

A SPATIALLY HETEROGENEOUS PREDATOR-PREY MODEL

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*This paper is dedicated to Sze-Bi Hsu,
with admiration for his pioneering mathematical work
and our deepest gratitude for his friendship.
At the occasion of his 70th anniversary*

ABSTRACT. This paper introduces a spatially heterogeneous diffusive predator-prey model unifying the classical Lotka–Volterra and Holling–Tanner ones through a prey saturation coefficient, $m(x)$, which is spatially heterogeneous and it is allowed to ‘degenerate’. Thus, in some patches of the territory the species can interact according to a Lotka–Volterra kinetics, while in others the prey saturation effects play a significant role on the dynamics of the species. As we are working under general mixed boundary conditions of non-classical type, we must invoke to some very recent technical devices to get some of the main results of this paper.

1. Introduction. This paper analyzes the existence and the uniqueness of coexistence states for the generalized spatially heterogeneous predator-prey model

$$\begin{cases} \mathcal{L}_1 u = \lambda u - a(x)u^2 - \tilde{b}(x) \frac{uv}{\tilde{\gamma}(x) + \tilde{m}(x)u} & \text{in } \Omega, \\ \mathcal{L}_2 v = \mu v + \tilde{c}(x) \frac{uv}{\tilde{\gamma}(x) + \tilde{m}(x)u} - d(x)v^2 & \text{in } \Omega, \\ \mathfrak{B}_1 u = \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega, \end{cases} \quad (1)$$

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where Ω is a bounded domain of \mathbb{R}^N whose boundary, $\partial\Omega$, is a $N - 1$ dimensional manifold of class C^2 , and \mathfrak{L}_1 and \mathfrak{L}_2 are second order uniformly elliptic operators of the form

$$\mathfrak{L}_k := -\operatorname{div}(A^k(x)\nabla) + \sum_{j=1}^N b_j^k(x)\partial_j + c^k(x), \quad k = 1, 2, \quad (2)$$

where, for every $k = 1, 2$, $A^k(x) := (a_{ij}^k(x))_{1 \leq i, j \leq N}$ is a symmetric matrix of order N such that

$$a_{ij}^k = a_{ji}^k \in W^{1,\infty}(\Omega) \quad \text{and} \quad b_j^k, c^k \in L^\infty(\Omega) \quad \text{for all} \quad 1 \leq i, j \leq N.$$

In this model, \mathfrak{B}_1 and \mathfrak{B}_2 are general boundary operators of mixed type such that, for every $k = 1, 2$ and $w \in \mathcal{C}(\bar{\Omega}) \cap \mathcal{C}^1(\Omega \cup \Gamma_1^k)$,

$$\mathfrak{B}_k w := \begin{cases} w & \text{on } \Gamma_0^k, \\ \partial_{\nu_k} w + \beta_k(x)w & \text{on } \Gamma_1^k, \end{cases} \quad (3)$$

where Γ_0^k and Γ_1^k are two closed and open disjoint subsets of $\partial\Omega$ such that

$$\Gamma_0^k \cup \Gamma_1^k = \partial\Omega.$$

In (3), $\beta_k \in \mathcal{C}(\Gamma_1^k; \mathbb{R})$ and $\nu_k \in \mathcal{C}^1(\Gamma_1^k; \mathbb{R}^N)$ is an outward pointing nowhere tangent vector field. Moreover, the functions coefficients $a(x)$, $\tilde{b}(x)$, $\tilde{c}(x)$, $d(x)$, $\tilde{\gamma}(x)$ and $\tilde{m}(x)$ are continuous in $\bar{\Omega}$ and satisfy $\tilde{b} \geq 0$, $\tilde{c} \geq 0$, $\tilde{m} \geq 0$ and

$$a(x) > 0, \quad d(x) > 0, \quad \tilde{\gamma}(x) > 0 \quad \text{for all} \quad x \in \bar{\Omega}. \quad (4)$$

Since $\tilde{\gamma}(x) > 0$ for all $x \in \bar{\Omega}$, the interaction coefficients between u and v in the setting of (1) can be equivalently expressed as

$$\tilde{b}(x) \frac{uv}{\tilde{\gamma}(x) + \tilde{m}(x)u} = \frac{\tilde{b}(x)}{\tilde{\gamma}(x)} \frac{uv}{1 + \frac{\tilde{m}(x)}{\tilde{\gamma}(x)}u}, \quad \tilde{c}(x) \frac{uv}{\tilde{\gamma}(x) + \tilde{m}(x)u} = \frac{\tilde{c}(x)}{\tilde{\gamma}(x)} \frac{uv}{1 + \frac{\tilde{m}(x)}{\tilde{\gamma}(x)}u}.$$

Thus, renaming

$$b(x) := \frac{\tilde{b}(x)}{\tilde{\gamma}(x)}, \quad c(x) := \frac{\tilde{c}(x)}{\tilde{\gamma}(x)}, \quad m(x) := \frac{\tilde{m}(x)}{\tilde{\gamma}(x)},$$

(1) can be finally written down as

$$\begin{cases} \mathfrak{L}_1 u = \lambda u - a(x)u^2 - b(x) \frac{uv}{1 + m(x)u} & \text{in } \Omega, \\ \mathfrak{L}_2 v = \mu v + c(x) \frac{uv}{1 + m(x)u} - d(x)v^2 & \text{in } \Omega, \\ \mathfrak{B}_1 u = \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega. \end{cases} \quad (5)$$

In this model, $a(x)$ and $d(x)$ satisfy (4) and

$$b \geq 0, \quad c \geq 0, \quad m \geq 0. \quad (6)$$

From an ecological point of view, (5) models the interaction between a prey with density u and a predator with density v in the inhabiting territory Ω , where both species are assumed to have a logistic growth, or decay, in the absence of each other. In the special case when $m = 0$, (5) provides us with a rather generalized diffusive counterpart of the classical Lotka–Volterra predator–prey model, while if $m(x)$ is a positive constant, it is a generalized heterogeneous counterpart of the diffusive Holling–Tanner model studied by A. Casal et al. [5]. Such kinetics take into account the saturation effects of the predator in the presence of a high population of preys;

the constant $m > 0$ measuring the predator saturation level (see, e.g., H. Freedman [18] and R. May [43]). In a non-spatial context, these predator-prey interactions had been already analyzed in the late seventies by S. B. Hsu [21], where a rather pioneering criterium for the global stability of the coexistence state was given (see also S. B. Hsu and T. W. Hwang [22]).

In (5), $m(x)$ measures the level of saturation of the predator at any particular location $x \in \Omega$ where $m(x) > 0$, while saturation effects do not play any role if $m(x) = 0$. Thus, (5) combines, within the same territory, the classical interactions of Lotka–Volterra type in the region $m^{-1}(0)$ with the Holling–Tanner functional responses in $\{x \in \Omega : m(x) > 0\}$. So, integrating at a single prototype model the classical Lotka–Volterra and Holling–Tanner kinetics. Throughout this paper, $\lambda > 0$ and $\mu \in \mathbb{R}$ are regarded as bifurcation parameters. In applications, $\lambda - c^1(x)$ and $\mu - c^2(x)$ are the growth rates of the prey and the predator in the absence of each other.

Although there is a huge amount of literature on this type of models, beginning with A. Casal et al. [5], in most of the available literature

$$\mathfrak{L}_1 = \mathfrak{L}_2 = -\Delta = -\sum_{j=1}^N \frac{\partial^2}{\partial x_j^2}$$

is the Laplace operator in \mathbb{R}^N , and either $\Gamma_1^1 = \Gamma_1^2 = \emptyset$, i.e., \mathfrak{B}_1 and \mathfrak{B}_2 equal the Dirichlet operator on $\partial\Omega$, or $\Gamma_0^1 = \Gamma_0^2 = \emptyset$, $\beta_1 = \beta_2 = 0$ and $\nu_1 = \nu_2$ is the exterior normal vector field; so, \mathfrak{B}_1 and \mathfrak{B}_2 equal the Neumann boundary operator. Among the contributions within the first category count those of R. Peng, M. X. Wang and W. Y. Chen [47], M. X. Wang and Q. Wu [49], H. Nie and J. Wu [44], G. Guo and J. Wu [19], [20], J. Zhou and C. Mu [52], J. Zhou and J. P. Shi [54], H. Jiang and L. Wang [24], H. Yuan, J. Wu, Y. Jia and H. Nie [50], S. Li, J. Wu and Y. Dong [29], and X. Feng, Y. Song and X. An [15]. Among those in the second category count P. Y. H. Pang and M. Wang [45], [46], Y. Du and S. B. Hsu [10], W. Ko and K. Ryu [25], [27], Y. Du and J. P. Shi [14], J. Zhou and C. Mu [53], Y. Jia, J. Wu and H. K. Xu [23], S. Li, J. Wu and Y. Dong [29], and X. Zeng, W. Zeng and L. Liu [51]. Another fraction of available literature, like K. Ryu and I. Ahn [48], [26] dealt with Robin boundary conditions. The paper of Y. Du and J. P. Shi [13] dealt with a model of a slightly different nature.

According to its greatest generality, the prototype (5) integrates almost all available models in the literature, except for the fact that we are not considering in this paper any kind of degeneracies for the function coefficients $a(x)$ and $d(x)$, which might provoke metasolutions, as discussed in J. López-Gómez [36] and the references there in. The first general Reaction-Diffusion systems incorporating spatial heterogeneities seem to be those introduced by J. López-Gómez in [31], later revisited in [33, Ch. 7]. Actually, as it will be shown later, most of the available results on the existence of coexistence states can be derived as a rather direct consequence of Theorem 7.2.2 of [33].

The main goal of this paper is characterizing the existence of coexistence states of (5) and analyzing their uniqueness in terms of the level of the saturation effects, measured by $m(x)$. As a result of our analysis we have found the next intriguing feature of the model (5). When $m(x) > 0$ for all $x \in \bar{\Omega}$, like in most of the existing papers, (5) cannot admit a coexistence state for

$$\mu \leq \sigma_0 \left[\mathfrak{L}_2 - \frac{c(x)}{m(x)}, \mathfrak{B}_2, \Omega \right],$$

where $\sigma_0[\mathfrak{L}_2 - c/m, \mathfrak{B}_2, \Omega]$ stands for the principal eigenvalue of $(\mathfrak{L}_2 - c/m, \mathfrak{B}_2, \Omega)$, whereas if

$$\Omega_0 \equiv \text{Int } m^{-1}(0) \neq \emptyset, \quad (7)$$

regardless the size and the internal structure of Ω_0 , (5) admits coexistence states for all $\mu < 0$.

As far as concerns the uniqueness, we have adopted the methodology of J. López-Gómez and R. M. Pardo [40], [41], to establish that the one-dimensional counterpart of (5) has a unique coexistence state if $m(x)$ is sufficiently small for all $x \in \Omega$, which enables us to recover the uniqueness theorems of [40] and [41]. Astonishingly, no real serious advance has been done on this particular issue in the last three decades, except for the multiplicity results of J. López-Gómez [42] and J. López-Gómez and E. Muñoz-Hernández [38] in the context of the periodic Lotka–Volterra predator model.

Although the techniques used in this paper are already classical, it should be emphasized that the construction of supersolutions and, hence, of a priori bounds, in the general case when $\beta_1(x)$ and $\beta_2(x)$ change of sign is far from straightforward and it uses a recent technical device introduced by D. Aleja et al. [1] based on Lemma 2.1 of the monograph [35]. Similarly, by the lack of singular perturbation results for logistic equations under general non-classical mixed boundary conditions, we must invoke the (very recent) Theorem 1.2 of S. Fernández-Rincón and J. López-Gómez [16]. Besides our extensions of the existing results here are far from straightforward, some of them are fraught with a number of technical difficulties whose resolution might contribute to facilitate our understanding of the effects of the spatial heterogeneities on the dynamics of Reaction Diffusion systems, much like Theorem 7.10 of [35] enhanced the mathematical analysis of the effects of the spatial heterogeneities in the context of degenerate problems.

