Discrete and Continuous Dynamical Systems - Series B

doi:10.3934/dcdsb.2023142

ON THE EFFECTS OF DENSITY-DEPENDENT EMIGRATION ON ECOLOGICAL MODELS WITH LOGISTIC AND WEAK ALLEE TYPE GROWTH TERMS

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(Communicated by Chris Cosner)

Abstract. We analyze the structure of positive steady states for a population model designed to explore the effects of habitat fragmentation, density dependent emigration, and Allee effect growth. The steady state reaction diffusion equation is:

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

where $f(s) = \frac{1}{a}s(1-s)(a+s)$ can represent either logistic-type growth ($a \geq 1$) or weak Allee affect growth ($a \in (0,1)$), $\lambda, \gamma > 0$ are parameters, Ω is a bounded domain in $\mathbb{R}^N$; $N > 1$ with smooth boundary $\partial\Omega$ or $\Omega = (0,1)$, $\frac{\partial u}{\partial \eta}$ is the outward normal derivative of u, and $g(u)$ is related to the relationship between density and emigration. In particular, we consider three forms of emigration: density independent emigration ($g = 1$), a negative density dependent emigration of the form $g(s) = \frac{1}{1+\beta s}$, and a positive density dependent emigration of the form $g(s) = 1 + \beta s$, where $\beta > 0$ is a parameter representing the interaction strength. We establish existence, nonexistence, and multiplicity results for ranges of λ depending on the choice of the function g. Our existence and multiplicity results are proved via the method of sub-super-solutions and study of certain eigenvalue problems. For the case $\Omega = (0,1)$, we also provide exact bifurcation diagrams for positive solutions for certain values of the parameters a, β and γ via a quadrature method and Mathematica computations. Our results shed light on the complex interactions of density dependent mechanisms on population dynamics in the presence of habitat fragmentation.

2020 *Mathematics Subject Classification.* Primary: 35J15, 35J25, 35J60.

Key words and phrases. Density-dependent emigration, Allee effect, Patch-level Allee effect, reaction diffusion model, habitat fragmentation.

The third author is supported by DMS-2150946 and the final author by DMS-2150947.

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1. Introduction.

1.1. Background and motivation.

As human-dominated habitat fragmentation continues at unprecedented levels, gaining a better understanding of consequences of density dependence is crucial for conservation efforts [15, 34, 22, 14, 38]. Habitat fragmentation not only results in reduced viable habitat or patch size, but also separates populations among much smaller residual patches which are surrounded by a human-modified "matrix" of varying degrees of hostility [34]. Theoretical population modeling has seen great success in predicting patch- and even landscape-level patterns in response to habitat fragmentation. In particular, the reaction diffusion framework has been successfully applied to better understand coupling of density dependent growth mechanisms with density dependent movement or dispersal (see, e.g., [6]). An advantage of the framework is its ability to handle space explicitly at the landscape-level, including modeling animal movement behavior differences when a patch boundary is reached [21, 16, 17, 12].

Traditionally, population models fix the patch size and consider a binary matrix with either immediate lethality (modeled using a Dirichlet boundary condition) or quality habitat (modeled as a Neumann boundary condition). More recently, authors have begun incorporating varying degrees of matrix hostility and changes in dispersal behavior upon reaching a patch boundary (see, e.g., [9], and especially for one-dimensional spatial domains, e.g., [29, 28] and the references therein). The authors in [12] provided a framework to link assumptions on individual growth and movement behavior to the landscape-level where patch size, matrix hostility, and response to habitat edge can all be studied in one-, two-, or three-dimensional landscapes. For the case of logistic growth, steady states of the unitless time independent reaction diffusion model studied in [12] satisfy:

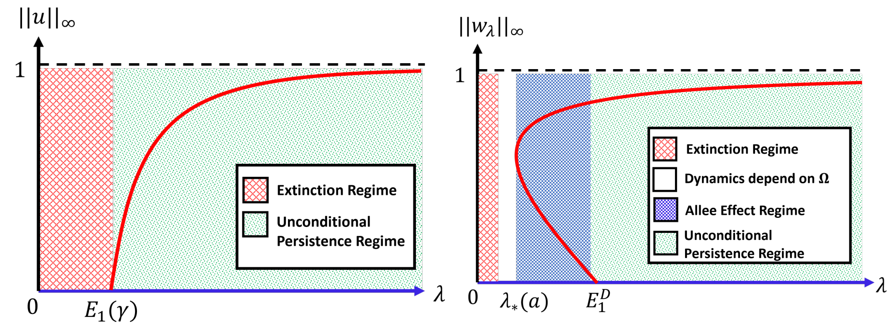
$$\begin{cases} -\Delta u = \lambda u(1-u);\ \Omega \\ \frac{\partial u}{\partial \eta} + \gamma\sqrt{\lambda} u = 0;\ \partial\Omega \end{cases} \tag{1}$$

where $\gamma > 0$ is a parameter quantifying matrix hostility, $\lambda > 0$ is a parameter proportional to patch size, Ω is a bounded habitat in $\mathbb{R}^N$; $N = 2, 3$ with smooth boundary $\partial\Omega$ and unit area or volume or $\Omega = (0, 1)$, and $\frac{\partial u}{\partial \eta}$ is the outward normal derivative of u. For a fixed M, γ, and $b > 0$, let $\overline{E}_1 = \overline{E}_1(M, b, \gamma)(> 0)$ be the principal eigenvalue of

$$\begin{cases} -\Delta \phi_0 = EM\phi_0;\ \Omega \\ \frac{\partial \phi_0}{\partial \eta} + \gamma\sqrt{E} b\phi_0 = 0;\ \partial\Omega. \end{cases} \tag{2}$$

See [18] for the existence and positivity of $\overline{E}_1$. The authors in [18] established an exact bifurcation diagram for positive solution of (1) showing that (1) has no positive solution for $\lambda \leq E_1(\gamma)$ and has a unique positive solution u_λ for $\lambda > E_1(\gamma)$, such that $\|u_\lambda\|_\infty \to 0$ as $\lambda \to E_1(\gamma)^+$, and $\|u_\lambda\|_\infty \to 1$ as $\lambda \to 0$ as shown in Figure 1(a), where we denote $E_1(\gamma) = \overline{E}_1(1, 1, \gamma)$.

Logistic-type growth (LTG) assumes a strictly negative density dependence between density and per-capita growth rate (see Figure 2). Notwithstanding, Allee effects, the positive effects of increasing density on fitness, have been observed empirically in the literature since they were first described in the early 1930's for cooperatively breeding species [1, 25]. Though difficult to detect, empirical support for Allee effects spans a wide diversity of taxa [10, 26, 37]. A common cause of an Allee effect in fitness is thought to be due to scarcity of reproductive opportunity



(A) Prototypical bifurcation diagram for (1).

(B) Prototypical bifurcation diagram for (3).

FIGURE 1. Prototypical bifurcation diagrams showing different regimes for logistic (left) and weak Allee effect (right) growth models.

at low densities [13, 27]. In the context of landscape ecology, Allee effects are particularly important and there is a growing list of studies that have examined the interplay between Allee effects and dispersal, broadly defined as movement between habitat patches [33]. An Allee effect is considered strong if per-capita growth rate is negative for small densities, and weak otherwise (in this case, WAG). See Figure 2 for a comparison of LTG and WAG. It is well known that population models with strong Allee effect growth will predict existence of a density threshold for which the population must remain above in order for persistence to be ensured [6]. However, a weak Allee effect growth is not sufficient to ensure existence of such a threshold.

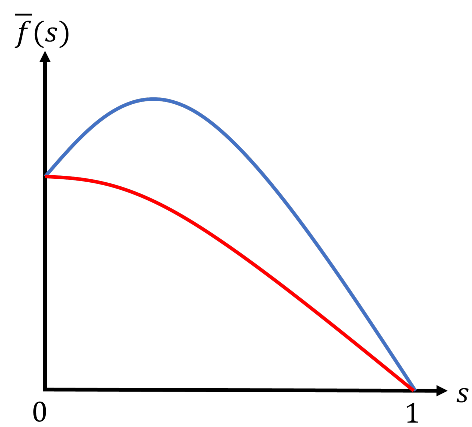


FIGURE 2. Prototypical shapes of per-capita growth rates when $a \in (0,1)$ (in blue) and $a \geq 1$ (in red).

The authors in [35] studied the WAG model with an immediately lethal matrix (i.e., Dirichlet boundary conditions)

$$\begin{cases} -\Delta w = \lambda \frac{1}{a} w(1-w)(a+w); \ \Omega \\ w = 0; \ \partial\Omega \end{cases} \tag{3}$$

where $a \in (0,1)$ represents the strength of the weak Allee growth term in the following sense: for $a \approx 1$, the range of densities for which the per-capita growth rate is increasing is small, i.e., low Allee strength, whereas, when $a \approx 0$, this range of densities is much larger, i.e., high Allee strength. They proved that, for $\lambda \geq E_1^D$, (3) has a positive solution w_λ such that $\|w_\lambda\|_\infty \longrightarrow 1$ as $\lambda \longrightarrow \infty$. Here, E_1^D is the principal eigenvalue of:

$$\begin{cases} -\Delta z = \lambda z; \ \Omega \\ \ z = 0; \ \partial\Omega. \end{cases} \tag{4}$$

Further, they established existence of at least two positive solutions for $\lambda \in (\lambda_*(a), E_1^D)$ and at least one positive solution for $\lambda = \lambda_*(a)$ for some $\lambda_*(a) \in (0, E_1^D)$ (see Figure 1(b)). For patch sizes with a $\lambda \in (\lambda_*(a), E_1^D)$, it is straightforward to show that initial density distributions, $u_0(x)$, with $\|u_0\|_\infty \approx 0$ yield time-dependent model predictions of extinction, whereas, when $u_0(x) \in [w_\lambda, 1); \Omega$, the model predicts persistence (see, e.g., [32], [11]). Thus, an Allee effect threshold is predicted by the model for this range of patch sizes, a phenomenon known in the literature as a patch-level Allee effect (PAE) (see, e.g., [6, 7, 8]). The strength of the PAE can be measured by computing the unitless distance of the PAE region, $(\lambda_*(a), E_1^D)$, i.e., PAE region length is defined as $E_1^D - \lambda_*(a)$. A larger length will imply that a larger range of patch sizes will be predicted to exhibit a PAE, and thus ecologists are more likely to find a PAE empirically. However, a length near zero will be practically impossible to observe empirically. See also [24, 31, 39] for related work on the studies of weak Allee growth models.

Population-dynamical consequences of an Allee effect can be affected by the relationship between conspecific density and the probability of emigrating from a patch. Although the most widely accepted view of emigration behavior is that species should exhibit a positive relationship between density and emigration [4, 5, 30], other forms of density-dependent emigration (DDE) exist. In a recent literature review of empirical studies, [20] found that 35% of the cases exhibited +DDE, 30% were density independent (DIE), 25% were -DDE, 6% were U-shaped (UDDE), and 4% were humped shaped (hDDE). Importantly, recent mathematical models have revealed that DDE forms with a negative slope (-DDE and UDDE) can also induce a PAE, even in a LTG model [8, 17, 20]. The authors in [11] studied a one-dimensional version of

$$\begin{cases} -\Delta u = \lambda f(u); \ \Omega \\ \alpha(u)\frac{\partial u}{\partial \eta} + \gamma\sqrt{\lambda}[1-\alpha(u)]u = 0; \ \partial\Omega \end{cases} \tag{5}$$

where $\alpha(u)$ is the probability of the population staying in the habitat upon it reaching the boundary, and $f(s) = \frac{1}{a}s(1-s)(a+s)$; $a > 0$. Equivalently, (5) can be written as

$$\begin{cases} -\Delta u = \lambda f(u); \ \Omega \\ \frac{\partial u}{\partial \eta} + \gamma\sqrt{\lambda}g(u)u = 0; \ \partial\Omega \end{cases} \tag{6}$$

where $g(s) = \frac{1-\alpha(s)}{\alpha(s)}$. Through numerical computations, they found that -DDE can enhance an already present PAE with WAG via enlarging the PAE region and even creating a PAE with LTG, whereas, +DDE can attenuate an already present PAE by shrinking the PAE region. They also reported that PAE region length was maximized with high matrix hostility, i.e., $\gamma \to \infty$, and minimized with low matrix hostility, i.e., $\gamma \approx 0$. Our focus in the present paper is to prove the computational results obtained in [11] for similar DDE forms and extend them to the higher-dimensional case, while connecting these results to those found in [18] and [35].

