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The diffusive Lotka–Volterra competition model in fragmented patches I: Coexistence☆

A. Acharya[a], S. Bandyopadhyay[a], J.T. Cronin[b], J. Goddard II[c,*], A. Muthunayake[d], R. Shivaji[a]

[a] Department of Mathematics and Statistics, University of North Carolina at Greensboro, Greensboro, NC 27412, USA
[b] Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA
[c] Department of Mathematics, Auburn University Montgomery, Montgomery, AL, 36124, USA
[d] Department of Mathematics, University of Miami, Coral Gables, FL 33146, USA

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ABSTRACT

It is an ecological imperative that we understand how changes in landscape heterogeneity affect population dynamics and coexistence among species residing in increasingly fragmented landscapes. Decades of research have shown the dispersal process to have major implications for individual fitness, species' distributions, interactions with other species, population dynamics, and stability. Although theoretical models have played a crucial role in predicting population level effects of dispersal, these models have largely ignored the conditional dependency of dispersal (e.g., responses to patch boundaries, matrix hostility, competitors, and predators). This work is the first in a series where we explore dynamics of the diffusive Lotka–Volterra (L–V) competition model in such a fragmented landscape. This model has been extensively studied in isolated patches, and to a lesser extent, in patches surrounded by an immediately hostile matrix. However, little attention has been focused on studying the model in a more realistic setting considering organismal behavior at the patch/matrix interface. Here, we provide a mechanistic connection between the model and its biological underpinnings and study its dynamics via exploration of nonexistence, existence, and uniqueness of the model's steady states. We employ several tools from nonlinear analysis, including sub-supersolutions, certain eigenvalue problems, and a numerical shooting method. In the case of weak, neutral, and strong competition, our results mostly match those of the isolated patch or immediately hostile matrix cases. However, in the case where competition is weak towards one species and strong towards the other, we find existence of a maximum patch size, and thus an intermediate range of patch sizes where coexistence is possible, in a patch surrounded by an intermediate hostile matrix when the weaker competitor has a dispersal advantage. These results support what ecologists have long theorized, i.e., a key mechanism

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* Corresponding author.
E-mail addresses: a_achary@uncg.edu (A. Acharya), s_bandyo@uncg.edu (S. Bandyopadhyay), jcronin@lsu.edu (J.T. Cronin), jgoddard@aum.edu (J. Goddard II), a.muthunayake@miami.edu (A. Muthunayake), r_shivaj@uncg.edu (R. Shivaji).

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promoting coexistence among competing species is a tradeoff between dispersal and competitive ability.

1. Introduction

1.1. Background and motivation

As a result of human activities, the landscapes within which species live have become increasingly more heterogeneous—suitable habitats are becoming fewer in number, smaller in size and more isolated. Compounding the problem, the matrix surrounding these habitat patches is becoming much more hostile (e.g., through urbanization or agricultural development) with elevated risks of mortality for those individuals who attempt to emigrate from a patch [1–3]. It is an ecological imperative that we understand how changes in landscape heterogeneity affect population dynamics and coexistence among species residing in these landscapes. Through decades of ecological research, it is clear that the dispersal process has major implications for individual fitness, species' distributions, interactions with other species, population dynamics and stability (e.g., [4–8]). In particular, theoretical studies have played an extremely important role in predicting population level effects of dispersal [9]. However, models have largely ignored the conditional dependency of dispersal; for example, the effects of an interspecific competitor or predator on dispersal (but see e.g., [10–12]). Theoretical studies of competing species in fragmented habitats typically model dispersal as a regional constant (e.g., [13]). This approach neglects realistic aspects of dispersal behavior that may affect the regional persistence of the competitors. These behaviors include the relationship between conspecific density and emigration, responses to boundary conditions and matrix hostility [10,12,14–17]. It has been hypothesized that intraspecific and interspecific competition may influence dispersal of a species differently [11,18,19], although this has rarely been tested experimentally [11]. Clearly, both theoretical and empirical investigations are needed that account for realistic aspects of animal movement behavior and interactions with other species to understand the effects of landscape heterogeneity on species population dynamics and coexistence.

Here, we explore dynamics of the diffusive Lotka–Volterra (L–V) competition model in a fragmented landscape, see Fig. 1. The model is built upon the reaction diffusion framework and includes a boundary condition designed to model effects of differential matrix hostility and behavior response to habitat edges between species. In the literature, the diffusive L–V competition model has been extensively studied in the case of a closed patch (reflecting boundary) and to a somewhat lesser degree in the case of an immediately lethal matrix (absorbing boundary). However, little attention has been paid to the diffusive L–V competition model in fragmented landscapes with a framework that allows for more realistic modeling of organismal behavior at the patch/matrix interface. To date, we have not found any work which considers long term behavior under combined effects of changes in matrix hostility and patch size (but see [20] &[21] where reversal of competitive dominance was studied as matrix hostility varied for fixed patch geometry). This paper is the first in a series of works exploring the dynamics of the diffusive L–V competition model in fragmented landscapes and focuses on the relationship between patch size and matrix hostility and coexistence. In an upcoming paper, we will explore how competitive dominance changes as patch size and matrix hostility vary. We note that results in the present work are in the spirit of those from [22] who studied the diffusive L–V competition model with reflecting boundary (Neumann boundary condition) and [23] who considered an absorbing boundary (Dirichlet boundary condition). The authors of those works did not explicitly consider structure of coexistence states as patch size or matrix hostility varied.

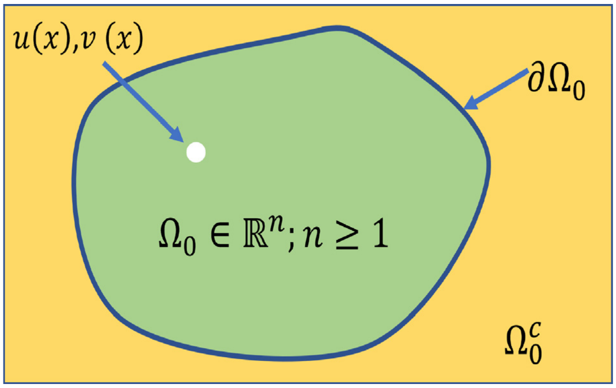


Fig. 1. Illustration of a fragmented habitat patch Ω_0 and surrounding exterior matrix Ω_0^c.

1.2. Model formulation

We present and study the diffusive Lotka–Volterra two species competition model coupled with boundary conditions which will allow study of the effects of habitat fragmentation on the system. The model is built upon the reaction diffusion framework which has seen tremendous success in studying spatially structured systems in the literature, see [24–30] and references therein for a detailed history of the framework. We assume that two species are dwelling in a single focal patch $\Omega_0 = \{\ell x \mid x \in \Omega\}$ with patch size $\ell > 0$ and $\Omega = (0,1)$ or $\Omega \subset \mathbb{R}^n$ having unit measure (e.g. if $n = 2$ then the area of Ω is one) and smooth boundary with $n = 2, 3$, that is surrounded by a hostile matrix, denoted by $\Omega_0^c = \mathbb{R}^n \setminus \overline{\Omega}_0$, where it is assumed that organisms experience exponential decay at fixed rate, say, $S_0 > 0$ (see Fig. 1). Denote the boundary of Ω_0 by $\partial\Omega_0$. The variable t represents time and x represents spatial location within the patch. The two organisms follow an unbiased random walk inside both patch and matrix, while on the patch/matrix interface a discontinuity between the density in the patch and matrix is allowed at the interface (via a biased random walk), while maintaining continuity in the flux (see e.g. [15,31,32]).

Here, organisms recognize the patch/matrix interface and modify their random walk movement probability (i.e. probability of an organism moving at a given time step in the random walk process), random walk step length (i.e. distance that an organism moves during a given time step), and/or probability of remaining in the patch (say α). In this patch-level setting, we equate dispersal from the patch to organisms reaching the patch/matrix interface, leaving the patch with probability $1-\alpha$ (taken to be constant), and entering the matrix, where they still have the opportunity to re-enter the patch at the interface. Following the derivation given in [33], the diffusive competitive Lotka–Volterra system becomes:

$$\begin{cases} u_t = D_1 \Delta u + r_1 u(1 - \frac{u}{K_1} - \frac{a_1}{K_1} v); & t > 0, x \in \Omega_0 \\ v_t = D_2 \Delta v + r_2 v(1 - \frac{v}{K_2} - \frac{a_2}{K_2} u); & t > 0, x \in \Omega_0 \\ u(0,x) = u_0(x); & x \in \Omega_0 \\ v(0,x) = v_0(x); & x \in \Omega_0 \\ D_1 \alpha_1 \frac{\partial u}{\partial \eta} + S_1^* \left[1 - \alpha_1\right] u = 0; & t > 0, x \in \partial\Omega_0 \\ D_2 \alpha_2 \frac{\partial v}{\partial \eta} + S_2^* \left[1 - \alpha_2\right] v = 0; & t > 0, x \in \partial\Omega_0 \end{cases} \tag{1}$$

and will exactly model the study system in the case of a one-dimensional patch in the sense that steady states of (1) and their stability properties will be exactly the same as those of the study system (see [33] and references therein). In the case of a simply connected, convex patch in two- or three-dimensions, the model will provide a reasonable approximation of the study system.

In this model, $D_i > 0$ represents patch diffusion rate, $r_i > 0$ patch intrinsic growth rate, $K_i > 0$ patch carrying capacity, $a_i \geq 0$ scale of competitive effect from the other competitor, $u_0(x), v_0(x)$ initial population density distributions in the patch, and α_i the probability of an individual remaining in the patch upon reaching the boundary ($i = 1$ for u and $i = 2$ for v). The term $\frac{\partial}{\partial \eta}$ denotes the outward normal derivative operator. From the derivation in [33], the nonnegative parameter $S_i = \frac{\sqrt{S_i^0 D_i^0}}{\kappa}$ represents the effective matrix hostility towards an organism and has units of length by time. The parameter $S_i^0 \geq 0$ represents matrix death rate, $D_i^0 > 0$ represents matrix diffusion rate, and κ encapsulates patch/matrix interface assumptions (see Table 1 in [33]), is independent of S_i^0, and may depend on D_i^0. For example, if a Type II Discontinuous Density is assumed at the interface then $S_i^* = \frac{\sqrt{S_i^0 D_i}}{\sqrt{D_i^0}}$ and is a strictly increasing function of matrix death rate for fixed D_i and D_i^0. The boundary is absorbing, i.e. all individuals that reach the boundary will emigrate, when $\alpha_i \equiv 0$, whereas the boundary is reflecting, i.e. the emigration rate is zero, when $\alpha_i \equiv 1$.

We now introduce a standard scaling,

$$\tilde{x} = \frac{x}{\ell}, \ \tilde{t} = r_1 t, \ \tilde{u} = \frac{u}{K_1}, \ \& \ \tilde{v} = \frac{v}{K_2}. \tag{2}$$

After applying this scaling and dropping the tilde, (1) becomes

$$\begin{cases} u_t = \frac{1}{\lambda}\Delta u + u(1 - u - b_1 v); & t > 0, x \in \Omega \\ v_t = \frac{D_0}{\lambda}\Delta v + r_0 v(1 - v - b_2 u); & t > 0, x \in \Omega \\ u(0,x) = u_0(x); & x \in \Omega \\ v(0,x) = v_0(x); & x \in \Omega \\ \frac{\partial u}{\partial \eta} + \sqrt{\lambda}\gamma_1 u = 0; & t > 0, x \in \partial\Omega \\ \frac{\partial v}{\partial \eta} + \sqrt{\lambda}\gamma_2 v = 0; & t > 0, x \in \partial\Omega \end{cases} \tag{3}$$

with corresponding steady state equation:

$$\begin{cases} -\Delta u = \lambda u(1 - u - b_1 v); \ \Omega \\ -\Delta v = \lambda r v(1 - v - b_2 u); \ \Omega \\ \frac{\partial u}{\partial \eta} + \sqrt{\lambda}\gamma_1 u = 0; \ \partial\Omega \\ \frac{\partial v}{\partial \eta} + \sqrt{\lambda}\gamma_2 v = 0; \ \partial\Omega \end{cases} \tag{4}$$

where $\lambda = \frac{r_1 \ell^2}{D_1}$, $r_0 = \frac{r_2}{r_1}$, $D_0 = \frac{D_2}{D_1}$, $r = \frac{r_0}{D_0}$, $b_i = \frac{a_i K_j}{K_i}$; $i, j = 1, 2$ and $i \neq j$, $\gamma_1 = \frac{S_1^*}{\sqrt{r_1 D_1}} \frac{1-\alpha_1}{\alpha_1}$, and $\gamma_2 = \frac{S_2^*}{\sqrt{r_1 D_1 D_0}} \frac{1-\alpha_2}{\alpha_2}$ are all unitless. Also, recall that Ω has length, area, or volume of one. Hence, for fixed r_1, r_2, D_1, D_2, the composite parameter λ is proportional to patch size squared, γ_1 is proportional to effective matrix hostility towards u, and γ_2 is proportional to effective matrix hostility towards v. The composite parameter b_i denotes scale of competitive effect of one organism onto the other, e.g., b_1 measures the competitive effect of v on u. We will consider $b_1, b_2 \in [0, 1)$ and $b_1 b_2 \neq 0$ as weak competition, $b_1 = 1 = b_2$ as neutral competition, either $0 < b_1 < 1 \leq b_2$ or $0 < b_2 < 1 \leq b_1$ as semistrong competition, and $b_1, b_2 \in [1, \infty)$ as strong competition.

In the case that $\gamma_1 = 0 = \gamma_2$, (3) becomes the classical diffusive homogeneous L–V competition model whose dynamics have been studied extensively (see, e.g., [22,34,35]). Here we recall a well known result (see, e.g., Section 12.4 in [36] and Theorems 3.6 & 4.3 in [37]) regarding coexistence for (3) in the reflecting boundary case:

Theorem 1.1 ([36,37]). *Let $r > 0$, $\gamma_1 = 0 = \gamma_2$, and $b_1, b_2 \geq 0$. Then for all $\lambda > 0$ the following hold:*

(A) If $b_1, b_2 < 1$ (weak competition) then (3) has a globally asymptotically stable coexistence state given by:

$$\left(\frac{1-b_1}{1-b_1 b_2}, \frac{1-b_2}{1-b_1 b_2}\right)$$

(B) If $b_1 < 1 \leq b_2$ or $b_2 < 1 \leq b_1$ (semistrong competition) then no coexistence state of (3) exists

(C) If $b_1 = 1 = b_2$ (neutral competition) then (3) has infinitely many asymptotically stable coexistence states of the form:

$$(c, 1-c)\,,\ c > 0$$

1.3. Single species model

Before stating our main results, we first recall the dynamics of the following single species model and discuss some important eigenvalue problems for which our coexistence results are built upon:

$$\begin{cases} W_t = \frac{1}{\lambda R}\Delta W + W(1-b-W);\ t > 0, x \in \Omega \\ W(0,x) = W_0(x);\ x \in \Omega \\ \frac{\partial W}{\partial \eta} + \sqrt{\lambda}\gamma W = 0;\ t > 0, x \in \partial\Omega \end{cases} \tag{5}$$

with corresponding steady state equation:

$$\begin{cases} -\Delta W = \lambda R W(1-b-W);\ \Omega \\ \frac{\partial W}{\partial \eta} + \sqrt{\lambda}\gamma W = 0;\ \partial\Omega \end{cases} \tag{6}$$

where $\gamma \geq 0$, W_0 is a smooth nonnegative function, and either (1) $b = 0$ with either $R = 1$ and $\gamma = \gamma_1$ or $R = r$ and $\gamma = \gamma_2$; (2) $b = b_1$, $R = 1$, and $\gamma = \gamma_1$; or (3) $b = b_2$, $R = r$, and $\gamma = \gamma_2$. From [38], the complete dynamics of (5) can be determined via the sign of the principal eigenvalue $\sigma_0 = \sigma_0(\lambda, R, b, \gamma)$ of

$$\begin{cases} -\Delta\phi_0 - \lambda R(1-b)\phi_0 = \sigma_0\phi_0;\ \Omega \\ \frac{\partial \phi_0}{\partial \eta} + \sqrt{\lambda}\gamma\phi_0 = 0;\ \partial\Omega \end{cases} \tag{7}$$

with corresponding eigenfunction ϕ_0 which can be chosen such that $\phi_0 > 0;\ \overline{\Omega}$ and $\|\phi_0\|_\infty = 1$. Also recall from [38] the eigenvalue problem,

$$\begin{cases} -\Delta\phi = R(1-b)E\phi;\ \Omega \\ \frac{\partial \phi}{\partial \eta} + \gamma\sqrt{E}\phi = 0;\ \partial\Omega. \end{cases} \tag{8}$$

For fixed $R, b,\ \&\ \gamma$, let $E_1(R, b, \gamma)$ denote the principal eigenvalue of (8) with corresponding eigenfunction ϕ which can be chosen such that $\phi > 0;\ \overline{\Omega}$. We will make the convention that $E_1(R, 0, \infty) = \frac{E_1^D}{R}$ where $E_1^D > 0$ is the principal eigenvalue of Laplace's equation with Dirichlet boundary conditions. Then from [38] we obtain:

Theorem 1.2 ([38]). *Let $R > 0$, $b \in [0, 1)$, and $\gamma \geq 0$.*

(a) If $\sigma_0 \geq 0$ $\left(\lambda \leq \frac{E_1(R,b,\gamma)}{1-b}\right)$ then $W \equiv 0$ is globally asymptotically stable and no positive solution exists for (6).

