Large saturation effects provoke multiplicity in spatially heterogeneous predator-prey models

Julián López-Gómez and Eduardo Muñoz-Hernández
Universidad Complutense de Madrid, Spain
Instituto de Matemática Interdisciplinar (IMI)

Abstract

This communication analyzes the diffusive spatially heterogeneous predator-prey model introduced by the authors in [16], which takes into account the saturation effects of the predator in the abundance of preys through a saturation coefficient $\gamma m(x) \gneq 0$ with $\|m\|_\infty = 1$. The main result establishes the existence of, at least, two coexistence states for sufficiently large $\gamma > 0$ in a region of the parameters where the Lotka–Volterra counterpart cannot admit any coexistence state, regardless the size and shapes of the logistic and interactions coefficients of the model.

1. Introduction

This communication analyzes the existence and multiplicity of coexistence states for the generalized spatially heterogeneous predator-prey model

$$\begin{cases} \mathfrak{L}_1 u = \lambda u - a(x)u^2 - b(x)\dfrac{uv}{1+\gamma m(x)u} & \text{in } \Omega, \\ \mathfrak{L}_2 v = \mu v + c(x)\dfrac{uv}{1+\gamma m(x)u} - d(x)v^2 & \text{in } \Omega, \\ \mathfrak{B}_1 u = \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega, \end{cases} \tag{1.1}$$

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 in Ω of the form

$$\mathfrak{L}_\kappa := -\mathrm{div}\,(A_\kappa(x)\nabla) + \sum_{j=1}^{N} b_{j,\kappa}(x)\partial_j + c_\kappa(x), \qquad \kappa = 1,2,$$

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

$$a_{ij,\kappa} = a_{ji,\kappa} \in W^{1,\infty}(\Omega) \quad \text{and} \quad b_{j,\kappa}, c_\kappa \in L^\infty(\Omega) \quad \text{for all} \quad 1 \le i,j \le N.$$

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

$$\mathfrak{B}_\kappa \xi := \begin{cases} \xi & \text{on } \Gamma_{0,\kappa}, \\ \partial_{\nu_\kappa}\xi + \beta_\kappa(x)\xi & \text{on } \Gamma_{1,\kappa}, \end{cases} \tag{1.2}$$

where $\Gamma_{0,\kappa}$ and $\Gamma_{1,\kappa}$ are two closed and open disjoint subsets of $\partial\Omega$ such that

$$\Gamma_{0,\kappa} \cup \Gamma_{1,\kappa} = \partial\Omega.$$

In (1.2), $\beta_\kappa \in C(\Gamma_{1,\kappa};\mathbb{R})$, and $\nu_\kappa \in C^1(\Gamma_{1,\kappa};\mathbb{R}^N)$ is an outward pointing nowhere tangent vector field. Moreover, the functions coefficients $a(x)$, $b(x)$, $c(x)$, $d(x)$ and $m(x)$ are continuous in $\bar\Omega$ and satisfy $b \gneq 0$, $c \gneq 0$, $m \ge 0$, and

$$a(x) > 0, \quad d(x) > 0 \qquad \text{for all } x \in \bar\Omega,$$

while $\gamma > 0$ and $\lambda, \mu \in \mathbb{R}$ are regarded as bifurcation parameters.

From an ecological point of view, (1.1) 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 $m = 0$, (1.1) 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 introduced by Casal et al. [4]. The kinetics in [4] took 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. In (1.1), the function $\gamma m(x)$ 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 $m(x) = 0$. Throughout this note, we assume that

$$\|m\|_\infty \equiv \max_{\bar{\Omega}} m = 1.$$

Thus, γ can be viewed as the maximal amplitude of the saturation effects of the predator. Under these general assumptions, (1.1) combines, within the same territory Ω, the classical interactions of Lotka–Volterra type in the region $m^{-1}(0)$ with the Holling-Tanner functional responses in $\{x \in \Omega : m(x) > 0\}$. In its greatest generality, (1.1) includes most of the existing models of this type in the literature. In applications, $\lambda - c_1(x)$ and $\mu - c_2(x)$ stand for the neat growth, or decay, rates of the prey and the predator in the absence of each other.

The main goal of this note is analyzing the dynamics of (1.1) when γ grows to infinity. Thus, it is natural to perform the change of variables

$$w := \gamma u, \qquad \varepsilon = \frac{1}{\gamma}.$$

According to it, the model (1.1) can be expressed as

$$\begin{cases} \mathfrak{L}_1 w = \lambda w - \varepsilon a(x) w^2 - b(x)\dfrac{wv}{1+m(x)w} & \text{in } \Omega, \\ \mathfrak{L}_2 v = \mu v - d(x) v^2 + \varepsilon c(x)\dfrac{wv}{1+m(x)w} & \text{in } \Omega, \\ \mathfrak{B}_1 w = \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega. \end{cases} \tag{1.3}$$

Hence, the problem of analyzing the dynamics of (1.1) for sufficiently large $\gamma > 0$ is equivalent to analyze the dynamics of (1.3) for sufficiently small $\varepsilon > 0$. Throughout this paper we will focus attention into (1.3) as a sort of shadow system perturbing from

$$\begin{cases} \mathfrak{L}_1 w = \lambda w - b(x)\dfrac{wv}{1+m(x)w} & \text{in } \Omega, \\ \mathfrak{L}_2 v = \mu v - d(x) v^2 & \text{in } \Omega, \\ \mathfrak{B}_1 w = \mathfrak{B}_2 v = 0 & \text{on } \partial\Omega, \end{cases} \tag{1.4}$$

which is an uncoupled problem.

