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Steady-state bifurcations of a diffusive–advective predator–prey system with hostile boundary conditions and spatial heterogeneity

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Abstract. In this paper, we consider a diffusive–advective predator–prey system in a spatially heterogeneous environment subject to a hostile boundary condition, where the interaction term is governed by a Holling type II functional response. We investigate the existence and global attractivity of both trivial and semi-trivial steady-state solutions and the existence and local stability of coexistence steady-state solutions, depending on the size of a key principal eigenvalue. In addition, we show that the effect of advection on the principal eigenvalue is monotonic for small advection rates, depending on the concavity of the resource distribution. For arbitrary advection rates, we consider two explicit resource distributions for which we can say precisely the behaviour of the principal eigenvalue as it depends on advection, highlighting that advection can either improve or impair a population's ability to persist, depending on the characteristics of the resource distribution. We present some numerical simulations to demonstrate the outcomes as they depend on the advection rates for the full predator–prey system. These insights highlight the intimate relationship between environmental heterogeneity, directed movement, and the hostile boundary. The methods employed include upper and lower solution techniques, bifurcation theory, spectral analysis, and the comparison principle.

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Keywords. Coexistence, Environmental heterogeneity, Local stability, Global stability, Bifurcation theory, Spectral analysis.

1. Introduction

Predator–prey systems are ubiquitous in nature and play a crucial role in maintaining the balance of ecosystems and have consequently received much attention in the modelling literature [2,10,13–15,17,18,20,29,34,45]. These systems involve the interaction between a predator species and its prey species. The Lotka–Volterra model is now considered a classical mathematical model for describing predator–prey interactions. First proposed by Alfred James Lotka [35] and Vito Volterra [42] in the early twentieth century, they have since become one of the most widely studied models in ecological dynamics [3,16,45].

More generally, reaction–diffusion equations and systems are a widely used tool in applied mathematics, including mathematical biology, chemistry, and physics. These equations have been successfully employed to model a variety of phenomena, such as pattern formation, chemical reactions, and population dynamics [5,38,39]. In spatial ecology, it is well recognized that the spatial distribution of resources in the natural world is often highly heterogeneous. Consequently, spatial heterogeneity has become a topic of increasing interest among researchers [1,8,20,30,47]. By incorporating spatial heterogeneity into reaction–diffusion equations, the classical heterogeneous diffusive predator–prey model can be expressed in the following general form [19]:

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$$
\begin{cases}
\dfrac{\partial u}{\partial t} - \nabla \cdot (d_1(x)\nabla u) = \lambda m_1(x)u - a(x)u^2 - b_1(x)\phi(u)v, & x \in \Omega,\ t > 0, \\
\dfrac{\partial v}{\partial t} - \nabla \cdot (d_2(x)\nabla v) = l m_2(x)v - d(x)v^2 + b_2(x)\phi(u)v, & x \in \Omega,\ t > 0, \\
B_1 u = B_2 v = 0, & x \in \partial\Omega,\ t > 0, \\
u(x,0) = u_0(x) \geq, \not\equiv 0,\ v(x,0) = v_0(x) \geq, \not\equiv 0, & x \in \Omega,
\end{cases} \tag{1.1}
$$

where $u(x,t)$ and $v(x,t)$ represent the population density of the prey and predator, respectively, in a smooth, bounded domain $\Omega \subset \mathbb{R}^n$. Here, λ and l are nonnegative constants, while d_1, d_2, m_1, m_2, a, b_1, b_2, d are nonnegative, continuous functions on $\overline{\Omega}$. B_1 and B_2 are boundary operators that may impose Neumann [20,30], Dirichlet [19], or Robin boundary conditions [5]. $\phi(u)$ represents the functional response of the predator which describes how the predator intake of prey changes with the current local prey density.

The prototypical Lotka–Volterra predator–prey model assumes a linear functional response, e.g. $\phi(u) = u$, which implies that predators have an unlimited appetite and can consume an infinite amount of prey; many works consider this modelling formulation, see, e.g. [2,13–15,29,34,45]. In a spatially homogeneous environment, that is, when all coefficients in model (1.1) are constant, Li [29] gives necessary and sufficient conditions for the existence of positive steady-state solutions under homogeneous Dirichlet boundary conditions; López-Gómez and Pardo [34] consider the uniqueness and stability of the coexistence steady state. Balt and Brown [2] discuss the bifurcation of steady-state solutions, and Yamada [45] studies the stability of the steady-state solution under homogeneous Dirichlet boundary conditions. When the environment is spatially heterogeneous, Dancer and Du [15] consider the nonnegative steady-state solutions of model (1.1) and demonstrated the influence of spatial heterogeneity, particularly when one (or more) coefficients vanish in an open subset of the domain.

In reality, however, predators have a finite capacity to consume prey. To better describe dynamics of predator–prey interactions, Holling [23,24] proposed three types of functional responses, including the Holling type I, II, and III functional response. The typical forms are

$$
\begin{aligned}
\text{Type (I)} : \phi(u) &= \begin{cases} cu, & 0 < u \leq u_*, \\ cu_* & u > u_*, \end{cases} \quad c > 0. \\
\text{Type (II)} : \phi(u) &= \frac{u}{1 + T_h u},\ u > 0,\ T_h > 0. \\
\text{Type (III)} : \phi(u) &= \frac{u^p}{1 + T_h u^p},\ u > 0,\ T_h > 0,\ p > 1.
\end{aligned}
$$

Among them, the Holling type II functional response is the most widely used. Many studies have investigated model (1.1) with a Holling type II functional response, see for example [3,17,18] for spatially homogeneous environments, or [20,30] for spatially heterogeneous environments. In [3], Balt and Brown utilized both local and global bifurcation theories to investigate the presence of positive solutions for (1.1) under Dirichlet boundary conditions. In [17] and [18], Du and Lou studied the existence and nonexistence of positive solutions under homogeneous Dirichlet boundary conditions and homogeneous Neumann boundary conditions, respectively. In [20], Du and Shi studied the effect of the degeneracy of the crowding function $a(x)$ on the prey population, while the asymptotic profile and stability of positive solutions are further explored in [30]. For predator–prey models with other types of functional responses, we refer readers to [6,7,31,36,40,41,43,46,47].

Due to spatial heterogeneity in the environment, populations may exhibit directed movement along the resource gradients. To account for this phenomenon, an advection term can be introduced. This phenomenon was first proposed by Belgacem and Cosner [1] where they consider the following:

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d\nabla u - au\nabla m(x)] + u\,[m(x) - u]\,, & x \in \Omega, t > 0, \\ u(x,t) = 0, & x \in \partial\Omega, t > 0. \end{cases} \tag{1.2}$$

Here, $u(x,t)$ denotes the density of the population at location x and time t, Ω is a bounded domain in $\mathbb{R}^n$ with a smooth boundary, $m(x)$ is the (sign-indefinite) intrinsic growth rate of population, and $a \in \mathbb{R}$ measures the tendency of population to move up ($a > 0$) or down ($a < 0$) the gradient of $m(x)$. For a more detailed biological interpretation, we refer readers to [1]. Reaction–diffusion–advection models of this type can be found in [4,8] for a single population or [9,32,33,37] for multiple interacting populations.

Inspired by [1], we consider the following Lotka–Volterra prey–predator diffusion–advection system with Holling type II functional response subject to homogeneous Dirichlet boundary conditions:

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d_1(x)\nabla u - \alpha_1 u\nabla m_1(x)] + u\left[m_1(x) - u - \frac{b_1(x)v}{1+T_h u}\right], & x \in \Omega, t > 0, \\ \dfrac{\partial v}{\partial t} = \nabla \cdot [d_2(x)\nabla v - \alpha_2 v\nabla m_2(x)] + v\left[m_2(x) + \frac{b_2(x)u}{1+T_h u} - v\right], & x \in \Omega, t > 0, \\ u(x,t) = v(x,t) = 0, & x \in \partial\Omega, t > 0, \\ u(x,0) = u_0(x) \geq, \not\equiv 0,\ v(x,0) = v_0(x) \geq, \not\equiv 0, & x \in \Omega, \end{cases} \tag{1.3}$$

where $u(x,t)$ and $v(x,t)$ represent the population densities of the prey and predator, respectively. The functions $m_1(x)$ and $m_2(x)$ represent the carrying capacity or intrinsic growth rate of populations u and v, respectively, with $m_1(x)$ and $m_2(x)$ being non-constant to reflect spatial heterogeneity of the environment. For simplicity, we assume $d_1(x) \equiv d_1, d_2(x) \equiv d_2$ and that $b_1(x) \equiv b_1, b_2(x) \equiv b_2$, so that the parameters $d_1, d_2 > 0$ are the constant dispersal rates of populations u and v, respectively, while the parameters b_1, $b_2 > 0$ are the predation rate and the conversion rate, respectively. The advective terms $\nabla \cdot [\alpha_1 u \nabla m_1(x)]$ ($\nabla \cdot [\alpha_2 v \nabla m_2(x)]$) indicate that species u (v) exhibit directed movement along the resource $m_1(x)$ ($m_2(x)$) with positive advection rate α_1 (α_2). Ω is a bounded domain in $\mathbb{R}^n (1 \leq n \leq 3)$ with smooth boundary $\partial\Omega$. The initial conditions of system (1.3) are assumed to satisfy the following compatibility condition:

$$u_0(x) = 0, \quad v_0(x) = 0, \quad x \in \partial\Omega. \tag{1.4}$$

For simplicity, in the rest of this paper, $m_1(x)$ and $m_2(x)$ are abbreviated as m_1 and m_2, respectively. Inspired by the change of variables described in [1], we let $\tilde{u} = e^{-(\alpha_1/d_1)m_1}u$, and $\tilde{v} = e^{-(\alpha_2/d_2)m_2}v$, denoting $\tilde{\alpha_1} = \alpha_1/d_1$, $\tilde{\alpha_2} = \alpha_2/d_2$ then dropping the tilde signs to transform system (1.3) into the following equivalent system:

$$\begin{cases} \dfrac{\partial u}{\partial t} = e^{-\alpha_1 m_1}\nabla \cdot [d_1 e^{\alpha_1 m_1}\nabla u] + u\left[m_1(x) - e^{\alpha_1 m_1}u - \frac{b_1 e^{\alpha_2 m_2}v}{1+T_h e^{\alpha_1 m_1}u}\right], & x \in \Omega, t > 0, \\ \dfrac{\partial v}{\partial t} = e^{-\alpha_2 m_2}\nabla \cdot [d_2 e^{\alpha_2 m_2}\nabla v] + v\left[m_2(x) + \frac{b_2 e^{\alpha_1 m_1}u}{1+T_h e^{\alpha_1 m_1}u} - e^{\alpha_2 m_2}v\right], & x \in \Omega, t > 0, \\ u(x,t) = v(x,t) = 0, & x \in \partial\Omega, t > 0, \\ u(x,0) = e^{-\alpha_1 m_1}u_0(x), v(x,0) = e^{-\alpha_2 m_2}v_0(x), & x \in \Omega. \end{cases} \tag{1.5}$$

Throughout the paper, we assume that both $m_1(x)$ and $m_2(x)$ satisfy the following hypothesis:

(H) $m_i(x) \in C^2(\overline{\Omega}),\ \max_{x\in\overline{\Omega}} m_i(x) > 0,\ i = 1, 2.$

In the present work, we are primarily interested in the steady-state solutions of (1.5). Denote by $\lambda = 1/d_1$, $l = 1/d_2$. The steady-state system corresponding to (1.5) is given by

$$\begin{cases} 0 = \nabla \cdot [e^{\alpha_1 m_1} \nabla u] + \lambda u e^{\alpha_1 m_1} \left[m_1(x) - e^{\alpha_1 m_1} u - \frac{b_1 e^{\alpha_2 m_2} v}{1 + T_h e^{\alpha_1 m_1} u} \right], & x \in \Omega, \\ 0 = \nabla \cdot [e^{\alpha_2 m_2} \nabla v] + l v e^{\alpha_2 m_2} \left[m_2(x) + \frac{b_2 e^{\alpha_1 m_1} u}{1 + T_h e^{\alpha_1 m_1} u} - e^{\alpha_2 m_2} v \right], & x \in \Omega, \\ u(x) = v(x) = 0, & x \in \partial\Omega. \end{cases} \tag{1.6}$$

We call $(0, 0)$ the trivial steady state, noting that it is always a solution. The semi-trivial steady state refers to a solution for which one variable is zero while the other variable is non-zero. A nontrivial steady-state solution refers to a solution for which both variables are nonzero. In ecological settings, a semi-trivial state implies that one populations persist while the other is extirpated, whereas a nontrivial steady-state solution implies that two populations can persist simultaneously, otherwise known as a coexistence steady state.

Let $\lambda_1, l_1, \widetilde{l}(\lambda), \widetilde{\lambda}(l)$ be the principal eigenvalues defined as in (4.1), (4.16) and (4.17). Our main results can be summarized as follows (see also Fig. 1):

(i) When $\lambda < \lambda_1$ and $l < l_1$, the only solution is the trivial steady-state solution $(0, 0)$, which is globally attractive (see Theorem 4.7).

(ii) As the parameter λ increases through λ_1, $(0, 0)$ loses its stability, and a spatially inhomogeneous semi-trivial steady-state solution $(u_\lambda, 0)$ bifurcating from $(0, 0)$ appears (see Theorem 4.1), which is globally attractive when $l < \widetilde{l}(\lambda)$ (see Theorem 4.5 for local stability and Theorem 4.8 for global stability). As the parameter l increases through $\widetilde{l}(\lambda)$, the semi-trivial steady-state solution $(u_\lambda, 0)$ loses stability, and a secondary bifurcation occurs at $l = \widetilde{l}(\lambda)$, leading to a spatially inhomogeneous coexistence steady-state solution (see Theorem 5.4). This coexistence steady-state solution exists near $l = \widetilde{l}(\lambda)$ and the condition for local asymptotic stability is given (see Theorem 5.9).

(iii) Similarly, when the parameter l passes through l_1, $(0, 0)$ becomes unstable, and a spatially inhomogeneous semi-trivial steady-state solution $(0, v_l)$ branches out from $(0, 0)$ (see Theorem 4.2) which is globally attractive when $\lambda < \widetilde{\lambda}(l)$ (see Theorem 4.5 for local stability and Theorem 4.9 for global stability). As the parameter λ increases through $\widetilde{\lambda}(l)$, the semi-trivial steady-state solution $(0, v_l)$ loses stability, and a secondary bifurcation occurs at $\lambda = \widetilde{\lambda}(l)$, branching out a spatially inhomogeneous coexistence steady-state solution (see Theorem 5.10), and the stability conditions for the coexistence steady-state solution near $\lambda = \widetilde{\lambda}(l)$ are given (see Theorem 5.13).

(iv) The trivial steady-state solution $(0, 0)$ is found to bifurcate at the point (λ_1, l_1), leading to a coexistence steady-state solution (see Theorem 5.1). In the neighbourhood of (λ_1, l_1), the coexistence state is locally asymptotically stable (see Theorem 5.3); moreover, the coexistence state is unique and connects coexistence solutions that bifurcate from $(u_\lambda, 0)$ at $l = \widetilde{l}(\lambda)$ and $(0, v_l)$ at $\lambda = \widetilde{\lambda}(l)$.

In addition to the results above, we investigate the effect of advection along the resource gradient on the population dynamics. We find that the impact of advection is monotonic depending on whether the resource function is convex or concave, at least for small rates of advection. If the resource function is convex, advection along the resource gradient is detrimental for the survival of the population by decreasing the size of the parameter region for which persistence is guaranteed. On the other hand, if the resource function is concave, advection along the resource gradient is beneficial to the survival of the population by increasing the size of the parameter region for which persistence is guaranteed. This is observed analytically in Corollary 6.2. In Sect. 6, we provide two key examples highlighting precise behaviour of the principal eigenvalue and therefore the effective growth rate of the population, with respect to the advection rate. Complementing these analytical insights, we present some numerical simulations to further explore the impacts of advection on the persistence or extirpation in full the predator–prey system.

