Numerical Algebra, Control and Optimization

doi:10.3934/naco.2024051

A Σ-SHAPED BIFURCATION CURVE FOR A CLASS OF REACTION DIFFUSION EQUATIONS AND AN APPLICATION TO AN ECOLOGICAL MODEL

Ananta Acharya[1], James T. Cronin[2], Nalin Fonseka[3], Jerome Goddard II[4], Alketa Henderson[5], Victor Munoz[5], and Ratnasingham Shivaji [*5]

[1]Department of Mathematical Sciences, Eastern New Mexico University Portales, NM 88130, USA

[2]Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

[3]Department of Mathematics, Actuarial Science, & Statistics, University of Central Missouri, Warrensburg, MO 64093, USA

[4]Department of Mathematics, Auburn University Montgomery, Montgomery, AL 36124, USA

[5]Department of Mathematics and Statistics, University of North Carolina at Greensboro, Greensboro, NC 27412, USA

Abstract. We analyze the structure of positive solutions to a class of steady state equations arising in modeling a prey population that grows logistically, experiences Holling Type III predation from a generalist predator, and exhibits an overall negative relationship between density and emigration rate (-DDE). In particular, the predator is assumed to operate on a different time scale than the prey and, thus, its density is held constant. Under some general hypotheses on the reaction term and boundary nonlinearity, we establish existence, nonexistence, and multiplicity results for certain ranges of a parameter which is proportional to patch size squared via the method of sub-super-solutions. In particular, we establish that the bifurcation curve of positive solutions for the steady state equation is at least Σ-shaped. In this case, there is a range of patch size where a patch-level Allee effect occurs, i.e., a situation where the trivial solution and at least one other positive steady state are stable arises for small patch sizes, and a non-Allee effect type bi-stability arises for a range of larger patch sizes. As an application of our result, we consider the case when Ω is a ball, the reaction term is exactly logistic growth with a Type III functional response and the boundary nonlinearity is a -DDE form with a fast decay rate and show that the hypotheses in our theorems are satisfied. Further, when $\Omega = (0, 1)$, we employ quadrature methods and computations using Wolfram Mathematica to show that the bifurcation diagram for positive solutions of this example is exactly Σ-shaped for certain values of the parameters. The occurrence of multiple steady states in real-world metapopulations can influence the fraction and distribution of occupied patches and cause uncertainty in predicting minimum patch size and density-area relationships.

2020 *Mathematics Subject Classification.* 35J15, 35J25, 35J30, 35J60, 35J66.

Key words and phrases. Reaction diffusion equations, existence, multiplicity, non-linear boundary conditions, Allee Effect, Σ-shaped bifurcation curves.

This work is supported by NSF grants Cronin (DMS-2150945 and DMS-2246724), Goddard (DMS-2150946 and DMS-2246725), and Shivaji (DMS-2150947 and DMS-2246723).

This paper is handled by Wandi Ding as the guest editor.

*Corresponding author: Ratnasingham Shivaji.

1. **Introduction.** In [18], the authors established certain existence and multiplicity results for positive solutions of the following steady state problem arising from a population model, namely,

$$\begin{cases} -\Delta u = \lambda\left(u - \frac{u^2}{K} - \frac{cu^2}{1+u^2}\right);\ x \in \Omega \\ \frac{\partial u}{\partial \eta} + \sqrt{\lambda}u = 0;\ x \in \partial\Omega \end{cases} \tag{1}$$

where a prey population and a generalist predator occupy a single habitat patch which is surrounded by a hostile matrix. Here, u represents the prey density in the patch, $\lambda > 0$ is proportional to patch size squared, prey exhibit logistic growth with $K > 0$ being the patch carrying capacity, and $\frac{cu^2}{1+u^2}$ represents a Holling Type III functional response of a predator population which is assumed to be at constant density (one could assume the time scale of the predator is much greater than the prey, leaving the predator's population dynamics as negligible) with composite parameter $c \geq 0$ representing maximal predation rate (see, e.g., [22], [23], and [24]). Specifically, a Type III response can arise in the situation where a generalist predator, which when it encounters this prey at low levels preys upon it at corresponding low levels. But, as the prey density reaches a certain threshold, the predator "switches" and begins to consume prey at higher levels. It is also assumed that either Ω is a bounded domain in $\mathbb{R}^N$; $N > 1$ with smooth boundary $\partial\Omega$ or $N = 1$ and $\Omega = (0, 1)$. In this scaled model, Ω has unit length, area, or volume and $\frac{\partial u}{\partial \eta}$ denotes the outward normal derivative of u. The details of the derivation of such a population model can be found in [13].

In [18], the authors proved that the bifurcation diagram of positive solutions for (1) is S-shaped for certain parameter values and ranges of λ-values (see Figure 1).

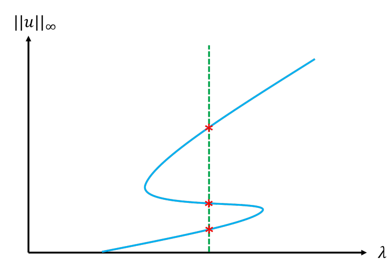

FIGURE 1. A prototypical S-shaped bifurcation diagram of positive solutions for (1).

The ecological interpretation of such a prediction is that patches with a λ-value such as the one illustrated by the dotted line in Figure 1 will have at least three positive steady states, say u_1, u_2, u_3 listed in ascending order of size. It is easy to see that this creates a dynamical structure that is at least bi-stable, i.e., the solution of the corresponding time-dependent problem with initial condition taken within $[u_1, u_2]$ will remain in this range for all time (see, e.g., [32]) and similarly for initial conditions taken within $[u_2, u_3]$. However, for this λ-value, the trivial solution is unstable. As this bifurcation diagram illustrates, the size of the patch plays a crucial role in determining if this predation mechanism will produce bi-stability or not. In other words, bi-stability only occurs for intermediate levels of patch size.

Allee effects, defined as the positive effects of increasing density on fitness, have also been shown to create a type of bi-stability in spatially heterogeneous models such as (1). In this case, the trivial solution and at least one other positive steady state are both stable, leading to prediction of a threshold for which the population must overcome in order to be predicted to persist. Allee effects were first described in the early 1930s for cooperatively breeding species [3, 26]. Although several causes of Allee effects have been proposed in the literature, scarcity of reproductive opportunities at low densities are thought to be a common cause for Allee effects (see [15, 30]). Other factors can be found in [11, 17, 27]. Although it can be difficult to detect (e.g., [35]), empirical support for Allee effects spans a wide diversity of taxa (see [11, 27]).

The authors have shown in a series of studies that a negative relationship between density and emigration from a patch into the matrix (-DDE) can generate a patch-level Allee effect in models without an explicit Allee effect type growth, see [8, 19, 21]. Although the most widely accepted view of emigration behavior is that species should exhibit positive DDE (+DDE) (see [5, 6, 31]), other forms of density-dependent emigration (DDE), including -DDE, exist. In a recent review of the empirical literature, [21] found that 35% of the cases exhibited +DDE, 30% were density independent (DIE), 25% were -DDE, 10% were non-monotonic. However, little is known about the dynamics of such an ecosystem where prey grow logistically, experience Type III predation, and exhibit -DDE. In particular, what interaction will the two mechanisms of Type III predation and -DDE have on predictions of persistence as the patch size is varied?

In this paper, we study a general class of steady state problems arising from a population model for prey that are growing logistically, experiencing Type III predation from a generalist predator, and exhibiting -DDE, namely:

$$\begin{cases} -\Delta u = \lambda f(u);\ x \in \Omega \\ \frac{\partial u}{\partial \eta} + \sqrt{\lambda}\gamma g(u)u = 0;\ x \in \partial\Omega \end{cases} \tag{2}$$

where the setup is the same as in (1) with the addition of the composite parameter γ which is proportional to matrix hostility and $g(u) = \frac{1-\alpha(u)}{\alpha(u)}$ with $\alpha(u)$ being the probability of an organism remaining in the patch upon reaching the boundary. We now make the following assumptions regarding the reaction term f and boundary nonlinearity g which will include the modeling situation discussed previously:
(H_1) : $f \in C([0,\infty),\mathbb{R})$ such that $f(0) = 0, f'(0) = 1$, there exists $r_0 \in (0,\infty)$ such that $f \in C^2([0,r_0])$, $f(r_0) = 0$, and $f(s)(s-r_0) \leq 0$ for $s \in [0,\infty)$,
(H_2) : $g \in C([0,\infty),(g_\infty, g_0])$ is a continuous function such that there exists g_0, g_∞ with $0 < g_\infty \leq g_0$, $g(0) = g_0$, and $\min\limits_{[0,\infty)} g(s) = g_\infty$.