We consider the following three DDE forms:

$$g(s) = \begin{cases} g_1(s) = 1 & ; \text{ Density Independent Emigration (DIE)} \\ g_2(s) = \frac{1}{1+\beta s}, \beta > 0 & ; \text{ Negative Density Dependent Emigration (-DDE)} \\ g_3(s) = 1 + \beta s, \beta > 0 & ; \text{ Positive Density Dependent Emigration (+DDE)} \end{cases}$$

and define $\underline{g} := \min_{s\in[0,1]} \{g(s)\} = \min\left\{1, \frac{1}{1+\beta}\right\}$. The unitless parameter $\beta \geq 0$ can be interpreted as the DDE strength in the following sense: if $\beta \approx 0$ then both +DDE and -DDE are well approximated by DIE, while, for large β-values, emigration rate approaches one and zero, respectively, for even small density levels. For brevity sake, we use the following abbreviations: WAG - Weak Allee Growth, LTG - Logistic Type Growth, and PAE - Patch Level Allee Effect. We consider two cases for the reaction term: Case I: $a \geq 1$ where f becomes LTG with decreasing per-capita growth rate ($\bar{f}(s) = \frac{f(s)}{s}$) and Case II: $a \in (0,1)$ where f becomes WAG since the per-capita growth rate ($\bar{f}$) is initially increasing. We study the structure of positive solutions to (6) as patch size (λ) and matrix hostility (γ) vary in each of the three DDE cases and two growth term cases. Note that non-trivial non-negative solutions u to (6) are such that $u \in (0,1); \overline{\Omega}$. This easily follows from the Hopf maximum principle.

1.2. **Main results.** We now state our main results.

Theorem 1.1. *Assume $\gamma > 0, a > 0$ are fixed.*

(a) Let $g = g_1$ (DIE), $g = g_2$, (-DDE) or $g = g_3$ (+DDE). Then:
  (i) If $\lambda \leq \overline{E}_1(M_0, \underline{g}, \gamma)$ where $M_0 = M_0(a) \geq 1$ is such that $f(s) < M_0 s$ for all $s \in (0,1]$, then (6) has no positive solution.
  (ii) If $\lambda > E_1(\gamma)$, then (6) has a positive solution u_λ s.t. $\|u_\lambda\|_\infty \to 1$ as $\lambda \to \infty$.

(b) Let $a \geq 1$ (LTG) and $g = g_1$ (DIE) or $a \geq 1$ (LTG) and $g = g_3$ (+DDE). Then for $\lambda > E_1(\gamma)$, (6) has a unique positive solution u_λ such that $\|u_\lambda\|_\infty \to 0$ as $\lambda \to E_1(\gamma)^+$ and $\|u_\lambda\|_\infty \to 1$ as $\lambda \to \infty$. Further, (6) has no positive solution for $\lambda \leq E_1(\gamma)$.

(c) Let $a \in (0,1)$ (WAG) and $g = g_1$ (DIE) or $a \in (0,1)$ (WAG) and $g = g_2$ (-DDE). Then there exists a $\overline{\lambda}_1(a,\gamma) \in (0, E_1(\gamma))$ such that (6) has a positive solution for $\lambda > \overline{\lambda}_1(a,\gamma)$ and a PAE occurs for $\lambda \in \left(\overline{\lambda}_1(a,\gamma), E_1(\gamma)\right)$. Furthermore, $\overline{\lambda}_1(a,\gamma) \to 0$ as $a \to 0$ and $\overline{\lambda}_1(a,\gamma) \to E_1(\gamma)$ as $a \to 1$.

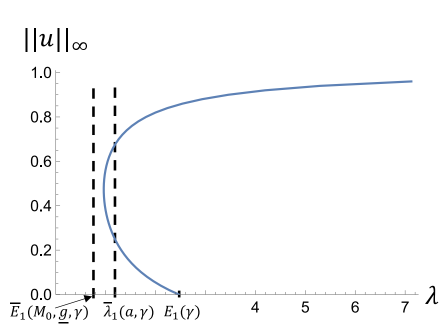
Remark 1.2. Here, our results do not exclude the possibility of a PAE occurring for $\lambda < \overline{\lambda}_1(a,\gamma)$, and hence it is not the same as $\lambda_*(a)$ for (1.3).

Theorem 1.3. *Let $g = g_1$ (DIE) or $g = g_2$ (-DDE), and $\lambda_0 \in (0, E_1(\gamma))$ be fixed. Then there exists an $\overline{a}_1(\gamma,\lambda_0) \in (0,1)$ such that for $a < \overline{a}_1(\gamma,\lambda_0)$ (6) has a positive solution for $\lambda > \lambda_0$ and a PAE occurs for $\lambda \in (\lambda_0, E_1(\gamma))$. Furthermore, $\overline{a}_1(\gamma,\lambda_0) \to 0$ as $\lambda_0 \to 0$ and $\overline{a}_1(\gamma,\lambda_0) \to 1$ as $\lambda_0 \to E_1(\gamma)$.*

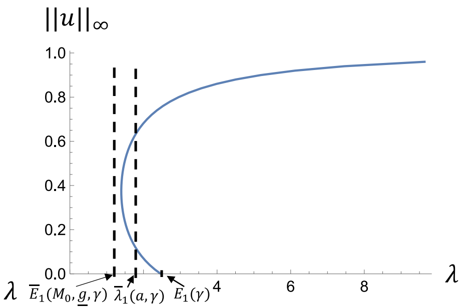
Remark 1.4. Here we note that PAE occurs for all $a < \overline{a}_1(\gamma,\lambda_0)$. PAE may or may not occur when $a = \overline{a}_1(\gamma,\lambda_0)$.

Remark 1.5.

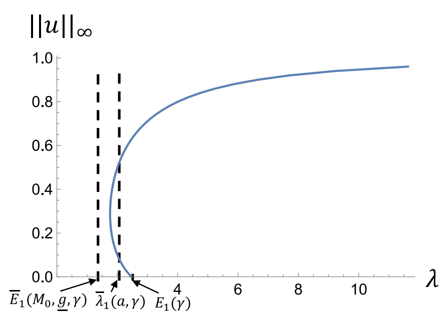
(A) Theorem 1.1*(b)* implies that, in the case $a \geq 1$ (LTG) and $g = g_1$ (DIE) or $g = g_3$ (+DDE), the bifurcation diagram for (6) illustrated in Figure 1 (a) is exact.



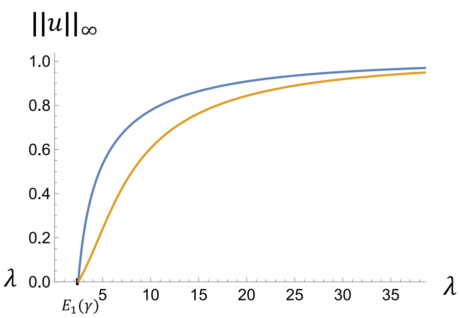
(A) Exact bifurcation diagram for the $g = g_1$ (DIE) case when $\gamma = 1, a = 0.3$.



(B) Exact bifurcation diagram for the $g = g_2$ (-DDE) case when $\gamma = 1, a = 0.3, \beta = 0.8$.



(C) Exact bifurcation diagram for the $g = g_3$ (+DDE) case when $\gamma = 1$, $a = 0.3, \beta = 0.8$.



(D) Exact bifurcation diagram when $a = 2, \gamma = 1$. Blue curve is for $g = g_1$ (DIE) case and the yellow curve is for the $g = g_3$ (+DDE) case when $\beta = 5$.

FIGURE 3. Exact bifurcation diagrams corresponding to Theorem 1.1 when $\Omega = (0, 1)$ via the quadrature method discussed in Section 4.

(B) Theorem 1.1*(c)(i)* shows that PAE region length increases as a decreases (increasing Allee effect strength), reaching its maximum as $a \to 0$.
(C) Theorem 1.1*(c)(ii)* conversely shows that the Allee effect strength needed to ensure a PAE occurs at λ_0 decreases as $\lambda_0 \to E_1(\gamma)$ and increases as $\lambda_0 \to 0$.

Next, we state results when the parameter β in g_2 and g_3 are allowed to vary.

Theorem 1.6. *Let $g = g_2$ (-DDE) and $\lambda_0 < E_1(\gamma)$ be fixed.*

(a) For $a > 0$ there exists $\overline{\beta}_1(a, \gamma, \lambda_0) > 0$ such that if $\beta > \overline{\beta}_1(a, \gamma, \lambda_0)$ then a PAE occurs for $\lambda \in \big[\lambda_0, E_1(\gamma)\big)$. Also $\overline{\beta}_1(a, \gamma, \lambda_0) \to \infty$ as $\lambda_0 \to 0$. Moreover, if $a \geq 1$ (LTG) then $\overline{\beta}_1(a, \gamma, \lambda_0) \to 0$ as $\lambda_0 \to E_1(\gamma)^-$.
(b) If $a \geq 1$ (LTG) then there exists $\overline{\beta}_2(\gamma, \lambda_0) > 0$ such that (6) has no positive solution for $\lambda \leq \lambda_0$ if $\beta \leq \overline{\beta}_2(\gamma, \lambda_0)$.

Theorem 1.7. *Let $a \in (0, 1)$ (WAG) and $\lambda_*(a)$ as in the discussion of positive solutions of (3). Then:*

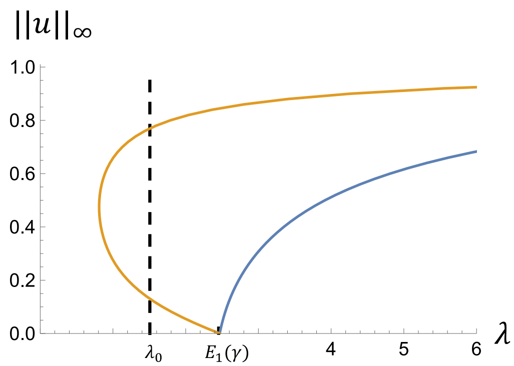


FIGURE 4. Exact bifurcation diagrams corresponding to Theorem 1.6 for $a = 2, \gamma = 1$, and $g = g_2$ (-DDE) with $\beta = 0.5$ (in blue) and $\beta = 5$ (in yellow) when $\Omega = (0, 1)$ via the quadrature method discussed in Section 4.

(a) If $g = g_1$ (DIE), $g = g_2$ (-DDE), or $g = g_3$ (+DDE) then there exists a $\overline{\gamma}_1(a) > 0$ such that if $\gamma > \overline{\gamma}_1(a)$ then there is a PAE for $\lambda \in [\lambda_*(a), E_1(\gamma))$ for all $\beta \geq 0$. Moreover, $\overline{\gamma}_1(a) \to 0$ as $a \to 0$ and $\overline{\gamma}_1(a) \to \infty$ as $a \to 1$.

(b) If $g = g_3$ (+DDE) then we have that

(i) For fixed $a \in (0, 1)$, there exists a $\overline{\lambda}_2(a, \gamma) \in (0, E_1(\gamma))$ and $\overline{\beta}_3(a, \gamma) > 0$ such that there is a PAE for $\lambda \in \big(\overline{\lambda}_2(a, \gamma), E_1(\gamma)\big)$ when $\beta < \overline{\beta}_3(a, \gamma)$. Moreover, $\overline{\beta}_3(a, \gamma) \to \infty$ as $a \to 0$.