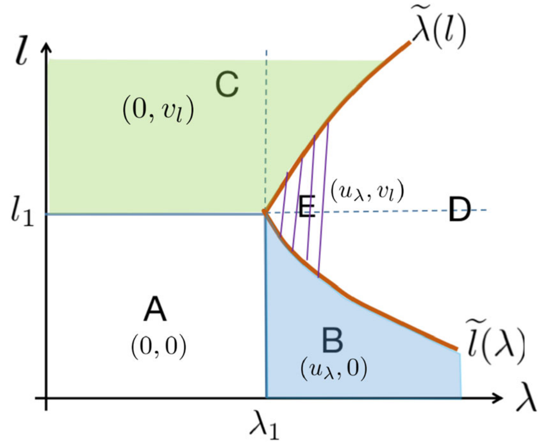

Fig. 1. A stability diagram showing the asymptotic behaviour of solutions depending on rates of diffusion in relation to two principal eigenvalues. In region A, $(0, 0)$ is a global attractor. In region B, $(u_\lambda, 0)$ is a global attractor. In region C, $(0, v_l)$ is a global attractor. In region D, $(0, 0)$, $(u_\lambda, 0)$ and $(0, v_l)$ all are unstable. Near $\widetilde{\lambda}(l)$ and $\widetilde{l}(\lambda)$, there exists coexistence steady state(s); in particular, there exists a unique coexistence steady state in region E bifurcating from $(0, 0)$ at the bifurcation point (λ_1, l_1), connecting the coexistence solution bifurcating from $(u_\lambda, 0)$ and the coexistence solution bifurcating from $(0, v_l)$

It is well known that dealing with steady-state solutions subject to homogeneous Dirichlet boundary conditions can be challenging, primarily because such solutions, except for the trivial solution, are spatially inhomogeneous. Of course, when a model has explicit environmental heterogeneity, nonconstant steady states are expected; the challenge in the case of homogeneous Dirichlet boundary conditions is that there are no nontrivial steady states *even when all other parameters are spatially homogeneous*. Moreover, the explicit expression of the spatially inhomogeneous steady-state solutions is crucial for the analysis of the corresponding linearized equations, and these linearized equations at the spatially inhomogeneous steady-state solutions are themselves spatially inhomogeneous. Complicating matters further, the diffusion–advection operator is not self-adjoint. There are various techniques available in the literature to investigate the existence of non-constant solutions, such as index theory [13], Leray–Schauder degree theory [27], Lyapunov–Schmidt reduction [37], iteration methods [28], or bifurcation theory [11]. In general, the bifurcation theorem [11] is typically applied when bifurcating from a simple eigenvalue. When considering bifurcations from a repeated eigenvalue, other methods must be employed.

The remainder of the paper is organized as follows: In Sect. 2, we give some basic conventions and preliminaries. The well-posedness of model (1.3) is given via the upper and lower solution method in Sect. 3. Section 4 is devoted to the existence and stability of trivial and semi-trivial steady-state solutions by the local bifurcation theory and spectral analysis. The global attractivity can be obtained via the comparison principle and continuity properties of a principal eigenvalue. In Sect. 5, we study the existence and stability of coexistence steady states bifurcating from the trivial and semi-trivial steady states near the bifurcation point. In Sect. 6, we discuss the effects of advection and spatial heterogeneity on species persistence and extinction and provide numerical simulations to compliment the theoretical insights.

Throughout this paper, we denote spaces by $X = H^2(\Omega, \mathbb{R}) \cap H_0^1(\Omega, \mathbb{R})$, $Y = L^2(\Omega, \mathbb{R})$. We also define the complexification of a linear space Z to be $Z_{\mathbb{C}} := Z \oplus iZ = \{x_1 + ix_2 | x_1, x_2 \in Z\}$, and denote the domain of a linear operator L by $\mathbb{D}(L)$, the kernel of L by $\mathbb{N}(L)$, and the range of L by $\mathbb{R}(L)$. For the complex-valued Hilbert space $Y_{\mathbb{C}}^2$, we use the standard inner product $\langle u, v\rangle = \int_\Omega \overline{u}(x)^{\mathrm{T}} v(x) \mathrm{d}x$.

2. Preliminaries

We first introduce the following eigenvalue problem:

$$\begin{cases} \nabla \cdot \left[e^{\alpha q(x)} \nabla \phi\right] + \lambda e^{\alpha q(x)} m(x)\phi = 0, & x \in \Omega, \\ \phi(x) = 0, & x \in \partial\Omega, \end{cases} \tag{2.1}$$

where $\alpha > 0$, $q(x) \in C^1(\Omega)$ is strictly positive in Ω, and $m(x) \in L^\infty(\Omega)$ may change sign in Ω. We say that a problem has a *principal eigenvalue* if it has a positive eigenfunction. It follows from [5,37] that (2.1) has some important properties which we highlight here for convenience.

Lemma 2.1. *The following hold.*

(i) *Problem* (2.1) *has a unique principal eigenvalue $\lambda_*(\alpha, q, m)$ with positive eigenfunction denoted by ϕ_1.*
(ii) *The principal eigenvalue $\lambda_*(\alpha, q, m)$ has a variational characterization given by*

$$\lambda_*(\alpha, q, m) = \inf_{\phi \in \Phi} \left[\frac{\int_\Omega e^{\alpha q(x)} |\nabla \phi|^2 \mathrm{d}x}{\int_\Omega e^{\alpha q(x)} m(x) \phi^2 \mathrm{d}x} \right], \tag{2.2}$$

where

$$\Phi = \left\{ \phi \in W_0^{1,2}(\Omega) : \phi = 0 \ \textit{in}\ \partial\Omega \ \text{and} \int_\Omega e^{\alpha q(x)} m(x)\phi^2 \mathrm{d}x > 0 \right\}.$$

(iii) $\lambda_*(\alpha, q, m_1) \le \lambda_*(\alpha, q, m_2)$ whenever $m_1(x) \le m_2(x)$ in Ω with strict inequality whenever $m_1(x) \not\equiv m_2(x)$.

We then consider the following initial boundary value problem:

$$\begin{cases} \theta_t = e^{-\alpha q(x)} \nabla \cdot \left[e^{\alpha q(x)} \nabla \theta\right] + \lambda \theta \left(m(x) - \theta\right), & x \in \Omega,\ t > 0, \\ \theta(x,t) = 0, & x \in \partial\Omega,\ t > 0, \\ \theta(x,0) = \theta_0(x) \ge, \not\equiv 0, & x \in \Omega. \end{cases} \tag{2.3}$$

The following can be found in, e.g. [1,22]

Proposition 2.2. *Suppose that* (H) *holds. Denote by $\lambda_* := \lambda_*(\alpha, q, m)$ the principal eigenvalue of* (2.1) *and let $\theta(\cdot, t)$ be the solution of* (2.3). *For any nontrivial initial data θ_0 we have the following dichotomy:*

(i) *if $\lambda \le \lambda_*$, then $\lim_{t\to\infty} \theta(\cdot, t) = 0$ in $C(\overline{\Omega})$.*
(ii) *if $\lambda > \lambda_*$, then $\lim_{t\to\infty} \theta(\cdot, t) = \theta_\alpha(\lambda)$ in $C(\overline{\Omega})$, where $\theta_\alpha(\lambda)$ is the unique positive steady state solving problem* (2.3).

Proposition 2.3. *Let $\theta_\alpha(\lambda)$ and λ_* be defined in Proposition* 2.2. *If $\lambda > \lambda_*$, then*

$$0 \le \theta_\alpha(\lambda) \le \max_{\overline{\Omega}}(m(x)).$$

Proof. It is not difficult to verify that 0 and $\max_{\overline{\Omega}}(m(x))$ are, respectively, a lower and upper solution to the steady-state equation corresponding to problem (2.3). Consequently, there exists a nontrivial steady state $\tilde{\theta}_\alpha(\lambda)$ solving problem (2.3) lying between the lower and upper solutions. Since $\theta_\alpha(\lambda)$ is unique, there holds $\theta_\alpha(\lambda) \equiv \overline{\theta}_\alpha(\lambda)$. □

3. Well-posedness

We use the upper and lower solution method to ensure the existence and boundedness of the solution to system (1.3).

Theorem 3.1. *Suppose that* (H) *and compatibility conditions* (1.4) *hold. Then, system* (1.3) *has a unique positive classical solution* $(u,v) \in [C^{2+\delta,1+\delta/2}(\overline{\Omega}\times[0,\infty))]^2$ *for some* $\delta \in (0,1)$*. Moreover,*

$$0 \le u \le M, \quad 0 \le v \le N, \tag{3.1}$$

where M *and* N *are positive constants defined in* (3.3) *and* (3.5).

Proof. According to [44], system (1.3) is a mixed quasi-monotonic system for $u,v \ge 0$. If $\overline{u},\overline{v},\underline{u},\underline{v}$ are nonnegative and satisfy

$$\begin{cases} \dfrac{\partial \overline{u}}{\partial t} - e^{-\alpha_1 m_1}\nabla\cdot[d_1 e^{\alpha_1 m_1}\nabla \overline{u}] \ge \overline{u}\left[m_1(x) - e^{\alpha_1 m_1}\overline{u} - \frac{b_1 e^{\alpha_2 m_2}\underline{v}}{1+T_h e^{\alpha_1 m_1}\overline{u}}\right], & \\ & x\in\Omega, t>0,\\ \dfrac{\partial \underline{v}}{\partial t} - e^{-\alpha_2 m_2}\nabla\cdot[d_2 e^{\alpha_2 m_2}\nabla \underline{v}] \le \underline{v}\left[m_2(x) + \frac{b_2 e^{\alpha_1 m_1}\underline{u}}{1+T_h e^{\alpha_1 m_1}\underline{u}} - e^{\alpha_2 m_2}\underline{v}\right], & x\in\Omega, t>0,\\ \dfrac{\partial \underline{u}}{\partial t} - e^{-\alpha_1 m_1}\nabla\cdot[d_1 e^{\alpha_1 m_1}\nabla \underline{u}] \le \underline{u}\left[m_1(x) - e^{\alpha_1 m_1}\underline{u} - \frac{b_1 e^{\alpha_2 m_2}\overline{v}}{1+T_h e^{\alpha_1 m_1}\overline{v}}\right], & x\in\Omega, t>0,\\ \dfrac{\partial \overline{v}}{\partial t} - e^{-\alpha_2 m_2}\nabla\cdot[d_2 e^{\alpha_2 m_2}\nabla \overline{v}] \ge \overline{v}\left[m_2(x) + \frac{b_2 e^{\alpha_1 m_1}\overline{u}}{1+T_h e^{\alpha_1 m_1}\overline{u}} - e^{\alpha_2 m_2}\overline{v}\right], & x\in\Omega, t>0,\\ \overline{u}\ge 0 \ge \underline{u},\ \overline{v}\ge 0\ge \underline{v}, & x\in\partial\Omega, t>0,\\ \overline{u}\ge e^{-\alpha_1 m_1}u_0 \ge \underline{u},\ \overline{v}\ge e^{-\alpha_2 m_2}v_0\ge \underline{v}, & x\in\Omega, t=0, \end{cases} \tag{3.2}$$

then $(\overline{u},\overline{v})$ and $(\underline{u},\underline{v})$ are called ordered upper and lower solutions (see, e.g. [44]) to system (1.3), respectively. Set

$$\underline{u}=\underline{v}=0,\ \overline{u}=M:=\max\left\{\frac{\max_{\overline{\Omega}}(m_1(x))}{e^{\min_{\overline{\Omega}}(\alpha_1 m_1(x))}},\ \max_{\Omega}(e^{-\alpha_1 m_1}u_0(x))\right\} \tag{3.3}$$

and let $\overline{v}$ solve

$$\begin{cases} \dfrac{\partial \overline{v}}{\partial t} - e^{-\alpha_2 m_2}\nabla\cdot[d_2 e^{\alpha_2 m_2}\nabla\overline{v}] = \overline{v}[m_2(x) + \frac{b_2 e^{\alpha_1 m_1}M}{1+T_h e^{\alpha_1 m_1}M} - e^{\alpha_2 m_2}\overline{v}], & x\in\Omega, t>0,\\ \overline{v}(x,t)=0, & x\in\Omega, t>0,\\ \overline{v}(x,0)=e^{-\alpha_2 m_2}v_0(x), & x\in\Omega, t=0. \end{cases} \tag{3.4}$$

From Propositions 2.2 and 2.3, problem (3.4) has a unique global solution. Furthermore,

$$\overline{v}\le N:=\max\left\{\frac{\max_{\overline{\Omega}}(m_2(x)+\frac{b_2 e^{\alpha_1 m_1}M}{1+T_h e^{\alpha_1 m_1}M})}{e^{\min_{\overline{\Omega}}(\alpha_2 m_2(x))}},\ \max_{\overline{\Omega}}\left\{e^{-\alpha_1 m_1}v_0(x)\right\}\right\} \tag{3.5}$$

Clearly, $(\overline{u},\overline{v}),(\underline{u},\underline{v})$ comprise a pair of ordered upper and lower solutions to system (1.3). Therefore, (1.3) has a unique global classical solution (u,v) satisfying

$$0=\underline{u}\le u\le\overline{u}=M \text{ and } 0=\underline{v}\le v\le\overline{v}=N,$$

in $\overline{\Omega}\times(0,\infty)$. The maximum principle implies that in fact the inequality is strict. □

4. Existence and global stability of trivial and semi-trivial steady-state solutions

For simplicity, denote by

$$\lambda_*(\alpha_1,m_1,m_1):=\lambda_1,\quad \lambda_*(\alpha_2,m_2,m_2):=l_1, \tag{4.1}$$

with corresponding eigenfunctions φ_1 and ψ_1, respectively.

4.1. Existence

Notice that system (1.6) always has the trivial solution $(0,0)$ along with the semi-trivial solutions $(u_\lambda, 0)$ and $(0, v_l)$, where u_λ and v_l are the unique solutions to

$$\begin{cases} \nabla\cdot[e^{\alpha_1 m_1}\nabla u] + \lambda u e^{\alpha_1 m_1}[m_1(x) - e^{\alpha_1 m_1}u] = 0, & x\in\Omega,\\ u(x) = 0, & x\in\partial\Omega. \end{cases} \tag{4.2}$$

and

$$\begin{cases} \nabla\cdot[e^{\alpha_2 m_2}\nabla v] + l v e^{\alpha_2 m_2}[m_2(x) - e^{\alpha_2 m_2}v] = 0, & x\in\Omega,\\ v(x) = 0, & x\in\partial\Omega. \end{cases} \tag{4.3}$$

respectively. Denote by

$$\begin{aligned} L_1 &= \nabla\cdot[e^{\alpha_1 m_1}\nabla] + \lambda_1 e^{\alpha_1 m_1} m_1(x),\\ L_2 &= \nabla\cdot[e^{\alpha_2 m_2}\nabla] + l_1 e^{\alpha_2 m_2} m_2(x),\\ L &= \begin{pmatrix} L_1 & 0\\ 0 & L_2\end{pmatrix}. \end{aligned} \tag{4.4}$$

Notice that

$$\begin{aligned} X &= \mathbb{N}(L_1)\oplus X_1 = \mathbb{N}(L_2)\oplus X_2, \text{ and } X^2 = \mathbb{N}(L)\oplus X_3,\\ Y &= \mathbb{N}(L_1)\oplus Y_1 = \mathbb{N}(L_2)\oplus Y_2, \text{ and } Y^2 = \mathbb{N}(L)\oplus Y_3, \end{aligned}$$

where

$$\begin{aligned} &\mathbb{N}(L_1) = \operatorname{span}\{\varphi_1\},\ \mathbb{N}(L_2) = \operatorname{span}\{\psi_1\},\\ &\mathbb{N}(L) = \operatorname{span}\{\Phi_1,\ \Psi_1\},\ \text{where } \Phi_1 = (\varphi_1, 0)^T,\ \Psi_1 = (0,\psi_1)^T,\\ &X_1 = \{y\in X : \langle\varphi_1, y\rangle = 0\},\ X_2 = \{y\in X : \langle\psi_1, y\rangle = 0\},\\ &X_3 = \{y\in X^2 : \langle\Phi_1, y\rangle = \langle\Psi_1, y\rangle = 0\},\\ &Y_1 = \mathbb{R}(L_1) = \{y\in Y : \langle\varphi_1, y\rangle = 0\},\ Y_2 = \mathbb{R}(L_2) = \{y\in Y : \langle\psi_1, y\rangle = 0\},\\ &Y_3 = \mathbb{R}(L_1) = \{y\in Y^2 : \langle\Phi_1, y\rangle = \langle\Psi_1, y\rangle = 0\}. \end{aligned}$$

We are now in a position to show some properties of u_λ and v_l.