We note that (H_2) ensures g represents an overall -DDE when $g_\infty < g_0$ or DIE or +DDE when $g_\infty = g_0$, and we will show that when $\max\limits_{[0,r_0]}\left\{\frac{f(s)}{s}\right\} = 1\ (= f'(0))$ the growth term is not of Allee effect type. Our aim is to derive sufficient conditions for which the bifurcation diagram of positive solutions for (2) is at least Σ-shaped. Ecologically, such a diagram will imply there are ranges of λ where a patch-level Allee effect arises and others where a non-Allee type bi-stability occurs.

First, we recall some results for certain eigenvalue problems from [20]. Namely, given $M, B, \gamma > 0$, let $\bar{E}_1(M,B,\gamma)$ be the principal eigenvalue of the problem:

$$\begin{cases} -\Delta\phi_0 = EM\phi_0;\ x \in \Omega \\ \frac{\partial \phi_0}{\partial \eta} + \sqrt{E}B\gamma\phi_0 = 0;\ x \in \partial\Omega \end{cases} \tag{3}$$

with corresponding normalized eigenfunction $\phi_0 > 0; x \in \overline{\Omega}$ such that $\|\phi_0\|_\infty = 1$. In the case of $M = 1, B = 1$ we denote $E_1(\gamma) = \bar{E}_1(1, 1, \gamma)$. Further, for a fixed $M, B, \gamma, \lambda > 0$, let $\sigma_0(M, B, \gamma)$ be the principal eigenvalue and $\phi_0 > 0; x \in \overline{\Omega}$ be the corresponding normalized eigenfunction of:

$$\begin{cases} -\Delta\phi_0 = (\sigma + \lambda M)\phi_0;\ x \in \Omega \\ \frac{\partial \phi_0}{\partial \eta} + \sqrt{\lambda} B\gamma\phi_0 = 0;\ x \in \partial\Omega \end{cases} \tag{4}$$

and $\sigma_1(M, B, \gamma)$ be the principal eigenvalue and $\phi_1 > 0; x \in \overline{\Omega}$ be the corresponding normalized eigenfunction of the related problem:

$$\begin{cases} -\Delta\phi_1 = (\sigma + \lambda M)\phi_1;\ x \in \Omega \\ \frac{\partial \phi_1}{\partial \eta} + \sqrt{\lambda} B\gamma\phi_1 = \sigma\phi_1;\ x \in \partial\Omega. \end{cases} \tag{5}$$

We note that $\operatorname{sgn}(\sigma_1) = \operatorname{sgn}(\sigma_0)$, $\sigma_0(M, B, \gamma) \geq 0$ for $\lambda \leq \bar{E}_1(M, B, \gamma)$, $\sigma_0(M, B, \gamma) < 0$ for $\lambda > \bar{E}_1(M, B, \gamma)$, and $\sigma_0(M, B, \gamma) \to 0$ as $\lambda \to \bar{E}_1(M, B, \gamma)$ (see [20]).
Let $R > 0$ be the radius of the largest ball that can be inscribed inside the domain Ω, $C_N := \frac{(N+1)^{N+1}}{2N^N}$ (> 1), $f^*(s) := \max_{r \in [0,s]} f(r)$, and given a $b > 0$, denote v_{μ_b} as the unique solution of:

$$\begin{cases} -\Delta v = 1;\ x \in \Omega \\ \frac{\partial v}{\partial \eta} + \gamma\mu_b g_\infty v = 0;\ x \in \partial\Omega \end{cases} \tag{6}$$

with $\mu_b = \sqrt{\frac{2bNC_N}{R^2 f(b)}}$.

Now, we state two further hypotheses regarding f:
(H_3) : there exist $a, b > 0$ such that $a < b < \frac{r_0}{C_N}$ and $\frac{a}{f^*(a)} / \frac{b}{f(b)} > \frac{2NC_N\|v_{\mu_b}\|_\infty}{R^2}$,
(H_4) : there exist $r_1 \in (0, b)$ and $r_2 \in (bC_N, r_0)$ such that f is non-decreasing in (r_1, r_2).

We now state our main results, with statements of stability understood in Lyapunov sense, e.g., see [7] or [32].

Theorem 1.1.

(i) *Let $(H_1), (H_2)$ hold and let $M_0 = \max_{[0,r_0]} \left\{\frac{f(s)}{s}\right\}$. Then (2) has no positive solution for $\lambda \leq \bar{E}_1(M_0, g_\infty, \gamma)$ and the trivial solution is asymptotically stable. For $\lambda > \bar{E}_1(1, g_0, \gamma)$, the trivial solution of (2) is unstable and there exists a positive solution of (2), u_λ, such that $\|u_\lambda\|_\infty \to r_0$ as $\lambda \to \infty$.*

(ii) *Let $(H_1), (H_2)$ hold and let $M_0 = \max_{[0,r_0]} \left\{\frac{f(s)}{s}\right\}$. Given a $\lambda_0 < \bar{E}_1(M_0, g_0, \gamma)$, there is a unique $b_0 \in (0, g_0)$ such that $\lambda_0 = \bar{E}_1(M_0, b_0, \gamma)$ and if $g(s) \geq \frac{b_0 - g_0}{r_0} s + g_0; s \in [0, r_0]$ then (2) has no positive solution for $\lambda \in (0, \lambda_0)$. In particular, if $M_0 = 1$ and $g_0 = g_\infty$ then (2) has no positive solution for $\lambda \leq \bar{E}_1(1, g_0, \gamma)$ and, thus, there is no patch-level Allee effect in this case.*

(iii) *Let* $(H_1), (H_2)$ *hold. Given a* $\lambda_1 \in \big(\bar{E}_1(1, g_\infty, \gamma), \bar{E}_1(1, g_0, \gamma)\big)$, *there exists a* $\lambda_0 \in (\bar{E}_1(1, g_\infty, \gamma), \lambda_1)$, *a corresponding* $b_0 \in (g_\infty, g_0)$ *such that* $\lambda_0 = \bar{E}_1(1, b_0, \gamma)$, *and a* $K_0(\lambda_1, f, \gamma, \Omega) > 0$ *such that if* $g(s) < b_0$ *for* $s \in [K_0(\lambda_1, f, \gamma, \Omega), r_0]$ *then* (2) *has at least two positive solutions for* $\lambda \in \big[\lambda_1, \bar{E}_1(1, g_0, \gamma)\big)$ *and a patch-level Allee effect occurs on this* λ*-range.*

(iv) *Let* (H_1), (H_2), (H_3), *&* (H_4) *hold. Then* (2) *has at least three positive solutions for*

$$\lambda \in \left(\max\left\{\bar{E}_1(1, g_0, \gamma), \frac{2bNC_N}{R^2 f(b)}\right\}, \min\left\{\frac{a}{\|v_{\mu_b}\|_\infty f^*(a)}, \frac{2r_2N}{f(b)R^2}\right\}\right).$$

Corollary 1.2. *Let* (H_1), (H_2), (H_3), *&* (H_4) *hold. Given a* $\lambda_1 \in \big(\bar{E}_1(1, g_\infty, \gamma), \bar{E}_1(1, g_0, \gamma)\big)$, *if* $g(s) < b_0$ *for* $s \in [K_0(\lambda_1, f, \gamma, \Omega), r_0]$ *(where* b_0 *and* K_0 *are as in Theorem* 1.1 *(iii)), then* (2) *has a positive solution* u_λ *for* $\lambda > \lambda_1$ *such that* $\|u_\lambda\|_\infty \to r_0$ *as* $\lambda \to \infty$, *at least two positive solutions for* $\lambda \in \big[\lambda_1, \bar{E}_1(1, g_0, \gamma)\big)$, *and at least three positive solutions for*

$$\lambda \in \left(\max\left\{\bar{E}_1(1, g_0, \gamma), \frac{2bNC_N}{R^2 f(b)}\right\}, \min\left\{\frac{a}{\|v_{\mu_b}\|_\infty f^*(a)}, \frac{2r_2N}{f(b)R^2}\right\}\right).$$

Remark 1.3. See [1] and [2] for studies where the authors have established a Σ-shaped bifurcation diagram for (2) when the boundary conditions are linear (i.e. $g(s) = 1$) and nonlinear respectively. In both studies, authors established their results assuming that $f(s)$ is an increasing function and hence their results do not apply to the reaction term $f(s) = s - \frac{s^2}{K} - \frac{cs^2}{1+s^2}$. See also [28], where the authors discuss a Σ-shaped bifurcation curve for an ecological model with semipositone structure and Dirichlet boundary conditions, namely when $f(s) = s - \frac{s^2}{K} - \frac{cs^2}{1+s^2} - \epsilon$; $\epsilon > 0$.

