac{\int_{\Omega} f(x)h(x)dx}{1 + \int_{\Omega} h(x)n(x)dx} \int_{\Omega} n(x)h(x)dx = \int_{\Omega} f(x)h(x)dx,$$

which implies the result.

Analogously, if u is a solution of (9), taking h as test function in (9) shows that

$$\int_{\Omega} e(x)u(x)dx = \frac{\int_{\Omega} f(x)h(x)dx}{1 + \int_{\Omega} h(x)n(x)dx}.$$

Then, substituting into (9) we conclude that u is the unique solution of (11).

Furthermore, if $f \in L^p(\Omega)$, by elliptic regularity, the unique solution of (10) belongs to $W^{2,p}(\Omega)$. \square

Along the paper, given a function $e \in C(\bar{\Omega})$, $e \geq 0$, $e \not\equiv 0$ in Ω , we denote by

$$A_e := \frac{\int_{\Omega} e(x)\varphi_1(x)dx}{1 + \int_{\Omega} e(x)\varphi_1(x)dx}.$$

Now, we are ready to state and prove the main result with respect to (8).

Theorem 3.2. *The nonlocal logistic equation (8) possesses a classical positive solution if, and only if, $\gamma > \lambda_1$. Moreover, it is unique if it exists, and it will be denoted by θ_γ .*

In addition, defining $\theta_{\lambda_1} \equiv 0$, the map $\gamma \in [\lambda_1, +\infty) \mapsto \theta_\gamma \in C_0^2(\bar{\Omega})$ is continuous, derivable and increasing. Furthermore, the following inequalities hold:

1.

$$\theta_\gamma \leq \omega_\gamma \leq \gamma \quad \text{in } \Omega.$$

2.

$$(\gamma - \lambda_1)A_e \leq \int_{\Omega} e(x)\theta_\gamma(x)dx \leq \gamma \frac{\|e\|_1}{1 + \|e\|_1}. \quad (12)$$

3.

$$\left(\frac{\gamma}{1 + \|e\|_1} - \lambda_1 \right) \varphi_1 \leq \theta_\gamma \leq \gamma(1 - A_e) + \lambda_1 A_e \quad \text{in } \Omega.$$

Proof. It is known the result about existence and uniqueness of positive solution of (8), see [5].

We will show that the map $\gamma \in [\lambda_1, +\infty) \mapsto \theta_\gamma$ is increasing. Fix $\lambda \in [\lambda_1, +\infty)$ and let $\mu > \lambda$, we claim that

$$\lambda - \int_{\Omega} e(x)\theta_\lambda(x)dx < \mu - \int_{\Omega} e(x)\theta_\mu(x)dx. \quad (13)$$

Suppose the contrary:

$$\lambda - \int_{\Omega} e(x)\theta_\lambda(x)dx \geq \mu - \int_{\Omega} e(x)\theta_\mu(x)dx. \quad (14)$$

Denoting $R_\delta := \delta - \int_{\Omega} e(x)\theta_\delta(x)dx$, we have that θ_λ and θ_μ are solutions of (6) with $\gamma = R_\lambda$ and $\gamma = R_\mu$, respectively, that is $\theta_\lambda = \omega_{R_\lambda}$ and $\theta_\mu = \omega_{R_\mu}$. Then, by (14), $\theta_\lambda \geq \theta_\mu$, and therefore

$$\int_{\Omega} e(x)\theta_\lambda(x)dx \geq \int_{\Omega} e(x)\theta_\mu(x)dx.$$

We get

$$\lambda - \int_{\Omega} e(x)\theta_\lambda(x)dx \leq \lambda - \int_{\Omega} e(x)\theta_\mu(x)dx < \mu - \int_{\Omega} e(x)\theta_\mu(x)dx,$$

which is an absurd.

By (13), we have $R_\lambda < R_\mu$ and by the monotonicity of the solution of (6) we obtain that $\theta_\lambda \leq \theta_\mu$. And, thus, we get the map, $\lambda \in [\lambda_1, +\infty) \mapsto \theta_\lambda$ is increasing. Using this fact, and the uniqueness of positive solution of (6), the continuity follows.

Now, we prove the differentiability of the map $\lambda \mapsto \theta_\lambda \in C_0^2(\bar{\Omega})$ using the Implicit Function Theorem. Define the map $\mathcal{H} : \mathbb{R} \times C_0^2(\bar{\Omega}) \mapsto C(\bar{\Omega})$ given by

$$\mathcal{H}(\gamma, w) := -\Delta w - w \left(\gamma - w - \int_{\Omega} e(x)w(x)dx \right).$$

It is clear that $\mathcal{H}(\gamma, \theta_\gamma) = 0$ and that

$$D_w \mathcal{H}(\gamma, \theta_\gamma)\xi = -\Delta \xi - \gamma \xi + 2\theta_\gamma \xi + \xi \int_{\Omega} e(x)\theta_\gamma(x)dx + \theta_\gamma \int_{\Omega} e(x)\xi(x)dx.$$

We denote

$$L := -\Delta - \gamma + 2\theta_\gamma(x) + \int_{\Omega} e(x)\theta_\gamma(x)dx.$$

Since $m(x) := -\gamma + 2\theta_\gamma + \int_{\Omega} e(x)\theta_\gamma(x)dx \in L^\infty(\Omega)$, the principal eigenvalue of $L = -\Delta + m(x)$ is well defined. We claim that

$$\lambda_1[L] > 0. \quad (15)$$

Indeed, in view of characterization of maximum principle (see, for instance, [9, Theorem 7.5.2]), to prove (15), it is sufficient to show that there exists a strict positive supersolution of the operator L . Indeed, since θ_γ is a positive solution of (8), it satisfies

$$L\theta_\gamma = -\Delta\theta_\gamma - \gamma\theta_\gamma + 2\theta_\gamma^2 + \theta_\gamma \int_{\Omega} e(x)\theta_\gamma(x)dx = \theta_\gamma^2 > 0 \quad \text{in } \Omega,$$

showing the claim. Therefore, we can apply Lemma 3.1 to conclude that $D_w \mathcal{H}(\gamma, \theta_\gamma)$ is an isomorphism. This concludes the proof of the differentiability.

Notice that θ_γ is a subsolution of (6), then by Proposition 1

$$\theta_\gamma \leq \omega_\gamma \leq \gamma \quad \text{in } \Omega.$$

Now, observe that $w = \theta_\gamma$ is a solution of the local logistic equation

$$-\Delta w = w \left(\gamma - \int_{\Omega} e(x) \theta_\gamma(x) dx - w \right) \quad \text{in } \Omega, \quad w = 0 \quad \text{on } \partial\Omega.$$

Then, using (7), we deduce that

$$\left(\gamma - \int_{\Omega} e(x) \theta_\gamma(x) dx - \lambda_1 \right) \varphi_1 \leq w = \theta_\gamma,$$

whence we conclude the lower inequality of (12).