This paper is organized as follows. Section 2 collects some preliminaries that are going to be used throughout this paper. Among them, the characterization of the strong maximum principle, [35, Th. 7.10], and the singular perturbation result established by [16, Th. 1.2]. Section 3 characterizes the linearized stability of the trivial and semitrivial positive solutions of (5). Section 4 derives some necessary conditions for the existence of a coexistence state of (5). Section 5 establishes that (5) possesses a coexistence state provided that any of the semitrivial positive solutions is linearly unstable. The analysis of A. Casal et al. [5] already established that this is far from characterizing the existence of a coexistence state when m is a positive constant, while, thanks to Theorem 3.1 of J. López-Gómez and R. M. Pardo [39], the instability of the semitrivial positive solutions characterizes the existence of a coexistence state in the classical diffusive Lotka–Volterra system under Dirichlet boundary conditions. Section 6 ascertains the nature of the local bifurcations to coexistence states from the semitrivial positive solutions. Finally, Section 7 delivers our main uniqueness result of coexistence states, establishing that, regardless the nodal structure of $m(x)$, in one spatial dimension, the problem (5) admits a unique coexistence state provided $\|m\|_{C(\bar{\Omega})}$ is sufficiently small.

2. Preliminaries. This section collects some well known results that are going to be used throughout this paper. As a direct consequence of the elliptic L^p -theory (see, e.g., Chapter 5 of [35]), it is apparent that any non-negative weak solution of (5), (u, v) , satisfies

$$u \in U_1 := \bigcap_{p=N}^{\infty} W_{\mathfrak{B}_1}^{2,p}(\Omega), \quad v \in U_2 := \bigcap_{p=N}^{\infty} W_{\mathfrak{B}_2}^{2,p}(\Omega),$$

where, for every $k = 1, 2$ and $p > N$, $W_{\mathfrak{B}_k}^{2,p}(\Omega)$ stands for the Sobolev space of the functions $w \in W^{2,p}(\Omega)$ such that $\mathfrak{B}_k w = 0$ on $\partial\Omega$. According to the Sobolev imbeddings (see, e.g., [35, Th. 4.5]), for every $p > N$, we have that

$$W^{2,p}(\Omega) \subset \mathcal{C}^{1,1-\frac{N}{p}}(\bar{\Omega}).$$

Hence, there is enough regularity along the boundary as to consider $\mathfrak{B}_k w$ in the classical sense. Actually, according to [35, Th. 5.11], (u, v) must be a strong solution of (5). In particular, u and v are twice classically differentiable almost everywhere in Ω and they are classical solutions in the sense of [35, Def. 4.1].

Throughout this paper, for any given $V \in L^\infty(\Omega)$ and $k = 1, 2$, we denote by

$$\sigma_0[\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega]$$

the principal eigenvalue of the linear eigenvalue problem

$$\begin{cases} (\mathfrak{L}_k + V)\varphi = \tau\varphi & \text{in } \Omega, \\ \mathfrak{B}_k\varphi = 0 & \text{on } \partial\Omega, \end{cases}$$

whose existence and uniqueness in our general setting was established in [35, Ch. 7]. It is folklore that the principal eigenvalue is the lowest real eigenvalue of the problem, as well as strictly dominant and algebraically simple. The associated principal eigenfunction, unique up to a multiplicative positive constant, can be taken strongly positive in Ω , $\varphi_k \gg 0$, in the sense that

$$\varphi_k(x) > 0 \text{ for all } x \in \Omega \cup \Gamma_1^k \text{ and } \frac{\partial \varphi_k}{\partial n}(x) < 0 \text{ for all } x \in \Gamma_0^k,$$

where n stands for the outward unit vector field to Ω . Throughout this paper we will use two important properties of the principal eigenvalue: its monotonicity with respect to the potential and the theorem of characterization of the strong maximum principle. They have been collected into the next two results. With the greatest generality in this paper, the next result goes back to S. Cano-Casanova and J. López-Gómez [4].

Theorem 2.1. *Let $V_1, V_2 \in L^\infty(\Omega)$ be such that $V_1 < V_2$. Then, for every $k = 1, 2$,*

$$\sigma_0[\mathfrak{L}_k + V_1, \mathfrak{B}_k, \Omega] < \sigma_0[\mathfrak{L}_k + V_2, \mathfrak{B}_k, \Omega].$$

Thus, the map $V \mapsto \sigma_0[\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega]$ is continuous and increasing.

The next characterization goes back to J. López-Gómez and M. Molina-Meyer [37] for cooperative systems under Dirichlet boundary conditions, and to H. Amann and J. López-Gómez [2] and J. López-Gómez [34] for general boundary conditions of mixed type. It is [35, Th. 7.10], where the interested reader is sent for further details.

Incidentally, simultaneously to [37], the equivalence between (a) and (b) was also established for the single equation under Dirichlet boundary conditions by H. Berestycki, L. Nirenberg and S. R. S. Varadhan [3] (see the Preface of [35] for any further details and a complete discussion).

Theorem 2.2. *For every $V \in L^\infty(\Omega)$ and $k = 1, 2$, the next conditions are equivalent:*

$$(a) \quad \sigma_0[\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega] > 0.$$

- (b) The tern $(\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega)$ admits a positive strict supersolution, $h \in U_k$, i.e., for some $h \in U_k$ such that $h \gtrsim 0$, the next estimates hold

$$\begin{cases} (\mathfrak{L}_k + V)h \geq 0 & \text{in } \Omega, \\ \mathfrak{B}_k h \geq 0 & \text{on } \partial\Omega, \end{cases}$$

with some of these inequalities strict.

- (c) The tern $(\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega)$ satisfies the strong maximum principle, i.e., $w \gg_k 0$ for every function $w \in U_k$ such that

$$\begin{cases} (\mathfrak{L}_k + V)w \geq 0 & \text{in } \Omega, \\ \mathfrak{B}_k w \geq 0 & \text{on } \partial\Omega, \end{cases}$$

with some of these inequalities strict. By $w \gg_k 0$, it is meant that

$$w(x) > 0 \text{ for all } x \in \Omega \cup \Gamma_1^k \text{ and } \frac{\partial w}{\partial n}(x) < 0 \text{ for all } x \in w^{-1}(0) \cap \Gamma_0^k.$$

Similarly, through this paper, we will often invoke the next result. In the special case when $\beta_k \geq 0$, it goes back to J. M. Fraile et al. [17, Th. 3.5]. In the general case when β_k changes of sign one can use the change of variable of S. Fernández-Rincón and J. López-Gómez [16, Sect. 3] to reduce the problem to the setting of [17], or one might derive it directly from Theorem 1.1 of D. Daners and J. López-Gómez [9].

Theorem 2.3. Suppose $\rho \in \mathbb{R}$ and $\xi \in C(\bar{\Omega}; (0, \infty))$. Then, for every $k = 1, 2$ and $V \in L^\infty(\Omega)$, the semilinear boundary value problem

$$\begin{cases} (\mathfrak{L}_k + V)w = \rho w - \xi(x)w^2 & \text{in } \Omega, \\ \mathfrak{B}_k w = 0 & \text{on } \partial\Omega, \end{cases} \quad (8)$$

admits a positive solution if, and only if,

$$\rho > \sigma_0[\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega].$$

Moreover, it is unique if it exists, and if we denote it by

$$w_{\rho,k} \equiv \theta_{[\mathfrak{L}_k + V, \rho, \xi]} \in U_k,$$

then $w_{\rho,k} \gg_k 0$ and the map $\rho \rightarrow w_{\rho,k}$ is point-wise increasing if

$$\rho > \sigma_0[\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega].$$

Furthermore,

$$\lim_{\rho \downarrow \sigma_0[\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega]} w_{\rho,k} = 0.$$

In other words, $w_{\rho,k}$ bifurcates from $w = 0$ at $\rho = \sigma_0[\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega]$.

More precisely, through this paper we denote by $\theta_{[\mathfrak{L}_k + V, \rho, \xi]}$ the maximal non-negative solution of (8). Thus,

$$\theta_{[\mathfrak{L}_k + V, \rho, \xi]} := 0 \quad \text{if } \rho \leq \sigma_0[\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega],$$

whereas

$$\theta_{[\mathfrak{L}_k + V, \rho, \xi]} \gg_k 0 \quad \text{if } \rho > \sigma_0[\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega].$$

J. M. Fraile et al. [17] also gave a version of Theorem 2.3 for the special case when $\rho \geq 0$ and ξ vanishes on some nice subdomain of Ω . Theorem 1.1 of D. Daners and J. López-Gómez [9] characterized the range of ρ 's for which (8) admits a positive solution under no additional restrictions on the nature of $\xi^{-1}(0)$. The next result, of technical nature, will be often invoked in this paper.

Lemma 2.4. *Under the assumptions of Theorem 2.3, $w_{\rho_2,k} \gg_k w_{\rho_1,k}$ if*

$$\rho_2 > \rho_1 > \sigma_0 [\mathfrak{L}_k + V, \mathfrak{B}_k, \Omega],$$

in the sense that $w_{\rho_2,k} - w_{\rho_1,k} \gg_k 0$. More generally, if \bar{u} is a positive strict supersolution of (8), then $\bar{u} \gg_k w_{\rho,k}$. Similarly, if \underline{u} is a positive strict subsolution of (8), then $\underline{u} \ll_k w_{\rho,k}$.

Proof. First we show that any positive strict supersolution of (8), \bar{u} , satisfies $\bar{u} \gg_k w_{\rho,k}$. Indeed,

$$\begin{aligned} \mathfrak{L}_k(\bar{u} - w_{\rho,k}) &\geq \rho\bar{u} - \xi(x)\bar{u}^2 - \rho w_{\rho,k} + \xi(x)w_{\rho,k}^2 \\ &= \rho(\bar{u} - w_{\rho,k}) - \xi(x)(\bar{u} + w_{\rho,k})(\bar{u} - w_{\rho,k}) \end{aligned}$$

and hence,

$$\begin{cases} [\mathfrak{L}_k + \xi(x)(\bar{u} + w_{\rho,k}) - \rho](\bar{u} - w_{\rho,k}) \geq 0 & \text{in } \Omega, \\ \mathfrak{B}_k(\bar{u} - w_{\rho,k}) \geq 0 & \text{on } \partial\Omega, \end{cases} \quad (9)$$

with some of these inequalities strict, for as \bar{u} is a strict supersolution of (8). On the other hand, by Theorem 2.1,

$$\sigma_0 [\mathfrak{L}_k + \xi(x)(\bar{u} + w_{\rho,k}) - \rho, \mathfrak{B}_k, \Omega] > \sigma_0 [\mathfrak{L}_k + \xi(x)w_{\rho,k} - \rho, \mathfrak{B}_k, \Omega] = 0,$$

because $\bar{u} \gtrsim 0$ and $\xi(x) > 0$ for all $x \in \Omega$. The last identity follows, by the Krein–Rutman theorem, from the fact that $w_{\rho,k}$ is a positive solution of (8). Therefore, according to Theorem 2.2, it follows from (9) that

$$\bar{u} - w_{\rho,k} \gg_k 0.$$

Now, suppose that \underline{u} is a positive strict subsolution of (8). Then,

$$\begin{aligned} \mathfrak{L}_k(w_{\rho,k} - \underline{u}) &\geq \rho w_{\rho,k} - \xi(x)w_{\rho,k}^2 - \rho\underline{u} + \xi(x)\underline{u}^2 \\ &= \rho(w_{\rho,k} - \underline{u}) - \xi(x)(w_{\rho,k} + \underline{u})(w_{\rho,k} - \underline{u}) \end{aligned}$$

and hence,

$$\begin{cases} [\mathfrak{L}_k + \xi(x)(w_{\rho,k} + \underline{u}) - \rho](w_{\rho,k} - \underline{u}) \geq 0 & \text{in } \Omega, \\ \mathfrak{B}_k(w_{\rho,k} - \underline{u}) \geq 0 & \text{on } \partial\Omega, \end{cases}$$

with some of these inequalities strict. Therefore, arguing as above yields

$$\underline{u} \ll_k w_{\rho,k}.$$

This ends the proof. \square

As a byproduct of Theorem 2.3, the next result holds

Corollary 1. *According to Theorem 2.3, (5) has a semitrivial positive solution of the form $(u, 0)$ if, and only if,*

$$\lambda > \sigma_{0,1} \equiv \sigma_0[\mathfrak{L}_1, \mathfrak{B}_1, \Omega]$$

and, in such case, $(u, 0) = (\theta_{[\mathfrak{L}_1, \lambda, a(x)]}, 0)$. Similarly, (5) has a semitrivial positive solution of the form $(0, v)$ if, and only if,

$$\mu > \sigma_{0,2} \equiv \sigma_0[\mathfrak{L}_2, \mathfrak{B}_2, \Omega]$$

and, in such case, $(0, v) = (0, \theta_{[\mathfrak{L}_2, \mu, d(x)]})$.