Theorem 1.1(i) shows that persistence of the prey is not possible when the patch size is too small, whereas prey can persist at a level which approaches the steady state value of the spatially homogeneous version of (2), i.e., r_0. The latter is due to the fact that larger patches develop a core area where organisms residing in this area are not likely to reach the patch/matrix interface and face mortality in the matrix. Theorem 1.1(ii) gives a sufficient condition for when the -DDE strength (which is measured by how fast g is allowed to decay to its minimum value g_∞) is not enough to ensure persistence for small patch sizes. Notice that $g_0 = g_\infty$ means that g represents non-negative DDE, and any patch-level Allee effect prediction has to come from the reaction term. When $\max\limits_{[0,r_0]}\left\{\frac{f(s)}{s}\right\} = 1$, there is no possibility for a positive solution below the bifurcation point, $\bar{E}_1(1, g_0, \gamma)$, and therefore no patch-level Allee effect is possible.

Theorem 1.1(iii) reveals the fact that if the prey species exhibits any level of -DDE (i.e., $g_\infty < g_0$) then a patch-level Allee effect is predicted as long as g decays quickly enough below a certain threshold. This threshold is related to the domain geometry through the eigenvalue problem (3) and the desired λ_1-value. Notice that the decay rate requirement is indeed tied to reaction term, f. The result in Theorem 1.1(iv) gives sufficient conditions for existence of a non-Allee type bi-stability for patch sizes in a certain range of values. Finally, Corollary 1.2 gives sufficient conditions for the bifurcation curve of positive solutions for (2) to be Σ-shaped (see Figure 2). In this case, the model predicts extinction for small patch sizes, a patch-level Allee effect for a range of patch sizes corresponding to $\lambda < \bar{E}_1(1, g_0, \gamma)$ and $\lambda \approx \bar{E}_1(1, g_0, \gamma)$, and a non-Allee type bi-stability for an intermediate range of patch sizes with λ-values in the range outlined in Theorem 1.1(iv).

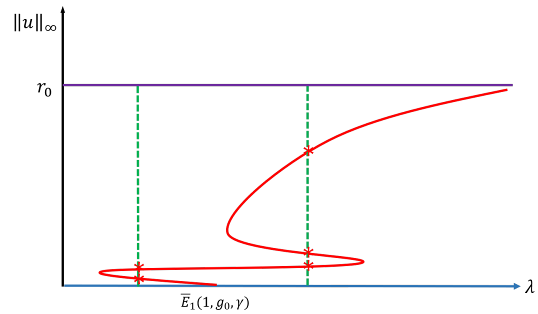

Figure 2. An expected bifurcation diagram for positive solutions of (2) when the hypotheses for Corollary 1.2 are satisfied.

We present some important preliminaries in Section 2, followed by proofs of Theorem 1.1 and Corollary 1.2 in Section 3. In Section 4, we discuss an example arising in ecological modeling for the case when Ω is a ball of radius $R > 0$ in $\mathbb{R}^N$; $N = 1, 2, 3$, and show that Theorem 1.1 and Corollary 1.2 hold for certain parameter values for this example. In Section 5, we computationally generate bifurcation diagrams of positive solutions for (2). In particular, our computational results indicate these bifurcation curves are exactly $\Sigma-$shaped for certain parameter values.

2. **Preliminaries.** In this section, we introduce definitions of a (strict) subsolution and a (strict) supersolution of (2) and state two sub-supersolution theorems that are used to prove existence and multiplicity results for positive solutions.
By a subsolution of (2) we mean $\psi \in C^2(\Omega) \cap C^1(\overline{\Omega})$ that satisfies

$$\begin{cases} -\Delta\psi \leq \lambda f(\psi);\ x \in \Omega \\ \frac{\partial\psi}{\partial\eta} + \sqrt{\lambda}\gamma g(\psi)\psi \leq 0;\ x \in \partial\Omega, \end{cases}$$

and by a supersolution of (2) we mean $Z \in C^2(\Omega) \cap C^1(\overline{\Omega})$ that satisfies

$$\begin{cases} -\Delta Z \geq \lambda f(Z);\ x \in \Omega \\ \frac{\partial Z}{\partial\eta} + \sqrt{\lambda}\gamma g(Z)Z \geq 0;\ x \in \partial\Omega. \end{cases}$$

By a strict subsolution (supersolution) of (2) we mean a subsolution (supersolution) which is not a solution.

Then the following results hold (see Thereoms 1 and 2 in [25]).

Lemma 2.1. *Let ψ and Z be a subsolution and a supersolution of (2) respectively such that $\psi \leq Z$. Then (2) has a solution $u \in C^2(\Omega) \cap C^1(\overline{\Omega})$ such that $u \in [\psi, Z]$.*

Lemma 2.2. *Let ψ_1 and Z_2 be a subsolution and a supersolution of (2) respectively such that $\psi_1 \leq Z_2$. Let ψ_2 and Z_1 be a strict subsolution and a strict supersolution of (2) respectively such that $\psi_2 \not\leq Z_1$ and $\psi_2, Z_1 \in [\psi_1, Z_2]$. Then (2) has at least three solutions u_1, u_2 and u_3 where $u_i \in [\psi_i, Z_i]$; $i = 1, 2$ and $u_3 \in [\psi_1, Z_2] \backslash ([\psi_1, Z_1] \cup [\psi_2, Z_2])$.*

Remark 2.3. Theorem 2 in [25] is established by the application of fixed-point theory ideas used in [4] (see Theorem 15.2). As in [4], Theorem 2 in [25] is also stated with the assumption $Z_1 < \psi_2$. For the proof of this theorem to go through, what is really needed is that the set $[\psi_1, Z_1] \cap [\psi_2, Z_2]$ is empty, which is true when $Z_1 < \psi_2$. However, for this set to be empty assuming $\psi_2 \not\leq Z_1$ is sufficient, and hence this three-solution theorem holds under this lesser assumption. This observation was noted in [34], and Lemma 2.2 is also stated with the assumption $\psi_2 \not\leq Z_1$.

3. **Proofs of Theorem 1.1 and Corollary 1.2.** In this section, we provide proofs of our main results. First, we make a note about K_0 referenced in Theorem 1.1.

Details of the constant K_0 in Theorem 1.1.

Given a $\lambda_1 \in \big(\bar{E}_1(1, g_\infty, \gamma), \bar{E}_1(1, g_0, \gamma)\big)$, we choose a $\lambda_0 \in (\bar{E}_1(1, g_\infty, \gamma), \lambda_1)$ and using the facts that $\bar{E}_1(M, B, \gamma)$ is strictly decreasing as a function of B and $\bar{E}_1(M, 0, \gamma) = 0$, there exists a unique $b_0 \in (g_\infty, g_0)$ such that $\lambda_0 = \bar{E}_1(1, b_0, \gamma)$. Now, for a fixed $\lambda > \lambda_1$, define $H(s) := (\lambda + \sigma_0)s - \lambda f(s)$, where $\sigma_0 = \sigma_0(1, b_0, \gamma)$ is the principal eigenvalue of (4) with corresponding eigenfunction ϕ_0. Then $H(0) = 0$ and $H'(0) = (\lambda + \sigma_0) - \lambda f'(0) = \sigma_0 < 0$ since $f'(0) = 1$ and $\sigma_0 < 0$ for $\lambda > \bar{E}_1(1, b_0, \gamma)$. This implies that $H(s) < 0$ for $s \approx 0$. Let $0 < s_\lambda < r_0$ be such that

$$H(s) = (\lambda + \sigma_0)s - \lambda f(s) < 0; \quad \text{for all } s \in (0, s_\lambda]. \tag{7}$$

Now, define

$$K_0 = K_0(\lambda_1, f, \gamma, \Omega) := \min_{\lambda \in \left[\lambda_1, \bar{E}_1(1, g_0, \gamma)\right]} \left\{ \min_{\overline{\Omega}} n\phi_0(x) \right\} \tag{8}$$

where

$$n := \min_{\lambda \in \left[\lambda_1, \bar{E}_1(1, g_0, \gamma)\right]} \{s_\lambda\}. \tag{9}$$

Next, we construct several sub- and supersolutions that are crucial to proving our results.

Construction of a subsolution ψ_1 when (H_1) & (H_2) hold for $\lambda > \bar{E}_1(1, g_0, \gamma)$.