On the other hand, consider $x_M \in \Omega$ such that $\theta_\gamma \leq \max_{x \in \bar{\Omega}} \theta_\gamma(x) = \theta_\gamma(x_M)$. Using that $-\Delta \theta_\gamma(x_M) \geq 0$, we get that

$$\theta_\gamma \leq \theta_\gamma(x_M) \leq \gamma - \int_{\Omega} e(x) \theta_\gamma(x) dx,$$

and using the lower inequality of (12), we obtain that

$$\theta_\gamma \leq \gamma - (\gamma - \lambda_1) A_e = \gamma(1 - A_e) + \lambda_1 A_e.$$

Finally, observe that

$$\theta_\gamma = \omega_{\gamma - \int_{\Omega} e \theta_\gamma} \leq \gamma - \int_{\Omega} e(x) \theta_\gamma(x) dx,$$

multiplying by e and integrating, we get that

$$\int_{\Omega} e(x) \theta_\gamma(x) dx \leq \gamma \frac{\|e\|_1}{1 + \|e\|_1}.$$

Going back to (8) we have that

$$-\Delta \theta_\gamma \geq \theta_\gamma \left(\frac{\gamma}{1 + \|e\|_1} - \theta_\gamma \right),$$

whence by Proposition 1, it follows that

$$\theta_\gamma \geq \left(\frac{\gamma}{1 + \|e\|_1} - \lambda_1 \right) \varphi_1 \quad \text{in } \Omega.$$

□

4. Bifurcation results. In this section, to simplify the notation, we will denote by $\theta_\lambda := \theta_{\lambda,a}$ and $\theta_\mu := \theta_{\mu,d}$, the unique positive solution of

$$\begin{cases} -\Delta u = u \left(\lambda - u - \int_{\Omega} a(x) u(x) dx \right) & \text{in } \Omega, \\ u = 0 & \text{on } \partial\Omega, \end{cases} \quad (16)$$

and

$$\begin{cases} -\Delta v = v \left(\mu - v - \int_{\Omega} d(x) v(x) dx \right) & \text{in } \Omega, \\ v = 0 & \text{on } \partial\Omega, \end{cases} \quad (17)$$

respectively, which exist for $\lambda > \lambda_1$ and $\mu > \lambda_1$. Moreover, we adopt the convention $\theta_{\lambda_1} = \theta_{\lambda_1,a} = \theta_{\lambda_1,d} = 0$.

Thus, notice that the semitrivial solutions $(u, 0) = (\theta_\lambda, 0)$ and $(0, v) = (0, \theta_\mu)$ of (1) are solutions of (16) and (17), respectively.

To carry out our main results in this section, we introduce the functions that delimit the region of coexistence states, namely, let $F, G : [\lambda_1, +\infty) \rightarrow \mathbb{R}$ given by

$$F(\lambda) := \lambda_1 \left[-\Delta - c_1 \theta_\lambda - c_2 \int_{\Omega} c(x) \theta_\lambda(x) dx \right]$$

and

$$G(\mu) := \lambda_1 \left[-\Delta - b_1 \theta_\mu - b_2 \int_{\Omega} b(x) \theta_\mu(x) dx \right].$$

It is evident that

$$F(\lambda_1) = G(\lambda_1) = \lambda_1.$$

The next lemma collects some basic properties of these functions under a suitable assumption about b_i and c_i ($i = 1, 2$).

Lemma 4.1. *Suppose $c_1, c_2 \geq 0$ (resp. $c_1, c_2 \leq 0$) and $(c_1, c_2) \neq (0, 0)$. Then, $F(\lambda)$ is continuous, decreasing (resp. increasing), and*

$$\lim_{\lambda \rightarrow +\infty} F(\lambda) = -\infty \quad (\text{resp.} \quad \lim_{\lambda \rightarrow +\infty} F(\lambda) = +\infty). \quad (18)$$

Analogously, suppose $b_1, b_2 \geq 0$ (resp. $b_1, b_2 \leq 0$) and $(b_1, b_2) \neq (0, 0)$. Then, $G(\mu)$ is continuous, decreasing (resp. increasing) and

$$\lim_{\mu \rightarrow +\infty} G(\mu) = -\infty \quad (\text{resp.} \quad \lim_{\mu \rightarrow +\infty} G(\mu) = +\infty). \quad (19)$$

Proof. The continuity and monotonicity follow from the continuity and monotonicity of the map $\lambda \in [\lambda_1, +\infty) \mapsto \theta_\lambda \in L^\infty(\Omega)$ and (5).

Using Theorem 3.2, we get that

$$\theta_\lambda(x) \geq \left(\frac{\lambda}{1 + \|a\|_1} - \lambda_1 \right) \varphi_1(x), \quad \int_{\Omega} c(x) \theta_\lambda(x) dx \geq \left(\frac{\lambda}{1 + \|a\|_1} - \lambda_1 \right) \|c\varphi_1\|_1.$$

Assume $c_1, c_2 \geq 0$ and $(c_1, c_2) \neq (0, 0)$. Then,

$$\begin{aligned} F(\lambda) &= \lambda_1 \left[-\Delta - c_1 \theta_\lambda - c_2 \int_{\Omega} c(x) \theta_\lambda(x) dx \right] \\ &\leq \lambda_1 \left[-\Delta - c_1 \left(\frac{\lambda}{1 + \|a\|_1} - \lambda_1 \right) \varphi_1 \right] - c_2 \left(\frac{\lambda}{1 + \|a\|_1} - \lambda_1 \right) \|c\varphi_1\|_1. \end{aligned}$$

Hence, $\lim_{\lambda \rightarrow +\infty} F(\lambda) = -\infty$.

Nevertheless, when $c_1, c_2 \leq 0$ and $(c_1, c_2) \neq (0, 0)$, we have that

$$F(\lambda) \geq \lambda_1 \left[-\Delta - c_1 \left(\frac{\lambda}{1 + \|a\|_1} - \lambda_1 \right) \varphi_1 \right] - c_2 \left(\frac{\lambda}{1 + \|a\|_1} - \lambda_1 \right) \|c\varphi_1\|_1,$$

whence we conclude that $\lim_{\lambda \rightarrow +\infty} F(\lambda) = +\infty$.

An analogous reasoning can be used to show the properties of the map $G(\mu)$. \square

Now we will present two bifurcation results. The first one is valid without any additional conditions on the parameters b_1, b_2, c_1 and c_2 .

By simplicity, we write $X = C_0^1(\bar{\Omega})$.

Theorem 4.2.

a) Fix $\mu > \lambda_1$ and regard $\lambda \in \mathbb{R}$ as the bifurcation parameter. Then, the point

$$(\lambda, u, v) = (G(\mu), 0, \theta_\mu)$$

is the unique bifurcation point to coexistence states from the semitrivial state $(\lambda, 0, \theta_\mu)$. Moreover, the component of coexistence states emanating from this point, say $\mathfrak{C}_{(\lambda, 0, v)}^+ \subset \mathbb{R} \times X \times X$, satisfies one of the following non excluding

alternatives: either is unbounded or there exists a positive solution $(\lambda^*, \theta_{\lambda^*})$ of (16) such that $\mu = F(\lambda^*)$ and $(\lambda^*, \theta_{\lambda^*}, 0) \in \overline{\mathfrak{C}_{(\lambda, 0, v)}^+}$.

b) Fix $\lambda > \lambda_1$ and regard $\mu \in \mathbb{R}$ as the bifurcation parameter. Then, the point

$$(\mu, u, v) = (F(\lambda), \theta_\lambda, 0)$$

is the unique bifurcation point to coexistence states from the semitrivial state $(\mu, \theta_\lambda, 0)$. Moreover, the component of coexistence states emanating from this point, say $\mathfrak{C}_{(\mu, u, 0)}^+ \subset \mathbb{R} \times X \times X$, satisfies one of the following non excluding alternatives: either is unbounded or there exists a positive solution (μ^*, θ_{μ^*}) of (17) such that $\lambda = G(\mu^*)$ and $(\mu^*, 0, \theta_{\mu^*}) \in \overline{\mathfrak{C}_{(\mu, u, 0)}^+}$.