By making the change of variable

$$\theta_{[\mathfrak{L}_k+V,\rho,\xi]} = \rho \psi_{[\mathfrak{L}_k+V,\rho,\xi]} \quad (10)$$

in the problem (8) and dividing the resulting differential equation by ρ^2 yields

$$\begin{cases} \frac{1}{\rho}(\mathfrak{L}_k + V)\psi_{[\mathfrak{L}_k+V,\rho,\xi]} = \psi_{[\mathfrak{L}_k+V,\rho,\xi]} - \xi(x)\psi_{[\mathfrak{L}_k+V,\rho,\xi]}^2 & \text{in } \Omega, \\ \mathfrak{B}_k\psi_{[\mathfrak{L}_k+V,\rho,\xi]} = 0 & \text{on } \partial\Omega. \end{cases}$$

Thus, thanks to Theorem 1.2 of S. Fernández-Rincón and J. López-Gómez [16], the next result holds.

Theorem 2.5. *Suppose $\rho > 0$ and $\xi \in C(\bar{\Omega}; (0, \infty))$. Then, for every compact subset, $K \subset \Omega \cup \Gamma_k^1$,*

$$\lim_{\rho \uparrow +\infty} \psi_{[\mathfrak{L}_k+V,\rho,\xi]} = \xi^{-1} \quad \text{uniformly in } K.$$

In other words,

$$\lim_{\rho \uparrow +\infty} \frac{\theta_{[\mathfrak{L}_k+V,\rho,\xi]}}{\rho} = \xi^{-1} \quad \text{uniformly in } K.$$

3. Linearized stability of the semitrivial positive solutions. This section analyzes the linearized stability of the semitrivial positive solutions of (5), which are given by $(\theta_{[\mathfrak{L}_1,\lambda,a]}, 0)$ if $\lambda > \sigma_{0,1}$, and $(0, \theta_{[\mathfrak{L}_2,\mu,d]})$ if $\mu > \sigma_{0,2}$. Their linearized stabilities provide us with their local attractive, or repulsive, characters as positive steady-state solutions of the associated parabolic model

$$\begin{cases} \partial_t u + \mathfrak{L}_1 u = \lambda u - a(x)u^2 - b(x)\frac{uv}{1+m(x)u} & x \in \Omega, \ t > 0, \\ \partial_t v + \mathfrak{L}_2 v = \mu v + c(x)\frac{uv}{1+m(x)u} - d(x)v^2 & x \in \Omega, \ t > 0, \\ \mathfrak{B}_1 u = \mathfrak{B}_2 v = 0 & x \in \partial\Omega, \ t > 0, \\ u(\cdot, 0) = u_0 \geq 0, \ v(\cdot, 0) = v_0 \geq 0, \end{cases} \quad (11)$$

where u_0 and v_0 are the initial distributions in the inhabiting area Ω of the species u and v . The next result provides us with the linearized stability of $(\theta_{[\mathfrak{L}_1,\lambda,a]}, 0)$.

Theorem 3.1. *Suppose $\lambda > \sigma_{0,1}$. Then, the semitrivial positive solution $(\theta_{[\mathfrak{L}_1,\lambda,a]}, 0)$ is linearly unstable (l.u.) if, and only if,*

$$\mu > \sigma_0 \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1,\lambda,a]}}{1+m\theta_{[\mathfrak{L}_1,\lambda,a]}}, \mathfrak{B}_2, \Omega \right], \quad (12)$$

while it is linearly stable (l.s.) if, and only if,

$$\mu < \sigma_0 \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1,\lambda,a]}}{1+m\theta_{[\mathfrak{L}_1,\lambda,a]}}, \mathfrak{B}_2, \Omega \right]. \quad (13)$$

Therefore, the curve

$$\mu = \Psi(\lambda) \equiv \sigma_0 \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1,\lambda,a]}}{1+m\theta_{[\mathfrak{L}_1,\lambda,a]}}, \mathfrak{B}_2, \Omega \right], \quad \lambda > \sigma_{0,1}, \quad (14)$$

provides us with the curve of change of stability of $(\theta_{[\mathfrak{L}_1,\lambda,a]}, 0)$, i.e., it is the curve of neutral stability of $(\theta_{[\mathfrak{L}_1,\lambda,a]}, 0)$.

Proof. The linearized stability of $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$ is determined by the signs of the eigenvalues of the linearization of (5) at $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$, i.e., by the signs of the τ 's for which the eigenvalue problem

$$\begin{cases} \mathfrak{L}_1 u = \lambda u - 2a\theta_{[\mathfrak{L}_1, \lambda, a]}u - b \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}}v + \tau u & \text{in } \Omega, \\ \mathfrak{L}_2 v = \mu v + c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}}v + \tau v & \text{in } \Omega, \\ \mathfrak{B}_1 u = \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega. \end{cases} \quad (15)$$

admits a nontrivial eigenfunction, (u, v) . First, we will look for eigenvalues with $v = 0$. Those are given by the values of τ for which the eigenvalue problem

$$\begin{cases} \mathfrak{L}_1 u = \lambda u - 2a\theta_{[\mathfrak{L}_1, \lambda, a]}u + \tau u & \text{in } \Omega, \\ \mathfrak{B}_1 u = 0 & \text{on } \partial\Omega, \end{cases} \quad (16)$$

admits a solution $u \neq 0$. Since, by definition,

$$\begin{cases} \mathfrak{L}_1 \theta_{[\mathfrak{L}_1, \lambda, a]} = \lambda \theta_{[\mathfrak{L}_1, \lambda, a]} - a\theta_{[\mathfrak{L}_1, \lambda, a]}^2 & \text{in } \Omega, \\ \mathfrak{B}_1 \theta_{[\mathfrak{L}_1, \lambda, a]} = 0 & \text{on } \partial\Omega, \end{cases}$$

it becomes apparent that

$$(\mathfrak{L}_1 + a\theta_{[\mathfrak{L}_1, \lambda, a]}) \theta_{[\mathfrak{L}_1, \lambda, a]} = \lambda \theta_{[\mathfrak{L}_1, \lambda, a]}$$

and hence, by the uniqueness of the principal eigenvalue (see, e.g., [33, Ch. 7]),

$$\lambda = \sigma_0[\mathfrak{L}_1 + a\theta_{[\mathfrak{L}_1, \lambda, a]}, \mathfrak{B}_1, \Omega].$$

Thus, by Theorem 2.1,

$$\sigma_0[\mathfrak{L}_1 + 2a\theta_{[\mathfrak{L}_1, \lambda, a]} - \lambda, \mathfrak{B}_1, \Omega] > \sigma_0[\mathfrak{L}_1 + a\theta_{[\mathfrak{L}_1, \lambda, a]} - \lambda, \mathfrak{B}_1, \Omega] = 0. \quad (17)$$

Consequently, since the principal eigenvalue is dominant, it becomes apparent that all the eigenvalues, τ , of (16) have a positive real part. So, they provide us with eigenfunctions on the stable manifold of the steady state solution $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$. Next, we will look for eigenfunctions of (15), (u, v) , with $v \neq 0$. Since $v \neq 0$ satisfies

$$\begin{cases} \mathfrak{L}_2 v = \mu v + c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}}v + \tau v & \text{in } \Omega, \\ \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega, \end{cases} \quad (18)$$

τ must be an eigenvalue of the differential operator

$$\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}} - \mu$$

in Ω subject to the boundary operator \mathfrak{B}_2 on $\partial\Omega$. By the dominance of the principal eigenvalue, all these eigenvalues are positive if (13) holds. Thus, $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$ is linearly stable under condition (13).

Now, suppose (12). Then,

$$\tau := \sigma_0 \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}} - \mu, \mathfrak{B}_2, \Omega \right] < 0$$

provides us with a negative eigenvalue of (18) and, for this choice, the first equation of (15) can be equivalently expressed as

$$\begin{cases} (\mathfrak{L}_1 + 2a\theta_{[\mathfrak{L}_1, \lambda, a]} - \lambda - \tau) u = -b \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}}v & \text{in } \Omega, \\ \mathfrak{B}_1 u = 0 & \text{on } \partial\Omega. \end{cases} \quad (19)$$

As $\tau < 0$, it follows from (17) that also

$$\sigma_0 [\mathfrak{L}_1 + 2a\theta_{[\mathfrak{L}_1, \lambda, a]} - \lambda - \tau, \mathfrak{B}_1, \Omega] > 0.$$

Thus, it follows from (19) that

$$u = -(\mathfrak{L}_1 + 2a\theta_{[\mathfrak{L}_1, \lambda, a]} - \lambda - \tau)^{-1} \left(b \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} v \right).$$

Therefore, (15) possesses a negative eigenvalue under (12). Hence, $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$ is linearly unstable, as claimed in the statement.

Lastly, thanks to the previous analysis, it becomes apparent that the curve (14) provides us with the set of values of the parameters λ and μ for which $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$ is linearly neutrally stable, i.e., is the curve of change of stability of this semitrivial solution. This ends the proof. \square

Similarly, the next result holds.

Theorem 3.2. *Suppose $\mu > \sigma_{0,2}$. Then, the semitrivial solution $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$ is linearly unstable (l.u.) if, and only if,*

$$\lambda > \sigma_0 [\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu, d]}, \mathfrak{B}_1, \Omega], \quad (20)$$

while it is linearly stable (l.s.) if, and only if,

$$\lambda < \sigma_0 [\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu, d]}, \mathfrak{B}_1, \Omega]. \quad (21)$$

Therefore, the curve

$$\lambda = \Phi(\mu) \equiv \sigma_0 [\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu, d]}, \mathfrak{B}_1, \Omega], \quad \mu > \sigma_{0,2}, \quad (22)$$

provides us with the curve of change of stability of $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$.