For a fixed $\lambda > 0$, let $\sigma_1 = \sigma_1(1, g_0, \gamma)$ be the principal eigenvalue with corresponding normalized eigenfunction $\phi_1 > 0$; $\overline{\Omega}$ of (5). We note that $\sigma_1 < 0$ for $\lambda > \bar{E}_1(1, g_0, \gamma)$. Let $\psi_1 := p_\lambda \phi_1$ for $p_\lambda > 0$ and $l(s) := (\lambda + \sigma_1)s - \lambda f(s)$. Then, we have $l(0) = 0$ and $l'(0) = (\lambda + \sigma_1) - \lambda f'(0) = \sigma_1 < 0$ since $f'(0) = 1$ and $\lambda > \bar{E}_1(1, g_0, \gamma)$. Therefore, $l(s) < 0; s \approx 0$. This implies that

$$-\Delta\psi_1 = p_\lambda(\lambda + \sigma_1)\phi_1 < \lambda f(p_\lambda \phi_1) = \lambda f(\psi_1); \ \Omega$$

for $p_\lambda \approx 0$. We also have

$$\begin{aligned}\frac{\partial \psi_1}{\partial \eta} + \sqrt{\lambda}\gamma g(\psi_1)\psi_1 &= p_\lambda\Big(\frac{\partial \phi_1}{\partial \eta} + \sqrt{\lambda}\gamma g(p_\lambda \phi_1)\phi_1\Big) \\ &= p_\lambda\Big(\Big(\sigma_1 - \sqrt{\lambda}\gamma g_0\Big)\phi_1 + \sqrt{\lambda}\gamma g(p_\lambda \phi_1)\phi_1\Big)\end{aligned}$$

$$= p_\lambda\Big(\sigma_1 + \sqrt{\lambda}\gamma\,(g(p_\lambda\phi_0) - g_0)\Big)\phi_1$$
$$< 0;\ \partial\Omega$$

for $p_\lambda \approx 0$, since $g(0) = g_0$ and $\sigma_1 < 0$. Hence, ψ_1 is a subsolution of (2) for $\lambda > \bar{E}_1(1, g_0, \gamma)$ and $p_\lambda \approx 0$.

Construction of a strict subsolution ψ_2 when (H_1), (H_2), (H_3), & (H_4) hold for $\lambda \in \left(\frac{2bNC_N}{R^2 f(b)}, \frac{2r_2 N}{f(b)R^2}\right)$.

Let $\tilde{g} \in C^1([0,\infty))$ be such that $\tilde{g}$ is nondecreasing on $[0, r_2), 0 \le \tilde{g}(s) \le f(s)$ on $[0, r_1)$ and $\tilde{g}(s) = f(s)$ on $[r_1, r_2)$. Then the following boundary value problem

$$\begin{cases} -\Delta w = \lambda \tilde{g}(w);\ x \in \Omega \\ \quad u = 0;\ x \in \partial\Omega \end{cases}$$

has a solution $\tilde{w}_\lambda \ge 0$ such that $\|\tilde{w}_\lambda\|_\infty \ge b$ for $\lambda \in \left(\frac{2bNC_N}{R^2 f(b)}, \frac{2r_2 N}{f(b)R^2}\right)$ provided (H_3) and (H_4) are satisfied (see [29]). Let $\psi_2 := \tilde{w}_\lambda$. Since $\tilde{g}(s) \le f(s)$ on $[0, r_0)$ and $\frac{\partial \tilde{w}_\lambda}{\partial \eta} < 0$ on $\partial\Omega$ by Hopf maximum principle, it is easy to show that ψ_2 is a strict subsolution of (2) for $\lambda \in \left(\frac{2bNC_N}{R^2 f(b)}, \frac{2r_2 N}{f(b)R^2}\right)$.

Construction of a strict subsolution ψ_3 when $(H_1), (H_2)$ are satisfied for $\lambda < \bar{E}_1(1, g_0, \gamma)$ when $g(s) < b_0$ for $s \in [K_0(\lambda_1, f, \gamma, \Omega), r_0]$.

Given a $\lambda_1 \in \left(\bar{E}_1(1, g_\infty, \gamma), \bar{E}_1(1, g_0, \gamma)\right)$, we choose a $\lambda_0 < \lambda_1$, there exists a unique $b_0 \in (g_\infty, g_0)$ such that $\lambda_0 = \bar{E}_1(1, b_0, \gamma)$. Now, recall n from (9), K_0 from (8), and $\sigma_0 = \sigma_0(1, b_0, \gamma)$ the principal eigenvalue of (4) with corresponding eigenfunction ϕ_0. Let $\lambda \in \left[\lambda_1, \bar{E}_1(1, g_0, \gamma)\right]$ and $\psi_3 := n\phi_0$, and assume that $g(s) < b_0$ for $s \in [K_0(\lambda_1, f, \gamma, \Omega), r_0]$. Then, from (7) we have

$$-\Delta\psi_3 = -n\Delta\phi_0 = n(\lambda + \sigma_0)\phi_0 < \lambda f(n\phi_0) = \lambda f(\psi_3);\ \Omega.$$

Further, since $g(s) < b_0$ for all $s \in [K_0, r_0]$, we have

$$\begin{aligned} \frac{\partial\psi_3}{\partial\eta} + \sqrt{\lambda}\gamma g(\psi_3)\psi_3 &= n\left(\frac{\partial\phi_0}{\partial\eta} + \sqrt{\lambda}\gamma g(n\phi_0)\phi_0\right) \\ &= n\sqrt{\lambda}\gamma\,(g(n\phi_0) - b_0)\,\phi_0 \\ &< 0;\ \partial\Omega. \end{aligned}$$

Hence, ψ_3 is a strict subsolution of (2) for $\lambda \in \left[\lambda_1, \bar{E}_1(1, g_0, \gamma)\right]$ with $\|\psi_3\|_\infty < r_0$.

Construction of a subsolution ψ_4 for $\lambda \gg 1$ such that $\|\psi_4\|_\infty \to r_0$ as $\lambda \to \infty$.

We note that the boundary value problem:

$$\begin{cases} -\Delta w = \lambda f(w);\ x \in \Omega \\ \quad w = 0;\ x \in \partial\Omega \end{cases}$$

has a solution w_λ for $\lambda \gg 1$ such that $0 \le w_\lambda \le r_0$ and $\|w_\lambda\|_\infty \to r_0$ as $\lambda \to \infty$ (see [10]).

Further, w_λ satisfies $\frac{\partial w_\lambda}{\partial \eta} + \sqrt{\lambda}\gamma g(w_\lambda)w_\lambda < 0$ on $\partial\Omega$ since $\frac{\partial w_\lambda}{\partial \eta} < 0$ on $\partial\Omega$ by Hopf's Maximum Principle. Therefore, $\psi_4 := w_\lambda$ is a subsolution of (2) for $\lambda \gg 1$ such that $\|\psi_4\|_\infty \to r_0$ as $\lambda \to \infty$.

Construction of a global supersolution Z_1 for $\lambda > 0$.

Let $Z_1 := r_0$. Then it is easy to see that Z_1 is a global supersolution of (2) for all $\lambda > 0$. Furthermore, it is easy to see from the maximum principle that any positive solution, u, of (2) will satisfy $\|u\|_\infty < Z_1 = r_0$.

Construction of a strict supersolution Z_2 when (H_1), (H_2), (H_3), & (H_4) hold for $\lambda \in \left(\frac{2bNC_N}{R^2 f(b)}, \frac{a}{\|v_{\mu_b}\|_\infty f^*(a)}\right)$.