(b) If $\sigma_0 < 0$ $\left(\lambda > \frac{E_1(R,b,\gamma)}{1-b}\right)$ then $W \equiv 0$ is unstable and there exists a unique globally asymptotically stable positive solution $W_{R,\gamma,b}$ for (6). Moreover, the following properties of $W_{R,\gamma,b}$ hold:

   (i) $\frac{-\sigma(R,b,\gamma,\lambda)}{\lambda r}\phi_0 \leq W_{R,\gamma,b} \leq 1;\ x \in \overline{\Omega}$

   (ii) For fixed x and λ

      (1) $W_{R,\gamma,b}$ is increasing in R for fixed b & γ

      (2) $W_{R,\gamma,b}$ is decreasing in b for fixed R & γ

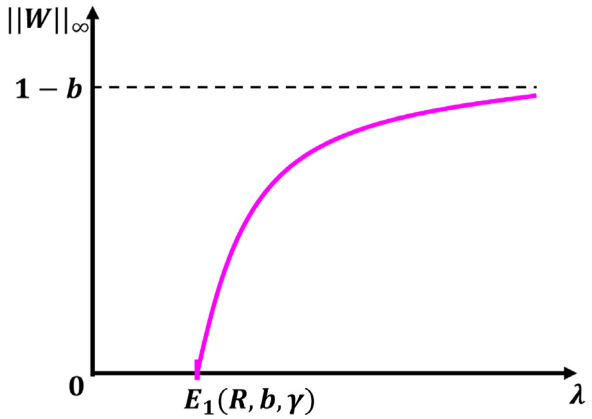


Fig. 2. Exact bifurcation diagram for positive solutions of (6).

(3) $W_{R,\gamma,b}$ *is decreasing in* γ *for fixed* R & b

(iii) $W_{R,\gamma,b} \to (1-b)$ *uniformly on every closed subset of* Ω *as* $\lambda \to \infty$.

See Fig. 2 for an exact bifurcation curve of positive solutions of (6).

Throughout the paper, we will consider either (1) $b = 0$ and define (i) $W_{1,\gamma_1} = W_{1,\gamma_1,0}$ and $E_1(1,\gamma_1) = E_1(1,0,\gamma_1)$ and (ii) $W_{r,\gamma_2} = W_{r,\gamma_2,0}$ and $E_1(r,\gamma_2) = E_1(r,0,\gamma_2)$, (2) $b = b_1$, $R = 1$, and $\gamma = \gamma_1$ and employ W_{1,γ_1,b_1} and $E_1(1,b_1,\gamma_1)$, or (3) $b = b_2$, $R = r$, and $\gamma = \gamma_2$ and employ W_{r,γ_2,b_2} and $E_1(r,b_2,\gamma_2)$.

Now, we consider the semitrivial steady states of (3) in which one population is present and the other is absent, namely:

$$\begin{cases} -\Delta W = \lambda W(1-W);\ \Omega \\ \frac{\partial W}{\partial \eta} + \sqrt{\lambda}\gamma_1\ W = 0;\ \partial\Omega \end{cases} \tag{9}$$

and

$$\begin{cases} -\Delta W = \lambda r W(1-W);\ \Omega \\ \frac{\partial W}{\partial \eta} + \sqrt{\lambda}\gamma_2 W = 0;\ \partial\Omega. \end{cases} \tag{10}$$

Hence, (9) is (6) with $R = 1$, $b = 0$, and $\gamma = \gamma_1$, represents the governing steady state equation for species u in the absence of v, and has unique positive solution $W \equiv W_{1,\gamma_1}$ whenever $\lambda > E_1(1,\gamma_1)$. Also, (10) is (6) with $R = r$, $b = 0$, and $\gamma = \gamma_2$, represents the governing steady state equation for the species v in the absence of u, and has unique positive solution $W \equiv W_{r,\gamma_2}$ whenever $\lambda > E_1(r,\gamma_2)$.

Let $\sigma_1 = \sigma_1(\lambda,\gamma_1)$ and $\sigma_2 = \sigma_2(\lambda,r,\gamma_2)$ be the principal eigenvalues of

$$\begin{cases} -\Delta\phi_1 - \lambda\phi_1 = \sigma_1\phi_1;\ \Omega \\ \frac{\partial\phi_1}{\partial\eta} + \sqrt{\lambda}\gamma_1\phi_1 = 0;\ \partial\Omega \end{cases} \tag{11}$$

and

$$\begin{cases} -\Delta\phi_2 - \lambda r\phi_2 = \sigma_2\phi_2;\ \Omega \\ \frac{\partial\phi_2}{\partial\eta} + \sqrt{\lambda}\gamma_2\phi_2 = 0;\ \partial\Omega, \end{cases} \tag{12}$$

with corresponding eigenfunctions ϕ_1, ϕ_2 which can be chosen such that $\phi_1, \phi_2 > 0;\ \overline{\Omega}$, respectively. The sign of these principal eigenvalues will determine whether or not a species can colonize the patch when rare.

Finally, we consider two eigenvalue problems involving W_{1,γ_1} and W_{r,γ_2}:

$$\begin{cases} -\Delta\phi_3 - \lambda r\left(1 - b_2 W_{1,\gamma_1}\right)\phi_3 = \sigma_3\phi_3;\ \Omega \\ \frac{\partial\phi_3}{\partial\eta} + \sqrt{\lambda}\gamma_2\phi_3 = 0;\ \partial\Omega \end{cases} \tag{13}$$

and

$$\begin{cases} -\Delta\phi_4 - \lambda\left(1 - b_1 W_{r,\gamma_2}\right)\phi_4 = \sigma_4\phi_4; \ \Omega \\ \frac{\partial\phi_4}{\partial\eta} + \sqrt{\lambda}\gamma_1\phi_4 = 0; \ \partial\Omega. \end{cases} \tag{14}$$

Let $\sigma_3 = \sigma_3(\lambda, r, \gamma_2)$, $\sigma_4 = \sigma_4(\lambda, \gamma_1)$ be the principal eigenvalues and ϕ_3, $\phi_4 > 0$; $\overline{\Omega}$ be the corresponding eigenfunctions of (13) and (14), respectively. The sign of σ_3 (σ_4) will ultimately determine if v (u) can invade the patch when rare if u (v) is near its equilibrium.

In the absence of competition (i.e., $b_1 = 0 = b_2$) the principal eigenvalues, $E_1(1, \gamma_1)$ and $E_1(r, \gamma_2)$, can be employed to determine when one species has an advantage over the other, in the sense that it has a smaller minimum patch size, allowing it to invade and colonize smaller patches than the other species. To see this, from the definition of λ we obtain the minimum patch size for u, $\ell_1^* = \sqrt{\frac{D_1 E_1(1,\gamma_1)}{r_1}}$ and for v, $\ell_2^* = \sqrt{\frac{D_1 E_1(r,\gamma_2)}{r_1}}$. Fixing r_1 and D_1, there are then three cases: (1) $E_1(1, \gamma_1) = E_1(r, \gamma_2)$ implying that $\ell_1^* = \ell_2^*$: neither species has an advantage as their minimum patch sizes are the same; (2) $E_1(1, \gamma_1) < E_1(r, \gamma_2)$ implying that $\ell_1^* < \ell_2^*$: u has an advantage being able to invade and colonize smaller patches than v; and (3) $E_1(1, \gamma_1) > E_1(r, \gamma_2)$ implying that $\ell_1^* > \ell_2^*$: v has an advantage being able to invade and colonize smaller patches than u. Crucial to this determination of advantage are the composite parameters, r, γ_1, γ_2, which encapsulate several biological mechanisms, i.e., r measures differences in the organisms in the patch and γ_1, γ_2 measure the combined effect of a hostile matrix on the respective organisms.

To see this, we first assume that the matrix affects both species the same and there is no competition, i.e., $\gamma_1 = \gamma_2$ and $b_1 = 0 = b_2$. Note that r can be written as $r = \frac{\frac{r_2}{D_2}}{\frac{r_1}{D_1}}$ and interpreted as a means to compare the two species by their patch growth-to-diffusion (G-D) ratio, defined as the ratio of patch intrinsic growth rate to patch diffusion rate. We employ Lemma 2.7(A) in Section 2 to explore the three cases: (1) if $r = 1$, then both growth to diffusion ratios are the same, $E_1(1, \gamma_1) = E_1(r, \gamma_1)$ implying that $\ell_1^* = \ell_2^*$, and neither species has a G-D advantage; (2) if $r > 1$ then v's growth to diffusion ratio is greater than u's, $E_1(1, \gamma_1) > E_1(r, \gamma_1)$ implying that $\ell_1^* > \ell_2^*$, and v has a G-D advantage in having a smaller minimum patch size; and (3) if $r < 1$ then u's ratio is greater than v's, $E_1(1, \gamma_1) < E_1(r, \gamma_1)$ implying that $\ell_1^* < \ell_2^*$, and u has a G-D advantage in having a smaller minimum patch size.

Secondly, we assume there is no overall difference in G-D ratios of the organisms and no competition, i.e., $r = 1$ and $b_1 = 0 = b_2$. The combined effect of matrix hostility and behavior response to detecting a patch edge is measured in the respective γ_i-value. For example, a large γ_1-value could indicate a high matrix mortality rate (i.e. $S_1^* \gg 1$) and/or a propensity of organisms to recognize the patch edge, bias their movement, and leave the patch with a high probability (i.e., $\alpha_1 \approx 0$). We employ Lemma 2.7(B) in Section 2 to explore the there are three cases: (1) if $\gamma_1 = \gamma_2$ then $E_1(1, \gamma_1) = E_1(1, \gamma_2)$, $\ell_1^* = \ell_2^*$, and the combined matrix effect benefits neither species over the other; (2) if $\gamma_1 > \gamma_2$ then $E_1(1, \gamma_1) > E_1(1, \gamma_2)$, $\ell_1^* > \ell_2^*$, and the combined matrix effect causes more mortality in u through interactions with the hostile matrix, and thus, gives v a smaller minimum patch size and a matrix advantage; and (3) if $\gamma_1 < \gamma_2$ then $E_1(1, \gamma_1) < E_1(1, \gamma_2)$, $\ell_1^* < \ell_2^*$, and the combined matrix effect causes more mortality in v through interactions with the hostile matrix, and thus, gives u a smaller minimum patch size and a matrix advantage. Since larger patches have a correspondingly larger core area within the patch where organisms have little chance of encountering mortality at the patch/matrix interface, any differential matrix effect acting on the system will be more pronounced for small patch sizes and diminish as the patch size goes to infinity. As we will see in the sections that follow, advantage in growth-to-diffusion ratio and combined matrix effect will play vital roles in predicting the outcome of this competition system.

1.4. Main results

In this subsection, we discuss nonexistence, existence, uniqueness, and stability of coexistence states of (3), i.e., positive solutions for (4). First, we state a result which provides sufficient conditions for nonexistence of positive solutions for (4).

Theorem 1.3 (*Nonexistence*). *For $r > 0$, $b_1, b_2 \geq 0$, and $\gamma_1, \gamma_2 \geq 0$, (4) has no positive solution if any of the following hold:*

(A) $\lambda \leq \max\{E_1(1, \gamma_1), E_1(r, \gamma_2)\}$
(B) $\gamma_1 = \gamma_2$ *and either of the following also hold:*

  (i) $b_2 \leq 1 \leq b_1$ *and* $1 \leq r \leq \frac{b_1}{b_2}$, *with at least one inequality being strict;*
  (ii) $b_1 \leq 1 \leq b_2$ *and* $\frac{b_1}{b_2} \leq r \leq 1$, *with at least one inequality being strict*

(C) $\gamma_1 > \gamma_2$, $b_2 \leq 1 \leq b_1$, *and* $1 \leq r \leq \frac{b_1}{b_2}$
(D) $\gamma_1 < \gamma_2$, $b_1 \leq 1 \leq b_2$, *and* $\frac{b_1}{b_2} \leq r \leq 1$
(E) $b_1 > 1$, $b_2 < \frac{b_1 - 1}{b_1}$, *and* $\lambda \gg 1$
(F) $b_2 > 1$, $b_1 < \frac{b_2 - 1}{b_2}$, *and* $\lambda \gg 1$
(G) $E_1(1, \gamma_1) < E_1(r, \gamma_2)$, $b_2 > 0$, *and* $\lambda < E_1(r, \gamma_2) + \delta(b_2)$, *for some* $\delta(b_2) > 0$
(H) $E_1(1, \gamma_1) > E_1(r, \gamma_2)$, $b_1 > 0$, *and* $\lambda < E_1(1, \gamma_1) + \delta(b_1)$, *for some* $\delta(b_1) > 0$.

We conjecture that the upper (lower) bounds on r in (B)(i) and (C) (respectively, (B)(ii) and (D)) and the upper bounds on b_2 in (E) and b_1 in (F) are all artificial, due to limitations in our proof method. Next, we present our main result giving sufficient conditions on coexistence of the competitors.

Theorem 1.4 (*Existence*). *Let $r^* = \frac{E_1(1,\gamma_2)}{E_1(1,\gamma_1)}$. For $r > 0$, $b_1, b_2 \geq 0$, and $\gamma_1, \gamma_2 \geq 0$ the following hold:*

(A) If $b_1, b_2 < 1$ then (4) has at least one positive solution, (u, v), for $\lambda > \max\left\{\frac{E_1(1,\gamma_1)}{1-b_1}, \frac{E_1(r,\gamma_2)}{1-b_2}\right\}$. Furthermore, every positive solution of (4), (u, v), will satisfy:

  (i) for $\lambda > \max\{E_1(1, \gamma_1), E_1(r, \gamma_2)\}$,

$$0 < u(x, \lambda) \leq W_{1,\gamma_1,0}(x, \lambda);\ \overline{\Omega},$$

$$0 < v(x, \lambda) \leq W_{r,\gamma_2,0}(x, \lambda);\ \overline{\Omega},$$

  (ii) for $\lambda > \max\left\{\frac{E_1(1,\gamma_1)}{1-b_1}, \frac{E_1(r,\gamma_2)}{1-b_2}\right\}$,

$$W_{1,\gamma_1,b_1}(x, \lambda) < u(x, \lambda) \leq W_{1,\gamma_1,0}(x, \lambda);\ \overline{\Omega},$$

$$W_{r,\gamma_2,b_2}(x, \lambda) < v(x, \lambda) \leq W_{r,\gamma_2,0}(x, \lambda);\ \overline{\Omega},$$

  (iii) if $r = 1$ and $\gamma_1 = \gamma_2$ (implying that $E_1(1, \gamma_1) = E_1(r, \gamma_2)$) then for $\lambda > E_1(1, \gamma_1)$,

$$u(x, \lambda) = \frac{1 - b_1}{1 - b_1 b_2} W_{1,\gamma_1,0}(x, \lambda);\ \overline{\Omega},$$
$$v(x, \lambda) = \frac{1 - b_2}{1 - b_1 b_2} W_{1,\gamma_1,0}(x, \lambda);\ \overline{\Omega}$$

(B) If $b_1 = b_2 = 1$, $\gamma_1 = \gamma_2$, and $r = 1$ (implying that $E_1(1, \gamma_1) = E_1(r, \gamma_2)$) then (4) has infinitely many positive solutions for $\lambda > E_1(1, \gamma_1)$, of the form:

$$(u(x, \lambda), v(x, \lambda)) = (sW_{1,\gamma_1,0}(x, \lambda), (1 - s)W_{1,\gamma_1,0}(x, \lambda))\,;\ \overline{\Omega},\ s \in (0, 1)$$

(C) If $b_1 < 1 \leq b_2$, $\gamma_1 > 0$, and $r > r^*$ (implying that $E_1(r,\gamma_2) < E_1(1,\gamma_1)$) then for $b_1 \approx 0$ there exist $\lambda_1(r,b_1,b_2,\gamma_1,\gamma_2), \lambda_2(r,b_2,\gamma_1,\gamma_2) > E_1(1,\gamma_1)$ such that (4) has at least one positive solution, (u,v), for $\lambda \in (\lambda_1,\lambda_2)$. Furthermore, (u,v) will satisfy:

$$W_{1,\gamma_1,b_1}(x,\lambda) < u(x,\lambda) < W_{1,\gamma_1,0}(x,\lambda);\ \overline{\Omega},$$

$$0 < v(x,\lambda) < W_{r,\gamma_2,0}(x,\lambda);\ \overline{\Omega}$$

(D) If $b_2 < 1 \leq b_1$, $\gamma_2 > 0$, and $r < r^*$ (implying that $E_1(r,\gamma_2) > E_1(1,\gamma_1)$) then for $b_2 \approx 0$ there exist $\lambda_1(r,b_1,b_2,\gamma_1,\gamma_2), \lambda_2(r,b_2,\gamma_1,\gamma_2) > E_1(r,\gamma_2)$ such that (4) has at least one positive solution, (u,v), for $\lambda \in (\lambda_1,\lambda_2)$. Furthermore, (u,v) will satisfy:

$$0 < u(x,\lambda) < W_{1,\gamma_1,0}(x,\lambda);\ \overline{\Omega},$$

$$W_{r,\gamma_2,b_2}(x,\lambda) < v(x,\lambda) < W_{r,\gamma_2,0}(x,\lambda);\ \overline{\Omega}$$

(E) If $b_1, b_2 > 1$, $\gamma_1 = \gamma_2$, and $r = 1$ (implying that $E_1(r,\gamma_2) = E_1(1,\gamma_1)$) then (4) has at least one positive solution for $\lambda > E_1(1,\gamma_1)$, given by:

$$(u(x,\lambda),v(x,\lambda)) = \left(\frac{1-b_1}{1-b_1b_2}W_{1,\gamma_1,0}(x,\lambda), \frac{1-b_2}{1-b_1b_2}W_{1,\gamma_1,0}(x,\lambda)\right);\ \overline{\Omega}.$$

Notice that (A)(i) of Theorem 1.4 holds for $b_1, b_2 \geq 0$ and the inequalities become strict if and only if $b_1, b_2 > 0$. We now present sufficient conditions for uniqueness of positive solutions of (4).