The plan of this note is the following. Section 2 collects some preliminaries. Section 3 gives some necessary and sufficient conditions for the existence of coexistence states of (1.1), as well as a local bifurcation result valid for all $\varepsilon \geq 0$. Section 4 ascertains the fine structure of the component of coexistence states of (1.4) bifurcating from the semitrivial positive solution of the form $(w, v) = (0, v)$ with $v > 0$. Finally, based on these results, in Section 5 we deliver our main multiplicity result for (1.3), with sufficiently small $\varepsilon > 0$. Essentially, as ε moves away from 0, a *metasolution* of (1.4) perturbs into a second coexistence state of (1.3) (see [13], if necessary, for the concept of metasolution).

2. Preliminaries

As a direct consequence of the elliptic L^p-theory, it is apparent that any non-negative weak solution of (1.3), (w, v), satisfies

$$u \in \mathscr{W}_1 := \bigcap_{p=N}^{\infty} W^{2,p}_{\mathfrak{B}_1}(\Omega), \qquad v \in \mathscr{W}_2 := \bigcap_{p=N}^{\infty} W^{2,p}_{\mathfrak{B}_2}(\Omega),$$

where, for every $\kappa = 1, 2$ and $p > N$, $W^{2,p}_{\mathfrak{B}_\kappa}(\Omega)$ stands for the Sobolev space of the functions $w \in W^{2,p}(\Omega)$ such that $\mathfrak{B}_\kappa w = 0$ on $\partial\Omega$. According to the Sobolev imbeddings, there is enough regularity on $\partial\Omega$ as to consider $\mathfrak{B}_\kappa$ in the classical sense, and (u, v) must be a strong solution of (1.1) (see, e.g., [12, Th. 5.11]).

For any given $V \in L^\infty(\Omega)$ and $\kappa = 1, 2$, we will denote by

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

the principal eigenvalue of the linear eigenvalue problem

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

whose existence and uniqueness in our general setting was established in [12, Ch. 7]. The associated principal eigenfunction, unique up to a multiplicative positive constant, can be taken strongly positive in Ω, $\varphi \gg_\kappa 0$, in the sense that

$$\varphi(x) > 0 \text{ for all } x \in \Omega \cup \Gamma_{1,\kappa} \text{ and } \frac{\partial \varphi}{\partial n}(x) < 0 \text{ for all } x \in \Gamma_{0,\kappa},$$

where n stands for the outward unit normal vector field to Ω. The following result, going back to Cano-Casanova and López-Gómez [3] in its present generality, establishes the monotonicity of the principal eigenvalue with respect to the potential.

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

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

Thus, the map $V \mapsto \sigma_0 [\mathfrak{L}_\kappa + V, \mathfrak{B}_\kappa, \Omega]$ is continuous in $L^\infty(\Omega)$ and increasing.

The next characterization is pivotal for analyzing elliptic equations or systems, as it is a key ingredient to infer most of our results. It goes back to López-Gómez and Molina-Meyer [14] for cooperative systems under Dirichlet boundary conditions, and to Amann and López-Gómez [2] and [11] for general boundary conditions of mixed type (see also [12, Th. 7.10] for further details).

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

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

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

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

with some of these inequalities strict.

(c) *The tern $(\mathfrak{L}_\kappa + V, \mathfrak{B}_\kappa, \Omega)$ satisfies the strong maximum principle, i.e., $w \gg_\kappa 0$ for every function $w \in \mathscr{W}_\kappa$ such that*

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

with some of these inequalities strict.

The next result is invoked when analyzing the logistic equation in our abstract setting here. For a detailed proof of Theorem 2.3 in the classical case when $\beta_\kappa \geq 0$ the reader is sent to Fraile et al. [8, Th. 3.5]. The general case when β_k changes of sign can be reduced to the classical case through the exponential change of variable of Fernández-Rincón and López-Gómez [7, Sect. 3]. Alternatively, see Theorem 1.1 of Daners and López-Gómez [6], though this change of variable goes back to [12, Ch. 2] in a linear context.