Let $Z_2 := \frac{av_{\mu_b}}{\|v_{\mu_b}\|_\infty}$, where v_{μ_b} is the unique positive solution of (6). Thus, we have

$$
\begin{aligned}
-\Delta Z_2 &= \frac{a}{\|v_{\mu_b}\|_\infty} \\
&> \lambda f^*(a) \\
&\geq \lambda f^*\left(\frac{av_{\mu_b}}{\|v_{\mu_b}\|_\infty}\right) \\
&\geq \lambda f\left(\frac{av_{\mu_b}}{\|v_{\mu_b}\|_\infty}\right) \\
&= \lambda f(Z_2); \Omega
\end{aligned}
$$

since $\lambda < \frac{a}{\|v_{\mu_b}\|_\infty f^*(a)}$ and $f^*(s) = \max_{t\in[0,s]} f(t)$. Now, since $\lambda > \frac{2bNC_N}{R^2 f(b)}$ and $g(s) \geq g_\infty$; $[0,\infty)$, we have

$$
\begin{aligned}
\frac{\partial Z_2}{\partial \eta} + \sqrt{\lambda}\gamma g(Z_2)Z_2 &= \frac{\partial\left(\frac{av_{\mu_b}}{\|v_{\mu_b}\|_\infty}\right)}{\partial \eta} + \sqrt{\lambda}\gamma g\left(\frac{av_{\mu_b}}{\|v_{\mu_b}\|_\infty}\right)\frac{av_{\mu_b}}{\|v_{\mu_b}\|_\infty} \\
&= \frac{a}{\|v_{\mu_b}\|_\infty}\left(\frac{\partial v_{\mu_b}}{\partial \eta} + \sqrt{\lambda}\gamma g\left(\frac{av_{\mu_b}}{\|v_{\mu_b}\|_\infty}\right)v_{\mu_b}\right) \\
&\geq \frac{a}{\|v_{\mu_b}\|_\infty}\left(\frac{\partial v_{\mu_b}}{\partial \eta} + \sqrt{\frac{2bNC_N}{R^2 f(b)}}\gamma g_\infty v_{\mu_b}\right) \\
&= \frac{a}{\|v_{\mu_b}\|_\infty}\left(\frac{\partial v_{\mu_b}}{\partial \eta} + \gamma\mu_b g_\infty v_{\mu_b}\right) \\
&= 0; \partial\Omega.
\end{aligned}
$$

Hence, Z_2 is a strict supersolution of (2) with $\|Z_2\|_\infty = a$.

Construction of a strict supersolution Z_3 when (H_1) holds for $\lambda < \bar{E}_1(1, g_0, \gamma)$.

For a fixed $\lambda > 0$, let $\sigma_1 = \sigma_1(1, g_0, \gamma)$ be the principal eigenvalue with corresponding normalized eigenfunction $\phi_1 > 0$; $\overline{\Omega}$ of (5). Recall that $\sigma_1 > 0$ for $\lambda < \bar{E}_1(1, g_0, \gamma)$. Let $Z_3 := \tilde{m}_\lambda \phi_1$ and $l(s) = (\lambda + \sigma_1)s - \lambda f(s)$. Then we have

$l(0)=0$ and $l'(0)=(\lambda+\sigma_1)-\lambda f'(0)=\sigma_1>0$ since $f'(0)=1$ and $\lambda<\bar{E}_1(1,g_0,\gamma)$. This implies that

$$-\Delta Z_3=\tilde{m}_\lambda(\lambda+\sigma_1)\phi_1>\lambda f(\tilde{m}_\lambda\phi_1)=\lambda f(Z_3);\ \Omega$$

for $\tilde{m}_\lambda\approx 0$. We also have

$$\begin{aligned}\frac{\partial Z_3}{\partial\eta}+\sqrt{\lambda}\gamma g(Z_3)Z_3&=\tilde{m}_\lambda\Big(\frac{\partial\phi_1}{\partial\eta}+\sqrt{\lambda}\gamma g(\tilde{m}_\lambda\phi_1)\phi_1\Big)\\&=\tilde{m}_\lambda\Big(\Big(\sigma_1-\sqrt{\lambda}\gamma g_0\Big)\phi_1+\sqrt{\lambda}\gamma g(\tilde{m}_\lambda\phi_1)\phi_1\Big)\\&=\tilde{m}_\lambda\phi_1\Big(\sqrt{\lambda}\gamma(g(\tilde{m}_\lambda\phi_1)-g_0)+\sigma_1\Big)\\&>0;\ \partial\Omega\end{aligned}$$

for $\tilde{m}_\lambda\approx 0$ since $g(0)=g_0$ and $\sigma_1>0$ for $\lambda<\bar{E}_1(1,g_0,\gamma)$. Hence, Z_3 is a strict supersolution of (2) for $\lambda<\bar{E}_1(1,g_0,\gamma)$ when $\tilde{m}_\lambda\approx 0$.

Finally, we provide proofs of our main results.

Proof of Theorem 1.1(i): Let (H_1), (H_2) hold and $M_0=\max\limits_{[0,r_0]}\left\{\frac{f(s)}{s}\right\}$.

We first prove non-existence for $\lambda<\bar{E}_1(M_0,g_\infty,\gamma)$.
Recall that $\sigma_0=\sigma_0(M_0,g_\infty,\gamma)>0$ for $\lambda<\bar{E}_1(M_0,g_\infty,\gamma)$. Assume u_λ is a positive solution of (2) for $\lambda<\bar{E}_1(M_0,g_\infty,\gamma)$. Then by Green's Second Identity, we have:

$$\begin{aligned}&\int_\Omega\Big(\phi_0\Delta u_\lambda-u_\lambda\Delta\phi_0\Big)dx\\&=\int_{\partial\Omega}\Big(\phi_0\frac{\partial u_\lambda}{\partial\eta}-u_\lambda\frac{\partial\phi_0}{\partial\eta}\Big)ds\\&=\int_{\partial\Omega}\Big(-\phi_0\sqrt{\lambda}\gamma g(u_\lambda)u_\lambda+u_\lambda\sqrt{\lambda}\gamma g_\infty\phi_0\Big)ds\\&=\int_{\partial\Omega}\gamma\phi_0u_\lambda\sqrt{\lambda}\Big(g_\infty-g(u_\lambda)\Big)ds\\&\le 0\end{aligned}\tag{10}$$

since $g(s)\ge g_\infty; s\in[0,r_0]$. On the other hand, we have

$$\begin{aligned}&\int_\Omega\Big(\phi_0\Delta u_\lambda-u_\lambda\Delta\phi_0\Big)dx\\&=\int_\Omega\Big(-\phi_0\lambda f(u_\lambda)+(M_0\lambda+\sigma_0)u_\lambda\phi_0\Big)dx\\&\ge\int_\Omega\Big(-\phi_0\lambda M_0u_\lambda+(M_0\lambda+\sigma_0)u_\lambda\phi_0\Big)dx\text{ since }f(u_\lambda)\le M_0u_\lambda\\&=\int_\Omega\phi_0u_\lambda\Big(-\lambda M_0+M_0\lambda+\sigma_0\Big)dx\\&=\int_\Omega\sigma_0\phi_0u_\lambda dx\\&>0\text{ since }\sigma_0>0\text{ for }\lambda<\bar{E}_1(M_0,g_\infty,\gamma).\end{aligned}\tag{11}$$

This is a contradiction. Thus, (2) has no positive solution for $\lambda<\bar{E}_1(M_0,g_\infty,\gamma)$. The stability properties of the trivial solution follow from a well-known argument as in [20] and are omitted.

Now we prove the existence of a positive solution u_λ for $\lambda > \bar{E}_1(1, g_0, \gamma)$. Recall the subsolution $\psi_1 = p_\lambda \theta_1$ and supersolution Z_1. We choose p_λ small enough so that $\psi_1 \le Z_1$. Then by Lemma 2.1, it follows that (2) has at least one positive solution u_λ such that $\psi_1 \le u_\lambda \le Z_1$ for $\lambda > \bar{E}_1(1, g_0, \gamma)$.

Now we prove that (2) has a positive solution u_λ such that $\|u_\lambda\|_\infty \to r_0$ as $\lambda \to \infty$.

Recall that for $\lambda \gg 1$, we have a supersolution Z_1 and subsolution ψ_4 of (2) such that $\|\psi_4\|_\infty \to r_0$ as $\lambda \to \infty$. By Lemma 2.1, (2) has a positive solution u_λ for $\lambda \gg 1$ such that $\|u_\lambda\|_\infty \to r_0$ as $\lambda \to \infty$. □

Proof of Theorem 1.1(ii): Let (H_1), (H_2) hold and let $M_0 = \max\limits_{[0,r_0]} \left\{ \frac{f(s)}{s} \right\}$.

Here, we show nonexistence of a positive solution when a certain growth requirement on g is met.