Theorem 4.1. *Suppose that* (H) *holds. Let λ_1 be defined as in* (4.1) *and φ_1 the eigenfunction. Then, there exists a $\lambda^* > \lambda_1$ and a continuously differentiable mapping $\lambda \mapsto (\zeta_\lambda, \beta_\lambda) \in X_1\times\mathbb{R}$ such that for any $\lambda\in(\lambda_1, \lambda^*)$, u_λ is the positive solution of* (4.2)*, where u_λ is given by*

$$u_\lambda = \beta_\lambda(\lambda-\lambda_1)[\varphi_1 + (\lambda-\lambda_1)\zeta_\lambda]. \tag{4.5}$$

Moreover, when $\lambda = \lambda_1$,

$$\beta_{\lambda_1} = \frac{\int_\Omega e^{\alpha_1 m_1} m_1(x)\varphi_1^2 \mathrm{d}x}{\lambda_1\int_\Omega e^{2\alpha_1 m_1}\varphi_1^3 \mathrm{d}x}, \tag{4.6}$$

and ζ_{λ_1} is the unique solution of the following equation:

$$L_1\zeta + e^{\alpha_1 m_1} m_1(x)\varphi_1 - \lambda_1\beta_{\lambda_1} e^{2\alpha_1 m_1}\varphi_1^2 = 0, \tag{4.7}$$

where L_1 is defined in (4.4)*.*

Proof. The assumption (H) implies that β_{λ_1} is positive. Note that

$$e^{\alpha_1 m_1}\varphi_1[m_1(x) - \lambda_1\beta_{\lambda_1}e^{\alpha_1 m_1}\varphi_1] \in \mathbb{R}(L_1).$$

Thus, β_{λ_1} and ζ_{λ_1} are well defined. Let $u = \beta(\lambda - \lambda_1)[\varphi_1 + (\lambda - \lambda_1)\zeta]$ as in (4.2). Then, we are able to define a nonlinear mapping $T : X_1 \times \mathbb{R}^2 \to Y$ by

$$\begin{aligned} T(\zeta, \beta, \lambda) = L_1\zeta + e^{\alpha_1 m_1}m_1(x)[\varphi_1 + (\lambda - \lambda_1)\zeta] \\ - \lambda\beta e^{2\alpha_1 m_1}[\varphi_1 + (\lambda - \lambda_1)\zeta]^2. \end{aligned} \tag{4.8}$$

An easy computation shows that $T(\zeta_{\lambda_1}, \beta_{\lambda_1}, \lambda_1) = 0$. The Fréchet derivative of T with respect to (ζ, β) at $(\zeta_{\lambda_1}, \beta_{\lambda_1}, \lambda_1)$ has the form:

$$D_{(\zeta,\beta)}T(\zeta_{\lambda_1}, \beta_{\lambda_1}, \lambda_1)[\widetilde{\zeta}, \widetilde{\beta}] = L_1\widetilde{\zeta} - \lambda_1\widetilde{\beta}e^{2\alpha_1 m_1}\varphi_1^2.$$

It is straightforward to verify that $D_{(\zeta,\beta)}T(\zeta_{\lambda_1}, \beta_{\lambda_1}, \lambda_1)$ is a bijection from $X_1 \times \mathbb{R}$ to Y. The implicit function theorem yields that there exists a $\lambda^* > \lambda_1$ and a continuously differentiable mapping $\lambda \mapsto (\zeta_\lambda, \beta_\lambda) \in X_1 \times \mathbb{R}$ such that $T(\zeta_\lambda, \beta_\lambda, \lambda) = 0$ for each $\lambda \in (\lambda_1, \lambda^*)$. □

Similarly, we have the following analog for v_l.

Theorem 4.2. *Suppose that* (H) *holds. Let l_1 be defined as in* (4.1) *and ψ_1 the eigenfunction. Then, there exists a $l^* > l_1$ and a continuously differentiable mapping $l \mapsto (\varepsilon_l, \gamma_l) \in X_2 \times \mathbb{R}$ such that for each $l \in (l_1, l^*)$, v_l is the positive solution of* (4.3)*, where v_l is given by*

$$v_l = \gamma_l(l - l_1)[\psi_1 + (l - l_1)\varepsilon_\lambda]. \tag{4.9}$$

Moreover, when $l = l_1$,

$$\gamma_{l_1} = \frac{\int_\Omega e^{\alpha_2 m_2}m_2(x)\psi_1^2 \mathrm{d}x}{l_1\int_\Omega e^{2\alpha_2 m_2}\psi_1^3 \mathrm{d}x}, \tag{4.10}$$

and ε_{l_1} is the unique solution of the following equation:

$$L_2\varepsilon + e^{\alpha_2 m_2}m_2(x)\psi_1 - l_1\gamma_{l_1}e^{2\alpha_2 m_2}\psi_1^2 = 0, \tag{4.11}$$

where L_2 is defined in (4.4)*.*

Remark 4.3. **Recall that from Proposition 2.2, the semi-trivial state $(u_\lambda, 0)$ exists if and only if $\lambda > \lambda_1$, and the semi-trivial state $(0, v_l)$ exists if and only if $l > l_1$.**

4.2. Local stability

The linearization operator of system (1.6) at $(0, 0)$ is:

$$L_0(\lambda, l) = \begin{pmatrix} \widetilde{L}_1 & 0 \\ 0 & \widetilde{L}_2 \end{pmatrix},$$

where

$$\widetilde{L}_1 = \nabla \cdot [e^{\alpha_1 m_1}\nabla] + \lambda e^{\alpha_1 m_1}m_1(x),\ \widetilde{L}_2 = \nabla \cdot [e^{\alpha_2 m_2}\nabla] + le^{\alpha_2 m_2}m_2(x).$$

By the Riesz–Schauder theory [21], we deduce that the spectrum of L_0 consists only of real eigenvalues. Hence, we have the following local stability result for the trivial steady state.

Theorem 4.4. *Suppose that* (H) *holds. Let λ_1 and l_1 be defined as in* (4.1)*. The trivial solution $(0, 0)$ is locally asymptotically stable if both $\lambda < \lambda_1$ and $l < l_1$, and it is unstable if at least one of $\lambda > \lambda_1$ or $l > l_1$ holds.*

The linearization operators of system (1.5) at $(u_\lambda, 0)$ and $(0, v_l)$ are:

$$L_\lambda(\lambda, l) = \begin{pmatrix} \widetilde{L}_1 - 2\lambda e^{2\alpha_1 m_1} u_\lambda & -\dfrac{\lambda b_1 e^{\alpha_1 m_1 + \alpha_2 m_2} u_\lambda}{1 + T_h e^{\alpha_1 m_1} u_\lambda} \\ 0 & \widetilde{L}_2 + \dfrac{l b_2 e^{\alpha_1 m_1 + \alpha_2 m_2} u_\lambda}{1 + T_h e^{\alpha_1 m_1} u_\lambda} \end{pmatrix}, \tag{4.12}$$

and

$$L_l(\lambda, l) = \begin{pmatrix} \widetilde{L}_1 - \lambda b_1 e^{\alpha_1 m_1 + \alpha_2 m_2} v_l & 0 \\ l b_2 e^{\alpha_1 m_1 + \alpha_2 m_2} v_l & \widetilde{L}_2 - 2l e^{2\alpha_2 m_2} v_l \end{pmatrix}, \tag{4.13}$$

respectively. One can readily check that the linear stability of $(u_\lambda, 0)$ and $(0, v_l)$ are determined by the respective principal eigenvalues of the following eigenvalue problems:

$$\begin{cases} \nabla \cdot [e^{\alpha_2 m_2} \nabla \chi] + l \chi e^{\alpha_2 m_2} \left[m_2(x) + \dfrac{b_2 e^{\alpha_1 m_1} u_\lambda}{1 + T_h e^{\alpha_1 m_1} u_\lambda} \right] = 0, & x \in \Omega, \\ \chi(x) = 0, & x \in \partial\Omega, \end{cases} \tag{4.14}$$

and

$$\begin{cases} \nabla \cdot [e^{\alpha_1 m_1} \nabla \kappa] + \lambda \kappa e^{\alpha_1 m_1} \left[m_1(x) - b_1 e^{\alpha_2 m_2} v_l \right] = 0, \quad x \in \Omega, \\ \kappa(x) = 0, \quad x \in \partial\Omega. \end{cases} \tag{4.15}$$

Denote by $(\widetilde{l}(\lambda), \widetilde{\chi}_1(\lambda))$ and $(\widetilde{\lambda}(l), \widetilde{\kappa}_1(l))$ the principal eigenpairs of (4.14) and (4.15), respectively. By the variational characterization (2.2), we have

$$\widetilde{l}(\lambda) := \lambda_* \left(\alpha_2, m_2, m_2 + \frac{b_2 e^{\alpha_1 m_1} u_\lambda}{1 + T_h e^{\alpha_1 m_1} u_\lambda} \right) = \inf_{\chi \in \Phi_1} \left[\frac{\int_\Omega e^{\alpha_2 m_2(x)} |\nabla \chi|^2 dx}{\int_\Omega e^{\alpha_2 m_2(x)} \left(m_2(x) + \dfrac{b_2 e^{\alpha_1 m_1} u_\lambda}{1 + T_h e^{\alpha_1 m_1} u_\lambda} \right) \chi^2 \mathrm{d}x} \right] \tag{4.16}$$

and

$$\widetilde{\lambda}(l) := \lambda_* \left(\alpha_1, m_1, m_1 - b_1 e^{\alpha_2 m_2} v_l \right) = \inf_{\kappa \in \Psi_1} \left[\frac{\int_\Omega e^{\alpha_1 m_1(x)} |\nabla \kappa|^2 dx}{\int_\Omega e^{\alpha_1 m_1(x)} \left(m_1(x) - b_1 e^{\alpha_2 m_2} v_l \right) \kappa^2 \mathrm{d}x} \right], \tag{4.17}$$

where

$$\Phi_1 = \left\{ \chi \in W_0^{1,2}(\Omega) : \chi = 0 \text{ on } \partial\Omega \text{ and } \int_\Omega e^{\alpha_2 m_2(x)} \left(m_2(x) + \frac{b_2 e^{\alpha_1 m_1} u_\lambda}{1 + T_h e^{\alpha_1 m_1} u_\lambda} \right) \chi^2 \mathrm{d}x > 0 \right\},$$
$$\Psi_1 = \left\{ \kappa \in W_0^{1,2}(\Omega) : \kappa = 0 \text{ on } \partial\Omega \text{ and } \int_\Omega e^{\alpha_1 m_1(x)} \left(m_1(x) - b_1 e^{\alpha_2 m_2} v_l \right) \kappa^2 \mathrm{d}x > 0 \right\}.$$

We then have the following local stability result for the semi-trivial steady states.

Theorem 4.5. *Suppose that* (H) *holds and let* $\widetilde{l}(\lambda)$ *and* $\widetilde{\lambda}(l)$ *be defined as in* (4.16) *and* (4.17)*. Then, we have the following dichotomies:*

- (i) *Suppose* $\lambda > \lambda_1$*. Then, the semi-trivial state* $(u_\lambda, 0)$ *is locally asymptotically stable whenever* $l < \widetilde{l}(\lambda)$ *and is unstable whenever* $l > \widetilde{l}(\lambda)$*.*
- (ii) *Suppose* $l > l_1$*. Then, the semi-trivial state* $(0, v_l)$ *is locally asymptotically stable whenever* $\lambda < \widetilde{\lambda}(l)$ *and is unstable whenever* $\lambda > \widetilde{\lambda}(l)$*.*

Notice that this behaviour is consistent with the *slower diffuser always wins!* result, where a smaller rate of diffusive movement is beneficial to population persistence in a spatially heterogeneous but temporally constant environment. Next, we introduce some useful properties of $\widetilde{l}(\lambda)$ and $\widetilde{\lambda}(l)$ following the efforts of [25,45].

Lemma 4.6. *The functions* $\widetilde{l}(\lambda)$ *and* $\widetilde{\lambda}(l)$ *defined in* (4.16) *and* (4.17) *satisfy the following properties:*

(i) (a) $\widetilde{l}(\cdot) \in C([\lambda_1, +\infty))$, *and* $\widetilde{l}(\lambda_1) = l_1$;
(b) $\widetilde{l}(\cdot) \in C^1((\lambda_1, +\infty))$, *and*

$$\lim_{\lambda \to \lambda_1} \widetilde{l}'(\lambda) = -\frac{l_1 \int_\Omega e^{\alpha_1 m_1} m_1(x) \varphi_1^2 \mathrm{d}x}{\lambda_1 \int_\Omega e^{2\alpha_1 m_1} \varphi_1^3 \mathrm{d}x} \cdot \frac{b_2 \int_\Omega e^{\alpha_1 m_1 + \alpha_2 m_2} \varphi_1 \psi_1^2 \mathrm{d}x}{\int_\Omega e^{\alpha_2 m_2} m_2(x) \psi_1^2 \mathrm{d}x} < 0. \tag{4.18}$$

(ii) (a) $\widetilde{\lambda}(\cdot) \in C([l_1, +\infty))$, *and* $\widetilde{\lambda}(l_1) = \lambda_1$;
(b) $\widetilde{\lambda}(\cdot) \in C^1((l_1, +\infty))$, *and*

$$\lim_{l \to l_1} \widetilde{\lambda}'(l) = \frac{\lambda_1 \int_\Omega e^{\alpha_2 m_2} m_2(x) \psi_1^2 \mathrm{d}x}{l_1 \int_\Omega e^{2\alpha_2 m_2} \psi_1^3 \mathrm{d}x} \cdot \frac{b_1 \int_\Omega e^{\alpha_1 m_1 + \alpha_2 m_2} \psi_1 \varphi_1^2 \mathrm{d}x}{\int_\Omega e^{\alpha_1 m_1} m_1(x) \varphi_1^2 \mathrm{d}x} > 0. \tag{4.19}$$

Proof. We give the proof for case (i) only as case (ii) follows in a similar fashion. Fix $h > 0$. By using the variational characterization (4.16) of $\widetilde{l}(\lambda)$ with the corresponding principal eigenfunction $\chi_1(\lambda)$, we obtain

$$\begin{aligned}
\widetilde{l}(\lambda) &= \frac{\int_\Omega e^{\alpha_2 m_2(x)} |\nabla \widetilde{\chi}_1(\lambda)|^2 \mathrm{d}x}{\int_\Omega e^{\alpha_2 m_2(x)} \left(m_2(x) + \dfrac{b_2 e^{\alpha_1 m_1} u_\lambda}{1 + T_h e^{\alpha_1 m_1} u_\lambda} \right) \widetilde{\chi}_1^2(\lambda) \mathrm{d}x} \\
&\le \frac{\int_\Omega e^{\alpha_2 m_2(x)} |\nabla \widetilde{\chi}_1(\lambda + h)|^2 \mathrm{d}x}{\int_\Omega e^{\alpha_2 m_2(x)} \left(m_2(x) + \dfrac{b_2 e^{\alpha_1 m_1} u_\lambda}{1 + T_h e^{\alpha_1 m_1} u_\lambda} \right) \widetilde{\chi}_1^2(\lambda + h) \mathrm{d}x} \\
&= \widetilde{l}(\lambda + h) \frac{\int_\Omega e^{\alpha_2 m_2(x)} \left(m_2(x) + \dfrac{b_2 e^{\alpha_1 m_1} u_{\lambda+h}}{1 + T_h e^{\alpha_1 m_1} u_{\lambda+h}} \right) \widetilde{\chi}_1^2(\lambda + h) \mathrm{d}x}{\int_\Omega e^{\alpha_2 m_2(x)} \left(m_2(x) + \dfrac{b_2 e^{\alpha_1 m_1} u_\lambda}{1 + T_h e^{\alpha_1 m_1} u_\lambda} \right) \widetilde{\chi}_1^2(\lambda + h) \mathrm{d}x},
\end{aligned} \tag{4.20}$$

where the first inequality follows from the definition of Φ_1, that is, $\chi_1(\lambda + h) \in \Phi_1$ for h sufficiently small, and the second equality follows from a direct manipulation and the variational characterization of the eigenvalue. Identical arguments yield

$$\widetilde{l}(\lambda + h) \le \widetilde{l}(\lambda) \frac{\int_\Omega e^{\alpha_2 m_2(x)} \left(m_2(x) + \dfrac{b_2 e^{\alpha_1 m_1} u_\lambda}{1 + T_h e^{\alpha_1 m_1} u_\lambda} \right) \widetilde{\chi}_1^2(\lambda) \mathrm{d}x}{\int_\Omega e^{\alpha_2 m_2(x)} \left(m_2(x) + \dfrac{b_2 e^{\alpha_1 m_1} u_{\lambda+h}}{1 + T_h e^{\alpha_1 m_1} u_{\lambda+h}} \right) \widetilde{\chi}_1^2(\lambda) \mathrm{d}x}. \tag{4.21}$$

Thus, the continuity of $\widetilde{l}$ holds on $[\lambda_1, +\infty)$ since $\lambda \mapsto u_\lambda$ is continuous over $[\lambda_1, +\infty)$. Moreover, it follows from the result of Kato [26, Ch. 5, §.4] that

$$\lim_{\lambda \to \lambda_1} \widetilde{\chi}_1(\lambda) = \psi_1 \text{ in } L^2(\Omega). \tag{4.22}$$

Finally, we have $\widetilde{l}(\lambda_1) \to l_1$ as $\lambda \to \lambda_1$ due to the fact that $\lim\limits_{\lambda \to \lambda_1} u_\lambda = 0$. This proves part (a).