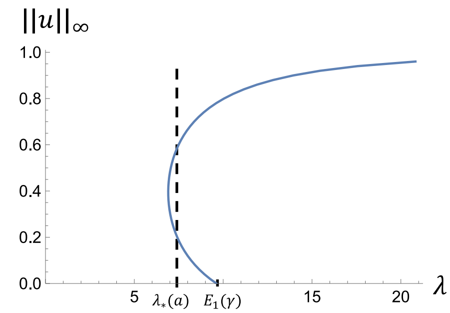
(ii) For fixed $\beta > 0$, there exists a $\overline{a}_2(\beta, \gamma) > 0$ and $\overline{\lambda}_3(a, \beta, \gamma) \in (0, E_1(\gamma))$ such that there is a PAE for $\lambda \in \big(\overline{\lambda}_3(a, \beta, \gamma), E_1(\gamma)\big)$ when $a < \overline{a}_2(\beta, \gamma)$. Furthermore, $\overline{\lambda}_3(a, \beta, \gamma) \to 0$ as $a \to 0$ and $\overline{a}_2(\beta, \gamma) \to 0$ as $\beta \to \infty$.

Remark 1.8. In the case $g = g_3$ (+DDE) with $a \in (0, 1)$, we conjecture that for a fixed γ there exists a $\beta(\gamma)$ such that for $\beta > \beta(\gamma)$ there will be no PAE for all $\lambda < E_1(\gamma)$. We base our conjecture on numerical observations when $\Omega = (0, 1)$ presented in Figures 5(b) and 11(a), also see [11].

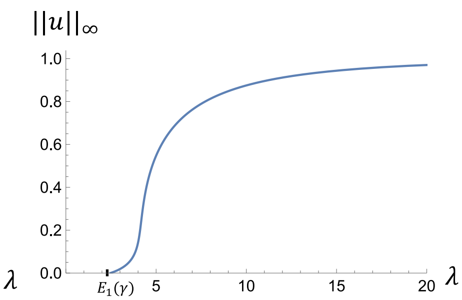
Remark 1.9. We note that Theorem 1.1(c)*(i)* and Theorem 1.7*(b)(ii)* imply that, in the case $g = g_1$ (DIE), $g = g_2$ (-DDE), and $g = g_3$ (+DDE), PAE occurs for all closed subsets of $(0, E_1(\gamma))$ as $a \to 0$.

Remark 1.10. We note that Theorem 1.6 implies that, in the case $g = g_2$ (-DDE) and $a > 0$, PAE occurs for all closed subsets of $(0, E_1(\gamma))$ as $\beta \to \infty$.

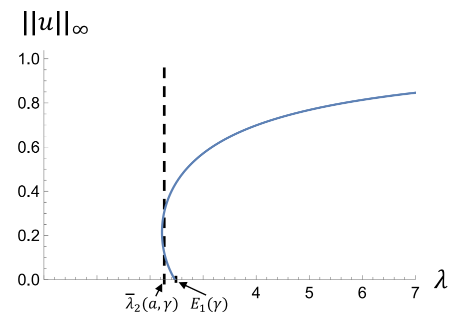
1.3. **Biological interpretation.** Theorem 1.1 establishes that for patches with size below a threshold, extinction is predicted for any form of DDE. For patch size with corresponding $\lambda > E_1(\gamma)$, Theorem 1.1 guarantees existence of at least one positive solution of (6) for any DDE form, and a unique (and hence globally asymptotically stable) positive solution of (6) for $a \geq 1$ (LTG) combined with either DIE or +DDE. As noted in [11], multiple positive solutions of 6 for $\lambda > E_1(\gamma)$ are possible in the one-dimensional case for -DDE. Theorem 1.1(c) shows that a PAE is predicted for DIE and -DDE solely based upon the strength of the Allee effect in the fitness. In fact, the PAE region increases in length as the Allee effect strength



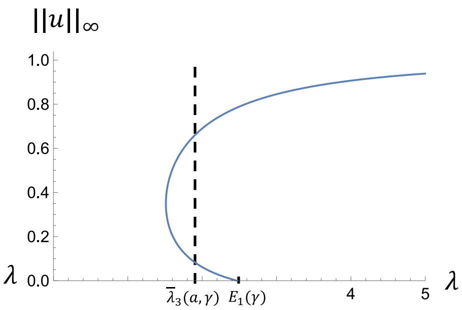
(A) Exact bifurcation diagram when $a = 0.3, \beta = 20$, and $\gamma = 50$.



(B) Exact bifurcation diagram when $a = 0.3, \beta = 20$, and $\gamma = 1$.



(C) Exact bifurcation diagram when $a = 0.6, \beta = 0.01$, and $\gamma = 1$.



(D) Exact bifurcation diagram when $a = 0.1, \beta = 10$, and $\gamma = 1$.

FIGURE 5. Exact bifurcation diagrams corresponding to Theorem 1.7 for $g = g_3$ (+DDE) case when $\Omega = (0,1)$ via the quadrature method discussed in Section 4.

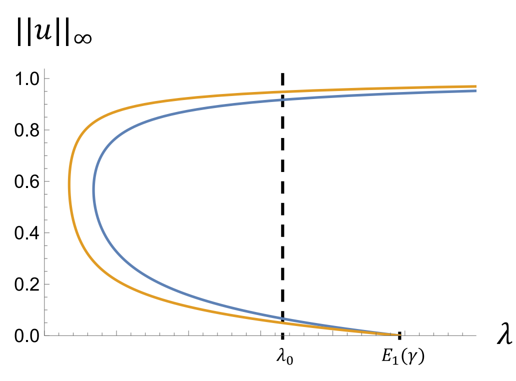


FIGURE 6. Exact bifurcation diagrams corresponding to Theorem 1.6 for $a = 0.3, \gamma = 1$, and $g = g_2$ (-DDE) with $\beta = 3$ (in blue) and $\beta = 5$ (in yellow) when $\Omega = (0,1)$ via the quadrature method discussed in Section 4.

increases (i.e., $a \to 0$). Also, given a patch with corresponding $\lambda < E_1(\gamma)$, the Allee effect strength must be quite strong to ensure a PAE occurs in this patch for $\lambda \approx 0$, and conversely, weak for $\lambda \approx E_1(\gamma)$.

Theorem 1.6 shows that for either LTG or WAG, a PAE can be guaranteed by taking a sufficiently strong DDE strength (i.e., $\beta \gg 1$). These results also coincide with previous work on similar models where -DDE was shown to induce a PAE under certain parameter ranges (see, e.g., [8]). Theorem 1.6 also provides some insight on the connection between patch size and the required DDE strength needed to ensure a PAE occurs. For patches with $\lambda \approx E_1(\gamma)$, weak DDE strength (i.e., $\beta \approx 0$) is sufficient to guarantee a PAE occurs, whereas, for patches with $\lambda \approx 0$, DDE strength must approach infinity. Also, in the LTG case, Theorem 1.6(b) shows existence of a minimum DDE strength required to ensure a PAE occurs given a fixed $\lambda_0 < E_1(\gamma)$.

A necessary condition for a PAE to occur is for the trivial solution of (6) to be asymptotically stable. This combined with the fact that the trivial solution of (6) is asymptotically stable for $\lambda < E_1(\gamma)$ and unstable for $\lambda > E_1(\gamma)$ (the proof of Theorem 2.1 in [11] goes through to higher dimensional case here) shows that the maximal Allee effect region is $(0, E_1(\gamma))$ for a given matrix hostility $\gamma > 0$. Also, since $E_1(\gamma) \to E_1^D$ as $\gamma \to \infty$, the maximal Allee effect region length is bounded above by E_1^D. Theorem 1.7(a) confirms an observation made in our computational results that as matrix hostility increases (i.e., $\gamma \to \infty$), a PAE is ensured for any DDE form (see also [11]). Moreover, increasing Allee effect strength lowers the threshold for matrix hostility needed to ensure a PAE.

Theorem 1.7(b) sheds some light on the observation first made by [11] and supported by our computational results in Figure 11(a) that a sufficiently strong +DDE can attenuate a PAE present under WAG. Our computational results also suggest that a PAE can even be completely counteracted by a sufficiently strong +DDE (see Figure 11(a)). Theorem 1.7(b)(i) shows that for a fixed Allee effect strength, a PAE will still occur if the +DDE strength is below a certain threshold that approaches infinity for increasing Allee effect strength (i.e., $a \to 0$). Theorem 1.7(b)(ii) illustrates that a similar situation is possible for fixed +DDE strength by making the Allee effect strength sufficiently strong. However, a proof that +DDE can completely counteract a PAE for a higher dimensional patch remains elusive. Finally, we note that our results connect PAE region length directly to 1) Allee effect strength for any of the three DDE forms and 2) DDE strength for -DDE in a rigorous way. In particular, we show that a PAE will occur for all closed subsets of $(0, E_1(\gamma))$ by either taking $a \to 0$ for any of the three DDE forms or $\beta \to \infty$ for -DDE.

1.4. **Structure of the paper.** We present preliminaries in Section 2. Our existence and multiplicity results are established via the method of sub-supersolutions. We construct the subsolutions and supersolutions to prove Theorems 1.1 - 1.7 in Section 3, and provide proofs of Theorems 1.1 - 1.7 in Section 4. Finally, in Section 5, we provide computational results consisting of bifurcation diagrams of positive solutions of (6) for various values of the parameters a, β, and γ when $\Omega = (0, 1)$ and show how they evolve as certain parameter values vary.

2. **Preliminaries.**

In this section, we introduce definitions of (strict) subsolution and (strict) supersolution of (6) and state a sub-supersolution theorem that is used to prove existence and multiplicity results of positive solutions.

By a subsolution of (6) we mean $\psi \in C^2(\Omega) \cap C^1(\overline{\Omega})$ that satisfies

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

By a supersolution of (6) we mean $Z \in C^2(\Omega) \cap C^1(\overline{\Omega})$ that satisfies

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

By a strict subsolution (supersolution) of (6) we mean a subsolution (supersolution) which is not a solution.
Then the following results hold (see [2], [23], and [36]):

Lemma 2.1. *Let ψ and Z be a subsolution and a supersolution of (6), respectively, such that $\psi \leq Z$. Then (6) 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 (6), respectively, such that $\psi_1 \leq Z_2$. Let ψ_2 and Z_1 be a strict subsolution and a strict supersolution of (6), respectively, such that ψ_2, $Z_1 \in [\psi_1, Z_2]$ and $\psi_2 \not\leq Z_1$. Then (6) has at least three solutions u_1, u_2 and u_3 where $u_i \in [\psi_i, Z_i]$; $i = 1, 2$ and $u_3 \in [\psi_1, Z_2] \backslash ([\psi_1, Z_1] \cup [\psi_2, Z_2])$.*

Finally, we recall Lemma 2.3 from [11] which gives a sufficient condition for a PAE to occur. It is easy to see that the proof given in [11] goes through for the higher dimensional case in (6).