Proof. The linearized stability of $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$ is determined by the signs of the τ 's for which the eigenvalue problem

$$\begin{cases} \mathfrak{L}_1 u = \lambda u - b\theta_{[\mathfrak{L}_2, \mu, d]} u + \tau u & \text{in } \Omega, \\ \mathfrak{L}_2 v = \mu v - 2d\theta_{[\mathfrak{L}_2, \mu, d]} v + c\theta_{[\mathfrak{L}_2, \mu, d]} u + \tau v & \text{in } \Omega, \\ \mathfrak{B}_1 u = \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega. \end{cases}$$

which can be equivalently written as

$$\begin{cases} (\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu, d]} - \lambda) u = \tau u & \text{in } \Omega, \\ (\mathfrak{L}_2 + 2d\theta_{[\mathfrak{L}_2, \mu, d]} - \mu) v = c\theta_{[\mathfrak{L}_2, \mu, d]} u + \tau v & \text{in } \Omega, \\ \mathfrak{B}_1 u = \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega. \end{cases} \quad (23)$$

As in the proof of Theorem 4.1, we first search for eigenvalues with $u = 0$. Those are given by the values of τ for which the eigenvalue problem

$$\begin{cases} (\mathfrak{L}_2 + 2d\theta_{[\mathfrak{L}_2, \mu, d]} - \mu) v = \tau v & \text{in } \Omega, \\ \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega, \end{cases} \quad (24)$$

admits a solution $v \neq 0$. Arguing as in the proof of Theorem 4.1, it becomes apparent that

$$\sigma_0 [\mathfrak{L}_2 + 2d\theta_{[\mathfrak{L}_2, \mu, d]} - \mu, \mathfrak{B}_2, \Omega] > \sigma_0 [\mathfrak{L}_2 + d\theta_{[\mathfrak{L}_2, \mu, d]} - \mu, \mathfrak{B}_2, \Omega] = 0.$$

Thus, since the principal eigenvalue is dominant, all eigenvalues of (24) have positive real part. So, these eigenvalues cannot destabilize $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$. Now, we will focus

attention on the eigenvalues τ with $u \neq 0$. Those are given by the eigenvalues of the problem

$$\begin{cases} (\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu, d]} - \lambda) u = \tau u & \text{in } \Omega, \\ \mathfrak{B}_1 u = 0 & \text{on } \partial\Omega. \end{cases} \quad (25)$$

Suppose (21) holds. Then,

$$\sigma_0 [\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu, d]} - \lambda, \mathfrak{B}_1, \Omega] > 0$$

and hence, since the principal eigenvalue is dominant, any other eigenvalue of (25), τ , has a positive real part. Thus, $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$ is linearly stable.

Now, suppose (20). Then,

$$\tau := \sigma_0 [\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu, d]} - \lambda, \mathfrak{B}_1, \Omega] < 0$$

provides us with a negative eigenvalue of (25) and the second equation of (23) can be equivalently expressed as

$$(\mathfrak{L}_2 + 2d\theta_{[\mathfrak{L}_2, \mu, d]} - \mu - \tau) v = c\theta_{[\mathfrak{L}_2, \mu, d]} u.$$

Thus, since

$$\sigma_0[\mathfrak{L}_2 + 2d\theta_{[\mathfrak{L}_2, \mu, d]} - \mu - \tau, \mathfrak{B}_2, \Omega] > \sigma_0[\mathfrak{L}_2 + d\theta_{[\mathfrak{L}_2, \mu, d]} - \mu, \mathfrak{B}_2, \Omega] = 0,$$

we find that

$$v = (\mathfrak{L}_2 + 2d\theta_{[\mathfrak{L}_2, \mu, d]} - \mu - \tau)^{-1} (c\theta_{[\mathfrak{L}_2, \mu, d]} u)$$

and therefore, (23) possesses a negative eigenvalue. Consequently, $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$ is linearly unstable. This ends the proof. \square

Subsequently, we will consider the curves of change of stability of the semitrivial solutions, $\lambda = \Phi(\mu)$ and $\mu = \Psi(\lambda)$, introduced in (22) and (14). As, according to Lemma 2.4, the map $\mu \mapsto \theta_{[\mathfrak{L}_2, \mu, d]}$ is increasing, it follows from Theorem 2.1 that $\Phi(\mu)$ is strictly increasing with respect to μ . Moreover, thanks to Theorem 2.5, it is easily seen that

$$\lim_{\mu \uparrow \infty} \Phi(\mu) = \lim_{\mu \uparrow \infty} \sigma_0 \left[\mathfrak{L}_1 + \mu b \frac{\theta_{[\mathfrak{L}_2, \mu, d]}}{\mu}, \mathfrak{B}_1, \Omega \right] = \infty,$$

because $\frac{b(x)}{d(x)} > 0$ for all $x \in \bar{\Omega}$. Moreover, owing to Theorems 2.3 and 2.1,

$$\lim_{\mu \downarrow \sigma_{0,2}} \Phi(\mu) = \sigma_{0,1}.$$

Therefore, the curve of change of stability of $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$, $\lambda = \Phi(\mu)$, passes through the point $(\sigma_{0,1}, \sigma_{0,2})$, it is increasing with respect to μ and

$$\lim_{\mu \uparrow \infty} \Phi(\mu) = \infty.$$

In particular, for every $\lambda > \sigma_{0,1}$ there exists a unique $\mu > \sigma_{0,2}$ such that $\lambda = \Phi(\mu)$. Similarly,

$$\lim_{\lambda \downarrow \sigma_{0,1}} \Psi(\lambda) = \sigma_{0,2}$$

and hence, the curve $\mu = \Psi(\lambda)$ also passes through $(\sigma_{0,1}, \sigma_{0,2})$. Moreover, since the mappings $\lambda \mapsto \theta_{[\mathfrak{L}_1, \lambda, a]}$ and $\zeta \mapsto \frac{\zeta}{1+m\zeta}$ are increasing, Theorem 2.1 reveals that $\Psi(\lambda)$ is strictly decreasing with respect to λ . Furthermore,

$$\Psi(\lambda) < \sigma_{0,2} \quad \text{for all } \lambda > \sigma_{0,1}.$$

As far as concerns the behavior of $\Psi(\lambda)$ for $\lambda \uparrow \infty$, we will differentiate two rather different situations.

Case 1. Suppose that

$$\text{Int } m^{-1}(0) \neq \emptyset.$$

Then, there exist $x_0 \in \Omega$ and $R > 0$ such that $\bar{B}_R(x_0) \subset \Omega$ and $m \equiv 0$ in $B_R(x_0)$. Thus, by Proposition 3.2 of S. Cano-Casanova and J. López-Gómez [4],

$$\Psi(\lambda) = \sigma_0 \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}}, \mathfrak{B}_2, \Omega \right] < \sigma_0 \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}}, \mathfrak{D}, B_R(x_0) \right].$$

Hence, since $m = 0$ on $B_R(x_0)$,

$$\Psi(\lambda) < \sigma_0 \left[\mathfrak{L}_2 - c\theta_{[\mathfrak{L}_1, \lambda, a]}, \mathfrak{D}, B_R(x_0) \right] \quad \text{for all } \lambda > \sigma_{0,1}.$$

On the other hand, thanks to Theorem 2.5,

$$\lim_{\lambda \uparrow \infty} \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{\lambda} = a^{-1} \quad \text{uniformly in } \bar{B}_R(x_0).$$

Therefore, much like in the classical Lotka–Volterra model ($m \equiv 0$),

$$\lim_{\lambda \uparrow \infty} \Psi(\lambda) = -\infty.$$

Case 2. Suppose that $m(x) > 0$ for all $x \in \bar{\Omega}$. Then, much like in the classical Holling–Tanner models with $m > 0$ constant, we may infer from Theorem 2.5 that

$$\begin{aligned} \lim_{\lambda \uparrow \infty} \Psi(\lambda) &= \lim_{\lambda \uparrow \infty} \sigma_0 \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}}, \mathfrak{B}_2, \Omega \right] \\ &= \lim_{\lambda \uparrow \infty} \sigma_0 \left[\mathfrak{L}_2 - c \frac{\frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{\lambda}}{\frac{1}{\lambda} + m \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{\lambda}}, \mathfrak{B}_2, \Omega \right] = \sigma_0 \left[\mathfrak{L}_2 - \frac{c}{m}, \mathfrak{B}_2, \Omega \right], \end{aligned}$$

in strong contrast with the previous case.

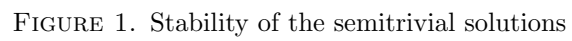
Figure 1 represents the curves $\mu = \Psi(\lambda)$ and $\lambda = \Phi(\mu)$ in Case 1. The curve $\mu = \Psi(\lambda)$ divides the half-plane $\lambda > \sigma_{0,1}$ into two regions. The solution $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$ is linearly asymptotically stable if $\mu < \Psi(\lambda)$, whereas it is linearly unstable if $\mu > \Psi(\lambda)$. Similarly, the curve $\lambda = \Phi(\mu)$ divides the half-plane $\mu > \sigma_{0,2}$ into two regions. The solution $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$ is linearly stable if $\lambda < \Phi(\mu)$, while it is linearly unstable if $\lambda > \Phi(\mu)$. In particular, the region enclosed by these curves,

$$\mu > \Psi(\lambda), \quad \lambda > \Phi(\mu), \quad (26)$$

which is the shadowed green region in Figure 1, is the region where any of the semitrivial positive solutions of (5) is linearly unstable. By the Lyapunov theorems, the semitrivial positive solutions are unstable in this region.

Figure 2 shows the stability of the trivial solution, $(0, 0)$ according to the each of the quadrants of the (λ, μ) plane centered at the point $(\sigma_{0,1}, \sigma_{0,2})$. At the light of the proofs of Theorems 3.1 and 3.2, checking these properties is straightforward. So, the technical details are omitted here.

4. Necessary conditions for the existence of coexistence states. The main result of this section establishes some necessary conditions for the existence of a coexistence state for (5). A coexistence state is a solution (u, v) with $u \gneq 0$ and $v \gneq 0$. These conditions are optimal in a sense to be precised later.



Theorem 4.1. *Suppose that (5) has a coexistence state, (u, v) . Then, $u \gg_1 0$, $v \gg_2 0$, and*

$$\lambda = \sigma_0 \left[\mathfrak{L}_1 + au + b \frac{v}{1+mu}, \mathfrak{B}_1, \Omega \right], \quad (27)$$

$$\mu = \sigma_0 \left[\mathfrak{L}_2 + dv - c \frac{u}{1+mu}, \mathfrak{B}_2, \Omega \right]. \quad (28)$$

Thus,

$$\lambda > \sigma_0 \left[\mathfrak{L}_1 + b \frac{\theta_{[\mathfrak{L}_2, \mu, d]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}}, \mathfrak{B}_1, \Omega \right], \quad \mu > \sigma_0 \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}}, \mathfrak{B}_2, \Omega \right]. \quad (29)$$

Proof. Let (u, v) be a coexistence state of (5). Then,

$$\begin{cases} \left(\mathfrak{L}_1 + au + b \frac{v}{1+mu} \right) u = \lambda u & \text{in } \Omega, \\ \left(\mathfrak{L}_2 + dv - c \frac{u}{1+mu} \right) v = \mu v & \text{in } \Omega, \\ \mathfrak{B}_1 u = \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega. \end{cases}$$

Thus, thanks to the uniqueness of the principal eigenvalue, (27) and (28) hold. Moreover, since u and v are principal eigenfunctions associated to each of these principal eigenvalues, it follows from [35, Ch. 7] that $u \gg_1 0$ and $v \gg_2 0$. Hence, by the first equation of (5),

$$\mathfrak{L}_1 u = \lambda u - au^2 - b \frac{uv}{1+mu} \leq \lambda u - au^2.$$

So, u is a positive strict subsolution of the problem

$$\begin{cases} \mathfrak{L}_1 w = \lambda w - a(x)w^2 & \text{in } \Omega, \\ \mathfrak{B}_1 w = 0 & \text{on } \partial\Omega. \end{cases} \quad (30)$$

To show the existence of large supersolutions of (30) we will use a technical device borrowed from D. Aleja et al. [1]. Since Ω is of class \mathcal{C}^2 , by [35, Lem. 2.1], there exist $\psi \in \mathcal{C}^2(\bar{\Omega})$ and $\gamma > 0$ such that

$$\frac{\partial \psi}{\partial \nu}(x) \geq \gamma > 0 \text{ for all } x \in \Gamma_1. \quad (31)$$

We claim that, for sufficiently large $C > 0$ and $M > 0$, the function

$$\bar{u}(x) := Ce^{M\psi(x)}, \quad x \in \bar{\Omega},$$

is a supersolution of (30). Indeed, for every $M > 0$ and $C > 0$, $\bar{u} > 0$ on Γ_0 . Moreover, for every $x \in \Gamma_1$,

$$\frac{\partial \bar{u}}{\partial \nu_1}(x) = CM \frac{\partial \psi}{\partial \nu_1}(x) e^{M\psi(x)} + C\beta_1(x) e^{M\psi(x)} = Ce^{M\psi(x)} \left(M \frac{\partial \psi}{\partial \nu_1}(x) + \beta_1(x) \right).$$

So, thanks to (31),

$$\frac{\partial \bar{u}}{\partial \nu_1}(x) \geq Ce^{M\psi(x)} (M\gamma + \beta_1(x)) > 0$$

for sufficiently large $M > 0$. Therefore,

$$\mathfrak{B}_1 \bar{u} \geq 0 \quad \text{on } \partial\Omega$$

for every $C > 0$ and sufficiently large $M > 0$. On the other hand, once fixed one of these M 's, it is easily seen that

$$\mathfrak{L}_1 \bar{u} = C\mathfrak{L}_1 e^{M\psi} \geq \lambda C e^{M\psi} - a(x)C^2 e^{2M\psi}$$

if, and only if,

$$e^{-M\psi} \mathfrak{L}_1 e^{M\psi} \geq \lambda - a(x) C e^{M\psi}$$

which holds true for sufficiently large $C > 0$, because $a(x) > 0$ and $e^{M\psi(x)} > 0$ for all $x \in \bar{\Omega}$. Consequently, \bar{u} provides us with a positive strict supersolution of (30) for sufficiently large $C > 0$ and $M > 0$.