We now proceed to show conclusion (b). Combining (4.20) and (4.21), we obtain

$$\widetilde{l}(\lambda+h)-\widetilde{l}(\lambda)\leq\widetilde{l}(\lambda)\frac{\int_\Omega e^{\alpha_2 m_2(x)}\left(\frac{b_2e^{\alpha_1 m_1}u_\lambda}{1+T_he^{\alpha_1 m_1}u_\lambda}-\frac{b_2e^{\alpha_1 m_1}u_{\lambda+h}}{1+T_he^{\alpha_1 m_1}u_{\lambda+h}}\right)\widetilde{\chi}_1^2(\lambda)\mathrm{d}x}{\int_\Omega e^{\alpha_2 m_2(x)}\left(m_2(x)+\frac{b_2e^{\alpha_1 m_1}u_{\lambda+h}}{1+T_he^{\alpha_1 m_1}u_{\lambda+h}}\right)\widetilde{\chi}_1^2(\lambda)\mathrm{d}x} \tag{4.23}$$

$$\widetilde{l}(\lambda+h)-\widetilde{l}(\lambda)\geq\widetilde{l}(\lambda)\frac{\int_\Omega e^{\alpha_2 m_2(x)}\left(\frac{b_2e^{\alpha_1 m_1}u_\lambda}{1+T_he^{\alpha_1 m_1}u_\lambda}-\frac{b_2e^{\alpha_1 m_1}u_{\lambda+h}}{1+T_he^{\alpha_1 m_1}u_{\lambda+h}}\right)\widetilde{\chi}_1^2(\lambda+h)\mathrm{d}x}{\int_\Omega e^{\alpha_2 m_2(x)}\left(m_2(x)+\frac{b_2e^{\alpha_1 m_1}u_{\lambda+h}}{1+T_he^{\alpha_1 m_1}u_{\lambda+h}}\right)\widetilde{\chi}_1^2(\lambda+h)\mathrm{d}x}. \tag{4.24}$$

Recalling the differentiability of u_λ with respect to λ, we divide (4.23) and (4.24) by h and let $h\to 0$ to obtain

$$\widetilde{l}'(\lambda)=\frac{\widetilde{l}(\lambda)\int_\Omega b_2e^{\alpha_1 m_1+\alpha_2 m_2(x)}\left(-\frac{u_\lambda}{1+T_he^{\alpha_1 m_1}u_\lambda}\right)'\widetilde{\chi}_1^2(\lambda)\mathrm{d}x}{\int_\Omega e^{\alpha_2 m_2(x)}\left(m_2(x)+\frac{b_2e^{\alpha_1 m_1}u_\lambda}{1+T_he^{\alpha_1 m_1}u_\lambda}\right)\widetilde{\chi}_1^2(\lambda)\mathrm{d}x} \tag{4.25}$$

for almost every $\lambda\in(\lambda_1,+\infty)$, where $'=\frac{d}{d\lambda}$ and

$$\left(-\frac{u_\lambda}{1+T_he^{\alpha_1 m_1}u_\lambda}\right)'=-\frac{u_\lambda'(1+T_he^{\alpha_1 m_1}u_\lambda)-u_\lambda T_he^{\alpha_1 m_1}u_\lambda'}{(1+T_he^{\alpha_1 m_1}u_\lambda)^2}. \tag{4.26}$$

By Theorem 4.1, we have

$$\lim_{\lambda\to\lambda_1}-u_\lambda'=-\frac{\int_\Omega e^{\alpha_1 m_1}m_1(x)\varphi_1^2\mathrm{d}x}{\lambda_1\int_\Omega e^{2\alpha_1 m_1}\varphi_1^3\mathrm{d}x}\varphi_1. \tag{4.27}$$

Inserting (4.22) and (4.27) into (4.25)–(4.26) yields (4.18). □

4.3. Global stability

We next investigate the global stability of $(0,0)$, $(u_\lambda,0)$ and $(0,v_l)$ via the maximum and comparison principle. First we note that system (1.5) can be rewritten as:

$$\begin{cases}\lambda\frac{\partial u}{\partial t}=e^{-\alpha_1 m_1}\nabla\cdot[e^{\alpha_1 m_1}\nabla u]+\lambda u\left[m_1(x)-e^{\alpha_1 m_1}u-\frac{b_1e^{\alpha_2 m_2}v}{1+T_he^{\alpha_1 m_1}u}\right], & x\in\Omega,t>0,\\ l\frac{\partial v}{\partial t}=e^{-\alpha_2 m_2}\nabla\cdot[e^{\alpha_2 m_2}\nabla v]+lv\left[m_2(x)+\frac{b_2e^{\alpha_1 m_1}u}{1+T_he^{\alpha_1 m_1}u}-e^{\alpha_2 m_2}v\right], & x\in\Omega,t>0,\\ u(x,t)=v(x,t)=0, & x\in\partial\Omega,t>0,\\ u(x,0)=e^{-\alpha_1 m_1}u_0(x),v(x,0)=e^{-\alpha_2 m_2}v_0(x), & x\in\Omega.\end{cases} \tag{4.28}$$

The following result gives the global asymptotic stability of the trivial steady state.

Theorem 4.7. *Suppose that* (H) *holds. Let λ_1 and l_1 be defined as in* (4.1).

If $\lambda<\lambda_1$ and $l<l_1$, then the trivial steady-state $(0,0)$ *of* (4.28) *is globally attractive among all nonnegative solutions.*

Proof. From Theorem 3.1, we have

$$\lambda\frac{\partial u}{\partial t}\leq e^{-\alpha_1 m_1}\nabla\cdot[e^{\alpha_1 m_1}\nabla u]+\lambda u\left(m_1(x)-e^{\alpha_1 m_1}u\right).$$

Then, $0 \le u \le U$ by the comparison principle, where U is the unique solution of

$$\begin{cases} \lambda \dfrac{\partial U}{\partial t} = e^{-\alpha_1 m_1}\nabla\cdot[e^{\alpha_1 m_1}\nabla U] + \lambda U[m_1(x) - e^{\alpha_1 m_1}U] = 0, & x\in\Omega, t>0, \\ U(x,t) = 0, & x\in\partial\Omega, t>0, \\ U(x,0) = u(x,0), & x\in\Omega. \end{cases} \tag{4.29}$$

Proposition 2.2 implies $\lim_{t\to\infty} U(\cdot,t) = 0$ in $\overline{\Omega}$. Therefore,

$$\limsup_{t\to\infty} u(\cdot,t) \le \limsup_{t\to\infty} U(\cdot,t) = 0 \text{ uniformly in } \overline{\Omega}. \tag{4.30}$$

Consequently, (4.30) implies that for any $\varepsilon > 0$ as small as we like, there exists a time T_ε such that

$$l\frac{\partial v}{\partial t} \le e^{-\alpha_2 m_2}\nabla\cdot[e^{\alpha_2 m_2}\nabla v] + lv(m_2(x)+\varepsilon) - le^{\alpha_2 m_2}v^2, \quad x\in\Omega, t\ge T_\varepsilon.$$

It follows from Lemma (2.1) (see also [37, Lemma 2.4]) that the principal eigenvalue in (2.2) depends monotonically on m, and so we have

$$l_1 = \lambda_*(\alpha_2, m_2, m_2) < \lambda_*(\alpha_2, m_2, m_2+\varepsilon) := l_\varepsilon$$

Since $l < l_1 < l_\varepsilon$, we combine Proposition 2.2 with the comparison principle to conclude that

$$\limsup_{t\to\infty} v(\cdot,t) \le \limsup_{t\to\infty} V(\cdot,t) = 0 \text{ uniformly in } x\in\overline{\Omega}, \tag{4.31}$$

where V uniquely solves

$$\begin{cases} l \dfrac{\partial V}{\partial t} = e^{-\alpha_2 m_2}\nabla\cdot[e^{\alpha_2 m_2}\nabla V] + lV[m_2(x) + \varepsilon - e^{\alpha_2 m_2}V] = 0, & x\in\Omega, t>0, \\ V(x,t) = 0, & x\in\partial\Omega, t>0, \\ V(x,0) = v(x,0), & x\in\Omega. \end{cases} \tag{4.32}$$

□

We then find the following global stability result for the semi-trivial steady state $(u_\lambda, 0)$.

Theorem 4.8. *Suppose that* (H) *holds. Let λ_1 and $\widetilde{l}(\lambda)$ be defined as in* (4.1) *and* (4.16)*, respectively, and assume that $\lambda > \lambda_1$ so the semi-trivial state $(u_\lambda, 0)$ exists. If $l < \tilde{l}(\lambda)$, then $(u_\lambda, 0)$ is globally attractive among all nonnegative solutions.*

Proof. Since $\lambda > \lambda_1$, there exists a unique steady-state solution u_λ of (4.2). By Proposition 2.2, any nontrivial solution of (4.29) satisfies

$$\lim_{t\to\infty} U(\cdot,t) = u_\lambda(\cdot) \text{ uniformly in } \overline{\Omega}.$$

Therefore, the comparison principle implies that

$$\limsup_{t\to\infty} u(\cdot,t) \le \limsup_{t\to\infty} U(\cdot,t) = u_\lambda(\cdot) \text{ uniformly in } \overline{\Omega}. \tag{4.33}$$

According to (4.33), we may argue as in the proof of Theorem 4.7 to conclude that for any $\varepsilon > 0$ as small as we like, there exists T_ε such that

$$l\frac{\partial v}{\partial t} \le e^{-\alpha_2 m_2}\nabla\cdot[e^{\alpha_2 m_2}\nabla v] + lv(m_2(x)+\varepsilon + \frac{b_2 e^{\alpha_1 m_1}u_\lambda}{1+T_h e^{\alpha_1 m_1}u_\lambda}), \quad x\in\Omega, t\ge T_\varepsilon,$$

Denote by

$$\widetilde{l}_\varepsilon(\lambda) := \lambda_*\left(\alpha_2, m_2, m_2+\varepsilon+\frac{b_2 e^{\alpha_1 m_1}u_\lambda}{1+T_h e^{\alpha_1 m_1}u_\lambda}\right)$$

By a similar argument used in Theorem 4.7, there holds $l < \widetilde{l}(\lambda) < \widetilde{l}_\varepsilon(\lambda)$.

For ε sufficiently small, the comparison principle then yields

$$\limsup_{t\to\infty} v(\cdot,t) \leq \limsup_{t\to\infty} V(\cdot,t) = 0 \text{ uniformly in } x \in \overline{\Omega}, \tag{4.34}$$

where V solves problem (4.32).

From (4.34), we conclude that there exists T'_ε such that

$$\lambda\frac{\partial u}{\partial t} \geq e^{-\alpha_1 m_1}\nabla\cdot[e^{\alpha_1 m_1}\nabla u] + \lambda u(m_1(x)-\varepsilon) - \lambda e^{\alpha_1 m_1}u^2,\ x\in\Omega, t\geq T'_\varepsilon.$$

Let $\lambda_\varepsilon := \lambda_*(\alpha_1, m_1, m_1-\varepsilon)$. Then $\lambda_\varepsilon < \lambda_1 < \lambda$, and thus by Proposition 2.2 and the comparison principle, it follows that

$$\limsup_{t\to\infty} u(\cdot,t) \geq \limsup_{t\to\infty} U_\varepsilon(\cdot,t) = u_\lambda^\varepsilon(\cdot) \text{ uniformly in } \overline{\Omega}, \tag{4.35}$$

where U_ε solves (4.29) with $m_1(x) := m_1(x)-\varepsilon$ and u_λ^ε is the associated, nontrivial steady-state solution whose existence is guaranteed for ε chosen sufficiently small. It is not difficult to see that $u_\lambda^\varepsilon \to u_\lambda$ uniformly in Ω as $\varepsilon \to 0^+$. Thus, we combine (4.33) and (4.35) and send ε to zero to conclude that

$$\lim_{t\to\infty} u(\cdot,t) = u_\lambda(\cdot) \text{ uniformly in } \overline{\Omega}. \tag{4.36}$$

□

In the same manner we can prove the following global stability result for the semi-trivial state $(0, v_l)$.

Theorem 4.9. *Suppose that* (H) *holds. Let l_1 and $\widetilde{\lambda}(l)$ be defined in* (4.1) *and* (4.15)*, respectively, and assume that $l > l_1$ so that $(0, v_l)$ exists. If $\lambda < \widetilde{\lambda}(l)$, then $(0, v_l)$ is globally attractive among all nonnegative solutions.*

5. Existence and local stability of coexistence steady-state solutions

In this section, we discuss the existence and local stability of coexistence steady-state solutions. We find that coexistence solutions can bifurcation from both trivial and semi-trivial solutions.

5.1. Bifurcation from the trivial solution $(0, 0)$

Theorem 5.1. *Suppose that* (H) *holds. Let λ_1, l_1, φ_1 and ψ_1 be defined in* (4.1)*. Then there exists a continuously differentiable mapping $s \mapsto (\widehat{\lambda}_1(s), \widehat{l}_1(s), \widehat{W}(s))$ for sufficiently small $|s|$ that satisfies*

$$\begin{cases} \widehat{\lambda}_1(s) = \lambda_1 + \widehat{\lambda}'_1(0)s + o(s), \\ \widehat{l}_1(s) = l_1 + \widehat{l}'_1(0)s + o(s), \\ \widehat{W}(s) = (\widehat{w}_1(s), \widehat{w}_2(s))^T \in X_3,\ \widehat{W}(0) = (0,0)^T \end{cases} \tag{5.1}$$

such that

$$\widehat{U}(s) = \begin{pmatrix} \widehat{u}(s) \\ \widehat{v}(s) \end{pmatrix} = \begin{pmatrix} s(\cos\omega\varphi_1 + \widehat{w}_1(s)) \\ s(\sin\omega\psi_1 + \widehat{w}_2(s)) \end{pmatrix},\ \omega \in \left(0, \frac{\pi}{2}\right) \tag{5.2}$$

is the bifurcating non-constant solution from the trivial solution $(0,0)$ at the bifurcation point (λ_1, l_1). Moreover,

$$\begin{aligned} \widehat{\lambda}'_1(0) &= \frac{\lambda_1\int_\Omega e^{\alpha_1 m_1}[e^{\alpha_1 m_1}\cos\omega\varphi_1^3 + b_1 e^{\alpha_2 m_2}\sin\omega\varphi_1^2\psi_1]\mathrm{d}x}{\int_\Omega e^{\alpha_1 m_1} m_1\varphi_1^2\mathrm{d}x}, \\ \widehat{l}'_1(0) &= \frac{l_1\int_\Omega e^{\alpha_2 m_2}[-b_2 e^{\alpha_1 m_1}\cos\omega\varphi_1\psi^2 + e^{\alpha_2 m_2}\sin\omega\psi_1^3]\mathrm{d}x}{\int_\Omega e^{\alpha_2 m_2} m_2\psi_1^2\mathrm{d}x}. \end{aligned} \tag{5.3}$$

Proof. Since we look for a solution with (1.6) of the form $(u, v) = (s(\cos\omega\varphi_1 + w_1), s(\sin\omega\psi_1 + w_2))$ with $(w_1, w_2)^T \in X_3$, we define a nonlinear mapping

$$H = (H_1, H_2) : B(\lambda_1, \delta) \times B(l_1, \delta) \times X_3 \times \mathbb{R} \to Y^2$$

by

$$\begin{aligned} &H_1(\lambda, l, w_1, w_2, s) \\ &\quad = \nabla\cdot[e^{\alpha_1 m_1}\nabla(\cos\omega\varphi_1 + w_1)] + \lambda(\cos\omega\varphi_1 + w_1)e^{\alpha_1 m_1} \\ &\qquad \left[m_1(x) - e^{\alpha_1 m_1}s(\cos\omega\varphi_1 + w_1) - \frac{b_1 e^{\alpha_2 m_2}s(\sin\omega\psi_1 + w_2)}{1 + T_h e^{\alpha_1 m_1}s(\cos\omega\varphi_1 + w_1)}\right], \\ &H_2(\lambda, l, w_1, w_2, s) \\ &\quad = \nabla\cdot[e^{\alpha_2 m_2}\nabla(\sin\omega\psi_1 + w_2)] + l(\sin\omega\psi_1 + w_2)e^{\alpha_2 m_2} \\ &\qquad \left[m_2(x) + \frac{b_2 e^{\alpha_1 m_1}s(\cos\omega\varphi_1 + w_1)}{1 + T_h e^{\alpha_1 m_1}s(\cos\omega\varphi_1 + w_1)} - e^{\alpha_2 m_2}s(\sin\omega\psi_1 + w_2)\right]. \end{aligned}$$

Clearly, $H(\lambda_1, l_1, 0, 0, 0) = 0$. The Fréchet derivative of $H(\lambda, l, w_1, w_2, s)$ with respect to (λ, l, w_1, w_2) at point $(\lambda_1, l_1, 0, 0)$ is a linear mapping from $\mathbb{R}^2 \times X_3$ to Y^2 with the form

$$\begin{cases} D_{(\lambda,l,w_1,w_2)}H_1(\lambda_1, l_1, 0, 0, 0)[\widetilde{\lambda}, \widetilde{l}, \widetilde{w}_1, \widetilde{w}_2] = L_1\widetilde{w}_1 + \widetilde{\lambda}e^{\alpha_1 m_1}m_1(x)\cos\omega\varphi_1, \\ D_{(\lambda,l,w_1,w_2)}H_2(\lambda_1, l_1, 0, 0, 0)[\widetilde{\lambda}, \widetilde{l}, \widetilde{w}_1, \widetilde{w}_2] = L_2\widetilde{w}_2 + \widetilde{l}e^{\alpha_2 m_2}m_2(x)\sin\omega\psi_1, \end{cases}$$

where L_1 and L_2 are defined in (4.4).