Proof. We will prove b). The proof of a) is similar.

Fix $\lambda > \lambda_1$. In order to apply unilateral bifurcation theorem's, we define the operator $\mathfrak{F} : \mathbb{R} \times X \times X \rightarrow X \times X$ given by

$$\mathfrak{F}(\mu, u, v) = \begin{bmatrix} u - (-\Delta)^{-1}(u(\lambda - u - \int_{\Omega} a(x)u(x)dx + b_1v + b_2 \int_{\Omega} b(x)v(x)dx)) \\ v - (-\Delta)^{-1}(v(\mu - v - \int_{\Omega} d(x)v(x)dx + c_1u + c_2 \int_{\Omega} c(x)u(x)dx)) \end{bmatrix}. \quad (20)$$

This operator is of class C^1 and, since $\lambda > \lambda_1$, there exists a unique positive solution of (16), denoted by θ_λ , that is $\mathfrak{F}(\mu, \theta_\lambda, 0) = (0, 0)$. Thus, we define

$$\begin{aligned} L(\mu) &:= D_{(u, v)} \mathfrak{F}(\mu, \theta_\lambda, 0) \\ &= \begin{bmatrix} I - (-\Delta)^{-1}(\lambda - 2\theta_\lambda - \int_{\Omega} a\theta_\lambda - \theta_\lambda \int_{\Omega} a \cdot) & -(-\Delta)^{-1}(b_1\theta_\lambda + b_2\theta_\lambda \int_{\Omega} b \cdot) \\ 0 & I - (-\Delta)^{-1}(\mu + c_1\theta_\lambda + c_2 \int_{\Omega} c\theta_\lambda) \end{bmatrix}. \end{aligned} \quad (21)$$

In order to find simple eigenvalues, let us determine the null space (or kernel) $N[L(\mu)]$. Observe that $(\xi, \eta) \in N[L(\mu)]$ if, and only if,

$$\begin{cases} -\Delta\xi - \lambda\xi + 2\theta_\lambda\xi + \xi \int_{\Omega} a\theta_\lambda + \theta_\lambda \int_{\Omega} a\xi = b_1\theta_\lambda\eta + b_2\theta_\lambda \int_{\Omega} b\eta & \text{in } \Omega, \\ -\Delta\eta - c_1\theta_\lambda\eta - c_2\eta \int_{\Omega} c\theta_\lambda = \mu\eta & \text{in } \Omega, \\ \xi = \eta = 0 & \text{on } \partial\Omega. \end{cases} \quad (22)$$

Thus, if $\mu = F(\lambda)$ the solutions of second equation are given by $C\varphi_{1, \mu}$, where $C \in \mathbb{R}$ and $\varphi_{1, \mu}$ denotes the unique positive eigenfunction associated to $F(\lambda)$ with $\|\varphi_{1, \mu}\|_\infty = 1$. Therefore, substituting η by $\varphi_{1, \mu}$ into the first equation of (22), it becomes apparently that

$$\begin{cases} -\Delta\xi - \lambda\xi + 2\theta_\lambda\xi + \xi \int_{\Omega} a\theta_\lambda + \theta_\lambda \int_{\Omega} a\xi = b_1\theta_\lambda\varphi_{1, \mu} + b_2\theta_\lambda \int_{\Omega} b\varphi_{1, \mu} & \text{in } \Omega, \\ \xi = 0 & \text{on } \partial\Omega. \end{cases} \quad (23)$$

Note that $a, \theta_\lambda, b_1\theta_\lambda\varphi_{1, \mu} + b_2\theta_\lambda \int_{\Omega} b\varphi_{1, \mu} \in L^\infty(\Omega)$. Moreover, by (15) we know that $\lambda_1[L] > 0$, where $L = -\Delta - \lambda + 2\theta_\lambda + \int_{\Omega} a\theta_\lambda$. Therefore, we can apply the Lemma 3.1 to conclude that (23) has a unique solution in $W^{2, p}(\Omega)$, $p > 1$, which will be denoted by ψ_μ .

Consequently, if $\mu = F(\lambda)$, the unique solutions of (22) are given by $(C\psi_\mu, C\varphi_{1, \mu})$, with $C \in \mathbb{R}$, which provides us with $N[L(F(\lambda))] = \text{span}[(\psi_\mu, \varphi_{1, \mu})]$.

To conclude that 0 is a simple eigenvalue of $L(F(\lambda))$, as discussed in [4], it remains to show that

$$L'(F(\lambda))(\psi_\mu, \varphi_{1,\mu}) := D_\mu L(F(\lambda))(\psi_\mu, \varphi_{1,\mu}) \notin R[D_{(u,v)}\mathfrak{F}(F(\lambda), \theta_\lambda, 0)], \quad (24)$$

where $R[T]$ will stand the range of T .

By direct calculation,

$$L'(F(\lambda))(\psi_\mu, \varphi_{1,\mu}) = \begin{bmatrix} 0 & 0 \\ 0 & -(-\Delta)^{-1} \end{bmatrix} \begin{bmatrix} \psi_\mu \\ \varphi_{1,\mu} \end{bmatrix} = (0, -(-\Delta)^{-1}(\varphi_{1,\mu})).$$

Suppose $(0, -(-\Delta)^{-1}(\varphi_{1,\mu})) \in R[D_{(u,v)}\mathfrak{F}(F(\lambda), \theta_\lambda, 0)]$. Then, there exists $(\xi, \eta) \in X \times X$ such that $D_{(u,v)}\mathfrak{F}(F(\lambda), \theta_\lambda, 0)(\xi, \eta) = (0, -(-\Delta)^{-1}(\varphi_{1,\mu}))$. In particular,

$$\eta - (-\Delta)^{-1}[(F(\lambda) + c_1\theta_\lambda + c_2 \int_\Omega c(x)\theta_\lambda(x)dx)\eta] = -(-\Delta)^{-1}(\varphi_{1,\mu}),$$

that is,

$$\begin{cases} -\Delta\eta - F(\lambda)\eta - c_1\theta_\lambda\eta - c_2\eta \int_\Omega c(x)\theta_\lambda(x)dx = -\varphi_{1,\mu} & \text{in } \Omega, \\ \eta = 0 & \text{on } \partial\Omega. \end{cases}$$

Taking $\varphi_{1,\mu}$ as test function and using that it is a positive eigenfunction associated to $F(\lambda) = \lambda_1[-\Delta - c_1\theta_\lambda - c_2 \int_\Omega c\theta_\lambda]$ yields

$$0 = \int_\Omega \nabla\eta \cdot \nabla\varphi_{1,\mu} - \int_\Omega \left(F(\lambda)\eta + c_1\theta_\lambda\eta + c_2\eta \int_\Omega c\theta_\lambda \right) \varphi_{1,\mu} = - \int_\Omega \varphi_{1,\mu}^2 < 0,$$

which is a contradiction. This establishes that (24) holds.