Theorem 1.5 (*Uniqueness*). *For $r > 0$, $b_1, b_2 < 1$, and $\gamma_1, \gamma_2 \geq 0$ the following hold:*

(A) If $b_1, b_2 < 1$, $r = 1$, and $\gamma_1 = \gamma_2$ then (4) has at most one positive solution for any $\lambda > 0$.

(B) For $\lambda > \max\{E_1(1,\gamma_1), E_1(r,\gamma_2)\}$ if

$$4 > \frac{b_1^2}{r}\sup_{\Omega}\left\{\frac{W_{1,\gamma_1}(x,\lambda)}{W_{r,\gamma_2}(x,\lambda)}\right\} + 2b_1b_2 + rb_2^2\sup_{\Omega}\left\{\frac{W_{r,\gamma_2}(x,\lambda)}{W_{1,\gamma_1}(x,\lambda)}\right\} \tag{15}$$

then (4) has at most one positive solution. In particular, if $b_1, b_2 \approx 0$ then (15) holds and (4) has a unique positive solution for $\lambda > \max\left\{\frac{E_1(1,\gamma_1)}{1-b_1}, \frac{E_1(r,\gamma_2)}{1-b_2}\right\}$.

Note that we provide a stronger uniqueness result for the asymmetric competition case (i.e. $b_1 = 0$) in Section 4.

Next we present results on stability of the semitrivial steady states for (3) and a condition for convergence to a coexistence state. We consider stability in the Lyapunov sense (see [36,39], for example).

Theorem 1.6 (*Stability*). *Suppose that $r > 0$, $b_1, b_2 \geq 0$, $\gamma_1, \gamma_2 \geq 0$, and $\lambda > 0$ are such that $\sigma_1, \sigma_2 < 0$. The following hold:*

(A) If $\sigma_3 > 0$ or $\sigma_4 > 0$ then $(W_{1,\gamma_1}, 0)$ or $(0, W_{r,\gamma_2})$ is asymptotically stable, respectively

(B) If $\sigma_3 < 0$ or $\sigma_4 < 0$ then $(W_{1,\gamma_1}, 0)$ or $(0, W_{r,\gamma_2})$ is unstable, respectively

(C) If $\sigma_3, \sigma_4 < 0$ then there exist a max–min $(\overline{u}, \underline{v})$ and a min–max $(\underline{u}, \overline{v})$ positive solution of (4) with $0 \leq \underline{u} \leq \overline{u} \leq W_{1,\gamma_1}$ and $0 \leq \underline{v} \leq \overline{v} \leq W_{r,\gamma_2}$ on $\overline{\Omega}$ such that:

  (i) if $\overline{u}(x) \leq u(0,x) \leq W_{1,\gamma_1}(x)$; Ω and $0 < v(0,x) \leq \underline{v}(x)$; Ω then the unique positive solution of (3), $(u(t,x), v(t,x))$, converges to $(\overline{u}, \underline{v})$ as $t \to \infty$.

  (ii) if $0 < u(0,x) \leq \underline{u}(x)$; Ω and $\overline{v}(x) \leq v(0,x) \leq W_{r,\gamma_2}(x)$; Ω then the unique positive solution of (3), $(u(t,x), v(t,x))$, converges to $(\underline{u}, \overline{v})$ as $t \to \infty$.

Table 1
Summary of coexistence and nonexistence results in the semistrong competition case comparing matrix effect, G-D ratio, minimum patch size in the absence of competition, and competitive effect. Recall that predictions of no coexistence are for all patch sizes, while predictions of coexistence in the semistrong case are only valid for a finite range of patch sizes (see Theorem 1.4). For each category, species advantage is given in parentheses, e.g., (N) represents neither species having an advantage, whereas (u) denotes u having an advantage over v in that category. Note that in Cases 1, 7, 13-15 we require $\gamma_2 > 0$, while in Cases 6, 10-12, 18 we require $\gamma_1 > 0$. The rightmost column shows where our results hold in the two extreme cases of 1) D: Dirichlet boundary condition (absorbing boundary) or 2) N: Neumann boundary condition (reflecting boundary). Note that R denotes Robin boundary condition which occurs when a $\gamma_i \in (0,\infty)$. For example, Case 10 still holds even if u faces an immediately lethal matrix (D) and v is completely isolated from matrix effects (N).

Case	Matrix effect	G-D Ratio	Minimum patch size	Competition	Predicted outcome	Other BCs
1	$\gamma_1 = \gamma_2$ (N)	$r < 1$ (u)	$E_1(1,\gamma_1) < E_1(r,\gamma_2)$ (u)	$b_2 < 1 \le b_1$ (v)	Coexistence for $b_2 \approx 0$	u, v: D
2	$\gamma_1 = \gamma_2$ (N)	$r = 1$ (N)	$E_1(1,\gamma_1) = E_1(r,\gamma_2)$ (N)	$b_2 < 1 \le b_1$ (v)	No Coexistence	u, v: D or N
3	$\gamma_1 = \gamma_2$ (N)	$r \in \left(1, \frac{b_1}{b_2}\right)$ (v)	$E_1(1,\gamma_1) > E_1(r,\gamma_2)$ (v)	$b_2 < 1 \le b_1$ (v)	No Coexistence	u, v: D
4	$\gamma_1 = \gamma_2$ (N)	$r \in \left(\frac{b_1}{b_2}, 1\right)$ (u)	$E_1(1,\gamma_1) < E_1(r,\gamma_2)$ (u)	$b_1 < 1 \le b_2$ (u)	No Coexistence	u, v: D
5	$\gamma_1 = \gamma_2$ (N)	$r = 1$ (N)	$E_1(1,\gamma_1) = E_1(r,\gamma_2)$ (N)	$b_1 < 1 \le b_2$ (u)	No Coexistence	u, v: D or N
6	$\gamma_1 = \gamma_2$ (N)	$r > 1$ (v)	$E_1(1,\gamma_1) > E_1(r,\gamma_2)$ (v)	$b_1 < 1 \le b_2$ (u)	Coexistence for $b_1 \approx 0$	u, v: D
7	$\gamma_1 > \gamma_2$ (v)	$r < r^*$ (u)	$E_1(1,\gamma_1) < E_1(r,\gamma_2)$ (u)	$b_2 < 1 \le b_1$ (v)	Coexistence for $b_2 \approx 0$	u: D, v : R
8	$\gamma_1 > \gamma_2$ (v)	$r = 1$ (N)	$E_1(1,\gamma_1) > E_1(r,\gamma_2)$ (v)	$b_2 < 1 \le b_1$ (v)	No Coexistence	u: D, v: N or R
9	$\gamma_1 > \gamma_2$ (v)	$r \in \left(1, \frac{b_1}{b_2}\right)$ (v)	$E_1(1,\gamma_1) > E_1(r,\gamma_2)$ (v)	$b_2 < 1 \le b_1$ (v)	No Coexistence	u: D, v: N or R
10	$\gamma_1 > \gamma_2$ (v)	$r \in (r^*, 1)$ (u)	$E_1(1,\gamma_1) > E_1(r,\gamma_2)$ (v)	$b_1 < 1 \le b_2$ (u)	Coexistence for $b_1 \approx 0$	u: D, v: N or R
11	$\gamma_1 > \gamma_2$ (v)	$r = 1$ (N)	$E_1(1,\gamma_1) > E_1(r,\gamma_2)$ (v)	$b_1 < 1 \le b_2$ (u)	Coexistence for $b_1 \approx 0$	u: D, v: N or R
12	$\gamma_1 > \gamma_2$ (v)	$r > 1$ (v)	$E_1(1,\gamma_1) > E_1(r,\gamma_2)$ (v)	$b_1 < 1 \le b_2$ (u)	Coexistence for $b_1 \approx 0$	u: D, v: N or R
13	$\gamma_1 < \gamma_2$ (u)	$r < 1$ (u)	$E_1(1,\gamma_1) < E_1(r,\gamma_2)$ (u)	$b_2 < 1 \le b_1$ (v)	Coexistence for $b_2 \approx 0$	u: N or R, v: D
14	$\gamma_1 < \gamma_2$ (u)	$r = 1$ (N)	$E_1(1,\gamma_1) < E_1(r,\gamma_2)$ (u)	$b_2 < 1 \le b_1$ (v)	Coexistence for $b_2 \approx 0$	u: N or R, v: D
15	$\gamma_1 < \gamma_2$ (u)	$r \in (1, r^*)$ (v)	$E_1(1,\gamma_1) < E_1(r,\gamma_2)$ (u)	$b_2 < 1 \le b_1$ (v)	Coexistence for $b_2 \approx 0$	u: N or R, v: D
16	$\gamma_1 < \gamma_2$ (u)	$r \in \left(\frac{b_1}{b_2}, 1\right)$ (u)	$E_1(1,\gamma_1) < E_1(r,\gamma_2)$ (u)	$b_1 < 1 \le b_2$ (u)	No Coexistence	u: N or R, v: D
17	$\gamma_1 < \gamma_2$ (u)	$r = 1$ (N)	$E_1(1,\gamma_1) < E_1(r,\gamma_2)$ (u)	$b_1 < 1 \le b_2$ (u)	No Coexistence	u: N or R, v: D
18	$\gamma_1 < \gamma_2$ (u)	$r > r^*$ (v)	$E_1(1,\gamma_1) > E_1(r,\gamma_2)$ (v)	$b_1 < 1 \le b_2$ (u)	Coexistence for $b_1 \approx 0$	u: R, v: D

(iii) $(\overline{u}, \underline{v}) = (\underline{u}, \overline{v})$ *if and only if there is a unique positive solution of* (4). *Moreover, this coexistence state is globally asymptotically stable.*

(iv) There does not exist an asymptotically stable positive solution of (4) *arbitrarily close to* $(W_{1,\gamma_1}, 0)$ *or* $(0, W_{r,\gamma_2})$.

In the absorbing boundary case (Dirichlet boundary condition), we have that $\gamma_1, \gamma_2 \to \infty$, $E_1(1,\gamma_1) = E_1^D$ and $E_1(r,\gamma_2) = \frac{E_1^D}{r}$, and Theorem 1.3 (A) & (B), Theorem 1.4 (A), (B), & (E), and Theorem 1.5 provide results similar to those in Theorems 3.1, 4.1, & 4.2 in [23]. In the reflecting boundary condition case (Neumann boundary condition, $\gamma_1 = 0 = \gamma_2$), we have that $E_1(1,\gamma_1) = 0 = E_1(r,\gamma_2)$ and Theorem 1.3 (A) & (B), Theorem 1.4 (A), (B), & (E) provide results similar to those in Theorems 3.6 & 4.3 of [37].

We close this subsection with a discussion of our results in the semistrong competitive case. In previous studies where both organisms were symmetrically affected by the matrix (i.e. either not at all via a reflecting boundary or facing the harsh reality of an immediately lethal matrix via an absorbing boundary), coexistence is not possible in the semistrong competition case with any G-D ratio and a reflecting boundary or when the G-D ratio is one in the absorbing boundary case (see, e.g., [22,23]). Interestingly, our results show that when organisms are differentially affected by the surrounding patch matrix coexistence is possible even in the semistrong case, at least for an intermediate range of patch sizes. Although our results do not prove necessity, they suggest that coexistence in this case requires counterbalancing of advantage and disadvantage in contrasting mechanisms. In Table 1 we summarize Theorems 1.3 and 1.4 in the semistrong case and provide a detailed comparison of advantage/disadvantage between the species. The Matrix Effect, G-D Ratio, and Competition columns denote appropriate parameter value ranges in our framework, as well as an indication of which species has an advantage in a particular category given that the remaining categories show no advantage for a particular species. For example, $r < 1$ in the G-D Ratio category indicates an advantage for u in the absence of competition and with the same matrix effect (i.e., $\gamma_1 = \gamma_2$). We note that the Matrix Effect and G-D Ratio columns together determine which species has the smallest minimum patch size (again in the absence of competition) which is denoted in the Minimum Patch Size column.

As a first example, Case 10 shows the matrix affects u more severely than v (either u has a higher emigration rate or higher effective matrix hostility relative to v) giving v the advantage in this category, while a G-D ratio less than one indicates that u either has a higher patch intrinsic growth rate or lower patch diffusion rate relative to v, which gives u the advantage in this category. However, $r > r^*$ indicates that between these contrasting mechanisms, the negative matrix effects on u overcome its G-D ratio advantage giving v a smaller minimum patch size requirement in the absence of competition. Thus, v has a combined advantage over u in the absence of competition. But, the effects of competition for resources in the patch are more severe towards v, giving u a competitive advantage. Our results then predict that coexistence is possible for an intermediate (finite) range of patch sizes as long as $b_1 \approx 0$ (meaning that the competitive effect of v onto u is sufficiently weak). This restriction on b_1 is reasonable since we have placed no upper bound on b_2. In fact, we would expect that for $b_2 \gg 1$ we must also have $b_1 \approx 0$ in order to still allow for coexistence. In this case, we see a balancing act between v's ability to invade and colonize smaller patches than u in the absence of competition and the ability of u to better compete with v for resources in a patch enables coexistence for a finite range of patch sizes. Our nonexistence results also indicate that in semistrong cases such as Case 10, coexistence is not possible for large patch sizes when $b_1 < \frac{b_2-1}{b_2}$. This nonexistence result is consistent with previous work where it has been shown that as patch size increases, a large enough core area develops in the patch where organisms are somewhat isolated from matrix effects (see, e.g., [29]). Thus, for large enough patch sizes, dynamics of the model begin to resemble those of the reflecting boundary case. Recall that coexistence is not possible for the semistrong case with a reflecting boundary condition. The Other BCs column gives some indication as to when our results are still valid in the extreme cases of an immediately lethal matrix (absorbing boundary or Dirichlet boundary condition (DBC)) and a completely isolated patch (reflecting boundary condition or Neumann boundary condition (NBC)). Interestingly, if $\gamma_1 \to \infty$ (u faces immediate mortality when encountering the patch/matrix interface, giving rise to an absorbing boundary condition) and $\gamma_2 = 0$ (v is completely isolated from matrix effects, giving rise to a reflecting boundary condition) then coexistence is still possible for an intermediate range of patch sizes.

We also note that as $\gamma_1 \to \gamma_2$ we have $r^* \to 1$ and Case 10 ceases to exist. A parallel scenario for Case 10 when $\gamma_1 = \gamma_2$ is found in Cases 4 & 6. Since $r^* = 1$, Case 4 indicates a scenario where neither species has a matrix effect advantage, but u retains an advantage in G-D ratio, and ultimately in minimum patch size. Our results show that if u has an advantage both in being able to colonize smaller patches (in the absence of competition) and better compete for resources in the patch then coexistence is not possible (we have already conjectured that our result in this case can be extended to cover $r \leq \frac{b_1}{b_2}$). In stark contrast, Case 6 shows a scenario where v's G-D ratio gives it an advantage in being able to colonize smaller patch sizes (in the absence of competition), combined with a counter-balanced advantage for u in competition for resources in the patch, allow for coexistence for an intermediate range of patch sizes when $b_1 \approx 0$. We also note that these results also hold when $\gamma_1, \gamma_2 \to \infty$ giving rise to an absorbing boundary for both u and v. Cases 1, 3, and 15 show a similar setting as Cases 4, 6, and 10 but with the roles of u and v being swapped.

Maintaining a matrix effect advantage for v ($\gamma_1 > \gamma_2$) but taking a G-D ratio such that $r < r^*$ leads us to Case 7 which is similar to Case 10 except that u's G-D ratio allows for an advantage in u being able to colonize smaller patches in the absence of competition. This advantage is offset by v's competitive advantage in the patch to allow coexistence in an intermediate range of patch sizes. A similar situation is found in Case 18, but where u and v roles are reversed. Unlike Cases 10 & 15, scenarios in Case 7 & 18 do not allow for either species to have a reflecting boundary condition.

When all mechanisms are either neutral with regard to awarding an advantage to one species over the other or favor the same organism when an advantage occurs, Cases 2, 5, 8, 9, 16, & 17 give predictions of no coexistence for all patch sizes. Finally, Cases 11 & 13 give scenarios where either the G-D ratio is neutral with respect to advantage or favors v, giving rise to v having an advantage in terms of colonizing smaller patches than u in the absence of competition. This offset by u's competitive advantage in the patch yields prediction of coexistence for an intermediate range of patch sizes. A symmetric set of cases is found in Cases 13 & 14 where the roles of u and v are reversed.