It is not difficult to check that this linear mapping is an isomorphism from $\mathbb{R}^2 \times X_3$ to Y^2. From the implicit function theorem, it follows that the continuously differentiable mapping defined in (5.1) exists and that there holds

$$H(\widehat{\lambda}_1(s), \widehat{l}_1(s), \widehat{W}(s)) = 0. \tag{5.4}$$

It is easily seen that $\widehat{U}(s)$ defined in (5.2) is a nonconstant solution of system (1.6) bifurcating from $(0, 0)$. Now we show (5.3) holds. Differentiating both sides of (5.4) with respect to s and taking $s = 0$, we find

$$\begin{cases} \nabla\cdot[e^{\alpha_1 m_1}\nabla\widehat{w}_1'(0)] + \widehat{\lambda}_1'(0)\cos\omega\varphi_1 e^{\alpha_1 m_1}m_1 + \lambda_1\widehat{w}_1'(0)e^{\alpha_1 m_1}m_1 \\ \quad - \lambda_1\cos\omega\varphi_1 e^{\alpha_1 m_1}(e^{\alpha_1 m_1}\cos\omega\varphi_1 + b_1 e^{\alpha_2 m_2}\sin\omega\psi_1) = 0, \\ \nabla\cdot[e^{\alpha_1 m_1}\nabla\widehat{w}_2'(0)] + \widehat{l}_1'(0)\sin\omega\psi_1 e^{\alpha_2 m_2}m_2 + l_1\widehat{w}_2'(0)e^{\alpha_2 m_2}m_2 \\ \quad - l_1\sin\omega\psi_1 e^{\alpha_2 m_2}(-b_2 e^{\alpha_1 m_1}\cos\omega\varphi_1 + e^{\alpha_2 m_2}\sin\omega\psi_1) = 0. \end{cases} \tag{5.5}$$

Multiplying both sides of the first and second equations of (5.5) by φ_1 and ψ_1, respectively, and then integrating the result over Ω give (5.3). □

Next, we study the stability of non-constant steady-state solutions by using spectral analysis. We consider the eigenvalue problem

$$L_{\widehat{U}}\xi = \mu(s)\xi \tag{5.6}$$

Here, $L_{\widehat{U}}$ is the linearization operator of system (1.6) at $(\widehat{\lambda}_1(s), \widehat{l}_1(s), \widehat{U}(s))$, which is given by

$$L_{\widehat{U}} = \begin{pmatrix} A & B \\ C & D \end{pmatrix},$$

where

$$A = \nabla\cdot[e^{\alpha_1 m_1}\nabla] + \widehat{\lambda}_1 e^{\alpha_1 m_1}\left[m_1 - 2e^{\alpha_1 m_1}\widehat{u} - \frac{b_1 e^{\alpha_2 m_2}\widehat{v}}{(1+T_h e^{\alpha_1 m_1}\widehat{u})^2}\right],$$
$$B = -\frac{\widehat{\lambda}_1 b_1 e^{\alpha_1 m_1+\alpha_2 m_2}\widehat{u}}{1+T_h e^{\alpha_1 m_1}\widehat{u}}, \qquad C = \frac{\widehat{l}_1 b_2 e^{\alpha_1 m_1+\alpha_2 m_2}\widehat{v}}{(1+T_h e^{\alpha_1 m_1}\widehat{u})^2},$$
$$D = \nabla\cdot[e^{\alpha_2 m_2}\nabla] + \widehat{l}_1 e^{\alpha_2 m_2}\left[m_2 - 2e^{\alpha_2 m_2}\widehat{v} + \frac{b_2 e^{\alpha_1 m_1}\widehat{u}}{1+T_h e^{\alpha_1 m_1}\widehat{u}}\right].$$

We now look for eigenfunctions $\xi = (\xi_1, \xi_2)^T$ of the form

$$\xi = \Phi_1 + p\Psi_1 + \eta, \tag{5.7}$$

where $\eta = (\eta_1, \eta_2)^T \in X_3$ and $p \in \mathbb{C}$. Substituting (5.7) into (5.6) implies the following equivalent system:

$$\begin{aligned}\mu(s)(\varphi_1+\eta_1) =& \nabla\cdot[e^{\alpha_1 m_1}\nabla(\varphi_1+\eta_1)] - \frac{\widehat{\lambda}_1 b_1 e^{\alpha_1 m_1+\alpha_2 m_2}\widehat{u}}{1+T_h e^{\alpha_1 m_1}\widehat{u}}(p\psi_1+\eta_2)\\ &+ \widehat{\lambda}_1 e^{\alpha_1 m_1}\left[m_1 - 2e^{\alpha_1 m_1}\widehat{u} - \frac{b_1 e^{\alpha_2 m_2}\widehat{v}}{(1+T_h e^{\alpha_1 m_1}\widehat{u})^2}\right](\varphi_1+\eta_1),\\ p\mu(s)(p\psi_1+\eta_2) =& \nabla\cdot[e^{\alpha_2 m_2}\nabla(p\psi_1+\eta_2)] + \frac{\widehat{l}_1 b_2 e^{\alpha_1 m_1+\alpha_2 m_2}\widehat{v}}{(1+T_h e^{\alpha_1 m_1}\widehat{u})^2}(\varphi_1+\eta_1)\\ &+ \widehat{l}_1 e^{\alpha_2 m_2}\left[m_2 - 2e^{\alpha_2 m_2}\widehat{v} + \frac{b_2 e^{\alpha_1 m_1}\widehat{u}}{1+T_h e^{\alpha_1 m_1}\widehat{u}}\right](p\psi_1+\eta_2).\end{aligned} \tag{5.8}$$

Multiplying the first and second equations of (5.8) by φ_1 and ψ_1, respectively, and integrating over Ω yields

$$\begin{aligned}\mu(s)\int_\Omega \varphi_1^2 \mathrm{d}x =& (\widehat{\lambda}_1 - \lambda_1)\int_\Omega e^{\alpha_1 m_1} m_1(\varphi_1+\eta_1)\varphi_1 \mathrm{d}x\\ &- \widehat{\lambda}_1 \int_\Omega e^{\alpha_1 m_1}\left(2e^{\alpha_1 m_1}\widehat{u} + \frac{b_1 e^{\alpha_2 m_2}\widehat{v}}{(1+T_h e^{\alpha_1 m_1}\widehat{u})^2}\right)(\varphi_1+\eta_1)\varphi_1 \mathrm{d}x\\ &- \widehat{\lambda}_1 b_1 \int_\Omega \frac{e^{\alpha_1 m_1+\alpha_2 m_2}\widehat{u}}{1+T_h e^{\alpha_1 m_1}\widehat{u}}(p\psi_1+\eta_2)\varphi_1 \mathrm{d}x,\end{aligned} \tag{5.9}$$

$$\begin{aligned}p\mu(s)\int_\Omega \psi_1^2 \mathrm{d}x =& (\widehat{l}_1 - l_1)\int_\Omega e^{\alpha_2 m_2} m_2(p\psi_1+\eta_2)\psi_1 \mathrm{d}x\\ &+ \widehat{l}_1 \int_\Omega e^{\alpha_2 m_2}\left(-2e^{\alpha_2 m_2}\widehat{v} + \frac{b_2 e^{\alpha_1 m_1}\widehat{u}}{1+T_h e^{\alpha_1 m_1}\widehat{u}}\right)(p\psi_1+\eta_2)\psi_1 \mathrm{d}x\\ &+ \widehat{l}_1 b_2 \int_\Omega \frac{e^{\alpha_1 m_1+\alpha_2 m_2}\widehat{v}}{(1+T_h e^{\alpha_1 m_1}\widehat{u})^2}(\varphi_1+\eta_1)\psi_1 \mathrm{d}x.\end{aligned} \tag{5.10}$$

Lemma 5.2. *Let $\mu(s)$ be defined as in (5.6). Then,*

$$\begin{aligned}\lim_{s\to 0}\frac{\mu(s)}{s} &= \mu'(0)\\ &= -\lambda_1 \cos\omega\left(\frac{\int_\Omega e^{2\alpha_1 m_1}\varphi_1^3 \mathrm{d}x + pb_1\int_\Omega e^{\alpha_1 m_1+\alpha_2 m_2}\varphi_1^2\psi_1 \mathrm{d}x}{\int_\Omega \varphi_1^2 \mathrm{d}x}\right)\\ &= -l_1 \sin\omega\left(\frac{\int_\Omega e^{2\alpha_2 m_2}\psi_1^3 \mathrm{d}x - \frac{b_2}{p}\int_\Omega e^{\alpha_1 m_1+\alpha_2 m_2}\varphi_1\psi_1^2 \mathrm{d}x}{\int_\Omega \psi_1^2 \mathrm{d}x}\right).\end{aligned} \tag{5.11}$$

Proof. Substituting (5.1) into (5.9) and (5.10), dividing both sides by s, and taking the limit yield (5.11). □

For simplicity of notation, we now write

$$\begin{aligned} k_{11} &:= \frac{\cos\omega \int_\Omega e^{2\alpha_1 m_1}\varphi_1^3 \mathrm{d}x}{\int_\Omega \varphi_1^2 \mathrm{d}x} > 0, \quad k_{12} := \frac{\cos\omega b_1 \int_\Omega e^{\alpha_1 m_1+\alpha_2 m_2}\varphi_1^2\psi_1 \mathrm{d}x}{\int_\Omega \varphi_1^2 \mathrm{d}x} > 0, \\ k_{21} &:= \frac{\sin\omega b_2 \int_\Omega e^{\alpha_1 m_1+\alpha_2 m_2}\varphi_1\psi_1^2 \mathrm{d}x}{\int_\Omega \psi_1^2 \mathrm{d}x} < 0, \ \ k_{22} := \frac{\sin\omega \int_\Omega e^{2\alpha_2 m_2}\psi_1^3 \mathrm{d}x}{\int_\Omega \psi_1^2 \mathrm{d}x} > 0. \end{aligned} \tag{5.12}$$

Then (5.11) can be rewritten as

$$\begin{aligned} \mu(s) &= -\lambda_1 s(k_{11} + pk_{12}) + o(s), \\ p\mu(s) &= -l_1 s(pk_{22} + k_{21}) + o(s). \end{aligned} \tag{5.13}$$

Substituting the first equation of (5.13) into the second equation and sending $s \to 0$ we obtain

$$\lambda_1 k_{12} p^2 + (\lambda_1 k_{11} - l_1 k_{22})p - l_1 k_{21} = 0. \tag{5.14}$$

This quadratic equation in the variable p has the two solutions

$$p_\pm = \frac{-(\lambda_1 k_{11} - l_1 k_{22}) \pm \sqrt{(\lambda_1 k_{11} - l_1 k_{22})^2 + 4\lambda_1 l_1 k_{12} k_{21}}}{2\lambda_1 k_{12}}. \tag{5.15}$$

Substituting (5.15) into the first equation of (5.13) gives

$$\mu_\pm(s) = -\frac{s}{2}(\lambda_1 k_{11} + l_1 k_{22} \pm \sqrt{(\lambda_1 k_{11} - l_1 k_{22})^2 + 4\lambda_1 l_1 k_{12} k_{21}}).$$

If $(\lambda_1 k_{11} - l_1 k_{22})^2 + 4\lambda_1 l_1 k_{12} k_{21} < 0$, then $\mathbb{R}e(\mu_\pm(s)) = -\frac{s}{2}(\lambda_1 k_{11} + l_1 k_{22}) < 0$ for s small. If $(\lambda_1 k_{11} - l_1 k_{22})^2 + 4\lambda_1 l_1 k_{12} k_{21} \geq 0$, then from (5.12), $k_{11}k_{22} - k_{12}k_{21} > 0$, we have $\mu_\pm(s) < 0$ for s small.

Consequently, we have the following local stability result.

Theorem 5.3. *The coexistence steady-state solution obtained in Theorem 5.1 is locally asymptotically stable near the bifurcation point (λ_1, l_1).*

5.2. Bifurcation from semi-trivial solutions $(u_\lambda, 0)$ and $(0, v_l)$

In this subsection, we employ the Crandall–Rabinowitz bifurcation theorem in [11] to discuss the secondary bifurcation from semi-trivial solutions $(u_\lambda, 0)$ and $(0, v_l)$.

We first consider the secondary bifurcation from the semi-trivial solution $(u_\lambda, 0)$. Fix $\lambda > \lambda_1$ and choose l as a free parameter. We define a nonlinear mapping $F : \mathbb{R} \times X^2 \to Y^2$ by

$$F(l, (u, v)) = \begin{pmatrix} \nabla \cdot [e^{\alpha_1 m_1}\nabla u] + \lambda u e^{\alpha_1 m_1}\left[m_1(x) - e^{\alpha_1 m_1}u - \frac{b_1 e^{\alpha_2 m_2}v}{1+T_h e^{\alpha_1 m_1}u}\right] \\ \nabla \cdot [e^{\alpha_2 m_2}\nabla v] + l v e^{\alpha_2 m_2}\left[m_2(x) + \frac{b_2 e^{\alpha_1 m_1}u}{1+T_h e^{\alpha_1 m_1}u} - e^{\alpha_2 m_2}v\right] \end{pmatrix}.$$

Obviously, $F(l, (u_\lambda, 0)) = \mathbf{0}$. The Fréchet derivative of F with respect to (u, v) at $(\widetilde{l}, (u_\lambda, 0))$ is given by

$$F_{(u,v)}\left(\widetilde{l}, (u_\lambda, 0)\right) = L_\lambda(\lambda, \widetilde{l}),$$

where L_λ is defined in (4.12). It is easily seen that

$$\mathcal{N}\left(F_{(u,v)}\left(\widetilde{l}, (u_\lambda, 0)\right)\right) = \mathrm{span}\left\{\begin{pmatrix} z_1 \\ z_2 \end{pmatrix}\right\} \neq \{0\},$$

where

$$z_1 = \left[\widetilde{L}_1 - 2\lambda e^{2\alpha_1 m_1}u_\lambda\right]^{-1}\left[\frac{\lambda b_1 e^{\alpha_1 m_1+\alpha_2 m_2}u_\lambda}{1+T_h e^{\alpha_1 m_1}u_\lambda}\widetilde{\chi}_1(\lambda)\right] \text{ and } z_2 = \widetilde{\chi}_1(\lambda). \tag{5.16}$$

Hence, $\dim\mathcal{N}\left(F_{(u,v)}\left(\widetilde{l},(u_\lambda,0)\right)\right)=1$. We claim that

$$\mathcal{R}\left(F_{(u,v)}\left(\widetilde{l},(u_\lambda,0)\right)\right)=\left\{(h_1,h_2)\in Y^2:\int_\Omega h_2\widetilde{\chi}_1(\lambda)\mathrm{d}x=0\right\}.$$

and $\operatorname{codim}\mathcal{R}\left(F_{(u,v)}\left(\widetilde{l},(u_\lambda,0)\right)\right)=1$. In fact, if

$$(h_1,h_2)\in\mathcal{R}\left(F_{(u,v)}\left(\widetilde{l},(u_\lambda,0)\right)\right),$$

then there exists a solution (u,v) such that

$$F_{(u,v)}\left(\widetilde{l},(u_\lambda,0)\right)[u,v]^T=(h_1,h_2)^T.$$

It follows from the eigenvalue problem that $\langle h_2,\widetilde{\chi}_1(\lambda)\rangle=0$. Moreover,

$$F_{(u,v)l}\left(\widetilde{l},(u_\lambda,0)\right)[z_1,z_2]=\begin{pmatrix}0\\ e^{\alpha_2m_2}\left(m_2(x)+\frac{b_2e^{\alpha_1m_1}u_\lambda}{1+T_he^{\alpha_1m_1}u_\lambda}\right)\widetilde{\chi}_1(\lambda)\end{pmatrix}$$
$$\notin\mathcal{R}\left(F_{(u,v)}\left(\widetilde{l},(u_\lambda,0)\right)\right)$$

as

$$\int_\Omega e^{\alpha_2m_2}\left(m_2(x)+\frac{b_2e^{\alpha_1m_1}u_\lambda}{1+T_he^{\alpha_1m_1}u_\lambda}\right)\widetilde{\chi}_1^2(\lambda)\mathrm{d}x=\frac{\int_\Omega e^{\alpha_2m_2}|\nabla\widetilde{\chi}_1(\lambda)|^2\mathrm{d}x}{\widetilde{l}(\lambda)}\neq0.$$

In view of the Crandall–Rabinowitz bifurcation theorem for simple eigenvalues [11, Theorem 1.17], there exists a positive constant δ and continuously differentiable functions

$$l:(-\delta,\delta)\to\mathbb{R},\ (\epsilon_1(s),\epsilon_2(s)):(-\delta,\delta)\to\mathbb{R}\left(F_{(u,v)}\left(\widetilde{l},(u_\lambda,0)\right)\right)$$

such that $l(0)=\widetilde{l}(\lambda)$ and $(\epsilon_1(0),\epsilon_2(0))=(0,0)$. If

$$\begin{cases}l(s)=\widetilde{l}(\lambda)+l'(0)s+o(s),\\ u(s)=u_\lambda+s(z_1+\epsilon_1(s)),\\ v(s)=s(z_2+\epsilon_2(s)),\end{cases}\tag{5.17}$$

where z_1 and z_2 are defined in (5.16), then $F(l(s),(u(s),v(s)))=0$. Summarizing, we have the following.