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

$$\begin{cases} (\mathfrak{L}_\kappa + V)w = \rho w - \xi(x)w^2 & \text{in } \Omega, \\ \mathfrak{B}_\kappa w = 0 & \text{on } \partial\Omega, \end{cases} \tag{2.1}$$

admits a positive solution if, and only if,

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

which is unique if it exists. Moreover, if we denote it by

$$w_{\rho,\kappa} \equiv \theta_{[\mathfrak{L}_\kappa + V, \rho, \xi]} \in \mathscr{W}_\kappa,$$

then $w_{\rho,k} \gg_\kappa 0$, the map $\rho \longrightarrow w_{\rho,\kappa}$ is point-wise increasing if

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

and $w_{\rho,\kappa}$ bifurcates from $w = 0$ at $\rho = \sigma_0 [\mathfrak{L}_\kappa + V, \mathfrak{B}_\kappa, \Omega]$. Furthermore, if $\bar{u}$ is a positive strict supersolution of (2.1)*, then $\bar{u} \gg_\kappa w_{\rho,\kappa}$. Similarly, if $\underline{u}$ is a positive strict subsolution of* (2.1)*, then $\underline{u} \ll_\kappa w_{\rho,\kappa}$.*

More precisely, through this note, we denote by $\theta_{[\mathfrak{L}_\kappa+V,\rho,\xi]}$ the maximal non-negative solution of (2.1). Hence, by Theorem 2.3,

$$\theta_{[\mathfrak{L}_\kappa+V,\rho,\xi]} := \begin{cases} 0 & \text{if } \rho \le \sigma_0\left[\mathfrak{L}_\kappa + V, \mathfrak{B}_\kappa, \Omega\right], \\ \gg_\kappa 0 & \text{if } \rho > \sigma_0\left[\mathfrak{L}_\kappa + V, \mathfrak{B}_\kappa, \Omega\right]. \end{cases}$$

Moreover, as a byproduct of Theorem 2.3, (1.1) 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, $(u,0) = \left(\theta_{[\mathfrak{L}_1,\lambda,a]}, 0\right)$. Similarly, (1.1) 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, $(0,v) = \left(0, \theta_{[\mathfrak{L}_2,\mu,d]}\right)$.

3. Coexistence regions and bifurcation of coexistence states from $(0, \theta_{[\mathfrak{L}_2,\mu,d]})$

In this section we are going to estimate the regions of the (λ,μ)–plane where the problem (1.1), or, equivalently, (1.3) has some coexistence state. Then, regardless the values of $\varepsilon > 0$ and $\mu > \sigma_{0,2}$, it is established the existence of a component of coexistence states bifurcating from the semitrivial curve $(0, \theta_{[\mathfrak{L}_2,\mu,d]})$ at a certain (unique) value of λ.

Next result collects some (optimal) necessary and sufficient conditions for the existence of coexistence states and, hence, it determines the coexistence regions of (1.3). It is a direct consequence of [16, Th. 4.1 & 5.1].

Theorem 3.1 *Suppose that, for some $\varepsilon > 0$, (1.3) has a coexistence state, (w,v). Then,*

$$\lambda > \varphi_\varepsilon(\mu) \equiv \sigma_0\Big[\mathfrak{L}_1 + b\tfrac{\theta_{[\mathfrak{L}_2,\mu,d]}}{1+m\theta_{[\mathfrak{L}_1,\lambda,\varepsilon a]}}, \mathfrak{B}_1, \Omega\Big] \quad \textit{and} \quad \mu > \Psi_\varepsilon(\lambda) \equiv \sigma_0\Big[\mathfrak{L}_2 - \varepsilon c\tfrac{\theta_{[\mathfrak{L}_1,\lambda,\varepsilon a]}}{1+m\theta_{[\mathfrak{L}_1,\lambda,\varepsilon a]}}, \mathfrak{B}_2, \Omega\Big]. \tag{3.1}$$

Conversely, under the following condition

$$\lambda > \Phi(\mu) \equiv \sigma_0\left[\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2,\mu,d]}, \mathfrak{B}_1, \Omega\right] \quad \textit{and} \quad \mu > \Psi_\varepsilon(\lambda), \tag{3.2}$$

the problem (1.3) *has, at least, a coexistence state.*

Figure 1 sketches the construction of the wedges (3.1) and (3.2) given by Theorem 3.1. By Theorem 2.1,

$$\varphi_\varepsilon(\mu) \equiv \sigma_0\left[\mathfrak{L}_1 + b\tfrac{\theta_{[\mathfrak{L}_2,\mu,d]}}{1+m\theta_{[\mathfrak{L}_1,\lambda,\varepsilon a]}}, \mathfrak{B}_1, \Omega\right] < \sigma_0\left[\mathfrak{L}_1 + b\theta_{[\mathfrak{L}_2,\mu,d]}, \mathfrak{B}_1, \Omega\right] \equiv \Phi(\mu), \qquad \text{for all } \mu > \sigma_{0,2}.$$

According to Theorem 3.1, (1.3) has a coexistence state in the solid area of Figure 1, whereas outside the union of the solid and dashed wedges of Figure 1, it cannot admit any coexistence state. Thus, the dashed wedge must contain the edge of the coexistence region. By the analysis already done in [16, Sec. 3], the global structure of the curve $\mu = \Psi_\varepsilon(\lambda)$ can change according to the nature of $m(x)$, as illustrated in Figure 1 and explained in its caption.