Lemma 2.3 ([11])**.** *For given $a, \beta > 0, \gamma > 0$, and $g = g_i; i = 1, 2, 3$, if (6) has at least one positive solution for $\lambda < E_1(\gamma)$ then the model predicts a patch-level Allee effect for the patch size corresponding to λ.*

3. **Construction of subsolutions and supersolutions to prove Theorems 1.1 - 1.7.** Here, we state a couple of eigenvalue problems which are crucial to our proofs and recall some properties of their respective principal eigenvalues. For $M, b, \lambda, \gamma > 0$, let $\sigma_0 = \sigma_0(M, b, \lambda, \gamma)$ be the principal eigenvalue and $\phi_0 > 0; \overline{\Omega}$ be the corresponding normalized eigenfunction of

$$\begin{cases} -\Delta\phi_0 - \lambda M\phi_0 = \sigma_0\phi_0;\ \Omega \\ \frac{\partial\phi_0}{\partial\eta} + \gamma\sqrt{\lambda}b\phi_0 = 0;\ \partial\Omega \end{cases} \tag{7}$$

and $\sigma_1 = \sigma_1(M, b, \lambda, \gamma)$ be the principal eigenvalue and $\phi_1 > 0; \overline{\Omega}$ be the corresponding normalized eigenfunction of

$$\begin{cases} -\Delta\phi_1 - \lambda M\phi_1 = \sigma_1\phi_1;\ \Omega \\ \frac{\partial\phi_1}{\partial\eta} + \gamma\sqrt{\lambda}b\phi_1 = \sigma_1\phi_1;\ \partial\Omega \end{cases} \tag{8}$$

Note that existence of both principle eigenvalues is standard (see, e.g., [6] and [3]). For simplicity of notation, we denote $\tilde{\sigma}_i = \sigma_i(1, 1, \gamma, \lambda)$ with corresponding eigenfunction $\tilde{\phi}_i$, $\hat{\sigma}_i = \sigma_i(1, r_1, \gamma, \lambda)$ for $r_1 > 1$ with corresponding eigenfunction $\hat{\phi}_i$, and $\overline{\sigma}_i = \sigma_i(1, b_0, \gamma, \lambda)$ for $b_0 \in (0, 1)$ with corresponding eigenfunction $\overline{\phi}_i$ each for $i = 0, 1$. The following lemma gives several useful properties of $\sigma_i(M, b, \lambda, \gamma)$ and $\overline{E}_1(M, b, \gamma)$ (see, e.g., [6], [18], and [3]).

Lemma 3.1. *Let $M, \gamma, b > 0$, $\sigma_0(M, b, \lambda, \gamma)$ denote the principal eigenvalue of (7), $\sigma_1(M, b, \lambda, \gamma)$ the principal eigenvalue of (8), and $\overline{E}_1(M, b, \gamma)$ the principal eigenvalue of (2). Then we have the following for $i = 0, 1$:*

(1) $\sigma_i(M,b,\lambda,\gamma)\geq 0$ *for* $\lambda\leq \overline{E}_1(M,b,\gamma)$
(2) $\sigma_i(M,b,\lambda,\gamma)< 0$ *for* $\lambda> \overline{E}_1(M,b,\gamma)$
(3) $\sigma_i(M,b,\lambda,\gamma)$ *is decreasing in* M *and increasing in* b *and* γ
(4) $sgn\,(\sigma_0(M,b,\lambda,\gamma)) = sgn\,(\sigma_1(M,b,\lambda,\gamma))$
(5) $\overline{E}_1(M,b,\gamma)$ *is decreasing in* M *and increasing in* b *and* γ
(6) $\overline{E}_1(M,b,\gamma)=\frac{\overline{E}_1\left(1,b,\frac{\gamma}{\sqrt{M}}\right)}{M}$.

Note that $f(0)=0$ and $f'(0)=1$.

Construction of a subsolution $\psi_1<1$ when $\lambda>E_1(\gamma)$ for $\gamma>0, a>0$, and any form of g.

We note that $\tilde{\sigma}_1<0$ for $\lambda>E_1(\gamma)$. Let $\psi_1:=\delta_1\tilde{\phi}_1$ for $\delta_1>0$ and $l(s)=(\tilde{\sigma}_1+\lambda)s-\lambda f(s)$. Then, we have $l(0)=0$ and $l'(0)=(\tilde{\sigma}_1+\lambda)-\lambda f'(0)=\tilde{\sigma}_1<0$ since $f'(0)=1$. Therefore, $l(s)<0; s\approx 0$. This implies that

$$-\Delta\psi_1=\delta_1(\lambda+\tilde{\sigma}_1)\tilde{\phi}_1<\lambda f(\delta_1\tilde{\phi}_1)=\lambda f(\psi_1);\ \Omega$$

for $\delta_1\approx 0$. We also have

$$\begin{aligned}\frac{\partial\psi_1}{\partial\eta}+\gamma\sqrt{\lambda}g(\psi_1)\psi_1&=\delta_1\Big(\frac{\partial\tilde{\phi}_1}{\partial\eta}+\gamma\sqrt{\lambda}g(\delta_1\tilde{\phi}_1)\tilde{\phi}_1\Big)\\&=\delta_1\Big(-\gamma\sqrt{\lambda}\tilde{\phi}_1+\tilde{\sigma}_1\tilde{\phi}_1+\gamma\sqrt{\lambda}g(\delta_1\tilde{\phi}_1)\tilde{\phi}_1\Big)\\&=\delta_1\tilde{\phi}_1\Big(\gamma\sqrt{\lambda}(g(\delta_1\tilde{\phi}_1)-1)+\tilde{\sigma}_1\Big)\\&<0;\ \partial\Omega\end{aligned}$$

for $\delta_1\approx 0$ since $g(0)=1$ and $\tilde{\sigma}_1<0$ for $\lambda>E_1(\gamma)$. Hence, ψ_1 is a subsolution of (6) for $\lambda>E_1(\gamma)$.

Construction of a subsolution ψ_2 when $\lambda>E_1^D$ such that $\|\psi_2\|_\infty\longrightarrow 1$ as $\lambda\longrightarrow\infty$for $\gamma>0, a>0$, and any form of g.

Consider the problem:

$$\begin{cases}-\Delta w=\lambda w(1-w);\ \Omega\\ \qquad w=0;\ \partial\Omega.\end{cases}\tag{9}$$

Let w_λ be the unique positive solution of (9) for $\lambda>E_1^D$ (see, e.g., [6]). We note that $\|w_\lambda\|_\infty\to 1$ as $\lambda\to\infty$. Let $\psi_2:=w_\lambda$. Then we have

$$\begin{aligned}-\Delta\psi_2&=\lambda\psi_2(1-\psi_2)\\&\leq\lambda\psi_2(1-\psi_2)(1+\frac{\psi_2}{a})\\&=\lambda f(\psi_2);\ \Omega.\end{aligned}$$

Also,

$$\frac{\partial\psi_2}{\partial\eta}+\gamma\sqrt{\lambda}g(\psi_2)\psi_2=\frac{\partial w_\lambda}{\partial\eta}<0;\ \partial\Omega$$

by the Hopf's Maximum Principle. Therefore, ψ_2 is a subsolution of (6) for $\lambda>E_1^D$ such that $\|\psi_2\|_\infty\longrightarrow 1$ as $\lambda\longrightarrow\infty$.

Construction of a strict subsolution ψ_3 in $\left(\overline{\lambda}_1(a,\gamma),\infty\right)$ for $\gamma>0, a\in(0,1)$ (WAG), and $g=g_1$ (DIE) or $g=g_2$ (-DDE), for some $\overline{\lambda}_1(a,\gamma)<E_1(\gamma)$.

For a fixed $\lambda > 0$, let $\tilde{\sigma}_0 = \sigma_0(1, 1, \lambda, \gamma)$ be the principal eigenvalue and $\tilde{\phi}_0 > 0$; $\overline{\Omega}$ be the corresponding normalized eigenfunction of (7) (here, $M = 1$ and $b = 1$). Let $\psi_3 = \delta_3 \tilde{\phi}_0$ with $\delta_3 > 0$ to be chosen later and $\tilde{m}_0 = \tilde{m}_0(\lambda) := \min_{\overline{\Omega}} \tilde{\phi}_0$. Then, since $1 - \frac{1}{a} < 0$ and $\tilde{\phi}_0 \leq 1; \overline{\Omega}$ we have

$$
\begin{aligned}
-\Delta\psi_3 - \lambda\psi_3(1-\psi_3)(1+\frac{\psi_3}{a}) &= \delta_3\left(\tilde{\sigma}_0\tilde{\phi}_0 + \left(1-\frac{1}{a}\right)\lambda\delta_3\tilde{\phi}_0^2 + \frac{\lambda\delta_3^2\left(\tilde{\phi}_0\right)^3}{a}\right)\\
&\leq \delta_3\left(\tilde{\sigma}_0 + \left(1-\frac{1}{a}\right)\lambda\delta_3\tilde{m}_0^2 + \frac{\lambda\delta_3^2}{a}\right)\\
&= \delta_3\frac{\lambda}{a}\left(\delta_3^2 + (a-1)\,\tilde{m}_0^2\delta_3 + \frac{a}{\lambda}\tilde{\sigma}_0\right);\ \Omega.
\end{aligned}
$$

Let $h(\delta) = \delta^2 + (a-1)\,\tilde{m}_0^2\delta + \frac{a}{\lambda}\tilde{\sigma}_0$. By the quadratic formula, the roots of h are given by

$$
\begin{aligned}
\delta_3^* &= \frac{\tilde{m}_0^2(1-a) - \sqrt{\tilde{m}_0^4(a-1)^2 - \frac{4a}{\lambda}\tilde{\sigma}_0}}{2}, \\
\delta_3^{**} &= \frac{\tilde{m}_0^2(1-a) + \sqrt{\tilde{m}_0^4(a-1)^2 - \frac{4a}{\lambda}\tilde{\sigma}_0}}{2}.
\end{aligned}
\tag{10}
$$

We note that if

$$
\frac{(a-1)^2}{a} > \frac{4\tilde{\sigma}_0}{\lambda\tilde{m}_0^4} \tag{11}
$$

then δ_3^* and δ_3^{**} are such that $\delta_3^* < \delta_3^{**}$. In fact, $\tilde{\sigma}_0 \geq 0$ for $\lambda \leq E_1(\gamma)$ giving that $0 < \delta_3^* \leq \delta_3^{**} < 1$, whereas, $\tilde{\sigma}_0 < 0$ when $\lambda > E_1(\gamma)$ giving that $\delta_3^* < 0$ and $\delta_3^{**} > 1$. Also, for a fixed $a \in (0, 1)$, (11) holds when $\lambda \approx E_1(\gamma)$ since $\tilde{\sigma}_0 \to 0^+$ and $\tilde{m}_0 \not\to 0$ as $\lambda \to E_1(\gamma)^-$.

Furthermore, for a fixed $\lambda \in (0, E_1(\gamma)]$, (11) holds when $a \approx 0$ since $\min_{[0,E_1(\gamma)]} \tilde{m}_0(\lambda) > 0$ and for a fixed $\lambda > E_1(\gamma)$, (11) holds for all $a > 0$ since $\tilde{\sigma}_0 < 0$ for $\lambda > E_1(\gamma)$. It is also easy to see that when $\lambda < E_1(\gamma)$, we have $\delta_3^* \to 0$ as $a \to 0$ or $\lambda \to E_1(\gamma)^-$ and $\delta_3^{**} \to \tilde{m}_0^2$ as $a \to 0$ and $\delta_3^{**} \to \tilde{m}_0^2(1-a)$ as $\lambda \to E_1(\gamma)^-$. This implies that for a given $a \in (0, 1)$, there exists a $\overline{\lambda}_1(a, \gamma) < E_1(\gamma)$ such that (11) holds for $\lambda \in \left(\overline{\lambda}_1(a, \gamma), \infty\right)$ and $\overline{\lambda}_1(a, \gamma) \to 0$ as $a \to 0$. Also, for a fixed $\lambda_0 \in (0, E_1(\gamma))$ there exists an $\overline{a}_1(\gamma, \lambda_0) \in (0, 1)$ such that (11) holds for $a \in (0, \overline{a}_1(\gamma, \lambda_0)$ and $\overline{a}_1(\gamma, \lambda_0) \to 1$ as $\lambda_0 \to E_1(\gamma)$.