Thus, we are able to apply Theorem 6.4.3 of [10] (see also [15]) to conclude that there exists a continuum \mathfrak{C} of solutions of (1) satisfying the global alternative of Rabinowitz. Moreover, following the proof of Theorem 7.2.2 of [10], we can conclude that there exists a subcontinuum, denoted by $\mathfrak{C}_{(\mu,u,0)}^+$, of coexistence states of (1) such that either:

1. $\mathfrak{C}_{(\mu,u,0)}^+$ is unbounded in $\mathbb{R} \times X \times X$;
2. There exists a positive solution (μ^*, θ_{μ^*}) of (17) such that $(\mu^*, 0, \theta_{\mu^*}) \in \overline{\mathfrak{C}_{(\mu,u,0)}^+}$ and

$$\lambda = \lambda_1 \left[-\Delta - c_1\theta_{\mu^*} - c_2 \int_\Omega c\theta_{\mu^*} \right] = G(\mu^*),$$

that is, the subcontinuum $\mathfrak{C}_{(\mu,u,0)}^+$ connects the two semitrivial curves;

3. There exists another positive solution of (16), e.g., (λ, ψ_λ) , with $\psi_\lambda \neq \theta_\lambda$ such that

$$(\lambda_1[-\Delta - b_1\psi_\lambda - b_2 \int_\Omega b\psi_\lambda], \psi_\lambda, 0) \in \overline{\mathfrak{C}_{(\mu,u,0)}^+};$$

4. $\lambda = \lambda_1$ and $(\lambda_1, 0, 0) \in \overline{\mathfrak{C}_{(\mu,u,0)}^+}$.

Since $\lambda > \lambda_1$, the alternative 4. is not true. Moreover, by uniqueness of solution of (16) (see Theorem 3.2), alternative 3. cannot occur. Consequently, the alternative 1. or 2. is satisfied. \square

Assuming an additional hypothesis about the sign of the parameters b_1, b_2, c_1, c_2 , we have the following bifurcation result:

Theorem 4.3. *a) Assume $b_1, b_2 \geq 0$, $(b_1, b_2) \neq (0, 0)$. Fix $\lambda < \lambda_1$ and regard $\mu \in \mathbb{R}$ as the bifurcation parameter. Then, the point*

$$(\mu, u, v) = (G^{-1}(\lambda), 0, \theta_\mu)$$

is the unique bifurcation point to coexistence states from the semitrivial state $(\mu, 0, \theta_\mu)$. Moreover, the component of coexistence states emanating from this point, say $\mathfrak{C}_{(\mu, 0, v)}^+ \subset \mathbb{R} \times X \times X$, is unbounded.

b) Assume $c_1, c_2 \geq 0$, $(c_1, c_2) \neq (0, 0)$. Fix $\mu < \lambda_1$ and regard $\lambda \in \mathbb{R}$ as the bifurcation parameter. Then, the point

$$(\lambda, u, v) = (F^{-1}(\mu), \theta_\lambda, 0)$$

is the unique bifurcation point to coexistence states from the semitrivial state $(\lambda, \theta_\lambda, 0)$. Moreover, the component of coexistence states emanating from this point, say $\mathfrak{C}_{(\lambda, u, 0)}^+ \subset \mathbb{R} \times X \times X$, is unbounded.

Proof. We will give some ideas the proof of b). The proof of a) is similar.

Fix $\mu < \lambda_1$ and consider the operator $\mathfrak{F} : \mathbb{R} \times X \times X \rightarrow X \times X$ defined in (20).

Since $F(\lambda)$ is a decreasing function such that $F((\lambda_1, +\infty)) = (-\infty, \lambda_1)$ (see Lemma 4.1) and $\mu < \lambda_1$, there exists a unique $\lambda = \lambda(\mu) > \lambda_1$ such that $\lambda = F^{-1}(\mu)$.

Arguing as in the previous result, we have that \mathfrak{F} is of class C^1 , $\mathfrak{F}(\lambda, \theta_\lambda, 0) = 0$ and $L(\lambda) := D_{(u,v)}\mathfrak{F}(\lambda, \theta_\lambda, 0)$ is given by (21). Moreover, $(\xi, \eta) \in N[L(F^{-1}(\mu))]$ if, and only if, (ξ, η) satisfies (22). Consequently, as a similar argument of the previous theorem, we obtain

$$N[L(F^{-1}(\mu))] = \text{span}[(\psi_\mu, \varphi_{1,\mu})].$$

Since the map $\lambda \mapsto \theta_\lambda$ is differentiable, then $\lambda \mapsto L(\lambda)$ is too. Let us to prove the transversality condition, i.e.,

$$L'(F^{-1}(\mu))(\psi_\mu, \varphi_{1,\mu}) := D_\lambda D_{(u,v)}\mathfrak{F}(F^{-1}(\mu), \theta_\lambda, 0)(\psi_\mu, \varphi_{1,\mu}) \notin R[D_{(u,v)}\mathfrak{F}(F^{-1}(\mu), \theta_\lambda, 0)].$$

A direct calculation shows

$$\begin{aligned} & L'(F^{-1}(\mu))(\psi_\mu, \varphi_{1,\mu}) \\ &= \begin{bmatrix} -(-\Delta)^{-1}(1 - 2\theta'_\lambda - \int_\Omega a\theta'_\lambda - \theta'_\lambda \int_\Omega a) & -(-\Delta)^{-1}(b_1\theta'_\lambda + b_2\theta'_\lambda \int_\Omega b) \\ 0 & -(-\Delta)^{-1}(c_1\theta'_\lambda + c_2 \int_\Omega c\theta'_\lambda) \end{bmatrix} \begin{bmatrix} \psi_\mu \\ \varphi_{1,\mu} \end{bmatrix}. \end{aligned}$$

If $L'(F^{-1}(\mu))(\psi_\mu, \varphi_{1,\mu}) \in R[D_{(u,v)}\mathfrak{F}(F^{-1}(\mu), \theta_\lambda, 0)]$, then there exists $(\xi, \eta) \in X \times X$ such that $D_{(u,v)}\mathfrak{F}(F^{-1}(\mu), \theta_\lambda, 0)(\xi, \eta) = L'(F^{-1}(\mu))(\psi_\mu, \varphi_{1,\mu})$. Consequently, η satisfies

$$\begin{cases} -\Delta\eta - c_1\theta_\lambda\eta - c_2\eta \int_\Omega c\theta_\lambda - \mu\eta = - \left(c_1\theta'_\lambda + c_2 \int_\Omega c\theta'_\lambda \right) \varphi_{1,\mu} & \text{in } \Omega, \\ \eta = 0 & \text{on } \partial\Omega. \end{cases}$$

Taking $\varphi_{1,\mu}$ as test function and using that it is a positive eigenfunction associated to $\mu = F(\lambda) = \lambda_1[-\Delta - c_1\theta_\lambda - c_2 \int_\Omega c\theta_\lambda]$ yields

$$\begin{aligned} 0 &= \int_\Omega \nabla\eta \cdot \nabla\varphi_{1,\mu} - \left(c_1\theta_\lambda\eta + c_2\eta \int_\Omega c\theta_\lambda - F(\lambda)\eta \right) \varphi_{1,\mu} = \\ &= - \int_\Omega \left(c_1\theta'_\lambda + c_2 \int_\Omega c\theta'_\lambda \right) \varphi_{1,\mu}^2 < 0, \end{aligned}$$

which is a contradiction. This establishes that (24) holds. Finally, arguing as in the previous theorem, we can conclude that there exists a unbounded continuum $\mathfrak{C}_{(\lambda,u,0)}^+$ emanating from the semitrivial solution $(\lambda, u, 0)$ at $(F^{-1}(\mu), \theta_\lambda, 0)$. \square

5. Proofs of the main results.

5.1. **Competition.** First, we show a priori bounds.