The overarching theme arising from our results as outlined in Table 1 is that advantage in either minimum patch size (in the absence of competition) or direct competitive effect and disadvantage in the other is sufficient to allow an intermediate (and finite) range of patch sizes for which coexistence occurs. Our results suggest that such a balancing act is necessary for coexistence. In fact, we conjecture that one of the conditions must hold in order to have coexistence in the semistrong competition case:

$$E_1(1,\gamma_1) < E_1(r,\gamma_2) \text{ and } b_2 < 1 \leq b_1 \tag{16}$$

$$E_1(1,\gamma_1) > E_1(r,\gamma_2) \text{ and } b_1 < 1 \leq b_2. \tag{17}$$

Computational results in the asymmetric case (see Section 4) certainly agree with this conjecture. From a mechanistic standpoint, these conditions are certainly consistent with intuition. In the case of (16), if for a given level of competitive effect of u onto v ($b_2 > 0$) a patch size was such that $\lambda \in (E_1(r,\gamma_2), E_1(r,\gamma_2) + \delta(b_2))$ (for $\delta(b_2) \approx 0$, whose existence is guaranteed by Theorem 1.3(G)) then a coexistence state is not be possible. In this case, we expect a range of patch sizes giving $\lambda \in (E_1(r,\gamma_2), E_1(r,\gamma_2) + \delta(b_2))$ where $(u,0)$ is globally asymptotically stable and $(0,v)$ is unstable. But, for sufficiently large patches the dynamics of (3) resemble that of the same model but with reflecting boundary conditions where coexistence is not possible, $(u,0)$ is unstable, and $(0,v)$ is globally asymptotically stable. Under the sufficient conditions listed in our results, we see that this reversal of competitive dominance as patch size increases yields an intermediate (finite) range of patch sizes where coexistence arises.

1.5. Structure of the paper

We will present some preliminary mathematical results in Section 2. Proofs of our main results are given in Section 3, followed by an analysis of the asymmetric competition case in Section 4. Finally, we discuss some consequences of our results in Section 5.

2. Mathematical preliminaries

Firstly, note that the general theory for reaction diffusion systems such as (3) is well established (e.g., see [29,36]). In fact, since (3) is a quasimonotone nonincreasing system, an application of Theorem 3.2 of Chapter 8 in [36] with subsolution $(0,0)$ and supersolution (M_1, M_2) ($M_1, M_2 \geq 1$) of (3) guarantees existence and uniqueness of a solution to (3). Also, solutions with nonnegative initial data exist and remain nonnegative and bounded for all time. Predictions of persistence, coexistence, and extinction in reaction diffusion systems can be explored via determination of the stability of the trivial steady state $(0,0)$ and semitrivial steady states $(u^*,0)$ and $(0,v^*)$, via determination of the sign of $\sigma_1, \sigma_2, \sigma_3$, and σ_4 (see, e.g., [29]). In fact, our main results show that the conventional view of "invasibility implies persistence" (see [29], for example) also holds for the model in the sense that instability of both the trivial and semitrivial steady states will imply a prediction that if an organism can invade the patch with small positive initial density then that the organism can colonize the patch and persist.

We now present and prove several preliminary results which will be crucial in proving our main results. Recall that we denote $W_{1,\gamma_1} = W_{1,\gamma_1,0}$ and $W_{r,\gamma_2} = W_{r,\gamma_2,0}$.

Lemma 2.1. *If $\lambda > \max\{E_1(1,\gamma_1), E_1(r,\gamma_2)\}$ and $\sigma_3, \sigma_4 < 0$ then (4) has a positive solution, (u,v), which for $m \approx 0$ satisfies:*

$$(m\phi_4, m\phi_3) < (u,v) < (W_{1,\gamma_1}, W_{r,\gamma_2});\ \overline{\Omega}$$

where σ_3, σ_4 are the principal eigenvalues with corresponding eigenfunctions ϕ_3, ϕ_4 of (13), (14), respectively.

Proof. Let $m > 0$ and define $\psi = (m\phi_4, m\phi_3)$ and $Z = (W_{1,\gamma_1}, W_{r,\gamma_2})$. By our choice of λ, $\sigma_1, \sigma_2 < 0$ ensuring that both W_{1,γ_1} and W_{r,γ_2} exist. We will now show that ψ and Z are a sub-supersolution pair for (4) (see [36], for example). First, we check (ψ_1, Z_2):

$$\begin{aligned} -\Delta\psi_1 - \lambda\psi_1(1-\psi_1-b_1Z_2) &= m\sigma_4\phi_4 + m\lambda\phi_4 - m\lambda b_1 W_{r,\gamma_2}\phi_4 - \lambda m\phi_4 \\ &\quad + \lambda m^2\phi_4^2 + m\lambda b_1 W_{r,\gamma_2}\phi_4 \\ &= m\phi_4[\sigma_4 + \lambda m\phi_4] \\ &< 0 \end{aligned} \tag{18}$$

for $m \approx 0$ since $\sigma_4 < 0$. Also, we have

$$\begin{aligned} -\Delta Z_2 - \lambda r Z_2(1-Z_2-b_2\psi_1) &= \lambda r W_{r,\gamma_2} - \lambda r W_{r,\gamma_2}^2 - \lambda r W_{r,\gamma_2} + \lambda r W_{r,\gamma_2}^2 \\ &\quad + \lambda r b_2 W_{r,\gamma_2} m\phi_4 \\ &= \lambda r b_2 W_{r,\gamma_2} m\phi_4 \\ &\geq 0 \end{aligned} \tag{19}$$

since $W_{r,\gamma_2}, \phi_4 > 0;\ \Omega$, $\lambda, r > 0$, and $b_2 \geq 0$. It is easy to see that

$$\frac{\partial\psi_1}{\partial\eta} + \sqrt{\lambda}\gamma_1\psi_1 = 0 = \frac{\partial Z_2}{\partial\eta} + \sqrt{\lambda}\gamma_2 Z_2. \tag{20}$$

Next, we check (Z_1, ψ_2):

$$\begin{aligned} -\Delta Z_1 - \lambda Z_1(1-Z_1-b_1\psi_2) &= \lambda W_{1,\gamma_1} - \lambda W_{1,\gamma_1}^2 - \lambda W_{1,\gamma_1} + \lambda W_{1,\gamma_1}^2 + \lambda b_1\ m W_{1,\gamma_1}\phi_3 \\ &= \lambda b_1\ m W_{1,\gamma_1}\phi_3 \\ &\geq 0 \end{aligned} \tag{21}$$

since $W_{1,\gamma_1}, \phi_3 > 0;\ \Omega$, $\lambda, r > 0$, and $b_1 \geq 0$. Also, we have

$$\begin{aligned} -\Delta\psi_2 - \lambda r\psi_2(1-\psi_2-b_2Z_1) &= m\sigma_3\phi_3 + m\lambda r\phi_3 - m\lambda r b_2 W_{1,\gamma_1}\phi_3 - m\lambda r\phi_3 \\ &\quad + m^2\lambda r\phi_3^2 + m\lambda r b_2 W_{1,\gamma_1}\phi_3 \\ &= m\phi_3[\sigma_3 + m\lambda r\phi_3] \\ &< 0 \end{aligned} \tag{22}$$

for $m \approx 0$ since $\sigma_3 < 0$. It is also easy to see that

$$\frac{\partial Z_1}{\partial\eta} + \sqrt{\lambda}\gamma_1 Z_1 = 0 = \frac{\partial\psi_2}{\partial\eta} + \sqrt{\lambda}\gamma_2\psi_2. \tag{23}$$

Also, we can choose $m \approx 0$ such that $\psi < Z;\ \overline{\Omega}$. Thus, ψ, Z are a strict sub-supersolution pair and Theorem 4.2 in Chapter 8 of [36] gives that (4) has at least one solution, (u,v), with

$$(\psi_1, \psi_2) < (u,v) < (Z_1, Z_2);\ \overline{\Omega}.\quad \square \tag{24}$$

Lemma 2.2. *If $\lambda > \max\{E_1(1,\gamma_1), E_1(r,\gamma_2)\}$ then the following hold:*

(A) $\sigma_3 \int_\Omega W_{r,\gamma_2}\phi_3 dx = \lambda r \int_\Omega W_{r,\gamma_2}\phi_3 \left[b_2 W_{1,\gamma_1} - W_{r,\gamma_2}\right] dx$
(B) $\sigma_4 \int_\Omega W_{1,\gamma_1}\phi_4 dx = \lambda \int_\Omega W_{1,\gamma_1}\phi_4 \left[b_1 W_{r,\gamma_2} - W_{1,\gamma_1}\right] dx.$

Proof. We only present a proof of (A) as the proof of (B) is similar. Using Green's Identity, we have:

$$\int_\Omega -\Delta W_{r,\gamma_2}\phi_3 + \Delta\phi_3 W_{r,\gamma_2} dx = \int_{\partial\Omega} -\frac{\partial W_{r,\gamma_2}}{\partial\eta}\phi_3 + \frac{\partial\phi_3}{\partial\eta}W_{r,\gamma_2} ds. \tag{25}$$

It is easy to see that the right-hand side of (25) is zero, thus

$$\begin{aligned} 0 = \int_\Omega -\Delta W_{r,\gamma_2}\phi_3 + \Delta\phi_3 W_{r,\gamma_2} dx &= \int_\Omega \lambda r W_{r,\gamma_2}\phi_3 - \lambda r W_{r,\gamma_2}^2\phi_3 - \sigma_3 W_{r,\gamma_2}\phi_3 - \lambda r W_{r,\gamma_2}\phi_3 \\ &\quad + \lambda r b_2 W_{1,\gamma_1} W_{r,\gamma_2}\phi_3 dx \\ &= \int_\Omega -\sigma_3 W_{r,\gamma_2}\phi_3 + \lambda r W_{r,\gamma_2}\phi_3 \left[b_2 W_{1,\gamma_1} - W_{r,\gamma_2}\right] dx \end{aligned} \tag{26}$$

or, equivalently,

$$\sigma_3 \int_\Omega W_{r,\gamma_2}\phi_3 dx = \int_\Omega \lambda r W_{r,\gamma_2}\phi_3 \left[b_2 W_{1,\gamma_1} - W_{r,\gamma_2}\right] dx. \quad \square \tag{27}$$

Lemma 2.3. *Considering σ_3, σ_4 as functions of $W_{1,\gamma_1}, W_{r,\gamma_2}$, respectively, the following hold:*

(A) σ_3, σ_4 is an increasing function of $W_{1,\gamma_1}, W_{r,\gamma_2}$, respectively
(B) If $\lambda > E_1(1, \gamma_1)$ then

$$\sigma_3(0) < \sigma_3(W_{1,\gamma_1}) < \sigma_3(1),$$

(C) If $\lambda > E_1(r, \gamma_2)$ then

$$\sigma_4(0) < \sigma_4(W_{r,\gamma_2}) < \sigma_4(1).$$

The proof of Lemma 2.3 follows from Corollary 2.2 in [29].

Lemma 2.4. *If (u, v) is a positive solution of (4) then the following holds:*

$$\lambda \int_\Omega uv\left[(1-r) + (rb_2 - 1)u + (r - b_1)v\right] dx = \sqrt{\lambda}(\gamma_1 - \gamma_2)\int_{\partial\Omega} uv ds. \tag{28}$$

Proof. Again by Green's Identity, we have that:

$$\int_\Omega -\Delta uv + \Delta vu dx = \int_{\partial\Omega} -\frac{\partial u}{\partial\eta}v + \frac{\partial v}{\partial\eta}u ds. \tag{29}$$

Thus, we have

$$\begin{aligned} \int_\Omega -\Delta uv + \Delta vu dx &= \int_\Omega \lambda u\left(1 - u - b_1 v\right) v \\ &\quad - \lambda r v\left(1 - v - b_2 u\right) u dx \\ &= \int_\Omega \lambda uv - \lambda u^2 v - \lambda b_1 uv^2 - \lambda ruv \\ &\quad + \lambda ruv^2 + \lambda r b_2 u^2 v dx \\ &= \lambda \int_\Omega uv\left[(1-r) + (rb_2 - 1)u + (r - b_1)v\right] dx \end{aligned} \tag{30}$$

and

$$\int_{\partial\Omega} -\frac{\partial u}{\partial\eta}v + \frac{\partial v}{\partial\eta}u ds = \sqrt{\lambda}(\gamma_1 - \gamma_2)\int_{\partial\Omega} uv ds \tag{31}$$

as desired. $\square$

Lemma 2.5. *Suppose that* $D(x) := 1 - r + (rb_2 - 1)u(x) + (r - b_1)v(x)$*. If* $r > 0,\ b_1, b_2 \geq 0,\ \gamma_1, \gamma_2 \geq 0$*, and* (u, v) *is a positive solution of* (4) *then the following hold:*

(A) if $b_1 \leq 1 \leq b_2$ *and* $\frac{b_1}{b_2} \leq r \leq 1$ *then* $D(x) \geq 0$
(B) if $b_2 \leq 1 \leq b_1$ *and* $1 \leq r \leq \frac{b_1}{b_2}$ *then* $D(x) \leq 0$.

Proof. To establish the result, we consider the following cases.

Case i: Assume that $r \leq \min\left\{b_1, \frac{1}{b_2}\right\}$, which implies that $rb_2 - 1 \leq 0$ and $r - b_1 \leq 0$. Since $u, v > 0;\ \Omega$, if $r \geq 1$ then we have that:

$$\begin{aligned} D(x) = 1 - r + (rb_2 - 1)u(x) + (r - b_1)v(x) &\leq 1 - r \\ &\leq 0;\ \Omega. \end{aligned} \tag{32}$$

Also, since $u, v \leq 1;\ \Omega$, if $r \geq \frac{b_1}{b_2}$ then we have that:

$$\begin{aligned} D(x) = 1 - r + (rb_2 - 1)u(x) + (r - b_1)v(x) &\geq 1 - r + rb_2 - 1 + r - b_1 \\ &= rb_2 - b_1 \\ &\geq 0;\ \Omega. \end{aligned} \tag{33}$$

Notice that for (32) to hold, it is necessary that $b_2 \leq 1 \leq b_1$ and for (33) to hold, that $b_1 \leq 1 \leq b_2$. Also, $D(x) < 0;\ \Omega$ in (32) ($D(x) > 0;\ \Omega$ in (33)) if at least one of the inequalities is strict.

Case ii: Assume that $b_1 \leq r \leq \frac{1}{b_2}$, which implies that $rb_2 - 1 \leq 0$ and $r - b_1 \geq 0$. Since $u > 0$ & $v \leq 1;\ \Omega$, if $b_1 \geq 1$ then we have that:

$$\begin{aligned} D(x) = 1 - r + (rb_2 - 1)u(x) + (r - b_1)v(x) &\leq 1 - r + r - b_1 \\ &\leq 1 - b_1 \\ &\leq 0;\ \Omega. \end{aligned} \tag{34}$$

Also, since $u \leq 1$ & $v > 0;\ \Omega$, if $b_2 \geq 1$ then we have that:

$$\begin{aligned} D(x) = 1 - r + (rb_2 - 1)u(x) + (r - b_1)v(x) &\geq 1 - r + rb_2 - 1 \\ &= r\,(b_2 - 1) \\ &\geq 0;\ \Omega. \end{aligned} \tag{35}$$

Again, notice that for (34) to hold, it is necessary that $b_2 \leq 1 \leq b_1$ and for (35) to hold, that $b_1 \leq 1 \leq b_2$. Also, $D(x) < 0;\ \Omega$ in (34) ($D(x) > 0;\ \Omega$ in (35)) if at least one of the inequalities is strict.

Case iii: Assume that $\frac{1}{b_2} \leq r \leq b_1$, which implies that $rb_2 - 1 \geq 0$ and $r - b_1 \leq 0$. Since $u > 0$ & $v \leq 1;\ \Omega$, if $b_1 \leq 1$ then we have that:

$$\begin{aligned} D(x) = 1 - r + (rb_2 - 1)u(x) + (r - b_1)v(x) &\geq 1 - r + r - b_1 \\ &= 1 - b_1 \\ &\geq 0;\ \Omega. \end{aligned} \tag{36}$$

Also, since $u \leq 1$ & $v > 0;\ \Omega$, if $b_2 \leq 1$ then we have that:

$$\begin{aligned} D(x) = 1 - r + (rb_2 - 1)u(x) + (r - b_1)v(x) &\leq 1 - r + rb_2 - 1 \\ &= r\,(b_2 - 1) \\ &\leq 0;\ \Omega. \end{aligned} \tag{37}$$

Again, notice that for (36) to hold, it is necessary that $b_1 \leq 1 \leq b_2$ and for (37) to hold, that $b_2 \leq 1 \leq b_1$. Also, $D(x) > 0;\ \Omega$ in (36) ($D(x) < 0;\ \Omega$ in (37)) if at least one of the inequalities is strict.

Case iv: Assume that $\max\left\{\frac{1}{b_2}, b_1\right\} \leq r \leq 1$, which implies that $rb_2 - 1 \geq 0$ and $r - b_1 \geq 0$. Since $u, v > 0;\ \Omega$, we have that:

$$\begin{aligned} D(x) = 1 - r + (rb_2 - 1)u(x) + (r - b_1)v(x) &\geq 1 - r \\ &\geq 0;\ \Omega. \end{aligned} \tag{38}$$

Also, since $u, v \leq 1;\ \Omega$, if $r \leq \frac{b_1}{b_2}$ then we have that:

$$\begin{aligned} D(x) = 1 - r + (rb_2 - 1)u(x) + (r - b_1)v(x) &\leq 1 - r + rb_2 - 1 + r - b_1 \\ &= rb_2 - b_1 \\ &\leq 0;\ \Omega. \end{aligned} \tag{39}$$

Again, notice that for (38) to hold, it is necessary that $b_1 \leq 1 \leq b_2$ and for (39) to hold, that $b_2 \leq 1 \leq b_1$. Also, $D(x) > 0;\ \Omega$ in (38) ($D(x) < 0;\ \Omega$ in (39)) if at least one of the inequalities is strict.