Now, for $\lambda \in \left(\overline{\lambda}_1(a, \gamma), \infty\right)$, $h(\delta_3) < 0$ for all $\delta_3 \in (\delta_3^*, \delta_3^{**})$. Hence, whenever $\delta_3 \in (\delta_3^*, \delta_3^{**})$ we must have

$$
-\Delta\psi_3 - \lambda\psi_3(1-\psi_3)(1+\frac{\psi_3}{a}) \leq \delta_3\frac{\lambda}{a}\left(\delta_3^2 + (a-1)\,\tilde{m}_0^2\delta_3 + \frac{a}{\lambda}\tilde{\sigma}_0\right) < 0;\ \Omega
$$

and

$$
\begin{aligned}
\frac{\partial\psi_3}{\partial\eta} + \gamma\sqrt{\lambda}g(\psi_3)\psi_3 &= \delta_3\left(\frac{\partial\tilde{\phi}_0}{\partial\eta} + \gamma\sqrt{\lambda}g(\delta_3\tilde{\phi}_0)\tilde{\phi}_0\right)\\
&= \delta_3\left(-\gamma\sqrt{\lambda}\tilde{\phi}_0 + \gamma\sqrt{\lambda}g(\delta_3\tilde{\phi}_0)\tilde{\phi}_0\right)\\
&= \delta_3\gamma\sqrt{\lambda}\tilde{\phi}_0\left(g(\delta_3\tilde{\phi}_0) - 1\right)
\end{aligned}
$$

$$\leq 0;\ \partial\Omega$$

since $g(s) \leq 1; s \in [0,1]$ when $g = g_1$ (DIE) or $g = g_2$ (-DDE). Hence, ψ_3 with $\delta_3 \in (\delta_3^*, \delta_3^{**})$ is a strict subsolution of (6) for $\lambda \in \big(\overline{\lambda}(a,\gamma), \infty\big)$.

Construction of a strict subsolution ψ_3^* in $\big(\overline{\lambda}_2(a,\gamma), \infty\big)$ when $a \in (0,1)$ (WAG) and $g = g_3$ (+DDE), for some $\overline{\lambda}_2(a,\gamma) < E_1(\gamma)$.
We choose $b = r_1$ with $r_1 > 1$ and $r_1 \approx 1$. Let $\hat{\sigma}_0 = \sigma_0(1, r_1, \lambda, \gamma)$ be the principle eigenvalue and $\hat{\phi}_0$ be the corresponding normalized eigenfunction of (7) and define $\psi_3^* := \hat{\delta}_3 \hat{\phi}_0$ with $\hat{\delta}_3 > 0$. Following the construction of ψ_3 but employing $\hat{\sigma}_0$, $\hat{\phi}_0$ and defining $\hat{m}_0 = \hat{m}_0(\lambda) := \min_{\overline{\Omega}} \hat{\phi}_0$, we can show that there exist $\hat{\delta}_3^*$ and $\hat{\delta}_3^{**}$ with $\hat{\delta}_3^* \leq \hat{\delta}_3^{**}$ and having all the same properties of $\delta_3^*, \delta_3^{**}$ by ensuring that $r_1 \approx 1$ (see (10)). Thus, there exists a $\overline{\lambda}_2(a,\gamma) > 0$ such that for $\lambda \in \big(\overline{\lambda}_2(a,\gamma), \infty\big)$ and $\hat{\delta}_3 \in (\hat{\delta}_3^*, \hat{\delta}_3^{**})$ we have

$$-\Delta\psi_3^* - \lambda\psi_3^*(1-\psi_3^*)(1+\frac{\psi_3^*}{a}) < 0;\ \Omega \tag{12}$$

and

$$\begin{aligned}\frac{\partial \psi_3^*}{\partial \eta} + \gamma\sqrt{\lambda} g(\psi_3^*)\psi_3^* &= -\gamma\sqrt{\lambda} r_1 \hat{\delta}_3\hat{\phi}_0 + \gamma\sqrt{\lambda}(1+\beta\hat{\delta}_3\hat{\phi}_0)\hat{\delta}_3\hat{\phi}_0 \\ &= \hat{\delta}_3\hat{\phi}_0\gamma\sqrt{\lambda}\left(\beta\hat{\delta}_3\hat{\phi}_0 + (1-r_1)\right) \\ &\leq \hat{\delta}_3\hat{\phi}_0\gamma\sqrt{\lambda}\left(\beta\hat{\delta}_3^{**} + (1-r_1)\right) \\ &< 0;\ \partial\Omega \end{aligned} \tag{13}$$

for $\beta < \overline{\beta}_3(a,\gamma) := \frac{r_1-1}{\hat{\delta}_3}$ since $\|\hat{\phi}_0\|_\infty \leq 1$. Thus, ψ_3^* is a strict subsolution of (6) for $\lambda \in \big(\overline{\lambda}_2(a,\gamma), \infty\big)$ when $\beta < \overline{\beta}_3(a,\gamma)$. Further, when $a \approx 0$ we can choose $\hat{\delta}_3 \approx 0$ such that inequalities (12) and (13) hold. Therefore, for a fixed $\beta > 0$ there exist $\overline{a}_2(\beta,\gamma) > 0$ and $\overline{\lambda}_3(a,\beta,\gamma)$ such that ψ_3^* is a strict subsolution of (6) for $\lambda \in \big(\overline{\lambda}_3(a,\beta,\gamma), \infty\big)$ when $a < \overline{a}_2(\beta,\gamma)$ and $\overline{\lambda}_3(a,\beta,\gamma) \to 0$ as $a \to 0$. Also, $\overline{a}_2(\beta,\gamma) \to 0$ as $\beta \to \infty$.

Construction of a strict subsolution ψ_4 in $\big[\lambda_0, E_1(\gamma)\big)$ when $a > 0$, $g = g_2$ (-DDE), and $\lambda_0 < E_1(\gamma)$ fixed when $\beta > \overline{\beta}_1(a,\gamma,\lambda_0)$ for some $\overline{\beta}_1(a,\gamma,\lambda_0) > 0$.
Let $\lambda_0 < E_1(\gamma)$ and $\tilde{\lambda}_0 \in (0, \lambda_0)$. Choose $M = 1$ and $b_0 \in (0,1)$ in (7) such that $\tilde{\lambda}_0 = E_1(1, b_0, \gamma)$. Next, for a fixed $\lambda > 0$, let $\overline{\sigma}_0 = \sigma_0(1, b_0, \lambda, \gamma)$ be the principal eigenvalue and $\overline{\phi}_0 > 0; \overline{\Omega}$ be the corresponding normalized eigenfunction of (7). We note that $\overline{\sigma}_0 < 0$ when $\lambda > \tilde{\lambda}_0$. Let $I = [\lambda_0, E_1(\gamma)]$ and define $H(s) := (\lambda + \overline{\sigma}_0)s - \lambda f(s)$ for $\lambda \geq \lambda_0$. Then, $H(0) = 0$ and $H'(0) = \overline{\sigma}_0 < 0$ since $f(0) = 0$, $f'(0) = 1$, and $\overline{\sigma}_0 < 0$. This implies that $H(s) < 0$ for $s \approx 0$. Let $s_\lambda \in (0,1)$ be such that

$$H(s) = (\lambda + \overline{\sigma}_0)s - \lambda f(s) < 0; \quad \text{for all } s \in (0, s_\lambda]. \tag{14}$$

Next, we define $K = K(a,\Omega) := \min_{\lambda\in I} \min_{\overline{\Omega}} \{\delta_4 \overline{\phi}_0\}$ where $\delta_4 := \min_{\lambda \in I}\{s_\lambda\}$. Observe that $0 < \delta_4 < 1$, and $\|\overline{\phi}_0\|_\infty \leq 1$ implies that $K < 1$. Let $\lambda \in I$ and define $\psi_4 := \delta_4\overline{\phi}_0$. From (14), we have

$$-\Delta\psi_4 = -\delta_4\Delta\overline{\phi}_0 = \delta_4(\lambda+\overline{\sigma}_0)\overline{\phi}_0 < \lambda f(\delta_4\overline{\phi}_0) = \lambda f(\psi_4);\ \Omega.$$

Next, since $\delta_4\overline{\phi}_0 \geq K$ we have

$$1+\beta\delta_4\overline{\phi}_0 \geq 1+\beta K;\ \partial\Omega.$$

This implies that

$$\frac{1}{1+\beta\delta_4\overline{\phi}_0} - b_0 \leq \frac{1}{1+\beta K} - b_0;\ \partial\Omega. \tag{15}$$

Let $\overline{\beta}_1 := \overline{\beta}_1(a,\gamma,\lambda_0)$ be such that $\frac{1}{1+\overline{\beta}_1 K} - b_0 = 0$. This implies that $\overline{\beta}_1(a,\gamma,\lambda_0) = \frac{1-b_0}{b_0 K}$. Observe that $\overline{\beta}_1(a,\gamma,\lambda_0) > 0$ and $\frac{1}{1+\beta K} - b_0 < 0$ for $\beta > \overline{\beta}_1(a,\gamma,\lambda_0)$. Now, for $\beta > \overline{\beta}_1(a,\gamma,\lambda_0)$, we have

$$\begin{aligned}\frac{\partial\psi_4}{\partial\eta} + \gamma\sqrt{\lambda}g(\psi_4)\psi_4 &= \delta_4\big(\frac{\partial\overline{\phi}_0}{\partial\eta} + \gamma\sqrt{\lambda}g(\delta_4\overline{\phi}_0)\phi_0\big)\overline{\phi}_0\big)\\ &= \delta_4\gamma\sqrt{\lambda}\overline{\phi}_0\Big(\frac{1}{1+\beta\delta_4\overline{\phi}_0} - b_0\Big)\\ &< 0;\ \partial\Omega\end{aligned}$$

by (15). Hence, ψ_4 is a strict subsolution of (6) for $\lambda \in I$ and $\beta > \overline{\beta}_1(a,\gamma,\lambda_0)$. Note that the prescribed behavior of $\overline{\beta}_1(a,\gamma,\lambda_0)$ follows from its form given above.

Construction of a strict subsolution ψ_5 in $[\lambda_*(a), E_1(\gamma)]$ for $a \in (0,1)$ (WAG), $\gamma > \overline{\gamma}_1(a)$ for some $\overline{\gamma}_1(a) > 0$, and any form of g.

Recall that (3) has a positive solution, $w_\lambda < 1; \overline{\Omega}$, for $\lambda \in [\lambda_*(a), E_1^D]$. We note that $E_1(\gamma)$ is an increasing continuous function of γ and $\lim_{\gamma\to\infty} E_1(\gamma) = E_1^D$. Then, there exists $\overline{\gamma}_1(a) > 0$ such that $E_1(\gamma) > \lambda_*(a)$ for $\gamma > \overline{\gamma}_1(a)$ (see Figure 7). Let $\psi_5 := w_\lambda$, for $\lambda \in [\lambda_*(a), E_1(\gamma)]$. It is straightforward to show that ψ_5 is a strict subsolution of (6) for $\lambda \in [\lambda_*(a), E_1(\gamma)]$ when $\gamma > \overline{\gamma}_1(a)$ since $\frac{\partial w_\lambda}{\partial\eta} < 0; \partial\Omega$.

We also note that the same argument as in the construction of ψ_3 holds in the case of (3) where $\tilde{\sigma}_0, \tilde{\phi}_0$ are replaced by appropriate versions of (7) but with Dirichlet boundary conditions. Using arguments from that subsection, it is straightforward to show that $\lambda_*(a) \to 0$ as $a \to 0$ and $\lambda_*(a) \to E_1^D$ as $a \to 1$. Thus, $\overline{\gamma}_1(a) \to 0$ as $a \to 0$ and $\overline{\gamma}_1(a) \to \infty$ as $a \to 1$.

Construction of a global supersolution Z_1 for $\lambda > 0$, $a > 0$, and any form of g.

Note that $Z_1 \equiv 1$ is a global supersolution of (6) for all $\lambda > 0$, $a > 0$, and any g_i.

Construction of a strict supersolution Z_2 for $\lambda \in (0, E_1(\gamma))$, $a > 0$, and any form of g.