Since $\theta_{[\mathfrak{L}_1,\lambda,\varepsilon a]} = \varepsilon^{-1}\theta_{[\mathfrak{L}_1,\lambda,a]}$, it is apparent that

$$\lim_{\varepsilon\downarrow 0}\varphi_\varepsilon(\mu) = \lim_{\varepsilon\downarrow 0}\sigma_0\left[\mathfrak{L}_1 + b\tfrac{\theta_{[\mathfrak{L}_2,\mu,d]}}{1+\frac{m}{\varepsilon}\theta_{[\mathfrak{L}_1,\lambda,a]}}, \mathfrak{B}_1, \Omega\right] = \sigma_0\left[\mathfrak{L}_1 + \left(1 - \chi_{\operatorname{int\,supp} m}\right) b(x)\theta_{[\mathfrak{L}_2,\mu,d]}, \mathfrak{B}_1, \Omega\right],$$

where, for any subset $A \subset \mathbb{R}^N$, χ_A stands for the characteristic function of the set A, i.e., $\chi_A(x) = 1$ if $x \in A$, and $\chi_A(x) = 0$ if $x \in \mathbb{R}^N \setminus A$. In the next section, it will become apparent that the function

$$\varphi_0(\mu) := \sigma_0\left[\mathfrak{L}_1 + \left(1 - \chi_{\operatorname{int\,supp} m}\right) b(x)\theta_{[\mathfrak{L}_2,\mu,d]}, \mathfrak{B}_1, \Omega\right], \qquad \mu > \sigma_{0,2}, \tag{3.3}$$

provides us with the left limiting curve to the region where the uncoupled model (1.4) possesses a coexistence state. The curve $\lambda = \varphi_0(\mu)$ has been also plotted in Figure 1 and, again by Theorem 2.1, $\varphi_0(\mu) < \varphi_\varepsilon(\mu)$ if $bm \gneq 0$.

According to Theorem 2.2, for every real number $e > \max\{-\sigma_{0,1}, -\sigma_{0,2}\}$ and $\kappa = 1,2$, $(\mathfrak{L}_\kappa + e, \mathfrak{B}_\kappa, \Omega)$ is an invertible operator with strongly positive inverse. Thus, the solutions of the problem (1.3) are the zeroes of the operator

$$\mathfrak{F} : \mathbb{R}\times\mathbb{R}\times\mathbb{R}\times C^1_{\mathfrak{B}_1}(\bar\Omega)\times C^1_{\mathfrak{B}_2}(\bar\Omega) \to \mathscr{W}_1 \times \mathscr{W}_2,$$

defined, for every $\lambda, \mu, \varepsilon \in \mathbb{R}$, $w \in C^1_{\mathfrak{B}_1}(\bar\Omega)$ and $v \in C^1_{\mathfrak{B}_2}(\bar\Omega)$, by

$$\mathfrak{F}(\lambda,\mu,\varepsilon,w,v) := \begin{pmatrix} w - (\mathfrak{L}_1 + e)^{-1}\left[(\lambda+e)w - \varepsilon a w^2 - b\frac{wv}{1+mw}\right] \\ v - (\mathfrak{L}_2 + e)^{-1}\left[(\mu+e)v - dv^2 + \varepsilon c\frac{wv}{1+mw}\right] \end{pmatrix}.$$

The next result shows the bifurcation to coexistence states from the semitrivial positive solution $(0, \theta_{[\mathfrak{L}_2,\mu,d]})$ along the curve $\lambda = \Phi(\mu)$. It is a direct consequence of the theorem of bifurcation from simple eigenvalues of Crandall and Rabinowitz [5]. It provides us with the local structure of the set of bifurcating coexistence states.