Enlarging C , if necessary, we also can get the estimate $u \leq \bar{u}$. Thus, (30) admits a positive solution, w_λ , such that

$$u \leq w_\lambda \leq \bar{u}.$$

By Theorem 2.3, $w_\lambda = \theta_{[\mathfrak{L}_1, \lambda, a]} \gg_1 0$ and $\lambda > \sigma_{0,1}$. So, due to Lemma 2.4,

$$u \ll_1 \theta_{[\mathfrak{L}_1, \lambda, a]} \ll_1 \bar{u} \quad (32)$$

as soon as \bar{u} is a strict supersolution of (30).

Going back to the second equation of (5), we also have that

$$\mathfrak{L}_2 v = \mu v - dv^2 + c \frac{uv}{1+mu} \geq \mu v - dv^2$$

and hence, v is a positive strict supersolution of

$$\begin{cases} \mathfrak{L}_2 w = \mu w - d(x)w^2 & \text{in } \Omega, \\ \mathfrak{B}_2 w = 0 & \text{on } \partial\Omega. \end{cases} \quad (33)$$

Suppose $\mu \leq \sigma_{0,2}$. Then, $\theta_{[\mathfrak{L}_2, \mu, d]} = 0$ and hence the next estimate holds

$$v \gg_1 \theta_{[\mathfrak{L}_2, \mu, d]}. \quad (34)$$

Now, suppose that $\mu > \sigma_{0,2}$. Then, $\theta_{[\mathfrak{L}_2, \mu, d]} \gg_2 0$ is the unique positive solution of (33) and (34) holds from Lemma 2.4. Thus, going back to the first equation of (5) and using (32) and (34), it becomes apparent that

$$\mathfrak{L}_1 u = \lambda u - au^2 - b \frac{uv}{1+mu} \leq \lambda u - au^2 - b \frac{\theta_{[\mathfrak{L}_2, \mu, d]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}} u.$$

Thus, u is a positive strict subsolution of the problem

$$\begin{cases} \left(\mathfrak{L}_1 + b \frac{\theta_{[\mathfrak{L}_2, \mu, d]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}} \right) w = \lambda w - aw^2 & \text{in } \Omega, \\ \mathfrak{B}_1 w = 0 & \text{on } \partial\Omega. \end{cases} \quad (35)$$

Arguing as above, it is easily seen that $\bar{u} := C e^{M\psi}$ also provides us with a supersolution of (35) for sufficiently large $M > 0$ and $C > 0$. Therefore, the problem (35) admits a positive solution in the interval $[u, \bar{u}]$. Consequently, by Theorem 2.3,

$$\lambda > \sigma_0 \left[\mathfrak{L}_1 + b \frac{\theta_{[\mathfrak{L}_2, \mu, d]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}} , \mathfrak{B}_1, \Omega \right],$$

which provides us with the first estimate of (29). Moreover, by Lemma 2.4,

$$0 \ll_1 u \ll_1 \theta_{[\mathfrak{L}_1 + b \frac{\theta_{[\mathfrak{L}_2, \mu, d]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}} , \lambda, a]} \ll_1 C e^{M\psi}. \quad (36)$$

Finally, since the mapping $u \mapsto \frac{u}{1+mu}$ is increasing, we can infer from (32) that

$$\mathfrak{L}_2 v = \mu v - dv^2 + c \frac{uv}{1+mu} < \mu v - dv^2 + c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}} v.$$

Thus, v provides us with a positive strict subsolution of

$$\begin{cases} \left(\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} \right) w = \mu w - dw^2 & \text{in } \Omega, \\ \mathfrak{B}_2 w = 0 & \text{on } \partial\Omega. \end{cases} \quad (37)$$

Since (37) admits strict supersolutions of the form $Ce^{M\psi}$ for sufficiently large $M > 0$ and $C > 0$, it becomes apparent that

$$\mu > \sigma_0 \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} , \mathfrak{B}_2, \Omega \right].$$

Moreover, according to Lemma 2.4,

$$v \ll_2 \theta \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} , \mu, d \right]. \quad (38)$$

This ends the proof. \square

5. Sufficient conditions for the existence of coexistence states. Our main existence theorem can be stated as follows.

Theorem 5.1. *Suppose (26) holds, i.e.,*

$$\begin{aligned} \lambda &> \Phi(\mu) \equiv \sigma_0[\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu, d]}, \mathfrak{B}_1, \Omega], \\ \mu &> \Psi(\lambda) \equiv \sigma_0 \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} , \mathfrak{B}_2, \Omega \right]. \end{aligned} \quad (39)$$

Then, (5) has, at least, one coexistence state. Moreover, when $\mu \leq \sigma_{0,2}$, by definition, $\theta_{[\mathfrak{L}_2, \mu, d]} = 0$ and hence, (39) becomes

$$\lambda > \sigma_{0,1}, \quad \mu > \sigma_0 \left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} , \mathfrak{B}_2, \Omega \right]. \quad (40)$$

In such case, (40) is not only sufficient but also necessary for the existence of a coexistence state.

In other words, according to Theorems 3.1 and 3.2, (5) admits a coexistence state if any of the existing semitrivial positive solutions is linearly unstable.

Proof. By fixing $\lambda > 0$ and regarding μ as the main bifurcation parameter the proof is a direct application of [33, Th. 7.2.2]. Indeed, since $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$ is a nondegenerate solution of

$$\begin{cases} \mathfrak{L}_1 u = \lambda u - a(x)u^2 & \text{in } \Omega, \\ \mathfrak{B}_1 u = 0 & \text{on } \partial\Omega, \end{cases} \quad (41)$$

by [33, Th. 7.2.2] there exists a continuum of coexistence states, \mathfrak{C} , in $\mathbb{R} \times U_1 \times U_2$ emanating from

$$(\mu, u, v) = (\Phi(\lambda), \theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$$

such that either

- (i) \mathfrak{C} is unbounded in $\mathbb{R} \times \mathcal{C}(\bar{\Omega}) \times \mathcal{C}(\bar{\Omega})$; or
- (ii) there exists a positive solution, $(\mu^*, \theta_{[\mathfrak{L}_2, \mu^*, d]})$ of

$$\begin{cases} \mathfrak{L}_2 v = \mu v - d(x)v^2 & \text{in } \Omega, \\ \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega, \end{cases} \quad (42)$$

such that $(\mu^*, 0, \theta_{[\mathfrak{L}_2, \mu^*, d]}) \in \bar{\mathfrak{C}}$.

Obviously, since (41) admits at most a unique positive solution, Alternative 3 of [33, Th. 7.2.2] cannot happen. Similarly, as we are assuming that $\lambda > \sigma_{0,1}$, Alternative 4 of [33, Th. 7.2.2] cannot occur neither. Subsequently, \mathcal{P}_μ stands for the μ -projection operator, $\mathcal{P}_\mu(\mu, u, v) = \mu$. Thanks to the estimates (36) and (38), it becomes apparent that $\mathcal{P}_\mu(\mathfrak{C})$ should be unbounded if Alternative (i) holds. On the other hand, by Theorem 4.1, (29) holds if (5) admits a coexistence state. Thus, $\mathcal{P}_\mu(\mathfrak{C})$ is bounded. Therefore, Alternative (ii) holds. To make sure that indeed $\mathcal{P}_\mu(\mathfrak{C})$ is bounded we can argue as follows. The second estimate of (29) shows that μ must be bounded below. The first one provides us with an upper bound for μ , because

$$\lim_{\mu \uparrow \infty} \sigma_0[\mathfrak{L}_1 + b \frac{\theta_{[\mathfrak{L}_2, \mu, d]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}}, \mathfrak{B}_1, \Omega] = \infty. \quad (43)$$

Note that (43) relies on the fact that, thanks to Theorem 2.5,

$$\lim_{\mu \uparrow \infty} \theta_{[\mathfrak{L}_2, \mu, d], \Omega} = \infty \quad (44)$$

uniformly on compact subsets of Ω .

The fact that $(\mu^*, 0, \theta_{[\mathfrak{L}_2, \mu^*, d]}) \in \bar{\mathfrak{C}}$ entails

$$\lambda = \sigma_0[\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu^*, d]}, \mathfrak{B}_1, \Omega].$$

Therefore, the continuum of coexistence states \mathfrak{C} bifurcates from $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$ at

$$\mu = \Phi(\lambda) \equiv \sigma_0\left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}}, \mathfrak{B}_2, \Omega\right] < \sigma_{0,2}$$

and from $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$ at $\mu^* > \sigma_{0,2}$. Figure 3 represents an admissible \mathfrak{C} .

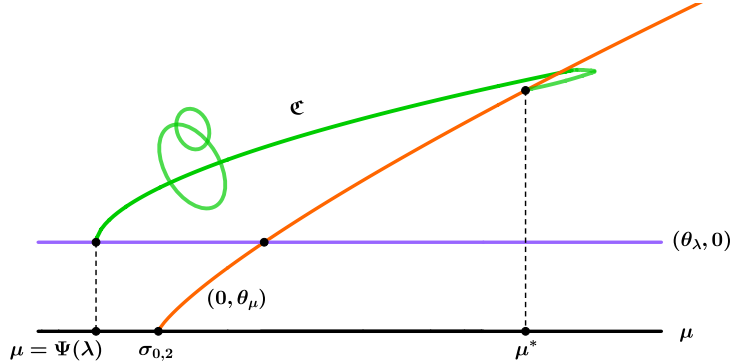


FIGURE 3. An admissible component \mathfrak{C}

Although we have not ascertained the bifurcation directions from the semitrivial states yet, it is apparent that (5) possesses a coexistence state for every $\mu \in (\Phi(\lambda), \mu^*)$, because, since \mathcal{P}_μ is continuous and \mathfrak{C} is connected, the projection $\mathcal{P}_\mu(\mathfrak{C})$ is also connected. From this fact, it is easily inferred that (5) has a coexistence state under condition (39).

When $\mu \leq \sigma_{0,2}$, by definition, $\theta_{[\mathfrak{L}_2, \mu, d]} = 0$. Thus, (39) reduces to (40). Combining Theorems 4.1 and 5.1 it is easily seen that (40) is not only sufficient but also necessary for the existence of a coexistence state. This ends the proof. \square

In the example of Figure 3 there exists $\varepsilon > 0$ such that (5) admits a coexistence state for all $\mu \in [\mu^*, \mu^* + \varepsilon]$, in complete agreement with Theorem 4.1.