Given a $\lambda_0 < \bar{E}_1(M_0, g_0, \gamma)$, there is a unique $b_0 \in (0, g_0)$ such that $\lambda_0 = \bar{E}_1(M_0, b_0, \gamma)$. Assume that $g(s) \ge \frac{b_0 - g_0}{r_0} s + g_0; s \in [0, r_0]$. Recall that $\sigma_0 = \sigma_0(M_0, b_0, \gamma) > 0$ for $\lambda < \bar{E}_1(M_0, b_0, \gamma)$. Assume u_λ is a positive solution of (2) for $\lambda < \bar{E}_1(M_0, b_0, \gamma)$. The argument in (11) from (i) goes through exactly. But, since $u_\lambda < r_0$ and $g(s) \ge \frac{b_0 - g_0}{r_0} s + g_0; s \in [0, r_0]$ we must have

$$
\begin{aligned}
&\int_\Omega \Big(\phi_0 \Delta u_\lambda - u_\lambda \Delta \phi_0 \Big) dx \\
&= \int_{\partial\Omega} \Big(\phi_0 \frac{\partial u_\lambda}{\partial \eta} - u_\lambda \frac{\partial \phi_0}{\partial \eta} \Big) ds \\
&= \int_{\partial\Omega} \Big(-\phi_0 \sqrt{\lambda} \gamma g(u_\lambda) u_\lambda + u_\lambda \sqrt{\lambda} \gamma b_0 \phi_0 \Big) ds \\
&= \int_{\partial\Omega} \gamma \phi_0 u_\lambda \sqrt{\lambda} \Big(b_0 - g(u_\lambda) \Big) ds \\
&\le \int_{\partial\Omega} \gamma \phi_0 u_\lambda \sqrt{\lambda} \Big(b_0 - g_0 + \frac{g_0 - b_0}{r_0} u_\lambda \Big) ds \\
&\le 0
\end{aligned}
\tag{12}
$$

Notice that a contradiction arises between (11) and (12), thus (2) has no positive solution for $\lambda < \lambda_0$. The second part follows since $M_0 = 1$ and $g_0 = g_\infty$ implies that $\bar{E}_1(M_0, g_\infty, \gamma) = \bar{E}_1(1, g_0, \gamma)$ and, thus, there is no positive solution for $\lambda < \bar{E}_1(1, g_0, \gamma)$. Since predictions of a patch-level Allee effect require existence of at least one positive solution of (2) where the trivial solution is asymptotically stable, (i) ensures that no such effect can happen in this case. □

Proof of Theorem 1.1(iii): Let (H_1) and (H_2) hold.

Here we show the existence of at least two positive solutions for $\lambda \in [\lambda_1, \bar{E}_1(1, g_0, \gamma))$ when $g(s) \le b_0$ for $s \ge K_0$.

Recall the strict subsolution $\psi_3 = n\phi_0$ for $\lambda \in [\lambda_1, \bar{E}_1(1, g_0, \gamma))$ with $\|\psi_3\|_\infty < r_0$, supersolution $Z_1 = r_0$ for $\lambda > 0$, and strict supersolution $Z_3 = \tilde{m}_\lambda \phi_1$ (with $\tilde{m}_\lambda \approx 0$) for $\lambda < \bar{E}_1(1, g_0, \gamma)$. Furthermore, $\psi_0 = 0$ is a solution and hence a subsolution of (2) for any $\lambda > 0$. Now, we choose $\tilde{m}_\lambda \approx 0$ such that $\psi_3 \not\le Z_3$ and $Z_3 \le Z_1$. Then, by Lemma 2.2, (2) has at least two positive solutions, say u_1 and u_2 for $\lambda \in [\lambda_1, \bar{E}_1(1, g_0, \gamma))$ where $u_1 \in [\psi_3, Z_1]$ and $u_2 \in [\psi_0, Z_1] \setminus ([\psi_0, Z_3] \cup [\psi_3, Z_1])$.

(Note: since $\psi_0 = 0$ is a solution, Lemma 2.2 can not guarantee a third positive solution in $[\psi_0, Z_3]$.) Finally, since the trivial solution is stable for $\lambda < \bar{E}_1(1, g_0, \gamma)$, solutions of the time dependent problem corresponding to (2) with initial conditions sufficiently small will tend towards zero. Furthermore, the solutions u_1, u_2 are also sub- and supersolutions, creating a region for which solutions of the time dependent problem corresponding to (2) with initial conditions in $[u_1, u_2]$ will be trapped in this range for all time. Hence, there is a patch-level Allee effect for $\lambda \in [\lambda_1, \bar{E}_1(1, g_0, \gamma))$. □

Proof of Theorem 1.1(iv): Let (H_1), (H_2), (H_3), & (H_4) hold.
Here we prove the existence of at least three positive solutions for $\lambda \in \left(\max\left\{E_1(\gamma), \frac{2bNC_N}{R^2 f(b)}\right\}, \min\left\{\frac{a}{\|v_{\mu_b}\|_\infty f^*(a)}, \frac{2r_2N}{f(b)R^2}\right\}\right)$**.**

Recall subsolution $\psi_1 = p_\lambda \phi_1$ for $\lambda > \bar{E}_1(1, g_0, \gamma)$, strict subsolution ψ_2 for $\lambda \in \left(\frac{2bNC_N}{R^2 f(b)}, \frac{2r_2N}{f(b)R^2}\right)$, supersolution Z_1 for $\lambda > 0$, and strict supersolution $Z_2 = \frac{av_{\mu_b}}{\|v_{\mu_b}\|_\infty}$ for $\lambda \in \left(\frac{2bNC_N}{R^2 f(b)}, \frac{a}{\|v_{\mu_b}\|_\infty f^*(a)}\right)$. Since $a < r_0$, we have $Z_2 < Z_1$. By construction we have $\|\psi_2\|_\infty > b > a = \|Z_2\|_\infty$. Choosing $p_\lambda \approx 0$ we have $\psi_1 \le \psi_2 \le Z_1$. Then, by Lemma (2.2) the result follows. □

Proof of Corollary 1.2:
We note that the proof of Corollary 1.2 is an immediate consequence of the proof of Theorem 1.1. □

4. **An application of Theorem 1.1 and Corollary 1.2 when Ω is a ball of radius R with $N = 1, 2, 3$.** Here we consider the following steady state logistic growth model with grazing in a spatially heterogeneous ecosystem:

$$\begin{cases} -\Delta u = \lambda f(u) = \lambda\left(u - \frac{u^2}{K} - \frac{cu^2}{1+u^2}\right);\ x \in \Omega \\ \frac{\partial u}{\partial \eta} + \sqrt{\lambda}\gamma g(u)u = 0;\ x \in \partial\Omega \end{cases} \tag{13}$$

where $\lambda > 0$, $K > 0$, $0 < c < 2$ and Ω is a ball of radius R in $\mathbb{R}^N$; $N = 1, 2, 3$ with smooth boundary $\partial\Omega$, and

$$g(s) = \begin{cases} 1 - ms\ ;\ 0 \le s \le \frac{1}{2m} \\ \frac{1}{2}\ ;\ s \ge \frac{1}{2m}, \end{cases}$$

where $m > 0$. We can easily see that (H_1), (H_2) are satisfied and $M_0 = 1$ for this example with $g_0 = 1$ and $g_\infty = \frac{1}{2}$. In [29], the authors proved the following properties of f. When $K \gg 1$, there exists a unique $r_0 > 0$ such that $f(r_0) = 0$ and $f(s)(s - r_0) \le 0$ for $s \in [0, \infty)$. Also, for $c \in \left(\frac{8}{3\sqrt{3}}, 2\right)$ and $K \gg 1$, they established constants $b > 0$, $c > 0$, $r_0 > 0$, $r_1 > 0$, and $r_2 > 0$ such that $c < r_1 < b < \frac{r_2}{C_N} < \frac{r_0}{C_N} < \infty$, $b \le \sqrt{Kc}$, $r_2 > \frac{K}{4}$, $f(s) > 0$ for $s \in (0, r_0)$, $f(s) < 0$ for $s \in (r_0, \infty)$, f is increasing on $(0, c) \cup (r_1, r_2)$, f is decreasing on $(c, r_1) \cup (r_2, \infty)$, $\lim_{K\to\infty} f(b) = \infty$, and $\lim_{K\to\infty} \frac{b}{f(b)} = 1$. Further, they chose $a \in (r_1, b)$ such that $f(a) = f^*(a) = f(c)$, and estimated a to be 1.5437 and $\frac{a}{f^*(a)}$ to be 11.4445 for $c \approx 2$ and $K \gg 1$. We now fix a $\lambda_1 \in \left(\bar{E}_1(1, \frac{1}{2}, \gamma), \bar{E}_1(1, 1, \gamma)\right)$, $\lambda_0 < \lambda_1$ with $\lambda_0 \approx \lambda_1$, and select the unique $b_0 \in (\frac{1}{2}, 1)$ such that $\lambda_0 = \bar{E}_1(1, b_0, \gamma)$. In this case, it is easy to show that the solution v_{μ_b} of (6) is

$$v_{\mu_b}(x) = \frac{R^2 - |x|^2}{2N} + \frac{1}{\gamma g_\infty} \frac{R}{N} \sqrt{\frac{f(b)}{m_0 b}}$$

where $m_0 = \frac{2NC_N}{R^2}$. Observe that $\|v_{\mu_b}\|_\infty$ decreases as γg_∞ increases, implying that $\frac{a}{\|v_{\mu_b}\|_\infty f^*(a)}$ increases and therefore the interval $\left(\frac{2bNC_N}{R^2 f(b)}, \frac{a}{\|v_{\mu_b}\|_\infty f^*(a)}\right)$ gets wider as γg_∞ increases. In the case when $\gamma g_\infty = 1$ it was shown in [18] that, for $N = 1, 2, 3$, $\frac{2bNC_N}{R^2 f(b)} < \frac{a}{\|v_{\mu_b}\|_\infty f^*(a)}$. Therefore by continuity, $\left(\frac{2bNC_N}{R^2 f(b)}, \frac{a}{\|v_{\mu_b}\|_\infty f^*(a)}\right)$ is feasible when $\gamma g_\infty \geq 1$. Thus $(H_3) - (H_4)$ are satisfied when $\gamma g_\infty \geq 1$, or equivalently, $\gamma > 2$.