Proposition 2. *Assume that $b_i, c_i \leq 0$ with $i = 1, 2$, $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$. If (u, v) is a coexistence state of (1), then:*

1.

$$u \leq \omega_\lambda \leq \lambda \quad \text{and} \quad v \leq \omega_\mu \leq \mu \quad \text{in } \Omega.$$

2.

$$\int_{\Omega} a(x)u(x)dx \leq \lambda \frac{\|a\|_1}{1 + \|a\|_1} \quad \text{and} \quad \int_{\Omega} d(x)v(x)dx \leq \mu \frac{\|d\|_1}{1 + \|d\|_1}.$$

3.

$$R_1(\lambda, \mu)\varphi_1 \leq u \quad \text{and} \quad R_2(\lambda, \mu)\varphi_1 \leq v \quad \text{in } \Omega,$$

where

$$R_1(\lambda, \mu) = \frac{\lambda}{1 + \|a\|_1} + \mu(b_1 + b_2\|b\|_1) - \lambda_1, \quad R_2(\lambda, \mu) = \frac{\mu}{1 + \|d\|_1} + \lambda(c_1 + c_2\|c\|_1) - \lambda_1.$$

Proof. Observe that in this case, if u and v are positive solutions of (1), then they are sub-solutions of (6) with $\gamma = \lambda$ and $\gamma = \mu$, respectively. By Proposition 1 we obtain the first paragraph.

On the other hand, if $u_M = \max u = u(x_M)$ we have that

$$u(x) \leq u_M \leq \lambda + b_1v(x_M) + b_2 \int_{\Omega} b(x)v(x)dx - \int_{\Omega} a(x)u(x)dx \leq \lambda - \int_{\Omega} a(x)u(x)dx.$$

Multiplying by $a(x)$ and integrating, we get the second paragraph.

For the third paragraph, using that $u \leq \lambda$ and the second paragraph, we have that

$$\begin{aligned} -\Delta v &= v \left(\mu - v - \int_{\Omega} d(x)v(x)dx + c_1u + c_2 \int_{\Omega} c(x)u(x)dx \right) \\ &\geq v \left(\frac{\mu}{1 + \|d\|_1} + (c_1 + c_2\|c\|_1)\lambda - v \right) \end{aligned}$$

and then, applying Proposition 1, we get that

$$v \geq R_2(\lambda, \mu)\varphi_1.$$

This completes the proof. \square

As an immediate consequence of Propositions 1 and 2 we deduce

Corollary 1. *Assume $b_i, c_i \leq 0$ with $i = 1, 2$, $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$. If $\lambda \leq \lambda_1$ or $\mu \leq \lambda_1$, then (1) does not admit coexistence states.*

In the following result we prove the competitive exclusion principle.

Proposition 3. *Assume that $b_i, c_i \leq 0$ with $i = 1, 2$, $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$. Fix $\lambda > \lambda_1$ (resp. $\mu > \lambda_1$), then there exists $\mu_c(\lambda)$ (resp. $\lambda_c(\mu)$) such that (1) does not admit coexistence states for $\mu > \mu_c(\lambda)$ (resp. $\lambda > \lambda_c(\mu)$).*

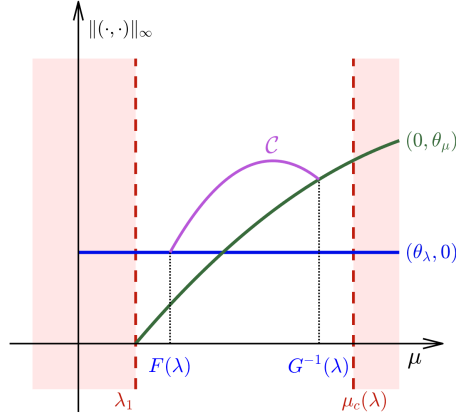


FIGURE 4. Bifurcation diagram (1) in the competition case

Proof. The proof of this result proceeds by contradiction. Observe that if u is a positive solution, then

$$\lambda = \lambda_1 \left[-\Delta + u + \int_{\Omega} au - b_1 v - b_2 \int_{\Omega} bv \right] > \lambda_1 \left[-\Delta - b_1 v - b_2 \int_{\Omega} bv \right]. \quad (25)$$

By Proposition 2, we get that

$$v \geq R_2(\lambda, \mu)\varphi_1, \quad \int_{\Omega} bv \geq R_2(\lambda, \mu)\|b\varphi_1\|_1,$$

and then by (25)

$$\lambda > \lambda_1[-\Delta - b_1 R_2(\lambda, \mu)\varphi_1] - b_2 R_2(\lambda, \mu)\|b\varphi_1\|_1,$$

a contradiction for μ large. \square

We are ready to prove Theorem 1.1 (see Figure 4).

Proof of Theorem 1.1. Fix $\lambda > \lambda_1$. Regarding μ as bifurcation parameter, by Theorem 4.2 from the semitrivial solution $(\theta_\lambda, 0)$ emanates a continuum $\mathfrak{C}_{(\mu, u, 0)}^+$ of coexistence states of (1) at $\mu = F(\lambda) > \lambda_1$. Thanks to Corollary 1 and Proposition 3, (1) does not admit coexistence states neither $\mu \leq \lambda_1$ nor $\mu > \mu_c(\lambda)$. Hence,

$$\text{Proj}_{\mathbf{R}}(\mathfrak{C}_{(\mu, u, 0)}^+) \subset (\lambda_1, \mu_c(\lambda)),$$

where given $(\mu, u, v) \in \mathfrak{C}_{(\mu, u, 0)}^+$ we have denoted $\text{Proj}_{\mathbf{R}}(\mu, u, v) = \mu$.