In Figure 4 we have represented the curve of change of stability of the semitrivial positive solutions $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$, $\lambda = \Phi(\mu)$, together with the curve

$$\lambda = \varphi(\mu) \equiv \sigma_0 \left[\mathfrak{L}_1 + b \frac{\theta_{[\mathfrak{L}_2, \mu, d]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} , \mathfrak{B}_1, \Omega \right] < \sigma_0 [\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu, d]}, \mathfrak{B}_1, \Omega] \equiv \Phi(\mu),$$

and the curve of change of stability of $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$, $\mu = \Psi(\lambda)$, in the special case when $m(x) > 0$ for all $x \in \bar{\Omega}$. In such case, we already know that

$$\lim_{\lambda \uparrow \infty} \Psi(\lambda) = \sigma_0 \left[\mathfrak{L}_2 - \frac{c}{m}, \mathfrak{B}_2, \Omega \right].$$

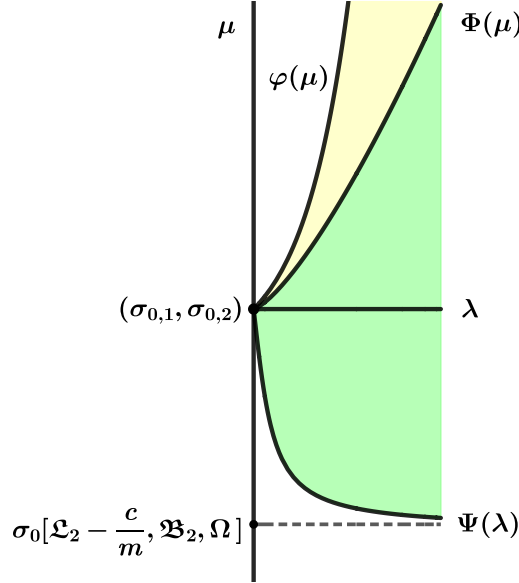
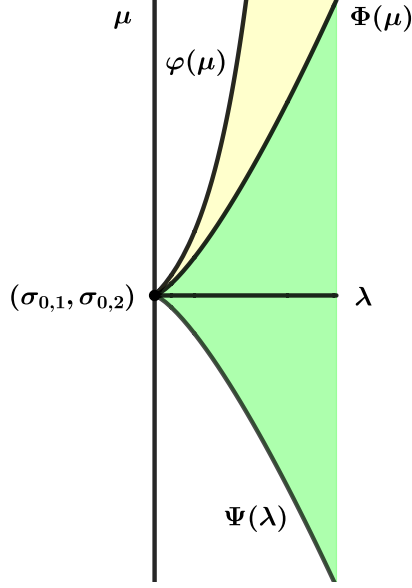


FIGURE 4. By Theorem 5.1, (5) admits a coexistence state for each (λ, μ) in the green region, while it cannot admit a coexistence state in the white one. Within the yellow region, (5) might admit, or not, a coexistence state as it will become apparent later.

Figure 5 represents the same curves in the most general case when $\text{Int } m^{-1}(0) \neq \emptyset$, which should be more realistic from a biological point of view. Note that, for every $\mu \in \mathbb{R}$, there exists $\lambda > \sigma_{0,1}$ such that (5) possesses a coexistence region, while in the case described in Figure 4, the problem (5) cannot admit a coexistence state if

$$\mu \leq \sigma_0 \left[\mathfrak{L}_2 - \frac{c}{m}, \mathfrak{B}_2, \Omega \right].$$

FIGURE 5. The coexistence wedges of Figure 4 when $\text{Int } m^{-1}(0) \neq \emptyset$.

6. Bifurcation to coexistence states from the semitrivial solutions. Throughout this section the solutions of (5) are viewed as zeroes of the operator

$$\mathfrak{F} : (\sigma_{0,1}, \infty) \times \mathbb{R} \times \mathcal{C}(\bar{\Omega}) \times \mathcal{C}(\bar{\Omega}) \rightarrow U_1 \times U_2,$$

defined by

$$\mathfrak{F}(\lambda, \mu, u, v) := \begin{pmatrix} u - (\mathfrak{L}_1 + \omega)^{-1} \left[(\lambda + \omega)u - au^2 - b\frac{uv}{1+mu} \right] \\ v - (\mathfrak{L}_2 + \omega)^{-1} \left[(\mu + \omega)v - dv^2 + c\frac{uv}{1+mu} \right] \end{pmatrix} \quad (45)$$

where ω is any real number satisfying

$$\omega > \max\{-\sigma_{0,1}, -\sigma_{0,2}\},$$

and, for every $k = 1, 2$, $(\mathfrak{L}_k + \omega)^{-1}$ stands for the resolvent operator of $(\mathfrak{L}_k + \omega, \mathfrak{B}_k, \Omega)$. The operator \mathfrak{F} is a compact perturbation of the identity map and hence it is Fredholm of index zero. Moreover, it is real analytic in an open region containing the positive cone $u \geq 0$.

Our first result establishes the structure of the set of coexistence states in a neighborhood of the bifurcation point

$$(\mu, u, v) = (\Psi(\lambda), \theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$$

for every $\lambda > \sigma_{0,1}$. As, due to Theorem 4.1, (5) cannot admit a coexistence state if $\mu < \Psi(\lambda)$, it is apparent that the bifurcation to coexistence states must be supercritical.

Theorem 6.1. *For every $\lambda > \sigma_{0,1}$, there exist $\varepsilon > 0$, and an analytic map*

$$(\mu, u, v) : (-\varepsilon, \varepsilon) \rightarrow \mathbb{R} \times U_1 \times U_2$$

such that

- (a) $(\mu(0), u(0), v(0)) = (\Psi(\lambda), \theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$.
- (b) $\mathfrak{F}(\lambda, \mu(s), u(s), v(s)) = 0$ for all $s \in (-\varepsilon, \varepsilon)$.
- (c) $u(s) > 0$ for all $s \in (-\varepsilon, \varepsilon)$, $v(s) > 0$ for all $s \in (0, \varepsilon)$ and $v(s) < 0$ for all $s \in (-\varepsilon, 0)$. Thus, for every $s \in (0, \varepsilon)$, $(u(s), v(s))$ is a coexistence state of (5) for $(\lambda, \mu) = (\lambda, \mu(s))$.
- (d) The set of solutions of (5) in a neighborhood of $(\Psi(\lambda), \theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$ consists of the curves $(\lambda, \mu, \theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$, $\mu \sim \Psi(\lambda)$, and $(\lambda, \mu(s), u(s), v(s))$, $s \in (-\varepsilon, \varepsilon)$.

Moreover, $\mu'(0) > 0$. Therefore, the bifurcation to coexistence states from $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$ at $\mu = \Psi(\lambda)$ is supercritical, in complete agreement with Theorem 4.1.

Proof. It is a direct consequence of the Theorem of M. G. Crandall and P. H. Rabinowitz [6] applied to the function \mathfrak{F} at the semitrivial branch $(\mu, \theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$. Indeed, by definition,

$$\mathfrak{F}(\lambda, \mu, \theta_{[\mathfrak{L}_1, \lambda, a]}, 0) = 0 \quad \text{for all } \mu \in \mathbb{R}.$$

Moreover, the Fréchet differential

$$\mathfrak{L}(\mu) := D_{(u,v)} \mathfrak{F}(\lambda, \mu, \theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$$

is the integral operator defined by

$$\mathfrak{L}(\mu)(u, v) = \begin{pmatrix} u - (\mathfrak{L}_1 + \omega)^{-1} \left[(\lambda + \omega)u - 2a\theta_{[\mathfrak{L}_1, \lambda, a]}u - b\frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}}v \right] \\ v - (\mathfrak{L}_2 + \omega)^{-1} \left[(\mu + \omega)v + c\frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}}v \right] \end{pmatrix}.$$

Thus,

$$N[\mathfrak{L}(\Psi(\lambda))] = \text{span}[\varphi_0], \quad \varphi_0 = \begin{pmatrix} u_1 \\ v_1 \end{pmatrix},$$

where

$$\begin{cases} (\mathfrak{L}_1 + 2a\theta_{[\mathfrak{L}_1, \lambda, a]} - \lambda)u_1 = -b\frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}}v_1, \\ \left(\mathfrak{L}_2 - c\frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}} \right)v_1 = \Psi(\lambda)v_1. \end{cases} \quad (46)$$

Hence, $v_1 \gg_2 0$ can be chosen as the principal eigenfunction associated to $\Psi(\lambda)$ normalized so that

$$\int_{\Omega} v_1^2(x) dx = 1.$$

On the other hand, by Theorem 2.1,

$$\sigma_0[\mathfrak{L}_1 + 2a\theta_{[\mathfrak{L}_1, \lambda, a]} - \lambda, \mathfrak{B}_1, \Omega] > \sigma_0[\mathfrak{L}_1 + a\theta_{[\mathfrak{L}_1, \lambda, a]}, \mathfrak{B}_1, \Omega] - \lambda = 0.$$

Thus, thanks to Theorem 2.2, the first equation of (46) yields

$$u_1 = -(\mathfrak{L}_1 + 2a\theta_{[\mathfrak{L}_1, \lambda, a]} - \lambda)^{-1} \left(d\frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1+m\theta_{[\mathfrak{L}_1, \lambda, a]}}\varphi_0 \right) \ll_1 0. \quad (47)$$

In order to apply the main theorem of [6] one should make sure that the next transversality condition holds

$$\mathfrak{L}'(\Psi(\lambda))\varphi_0 \notin R[\mathfrak{L}(\Psi(\lambda))], \quad (48)$$

where $\mathfrak{L}'(\mu)$ stands for the derivative of $\mathfrak{L}(\mu)$ with respect to μ . Since

$$\mathfrak{L}'(\Psi(\lambda))(u, v) = \begin{pmatrix} 0 \\ -(\mathfrak{L}_2 + \omega)^{-1}v \end{pmatrix},$$

(48) can be expressed as

$$\begin{pmatrix} 0 \\ -(\mathfrak{L}_2 + \omega)^{-1}v_1 \end{pmatrix} \notin R[\mathfrak{L}(\Psi(\lambda))].$$

On the contrary, assume that

$$\mathfrak{L}(\Psi(\lambda))(u, v) = \begin{pmatrix} 0 \\ -(\mathfrak{L}_2 + \omega)^{-1}v_1 \end{pmatrix}$$

for some (u, v) . Then,

$$v - (\mathfrak{L}_2 + \omega)^{-1} \left[(\Psi(\lambda) + \omega)v + c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}}v \right] = -(\mathfrak{L}_2 + \omega)^{-1}v_1$$

and hence, $v \in U_2$ satisfies

$$\left[\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} - \Psi(\lambda) \right] v = -v_1,$$

which is impossible, because $-v_1 \ll_2 0$ cannot be orthogonal in $L^2(\Omega)$ to the principal eigenfunction, $v_1^* \gg_2 0$, of the differential operator

$$\mathfrak{L}_2^* - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} - \Psi(\lambda),$$

where \mathfrak{L}_2^* stands for the adjoint operator of $(\mathfrak{L}_2, \mathfrak{B}_2, \Omega)$. Therefore, the main theorem of [6] can be applied to get the first assertions of the theorem. It remains to prove that $\mu'(0) > 0$. Setting

$$(\mu(s), u(s), v(s)) = \left(\Psi(\lambda) + \sum_{j=1}^{\infty} s^j \mu_j, \theta_{[\mathfrak{L}_1, \lambda, a]} + \sum_{j=1}^{\infty} s^j u_j, \sum_{j=1}^{\infty} s^j v_j \right), \quad s \sim 0,$$

substituting in (5) and taking into account the definitions of $\Psi(\lambda)$, u_1 and v_1 , it becomes apparent that

$$\left(\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} - \Psi(\lambda) \right) v_2 = \left(\mu_1 + \frac{cu_1}{(1 + m\theta_{[\mathfrak{L}_1, \lambda, a]})^2} - dv_1 \right) v_1. \quad (49)$$

Therefore, the Fredholm's alternative yields

$$\mu_1 = \int_{\Omega} dv_1^2 v_1^* - \int_{\Omega} \frac{cu_1}{(1 + m\theta_{[\mathfrak{L}_1, \lambda, a]})^2} v_1 v_1^*, \quad (50)$$

provided that v_1^* is normalized so that

$$\int_{\Omega} v_1(x) v_1^*(x) dx = 1.$$

By (47), $u_1 \ll_1 0$ in Ω . Thus, by (50), $\mu_1 > 0$ for all $\lambda > \sigma_{0,1}$. This ends the proof. \square

The next result provides us with the local structure of the set of coexistence states bifurcating from

$$(\lambda, u, v) = (\Phi(\mu), 0, \theta_{[\mathfrak{L}_2, \mu, d]})$$

for every $\mu > \sigma_{0,2}$.