We also note that for $N = 1, 2, 3$, we have $\frac{2bNC_N}{R^2 f(b)} = \frac{m_0 b}{f(b)} > \frac{5m_0}{8} > B_D > E_1(\gamma)$ for $c \in \left(\frac{8}{3\sqrt{3}}, 2\right)$ and $K \gg 1$, where B_D is the principal eigenvalue of $-\Delta$ with Dirichlet boundary condition (see [18]). Further, we note that $g(s) \leq b_0$ for $s \in [K_0, r_0]$ when $m \gg 1$.

Thus, our example satisfies all the hypotheses of Theorem 1.1, and therefore they can be applied to our example yielding a structure of positive solutions at least like the one illustrated in Figure 2. □

5. Computational results when $\Omega = (0, 1)$.

We note that in the one-dimensional case, (13) reduces to

$$\begin{cases} -u'' = \lambda \tilde{f}(u) = \lambda \left(u - \frac{u^2}{K} - \frac{cu^2}{1+u^2}\right); \ x \in (0,1) \\ -u'(0) + \sqrt{\lambda}\gamma g(u(0))u(0) = 0 \\ u'(1) + \sqrt{\lambda}\gamma g(u(1))u(1) = 0, \end{cases} \tag{14}$$

where

$$g(s) = \begin{cases} 1 - ms \ ; \ 0 \leq s \leq \frac{1}{2m} \\ \frac{1}{2} \ ; \ s \geq \frac{1}{2m}. \end{cases}$$

In this case, we note that the positive solutions of (14) can be completely analyzed by a quadrature method (see [12]). Since $h(s) = g(s)s$ is increasing for all $s > 0$, it follows that the solutions of (14) are symmetric about $x = \frac{1}{2}$ with $u(0) = u(1) := q$ and $\|u\|_\infty := \rho$. Namely, the solutions take the shape as in Figure 3.

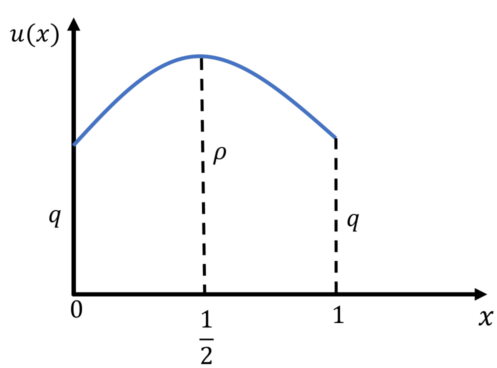

FIGURE 3. The shape of symmetric positive solutions of (14).

Further, the numerically approximated bifurcation diagrams for positive solutions to (14) are described by the equations:

$$\lambda = 2\Big(\int_{q(\rho)}^{\rho} \frac{ds}{\sqrt{F(\rho)-F(s)}}\Big)^2 \tag{15}$$

and

$$2[F(\rho)-F(q)] = \gamma^2(g(q))^2q^2 \tag{16}$$

where, $F(s) = \int_0^s f(t)dt$ (see [12] for details). Note that for a given $\rho \in (0, r_0)$, where r_0 is defined as in (H_1) (i.e., the falling zero for f), there exists a unique $q = q(\rho) \in (0, \rho)$ that satisfies (15) and (16).

Below we provide bifurcation diagrams for the positive solutions of (14) via Mathematica computation of (15)-(16). Note that the bifurcation diagrams here are not drawn to scale.

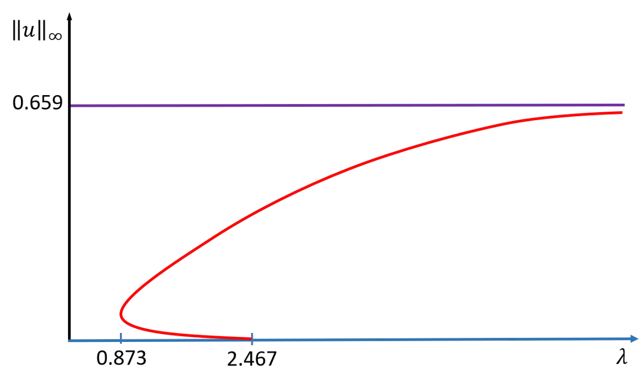

FIGURE 4. An approximate bifurcation diagram of positive solutions for (14) when $\gamma = 1; K = 5; c = 1.89$, $m = 1000$.

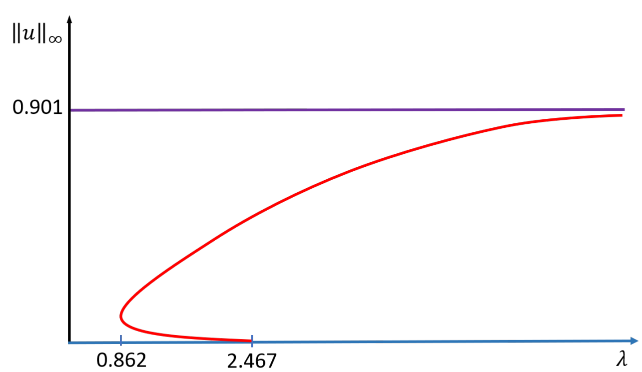

FIGURE 5. An approximate bifurcation diagram of positive solutions for (14) when $\gamma = 1; K = 15; c = 1.89$, $m = 1000$.

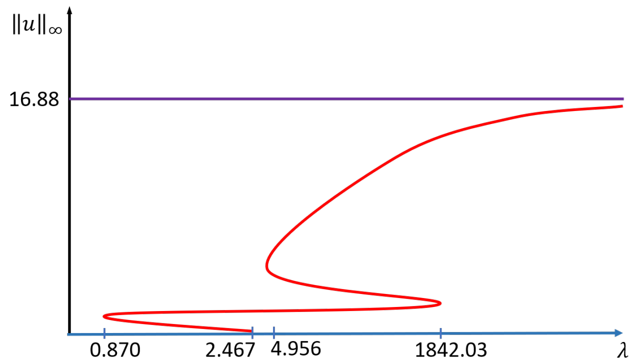

FIGURE 6. An approximate bifurcation diagram of positive solutions for (14) when $\gamma = 1; K = 19; c = 1.89$, $m = 1000$.

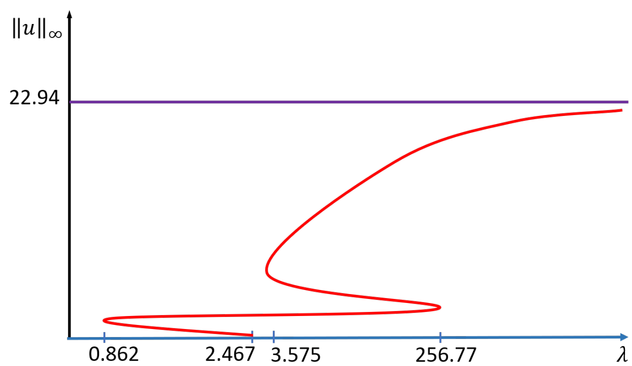

FIGURE 7. An approximate bifurcation diagram of positive solutions for (14) when $\gamma = 1; K = 25; c = 1.89$, $m = 1000$.

Our numerical results show that when K is relatively small the population does not exhibit multiple positive steady states for patch sizes bigger than $E_1(\gamma)$. However, for bigger K-values we observe the existence of three positive steady states for patch sizes bigger than $E_1(\gamma)$ for a certain range of λ. For this set of parameter values, we observe a patch-level Allee effect for a certain range of λ which is a consequence of a strong negative density-dependent dispersal (i.e., $m \gg 1$ causes the probability of remaining in the patch to approach 100% for even very small density values). Further, when K is very large, our model predicts existence of four positive steady states for patch sizes smaller than $E_1(\gamma)$ and three positive steady states for patch sizes bigger than $E_1(\gamma)$ for a certain range of λ-values.