The result now follows for (A) from (33), if $\frac{1}{b_2} \leq b_1$ then (36) or if $\frac{1}{b_2} > b_1$ then (35), and (38), and for (B) from (32), if $\frac{1}{b_2} \leq b_1$ then (37) or if $\frac{1}{b_2} > b_1$ then (34), and (39). $\square$

Lemma 2.6. *If $b_1, b_2 < 1$ and (u, v) is a positive solution of (4) then the following hold:*

(A) if $z(x)$ is a smooth function that satisfies

$$\begin{cases} -\Delta z = \lambda z\,(1 - u - v)\,;\ \Omega \\ \frac{\partial z}{\partial \eta} + \sqrt{\lambda}\gamma_1 z = 0;\ \partial\Omega \end{cases} \tag{40}$$

then $z(x) \equiv 0$

(B) if $z(x)$ is a smooth function that satisfies

$$\begin{cases} -\Delta z = \lambda r z\,(1 - u - v)\,;\ \Omega \\ \frac{\partial z}{\partial \eta} + \sqrt{\lambda}\gamma_2 z = 0;\ \partial\Omega \end{cases} \tag{41}$$

then $z(x) \equiv 0$.

Proof. We only provide a proof for (A) as the proof for (B) is similar. Note that when $\mu = 0$, $w \equiv u$ is a solution of

$$\begin{cases} -\Delta w - \lambda w\,(1 - u - b_1 v) = \mu w;\ \Omega \\ \frac{\partial w}{\partial \eta} + \sqrt{\lambda}\gamma_1 w = 0;\ \partial\Omega. \end{cases} \tag{42}$$

Since $u > 0;\ \Omega$, the principal eigenvalue μ_1 of (42) is zero. But, for any $\phi \neq 0$ smooth we must have:

$$\mu_1 = 0 \leq \frac{\int_\Omega |\nabla\phi|^2 - \lambda\,(1 - u - b_1 v)\,\phi^2 dx + \int_{\partial\Omega} \sqrt{\lambda}\gamma_1 \phi^2 ds}{\int_\Omega \phi^2 dx} \tag{43}$$

(this can be seen from page 97 of [29]). But, we also have

$$\int_\Omega -\Delta z z dx = \int_{\partial\Omega} -\frac{\partial z}{\partial \eta} z ds + \int_\Omega |\nabla z|^2 dx \tag{44}$$

where

$$\int_\Omega -\Delta z z dx = \int_\Omega \lambda\,(1 - u - v)\,z^2 dx \tag{45}$$

and

$$\int_{\partial\Omega} -\frac{\partial z}{\partial \eta} z ds = \int_{\partial\Omega} \sqrt{\lambda}\gamma_1 z^2 ds \tag{46}$$

implying that

$$\int_{\Omega} |\nabla z|^2 \, dx - \int_{\Omega} \lambda \left(1 - u - v\right) z^2 dx + \int_{\partial\Omega} \sqrt{\lambda}\gamma_1 z^2 ds = 0. \tag{47}$$

Now, using (43) we have

$$\begin{aligned} 0 = \int_{\Omega} |\nabla z|^2 \, dx - \int_{\Omega} \lambda \left(1 - u - b_1 v\right) z^2 dx + \int_{\partial\Omega} \sqrt{\lambda}\gamma_1 z^2 ds + \int_{\Omega} \lambda(1-b_1) v z^2 dx \\ \geq \int_{\Omega} \lambda(1-b_1) v z^2 dx \end{aligned} \tag{48}$$

implying that

$$\int_{\Omega} \lambda(1-b_1) v z^2 dx \leq 0. \tag{49}$$

But, this is a contraction since $\lambda > 0, b_1 < 1$, and $v > 0$. Hence, $z \equiv 0$ as desired. □

Lemma 2.7. *The principal eigenvalue, $E_1(r,\gamma)$, which is defined in (8) has the following properties for all $r > 0$ and $\gamma \geq 0$ (note that $b = 0$ throughout this result):*

(A) For fixed $\gamma > 0$

- *(i) $E_1(r,\gamma)$ is a decreasing function of r*
- *(ii) $E_1(r,\gamma) \to 0$ as $r \to \infty$*
- *(iii) $E_1(r,\gamma) \to \infty$ as $r \to 0^+$*

(B) For fixed $r > 0$

- *(i) $E_1(r,\gamma)$ is an increasing function of γ*
- *(ii) $E_1(r,\gamma) \to \frac{E_1^D}{r}$ as $\gamma \to \infty$*
- *(iii) $E_1(r,\gamma) \to 0$ as $\gamma \to 0^+$*

(C) $E_1(r,\gamma) = \frac{E_1(1,\gamma)}{r}$

(D) Fix $\gamma_1 > 0$ and $\gamma_2 \geq 0$ and let $r^* = \frac{E_1(1,\gamma_2)}{E_1(1,\gamma_1)}$,

- *(i) if $r < r^*$ then $E_1(1,\gamma_1) < E_1(r,\gamma_2)$*
- *(ii) if $r = r^*$ then $E_1(1,\gamma_1) = E_1(r,\gamma_2)$*
- *(iii) if $r > r^*$ then $E_1(1,\gamma_1) > E_1(r,\gamma_2)$*
- *(iv) if $\gamma_1 > \gamma_2$ then $r^* < 1$*
- *(v) if $\gamma_1 = \gamma_2$ then $r^* = 1$*
- *(vi) if $\gamma_1 < \gamma_2$ then $r^* > 1$.*

The proof of (A) – (C) can be found in [17] and (D) follows immediately from (C).

We close this section by discussing two computational methods that we will employ to numerically study the structure of positive solutions of (4) in the asymmetric competition case in Section 4.

2.1. Quadrature method

Here, we recall in detail the quadrature method derived in [38] which we use to approximate the unique positive solution u $(= u_\lambda)$ of (9) in the case of a one-dimensional patch. We note that such a quadrature method for the Dirichlet boundary condition case was first introduced in [40]. Let $f(u) = u(1-u)$, $\Omega = (0,1)$, and u be a positive solution to (9). Since (9) is autonomous, u must be symmetric about $x = \frac{1}{2}$, increasing on $\left(0, \frac{1}{2}\right)$, and decreasing on $\left(\frac{1}{2}, 1\right)$. Let $u(0) = u(1) = q$ and $\|u\|_\infty = u\left(\frac{1}{2}\right) = \rho$. Also, note that $u'\left(\frac{1}{2}\right) = 0$. See Fig. 3 for an illustration of the structure of u.

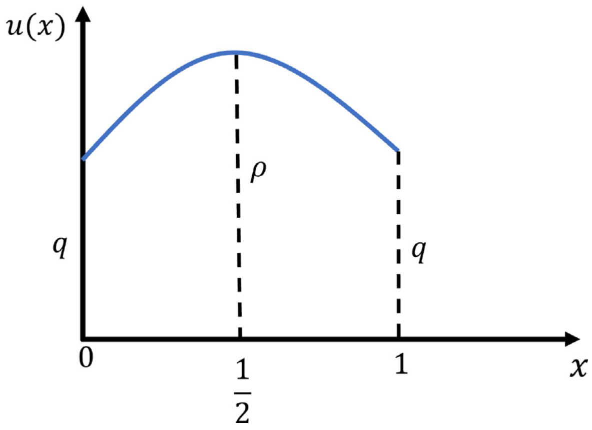


Fig. 3. Shape of a positive solution, u, to (9).

Multiplying the differential equation in (9) by u' we have

$$-u''u' = \lambda f(u)u'. \tag{50}$$

By integrating both sides, we obtain

$$-\frac{[u'(x)]^2}{2} = \lambda F(u(x)) + C \tag{51}$$

where $F(s) = \int_0^s f(t)dt$. Now, applying $u'\left(\frac{1}{2}\right) = 0$ and $u\left(\frac{1}{2}\right) = \rho$ we must have that $C = -\lambda F(\rho)$. Thus

$$u'(x) = \sqrt{2\lambda(F(\rho) - F(u(x))}; \quad x \in \left[0, \frac{1}{2}\right]. \tag{52}$$

Further integration from 0 to x; $x \in \left[0, \frac{1}{2}\right)$ yields

$$\int_0^x \frac{u'(x)ds}{\sqrt{F(\rho) - F(u(s))}} = \sqrt{2\lambda}x. \tag{53}$$

Through a change of variables and using the fact that $u(0) = q$ we have

$$\int_q^{u(x)} \frac{ds}{\sqrt{F(\rho) - F(s)}} = \sqrt{2\lambda}x; \quad x \in \left[0, \frac{1}{2}\right). \tag{54}$$

Now, letting $x \to \frac{1}{2}$, we have

$$\sqrt{2}\int_q^{\rho} \frac{ds}{\sqrt{F(\rho) - F(s)}} = \sqrt{\lambda}. \tag{55}$$

For the improper integral in (55) to exist, we must have $f(\rho) > 0$ and $F(\rho) > F(s); s \in [0, \rho)$. Hence, in this case we require $\rho \in (0, 1)$. Using the boundary conditions in (9), we note that ρ and q must satisfy

$$F(\rho) = \frac{2F(q) + \gamma_2^2 q^2}{2}. \tag{56}$$

It is easy to verify that given $\rho \in (0, 1)$, there exists a unique $q = q(\rho) \in (0, \rho)$ satisfying (56). Also,

$$G(\rho) = \sqrt{2}\int_{q(\rho)}^{\rho} \frac{ds}{\sqrt{F(\rho) - F(s)}} \tag{57}$$

is well defined and continuous on $(0,1)$. Further, if λ, ρ, and $q(\rho)$ satisfy

$$\sqrt{\lambda} = G(\rho) = \sqrt{2}\int_{q(\rho)}^{\rho} \frac{ds}{\sqrt{F(\rho)-F(s)}}, \tag{58}$$

then it can be shown that for each $x \in \left[0, \frac{1}{2}\right)$ there is a unique $u(x) \in [0,\rho)$ that satisfies the equation

$$\int_{q(\rho)}^{u(x)} \frac{ds}{\sqrt{F(\rho)-F(s)}} = \sqrt{2\lambda}x. \tag{59}$$

Now, defining $u\left(\frac{1}{2}\right) = \rho$, and $u(x) = u(1-x)$ for $x \in \left(\frac{1}{2}, 1\right]$, it can then be shown that $u \in C^2[0,1]$ and satisfies (6).

Hence (58), namely $S = \{(\lambda,\rho) \mid \rho \in (0,1),\ G(\rho) = \sqrt{\lambda}\}$, describes the bifurcation diagram for positive solutions of (6). For given λ, ρ, and q satisfying (56) and (58), we will also use (59) to numerically approximate u.

2.2. Shooting method

In this subsection, we discuss a numerical shooting method which will be employed to approximate the positive solution v of (4) in the asymmetric competition case when $b_1 = 0$, namely:

$$\begin{cases} -v'' = \lambda r v\left[1 - v - b_2 u\right];\ (0,1) \\ -v'(0) + \sqrt{\lambda}\gamma_2 v(0) = 0 \\ v'(1) + \sqrt{\lambda}\gamma_2 v(1) = 0 \end{cases} \tag{60}$$

where $u = W_{1,\gamma_1,0}$ is the unique positive solution of (6) and is numerically approximated using the quadrature method.

Let $v(0) = \delta$ and $v' = z$. Then we obtain the following system of ordinary differential equations:

$$\begin{cases} v' = z;\ (0,1) \\ -z' = \lambda v(1 - v - b_2 W_{1,\gamma_1});\ (0,1) \\ z(1) = -\sqrt{\lambda}\gamma_1 v(1) \\ v(0) = \delta \\ z(0) = \sqrt{\lambda}\gamma_1 \delta. \end{cases} \tag{61}$$

For a given value of $\delta > 0$, we employ the `ParametricNDSolve` command in Wolfram Mathematica (which uses the "Runge–Kutta" numerical method) to approximate solutions of (61). This process can be explained as shooting from $x = 0$ (where $v(0) = \delta$ and $z(0) = \sqrt{\lambda}\gamma_1\delta$) and checking at $x = 1$ to see if $z(1) = -\sqrt{\lambda}\gamma_1 v(1)$ (see Fig. 4).

3. Proof of main results

In this section, we provide proofs of our main results.

3.1. Proof of Theorem 1.3

Assume that (u, v) is a positive solution of (4) for a fixed $\lambda > 0$.
(A) First, assume that $\lambda \le E_1(1,\gamma_1)$ which implies that $\sigma_1 \ge 0$ (see Theorem 1.2). Using Green's Identity and the eigenfunction corresponding to σ_1, we have that:

$$\int_{\Omega} -\Delta u \phi_1 + \Delta\phi_1 u dx = \int_{\partial\Omega} -\frac{\partial u}{\partial \eta}\phi_1 + \frac{\partial \phi_1}{\partial \eta} u ds. \tag{62}$$

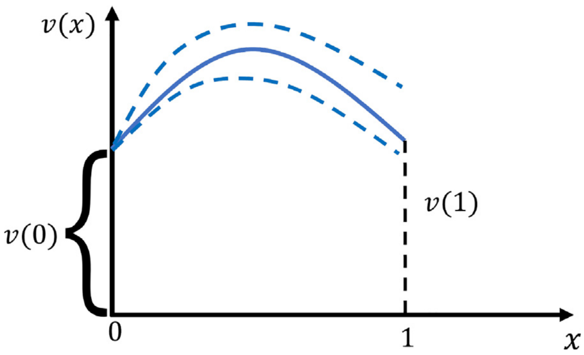


Fig. 4. Illustration of shooting from $x = 0$ to $x = 1$. Dotted lines indicate δ-values which yield solutions, v, that do not satisfy the boundary condition at $x = 1$, whereas the solid line represents values that do satisfy the boundary condition.

But, the right-hand-side of (62) is clearly equal to zero, and we also have:

$$\begin{aligned}\int_\Omega -\Delta u\phi_1 + \Delta\phi_1 u dx &= \int_\Omega \lambda u\phi_1 (1 - u - b_1 v) - u(\sigma_1\phi_1 + \lambda\phi_1) dx \\ &= \int_\Omega \lambda u\phi_1 - \lambda u^2\phi_1 - \lambda b_1 uv\phi_1 - \sigma_1\phi_1 u - \lambda u\phi_1 dx \\ &= \int_\Omega -u\phi_1 (u + b_1 v + \sigma_1) dx \\ &< 0 \end{aligned} \tag{63}$$

since $u, v, \phi_1 > 0;\ \Omega$ and $\sigma_1 \geq 0$. This contradiction ensures that no positive solution of (4) exists when $\lambda \leq E_1(1, \gamma_1)$. An almost identical argument follows when $\lambda \leq E_1(r, \gamma_2)$.

(B) – (D) Note that these parts follow immediately from Lemmas 2.4 and 2.5. For example, we provide a proof of (C): Note that (A) implies that $\lambda > \max\{E_1(1, \gamma_1), E_1(r, \gamma_2)\}$. Now, assuming $\gamma_1 > \gamma_2$ ensures that the right-hand-side of (28) is strictly positive, whereas the left-hand-side of (28) is nonpositive from Lemma 2.5 when $b_2 \leq 1 \leq b_1$ and $1 \leq r \leq \frac{b_1}{b_2}$ (since $u, v > 0;\ \Omega$ and $\lambda > 0$). This contradiction implies that no positive solution of (4) exists when $b_2 \leq 1 \leq b_1$ and $1 \leq r \leq \frac{b_1}{b_2}$.