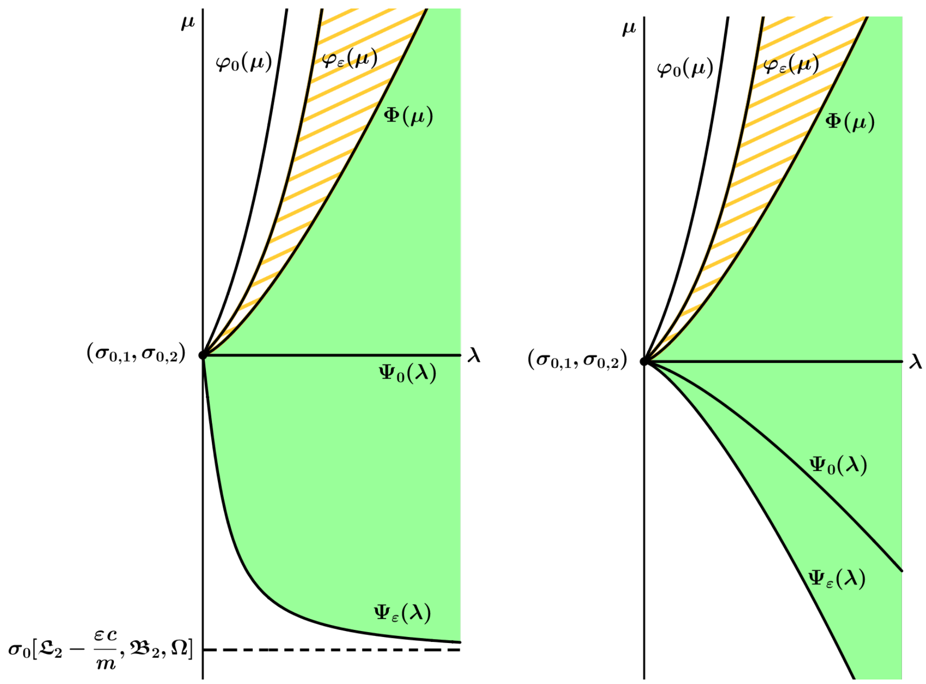

Fig. 1 The coexistence regions of (1.3) according to Theorem 3.1 if $m(x) > 0$ for all $x \in \bar{\Omega}$ (left picture) or int $m^{-1}(0) \neq \emptyset$ (right picture). When $m(x) > 0$ for all $x \in \bar{\Omega}$ the curve $\mu = \Psi_\varepsilon(\lambda)$, $\lambda > \sigma_{0,1}$, inherits the same asymptotic behavior as in the classical Holling–Tanner case when $m(x) \equiv m > 0$, whereas in case int $m^{-1}(0) \neq \emptyset$ it possesses the same asymptotic features as in the classical Lotka–Volterra model with $m \equiv 0$.

Theorem 3.2 *For every $\mu > \sigma_{0,2}$ and $\varepsilon \in \mathbb{R}$, there exist $\delta = \delta(\mu, \varepsilon) > 0$ and an analytic map $(\lambda, w, v) : (-\delta, \delta) \to \mathbb{R} \times \mathscr{W}_1 \times \mathscr{W}_2$ such that:*

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

(ii) $\mathfrak{F}(\lambda(s), \mu, \varepsilon, w(s), v(s)) = 0$ *for all* $s \in (-\delta, \delta)$.

(iii) $v(s) \gg_2 0$ *if* $s \in (-\delta, \delta)$, $w(s) \gg_1 0$ *if* $s \in (0, \delta)$ *and* $w(s) \ll_1 0$ *if* $s \in (-\delta, 0)$.

(iv) *The set of solutions of* (1.3) *in a neighborhood of* $(\lambda, w, v) = \big(\Phi(\mu), 0, \theta_{[\mathfrak{L}_2,\mu,d]}\big)$ *consists of the curves* $\big(\lambda, 0, \theta_{[\mathfrak{L}_2,\mu,d]}\big)$, $\lambda \sim \Phi(\mu)$, *and* $(\lambda(s), w(s), v(s))$, $s \in (-\delta, \delta)$.

Moreover, there are two functions $w_1, w_1^* \gg_1 0$ *such that*

$$\lambda'(0) = \int_\Omega \big(\varepsilon a - b\theta_{[\mathfrak{L}_2,\mu,d]}\big)\, w_1^2 w_1^* + \int_\Omega b\, \big(\mathfrak{L}_2 + 2d\theta_{[\mathfrak{L}_2,\mu,d]} - \mu\big)^{-1}\big(\varepsilon c \theta_{[\mathfrak{L}_2,\mu,d]} w_1\big)\, w_1 w_1^*. \tag{3.4}$$

Remark 3.3 As the dependence of $\mathfrak{F}$ on $\varepsilon \in \mathbb{R}$ is also analytic, by the implicit function theorem used in the proof of the theorem of Crandall and Rabinowitz [5], it becomes apparent that the bifurcated curve

$$(\lambda(s), w(s), v(s)) \equiv (\lambda(s,\varepsilon), w(s,\varepsilon), v(s,\varepsilon))$$

also is analytic with respect to the parameter ε.

4. The coexistence states of the uncoupled problem (1.4)

This section determines the set of coexistence states of the limiting shadow problem (1.4). As v satisfies

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

the condition $\mu > \sigma_{0,2} \equiv \sigma_0[\mathfrak{L}_2, \mathfrak{B}_2, \Omega]$ is imperative so that (1.4) can have a coexistence state. Otherwise, $v = 0$ for any component-wise nonnegative solution, (w, v), of (1.4). Thus, throughout this section, we assume that

$\mu > \sigma_{0,2}$. In such case, by Theorem 2.3, for every coexistence state (w, v) of (1.4), necessarily $v = \theta_{[\mathfrak{L}_2,\mu,d]} \gg_2 0$, and $w \gg_1 0$ is a positive solution of the associated problem

$$\begin{cases} \mathfrak{L}_1 w = \lambda w - b(x)\theta_{[\mathfrak{L}_2,\mu,d]} \dfrac{w}{1+m(x)w} & \text{in } \Omega, \\ \mathfrak{B}_1 w = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.1}$$

The next result ascertains the range of λ's where (4.1) has a coexistence state.