For a fixed $\lambda > 0$, recall $\tilde{\sigma}_1 = \sigma_1(1,1,\lambda,\gamma)$ is the principal eigenvalue and $\tilde{\phi}_1 > 0; \overline{\Omega}$ the corresponding normalized eigenfunction of (8) (here, $M = 1$ and $b = 1$). We note that $\tilde{\sigma}_1 > 0$ for $\lambda < E_1(\gamma)$ (see Lemma 3.1). Let $Z_2 := m_2\tilde{\phi}_1$ and $l(s) = (\tilde{\sigma}_1+\lambda)s - \lambda f(s)$. Since $f(0) = 0$ and $f'(0) = 1$, we have $l(0) = 0$ and $l'(0) = (\tilde{\sigma}_1+\lambda) - \lambda f'(0) = \tilde{\sigma}_1 > 0$ giving that $l(s) > 0$ for $s \approx 0$. This implies that

$$-\Delta Z_2 = m_2(\lambda+\tilde{\sigma}_1)\tilde{\phi}_1 > \lambda f(m_2\tilde{\phi}_1) = \lambda f(Z_2);\ \Omega$$

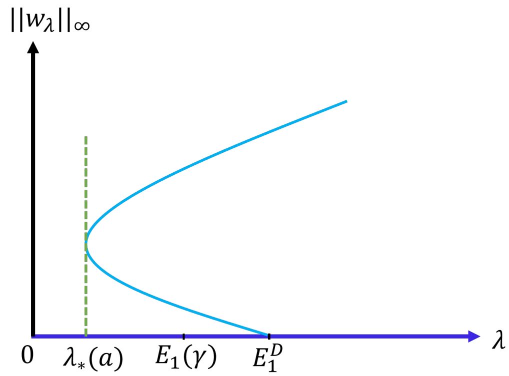


FIGURE 7. Representation of $\lambda_*(a), E_1(\gamma)$, and E_1^D on a prototypical bifurcation diagram for (3).

and

$$\begin{aligned}\frac{\partial Z_2}{\partial \eta}+\gamma\sqrt{\lambda}g(Z_2)Z_2 &= m_2\Big(\frac{\partial \tilde{\phi}_1}{\partial \eta}+\gamma\sqrt{\lambda}g(m_2\tilde{\phi}_1)\tilde{\phi}_1\Big)\\ &= m_2\Big(-\gamma\sqrt{\lambda}\tilde{\phi}_1+\tilde{\sigma}_1\tilde{\phi}_1+\gamma\sqrt{\lambda}g(m_2\tilde{\phi}_1)\tilde{\phi}_1\Big)\\ &= m_2\tilde{\phi}_1\Big(\gamma\sqrt{\lambda}(g(m_2\tilde{\phi}_1)-1)+\tilde{\sigma}_1\Big)\\ &> 0;\ \partial\Omega\end{aligned}$$

for $m_2 \approx 0$ since $g(0) = 1$. Hence, Z_2 is a strict supersolution of (6) for $\lambda < E_1(\gamma)$ and $m_2 \approx 0$.

Construction of a small supersolution Z_3 for $\lambda > E_1(\gamma)$ and $\lambda \approx E_1(\gamma)$ when $a \geq 1$ (LTG) and $g = g_1$ (DIE) or $g = g_3$ (+DDE).

For a fixed $\lambda > 0$, recall $\tilde{\sigma}_0 = \sigma_0(1, 1, \lambda, \gamma)$ is the principal eigenvalue and $\tilde{\phi}_0 > 0; \overline{\Omega}$ is the corresponding normalized eigenfunction of (7) (here, $M = 1$ and $b = 1$). We note that $\tilde{\sigma}_0 < 0$ for $\lambda > E_1(\gamma)$ (see Lemma 3.1). Define $Z_3 := m_3\tilde{\phi}_0$, where $m_3 > 0$ is such that $m_3^2 = \frac{-\tilde{\sigma}_0}{\lambda \min_{\overline{\Omega}}\{\tilde{\phi}_0^2\}}$. We note that for $\lambda \approx E_1(\gamma)$ we can assume $m_3\phi_0 < 1$ since $\tilde{\sigma}_0 \to 0$ and $\min_{\overline{\Omega}}\left\{\tilde{\phi}_0^2\right\} \not\to 0$ when $\lambda \to E_1(\gamma)^+$. Then we have

$$\begin{aligned}-\Delta Z_3-\lambda f(Z_3) &= m_3(\lambda+\tilde{\sigma}_0)\tilde{\phi}_0-\lambda m_3\tilde{\phi}_0(1-m_3\tilde{\phi}_0)\big(1+\frac{m_3\tilde{\phi}_0}{a}\big)\\ &\geq m_3(\lambda+\tilde{\sigma}_0)\tilde{\phi}_0-\lambda m_3\tilde{\phi}_0(1-m_3\tilde{\phi}_0)\big(1+m_3\tilde{\phi}_0\big)\\ &= m_3\tilde{\phi}_0(\tilde{\sigma}_0+\lambda m_3^2\tilde{\phi}_0^2)\\ &\geq 0;\ \Omega\end{aligned}$$

since $a \geq 1$. Also, we have

$$\frac{\partial Z_3}{\partial \eta}+\gamma\sqrt{\lambda}g(Z_3)Z_3 \geq \frac{\partial Z_3}{\partial \eta}+\gamma\sqrt{\lambda}Z_3 = 0;\ \partial\Omega$$

since $g \geq 1; [0, 1]$ when $g = g_1$ (DIE) or $g = g_3$ (+DDE). This implies that Z_3 is a supersolution of (6) when $\lambda > E_1(\gamma)$. Since $\tilde{\sigma}_0 \to 0$ as $\lambda \to E_1(\gamma)^+$, $m_3 \to 0$ as

$\lambda \to E_1(\gamma)^+$ and, hence, $\|Z_3\|_\infty \to 0$ as $\lambda \to E_1(\gamma)^+$.

For convenience of the reader, we summarize construction of these subsolutions and supersolutions in Tables 1 and 2, respectively.

Name	a**-Value**	**DDE**	**Conditions**
$\psi_1 = \delta_1\tilde{\phi}_1$	$a > 0$	Any DDE	$\beta > 0$, $\lambda > E_1(\gamma)$, and $\delta_1 \approx 0$
$\psi_2 = w_\lambda$	$a > 0$	Any DDE	$\lambda > E_1^D$
$\psi_3 = \delta_3\tilde{\phi}_0$ (strict)	$a \in (0,1)$	DIE or -DDE	For fixed $\beta > 0$ & $a \in (0,1)$, $\lambda \in (\overline{\lambda}_1(a,\gamma), \infty)$ for some $\overline{\lambda}_1(a,\gamma) < E_1(\gamma)$ or for fixed $\lambda_0 \in (0, E_1(\gamma))$ and $a < \overline{a}_1(\gamma, \lambda_0)$ for some $\overline{a}_1(\gamma,\lambda_0) \in (0,1)$
$\psi_3^* = \hat{\delta}_3\hat{\phi}_0$ (strict)	$a \in (0,1)$	+DDE	For fixed $a \in (0,1)$, $\lambda \in (\overline{\lambda}_2(a,\gamma), \infty)$ and $\beta < \overline{\beta}_3(a,\gamma)$ for some $\overline{\lambda}_2(a,\gamma) < E_1(\gamma)$ and $\overline{\beta}_3(a,\gamma) > 0$ or for fixed $\beta > 0$, $\lambda \in (\overline{\lambda}_3(a,\gamma), \infty)$ and $a < \overline{a}_2(\beta,\gamma)$, for some $\overline{a}_2(\beta,\gamma) \in (0,1)$ and $\overline{\lambda}_3(a,\beta,\gamma) < E_1(\gamma)$
$\psi_4 = \delta_4\overline{\phi}_0$ (strict)	$a > 0$	-DDE	For fixed $\lambda_0 \in (0, E_1(\gamma))$, $\beta > \overline{\beta}_1(a,\gamma,\lambda_0)$ for some $\overline{\beta}_1(a,\gamma,\lambda_0) > 0$
$\psi_5 = w_\lambda$ (strict)	$a \in (0,1)$	Any DDE	For fixed $a \in (0,1)$, $\lambda \in [\lambda_*(a), E_1^D]$, and $\gamma > \overline{\gamma}_1(a)$ for some $\overline{\gamma}_1(a) > 0$

TABLE 1. Summary of subsolutions used to prove our main results.

Name	a**-Value**	**DDE**	**Conditions**
$Z_1 \equiv 1$ (global)	$a > 0$	Any DDE	$\lambda > 0$
$Z_2 = m_2\tilde{\phi}_1$ (strict)	$a > 0$	Any DDE	$\lambda < E_1(\gamma)$ and $m_2 \approx 0$
$Z_3 = m_3\tilde{\phi}_0$	$a \geq 1$	DIE or +DDE	For $\lambda > E_1(\gamma)$ and $\lambda \approx E_1(\gamma)$ $m_3 = \frac{-\tilde{\sigma}_0}{\lambda \min_{\overline{\Omega}}\{\tilde{\phi}_0^2\}}$

TABLE 2. Summary of supersolutions used to prove our main results.

4. **Proofs of Theorems 1.1 - 1.7.** We provide proofs our main results in this section. We note that by Lemma 3.1 if $\lambda < E_1(\gamma)$ then $\tilde{\sigma_0}, \tilde{\sigma_1} > 0$ which implies that the trivial solution of (6) is asymptotically stable (see [19]). By Lemma 2.3, it suffices to show existence of at least one positive solution for a given $\lambda < E_1(\gamma)$ to ensure a PAE occurs for a patch with size corresponding to λ.

Proof of Theorem 1.1:
(a) Let $g = g_1$ (DIE), $g = g_2$ (-DDE), or $g = g_3$ (+DDE).
(a)(i) We prove here non-existence of a positive solution for $\lambda \leq \overline{E}_1(M_0, \underline{g}, \gamma)$.
Let $M_0 = M_0(a) \geq 1$ be such that $f(s) < M_0 s$ for all $s \in (0,1)$, $\overline{E}_1(M_0, \underline{g}, \gamma)$ be the principal eigenvalue of (2), and $\sigma_0(M_0, \underline{g}, \lambda, \gamma)$ be the principal eigenvalue and $\phi_0 > 0; \overline{\Omega}$ be the corresponding normalized eigenfunction of (7). Recall, $\underline{g} = \min_{s\in[0,1]} \{g(s)\}$.
We note that $\overline{E}_1(M_0, \underline{g}, \gamma) \leq E_1(\gamma)$ and $\sigma_0(M_0, \underline{g}, \lambda, \gamma) \geq 0$ when $\lambda \leq \overline{E}_1(M_0, \underline{g}, \gamma)$ (see Lemma 3.1). Suppose u_λ is a positive solution of (6) for $\lambda \leq \overline{E}_1(M_0, \underline{g}, \gamma)$. Then by Green's Second Identity we have:

$$\begin{aligned}
\int_\Omega \Big(\phi_0 \Delta u_\lambda - u_\lambda \Delta \phi_0\Big) dx &= \int_{\partial\Omega} \Big(\phi_0 \frac{\partial u_\lambda}{\partial \eta} - u_\lambda \frac{\partial \phi_0}{\partial \eta}\Big) ds \\
&= \int_{\partial\Omega} \Big(-\phi_0 \gamma \sqrt{\lambda} g(u_\lambda) u_\lambda + \gamma u_\lambda \sqrt{\lambda} \underline{g} \phi_0\Big) ds \\
&= \int_{\partial\Omega} \gamma \phi_0 u_\lambda \sqrt{\lambda} \Big(\underline{g} - g(u_\lambda)\Big) ds \\
&\leq 0.
\end{aligned}$$

On the other hand, we have

$$\begin{aligned}
\int_\Omega \Big(\phi_0 \Delta u_\lambda - u_\lambda \Delta \phi_0\Big) dx &= \int_\Omega \Big(-\phi_0 \lambda f(u_\lambda) + (M_0 \lambda + \sigma_0(M_0, \underline{g}, \lambda, \gamma)) u_\lambda \phi_0\Big) dx \\
&> \int_\Omega \Big(-\phi_0 \lambda M_0 u_\lambda + (M_0 \lambda + \sigma_0(M_0, \underline{g}, \lambda, \gamma)) u_\lambda \phi_0\Big) dx \\
&= \int_\Omega \sigma_0(M_0, \underline{g}, \lambda, \gamma) \phi_0 u_\lambda dx \\
&\geq 0
\end{aligned}$$

since $f(u_\lambda) < M_0 u_\lambda; u_\lambda \in (0,1)$ and $\sigma_0(M_0, \underline{g}, \lambda, \gamma) \geq 0$ for $\lambda \leq \overline{E}_1(M_0, \underline{g}, \gamma)$. This is a contradiction. Thus, (6) has no positive solution for $\lambda \leq \overline{E}_1(M_0, \underline{g}, \gamma)$.