(E) Assume that $b_1 > 1$ and $b_2 < \frac{b_1 - 1}{b_1}$. Since we wish to prove nonexistence for large λ-values, it suffices to show nonexistence for $\lambda > \frac{E_1(r,\gamma_2)}{1-b_2}$. Using Green's Identity, we have:

$$\int_\Omega -\Delta u W_{1,\gamma_1} + \Delta W_{1,\gamma_1} u dx = \int_{\partial\Omega} -\frac{\partial u}{\partial\eta} W_{1,\gamma_1} + \frac{\partial W_{1,\gamma_1}}{\partial\eta} u ds. \tag{64}$$

But, the right-hand-side of (64) is clearly equal to zero and the left-hand-side becomes:

$$\begin{aligned}\int_\Omega -\Delta u W_{1,\gamma_1} + \Delta W_{1,\gamma_1} u dx &= \int_\Omega \lambda u (1 - u - b_1 v) W_{1,\gamma_1} - \lambda W_{1,\gamma_1} (1 - W_{1,\gamma_1}) u dx \\ &= \int_\Omega \lambda u W_{1,\gamma_1} [W_{1,\gamma_1} - (u + b_1 v)] dx \\ &< \int_\Omega \lambda u W_{1,\gamma_1} [W_{1,\gamma_1} - b_1 W_{r,\gamma_2,b_2}] dx \end{aligned} \tag{65}$$

since $u > 0;\ \Omega$ and $v \geq W_{r,\gamma_2,b_2};\ \Omega$ (see proof of (D) in Theorem 1.4 and note that for $\lambda > \frac{E_1(r,\gamma_2)}{1-b_2}$, Theorem 1.2 ensures that W_{r,γ_2,b_2} exists). Also, Theorem 1.2 ensures that:

$$W_{1,\gamma_1} - b_1 W_{r,\gamma_2,b_2} \to 1 - b_1(1 - b_2) \text{ on all closed subsets of } \Omega \text{ as } \lambda \to \infty. \tag{66}$$

Since $b_1 > 1$ and $b_2 < \frac{b_1-1}{b_1}$, we have that $1 - b_1(1-b_2) < 0$ and can choose $\lambda \gg 1$ such that $\int_\Omega \lambda u W_{1,\gamma_1}\left[W_{1,\gamma_1} - b_1 W_{r,\gamma_2,b_2}\right] dx < 0$, which is a contradiction.
(F) We omit this proof as it is almost identical to the one in (E).
(G) Here, we show that there exists $\delta(b_2) > 0$ such that (4) has no positive solution for $\lambda < E_1(r,\gamma_2)+\delta(b_2)$. If $\lambda \le E_1(1,\gamma_1)$ then from (A) (4) has no positive solution. Thus, we assume (u,v) is a positive solution of (4) for some $\lambda \in (E_1(1,\gamma_1), E_1(r,\gamma_2))$, which implies that $\sigma_2 > 0$. By Green's Identity, we obtain:

$$\int_\Omega -\Delta v\phi_2 + \Delta\phi_2 v dx = \int_{\partial\Omega} -\frac{\partial v}{\partial\eta}\phi_2 + \frac{\partial\phi_2}{\partial\eta} v ds, \tag{67}$$

and it is easy to see that the right-hand-side of (67) is zero. Now, we also have that:

$$\begin{aligned}
\int_\Omega -\Delta v\phi_2 + \Delta\phi_2 v dx &= \int_\Omega \lambda r v(1 - v - b_2 u)\phi_2 - (\lambda r + \sigma_2)\phi_2 v dx \\
&= \int_\Omega (-\lambda r - \sigma_2 + \lambda r - \lambda r v - \lambda r b_2 u)\,\phi_2 v dx \\
&= \int_\Omega (-\sigma_{2,\lambda} - \lambda r v - \lambda r b_2 u)\,\phi_2 v dx \\
&= \lambda r \int_\Omega \left(\frac{-\sigma_2}{\lambda r} - v - b_2 u\right)\phi_2 v dx \qquad (68)\\
&\le \lambda r \int_\Omega \left(\frac{-\sigma_{2,\lambda}}{\lambda r} - v - b_2 \min_{\overline{\Omega}}\{u\}\right)\phi_2 v dx \\
&\le \lambda r \int_\Omega \left(\frac{-\sigma_2}{\lambda r} - b_2 \min_{\overline{\Omega}}\{u\}\right)\phi_2 v dx, \qquad (69)
\end{aligned}$$

which gives rise to a contradiction since $\sigma_2 > 0$. Further, from (68), we have $0 \le \min_{\overline{\Omega}}\{u\}\left[\frac{-\sigma_2}{\lambda r \min_{\overline{\Omega}}\{u\}} - b_2\right]$ and we note that $\sigma_2 \to 0$ when $\lambda \to E_1(r,\gamma_2)$ and $\sigma_2 < 0$ when $\lambda > E_1(r,\gamma_2)$. Since $b_2 > 0$, there exists a $\delta(b_2) > 0$ such that (4) has no positive solution for $\lambda \in [E_1(r,\gamma_2), E_1(r,\gamma_2)+\delta(b_2))$ and hence a positive solution does not exist for $\lambda < E_1(r,\gamma_2)+\delta(b_2)$. Furthermore, it is clear that a necessary condition for existence of a positive solution is $H(\lambda, r) = \frac{-\sigma_2}{\lambda r \min_{\overline{\Omega}} u} \ge b_2$, as desired.
(H) We omit this proof as it is almost identical to the one in (G). □

3.2. Proof of Theorem 1.4

(A) Assume that $b_1, b_2 < 1$ and $\lambda > \max\left\{\frac{E_1(r,\gamma_2)}{1-b_2}, \frac{E_1(1,\gamma_1)}{1-b_1}\right\}$. We first prove existence of a positive solution of (4). Note that this implies $\sigma_1, \sigma_2 < 0$ ensuring that $W_{1,\gamma_1}, W_{r,\gamma_2}$ (the unique positive solution of (6) with $R = 1$ and $R = r$, respectively) both exist. Now consider $\sigma_3(W_{1,\gamma_1})$ with $W_{1,\gamma_1} \equiv 1$ and $\sigma_4(W_{r,\gamma_2})$ with $W_{r,\gamma_2} \equiv 1$, namely,

$$\begin{cases} -\Delta\phi_3 - \lambda r\,(1-b_2)\,\phi_3 = \sigma_3\phi_3;\ \Omega \\ \frac{\partial\phi_3}{\partial\eta} + \sqrt{\lambda}\gamma_2\phi_3 = 0;\ \partial\Omega \end{cases} \tag{70}$$

and

$$\begin{cases} -\Delta\phi_4 - \lambda\,(1-b_1)\,\phi_4 = \sigma_4\phi_4;\ \Omega \\ \frac{\partial\phi_4}{\partial\eta} + \sqrt{\lambda}\gamma_1\phi_4 = 0;\ \partial\Omega. \end{cases} \tag{71}$$

By Lemma 2.3, we have that $\sigma_3(W_{1,\gamma_1}) < \sigma_3(1)$ and $\sigma_4(W_{r,\gamma_2}) < \sigma_4(1)$, thus by Lemma 2.1 it suffices to show that $\sigma_3(1), \sigma_4(1) < 0$ in order to prove existence. Comparing (70) with (8), uniqueness of the principal eigenvalue ensures that

$$\begin{aligned} \sigma_3(1) + \lambda r(1-b_2) &= E_1(R,\gamma)R \\ \gamma &= \gamma_2, \end{aligned} \tag{72}$$

or equivalently,

$$\sigma_3(1) = E_1(R,\gamma)R - \lambda r(1-b_2). \tag{73}$$

Taking $\sigma_3(1) = 0$, we see that $R = r(1-b_2)$ and $\lambda = E_1(r(1-b_2),\gamma_2) = \frac{E_1(r,\gamma_2)}{1-b_2}$, using Lemma 2.7. Also, using (73) we have that $\sigma_3(1) < 0$ for $\lambda > \frac{E_1(r,\gamma_2)}{1-b_2}$.

Similarly, comparing (71) with (8), uniqueness of the principal eigenvalue ensures that

$$\begin{aligned} \sigma_4(1) + \lambda(1-b_1) &= E_1(R,\gamma)R \\ \gamma &= \gamma_1, \end{aligned} \tag{74}$$

or equivalently,

$$\sigma_4(1) = E_1(R,\gamma)R - \lambda(1-b_1). \tag{75}$$

Again, taking $\sigma_4(1) = 0$, we see that $R = (1-b_1)$ and $\lambda = E_1((1-b_1),\gamma_1) = \frac{E_1(1,\gamma_1)}{1-b_1}$, using Lemma 2.7. Using (75), we have that $\sigma_4(1) < 0$ for $\lambda > \frac{E_1(1,\gamma_1)}{1-b_1}$. Thus, for $\lambda > \max\left\{\frac{E_1(r,\gamma_2)}{1-b_2}, \frac{E_1(1,\gamma_1)}{1-b_1}\right\}$, Lemma 2.1 ensures existence of a positive solution of (4) with $(m\phi_4, m\phi_3) \le (u,v) \le (W_{1,\gamma_1}, W_{r,\gamma_2});\ \overline{\Omega}$ for $m \approx 0$.
(i) Now assume (u,v) is any positive solution of (4) with $\lambda > \max\{E_1(r,\gamma_2), E_1(1,\gamma_1)\}$. Then (u,v) also satisfies:

$$\begin{cases} -\Delta u - \lambda u\,(1-u) = -\lambda b_1 uv < 0;\ \Omega \\ \frac{\partial u}{\partial \eta} + \sqrt{\lambda}\gamma_1 u = 0;\ \partial\Omega \end{cases} \tag{76}$$

implying that u is a strict subsolution of (9). Since $Z \equiv M > 1$ is a supersolution of (9) and $u \le M;\ \overline{\Omega}$, uniqueness of W_{1,γ_1} gives that $u \le W_{1,\gamma_1};\ \overline{\Omega}$. A similar argument gives that $v \le W_{r,\gamma_2};\ \overline{\Omega}$.
(ii) We assume (u,v) is any positive solution of (4) with $\lambda > \max\left\{\frac{E_1(1,\gamma_1)}{1-b_1}, \frac{E_1(r,\gamma_2)}{1-b_2}\right\}$ (which implies that $W_{1,\gamma_1,b_1}, W_{r,\gamma_2,b_2}$ both exist). Now, since $v \le W_{r,\gamma_2} \le 1;\ \overline{\Omega}$, we have that (u,v) satisfies:

$$\begin{cases} -\Delta u - \lambda u\,(1-u-b_1) \ge -\Delta u - \lambda u(1-u-b_1 v) = 0;\ \Omega \\ \frac{\partial u}{\partial \eta} + \sqrt{\lambda}\gamma_1 u = 0;\ \partial\Omega \end{cases} \tag{77}$$

implying that u is a supersolution of (6) with $R = 1, b = b_1$, and $\gamma = \gamma_1$. Using the principal eigenfunction, ϕ_0, corresponding to σ_1 (which is negative by our choice of λ) gives that $\psi = m\phi_0$ is a subsolution of (6) with $R = 1, b = b_1$, and $\gamma = \gamma_1$ and satisfies $m\phi_0 < u;\ \overline{\Omega}$ both by choosing $m \approx 0$. Uniqueness of W_{1,γ_1,b_1} (the positive solution of (6) with $R = 1, b = b_1$, and $\gamma = \gamma_1$) gives that $W_{1,\gamma_1,b_1} \le u;\ \overline{\Omega}$. A similar argument shows that $W_{r,\gamma_2,b_2} \le v;\ \overline{\Omega}$.
(iii) Finally, assume that $r = 1$ and $\gamma_1 = \gamma_2$. We will show that $\left(\frac{1-b_1}{1-b_1b_2}W_{1,\gamma_1}, \frac{1-b_2}{1-b_1b_2}W_{r,\gamma_2}\right)$ will satisfy (4). To that end, we see that:

$$\begin{aligned} -\Delta u - \lambda u(1-u-b_1 v) &= \frac{1-b_1}{1-b_1b_2}\lambda W_{1,\gamma_1}(1-W_{1,\gamma_1}) \\ &\quad - \lambda\left(\frac{1-b_1}{1-b_1b_2}\right)W_{1,\gamma_1}\left(1 - \frac{1-b_1}{1-b_1b_2}W_{1,\gamma_1} - \frac{b_1(1-b_2)}{1-b_1b_2}W_{1,\gamma_1}\right) \\ &= \frac{1-b_1}{1-b_1b_2}\lambda W_{1,\gamma_1}\left[1 - W_{1,\gamma_1} - 1 + \frac{1-b_1}{1-b_1b_2}W_{1,\gamma_1} + \frac{b_1(1-b_2)}{1-b_1b_2}W_{1,\gamma_1}\right] \\ &\quad + \frac{1-b_1}{1-b_1b_2}\lambda W_{1,\gamma_1}^2\left[\frac{b_1b_2 - 1 + 1 - b_1 + b_1 - b_1b_2}{1-b_1b_2}\right] \\ &= 0 \end{aligned} \tag{78}$$

and

$$\frac{\partial u}{\partial \eta} + \sqrt{\lambda}\gamma_1 u = -\left(\frac{1-b_1}{1-b_1b_2}\right)W_{1,\gamma_1}\sqrt{\lambda}\gamma_1 + \left(\frac{1-b_1}{1-b_1b_2}\right)W_{1,\gamma_1}\sqrt{\lambda}\gamma_1 = 0;\ \partial\Omega. \tag{79}$$

A similar argument holds for v. Theorem 1.5 gives uniqueness of the solution in this case.

(B) Assume that $b_1 = b_2 = 1, \gamma_1 = \gamma_2$, and $r = 1$ and $\lambda > E_1(1,\gamma_1)$. Notice that $\sigma_1 < 0$ in this case ensuring existence of W_{1,γ_1}. Fix $s \in (0,1)$ and let $(u,v) = (sW_{1,\gamma_1}, (1-s)W_{1,\gamma_1})$. We will first show that (u,v) is a solution of (4). To that end, we see that:

$$\begin{aligned} -\Delta u - \lambda u(1-u-v) &= -\Delta sW_{1,\gamma_1} - \lambda sW_{1,\gamma_1}\left(1 - sW_{1,\gamma_1} - (1-s)W_{1,\gamma_1}\right) \\ &= s\left[-\Delta W_{1,\gamma_1} - \lambda W_{1,\gamma_1}\left(1 - W_{1,\gamma_1}\right)\right] \\ &= 0 \end{aligned} \tag{80}$$

and

$$\begin{aligned} -\Delta v - \lambda v(1-v-u) &= -\Delta(1-s)W_{1,\gamma_1} - \lambda(1-s)W_{1,\gamma_1}\left(1 - (1-s)W_{1,\gamma_1} - sW_{1,\gamma_1}\right) \\ &= (1-s)\left[-\Delta W_{1,\gamma_1} - \lambda W_{1,\gamma_1}\left(1 - W_{1,\gamma_1}\right)\right] \\ &= 0 \end{aligned} \tag{81}$$

with

$$\begin{aligned} \frac{\partial u}{\partial \eta} + \sqrt{\lambda}\gamma_1 u &= \frac{\partial sW_{1,\gamma_1}}{\partial \eta} + \sqrt{\lambda}\gamma_1 sW_{1,\gamma_1} \\ &= s\left[\frac{\partial W_{1,\gamma_1}}{\partial \eta} + \sqrt{\lambda}\gamma_1 W_{1,\gamma_1}\right] \\ &= 0 \end{aligned} \tag{82}$$

and

$$\begin{aligned} \frac{\partial v}{\partial \eta} + \sqrt{\lambda}\gamma_1 v &= \frac{\partial(1-s)W_{1,\gamma_1}}{\partial \eta} + \sqrt{\lambda}\gamma_1(1-s)W_{1,\gamma_1} \\ &= (1-s)\left[\frac{\partial W_{1,\gamma_1}}{\partial \eta} + \sqrt{\lambda}\gamma_1 W_{1,\gamma_1}\right] \\ &= 0. \end{aligned} \tag{83}$$

Now, we will show that all positive solutions of (4) must have this form. Assume that (u,v) is a positive solution of (4). Following the same argument as in the proof of Lemma 2.6, the principal eigenvalue of (42) with $b_1 = 1$, μ_1, must be zero. But, both u and v satisfy (42) and since μ_1 is simple, we must have that $u = cv$ where $c > 0$. Substituting (u,v) into (4) yields:

$$\begin{aligned} -\Delta u - \lambda u(1-u-v) &= -\Delta u - \lambda u\left(1 - u - \frac{1}{c}u\right) \\ &= -\Delta u - \lambda u\left(1 - \left(1 + \frac{1}{c}\right)u\right) \end{aligned} \tag{84}$$

and

$$\begin{aligned} -\Delta v - \lambda v(1-v-u) &= -\Delta v - \lambda v\left(1 - v - cv\right) \\ &= -\Delta v - \lambda v\left(1 - (1+c)v\right). \end{aligned} \tag{85}$$

It is now easy to see that $u = \frac{c}{c+1}W_{1,\gamma_1}$ and $v = \frac{1}{1+c}W_{r,\gamma_2}$. Let $s = \frac{c}{c+1} \in (0,1)$ which gives that $1-s = \frac{1}{1+c}$, as desired.

(C) In this case, we assume that $b_1 < 1 \le b_2$, $\gamma_1 > 0$, and $r > r^*$ (note that if $\gamma_2 = 0$ then there is no restriction on r), for which Lemma 2.7 implies that $E_1(r,\gamma_2) < E_1(1,\gamma_1)$. Fix $b_2 \ge 1$. By Lemma 2.1, it suffices to show that $\sigma_3(W_{1,\gamma_1}), \sigma_4(W_{r,\gamma_2}) < 0$. Since $E_1(r,\gamma_2) < E_1(1,\gamma_1)$, we have that $W_{1,\gamma_1}(x, E_1(1,\gamma_1)) \equiv 0$ and $W_{r,\gamma_2}(x, E_1(1,\gamma_1)) > 0$; Ω. This implies that there exists a

$\lambda_2(b_2) > (\approx) E_1(1,\gamma_1)$ such that $b_2 W_{1,\gamma_1}(x,\lambda) < W_{r,\gamma_2}(x,\lambda);\ \Omega$ for $\lambda \in (E_1(1,\gamma_1), \lambda_2(b_2))$. Now, fix $\lambda_0 \in (E_1(1,\gamma_1), \lambda_2(b_2))$ and choose b_1 such that

$$b_1 < n_1(\lambda_0) := \min_{\Omega} \{W_{1,\gamma_1}(x,\lambda_0)\}. \tag{86}$$

Since $W_{r,\gamma_2}(x,\lambda) < 1;\ \Omega$, this choice ensures that $b_1 < \frac{W_{1,\gamma_1}(x,\lambda)}{W_{r,\gamma_2}(x,\lambda)};\ \Omega$ for $\lambda \in (\lambda_1(b_1,b_2), \lambda_2(b_2))$ where $\lambda_1(b_1,b_2) := \lambda_0 - \delta_1$ for some $\delta_1(b_1,b_2) > (\approx)\ 0$. Thus, for $\lambda \in (\lambda_1(b_1,b_2), \lambda_2(b_2))$ and $b_1 < n_1(\lambda_0)$, we must have

$$b_2 W_{1,\gamma_1}(x,\lambda) - W_{r,\gamma_2}(x,\lambda) < 0;\ \Omega \tag{87}$$

$$b_1 W_{r,\gamma_2}(x,\lambda) - W_{1,\gamma_1}(x,\lambda) < 0;\ \Omega. \tag{88}$$

Lemma 2.2 now gives that $\sigma_3(W_{1,\gamma_1}), \sigma_4(W_{r,\gamma_2}) < 0$ for $\lambda \in (\lambda_1(b_1,b_2), \lambda_2(b_2))$. The furthermore statement follows from the proof of (A)(i)-(ii) for the bounds on u and from Lemma 2.1 for the bounds on v, as desired.