Lemma 4.1 *Suppose $bm \gneq 0$ and $w \neq 0$ is a positive solution of* (4.1)*. Then, $w \gg_1 0$ and*

$$\sigma_{0,1} \leq \varphi_0(\mu) < \lambda = \sigma_0\left[\mathfrak{L}_1 + \tfrac{b(x)\theta_{[\mathfrak{L}_2,\mu,d]}}{1+m(x)w}, \mathfrak{B}_1, \Omega\right] < \Phi(\mu), \tag{4.2}$$

where $\varphi_0(\mu)$ and $\Phi(\mu)$ are the functions defined in (3.3) *and* (3.2)*, respectively.*

According to Theorem 3.2, there is a bifurcation to positive solutions of (4.1) from $(w, v) = (0, \theta_{[\mathfrak{L}_2,\mu,d]})$ at $\lambda = \Phi(\mu)$, which is subcritical, because

$$\lambda'(0) = -\int_\Omega b\theta_{[\mathfrak{L}_2,\mu,d]} w_1^2 w_1^* < 0. \tag{4.3}$$

Set $\mathfrak{F}_0(\lambda, \mu, w, v) \equiv \mathfrak{F}(\lambda, \mu, 0, w, v)$, and let denote by $\mathscr{S}_0$ the set of nontrivial solutions of (4.1) defined by

$$\mathscr{S}_0 := \{(\lambda, \mu, w, \theta_{[\mathfrak{L}_2,\mu,d]}) \in \mathfrak{F}_0^{-1}(0) \ : \ w \neq 0\} \cup \{(\lambda, \mu, 0, \theta_{[\mathfrak{L}_2,\mu,d]}) \ : \ \lambda \in \Sigma(\mathscr{L}(\lambda))\},$$

where $\Sigma(\mathscr{L}(\lambda))$ stands for the generalized spectrum of the Fredholm curve

$$\mathscr{L}(\lambda) := D_{(w,v)}\mathfrak{F}_0(\lambda, \mu, 0, \theta_{[\mathfrak{L}_2,\mu,d]}).$$

The next result establishes that the component $\mathscr{C}_0^+$ of positive solutions of $\mathscr{S}_0$ with $(\Phi(\mu), \mu, 0, \theta_{[\mathfrak{L}_2,\mu,d]}) \in \bar{\mathscr{C}}_0^+$ satisfies

$$\mathcal{P}_\lambda(\mathscr{C}_0^+) = (\varphi_0(\mu), \Phi(\mu)), \tag{4.4}$$

where $\mathcal{P}_\lambda$ stands for the λ-projection operator, $\mathcal{P}_\lambda(\lambda, \mu, w, \theta_{[\mathfrak{L}_2,\mu,d]}) \equiv \lambda$. Moreover, it shows that $\mathscr{C}_0^+$ is unbounded at $\lambda = \varphi_0(\mu)$ and it provides us with its fine structure nearby $\lambda = \Phi(\mu)$ and $\lambda = \varphi_0(\mu)$. This is a crucial information to obtain the main multiplicity result of this note for (1.3) with sufficiently small $\varepsilon > 0$.

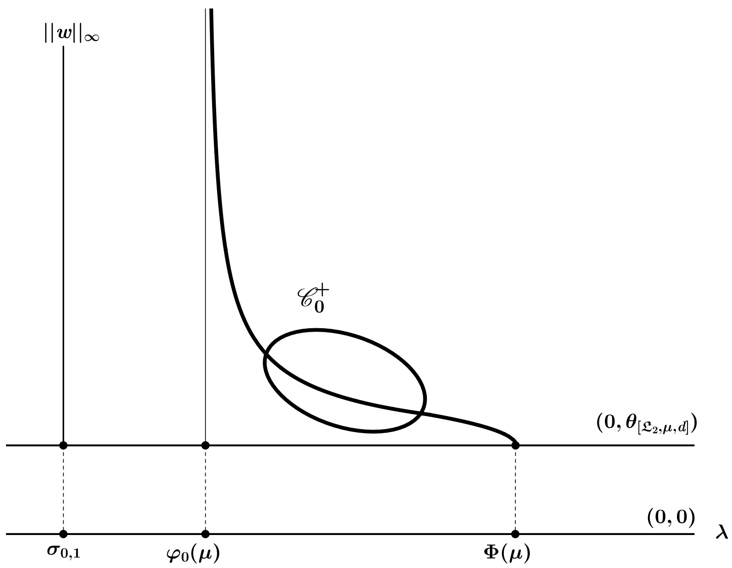

Fig. 2 An admissible component $\mathscr{C}_0^+$ in case $bm \gneq 0$.

Theorem 4.2 *The component $\mathscr{C}_0^+$ satisfies* (4.4)*. Moreover, for every sequence of positive solutions, in $\mathscr{C}_0^+$, $\{(\lambda_n, \mu, w_n, \theta_{[\mathfrak{L}_2,\mu,d]})\}_{n\geq 1}$, such that* $\lim_{n\to\infty} \lambda_n = \varphi_0(\mu)$*, necessarily*

$$\lim_{n\to\infty} \|w_n\|_\infty = +\infty. \tag{4.5}$$

On the other hand, in a neighborhood of $(\lambda, \mu, w, \theta_{[\mathfrak{L}_2,\mu,d]}) = (\Phi(\mu), \mu, 0, \theta_{[\mathfrak{L}_2,\mu,d]})$ *in* $\mathbb{R}\times\mathbb{R}\times\mathscr{W}_1\times\{\theta_{[\mathfrak{L}_2,\mu,d]}\}$, $\mathscr{C}_0^+$ *consists of the analytic curve* $(\lambda(s), \mu, w(s), \theta_{[\mathfrak{L}_2,\mu,d]})$ *given by Theorem* 3.2. *Actually, there exists* $r > 0$ *such that, for every* $\lambda \in [\Phi(\mu) - r, \Phi(\mu))$, (4.1) *has a unique positive solution. Moreover, for sufficiently small* $r > 0$, *this positive solution is linearly unstable with one-dimensional unstable manifold.*