Theorem 6.2. *For every $\mu > \sigma_{0,2}$, there exist $\varepsilon > 0$, and an analytic map*

$$(\lambda, u, v) : (-\varepsilon, \varepsilon) \rightarrow \mathbb{R} \times U_1 \times U_2$$

such that

- (a) $(\lambda(0), u(0), v(0)) = (\Phi(\mu), 0, \theta_{[\mathfrak{L}_2, \mu, d]})$.
- (b) $\mathfrak{F}(\lambda(s), \mu, u(s), v(s)) = 0$ for all $s \in (-\varepsilon, \varepsilon)$.
- (c) $v(s) > 0$ for all $s \in (-\varepsilon, \varepsilon)$, $u(s) > 0$ for all $s \in (0, \varepsilon)$ and $u(s) < 0$ for all $s \in (-\varepsilon, 0)$. Thus, for every $s \in (0, \varepsilon)$, $(u(s), v(s))$ is a coexistence state of (5) for $(\lambda, \mu) = (\lambda(s), \mu)$.
- (d) The set of solutions of (5) in a neighborhood of $(\lambda, \Phi(\mu), 0, \theta_{[\mathfrak{L}_2, \mu, d]})$ consists of the curves $(\lambda, \mu, 0, \theta_{[\mathfrak{L}_2, \mu, d]})$, $\lambda \sim \Phi(\mu)$, and $(\lambda(s), \mu, u(s), v(s))$, $s \in (-\varepsilon, \varepsilon)$.

Moreover,

$$\lambda'(0) = \int_{\Omega} (a - b m \theta_{[\mathfrak{L}_2, \mu, d]}) u_1^2 u_1^* + \int_{\Omega} b (\mathfrak{L}_2 + 2d \theta_{[\mathfrak{L}_2, \mu, d]} - \mu)^{-1} (c \theta_{[\mathfrak{L}_2, \mu, d]} u_1) u_1 u_1^*, \quad (51)$$

where $u_1 \gg_1 0$ is the principal eigenfunction of $\Phi(\mu)$, normalized so that $\int_{\Omega} u_1^2 = 1$, and $u_1^* \gg_1 0$ stands for the principal eigenfunction associated to $\mathfrak{L}_1^* + b \theta_{[\mathfrak{L}_2, \mu, d]} - \Phi(\mu)$, normalized so that $\int_{\Omega} u_1 u_1^* = 1$.

Proof. As the previous theorem, this result also is a direct consequence of the main theorem of [6] applied to the function \mathfrak{F} at the semitrivial branch $(\lambda, 0, \theta_{[\mathfrak{L}_2, \mu, d]})$. Indeed, by definition,

$$\mathfrak{F}(\lambda, \mu, 0, \theta_{[\mathfrak{L}_2, \mu, d]}) = 0 \quad \text{for all } \mu \in \mathbb{R}.$$

Moreover, the Fréchet differential

$$\mathfrak{M}(\lambda) := D_{(u,v)} \mathfrak{F}(\lambda, \mu, 0, \theta_{[\mathfrak{L}_2, \mu, d]})$$

is given by

$$\mathfrak{M}(\lambda)(u, v) = \begin{pmatrix} u - (\mathfrak{L}_1 + \omega)^{-1} [(\lambda + \omega)u - b \theta_{[\mathfrak{L}_2, \mu, d]} u] \\ v - (\mathfrak{L}_2 + \omega)^{-1} [(\mu + \omega)v - 2d \theta_{[\mathfrak{L}_2, \mu, d]} v + c \theta_{[\mathfrak{L}_2, \mu, d]} u] \end{pmatrix}.$$

Thus,

$$N[\mathfrak{M}(\Phi(\mu))] = \text{span}[\varphi_0], \quad \varphi_0 = \begin{pmatrix} u_1 \\ v_1 \end{pmatrix},$$

where

$$\begin{cases} (\mathfrak{L}_1 + b \theta_{[\mathfrak{L}_2, \mu, d]}) u_1 = \Phi(\mu) u_1, \\ (\mathfrak{L}_2 + 2d \theta_{[\mathfrak{L}_2, \mu, d]} - \mu) v_1 = c \theta_{[\mathfrak{L}_2, \mu, d]} u_1. \end{cases} \quad (52)$$

Hence, $u_1 \gg_1 0$ can be chosen as the principal eigenfunction associated to $\Phi(\mu)$ normalized so that

$$\int_{\Omega} u_1^2(x) dx = 1.$$

By Theorem 2.1,

$$\sigma_0 [\mathfrak{L}_2 + 2d \theta_{[\mathfrak{L}_2, \mu, d]} - \mu, \mathfrak{B}_2, \Omega] > \sigma_0 [\mathfrak{L}_2 + d \theta_{[\mathfrak{L}_2, \mu, d]}, \mathfrak{B}_2, \Omega] - \mu = 0.$$

So, due to Theorem 2.2, we find from the second equation of (52) that

$$v_1 = (\mathfrak{L}_2 + 2d\theta_{[\mathfrak{L}_2, \mu, d]} - \mu)^{-1} (c\theta_{[\mathfrak{L}_2, \mu, d]}u_1) \gg_2 0. \quad (53)$$

To apply the main theorem of [6] one should make sure that the next condition holds

$$\mathfrak{M}'(\Phi(\mu))\varphi_0 \notin R[\mathfrak{M}(\Phi(\mu))], \quad (54)$$

where $\mathfrak{M}'(\lambda)$ stands for the derivative of $\mathfrak{M}(\lambda)$ with respect to λ . Since

$$\mathfrak{M}'(\Phi(\mu))(u, v) = \begin{pmatrix} -(\mathfrak{L}_1 + \omega)^{-1}u \\ 0 \end{pmatrix},$$

(54) can be written as

$$\begin{pmatrix} -(\mathfrak{L}_1 + \omega)^{-1}u_1 \\ 0 \end{pmatrix} \notin R[\mathfrak{M}(\Phi(\mu))].$$

On the contrary, assume that there exists (u, v) such that

$$\mathfrak{M}(\Phi(\mu))(u, v) = \begin{pmatrix} -(\mathfrak{L}_1 + \omega)^{-1}u_1 \\ 0 \end{pmatrix}.$$

Then,

$$u - (\mathfrak{L}_1 + \omega)^{-1}[(\Phi(\mu) + \omega)u - b\theta_{[\mathfrak{L}_2, \mu, d]}u] = -(\mathfrak{L}_1 + \omega)^{-1}u_1$$

and hence, $u \in U_1$ satisfies

$$[\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu, d]} - \Phi(\mu)]u = -u_1,$$

which is impossible, because $-u_1 \ll_1 0$ cannot be orthogonal in $L^2(\Omega)$ to the principal eigenfunction, $u_1^* \gg_1 0$, of the differential operator

$$\mathfrak{L}_1^* + b\theta_{[\mathfrak{L}_2, \mu, d]} - \Phi(\mu),$$

where \mathfrak{L}_1^* stands for the adjoint operator of $(\mathfrak{L}_1, \mathfrak{B}_1, \Omega)$. Therefore, thanks to the main theorem of [6], the first assertions of the theorem follow readily. It remains to find out $\lambda'(0)$. Setting

$$(\lambda(s), u(s), v(s)) = \left(\Phi(\mu) + \sum_{j=1}^{\infty} s^j \lambda_j, \sum_{j=1}^{\infty} s^j u_j, \theta_{[\mathfrak{L}_2, \mu, d]} + \sum_{j=1}^{\infty} s^j v_j \right), \quad s \sim 0,$$

substituting in (5) and taking into account the definitions of $\Phi(\mu)$, u_1 and v_1 , it is easily seen that

$$(\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2, \mu, d]} - \Phi(\mu))v_2 = (\lambda_1 + bm\theta_{[\mathfrak{L}_2, \mu, d]}u_1 - au_1 - bv_1)u_1.$$

Consequently, choosing u_1^* such that $\int_{\Omega} u_1 u_1^* = 1$, combining the Fredholm's alternative with (53), the identity (51) holds. This ends the proof. \square

As a byproduct of (51), the next result holds.

Theorem 6.3. *Let $\mathfrak{m} \in \mathcal{C}(\bar{\Omega})$ be such that $\mathfrak{m} \gtrsim 0$ and consider $m = M\mathfrak{m}$, where $M > 0$ is a positive constant. Then, for every $\mu > \sigma_{0,2}$, there exist $M_1, M_2 > 0$ such that $M_1 < M_2$ and*

- (a) $\lambda'(0) > 0$ if $M < M_1$.
- (b) $\lambda'(0) < 0$ if $M > M_2$.

Moreover, when $\lambda'(0) < 0$, there exists $\varepsilon > 0$ such that, for every $\lambda \in (\Phi(\mu) - \varepsilon, \Phi(\mu))$, the problem (5) possesses, at least, two coexistence states.

Proof. The first assertion of the theorem is a direct consequence of (51), for as there exist $x_0 \in \Omega$ and $\eta > 0$ such that $x \in \Omega$ and $\mathfrak{m}(x) > 0$ if $|x - x_0| \leq \eta$.

The second assertion of the theorem can be inferred with the next argument. Suppose $\lambda'(0) < 0$. Then, the bifurcation to coexistence states from the curve $(\lambda, u, v) = (\lambda, 0, \theta_{[\mathfrak{L}_2, \mu, d]})$ at $\lambda = \Phi(\mu)$ is subcritical. Moreover, by Theorem 3.2, $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$ is linearly unstable if $\lambda < \Phi(\mu)$. Thus, thanks to the exchange stability principle of M. G. Crandall and P. H. Rabinowitz [7], the coexistence state $(\lambda(s), \mu, u(s), v(s))$ must be linearly unstable with one-dimensional unstable manifold for sufficiently small $s > 0$. Thus, its fixed point index, as discussed in [30], equals -1 . Therefore, adapting the technical devices of [30] it readily follows the existence of a further coexistence state for sufficiently close $\lambda < \Phi(\mu)$, because the total index of the underlying fixed point operator equals 1, and, whenever $\lambda < \Phi(\mu)$, the local fixed point indices of $(0, 0)$ and $(\theta_{[\mathfrak{L}_1, \lambda, a]}, 0)$ equal 0, while the local index of $(0, \theta_{[\mathfrak{L}_2, \mu, d]})$ equals 1. The technical details of these calculations are omitted here. \square

As suggested by the numerical experiments of A. Casal et al. [5] (see Figure 3 and the subsequent discussion of [5]), even in the simplest prototypes of model (5), the fact that $\lambda'(0) > 0$ in Theorem 6.2 does not necessarily guarantee the uniqueness of the coexistence state. This crucial feature was later exploited by Y. Du and Y. Lou [11], [12], where, in addition, a rigorous proof of the Hopf bifurcation documented in [5] was given.

7. Uniqueness of the coexistence state in the 1-d model. The main result of this section is a substantial improvement of the classical uniqueness 1-d theorem of J. López-Gómez and R. M. Pardo [40], later sharpened by A. Casal et al. [5], E. N. Dancer et al. [8], and J. López-Gómez and R. M. Pardo [41], and revisited in [42] in a rather different context. It can be stated as follows.