On the other hand, thanks to Proposition 2 we have that $\|u\|_\infty, \|v\|_\infty \leq C$ for all $(\mu, u, v) \in \mathfrak{C}_{(\mu, u, 0)}^+$. By elliptic regularity, we get that

$$\|u\|_X, \|v\|_X \leq C,$$

and hence $\mathfrak{C}_{(\mu, u, 0)}^+$ is bounded. Hence, by Theorem 4.2 there exists a positive solution (μ^*, θ_{μ^*}) of (17) such that $\lambda = G(\mu^*)$ and $(\mu^*, 0, \theta_{\mu^*}) \in \overline{\mathfrak{C}_{(\mu, u, 0)}^+}$. Hence, we obtain that

$$(F(\lambda), G^{-1}(\lambda)) \subset \text{Proj}_{\mathbf{R}}(\mathfrak{C}_{(\mu, u, 0)}^+).$$

This concludes the proof. \square

5.2. Prey-predator.

Proposition 4. *Assume that $c_i \leq 0 \leq b_i$ with $i = 1, 2$ and $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$. If (u, v) is a coexistence state of (1), then*

$$R_3(\lambda, \mu)\varphi_1 \leq u \leq \lambda + \mu(b_1 + b_2\|b\|_1) \quad \text{and} \quad v \leq \omega_\mu \leq \mu,$$

where

$$R_3(\lambda, \mu) = \frac{1}{1 + \|a\|_1}(\lambda - \mu(b_1 + b_2\|b\|_1)\|a\|_1) - \lambda_1.$$

Proof. It is clear that $v \leq \mu$ by the same argument as the above Proposition. Thus

$$-\Delta u \leq u \left(\lambda - u - \int_{\Omega} a(x)u(x)dx + b_1\mu + b_2\|b\|_1\mu \right) \leq u(\lambda - u + \mu(b_1 + b_2\|b\|_1)).$$

Then, u is a subsolution of (6). By Proposition 1 we have that

$$u \leq \lambda + \mu(b_1 + b_2\|b\|_1).$$

Moreover, since $b_i \geq 0$, if $u_M = \max_{x \in \Omega} u(x)$ we conclude that

$$u(x) \leq u_M \leq \lambda - \int_{\Omega} a(x)u(x)dx + \mu(b_1 + b_2\|b\|_1),$$

and then,

$$\int_{\Omega} a(x)u(x)dx \leq \frac{\|a\|_1}{1 + \|a\|_1}(\lambda + \mu(b_1 + b_2\|b\|_1)).$$

Hence,

$$-\Delta u \geq u \left(\lambda - u - \int_{\Omega} a(x)u(x)dx \right) \geq u \left(\frac{\lambda}{1 + \|a\|_1} - \frac{\|a\|_1}{1 + \|a\|_1}(\mu(b_1 + b_2\|b\|_1)) - u \right)$$

and then

$$u \geq R_3(\lambda, \mu)\varphi_1. \quad \square$$

Again, we can conclude that

Corollary 2. *Assume that $c_i \leq 0 \leq b_i$ with $i = 1, 2$ and $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$. If $\lambda + \mu(b_1 + b_2\|b\|_1) \leq 0$ or $\mu \leq \lambda_1$, then (1) does not admit coexistence states.*

Now, we show a non-existence result.

Proposition 5. *Assume that $c_i \leq 0 \leq b_i$ for $i = 1, 2$ and $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$. Fix $\mu > \lambda_1$, then there exists $\lambda_p(\mu)$ such that (1) does not admit coexistence states for $\lambda > \lambda_p(\mu)$.*

Proof. Suppose that (u, v) is a coexistence state of (1). Using Proposition 4 we get

$$\begin{aligned} -\Delta v &= v \left(\mu - v - \int_{\Omega} d(x)v(x)dx + c_1u + c_2 \int_{\Omega} cu \right) \\ &\leq v(\mu + c_1R_3(\lambda, \mu)\varphi_1 + c_2R_3(\lambda, \mu)\|\varphi_1c\|_1). \end{aligned}$$

Therefore, multiplying by φ_1 and integrating, we get

$$0 \leq (\mu - \lambda_1 + c_2R_3(\lambda, \mu)\|\varphi_1c\|_1) \int_{\Omega} v\varphi_1 + c_1R_3(\lambda, \mu) \int_{\Omega} v\varphi_1^2,$$

a contradiction for λ large. \square

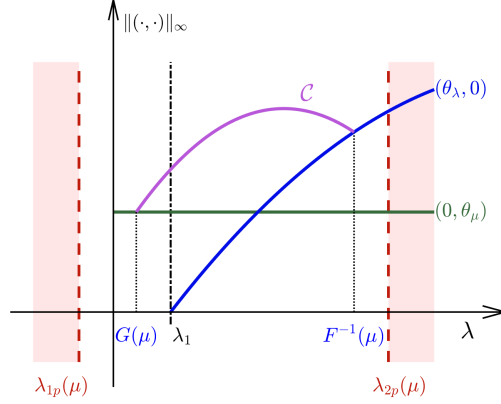


FIGURE 5. Bifurcation diagram (1) in the prey-predator case

Proof of Theorem 1.2. Fix $\mu > \lambda_1$ and consider λ as a parameter (see Figure 5). By Theorem 4.2 from the semitrivial solution $(0, \theta_\mu)$ emanates a continuum $\mathfrak{C}_{(\lambda, 0, v)}^+$ of coexistence states of (1) at $\lambda = G(\mu)$. Thanks to Corollary 2 and Proposition 5, (1) does not admit positive solution neither $\lambda < \lambda_{1p}(\mu)$ nor $\lambda > \lambda_{2p}(\mu)$. On the other hand, thanks to the a priori bounds of positive solutions, $\mathfrak{C}_{(\lambda, 0, v)}^+$ is bounded. Hence, we conclude that

$$(G(\mu), F^{-1}(\mu)) \subset \text{Proj}_{\mathbf{R}}(\mathfrak{C}_{(\lambda, 0, v)}^+).$$

The proof is completed. \square

5.3. Cooperation. We assume that a weak local cooperation occurs, that is $b_1 c_1 < 1$. We are going to obtain two different regimes of cooperation. In the first one, all the cooperation coefficients are small.

Proposition 6. (*Weak nonlocal cooperation*) Assume $b_i, c_i \geq 0$ for $i = 1, 2$, $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$ and

$$(H_w) \quad (b_1 + b_2 \|b\|_1)(c_1 + c_2 \|c\|_1) < 1.$$

Then, if (u, v) is a coexistence state of (1), we have

$$u \leq \frac{\lambda + \mu(b_1 + b_2 \|b\|_1)}{1 - (b_1 + b_2 \|b\|_1)(c_1 + c_2 \|c\|_1)}, \quad v \leq \frac{\mu + \lambda(c_1 + c_2 \|c\|_1)}{1 - (b_1 + b_2 \|b\|_1)(c_1 + c_2 \|c\|_1)}.$$

Proof. Let (u, v) be a coexistence state of (1), then there exists $x_M \in \Omega$ such that $u(x_M) = \max_{\bar{\Omega}} u(x) := u_M$. Since $-\Delta u(x_M) \geq 0$, we have that

$$\begin{aligned} u_M + \int_{\Omega} a(x)u(x)dx &\leq \lambda + b_1 v(x_M) + b_2 \int_{\Omega} b(x)v(x)dx \\ &\leq \lambda + b_1 v_M + b_2 \int_{\Omega} b(x)v(x)dx \leq \lambda + v_M(b_1 + b_2 \|b\|_1), \end{aligned} \quad (26)$$

with $v_M = \max_{\overline{\Omega}} v(x)$. Analogously,

$$v_M + \int_{\Omega} d(x)v(x)dx \leq \mu + c_1 u_M + c_2 \int_{\Omega} c(x)u(x)dx \leq \mu + u_M(c_1 + c_2\|c\|_1). \quad (27)$$

From these inequalities, one can derive

$$u_M \leq \lambda + v_M(b_1 + b_2\|b\|_1), \quad v_M \leq \mu + u_M(c_1 + c_2\|c\|_1), \quad (28)$$

and using (H_w) , we obtain the result. \square

As consequence, we obtain

Corollary 3. *Assume that $b_i, c_i \geq 0$ for $i = 1, 2$ and $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$ and (H_w) . Fix $\lambda \in \mathbb{R}$ (resp. $\mu \in \mathbb{R}$), then there exists $\mu_{ws}(\lambda)$ (resp. $\lambda_{ws}(\mu)$) such that (1) does not admit coexistence state for $\mu < \mu_{ws}(\lambda)$ (resp. $\lambda < \lambda_{ws}(\mu)$).*