Furthermore, there exists $r > 0$ *such that, for every* $\lambda \in (\varphi_0(\mu), \varphi_0(\mu)+r]$, (4.1) *has a unique positive solution,* $(\lambda, \mu, w_\lambda, \theta_{[\mathfrak{L}_2,\mu,d]})$, *which is non-degenerate. Thus, for these values of* λ, $\mathscr{C}_0^+$ *consists of an analytic curve of positive solutions bifurcating from* $+\infty$ *at* $\lambda = \varphi_0(\mu)$.

Figure 2 shows an admissible component $\mathscr{C}_0^+$ of positive solutions of (4.1) adjusted to the patterns of Theorem 4.2. Although (4.1) has a unique positive solution for λ sufficiently close to either $\Phi(\mu)$, or $\varphi_0(\mu)$, the problem might possess an arbitrarily large number of positive solutions for some intermediate range of values of the parameter λ, as illustrated in Figure 2.

5. An optimal multiplicity result for the original model

The next multiplicity result is the main theorem of this communication. Recall that, owing to Theorem 3.1, for every $\mu > \sigma_{0,2}$, (1.3) has a coexistence state if $\lambda > \Phi(\mu)$. Moreover, in such case, $\lambda > \varphi_\varepsilon(\mu)$.

Theorem 5.1 *Fix* $\lambda^* \in (\varphi_0(\mu), \Phi(\mu))$. *Then, there exists* $\varepsilon_0 \equiv \varepsilon_0(\lambda^*) > 0$ *such that, for every* $\varepsilon \in (0, \varepsilon_0)$, (1.3) *possesses a component* $\mathscr{C}_\varepsilon^+$ *of coexistence states satisfying the following properties*:

(a) $\mathcal{P}_\lambda\left(\mathscr{C}_\varepsilon^+\right) = [\lambda_T, +\infty)$ *for some* $\lambda_T \equiv \lambda_T(\varepsilon) \in (\varphi_\varepsilon(\mu), \lambda^*]$.

(b) *For every* $\lambda \in [\lambda^*, \Phi(\mu))$, (1.3) *has, at least, two different coexistence states.*

(c) $\mathscr{C}_\varepsilon^+$ *is an analytic curve, with respect to the parameter* λ, *in a neighborhood of*

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

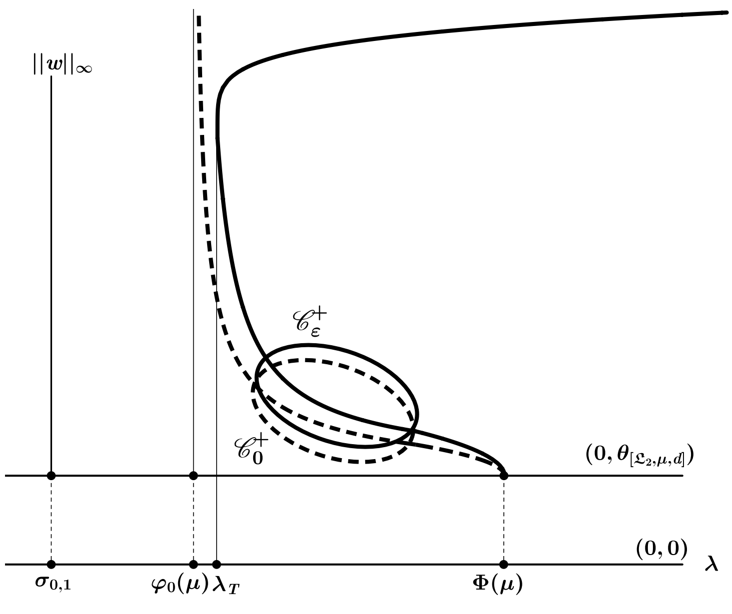

Fig. 3 The components $\mathscr{C}_0^+$ (dashed line) and $\mathscr{C}_\varepsilon^+$ (solid line) for small $\varepsilon > 0$

Naturally, $\mathscr{C}_\varepsilon^+$ is the perturbation of the component $\mathscr{C}_0^+$ constructed in Section 4 as $\varepsilon > 0$ leaves $\varepsilon = 0$. Figure 3 shows an admissible component $\mathscr{C}_\varepsilon^+$ (solid line) perturbing from $\mathscr{C}_0^+$ (dashed line) and satisfying Theorem 5.1. Roughly spoken, the proof of Theorem 5.1 relies on the following features:

- The existence of a priori bounds for the coexistence states of the problem (1.4). These bounds can be derived as an application of Theorems 2.2 and 2.3. The existence of a priori bounds together with [10, Th. 7.2.2] guarantee that the component $\mathscr{C}_\varepsilon^+$ is unbounded in λ, i.e., $\mathcal{P}_\lambda\left(\mathscr{C}_\varepsilon^+\right)$ should contain an interval of the form $[\hat{\lambda}, +\infty)$ for some $\hat{\lambda} > \varphi_0(\mu)$.