Theorem 7.1. *Suppose that $\Omega = (p, q)$ for some real numbers $p < q$, that $\lambda > \sigma_{0,1}$, $\lambda > \Phi(\mu)$, $\mu > \Psi(\lambda)$, and that (37) admits a positive supersolution, \bar{v} , such that*

$$\bar{v} \leq \frac{a}{bm}. \quad (55)$$

Then, (5) possesses a unique coexistence state.

Proof. The existence of a coexistence state is guaranteed by Theorem 5.1. Let (u, v) , (\tilde{u}, \tilde{v}) be two arbitrary coexistence states of (5). Then,

$$\begin{cases} [\mathfrak{L}_1 - \lambda + a(u + \tilde{u})](u - \tilde{u}) + b \left(\frac{uv}{1 + mu} - \frac{\tilde{u}\tilde{v}}{1 + m\tilde{u}} \right) = 0, \\ [\mathfrak{L}_2 - \mu + d(v + \tilde{v})](v - \tilde{v}) - c \left(\frac{uv}{1 + mu} - \frac{\tilde{u}\tilde{v}}{1 + m\tilde{u}} \right) = 0. \end{cases} \quad (56)$$

Moreover,

$$\begin{aligned} \frac{uv}{1 + mu} - \frac{\tilde{u}\tilde{v}}{1 + m\tilde{u}} &= \frac{\tilde{v}}{(1 + mu)(1 + m\tilde{u})}(u - \tilde{u}) + \frac{u(1 + m\tilde{u})}{(1 + mu)(1 + m\tilde{u})}(v - \tilde{v}) \\ &= \frac{\tilde{v}}{(1 + mu)(1 + m\tilde{u})}(u - \tilde{u}) + \frac{u}{1 + mu}(v - \tilde{v}). \end{aligned}$$

Thus, setting

$$\begin{aligned}\tilde{\mathfrak{L}}_1 &:= \mathfrak{L}_1 - \lambda + a(u + \tilde{u}) + b \frac{\tilde{v}}{(1 + mu)(1 + m\tilde{u})}, \\ \tilde{\mathfrak{L}}_2 &:= \mathfrak{L}_2 - \mu + d(v + \tilde{v}) - c \frac{u}{1 + mu},\end{aligned}$$

and

$$\varphi_1 := u - \tilde{u}, \quad \varphi_2 := v - \tilde{v},$$

it is apparent that (56) can be expressed as

$$\begin{cases} \tilde{\mathfrak{L}}_1 \varphi_1 = -b \frac{u}{1 + mu} \varphi_2 & \text{in } (p, q), \\ \tilde{\mathfrak{L}}_2 \varphi_2 = c \frac{\tilde{v}}{(1 + mu)(1 + m\tilde{u})} \varphi_1 & \text{in } (p, q), \\ \mathfrak{B}_1 u = \mathfrak{B}_2 v = 0 & \text{on } \{p, q\}. \end{cases} \quad (57)$$

On the other hand, according to the proof of Theorem 4.1, we already know that $\tilde{v} \gg_2 0$ is a positive strict subsolution of

$$\begin{cases} \left(\mathfrak{L}_2 - c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} \right) w = \mu w - dw^2 & \text{in } \Omega, \\ \mathfrak{B}_2 w = 0 & \text{on } \partial\Omega. \end{cases} \quad (58)$$

Moreover, we are assuming that (58) admits a positive strict supersolution, \bar{v} , satisfying (55). Consequently, by Lemma 2.4, it becomes apparent that

$$\tilde{v} \lesssim w \lesssim \bar{v} \leq \frac{a}{bm},$$

where w stands for the unique positive solution of (58), which exists because $\mu > \Psi(\lambda)$. As this estimate implies

$$a \gtrsim bm\tilde{v} \geq \frac{bm\tilde{v}}{(1 + mu)(1 + m\tilde{u})} = \frac{1}{u} \frac{b\tilde{v}(1 + mu) - b\tilde{v}}{(1 + mu)(1 + m\tilde{u})}$$

one has that

$$au + \frac{b\tilde{v} - b\tilde{v}(1 + mu)}{(1 + mu)(1 + m\tilde{u})} \gtrsim 0$$

or, equivalently,

$$au + \frac{b\tilde{v}}{(1 + mu)(1 + m\tilde{u})} \gtrsim \frac{b\tilde{v}}{1 + m\tilde{u}},$$

which implies

$$\sigma_0[\tilde{\mathfrak{L}}_1, \mathfrak{B}_1, (p, q)] > \sigma_0\left[\mathfrak{L}_1 - \lambda + a\tilde{u} + b \frac{\tilde{v}}{1 + m\tilde{u}}, \mathfrak{B}_1, (p, q)\right] = 0.$$

Similarly, by Theorem 2.1,

$$\sigma_0[\tilde{\mathfrak{L}}_2, \mathfrak{B}_2, (p, q)] > \sigma_0\left[\mathfrak{L}_2 - \mu + dv - c \frac{u}{1 + mu}, \mathfrak{B}_2, (p, q)\right] = 0.$$

Thus, owing to the next lemma, we can infer that $(\varphi_1, \varphi_2) = (0, 0)$ is the unique solution of (57). Therefore, $(u, v) = (\tilde{u}, \tilde{v})$. The proof is complete. \square

Lemma 7.2. *Suppose that $\Omega = (p, q)$ for some real numbers $p < q$ and that $\alpha, \beta \in \mathcal{C}(\bar{\Omega})$ satisfy $\alpha(x) > 0$ and $\beta(x) > 0$ for all $x \in (p, q)$. Then, $(u, v) = (0, 0)$ is the unique solution of*

$$\begin{cases} \tilde{\mathcal{L}}_1 u = -\alpha v & \text{in } (p, q), \\ \tilde{\mathcal{L}}_2 v = \beta u & \text{in } (p, q), \\ \mathfrak{B}_1 u = \mathfrak{B}_2 v = 0 & \text{on } \{p, q\}. \end{cases} \quad (59)$$

Proof of Lemma 7.2. Let (u, v) be a solution of (59). To show that $(u, v) = (0, 0)$ we will argue by contradiction assuming that $(u, v) \neq (0, 0)$. Suppose $u \neq 0$. Then, it follows from the v -equation of (59) that $v \neq 0$. Similarly, if $v \neq 0$, the u -equation implies that $u \neq 0$. Thus, $u \neq 0$ and $v \neq 0$. Suppose $u \geq 0$. Then, since $\tilde{\mathcal{L}}_2^{-1}$ is strongly positive, we can infer from the v -equation of (59) that $v \gg_2 0$. But, in such case, the right hand side of the u -equation of (59) becomes negative and hence, since $\tilde{\mathcal{L}}_1^{-1}$ is strongly positive, we can infer that also $u \ll_1 0$, which is impossible. Therefore, u changes of sign in (p, q) . This argument can be easily adapted to show that v must change of sign too. Adapting the proof of [8], it is easily seen that the zeros of u and v are isolated, i.e., they cannot accumulate in (p, q) . Thus, there is a partition of $[p, q]$,

$$Q := \{p = x_0 < x_1 < x_2 < \dots < x_{m-1} < x_m = q\}, \quad m \geq 2,$$

such that

$$\begin{aligned} u(x) &> 0 \text{ for all } x \in (x_{2j}, x_{2j+1}), \quad j \geq 0, \quad 2j+1 \leq m, \\ u(x) &< 0 \text{ for all } x \in (x_{2j-1}, x_{2j}), \quad j \geq 1, \quad 2j \leq m, \\ u(x_j) &= 0 \text{ for all } j \in \{1, \dots, m-1\} \text{ and } \mathfrak{B}_1 u(p) = \mathfrak{B}_1 u(q) = 0. \end{aligned} \quad (60)$$

We claim that

$$v(x_{2j}) > 0, \quad v(x_{2j+1}) < 0, \quad x_{2j}, x_{2j+1} \in Q \setminus \{p, q\}.$$

Indeed, by (60), we have that $u(x) > 0$ for all $x \in (x_0, x_1)$, $\mathfrak{B}_1 u(x_0) = 0$ and $u(x_1) = 0$. Thus, owing to (59), we find that

$$\tilde{\mathcal{L}}_2 v = \beta u > 0 \quad \text{in } (x_0, x_1).$$

Moreover, $\mathfrak{B}_2 v(x_0) = 0$. Suppose that $v(x_1) \geq 0$. As, according to [4, Pr. 3.2], the operator $\tilde{\mathcal{L}}_2$ subject to the boundary conditions

$$\mathfrak{B}_2 v(x_0) = 0, \quad v(x_1) = 0,$$

in the interval (x_0, x_1) has a positive principal eigenvalue, from Theorem 2.2 it becomes apparent that $v(x) > 0$ for all $x \in (x_0, x_1)$. Thus, going back to (59) yields

$$\tilde{\mathcal{L}}_1 u = -\alpha v < 0 \quad \text{in } (x_0, x_1).$$

As due to [4, Pr. 3.2], the operator $\tilde{\mathcal{L}}_1$ subject to the boundary conditions

$$\mathfrak{B}_1 u(x_0) = 0, \quad u(x_1) = 0,$$

in the interval (x_0, x_1) has a positive principal eigenvalue, Theorem 2.2 also implies that $u(x) < 0$ for all $x \in (x_0, x_1)$, which is a contradiction. Therefore, $v(x_1) < 0$. The previous argument can be easily adapted to show that $v(x_2) > 0$, $v(x_3) < 0$, ... and so on and so forth.

If m is odd, one has that

$$u(x) > 0 \text{ for all } x \in (x_m, q) \text{ and } v(x_m) > 0, \quad (61)$$

while, if m is even,

$$u(x) < 0 \text{ for all } x \in (x_{2k+1}, q) \text{ and } v(x_{2k+1}) < 0.$$

Suppose that m is odd. Then, (61) holds and hence, by (59),

$$\tilde{\mathfrak{L}}_2 v = \beta u > 0 \text{ in } (x_{2k}, q).$$

Since $v(x_{2k}) > 0$ and $\mathfrak{B}_2 v(q) = 0$, arguing as above, it follows from [4, Pr. 3.2] and Theorem 2.2 that $v(x) > 0$ for all $x \in (x_{m-1}, q)$. Thus,

$$\tilde{\mathfrak{L}}_1 u = -\alpha v < 0 \text{ in } (x_{m-1}, q)$$

and therefore, since $u(x_{m-1}) = 0$ and $\mathfrak{B}_u(q) = 0$, it becomes apparent that $u(x) < 0$ for all $x \in (x_{m-1}, q)$, which contradicts (61). A similar contradiction can be reached when, instead, m is even. These contradictions end the proof. \square

Since

$$\frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} \leq \theta_{[\mathfrak{L}_1, \lambda, a]},$$

we have that

$$-c \frac{\theta_{[\mathfrak{L}_1, \lambda, a]}}{1 + m\theta_{[\mathfrak{L}_1, \lambda, a]}} \geq -c\theta_{[\mathfrak{L}_1, \lambda, a]},$$

and hence, any positive strict supersolution, \bar{v} of

$$\begin{cases} (\mathfrak{L}_2 - c\theta_{[\mathfrak{L}_1, \lambda, a]}) w = \mu w - dw^2 & \text{in } \Omega, \\ \mathfrak{B}_2 w = 0 & \text{on } \partial\Omega, \end{cases} \quad (62)$$

provides us with a positive strict supersolution of (58). On the other hand, arguing as in the proof of Theorem 4.1 it becomes apparent that (62) admits a positive strict supersolution of the form

$$\bar{v} = Ce^{M\psi}$$

for sufficiently large constants $C > 0$ and $M > 0$, independent of $m(x)$. Therefore, the assumption (55) of Theorem 7.1 holds true as soon as

$$Ce^{M\psi} \leq \frac{a}{bm}. \quad (63)$$

Consequently, the uniqueness of a coexistence state occurs for sufficiently small $m(x)$, in complete agreement with the available results in the literature.

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