The biologically necessary criteria for Σ-shaped bifurcation curves and multiple steady states over a range of patch sizes include -DDE in the prey population and a Holling type III functional response by the predator. One-fourth of the published studies in ecology find -DDE [21] and this emigratory response can generate a patch-level Allee effect [8, 19, 21]. A type III functional response is known to arise when generalist predators respond to changing prey abundance by switching

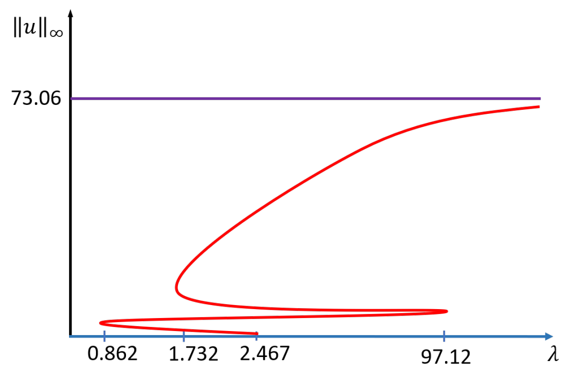

FIGURE 8. An approximate bifurcation diagram of positive solutions for (14) when $\gamma = 1; K = 75; c = 1.89$, $m = 1000$.

to more profitable prey [16, 33, 36]. Density dependent emigration, predation following a Type III functional response, and interplay with landscape-level elements such as patch size and matrix hostility combine in determining the number of positive steady states. Multiple steady states can influence regional persistence of the prey metapopulation by altering the fraction and distribution of occupied patches and causing uncertainty in the predictability of minimum patch size and density-area relationships [9, 14].

Acknowledgments: The authors sincerely thank the anonymous referees for their suggestions.

REFERENCES

[1] A. Acharya, N. Fonseka, J. Quiroa and R. Shivaji, Σ-shaped bifurcation curves, *Advances in Nonlinear Analysis*, **10** (2021), 1255-1266.

[2] A. Acharya, N. Fonseka, A. Henderson and R. Shivaji, ∑-shaped bifurcation curves influenced by nonlinear boundary conditions for classes of reaction diffusion systems, to appear in *Topological Methods in Nonlinear Analysis*.

[3] W. C. Allee, *Animal Aggregations, A Study in General Sociology*, University of Chicago Press, Chicago, Illinois, USA, 1931.

[4] H. Amann, Fixed point equations and nonlinear eigenvalue problems in ordered banach spaces, *SIAM review*, **18** (1976), 620-709.

[5] P. Amarasekare, The role of density-dependent dispersal in source-sink dynamics, *Journal of Theoretical Biology*, **226** (2004), 159-168,

[6] D. E. Bowler and T. G. Benton, Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics, *Biological Reviews*, **80** (2005), 205-225,

[7] R. S. Cantrell and C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*, Mathematical and Computational Biology, Wiley, Chichester, 2003.

[8] R. S. Cantrell and C. Cosner, Density dependent behavior at habitat boundaries and the allee effect, *Bulletin of Mathematical Biology*, **69** (2007), 2339-2360.

[9] R. S. Cantrell, C. Cosner and W. F. Fagan, How predator incursions affect critical patch size: The role of the functional response, *The American Naturalist*, **158** (2001), 368-375,

[10] P. Clément and G. Sweers, Existence and multiplicity results for a semilinear elliptic eigenvalue problem, *Annali della Scuola Normale Superiore di Pisa-Classe di Scienze*, **14** (1987), 97-121.

[11] F. Courchamp, L. Berec and J. Gascoigne, *Allee Effects in Ecology and Conservation*, Oxford University Press, 2008.

[12] J. T. Cronin, N. Fonseka, J. Goddard, J. Leonard and R. Shivaji, Modeling the effects of density dependent emigration, weak allee effects, and matrix hostility on patch-level population persistence, *Mathematical Biosciences and Engineering*, **17** (2020), 1718.

[13] J. T. Cronin, J. Goddard and R. Shivaji, Effects of patch-matrix composition and individual movement response on population persistence at the patch level, *Bulletin of Mathematical Biology*, **81** (2019), 3933-3975.

[14] J. T. Cronin, J. Goddard II, A. Muthunayake, J. Quiroa and R. Shivaji, Predators-induced prey dispersal can cause hump-shaped density-area relationships in prey populations, *Journal of Mathematical Biology*, **88** (2024), 1-31.

[15] B. Dennis, Allee effects: population growth, critical density, and the chance of extinction, *Natural Resource Modelling*, **3** (1989), 481-538.

[16] J. S. Elkinton, A. M. Liebhold and R.-M. Muzika, Effects of alternative prey on predation by small mammals on gypsy moth pupae, *Population Ecology*, **46** (2004), 171-178,

[17] M. Fischer, M. Hock and M. Paschke, Low genetic variation reduces cross-compatibility and offspring fitness in populations of a narrow endemic plant with a self-incompatibility system, *Conservation Genetics*, **4** (2003), 325-336,

[18] N. Fonseka, R. Shivaji, B. Son and K. Spetzer, Classes of reaction diffusion equations where a parameter influences the equation as well as the boundary condition, *Journal of Mathematical Analysis and Applications*, **476** (2019), 480-494.

[19] J. Goddard II, Q. Morris, C. Payne and R. Shivaji, A diffusive logistic equation with u-shaped density dependent dispersal on the boundary, *Topological Methods in Nonlinear Analysis*, **53** (2019), 335-349.

[20] J. Goddard II, Q. A. Morris, S. B. Robinson and R. Shivaji, An exact bifurcation diagram for a reaction-diffusion equation arising in population dynamics, *Boundary Value Problems*, **2018** (2018), 1-17.

[21] R. R. Harman, J. Goddard II, R. Shivaji and J. T. Cronin, Frequency of occurrence and population-dynamic consequences of different forms of density-dependent emigration, *American Naturalist*, **195** (2020), 851-867.

[22] C. S. Holling, The components of predation as revealed by a study of small-mammal predation of the european pine sawfly, *The Canadian Entomologist*, **91** (1959), 293-320.

[23] C. S. Holling, Principles of insect predation, *Annual Review of Entomology*, **6** (1961), 163-182,

[24] C. S. Holling, The functional response of invertebrate predators to prey density, *Memoirs of the Entomological Society of Canada*, **98** (1966), 5-86,

[25] F. Inkmann, Existence and multiplicity theorems for semilinear elliptic equations with nonlinear boundary conditions, *Indiana University Mathematics Journal*, **31** (1982), 213-221.

[26] N. Knowlton, Thresholds and multiple stable states in coral reef community dynamics, *Integrative and Comparative Biology*, **32** (1992), 674-682,

[27] A. M. Kramer, B. Dennis, A. M. Liebhold and J. M. Drake, The evidence for allee effects, *Population Ecology*, **51** (2009), 341-354,

[28] E. K. Lee, S. Sasi and R. Shivaji, An ecological model with a Σ-shaped bifurcation curve, *Nonlinear Analysis, Series B: Real World Applications*, **13** (2012), 634-642.

[29] E. Lee, S. Sasi and R. Shivaji, S-shaped bifurcation curves in ecosystems, *Journal of mathematical analysis and applications*, **381** (2011), 732-741.

[30] M. A. Lewis and P. Kareiva, Allee dynamics and the spread of invading organisms, *Theoretical Population Biology*, **43** (1993), 141-158.

[31] E. Matthysen, *Multicausality of Dispersal: A Review*, Oxford University Press, United Kingdom, 2012.

[32] C. V. Pao, *Nonlinear Parabolic and Elliptic Equations*, Plenum Press, New York, 1992.

[33] O. Sarnelle and A. E. Wilson, Type iii functional response in daphnia, *Ecology*, **89** (2008), 1723-1732,

[34] R. Shivaji, A remark on the existence of three solutions via sub-super solutions, in *Nonlinear Analysis and Applications*, CRC Press, 1987, 561-566.

[35] R. M. Sibly, D. Barker, M. C. Denham, J. Hone and M. Pagel, On the regulation of populations of mammals, birds, fish, and insects, *Science*, **309** (2005), 607-610.

[36] B. Tschanz, L.-F. Bersier and S. Bacher, Functional responses: A question of alternative prey and predator density, *Ecology*, **88** (2007), 1300-1308,

Received April 2024; final revision October 2024; early access November 2024.