(D) In this case, we assume that $b_2 < 1 \le b_1$, $\gamma_2 > 0$, and $r < r^*$ (note that if $\gamma_1 = 0$ then there is no restriction on r), for which Lemma 2.7 implies that $E_1(1,\gamma_1) < E_1(r,\gamma_2)$. Fix $b_1 \ge 1$. By Lemma 2.1, it suffices to show that $\sigma_3(W_{1,\gamma_1}), \sigma_4(W_{r,\gamma_2}) < 0$. Since $E_1(1,\gamma_1) < E_1(r,\gamma_2)$, we have that $W_{r,\gamma_2}(x, E_1(r,\gamma_2)) \equiv 0$ and $W_{1,\gamma_1}(x, E_1(r,\gamma_2)) > 0;\ \Omega$. This implies that there exists a $\lambda_2(b_1) > (\approx) E_1(r,\gamma_2)$ such that $b_1 W_{r,\gamma_2}(x,\lambda) < W_{1,\gamma_1}(x,\lambda);\ \Omega$ for $\lambda \in (E_1(r,\gamma_2), \lambda_2(b_1))$. Now, fix $\lambda_0 \in (E_1(r,\gamma_2), \lambda_2(b_2))$ and choose b_2 such that

$$b_2 < n_2(\lambda_0) := \min_{\Omega} \{W_{r,\gamma_2}(x,\lambda_0)\}. \tag{89}$$

Since $W_{1,\gamma_1}(x,\lambda) < 1;\ \Omega$, this choice ensures that $b_2 < \frac{W_{r,\gamma_2}(x,\lambda)}{W_{1,\gamma_1}(x,\lambda)};\ \Omega$ for $\lambda \in (\lambda_1(b_1,b_2), \lambda_2(b_2))$ where $\lambda_1(b_1,b_2) := \lambda_0 - \delta_2$ for some $\delta_2(b_1,b_2) > (\approx)\ 0$. Thus, for $\lambda \in (\lambda_1(b_1,b_2), \lambda_2(b_2))$ and $b_2 < n_2(\lambda_0)$, we must have

$$b_2 W_{1,\gamma_1}(x,\lambda) - W_{r,\gamma_2}(x,\lambda) < 0;\ \Omega \tag{90}$$

$$b_1 W_{r,\gamma_2}(x,\lambda) - W_{1,\gamma_1}(x,\lambda) < 0;\ \Omega. \tag{91}$$

Lemma 2.2 now gives that $\sigma_3(W_{1,\gamma_1}), \sigma_4(W_{r,\gamma_2}) < 0$ for $\lambda \in (\lambda_1(b_1,b_2), \lambda_2(b_2))$. The furthermore statement follows from the proof of (A)(i) for the bounds on v and from Lemma 2.1 for the bounds on u, as desired.

(E) In the case of $b_1, b_2 > 1$, the argument in (A)(ii) gives existence of at least one positive solution of the specified form. However, uniqueness is still open. □

3.3. *Proof of Theorem 1.5*

(A) We assume that $b_1, b_2 < 1, r = 1$, and $\gamma_1 = \gamma_2$. Now, suppose that (u,v) is any positive solution of (4), for which we rewrite as:

$$\begin{cases} -\Delta u - \lambda u(1-u-v) - \lambda(1-b_1)uv = 0;\ \Omega \\ -\Delta v - \lambda v(1-v-u) - \lambda(1-b_2)uv = 0;\ \Omega \\ \frac{\partial u}{\partial \eta} + \sqrt{\lambda}\gamma_1 u = 0;\ \partial\Omega \\ \frac{\partial v}{\partial \eta} + \sqrt{\lambda}\gamma_1 v = 0;\ \partial\Omega. \end{cases} \tag{92}$$

Now, multiply the first and third equations in (92) by $(1-b_2)$ and the second and fourth equations by $(1-b_1)$ and subtract the second from the first and then the fourth from the third giving:

$$\begin{cases} -\Delta\psi - \lambda\psi(1-u-v) = 0;\ \Omega \\ \frac{\partial \psi}{\partial \eta} + \sqrt{\lambda}\gamma_1 \psi = 0;\ \partial\Omega \end{cases} \tag{93}$$

where $\psi = (1-b_2)u - (1-b_1)v$. By Lemma 2.6, $\psi \equiv 0$ giving that $(1-b_2)u \equiv (1-b_1)v$. In other words, we have that $v = Ru$ and $R = \frac{1-b_2}{1-b_1}$. But, this gives

$$1 + Rb_1 = 1 + \frac{b_1(1-b_2)}{1-b_1} = \frac{1-b_1b_2}{1-b_1} \tag{94}$$

and hence

$$\begin{aligned} 0 &= -\Delta u - \lambda u(1-u-b_1v) \\ &= -\Delta u - \lambda u\left(1-(1+Rb_1)u\right) \\ &= -\Delta u - \lambda u\left(1-\left(\frac{1-b_1b_2}{1-b_1}\right)u\right);\ \Omega. \end{aligned} \tag{95}$$

Thus, u satisfies

$$\begin{cases} -\Delta u - \lambda u\left(1-\left(\frac{1-b_1b_2}{1-b_1}\right)u\right) = 0;\ \Omega \\ \frac{\partial u}{\partial \eta} + \sqrt{\lambda}\gamma_1 u = 0;\ \partial\Omega. \end{cases} \tag{96}$$

From Theorem 1.2, it is now easy to see that $u = \frac{1-b_1}{1-b_1b_2}W_{1,\gamma_1}$ and, since $v = Ru$, $v = \frac{1-b_2}{1-b_1b_2}W_{1,\gamma_1}$. This fact combined with Theorem 1.4(A) (ii) & (iii) gives the result.

(B) Here, we assume that $r > 0, \gamma_1, \gamma_2 > 0$, and $b_1, b_2 < 1$ with (u_1, v_1) and (u_2, v_2) both positive solutions of (4). Let $p = u_1 - u_2$ and $q = v_1 - v_2$. Then we must have

$$\begin{aligned} -\Delta p &= \lambda u_1(1-u_1-b_1v_1) - \lambda u_2(1-u_2-b_1v_2) \\ &= \lambda u_1 - \lambda u_1^2 - \lambda b_1u_1v_1 - \lambda u_2 + \lambda u_2^2 + \lambda b_1u_2v_2 + \lambda u_1u_2 \\ &+ \lambda b_1u_2v_1 - \lambda u_1u_2 - \lambda b_1u_2v_1 \\ &= \lambda(u_1-u_2)(1-u_1-b_1v_1) - \lambda u_2(u_1-u_2) - \lambda b_1u_2(v_1-v_2) \\ &= \lambda p(1-u_1-b_1v_1) - \lambda u_2 p - \lambda b_1u_2 q;\ \Omega \end{aligned}$$

and, similarly,

$$-\Delta q = \lambda rq(1-v_2-b_2u_2) - \lambda rb_2vp - \lambda rv_1q;\ \Omega. \tag{97}$$

Also,

$$\frac{\partial p}{\partial \eta} + \sqrt{\lambda}\gamma_1 p = \frac{\partial u_1}{\partial \eta} - \frac{\partial u_2}{\partial \eta} + \sqrt{\lambda}\gamma_1(u_1-u_2) = 0;\ \partial\Omega \tag{98}$$

and, similarly,

$$\frac{\partial q}{\partial \eta} + \sqrt{\lambda}\gamma_2 q = 0;\ \partial\Omega. \tag{99}$$

Thus, (p, q) satisfies

$$\begin{cases} -\Delta p - \lambda p(1-u_1-b_1v_1) + \lambda u_2 p + \lambda b_1u_2 q = 0;\ \Omega \\ -\Delta q - \lambda rq(1-v_2-b_2u_2) + \lambda rb_2v_1 p + \lambda rv_1 q = 0;\ \Omega \\ \frac{\partial p}{\partial \eta} + \sqrt{\lambda}\gamma_1 p = 0;\ \partial\Omega \\ \frac{\partial q}{\partial \eta} + \sqrt{\lambda}\gamma_2 q = 0;\ \partial\Omega. \end{cases} \tag{100}$$

From the proof of Lemma 2.6, if z is a smooth function that satisfies

$$\begin{cases} -\Delta z = \lambda z(1-u-b_1v);\ \Omega \\ \frac{\partial z}{\partial \eta} + \sqrt{\lambda}\gamma_1 z = 0;\ \partial\Omega \end{cases} \tag{101}$$

then z also satisfies

$$\int_\Omega |\nabla z|^2\,dx - \int_\Omega \lambda(1-u-b_1v)z^2dx + \int_{\partial\Omega} \sqrt{\lambda}\gamma_1 z^2 ds \geq 0. \tag{102}$$

Similarly, if w satisfies

$$\begin{cases} -\Delta w = \lambda r w(1 - v - b_2 u); \ \Omega \\ \frac{\partial w}{\partial \eta} + \sqrt{\lambda}\gamma_2 w = 0; \ \partial\Omega \end{cases} \tag{103}$$

then w also satisfies

$$\int_\Omega |\nabla w|^2 \, dx - \int_\Omega \lambda(1 - v - b_2 u) w^2 dx + \int_{\partial\Omega} \sqrt{\lambda}\gamma_2 w^2 ds \geq 0. \tag{104}$$

Hence, the following hold:

$$\int_\Omega z \left[-\Delta z - \lambda z(1 - u_1 - b_1 v_1)\right] dx \geq 0 \tag{105}$$

$$\int_\Omega w \left[-\Delta w - \lambda r w(1 - v_2 - b_2 u_2)\right] dx \geq 0. \tag{106}$$

Now, we multiply the first equation in (100) by p and the second by q and integrating both of them over Ω yields

$$\int_\Omega p \left[-\Delta p - \lambda p(1 - u_1 - b_1 v_1)\right] + \lambda u_2 p^2 + \lambda b_1 u_2 pq dx = 0 \tag{107}$$

$$\int_\Omega q \left[-\Delta q - \lambda r q(1 - v_2 - b_2 u_2)\right] + \lambda r b_2 v_1 pq + \lambda r v_1 q^2 dx = 0. \tag{108}$$

Adding (107) to (108) gives

$$\int_\Omega p \left[-\Delta p - \lambda p(1 - u_1 - b_1 v_1)\right] + q \left[-\Delta q - \lambda r q(1 - v_2 - b_2 u_2)\right] + \lambda u_2 p^2 + \lambda b_1 u_2 pq + \lambda r b_2 v_1 pq + \lambda r v_1 q^2 dx = 0. \tag{109}$$

Employing (105) and (106) we further obtain

$$\lambda \int_\Omega u_2 p^2 + (b_1 u_2 + r b_2 v_1) pq + r v_1 q^2 dx \leq 0. \tag{110}$$

Define $Q_x(s,t) := u_2(x)s^2 + \left[b_1 u_2(x) + r b_2 v_1(x)\right] st + r v_1(x) t^2$. If $Q_x(s,t)$ is positive definite for all $x \in \Omega$ then $p, q \equiv 0$ proving uniqueness. To that end, if the following holds then we are ensured the result:

$$(b_1 u_2 + r b_2 v_1)^2 - 4 u_2 r v_1 < 0, \tag{111}$$

or equivalently,

$$4 > \frac{b_1^2}{r}\frac{u_2}{v_1} + 2 b_1 b_2 + r b_2^2 \frac{v_1}{u_1}; \ \Omega. \tag{112}$$

It is now clear that if (15) holds then so does (111), giving the result. The final statement of the theorem follows immediately from the fact that both W_{1,γ_1} and W_{r,γ_2} are bounded above and below (and in this case, away from zero). Thus, taking $b_1, b_2 \approx 0$ and $\lambda > \max\left\{\frac{E_1(1,\gamma_1)}{1-b_1}, \frac{E_1(r,\gamma_2)}{1-b_2}\right\}$, Theorem 1.3 and the previous argument together ensure existence of a unique positive solution for (4). □

3.4. Proof of Theorem 1.6

Here, we assume that $r > 0, b_1, b_2 \geq 0$, $\gamma_1, \gamma_2 \geq 0$, and $\lambda > 0$ are such that $\sigma_1, \sigma_2 < 0$. We note that (A) and (B) are standard, omit their proofs, and direct the interested reader to, e.g., [39]. In particular, the author in [39] proves in Theorem 7.6.2 that if a positive solution, (u, v), of (4) is stable then it is also asymptotically stable. (Even though Theorem 7.6.2 specifically addresses a quasimonotone nondecreasing system, a change of variables as suggested in [39] allows the theorem to apply to our quasimonotone nonincreasing system, see also [36]). Also, note that (i)–(iii) of (C) follows immediately from our construction of sub- and supersolutions of (4) in Lemma 2.1 and Theorems 5.2 and 5.5 in Chapter 10 of [36].

To prove (iv) of (C), fix $\lambda > 0$ such that $\sigma_3, \sigma_4 < 0$ and assume that there exists a sequence of asymptotically stable positive solutions of (4), $\{(u_n, v_n)\}_{n=1}^{\infty}$, converging to $(0, W_{r,\gamma_2})$ as $n \to \infty$. Choose $N > 1$ such that for all $n > N$ we have

$$\frac{-\sigma_4}{\lambda} > \left|u_n - b_1\left(W_{r,\gamma_2} - v_n\right)\right|;\ \overline{\Omega}. \tag{113}$$

Thus, there exists an $\epsilon > 0$ such that

$$\frac{-\sigma_4}{\lambda} > \epsilon > \left|u_n - b_1\left(W_{r,\gamma_2} - v_n\right)\right|;\ \overline{\Omega}. \tag{114}$$

Now, we have that:

$$\begin{aligned} u_t &= \frac{1}{\lambda}\Delta u + u(1 - u - b_1 v) \\ &= \frac{1}{\lambda}\Delta u + u\left(1 - b_1 W_{r,\gamma_2} - [u - b_1(W_{r,\gamma_2} + v)]\right) \\ &\geq \frac{1}{\lambda}\Delta u + u\left(1 - b_1 W_{r,\gamma_2} - \epsilon\right);\ t > 0, x \in \Omega \end{aligned} \tag{115}$$

as long as $\epsilon > |u - b_1(W_{r,\gamma_2} + v)|$. Fix an $n > N$ and $u(0,x), v(0,x) > 0;\ \overline{\Omega}$ with $u(0,x) \approx 0$ and $v(0,x) \approx W_{r,\gamma_2}$ on $\overline{\Omega}$. There must exist a $K > 0$ such that $u(0,x) > K\phi_4(x);\ \overline{\Omega}$, where ϕ_4 is the eigenfunction corresponding to σ_4, chosen such that $\phi_4(x) > 0;\ \overline{\Omega}$ and $\|\phi_4\|_\infty = 1$. Also, we can choose $t_0 > 0$ such that

$$\frac{-\sigma_4}{\lambda} > \epsilon > \left|u(t,x) - b_1\left(W_{r,\gamma_2} - v(t,x)\right)\right|;\ x \in \overline{\Omega} \tag{116}$$

for all $t > t_0$.

Define $\psi(t,x) = Ke^{\left(\frac{-\sigma_4}{\lambda} - \epsilon\right)t}\phi_4(x)$ and $h(x) = 1 - b_1 W_{r,\gamma_2}$. For all $t > 0$, we have that:

$$\begin{aligned} \psi_t - \frac{1}{\lambda}\Delta\psi - (h(x) - \epsilon)\psi &= K\left(\frac{-\sigma_4}{\lambda} - \epsilon\right)e^{\left(\frac{-\sigma_4}{\lambda} - \epsilon\right)t}\phi_4(x) \\ &\quad + \frac{K}{\lambda}e^{\left(\frac{-\sigma_4}{\lambda} - \epsilon\right)t}\left[\sigma_4 + \lambda h(x)\right]\phi_4(x) - Ke^{\left(\frac{-\sigma_4}{\lambda} - \epsilon\right)t}\left[h(x) - \epsilon\right]\phi_4(x) \\ &= 0 \end{aligned} \tag{117}$$

and, clearly,

$$\frac{\partial\psi}{\partial\eta} + \sqrt{\lambda}\gamma_1\psi = 0. \tag{118}$$

Thus, $u(t,x)$ is a supersolution and $\psi(t,x)$ is a solution of:

$$\begin{cases} W_t = \frac{1}{\lambda}\Delta W + (h(x) - \epsilon)W; & t > 0, x \in \Omega \\ W(0,x) = K\phi_4(x); & x \in \Omega \\ \frac{\partial W}{\partial\eta} + \sqrt{\lambda}\gamma_1\ W = 0; & t > 0, x \in \partial\Omega. \end{cases} \tag{119}$$

A standard argument now implies that $u(t,x) \geq \psi(t,x) = Ke^{\left(\frac{-\sigma_4}{\lambda} - \epsilon\right)t}\phi_4(x);\ x \in \overline{\Omega}$ for $t > t_0$. But, our choice of ϵ implies that $\frac{-\sigma_4}{\lambda} - \epsilon > 0$ giving that $u(t,x)$ is unbounded as $t \to \infty$. This is a contradiction, and hence, no such sequence can exist. An almost identical argument holds for the case that (u_n, v_n) converges to $(W_{1,\gamma_1}, 0)$ as $t \to \infty$ and is omitted. □

4. The asymmetric competition case

In this section, we explore the special case of asymmetric competition, where the competitive effect of v onto u is negligible, i.e., $b_1 = 0$, and in either the weak ($b_2 < 1$) or semistrong ($b_2 \geq 1$) cases. Here, (4) becomes

$$\begin{cases} -\Delta u = \lambda u(1-u); & \Omega \\ \frac{\partial u}{\partial \eta} + \sqrt{\lambda}\gamma_1 u = 0; & \partial\Omega \end{cases} \tag{120}$$

and

$$\begin{cases} -\Delta v = \lambda r v(1-v-b_2 u); & \Omega \\ \frac{\partial v}{\partial \eta} + \sqrt{\lambda}\gamma_2 v = 0; & \partial\Omega. \end{cases} \tag{121}$$

Notice that $u = W_{1,\gamma_1,0}$, and thus Theorem 1.2 gives the complete structure of positive solutions for (120). We first state an analytical result regarding uniqueness of positive solutions for (121) which improves Theorem 1.5.