- The use of the implicit function to make sure that $\mathscr{C}_\varepsilon^+$ consists of two arcs of analytic λ-curve for $\lambda \sim \varphi_0(\mu)$ and $\lambda \sim \Phi(\mu)$ and sufficiently small $\varepsilon > 0$, and the construction of an open isolating neighborhood, $\mathcal{O}$, for a certain subcomponent of $\mathscr{C}_0^+$ joining these two arcs.
- Showing that, for sufficiently small $\varepsilon > 0$, the isolating neighborhood also packages the components $\mathscr{C}_\varepsilon^+$.
- Using the fixed point index in cones, as axiomatized by Amann [1], to infer the multiplicity result as in [9]. According to it, the existence of a second coexistence state for all $\lambda \geq \lambda^*$ holds.

Remark 5.2 According to Theorem 3.2 and [10, Th. 7.2.2], the existence of a $\lambda^* \in (\varphi_\varepsilon(\mu), \Phi(\mu))$ such that, for every $\lambda \in [\lambda^*, \Phi(\mu))$, (1.3) has, at least, two coexistence states is guaranteed if $\lambda'(0) < 0$. This occurs for sufficiently small ε, which might be larger than the ε_0 given by Theorem 5.1; at least, for $\varepsilon \in (0, \varepsilon^*)$, where ε^* satisfies $\lambda'(0, \varepsilon^*) = 0$.

Acknowledgements

This communication has been written under the auspices of the Ministry of Science and Innovation of Spain, under Research Grant PID2021-123343NB-I00, and of the IMI of Complutense University. The second author, ORCID 0000-0003-1184-6231, has been also supported by contract CT42/18-CT43/18 of Complutense University of Madrid.

References

[1] Herbert Amann. Fixed point equations and nonlinear eigenvalue problems in ordered Banach spaces. *SIAM Rev.*, 18:620–709, 1976.

[2] Herbert Amann and Julián López-Gómez. A priori bounds and multiple solutions for superlinear indefinite elliptic problems. *J. Diff. Equations*, 146(2):336–374, 1998.

[3] Santiago Cano-Casanova and Julián López-Gómez. Properties of the principal eigenvalues of a general class of non-classical mixed boundary value problems. *J. Diff. Equations*, 178:123–211, 2002.

[4] Alfonso Casal, Chris Eilbeck and Julián López-Gómez. Existence and uniqueness of coexistence states for a predator-prey model with diffusion. *Diff. Int. Eqns.*, 7:411–439, 1994.

[5] Michael G. Crandall and Paul H. Rabinowitz. Bifurcation from simple eigenvalues. *J. Funct. Anal.*, 8:321–340, 1971.

[6] Daniel Daners and Julián López-Gómez. Global dynamics of generalized logistic equations. *Adv. Nonl. Studies*, 18:217–233, 2018.

[7] Sergio Fernández-Rincón and Julián López-Gómez. The singular perturbation problem for a class of generalized logistic equations under non-classical mixed boundary conditions. *Adv. Nonl. Studies*, 19:1–27, 2019.

[8] José María Fraile, Pablo Koch Medina, Julián López-Gómez, and Sandro Merino. Elliptic eigenvalue problems and unbounded continua of positive solutions of a semilinear elliptic equation. *J. Diff. Equations*, 127:295–319, 1995.

[9] Julián López-Gómez. Positive periodic solutions of Lotka-Volterra reaction-diffusion systems. *Diff. Int. Eqns.*, 5(1):55–72, 1992.

[10] Julián López-Gómez. *Spectral Theory and Nonlinear Functional Analysis*. Research Notes in Mathematics 426, Chapman & Hall/CRC Press, Boca Raton, FL, 2001.

[11] Julián López-Gómez. Classifying smooth supersolutions for a general class of elliptic boundary value problems. *Adv. Diff. Eqns.*, 8:1025–1042, 2003.

[12] Julián López-Gómez. *Linear Second Order Elliptic Operators*. World Scientific, Singapore, 2013.

[13] Julián López-Gómez. *Metasolutions of Parabolic Equations in Population Dynamics*. CRC Press, Boca Raton, 2015.

[14] Julián López-Gómez and Marcela Molina-Meyer. The maximum principle for cooperative weakly elliptic systems and some applications. *Diff. Int. Eqns*, 7:383–398, 1994.

[15] Julián López-Gómez and Eduardo Muñoz-Hernández. A spatially heterogeneous predator-prey model. *DCDS-Series B*, 26(4):2085–2113, 2021.

[16] Julián López-Gómez and Eduardo Muñoz-Hernández. Multiplicity in a spatially heterogeneous predator-prey model. *In preparation*, 2023.