In the following result, we obtain a priori bounds even for b_2 and/or c_2 large. To be precise, we need to introduce the function

$$H(x) := \begin{cases} \frac{(a_M + C)(d_M + C) - c_1(b_1 a_M d_M + x C b_L)}{c_L(x b_L(1 - b_1 c_1) + b_1 C)} & x \in \left[\frac{b_1 d_M}{b_L}, \frac{d_M + C}{c_1 b_L} \right], \\ \frac{c_1 a_M}{c_L} & x > \frac{d_M + C}{c_1 b_L}, \end{cases}$$

where

$$C = \frac{1 - b_1 c_1}{\|\varphi_1\|_1}.$$

Since

$$H\left(\frac{d_M + C}{c_1 b_L}\right) = \frac{c_1 a_M}{c_L},$$

H is continuous. Moreover, it is evident that H is decreasing in $\left[\frac{b_1 d_M}{b_L}, \frac{d_M + C}{c_1 b_L} \right]$ and

$$H\left(\frac{b_1 d_M}{b_L}\right) = \frac{a_M + C}{b_1 c_L}.$$

In Figure 6 we have represented in the (b_2, c_2) -plane the regions defined by (H_w) and (H_s) .

Proposition 7. *(Strong nonlocal cooperation) Assume $b_i, c_i > 0$ with $b_1 c_1 < 1$, $b(x), c(x) > 0$ for $x \in \overline{\Omega}$ and*

$$(H_s) \quad b_2 > b_1 d_M / b_L, \quad c_2 > H(b_2).$$

If (u, v) is a coexistence state of (1), we have

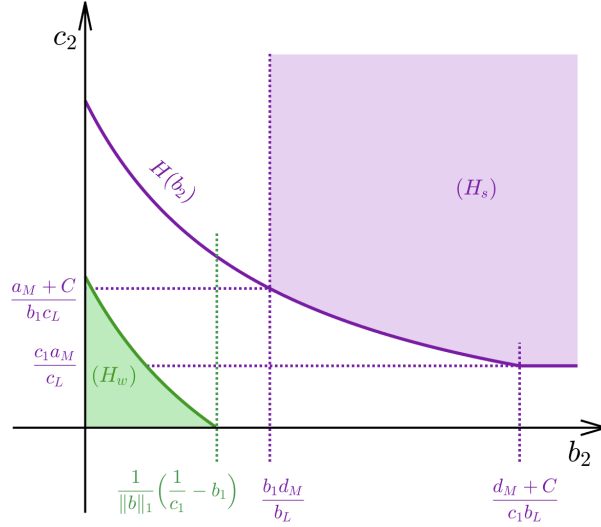
$$\|u\|_{\infty} \leq C_1, \quad \|v\|_{\infty} \leq C_2.$$

Moreover, fix $\lambda > \lambda_1$ (resp. $\mu > \lambda_1$), there exists $\mu_{ss}(\lambda)$ (resp. $\lambda_{ss}(\mu)$) such that for $\mu > \mu_{ss}(\lambda)$ (resp. $\lambda > \lambda_{ss}(\mu)$) system (1) does not admit coexistence states.

Proof. We consider the auxiliary problem:

$$\begin{cases} -\Delta u = u(\gamma_1 - u + b_1 v) & \text{in } \Omega, \\ -\Delta v = v(\gamma_2 - v + c_1 u) & \text{in } \Omega, \\ u = v = 0 & \text{on } \partial\Omega. \end{cases} \quad (29)$$

Since $b_1 c_1 < 1$, there exists a unique positive solution $(\hat{u}_{\gamma_1, \gamma_2}, \hat{v}_{\gamma_1, \gamma_2})$ of (29) (see Theorem 5.1 in [7]).

FIGURE 6. Regions in the (b_2, c_2) -plane defined by (H_w) and (H_s) .

Now, we intend to find a lower bound of solution of (29). For this we consider,

$$(\underline{u}, \underline{v}) = (\varepsilon_1 \varphi_1, \varepsilon_2 \varphi_1),$$

ε_1 and ε_2 are positive constants such that:

$$\begin{cases} \varepsilon_1 - b_1 \varepsilon_2 = \gamma_1 - \lambda_1, \\ \varepsilon_2 - c_1 \varepsilon_1 = \gamma_2 - \lambda_1. \end{cases} \quad (30)$$

That is,

$$\begin{cases} \varepsilon_1 = \frac{b_1(\gamma_2 - \lambda_1) + (\gamma_1 - \lambda_1)}{1 - b_1 c_1}, \\ \varepsilon_2 = \frac{c_1(\gamma_1 - \lambda_1) + (\gamma_2 - \lambda_1)}{1 - b_1 c_1}. \end{cases} \quad (31)$$

Observe that, thanks to (30) and $\|\varphi_1\|_\infty = 1$,

$$\begin{aligned} -\Delta \underline{u} &= \varepsilon_1 \lambda_1 \varphi_1 \leq \varepsilon_1 \varphi_1 (\gamma_1 - \varepsilon_1 \varphi_1 + b_1 \varepsilon_2 \varphi_1) = \underline{u} (\gamma_1 - \underline{u} + b_1 \underline{v}), \\ -\Delta \underline{v} &= \varepsilon_2 \lambda_1 \varphi_1 \leq \varepsilon_2 \varphi_1 (\gamma_2 - \varepsilon_2 \varphi_1 + c_1 \varepsilon_1 \varphi_1) = \underline{v} (\gamma_2 - \underline{v} + c_1 \underline{u}). \end{aligned}$$

Then, $(\underline{u}, \underline{v})$ is a subsolution of the problem (29) with $\varepsilon_1, \varepsilon_2$ defined by (30). Therefore,

$$\begin{aligned} \varepsilon_1 \varphi_1 &\leq \hat{u}_{\gamma_1, \gamma_2}, \\ \varepsilon_2 \varphi_1 &\leq \hat{v}_{\gamma_1, \gamma_2}. \end{aligned} \quad (32)$$

Now, let (u, v) be a coexistence state of (1), then (u, v) is the solution of (29) with

$$\begin{aligned}\gamma_1 &= \lambda - \int_{\Omega} a(x)u(x)dx + b_2 \int_{\Omega} b(x)v(x) dx, \\ \gamma_2 &= \mu - \int_{\Omega} d(x)v(x) dx + c_2 \int_{\Omega} c(x)u(x) dx.\end{aligned}$$