Theorem 5.4. *Suppose that* (H) *holds. Let* $\lambda>\lambda_1$. *Then, the solutions of* $F(l,(u,v))=0$ *near the bifurcation point* $(\widetilde{l}(\lambda),(u_\lambda,0))$ *are in a form of*

$$\Gamma=\{(l(s),(u(s),v(s))):-\delta<s<\delta\},$$

where δ *is a positive constant and* $l(s)$, $u(s)$ *and* $v(s)$ *are defined in* (5.17).

In what follows, we utilize the stability exchange theorem introduced in [12] to establish the stability of the bifurcation solution $(l(s),(u(s),v(s)))$.

Theorem 5.5. *Let* $\Gamma=\{(l(s),(u(s),v(s))):-\delta<s<\delta\}$ *be the non-trivial curve found in Theorem* 5.4. *Then, there exists continuously differentiable function*

$$r:(\widetilde{l}(\lambda)-\varepsilon,\widetilde{l}(\lambda)+\varepsilon)\to\mathbb{R},\ \tau=(\tau_1,\tau_2):(\widetilde{l}(\lambda)-\varepsilon,\widetilde{l}(\lambda)+\varepsilon)\to X^2,$$
$$\pi:(-\delta,\delta)\to\mathbb{R},\ \rho=(\rho_1,\rho_2):(-\delta,\delta)\to X^2,$$

such that

$$\begin{aligned}&F_{(u,v)}(l,(u_\lambda,0))\tau(l)=r(l)K\tau(l),\quad l\in(\widetilde{l}(\lambda)-\varepsilon,\widetilde{l}(\lambda)+\varepsilon),\\&F_{(u,v)}(l(s),(u(s,\cdot),v(s,\cdot)))\rho(s)=\pi(s)K\rho(s),\quad s\in(-\delta,\delta),\end{aligned}\tag{5.18}$$

where $r(\widetilde{l}(\lambda)) = \pi(0) = 0$, $\tau(\widetilde{l}(\lambda)) = \rho(0) = (z_1, z_2)$, $K : X^2 \to Y^2$ *is the inclusion map with* $K(u) = u$. *Moreover, near* $s = 0$ *the functions* $\pi(s)$ *and* $-sl'(s)r'(\widetilde{l}(\lambda))$ *have the same zeroes and, whenever* $\pi(s) \neq 0$, *they share the same sign and satisfy*

$$\lim_{s\to 0} \frac{-sl'(s)r'(\widetilde{l}(\lambda))}{\pi(s)} = 1. \tag{5.19}$$

To determine the sign of $\pi(s)$, we require the following lemmas.

Lemma 5.6. *Let* $l(s)$ *be defined in* (5.17). *Then*

$$l'(0) = \frac{\widetilde{l}(\lambda)\int_\Omega e^{\alpha_2 m_2}\left(e^{\alpha_2 m_2} z_2 - \frac{b_2 e^{\alpha_1 m_1} z_1}{(1+T_h e^{\alpha_1 m_1} u_\lambda)^2}\right) z_2 \widetilde{\chi}_1(\lambda)\mathrm{d}x}{\int_\Omega e^{\alpha_2 m_2}\left(m_2(x) + \frac{b_2 e^{\alpha_1 m_1} u_\lambda}{1+T_h e^{\alpha_1 m_1} u_\lambda}\right) z_2 \widetilde{\chi}_1(\lambda)\mathrm{d}x},$$

where z_1 *and* z_2 *are defined in* (5.16).

Proof. Substituting (5.17) into the second equation of (1.6) yields

$$\begin{aligned} 0 =& \nabla\cdot[e^{\alpha_2 m_2}\nabla(z_2+\epsilon_2(s))] \\ &+ l(s)(z_2+\epsilon_2(s))e^{\alpha_2 m_2}\left[m_2(x) + \frac{b_2 e^{\alpha_1 m_1}(u_\lambda + s(z_1+\epsilon_1(s)))}{1+T_h e^{\alpha_1 m_1}(u_\lambda + s(z_1+\epsilon_1(s)))} - e^{\alpha_2 m_2} s(z_2+\epsilon_2(s))\right]. \end{aligned} \tag{5.20}$$

One can differentiate both sides of the equation above with respect to s and then evaluate the result at $s = 0$ to find

$$\begin{aligned} 0 =& \nabla\cdot[e^{\alpha_2 m_2}\nabla(\epsilon_2'(0))] + l'(0) z_2 e^{\alpha_2 m_2}\left(m_2(x) + \frac{b_2 e^{\alpha_1 m_1} u_\lambda}{1+T_h e^{\alpha_1 m_1} u_\lambda}\right) \\ &+ \widetilde{l}(\lambda)\epsilon_2'(0) e^{\alpha_2 m_2}\left(m_2(x) + \frac{b_2 e^{\alpha_1 m_1} u_\lambda}{1+T_h e^{\alpha_1 m_1} u_\lambda}\right) + \widetilde{l}(\lambda) z_2 e^{\alpha_2 m_2}\left(\frac{b_2 e^{\alpha_1 m_1} z_1}{(1+T_h e^{\alpha_1 m_1} u_\lambda)^2} - e^{\alpha_2 m_2} z_2\right). \end{aligned}$$

By multiplying both sides of the equation above with $\widetilde{\chi}(\lambda)$ and integrating over Ω, and then using the fact that $\widetilde{\chi}(\lambda)$ is the principal eigenvalue of (4.14), the desired conclusion can be readily derived. □

Remark 5.7. **Note that the sign of $l'(0)$ depends on the sign of Q, where**

$$Q := \widetilde{l}(\lambda)\int_\Omega e^{\alpha_2 m_2}\left(e^{\alpha_2 m_2} z_2 - \frac{b_2 e^{\alpha_1 m_1} z_1}{(1+T_h e^{\alpha_1 m_1} u_\lambda)^2}\right) z_2 \widetilde{\chi}_1(\lambda)\mathrm{d}x. \tag{5.21}$$

Moreover,

$$\lim_{\lambda\to\lambda_1} Q = \int_\Omega e^{2\alpha_2 m_2}\psi_1^3 \mathrm{d}x > 0.$$

Lemma 5.8. *Let* $r(l)$ *be defined as in Theorem* 5.5, *and let* $z_2 = \widetilde{\chi}_1(\lambda)$ *be defined as in* (5.16). *Then, we have*

$$r'(\widetilde{l}(\lambda)) = \frac{\int_\Omega e^{\alpha_2 m_2}\left(m_2(x) + \frac{b_2 e^{\alpha_1 m_1} u_\lambda}{1+T_h e^{\alpha_1 m_1} u_\lambda}\right)\widetilde{\chi}_1(\lambda)^2 \mathrm{d}x}{\int_\Omega \widetilde{\chi}_1(\lambda)^2 \mathrm{d}x} > 0. \tag{5.22}$$

Proof. Differentiating both sides of (5.18) with respect to l, evaluating at $\widetilde{l}(\lambda)$, and then taking the inner product with $(0, z_2)^{\mathrm{T}}$ give (5.22). □

Combining Theorem 5.5, Lemmas 5.6 and 5.8, we conclude with the following theorem.

Theorem 5.9. *For* $s > 0$ *sufficiently small, let* $(u(s), v(s))$ *be the coexistence state defined in Theorem* 5.4 *and let* Q *be defined as in* (5.21). *The following dichotomy holds.*

(i) *If* $Q > 0$, *then* $\pi(s) < 0$, *and any coexistence state* $(u(s), v(s))$ *is locally asymptotically stable.*

(ii) *If $Q < 0$, then $\pi(s) > 0$, and any coexistence state $(u(s), v(s))$ is unstable.*

Similar arguments apply to the case of bifurcation from the semi-trivial state $(0, v_l)$. Define a nonlinear mapping $G : \mathbb{R} \times X^2 \to Y^2$ by

$$G(\lambda, (u, v)) = \begin{pmatrix} \nabla \cdot [e^{\alpha_1 m_1} \nabla u] + \lambda u e^{\alpha_1 m_1} \left[m_1(x) - e^{\alpha_1 m_1} u - \frac{b_1 e^{\alpha_2 m_2} v}{1 + T_h e^{\alpha_1 m_1} u} \right] \\ \nabla \cdot [e^{\alpha_2 m_2} \nabla v] + l v e^{\alpha_2 m_2} \left[m_2(x) + \frac{b_2 e^{\alpha_1 m_1} u}{1 + T_h e^{\alpha_1 m_1} u} - e^{\alpha_2 m_2} v \right] \end{pmatrix}.$$

Clearly, $G(\lambda, (0, v_l)) = 0$ and

$$G_{(u,v)} \left(\widetilde{\lambda}, (0, v_l) \right) = L_l(\widetilde{\lambda}, l),$$

where L_l is defined in (4.13). It follows immediately that

(i)

$$\mathbb{N} \left(G_{(u,v)} \left(\widetilde{\lambda}, (0, v_l) \right) \right) = \text{span} \left\{ \begin{pmatrix} \overline{z}_1 \\ \overline{z}_2 \end{pmatrix} \right\} \neq \{0\},$$

where

$$\overline{z}_1 = \widetilde{\kappa}_1(l) \text{ and } \overline{z}_2 = \left[\widetilde{L}_2 - 2 l e^{2\alpha_2 m_2} v_l \right]^{-1} \left[-l b_2 e^{\alpha_1 m_1 + \alpha_2 m_2} v_l \widetilde{\kappa}_1(l) \right], \tag{5.23}$$

and

(ii) $\dim \mathbb{N} \left(G_{(u,v)} \left(\widetilde{\lambda}, (0, v_l) \right) \right) = \text{codim} \mathbb{R} \left(G_{(u,v)} \left(\widetilde{\lambda}, (0, v_l) \right) \right) = 1$, and

$$\mathbb{R} \left(G_{(u,v)} \left(\widetilde{\lambda}, (0, v_l) \right) \right) = \left\{ (h_1, h_2) \in Y^2 : \int_\Omega h_1 \widetilde{\kappa}_1(\lambda) \mathrm{d}x = 0 \right\}.$$

Theorem 5.10. *Suppose that* (H) *holds. Let $l > l_1$ be fixed. Then there exists a positive constant δ and continuously differentiable functions*

$$\lambda : (-\delta, \delta) \mapsto \mathbb{R}, \ (\overline{\epsilon}_1(s), \overline{\epsilon}_2(s)) : (-\delta, \delta) \mapsto \mathbb{R} \left(G_{(u,v)} \left(\widetilde{\lambda}, (0, v_l) \right) \right)$$

such that $\lambda(0) = \widetilde{\lambda}(l)$, $(\overline{\epsilon}_1(0), \overline{\epsilon}_2(0)) = (0, 0)$. Moreover, the solutions of $G(\lambda, (u, v)) = 0$ near the bifurcation point $(\widetilde{\lambda}(l), (0, v_l))$ are in the form

$$\overline{\Gamma} = \{ (\lambda(s), (u(s), v(s))) : -\delta < s < \delta \}.$$

Here, λ, u and v are given by:

$$\begin{cases} \lambda(s) = \widetilde{\lambda}(l) + \lambda'(0) s + o(s), \\ u(s) = s(\overline{z}_1 + \overline{\epsilon}_1(s)), \\ v(s) = v_l + s(\overline{z}_2 + \overline{\epsilon}_2(s)), \end{cases} \tag{5.24}$$

where $\overline{z}_1$ and $\overline{z}_2$ are defined in (5.23).

Lemma 5.11. *Let $\lambda(s)$ be defined in* (5.24)*. Then,*

$$\lambda'(0) = \frac{\widetilde{\lambda}(l) \int_\Omega e^{\alpha_1 m_1} \left(e^{\alpha_1 m_1} \overline{z}_1 - b_1 e^{\alpha_2 m_2} \overline{z}_2 \right) \overline{z}_1 \widetilde{\kappa}_1(l) \mathrm{d}x}{\int_\Omega e^{\alpha_1 m_1} \left(m_1(x) - b_1 e^{\alpha_2 m_2} v_l \right) \overline{z}_1 \widetilde{\kappa}_1(l) \mathrm{d}x},$$

where $\overline{z}_1$ and $\overline{z}_2$ are defined in (5.23)*. Moreover, if we let*

$$\overline{Q} := \widetilde{\lambda}(l) \int_\Omega e^{\alpha_1 m_1} \left(e^{\alpha_1 m_1} \overline{z}_1 - b_1 e^{\alpha_2 m_2} \overline{z}_2 \right) \overline{z}_1 \widetilde{\kappa}_1(l) \mathrm{d}x, \tag{5.25}$$

there holds

$$\lim_{l \to l_1} \overline{Q} = \int_\Omega e^{2\alpha_1 m_1} \varphi_1^3 \mathrm{d}x > 0.$$

Theorem 5.12. *Let* $\overline{\Gamma} = \{(\lambda(s),(u(s),v(s))) : -\delta < s < \delta\}$ *be the non-trivial curve found in Theorem 5.10. Then, there exist continuously differentiable functions* $\overline{r} : (\widetilde{\lambda}(l)-\varepsilon, \widetilde{\lambda}(l)+\varepsilon) \mapsto \mathbb{R}$, $\overline{\tau} = (\overline{\tau}_1, \overline{\tau}_2) : (\widetilde{\lambda}(l)-\varepsilon, \widetilde{\lambda}(l)+\varepsilon) \mapsto X^2$, $\pi : (-\delta,\delta) \mapsto \mathbb{R}$, $\overline{\rho} = (\overline{\rho}_1, \overline{\rho}_2) : (-\delta,\delta) \mapsto X^2$, *such that*

$$\begin{aligned} G_{(u,v)}(\lambda,(0,v_l))\overline{\tau}(\lambda) &= \overline{r}(\lambda)K\overline{\tau}(\lambda), \quad \lambda \in (\widetilde{\lambda}(l)-\varepsilon, \widetilde{\lambda}(l)+\varepsilon), \\ G_{(u,v)}(\lambda(s),(u(s,\cdot),v(s,\cdot)))\overline{\rho}(s) &= \overline{\pi}(s)K\overline{\rho}(s), \quad s \in (-\delta,\delta), \end{aligned} \tag{5.26}$$

where $\overline{r}(\widetilde{\lambda}(l)) = \overline{\pi}(0) = 0$, $\overline{\tau}(\widetilde{\lambda}(l)) = \overline{\rho}(0) = (\overline{z}_1, \overline{z}_2)$, *and* $K : X^2 \to Y^2$ *is the inclusion map with* $K(u) = u$. *Moreover, near* $s = 0$ *the functions* $\overline{\pi}(s)$ *and* $-s\lambda'(s)\overline{r}'(\widetilde{\lambda}(l))$ *have the same zeroes and, whenever* $\overline{\pi}(s) \neq 0$, *they share the same sign and satisfy*

$$\lim_{s\to 0} \frac{-s\lambda'(s)\overline{r}'(\widetilde{\lambda}(l))}{\overline{\pi}(s)} = 1. \tag{5.27}$$