(a)(ii) Here, we prove existence of a positive solution, u_λ, for $\lambda > E_1(\gamma)$ such that $\|u_\lambda\|_\infty \to 1$ as $\lambda \to \infty$.
Recall the subsolution $\psi_1 = \delta_1 \tilde{\phi}_1$ for $\lambda > E_1(\gamma)$ and the supersolution $Z_1 \equiv 1$. Since $\psi_1 < Z_1$, by Lemma 2.1 it follows that (6) has a positive solution in $[\psi_1, Z_1]$ for $\lambda > E_1(\gamma)$. Also, recall the subsolution $\psi_2 = w_\lambda < 1; \overline{\Omega}$ for $\lambda > E_1^D$. Then by Lemma 2.1 it follows that (6) has a positive solution in $[\psi_2, Z_1]$ for $\lambda > E_1^D$. This implies that (6) has a positive solution u_λ for $\lambda > E_1(\gamma)$ such that $\|u_\lambda\|_\infty \longrightarrow 1$ as $\lambda \longrightarrow \infty$ since $\|\psi_2\|_\infty \longrightarrow 1$ as $\lambda \longrightarrow \infty$.

(b) When $a \geq 1$ and $g = g_1$ (DIE) or $g = g_3$ (+DDE), we prove that (6) has a unique positive solution, u_λ, for $\lambda > E_1(\gamma)$ such that $\|u_\lambda\|_\infty \to 0$ as $\lambda \to E_1(\gamma)^+, \|u_\lambda\|_\infty \to 1$ as $\lambda \to \infty$, and has no positive solution for $\lambda \leq E_1(\gamma)$.
First, we establish uniqueness. Suppose that (6) has two distinct positive solutions, u_1, u_2, for $\lambda > E_1(\gamma)$. Since $Z_1 \equiv 1$ is a global supersolution, it follows that (6) has a maximal solution. Without loss of generality suppose $u_2 > u_1$. Then by Green's Second Identity we have

$$\int_\Omega (\Delta u_1 u_2 - \Delta u_2 u_1) dx = \int_{\partial\Omega} \Big(\frac{\partial u_1}{\partial \eta} u_2 - \frac{\partial u_2}{\partial \eta} u_1\Big) ds$$

$$
\begin{aligned}
&= \int_{\partial\Omega} \Big(-\gamma\sqrt{\lambda} g(u_1) u_1 u_2 + \gamma\sqrt{\lambda} g(u_2) u_2 u_1 \Big) ds \\
&= \int_{\partial\Omega} \gamma\sqrt{\lambda} u_1 u_2 \Big(g(u_2) - g(u_1) \Big) ds \\
&\geq 0,
\end{aligned}
$$

since g is non-decreasing and $u_2 > u_1$. We note that $\frac{f(s)}{s}$ is decreasing for $a \geq 1$, giving that

$$
\begin{aligned}
\int_{\Omega} (\Delta u_1 u_2 - \Delta u_2 u_1) dx &= \int_{\Omega} \Bigg(-\lambda f(u_1) u_2 + \lambda f(u_2) u_1 \Bigg) ds \\
&= \int_{\Omega} \lambda u_1 u_2 \Bigg(\frac{f(u_2)}{u_2} - \frac{f(u_1)}{u_1} \Bigg) ds \\
&< 0
\end{aligned}
$$

since $u_2 > u_1$. This is a contradiction. Hence, (6) has at most one positive solution for $\lambda > E_1(\gamma)$.

Next, we note that existence of a positive solution u_λ for $\lambda > E_1(\gamma)$ such that $\|u_\lambda\|_\infty \to 1$ as $\lambda \to \infty$ follows from the proof in $(a)(ii)$. Now, we prove that $\|u_\lambda\|_\infty \to 0$ as $\lambda \to E_1(\gamma)^+$. Recall the subsolution $\psi_1 = \delta_1 \tilde{\phi}_1$ and supersolution $Z_3 = m_3 \tilde{\phi}_0$ and choose δ_1 small enough such that $\psi_1 \leq Z_3$. Then, by Lemma 2.1, (6) has a positive solution $v_\lambda \in [\psi_1, Z_3]$ such that $\|v_\lambda\|_\infty \to 0$ as $\lambda \to E_1(\gamma)^+$ since $\|Z_3\|_\infty \to 0$ as $\lambda \to E_1(\gamma)^+$. But, uniqueness of positive solutions of (6) proved above implies that $v_\lambda \equiv u_\lambda$. Hence, we have $\|u_\lambda\|_\infty \to 0$ as $\lambda \to E_1(\gamma)^+$. Finally, non-existence for $\lambda \leq E_1(\gamma)$ follows from the non-existence proof in $(a)(i)$ by setting $M_0 = 1$ and $\underline{g} = 1$.

(c) Let $a \in (0,1)$ (WAG) and $g = g_1$ (DIE) or $g = g_2$ (-DDE). Here, we prove that (6) has at least one positive solution for $\lambda > \overline{\lambda}_1(a,\gamma)$, a PAE occurs for $\lambda \in (\overline{\lambda}_1(a,\gamma), E_1(\gamma))$, and $\overline{\lambda}_1(a,\gamma)$ has the specified properties, where $\overline{\lambda}_1(a,\gamma)$ is as in the construction of the subsolution ψ_3.
First, we note that $\psi_0 \equiv 0$ is a solution and hence a subsolution of (6) for $\lambda > 0$. Recall the strict subsolution $\psi_3 = \delta_3 \tilde{\phi}_0 \leq 1; \overline{\Omega}$ for $\lambda \in \big(\overline{\lambda}(a,\gamma), \infty\big)$, strict supersolution $Z_2 = m_2 \tilde{\phi}_1 \leq 1; \overline{\Omega}$ (with $m_2 \approx 0$) for $\lambda < E_1(\gamma)$, and supersolution $Z_1 \equiv 1$ for $\lambda > 0$. We can choose m_2 small enough such that $\psi_3 \not\leq Z_2$. By Lemma 2.2, (6) has at least two positive solutions, $u_1 \in [\psi_3, Z_1]$ and $u_2 \in [\psi_0, Z_1] \backslash ([\psi_0, Z_2] \cup [\psi_3, Z_1])$, for $\lambda \in \big(\overline{\lambda}(a,\gamma), E_1(\gamma)\big)$. Since $\psi_0 \equiv 0$ is a solution, Lemma 2.2 can only guarantee existence of at least two positive solutions for (6). Hence, there is a PAE for $\lambda \in \big(\overline{\lambda}(a,\gamma), E_1(\gamma)\big)$. The specified properties of $\overline{\lambda}_1(a,\gamma)$ follow from the construction of ψ_3.
Secondly, recall the strict subsolutions ψ_3 for $\lambda \in \big(\overline{\lambda}_1(a,\gamma), \infty\big)$ and the global supersolution $Z_1 \equiv 1$ for all $\lambda > 0$. Thus, (6) has at least one positive solution for $\lambda \in \big(\overline{\lambda}(a,\gamma), \infty\big)$ by Lemma 2.1.

Proof of Theorem 1.3: The proof is similar to (c) and is thus omitted. □

Proof of Theorem 1.6:
Let $g = g_2$ (-DDE) and $\lambda_0 < E_1(\gamma)$.
(a) Here, we show here that for $a > 0$ there exists a $\overline{\beta}_1(a,\gamma,\lambda_0) > 0$ such that (6) has a PAE for $\lambda \in \big[\lambda_0, E_1(\gamma)\big)$ when $\beta > \overline{\beta}_1(a,\gamma,\lambda_0)$ and $\overline{\beta}_1(a,\gamma,\lambda_0)$ has the prescribed properties.

We note that $\psi_0 \equiv 0$ is a solution and hence a subsolution of (6). Recall the strict subsolution $\psi_4 = \delta_4\overline{\phi}_0 \leq 1; \overline{\Omega}$ for $\lambda \in [\lambda_0, E_1(\gamma)]$ when $\beta > \overline{\beta}_1(a,\gamma,\lambda_0)$, strict supersolution $Z_2 = m_2\tilde{\phi}_1 \leq 1; \overline{\Omega}$ (with $m_2 \approx 0$) for $\lambda < E_1(\gamma)$, and supersolution $Z_1 \equiv 1$ for $\lambda > 0$. We can also choose m_2 small enough such that $\psi_4 \not\leq Z_2$. By Lemma 2.2, (6) has at least two positive solutions, $u_1 \in [\psi_4, Z_1]$ and $u_2 \in [\psi_0, Z_1]\backslash([\psi_0, Z_2] \cup [\psi_4, Z_1])$, for $\lambda \in \big[\lambda_0, E_1(\gamma)\big)$. Since $\psi_0 \equiv 0$ is a solution, Lemma 2.2 can only guarantee existence of at least two positive solutions. Hence, there is a PAE for $\lambda \in \big[\lambda_0, E_1(\gamma)\big)$. Moreover, the prescribed properties of $\overline{\beta}_1(a,\gamma,\lambda_0)$ follow from the construction of ψ_4.

(b) We now show that if $a \geq 1$ (LTG) then there exists a $\overline{\beta}_2(\gamma,\lambda_0) > 0$ such that (6) has no positive solution for $\lambda \leq \lambda_0$ when $\beta \leq \overline{\beta}_2(\gamma,\lambda_0)$.
Choose $b_0 \in (0,1)$ in (7) such that $\lambda_0 = \overline{E}_1(1, b_0, \gamma)$ (see Lemma 3.1). For a given $\lambda \leq \lambda_0$, recall that $\overline{\sigma}_0 = \sigma_0(1, b_0, \lambda, \gamma)$ is the principal eigenvalue and $\overline{\phi}_0 > 0; \overline{\Omega}$ is the corresponding normalized eigenfunction of (7). We note that $\overline{\sigma}_0 \geq 0$ for $\lambda \leq \lambda_0$. (see Lemma 3.1). Now, suppose that (6) has a positive solution, u_λ, for $\lambda \leq \lambda_0$. Then we have $1 + \beta u_\lambda < 1 + \beta; \partial\Omega$. This implies that

$$b_0 - \frac{1}{1+\beta u_\lambda} < b_0 - \frac{1}{1+\beta};\ \partial\Omega.$$