By (32) and (31)

$$\begin{aligned}\frac{\lambda - \lambda_1 - \int_{\Omega} au dx + b_2 \int_{\Omega} bv dx + b_1 \left(\mu - \lambda_1 - \int_{\Omega} dv dx + c_2 \int_{\Omega} cu dx \right)}{1 - b_1 c_1} \varphi_1 &\leq u \\ \frac{\mu - \lambda_1 - \int_{\Omega} dv dx + c_2 \int_{\Omega} cu dx + c_1 \left(\lambda - \lambda_1 - \int_{\Omega} au dx + b_2 \int_{\Omega} bv dx \right)}{1 - b_1 c_1} \varphi_1 &\leq v\end{aligned}$$

then, by integrating

$$\begin{aligned}A_1 \int_{\Omega} u dx + B_1 \int_{\Omega} v dx &\leq R_1 \\ B_2 \int_{\Omega} v dx + A_2 \int_{\Omega} u dx &\leq R_2\end{aligned}\tag{33}$$

with

$$\begin{aligned}A_1 &= c_2 b_1 c_L - a_M - C, & B_1 &= b_2 b_L - b_1 d_M, \\ A_2 &= c_2 c_L - c_1 a_M, & B_2 &= b_2 c_1 b_L - d_M - C, \\ R_1 &= \lambda_1 - \lambda + b_1(\lambda_1 - \mu), & R_2 &= \lambda_1 - \mu + c_1(\lambda_1 - \lambda).\end{aligned}$$

First, observe that since $b_1 c_1 < 1$, we have that

$$b_1 < \frac{d_M + C}{c_1 d_M}.$$

1. Assume that $b_2 \in (\frac{b_1 d_M}{b_L}, \frac{d_M + C}{c_1 b_L}]$. Then, $B_2 \leq 0 < B_1$. We distinguish two cases:

(a) Assume that $c_2 \in (\frac{c_1 a_M}{c_L}, \frac{a_M + C}{b_1 c_L}]$. In this case $A_1 \leq 0 < A_2$. Then, assuming that

$$D := B_1 A_2 - A_1 B_2 > 0,\tag{34}$$

we can conclude that

$$\int_{\Omega} u dx \leq \frac{T_1}{D}, \quad \int_{\Omega} v dx \leq \frac{T_2}{D},\tag{35}$$

where

$$T_1 = R_2 B_1 - B_2 R_1, \quad T_2 = R_1 A_2 - R_2 A_1.$$

Observe that (34) is equivalent to

$$c_2 > H(b_2).$$

(b) Assume that $c_2 \in (\frac{a_M + C}{b_1 c_L}, +\infty)$. In this case, $A_1, A_2 > 0$. Then, we can easily conclude that

$$\int_{\Omega} u dx \leq \frac{R_1}{A_1}, \quad \int_{\Omega} v dx \leq \frac{R_1}{B_1}.$$

2. Assume that $b_2 > \frac{d_M + C}{c_1 b_L}$. Then, $B_1, B_2 > 0$.

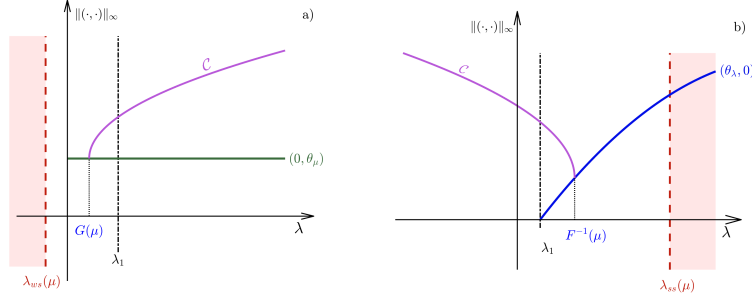


FIGURE 7. Bifurcation diagram (1) in the symbiosis case

- (a) Assume that $c_2 \in (\frac{c_1 a_M}{c_L}, \frac{a_M + C}{b_1 c_L}]$. In this case $A_1 \leq 0 < A_2$, and from the second equation we deduce that

$$\int_{\Omega} u \, dx \leq \frac{R_2}{A_2}, \quad \int_{\Omega} v \, dx \leq \frac{R_2}{B_2}.$$

- (b) Assume that $c_2 > \frac{a_M + C}{b_1 c_L}$. In this case $A_1, A_2 > 0$, again the result is deduced easily, in fact

$$\int_{\Omega} u \, dx \leq \min \left\{ \frac{R_1}{A_1}, \frac{R_2}{A_2} \right\}, \quad \int_{\Omega} v \, dx \leq \min \left\{ \frac{R_1}{B_1}, \frac{R_2}{B_2} \right\}.$$

Hence, in all the cases, we have obtained that

$$\int_{\Omega} u \leq E_1, \quad \int_{\Omega} v \leq E_2$$

and as consequence

$$\begin{cases} -\Delta u \leq u(\lambda + b_2 b_M E_2 - u + b_1 v) & \text{in } \Omega, \\ -\Delta v \leq v(\mu + c_2 c_M E_1 - v + c_1 u) & \text{in } \Omega, \\ u = v = 0 & \text{on } \partial\Omega, \end{cases} \quad (36)$$

whence we deduce thanks to $b_1 c_1 < 1$ that

$$\|u\|_{\infty} \leq C_1, \quad \|v\|_{\infty} \leq C_2.$$

With respect to the non-existence result, observe that, fixed $\lambda \in \mathbb{R}$, $R_1 < 0$, $R_2 < 0$, $T_1 < 0$ and $T_2 < 0$ for μ large. This concludes the proof. \square

Proof of Theorem 1.3. a) Assume that $b_i, c_i \geq 0$ for $i = 1, 2$, $(b_1, b_2) \neq (0, 0) \neq (c_1, c_2)$ and (H_w) .

Fix $\mu > \lambda_1$ (see Figure 7 a)). By Theorem 4.2 from the semitrivial solution $(0, \theta_{\mu})$ emanates a continuum $\mathfrak{C}_{(\lambda, 0, v)}^+$ of coexistence states of (1) at $\lambda = G(\mu)$. Since $F(\lambda) < \lambda_1$ for $\lambda > \lambda_1$, it is not possible the existence of $\lambda^* > \lambda_1$ such that $\mu = F(\lambda^*)$. Hence by Theorem 4.2, \mathfrak{C} is unbounded. By Proposition 6, any coexistence state $(u, v) \in \mathfrak{C}_{(\lambda, 0, v)}^+$ is bounded when λ belongs to a bounded subset of \mathbb{R} , and then we can conclude that

$$(G(\mu), +\infty) \subset \text{Proj}_{\mathbb{R}}(\mathfrak{C}_{(\lambda, 0, v)}^+).$$

In a similar way, we can show that for $\lambda > \lambda_1$ fixed we get

$$(F(\lambda), +\infty) \subset \text{Proj}_{\mathbf{R}}(\mathfrak{C}_{(\mu, u, 0)}^+).$$

b) Assume now that (H_s) .

Fix $\mu < \lambda_1$ (see Figure 7 b)). Then, by Theorem 4.3 from the semitrivial solution $(\theta_\lambda, 0)$ bifurcates at $\lambda = F^{-1}(\mu)$ an unbounded continuum $\mathfrak{C}_{(\lambda, u, 0)}^+$ of coexistence states of (1). Thanks to Proposition 7, we have a priori bounds of the solutions and non-existence of coexistence states for λ large, we conclude

$$(-\infty, F^{-1}(\mu)) \subset \text{Proj}_{\mathbf{R}}(\mathfrak{C}_{(\lambda, u, 0)}^+).$$

In a similar way, for $\lambda < \lambda_1$ we show that

$$(-\infty, G^{-1}(\lambda)) \subset \text{Proj}_{\mathbf{R}}(\mathfrak{C}_{(\mu, 0, v)}^+).$$

□

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