Theorem 5.13. *Let* $(u(s),v(s))$ *be the coexistence states found in Theorem 5.10 for* $s > 0$ *sufficiently small and let* $\overline{Q}$ *be defined as in (5.25). The following dichotomy holds.*

(i) *If* $\overline{Q} > 0$, *then* $\overline{\pi}(s) < 0$, *and any coexistence state* $(u(s),v(s))$ *is locally asymptotically stable.*
(ii) *If* $\overline{Q} < 0$, *then* $\overline{\pi}(s) > 0$, *and any coexistence state* $(u(s),v(s))$ *is unstable.*

Remark 5.14. **By the global bifurcation theory, similar to results found in [25,45] for example, there exists a continuum of nontrivial steady-state solutions joining Γ and $\overline{\Gamma}$, and this continuum is the nontrivial steady-state solutions bifurcating from the trivial solution $(0,0)$.**

Remark 5.15. **It is worth noting that when m_1, m_2 are constant and $T_h = 0$, the findings in [45] match those presented here for $\alpha_1 = \alpha_2 = 0$, and as such, are considered optimal in this scenario. Moreover, we emphasize that the approach used in this paper is also applicable to the diffusion–advection–competition model.**

6. The effects of advection and spatial heterogeneity

In this section, we study the combined effects of advection and spatial heterogeneity on the asymptotic behaviour of the system. To this aim, we discuss the continuous differentiability of $\lambda_1(\alpha_1)$ with respect to the advection rate α_1, where $\lambda_1(\alpha_1)$ is the principal eigenvalue of the eigenvalue problem

$$\begin{cases} \nabla \cdot \left[e^{\alpha m_1(x)}\nabla\phi\right] + \lambda e^{\alpha m_1(x)} m_1(x)\phi = 0, & x \in \Omega, \\ \phi(x) = 0, & x \in \partial\Omega. \end{cases} \tag{6.1}$$

Since the local dependence of $l_1(\alpha_2)$ on α_2 can be argued similarly, we do not give a detailed argument. This follows from the implicit function theorem, see for example the discussion in [1].

Theorem 6.1. *Let* $\lambda_1(\alpha_1)$ *be the principal eigenvalue of problem (6.1). Then* $\lambda_1(\alpha_1)$ *is continuously differentiable with respect to* α_1. *Moreover, there holds*

$$\lambda_1'(\alpha_1) = \int_\Omega \frac{\phi_1^2}{2} \nabla \cdot [e^{\alpha_1 m_1}\nabla m_1] \mathrm{d}x, \tag{6.2}$$

where ϕ_1 *is the positive eigenfunction corresponding to* λ_1 *satisfying the normalization condition*

$$\int_\Omega m_1 e^{\alpha_1 m_1}\phi_1^2 \mathrm{d}x = 1.$$

Proof. Define $E = \{\phi \in C^{2+\theta}(\overline{\Omega}) : \phi = 0 \text{ on } \partial\Omega\}$, where $\theta \in (0,1)$, and a linear mapping $\Pi : \mathbb{R} \times E \times \mathbb{R} \mapsto C^{\theta}(\overline{\Omega}) \times \mathbb{R}$ by

$$\Pi(\lambda, \phi, \alpha_1) = \begin{pmatrix} \nabla \cdot \left[e^{\alpha_1 m_1(x)} \nabla \phi\right] + \lambda e^{\alpha_1 m_1(x)} m_1(x)\phi \\ \int_\Omega m_1 e^{\alpha_1 m_1} \phi^2 dx - 1 \end{pmatrix}$$

Obviously, $\Pi(\lambda_1, \phi_1, \alpha_1) = \mathbf{0}$. The Fréchet derivative of Π with respect to (λ, ϕ) is a bijection, where

$$D_{(\lambda,\phi)}\Pi(\lambda_1, \phi_1, \alpha_1)[t, r] = \begin{pmatrix} \nabla \cdot \left[e^{\alpha m_1(x)} \nabla r\right] + \lambda_1 e^{\alpha_1 m_1(x)} m_1(x) r + t e^{\alpha_1 m_1(x)} m_1(x)\phi_1 \\ 2\int_\Omega m_1 e^{\alpha_1 m_1} \phi_1 r \mathrm{d}x \end{pmatrix}.$$

In fact, if $D_{(\lambda,\phi)}\Pi(\lambda_1, \phi_1, \alpha_1)[t, r] = (0, 0)$, i.e. there holds

$$\begin{cases} \nabla \cdot \left[e^{\alpha m_1(x)} \nabla r\right] + \lambda_1 e^{\alpha_1 m_1(x)} m_1(x) r + t e^{\alpha_1 m_1(x)} m_1(x)\phi_1 = 0, \\ 2\int_\Omega m_1 e^{\alpha_1 m_1} \phi_1 r \mathrm{d}x = 0, \end{cases} \tag{6.3}$$

then multiplying both sides of the first equation of (6.3) by ϕ_1 and integrating by parts yield

$$t \int_\Omega m_1 e^{\alpha_1 m_1} \phi_1^2 \mathrm{d}x = 0,$$

which implies $t = 0$ as $\int_\Omega m_1 e^{\alpha_1 m_1} \phi_1^2 \mathrm{d}x = 1$. Moreover, due to the properties of principal eigenvalue λ_1, it must be the case that $r = c\phi$ for some $c \in \mathbb{R}$. Substituting $r = c\phi$ into the second equation of (6.3), we find $r = 0$. This implies $D_{(\lambda,\phi)}\Pi(\lambda_1, \phi_1, \alpha_1)[t, r]$ is injective.

To show $D_{(\lambda,\phi)}\Pi(\lambda_1, \phi_1, \alpha_1)[t, r]$ is surjective, for any $(h, j) \in C^{\theta}(\overline{\Omega}) \times \mathbb{R}$, we consider the problem $D_{(\lambda,\phi)}\Pi(\lambda_1, \phi_1, \alpha_1)[t, r] = (h, j)$, that is

$$\begin{cases} \nabla \cdot \left[e^{\alpha m_1(x)} \nabla r\right] + \lambda_1 e^{\alpha_1 m_1(x)} m_1(x) r = h - t e^{\alpha_1 m_1(x)} m_1(x)\phi_1, \\ 2\int_\Omega m_1 e^{\alpha_1 m_1} \phi_1 r \mathrm{d}x = j. \end{cases} \tag{6.4}$$

Multiplying both sides of the first equation of (6.4) by ϕ_1 gives that

$$t = \frac{\int_\Omega h\phi_1 \mathrm{d}x}{\int_\Omega m_1 e^{\alpha_1 m_1} \phi_1^2 \mathrm{d}x}.$$

We then look for r of the form $r = q\phi_1 + z$ with $\int_\Omega m_1 e^{\alpha_1 m_1} z\phi_1 \mathrm{d}x = 0$. From the second equation of (6.4), we obtain $q = \frac{j}{2\int_\Omega m_1 e^{\alpha_1 m_1} \phi_1^2 \mathrm{d}x}$.

Therefore, $D_{(\lambda,\phi)}\Pi(\lambda_1, \phi_1, \alpha_1)[t, r]$ is a bijection. By the implicit function theorem, there exists λ_1 and a continuously differentiable mapping $\alpha_1 \mapsto (\lambda_1(\alpha_1), \phi_1(\alpha_1))$ from $\mathbb{R}$ to $\mathbb{R} \times E$ such that

$$\Pi(\lambda_1(\alpha_1), \phi_1(\alpha_1), \alpha_1) = 0. \tag{6.5}$$

Differentiating both sides of the first equation of (6.5) with respect to α_1, we have

$$\nabla \cdot [m_1 e^{\alpha_1 m_1} \nabla \phi_1] + \nabla \cdot [e^{\alpha_1 m_1} \nabla \phi_1'] + \lambda_1'(\alpha_1) e^{\alpha_1 m_1} m_1 \phi_1 + \lambda_1 e^{\alpha_1 m_1} m_1^2 \phi_1 + \lambda_1 e^{\alpha_1 m_1} m_1 \phi_1' = 0. \tag{6.6}$$

Multiplying (6.6) by ϕ_1 and using the normalization condition, we conclude that

$$\begin{aligned}\lambda_1'(\alpha_1) &= -\int_\Omega \phi_1 \nabla\cdot[m_1 e^{\alpha_1 m_1}\nabla\phi_1]\,\mathrm{d}x - \int_\Omega \lambda_1 m_1^2 e^{\alpha_1 m_1}\phi_1^2 \mathrm{d}x \\ &= -\left(\int_\Omega m_1\phi_1\nabla\cdot[e^{\alpha_1 m_1}\nabla\phi_1]\,\mathrm{d}x + \int_\Omega \phi_1\nabla m_1 e^{\alpha_1 m_1}\nabla\phi_1\mathrm{d}x\right) - \int_\Omega \lambda_1 m_1^2 e^{\alpha_1 m_1}\phi_1^2\mathrm{d}x \\ &= \int_\Omega \lambda_1 m_1^2 e^{\alpha_1 m_1}\phi_1^2\mathrm{d}x - \int_\Omega \nabla\left(\frac{\phi_1^2}{2}\right)\nabla m_1 e^{\alpha_1 m_1}\mathrm{d}x - \int_\Omega \lambda_1 m_1^2 e^{\alpha_1 m_1}\phi_1^2\mathrm{d}x \\ &= -\int_\Omega \nabla\left(\frac{\phi_1^2}{2}\right)\nabla m_1 e^{\alpha_1 m_1}\mathrm{d}x \\ &= \int_\Omega \frac{\phi_1^2}{2}\nabla\cdot[e^{\alpha_1 m_1}\nabla m_1]\mathrm{d}x.\end{aligned} \tag{6.7}$$

□

Notice that when $\alpha_1 = 0$, $\lambda_1'(0) = \int_\Omega \frac{\phi_1^2}{2}\Delta m_1 \mathrm{d}x$. Hence, the sign of λ_1' depends on the sign of Δm near $\alpha_1 = 0$, giving us the following corollary.

Corollary 6.2. *Let λ_1 be the principal eigenvalue of eigenvalue problem (6.1). Near $\alpha_1 = 0$, it is true that*

(i) *if $\Delta m_1(x) < 0$ for all $x \in \Omega$, then λ_1 is decreasing with respect to α_1.*

(ii) *if $\Delta m_1(x) > 0$ for all $x \in \Omega$, then λ_1 is increasing with respect to α_1.*

Remark 6.3. **In fact, if $\Delta m_1(x) > 0$, λ_1 is increasing for *all* $\alpha_1 \geq 0$. This is readily observed upon expansion of (6.7), where we are left with terms $|\nabla m_1|^2 \geq 0$ and $\Delta m_1 > 0$ so that $\lambda_1'(\alpha_1) > 0$ for all $\alpha_1 \geq 0$.**

From a biological perspective, Theorem 6.1 demonstrates that the effect of advection along the gradient of the environmental resource on population persistence and extinction depends intimately on the spatial heterogeneity of the environment. Whether advection is beneficial or detrimental to population persistence can be understood in terms of increases or decreases of the eigenvalue $\lambda_1(\alpha_1)$ with respect to α_1. To exemplify this, recall that by Theorem 4.7, $(0, 0)$ is globally asymptotically stable whenever $\lambda < \lambda_1$ and $l < l_1$. Therefore, if $\lambda_1(\alpha_1)$ increases with respect to α_1, the parameter window for which deterministic extinction is predicted increases contemporaneously. On the other hand, when $\lambda_1(\alpha_1)$ decreases, this window decreases. Note that $\lambda_1 = d_1^{-1}$ is introduced as the intermediate parameter. In this sense, *a larger value of λ_1 is detrimental to population persistence as a smaller rate of diffusion is required to compensate*. Notice also that this is consistent with typical behaviour observed in diffusive systems: a smaller rate of diffusion is preferred when resources are constant in time.

Subsequently, Corollary 6.2 leads to the following insight: if the resource function is strictly concave, then advection along the gradient of the environmental resource is beneficial to the species survival, at least for small α_1; however, if the resource function for species survival is strictly convex, then advection along the gradient of the environmental resource is *always* detrimental to the species' survival! This highlights a delicate balance between a hostile boundary, the distribution of resources across space, and the rate of movement towards resource peaks. Of note is the fact that when resource peaks concentrate near the boundary, advection is detrimental; this is in contrast to a single resource peak appearing in the interior of the domain, where advection may or may not improve outcomes for local populations.

To explore such insights further, we consider two special forms of the resource distribution satisfying some special properties. These properties, paired with Proposition 6.2, will give analytical insights into the behaviour of $\lambda_1(\alpha_1)$ and how it affects a single population. We then use numerical simulation to explore the impact of advection in the predator–prey system. In what follows, we fix $\lambda = l = 2^{-1}$, $b_1(x) = b_2(x) \equiv 1$, $m = 1$ and vary the special heterogeneity and advection rates in a fixed domain $\Omega = (0, L)$.

Example 1. Choose $m_1(x) = \sigma(x-x_0)^2 + c(\sigma, x_0)$ for $\sigma \in \mathbb{R}\backslash\{0\}$ and $x_0 \in (0, L)$. The constant $c(\sigma, x_0)$ is given by

$$c(\sigma, L) = m_0 - \sigma \int_0^L (x-x_0)^2 \mathrm{d}x, \tag{6.8}$$

which is chosen such that the average amount of resources is held fixed at $m_0 > 0$ for varying σ, x_0. By symmetry, we may consider only $x_0 \in (0, \frac{L}{2}]$ without loss of generality. Expanding the right-hand side of the final line of (6.7) yields

$$\lambda_1'(\alpha_1) = \int_0^L \frac{\phi_1^2}{2} e^{\alpha_1 m_1}[\alpha_1|(m_1)_x|^2 + (m_1)_{xx}]\mathrm{d}x. \tag{6.9}$$

We consider three cases.

(a) $\sigma > 0$, $x_0 \in (0, \frac{L}{2}]$. In this case, the function is concave up, i.e. $(m_1)_{xx} = 2\sigma > 0$, and hence $\lambda_1'(\alpha_1) > 0$ for all $\alpha_1 \geq 0$. Therefore, $\lambda_1(\alpha_1)$ is strictly increasing and advection towards resource peaks is detrimental to the population's persistence.

(b) $\sigma < 0$, $x_0 \in (0, \frac{L}{2})$. In this case, the function is concave down with a single peak somewhere away from the centre or boundary of the domain. We may compute $(m_1)_x = 2\sigma(x-x_0)$ and $(m_1)_{xx} = 2\sigma$ to find that

$$\alpha_1|(m_1)_x|^2 + (m_1)_{xx} = \sigma(4\sigma\alpha_1(x-x_0)^2 + 2) < 0,$$

for any $\alpha_1 > 0$ satisfying

$$\alpha_1 < \frac{1}{2\max\{x_0, L/2 - x_0\}^2|\sigma|}.$$

Therefore, $\lambda_1(\alpha_1)$ is strictly decreasing for $\alpha_1 \ll 1$, and a small amount of advection towards resource peaks will enhance the likelihood of population persistence, though it is not necessarily true for α_1 large.

(c) $\sigma < 0$, $x_0 = \frac{L}{2}$. In this case, the function is concave down, symmetric about $x = \frac{L}{2}$ with a single resource peak located at $\frac{L}{2}$. We then make the following informal assertions without proof: since $m_1(x)$ is symmetric about $x = \frac{L}{2}$, so is its eigenfunction ϕ_1. The eigenfunction is also concave down with a unique maximum located at $x = \frac{L}{2}$. Therefore, $(m_1)_x > 0$ and $(\phi_1)_x > 0$ over $(0, \frac{L}{2})$, while $(m_1)_x < 0$ and $(\phi_1)_x < 0$ over $(0, \frac{L}{2})$. Then, integrating by parts in (6.7) and applying the boundary condition satisfied by ϕ_1 gives

$$\lambda_1'(\alpha_1) = -\int_0^L e^{\alpha_1 m_1}(m_1)_x \phi_1 (\phi_1)_x \mathrm{d}x.$$

Splitting this integral into the regions $(0, \frac{L}{2})$ and $(\frac{L}{2}, L)$ using the sign-definite nature of $(m_1)_x$ and $(\phi_1)_x$ in their respective regions yield

$$\lambda_1'(\alpha_1) = -\int_0^L e^{\alpha_1 m_1}\phi_1|(m_1)_x||(\phi_1)_x|\mathrm{d}x < 0.$$

Hence, $\lambda_1(\alpha_1)$ is strictly decreasing and advection towards resource peaks at *any* rate is beneficial to the likelihood of persistence for the population.