Let $\overline{\beta}_2 := \overline{\beta}_2(\gamma,\lambda_0)$ be such that $b_0 - \frac{1}{1+\overline{\beta}_2(\gamma,\lambda_0}=0$ which implies $\overline{\beta}_2(\gamma,\lambda_0) = \frac{1-b_0}{b_0}$. Since $b_0 < 1$, we have that $\overline{\beta}_2(\gamma,\lambda_0) > 0$. Note that $b_0 - \frac{1}{1+\beta} \leq 0$ for $\beta \leq \overline{\beta}_2(\gamma,\lambda_0)$. Then by Green's Second Identity we have

$$\begin{aligned}
\int_\Omega \Big(\Delta u_\lambda \overline{\phi}_0 - u_\lambda \Delta\overline{\phi}_0\Big)dx &= \int_{\partial\Omega} \Big(\frac{\partial u_\lambda}{\partial\eta}\overline{\phi}_0 - \frac{\partial\overline{\phi}}{\partial\eta}u_\lambda\Big)ds \\
&= \int_{\partial\Omega} \Big(-\gamma\sqrt{\lambda}g(u_\lambda)u_\lambda\overline{\phi}_0 + \gamma\sqrt{\lambda}b_0\overline{\phi}_0 u_\lambda\Big)ds \\
&= \int_{\partial\Omega} \gamma\sqrt{\lambda}u_\lambda\overline{\phi}_0\Big(b_0 - g(u_\lambda)\Big)ds \\
&= \int_{\partial\Omega} \gamma\sqrt{\lambda}u_\lambda\overline{\phi}_0\Big(b_0 - \frac{1}{1+\beta u_\lambda}\Big)ds \\
&< \int_{\partial\Omega} \gamma\sqrt{\lambda}u_\lambda\overline{\phi}_0\Big(b_0 - \frac{1}{1+\beta}\Big)ds \\
&\leq 0
\end{aligned}$$

for $\beta \leq \overline{\beta}_2(\gamma,\lambda_0)$.
On the other hand, noting that $1 + \frac{u_\lambda}{a} \leq 1 + u_\lambda; \Omega$ for $a \geq 1$, we have

$$\int_\Omega \Big(\Delta u_\lambda \overline{\phi}_0 - u_\lambda \Delta\overline{\phi}_0\Big)dx = \int_\Omega \Big(-\overline{\phi}_0\lambda u_\lambda(1-u_\lambda)(1+\frac{u_\lambda}{a}) + (\lambda+\overline{\sigma}_0)\overline{\phi}_0 u_\lambda\Big)dx$$

$$\begin{aligned} &\geq \int_\Omega \Big((\lambda+\overline{\sigma}_0)\overline{\phi}_0 u_\lambda - \overline{\phi}_0 \lambda u_\lambda (1-u_\lambda)(1+u_\lambda)\Big) dx \\ &= \int_\Omega \overline{\phi}_0 u_\lambda \Big(\lambda + \overline{\sigma}_0 - \lambda + \lambda u_\lambda^2 \Big) dx \\ &= \int_\Omega \overline{\phi}_0 u_\lambda \Big(\overline{\sigma}_0 + \lambda u_\lambda^2 \Big) dx \\ &> 0 \end{aligned}$$

since $\overline{\sigma}_0 \geq 0$ for $\lambda \leq \lambda_0$. This is a contradiction. Hence, when $\beta \leq \overline{\beta}_2(\gamma, \lambda_0)$ (6) has no positive solution for $\lambda \leq \lambda_0$. □

Proof of Theorem 1.7:
Let $a \in (0,1)$ (WAG) and $\lambda_*(a)$ be as in the discussion of positive solutions of (3).
(a) Let $g = g_1$ (DIE), $g = g_2$ (-DDE), or $g = g_3$ (+DDE) and $\lambda \in [\lambda_*(a), E_1(\gamma))$. Recall the strict subsolution $\psi_5 = w_\lambda < 1; \overline{\Omega}$ for $\lambda \in [\lambda_*(a), E_1(\gamma))$ when $\gamma > \overline{\gamma}(a)$, supersolution $Z_1 \equiv 1$ for $\lambda > 0$, and strict supersolution $Z_2 = m_2\tilde{\phi}_1 \leq 1; \overline{\Omega}$ (with $m_2 \approx 0$) for $\lambda < E_1(\gamma)$. We note that $\psi_0 \equiv 0$ is a solution and hence a subsolution of (6) and that $\|\psi_5\|_\infty < 1 = Z_1$. We can also choose m_2 small enough such that $\psi_5 \not\leq Z_2$. By Lemma 2.2, (6) has at least two positive solutions, $u_1 \in [\psi_5, Z_1]$, and $u_2 \in [\psi_0, Z_1] \backslash ([\psi_0, Z_2] \cup [\psi_5, Z_1])$, for $\lambda \in [\lambda_*(a), E_1(\gamma))$. Since $\psi_0 \equiv 0$ is a solution, Lemma 2.2 can only guarantee existence of at least two positive solutions for (6). Hence, there is a PAE for $\lambda \in [\lambda_*(a), E_1(\gamma))$ when $\gamma > \overline{\gamma}_1(a)$. The prescribed properties of $\lambda_*(a)$ follow from the construction of ψ_5.
(b) This proof is similar to that of Theorem 1.1 (c)(i) & (ii) using the subsolution ψ_3^* instead of ψ_3, and is thus omitted. □

5. **Computational results when $\Omega = (0,1)$.** We note that in the one-dimensional case with $\Omega = (0,1)$, (6) reduces to

$$\begin{cases} -u'' = \lambda f(u); \ (0,1) \\ -u'(0) + \gamma\sqrt{\lambda} g(u(0))u(0) = 0 \\ u'(1) + \gamma\sqrt{\lambda} g(u(1))u(1) = 0. \end{cases} \tag{16}$$

In this case, we note that the positive solutions of (16) can be completely analyzed by the quadrature method. Since $h(s) = g(s)s$ is increasing for all $s > 0$, it follows that the solutions are symmetric about $x = \frac{1}{2}$ with $u(0) = u(1)$ and $\|u\|_\infty = \rho$ (see [11]). Namely, positive solutions of (16) take the shape as illustrated in Figure 8. Further, the exact bifurcation diagrams for positive solutions to (16) are described by the equations (see [11]):

$$\lambda = 2\Big(\int_{q(\rho)}^{\rho} \frac{ds}{\sqrt{F(\rho) - F(s)}} \Big)^2 \tag{17}$$

and

$$2[F(\rho) - F(q)] = \gamma^2 q^2 (g(q))^2 \tag{18}$$

where, $\rho = u(\frac{1}{2})$, $q = u(0) = u(1)$, and $F(s) = \int_0^s f(t)dt$.

In what follows, we provide some bifurcation diagrams obtained via Mathematica computations of (17)-(18) for the cases DIE, -DDE, and +DDE.

Figure 9 shows an evolution of bifurcation curves as a and γ vary in the case of DIE. When $a \in (0,1)$, the bifurcation curves reveal a PAE. There is no PAE for

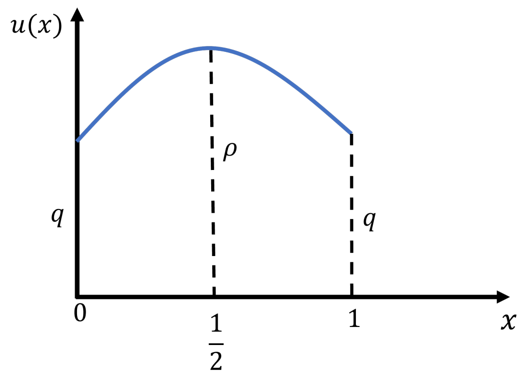
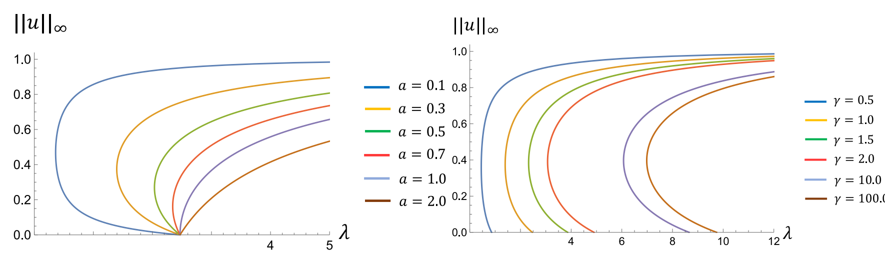


FIGURE 8. A prototypical shape of a positive solution of (16), where $\rho = \|u\|_\infty$ and $q = u(0) = u(1)$.

$a \geq 1$. Further, as a increases the PAE region length decreases and is equal to zero for $a \geq 1$ (see Figure 9(a). In Figure 9(b), we observe that as γ increases the PAE region length and $E_1(\gamma)$ increase.



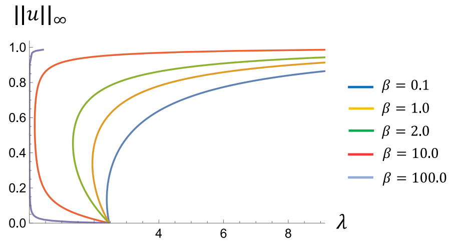
(A) Exact bifurcation curves for various $a > 0$ when $\gamma = 1$.

(B) Exact bifurcation curves for various $\gamma > 0$ when $a = 0.3$.

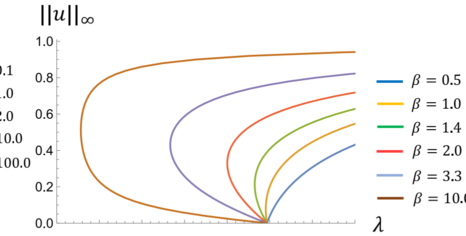
FIGURE 9. Exact bifurcation diagrams for (16) when $g(s) = g_1(s) \equiv 1$ as a and γ vary.

Figure 10 shows an evolution of bifurcation curves as β varies in the case of -DDE. We observe that the PAE region length increases as β increases indicating that when strength of the -DDE relationship (i.e., β) increases, a PAE occurs over a wider range of patch sizes. The PAE always persists for all $\beta > 0$ when $a \in (0, 1)$ (see Figure 10(a)). Figure 10(b) shows that, when $a \geq 1$, PAE is present only for large β. We observe that the PAE region length increases as β increases, and no PAE is present when $\beta \approx 0$.

Figure 11 shows an evolution of bifurcation curves as β varies in the case of +DDE. We observe that PAE region length decreases as β increases. When $a \in (0, 1)$ (see Figure 11(a)), bifurcation curves show that PAE is present for $\beta \approx 0$ and PAE disappears for larger β. Figure 11(b) shows that when $a \geq 1$ and $\beta > 0$, (16) has no positive solution for $\lambda \leq E_1(\gamma)$ and a unique positive solution for $\lambda > E_1(\gamma)$.

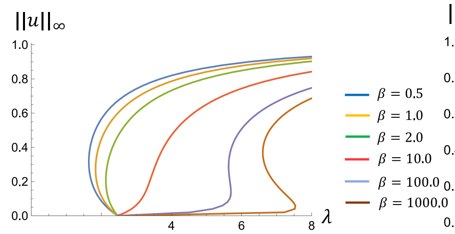


(A) Exact bifurcation curves for various β-values when $a = 0.8$, and $\gamma = 1$.

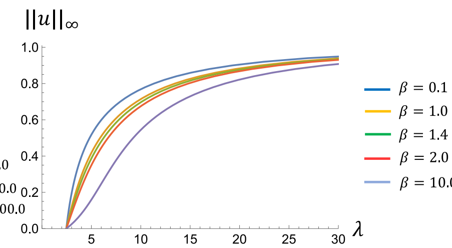


(B) Exact bifurcation curves for various β-values when $a = 2$, and $\gamma = 1$.

FIGURE 10. Exact bifurcation curves when $a = 0.8$ and $a = 2$ with varying $\beta > 0$ when $g(s) = g_2(s) = \frac{1}{1+\beta s}$ and $\gamma = 1$.



(A) Exact bifurcation curves for different $\beta > 0$ when $a = 0.3$ and $\gamma = 1$.



(B) Exact bifurcation curves for different $\beta > 0$ when $a = 2$ and $\gamma = 1$.

FIGURE 11. Exact bifurcation curves when $a = 0.3$ and $a = 2$ with varying $\beta > 0$ when $g(s) = g_3(s) = 1 + \beta s$ and $\gamma = 1$.

Acknowledgments. We would like to thank the anonymous reviewers for their helpful comments which greatly improved the manuscript.

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Received March 2023; revised July 2023; early access August 2023.