These three cases demonstrate the intimate relation between the rate of advection, the nature of the spatial heterogeneity, and the hostile boundary condition. In case (a), any advection rate pushes the population towards the hostile boundary, which decreases the parameter regime for which the population may persist. One may intuit that if the resource peak is located in the domain's interior (i.e. concavity changes), advection will point away from the hostile boundary and enlarge the parameter regime for which persistence is a possibility. Indeed, case (b) demonstrates this but is guaranteed for small advection rates only, suggesting that for large enough advection rates, the push *away* from one boundary point may result in a push *towards* the opposing boundary point. However, if the resource function is symmetric about the centre of the domain, the push from the left and right boundary points are in perfect balance, and any amount of advection towards the resource peak is beneficial. This is what was informally demonstrated in case (c). Together, these results demonstrate that $\lambda_1(\alpha_1)$ is sometimes monotonic, but may also be nonmonotone for some particular forms of environmental heterogeneity.

These insights apply to the single-species model only; the full predator–prey system has additional complexity worth investigating further. In Fig. 2, we explore this scenario for the full predator–prey system when we choose $m_1 = m_2 = \sigma(x - x_0)^2 + c(\sigma, L)$ for particular choices of σ and x_0. In the first row, we observe expected behaviour from case (a): increasing advection is detrimental to both populations, where we observe extirpation of the prey for over half of the shown parameter regime. In cases where the prey population persists, improvement is due to the detrimental effect of advection on the predator population. In the middle row, we have case (b), where we observe nonmonotone behaviour in the average population sizes for both the prey and the predator. This suggests that in case (b), extirpation is expected for sufficiently large advection rates. In the third row, we find case (c), with a function that is concave down and symmetric about $x_0 = 5$, the centre of the domain. We again observe nonmonotone behaviour for both populations, indicating that the monotone behaviour explored in case (c) for the single species model does not hold in the predator–prey system.

Example 2. Motivated by Example 1 case (b), we construct a function for which we know precisely the sign of the derivative of λ_1. Choose $m_1 = \frac{\ln(\sigma x + m_0)}{\sigma}$ for $\sigma > 0$ and $m_0 \geq 1$ fixed. In this case, the function is concave down, but the resource peak always appears at the boundary point L. We may then compute $(m_1)_x = (\sigma x + m_0)^{-1}$ and $(m_1)_{xx} = -\sigma(\sigma x + m_0)^{-2}$, whence

$$\alpha_1 |(m_1)_x|^2 + (m_1)_{xx} = \frac{\alpha_1 - \sigma}{(\sigma x + m_0)^2} \begin{cases} < 0, & \alpha_1 < \sigma; \\ = 0, & \sigma = \alpha_1; \\ > 0, & \alpha_1 > \sigma. \end{cases}$$

Therefore, for any $\sigma > 0$ fixed, we know the precise behaviour of $\lambda_1(\alpha_1)$: $\lambda_1(\alpha_1)$ is strictly decreasing in $(0, \sigma)$, reaches a unique minimal value at $\alpha_1 = \sigma$, after which $\lambda_1(\alpha_1)$ is strictly increasing. In particular, this suggests that for $\lambda > \lambda_1(\sigma)$ chosen sufficiently close to $\lambda_1(\sigma)$, there exists a neighbourhood (α_*, α^*) about $\alpha_1 = \sigma$ for which the population persist for $\alpha_1 \in (\alpha_*, \alpha^*)$, while the population is extirpated otherwise. As such, there is an optimal range of rate of advection required to ensure the persistence of the population. In Fig. 3, we explore this scenario for the full predator–prey system. We observe behaviour consistent with the single-species insights obtained in Example 2: with the chosen parameters, we observe nonmonotone behaviour along the lines $\alpha_1 = 2$ and $\alpha_2 = 2$. Indeed, we observe increasing then decreasing behaviour for the prey when $\alpha_2 = 2$, but the decreasing then increasing behaviour of the predator appears to be offset by the absence of the prey.

7. Discussion

Understanding predator–prey systems, particularly in spatially heterogeneous environments, remains a subject of considerable importance for theoretical biology and ecology. Myriad factors affect the dynamics of such systems, and the inclusion of diffusive–advective interactions presents a valuable perspective for capturing the essence of many scenarios known to occur in the natural world.

Different from most literature related to predator–prey systems [6,20,40], the boundary conditions we consider here are Dirichlet boundary conditions. It is usually difficult to analyse systems under Dirichlet boundary conditions. Compared with the single population model considered in [1], we considered two populations of predator–prey systems with advective motion along the gradient direction of the heterogeneous environment, we found that the system produces richer dynamics and gave the impact of the

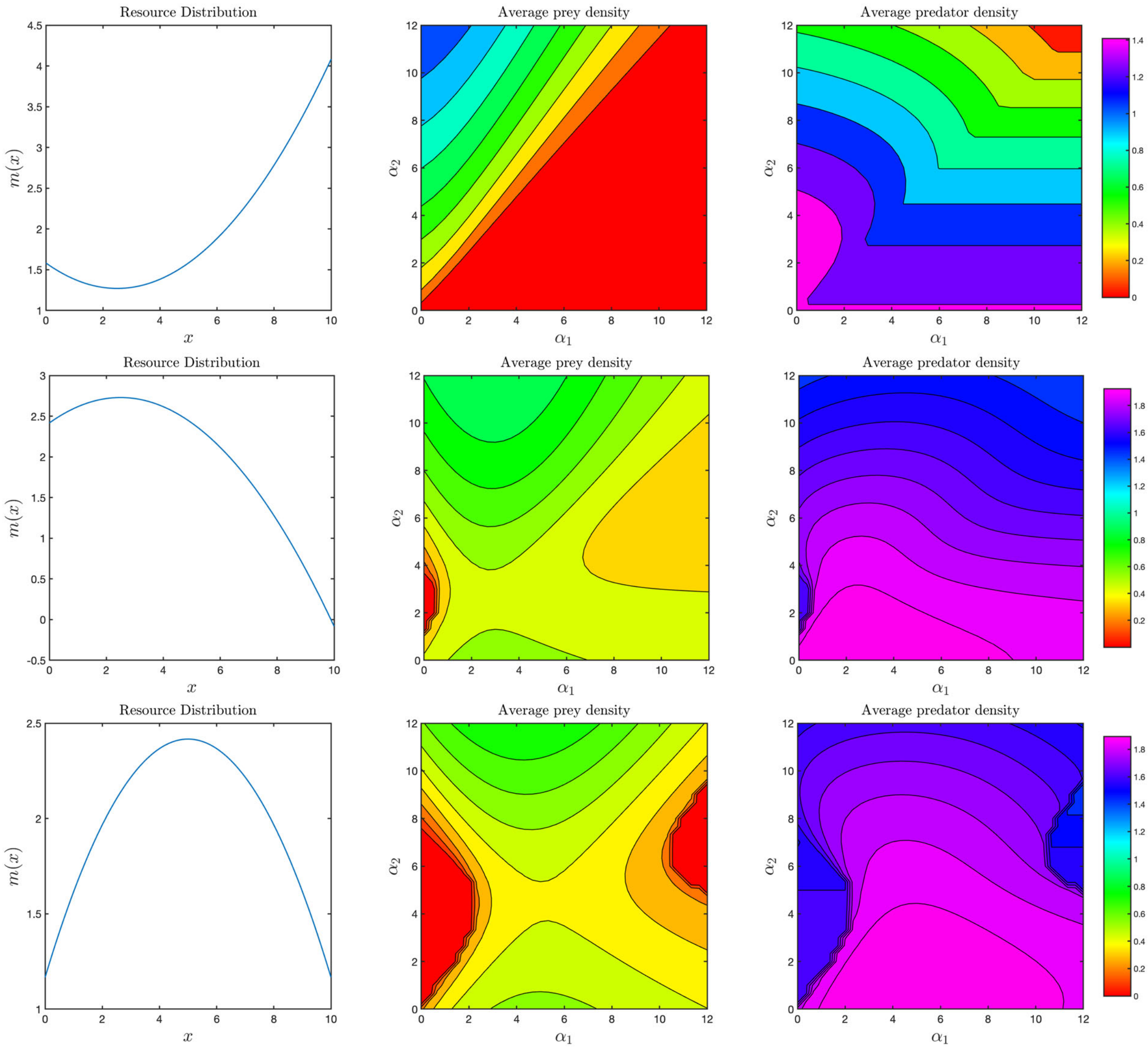

Fig. 2. Global dynamics of the predator–prey system (1.3) depending on advection rates α_1,$\alpha_2 \geq 0$ in the domain $\Omega = (0, 10)$. In each of these simulation sets, we fix the following parameters: $d_1 = d_2 = 2$, $b_1 = b_2 = 1$, $m = 1$. In the left column, we see the profile of the resource distribution $m_1 = m_2 := m(x)$ as defined in Example 1. Choosing $m_0 = 2$ so that the average resource density is held fixed, we fix the following three sets of parameters: $(\sigma, x_0) = (0.05, 2.5)$, $(\sigma, x_0) = (-0.05, 2.5)$, and $(\sigma, x_0) = (-0.05, 5.0)$ from top to bottom. We explore the solution behaviour for $\alpha_i \in [0, 12]$, $i = 1, 2$, where we see the average prey and predator density in the middle and right columns, respectively

heterogeneous environment on population dynamics. Our study applies not only to a diffusive–advective predator–prey system in a spatially heterogeneous environment, with predator–prey interactions described by a Holling type II functional response, but also to the competing systems. Of note is the inclusion of directed movement up the resource gradient, which can significantly impact the system's asymptotic behaviour. Therefore, our result is a generalization of the result in [45] since the advection term is not considered in [45]. By applying several analytical tools, including bifurcation theory, upper and lower solution techniques, spectral analysis, and the comparison principle, we have begun to unravel a deeper

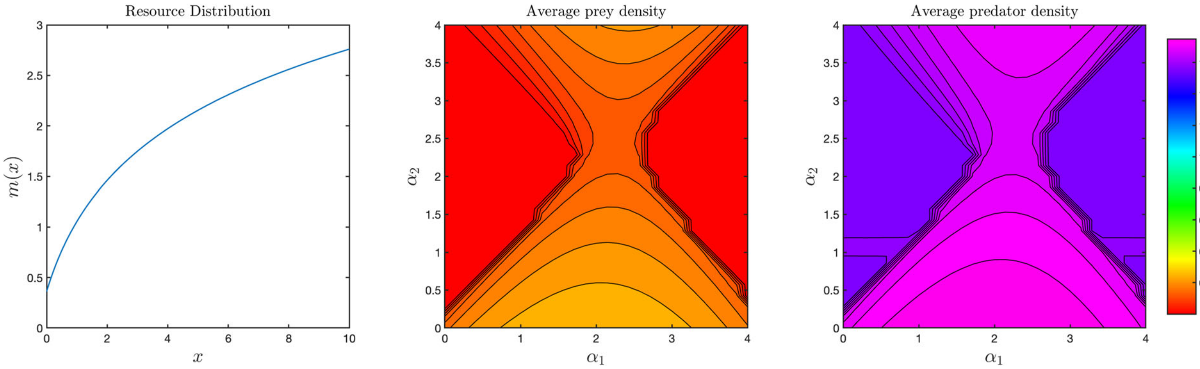

FIG. 3. Global dynamics of the predator–prey system (1.3) depending on advection rates α_1,$\alpha_2 \geq 0$ in the domain $\Omega = (0, 10)$. In each of these simulation sets, we fix the following parameters: $d_1 = d_2 = 2$, $b_1 = b_2 = 1$, $m = 1$. In the left column, we see the profile of the resource distribution $m_1 = m_2 := m(x)$ as defined in Example 2 with $\sigma = 1.0$ and shifted by a constant so that the average resource distribution is fixed at 1. We explore the solution behaviour for $\alpha_i \in [0, 4]$, $i = 1, 2$, where we see the average prey and predator density in the middle and right columns, respectively

understanding of the dynamical behaviour of such predator–prey systems. Of note is the application of these tools to a predator–prey system, where such tools are typically employed in a competition system setting. Consistent with existing results, we proved the existence and uniqueness of the semi-trivial steady states and the global asymptotic stability of the trivial and semi-trivial states in some instances. Moreover, we proved the existence and stability of the positive steady state for a predator–prey system with advection, which appears to be new for the system considered here.

Including advection, represented by the rates α_1, α_2, adds depth to the study by investigating how directed movement along a resource gradient influences predator–prey dynamics. Advection is especially significant because it can play a crucial role in determining how efficiently resources can be exploited in space, given the landscape's heterogeneity. Of particular note are the potential implications for conservation ecology in urban environments when considering the combined effects of spatial heterogeneity, directed movement, and a hostile boundary condition.

One of the most intriguing outcomes observed in our results was the nuanced impact of advection on population persistence. Depending on the form of the resource density function, advection can either promote or hinder persistence. This is best understood when the resource density is either strictly concave or strictly convex. When the resource density is concave with a single peak appearing in the interior of the domain, a small amount of advection increases the possibility for persistence through a decrease in the size of the principal eigenvalue; on the other hand, when the resource density is convex with resource peaks appearing on the boundary, any amount of advection always decreases the possibility for persistence through an increase in the size of the principal eigenvalue. There is an intuitive understanding of this phenomenon: when the resource gradient points towards the domain boundary, the population is pushed towards the hostile boundary. Of note is the fact that the principal eigenvalue is *always increasing* in this case, suggesting that the benefit of concentrating near peak resources along the boundary will never outweigh the detriment of occupying areas near the hostile boundary. Interestingly, the behaviour of the principal eigenvalue is not so clear when a single resource peak exists in the interior of the domain. To explore such curiosities, we presented two forms of environmental heterogeneity, each depending on two parameters. The first example, a simple parabola, provides analytical evidence of cases where $\lambda_1(\alpha_1)$ is either monotonically decreasing or increasing, in which case directed movement is always a benefit or drawback, respectively, to a population's persistence. The second example, a carefully constructed logarithmic function, has precise nonmonotone behaviour. Of particular interest is the existence of an optimal window of advection rates for which the population will persist. These analytical insights, applicable to the single-species model for which there is no species–species interaction, are complemented by numerical simulation of the full predator–prey system. Similar to the analytical insights, we observe both monotone and nonmonotone behaviours with respect to advection as demonstrated by the simulated global dynamics of the system. These results have significant implications for conservation efforts, where efforts are often made to retain as much natural habitat as possible. These results suggest that, in addition to habitat retention, a possibly hostile boundary (e.g. in or near urban centres), the distribution of resources in relation to the boundary, combined with species-specific traits must be considered as important factors.

These results also suggest some intriguing lines of inquiry for future research. We briefly highlight the following:

- **Generalist Predators:** The assumption of the strict positivity of $m_2(x)$ somewhere in Ω indicates that the predator, being a generalist, not only feeds on the prey but also has access to additional resources independent of the predator. How might these findings change if the predator's diet is more specialized, relying more heavily on the prey species? More precisely, how do the dynamics change when $m_2(x) \leq 0$ over all of Ω?
- **Adaptive behaviour:** It is assumed that the prey has an ability to move up the resource gradient, but does not have any change in movement in relation to the presence of a predator. This assumes the prey is a 'no-brainer', in some sense, moving towards higher resource density areas no matter what. A more realistic model may consider the possibility of directed movement *away* from the predator by the prey, potentially improving the possibility for persistence. This would make the system of equation nonlinear at a higher order, increasing the difficulty of study significantly.
- **External Factors:** Environmental disturbances, such as climatic events and anthropogenic habitat disturbances, could modify a species' advection patterns. Investigating how sudden changes in advection might influence the dynamics would be of significant interest. This could be considered through time-dependent advection rates, changing in relation to the current state of the predator/prey and the local environmental quality.

We hope that this effort sheds light on the complex interplay of diffusion, advection, and spatial heterogeneity on predator–prey dynamics, with the findings having possible implications for habitat management, conservation, and our broader understanding of population dynamics. Such insights underscore the necessity of a holistic perspective when assessing such systems, where individual components cannot be isolated from the rest, and where the synergies between them can lead to outcomes that are sometimes counterintuitive.

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Data availability This article describes entirely theoretical research; data sharing was not applicable to this article as no datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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