Theorem 4.1 (*Uniqueness*). *There is at most one positive solution for (121) for all $\lambda > 0$.*

A proof of Theorem 4.1 is presented at the end of this section.

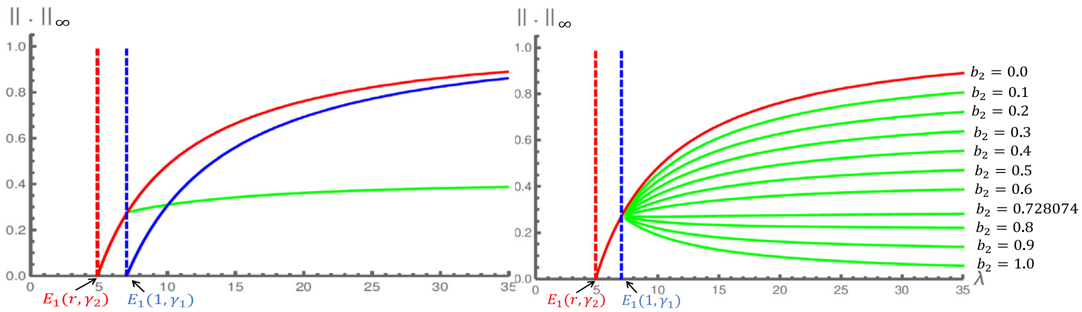
Next, we explore the structure of positive solutions for (121) in the case of $\Omega = (0,1)$. Using the quadrature method discussed in Section 2.1 and Mathematica, we numerically approximate the unique positive solution of (120), u, guaranteed by Theorem 1.2. Using this approximation, we next employ the shooting method discussed in Section 2.2 to numerically approximate positive solutions of (121) and generate bifurcation diagrams of the positive solutions of (4). Based on our analysis, we obtain the following Computational Results 4.1–4.3. Here, we chose values of r, γ_1, γ_2 so that we obtain results for three different cases: $E_1(r,\gamma_2) < E_1(1,\gamma_1)$, $E_1(r,\gamma_2) > E_1(1,\gamma_1)$ and $E_1(r,\gamma_2) = E_1(1,\gamma_1)$.

Computational Results 4.1 ($E_1(r,\gamma_2) < E_1(1,\gamma_1)$). *If r, γ_1, and γ_2 are fixed such that $E_1(r,\gamma_2) < E_1(1,\gamma_1)$ and $b_2 \geq 0$ then the following hold:*

(a) If $b_2 < 1$ (weak competition) or $b_2 = 1$ (semistrong competition) then (121) has a positive solution for $\lambda > E_1(r,\gamma_2)$ (see Fig. 5(a)). Moreover, there exists a positive constant $b_2^* < 1$ such that for $b_2 = b_2^*$, $\|v\|_\infty$ is a constant for any $\lambda > E_1(1,\gamma_1)$. Also, for $\lambda > E_1(1,\gamma_1)$ and any $b_2 < b_2^*$, $\|v\|_\infty$ increases in λ, and for any $b_2 > b_2^*$, $\|v\|_\infty$ decreases in λ. Furthermore, for $b_2 \leq 1$, $\|v\|_\infty \to 1 - b_2$ as $\lambda \to \infty$. (See Fig. 5(b)).

(b) If $b_2 > 1$ (semistrong competition) then there exists a $\lambda_{\max} > E_1(1,\gamma_1)$, a maximum patch size (see Fig. 6), such that (121) has no positive solution for $\lambda > \lambda_{\max}$. Moreover, $\lambda_{\max}$ decreases in b_2 and γ_2 and increases in r and γ_1, for fixed values of the remaining parameters. (See Figs. 6–10).

Figs. 5–6 illustrate Computational Result 4.1. In particular, Figs. 7–10 give some insight into the behavior of $\lambda_{\max}$ as r, b_2, γ_1, and γ_2 vary, with Figs. 8 and 10 showing behavior for two parameters changing simultaneously. Two interesting cases arise here: 1) for weak competition ($b_2 < 1$) existence of such a b_2^* where $\|v\|_\infty$ remains constant for all patch sizes yielding a $\lambda > E_1(1,\gamma_1)$ and 2) for the special case of $b_2 = 1$ (semistrong competition) the counterintuitive fact that as the patch size becomes large, $\|v\|_\infty \to 0$. For (1), a careful balancing of increased competitive pressure on v generated by u's increasing density and v's own increasing density both as patch size increases seems to be a reasonable explantation of this phenomenon. The interesting case (2) shows $b_2 = 1$ as the boundary separating predictions of no maximum patch size for $b_2 < 1$ and existence of a maximum patch size when $b_2 > 1$. Our computational results here are consistent with our analytical results in Theorem 1.3 (E) & (F) for existence of a maximum patch size when $b_2 > 1$, and even suggest that the upper bounds on b_1 in (E) and b_2 in (F) are artificial.



(a) Fixed $b_2 = 0.6$. (b) Different values of $b_2 \leq 1$.

Fig. 5. Bifurcation diagrams for (4) with various b_2-values and $r = 1, \gamma_1 = 4$, and $\gamma_2 = 2$ implying that $E_1(r,\gamma_2) < E_1(1,\gamma_1)$ and $b_2^* \approx 0.728074$. The blue curve represents the u-component of (u,v), as well as $(u,0)$, green represents the v-component of (u,v), and red represents $(0,v)$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

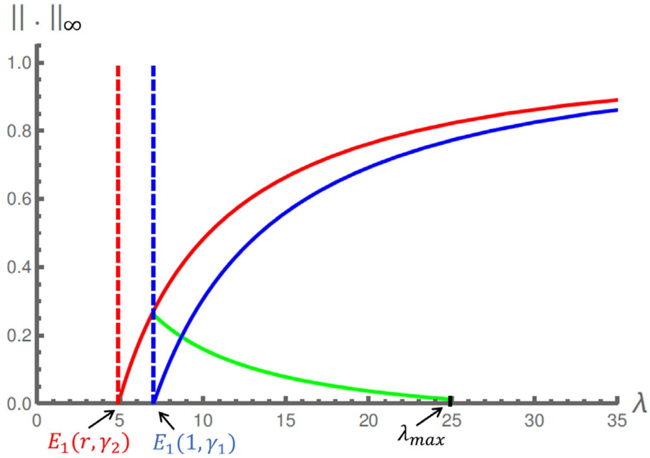


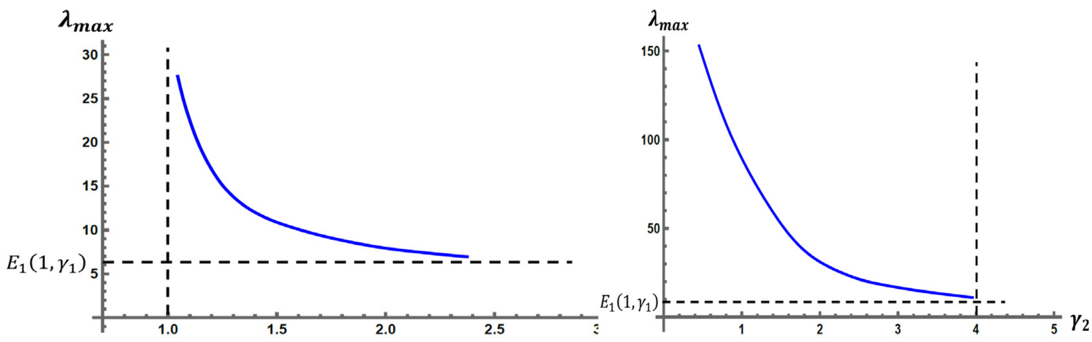
Fig. 6. Bifurcation diagram for (4) showing existence of a maximum patch size, $\lambda_{\max}$, when $b_2 = 1.1$ and $r = 1, \gamma_1 = 4$, and $\gamma_2 = 2$ imply that $E_1(r,\gamma_2) < E_1(1,\gamma_1)$. The blue curve represents the u-component of (u,v), as well as $(u,0)$, green represents the v-component of (u,v), and red represents $(0,v)$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Our computational analysis of the behavior of $\lambda_{\max}$ with respect to r, b_2, γ_1, and γ_2 is fairly consistent with intuition. Fig. 7 shows that $\lambda_{\max}$ increases as b_2 (scale of competitive pressure of u onto v) and γ_2 (v's matrix effect) decrease, both of which promote increasing v density in the patch, whereas Fig. 9 shows $\lambda_{\max}$ increases as r (G-D ratio, recall $r > 1$ implies an advantage for v) and γ_1 (u's matrix effect) increase, both of which promote increasing v density in the patch. The heatmap plots in Figs. 8 & 10 confirm that b_2 and γ_2 work in tandem to affect $\lambda_{\max}$, and similarly for r and γ_1.

Computational Results 4.2 ($E_1(r,\gamma_2) > E_1(1,\gamma_1)$)**.** *If r, γ_1, and γ_2 are fixed such that $E_1(r,\gamma_2) > E_1(1,\gamma_1)$ and $b_2 < 1$ (weak competition) then the following hold:*

(a) There exists a minimum patch size $\lambda_{\min} > E_1(r,\gamma_2)$ such that (4) has a positive solution for $\lambda > \lambda_{\min}$ and no positive solution for $\lambda \leq \lambda_{\min}$. Furthermore, $\|v\|_\infty \to 1 - b_2$ as $\lambda \to \infty$ (see Fig. 11).

(b) The minimum patch size $\lambda_{\min}$ increases in b_2 and γ_2 and decreases in r and γ_1, for fixed values of the remaining parameters. Moreover, $\lambda_{\min} \to \infty$ as $b_2 \to 1$, but for a fixed $b_2 < 1$, if $\gamma_1 \to \infty$, $\lambda_{\min}$ is bounded. (see Figs. 12–15).



(a) Plot of b_2 vs $\lambda_{\max}$ (maximum patch size). (b) Plot of γ_2 vs $\lambda_{\max}$ (maximum patch size).

Fig. 7. Variations of $\lambda_{\max}$ with respect to b_2 and γ_2 when $r = 1$ and $\gamma_1 = 4$. In (a), $\gamma_2 = 2$, while $\gamma_2 \in (0, 4)$ in (b) is taken to maintain $E_1(r, \gamma_2) < E_1(1, \gamma_1)$.

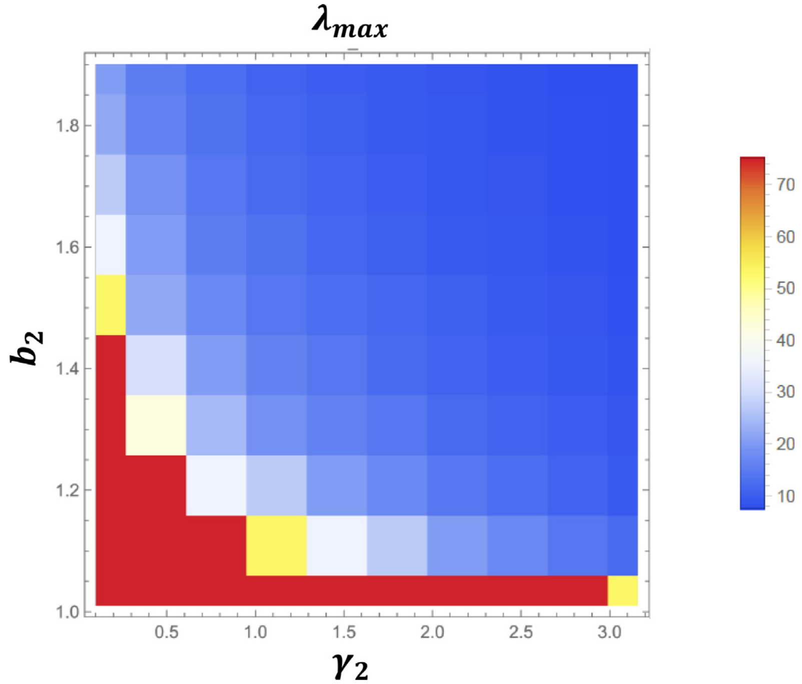
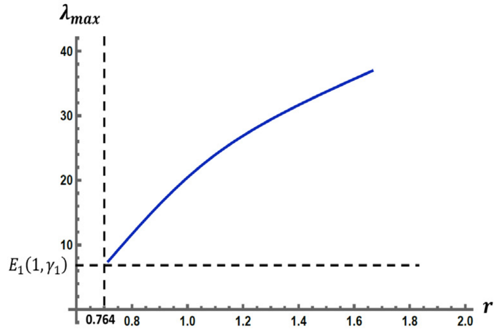


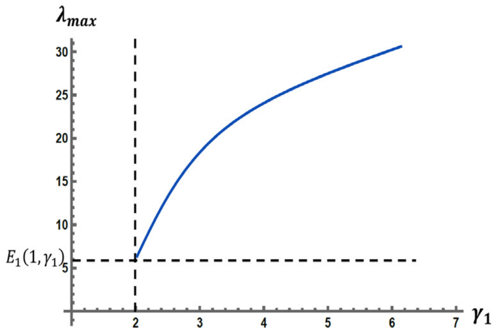
Fig. 8. Heatmap plot showing combined effects of b_2 and γ_2 on $\lambda_{\max}$ for $r = 1$ and $\gamma_1 = 4$.

Figs. 11 & 12 illustrate Computational Result 4.2. In particular, Figs. 12–15 give some insight into the behavior of $\lambda_{\min}$ as r, b_2, γ_1, and γ_2 vary, with Figs. 13 and 15 showing behavior for two parameters changing simultaneously. In fact, Figs. 11(b) & 12(a) give some insight as to why coexistence is lost for all patch sizes when $b_2 > 1$ (see Theorem 1.3(D)), by examining behavior of $\lambda_{\min}$ as $b_2 \to 1$. As can be seen in these figures, $\lambda_{\min} \to \infty$ as $b_2 \to 1$, implying that coexistence in not possible for $b_2 > 1$. These computational results also support our conjecture that the lower bound on r in Theorem 1.3(D) is artificial. Theorem 1.3(G) is also illustrated in Fig. 11 in that $\lambda_{\min} > E_1(r, \gamma_2)$. In other words, competition effects from u onto v cause a larger minimum patch size requirement than what would be needed in the absence of competition.

Our computational analysis of the behavior of $\lambda_{\min}$ with respect to r, b_2, γ_1, and γ_2 is again fairly consistent with intuition. Fig. 12 shows that $\lambda_{\min}$ decreases as b_2 (scale of competitive pressure of u onto v) or γ_2 (v's matrix effect) decrease, both of which promote increasing v density in the patch, whereas Fig. 14



(a) Plot of r versus $\lambda_{\max}$ (maximum patch size).



(b) Plot of γ_1 versus $\lambda_{\max}$ (maximum patch size).

Fig. 9. Variations of $\lambda_{\max}$ with respect to r and γ_1 for $b = 1.1$ and $\gamma_2 = 2$. In (a), $r > 0.764$ and $\gamma_1 = 4$, while $r = 1$ and $\gamma_1 > 2$ in (b) is taken to maintain $E_1(r,\gamma_2) < E_1(1,\gamma_1)$.

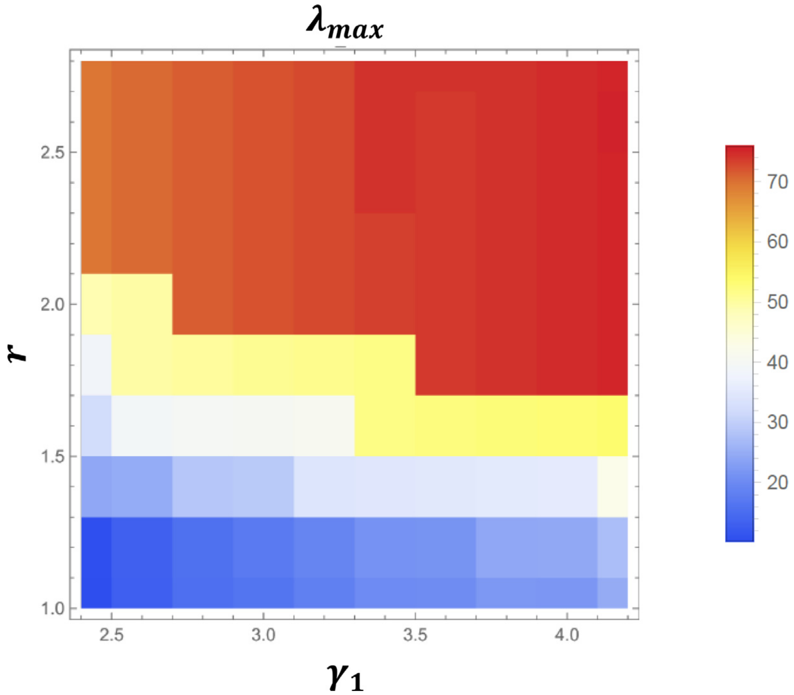
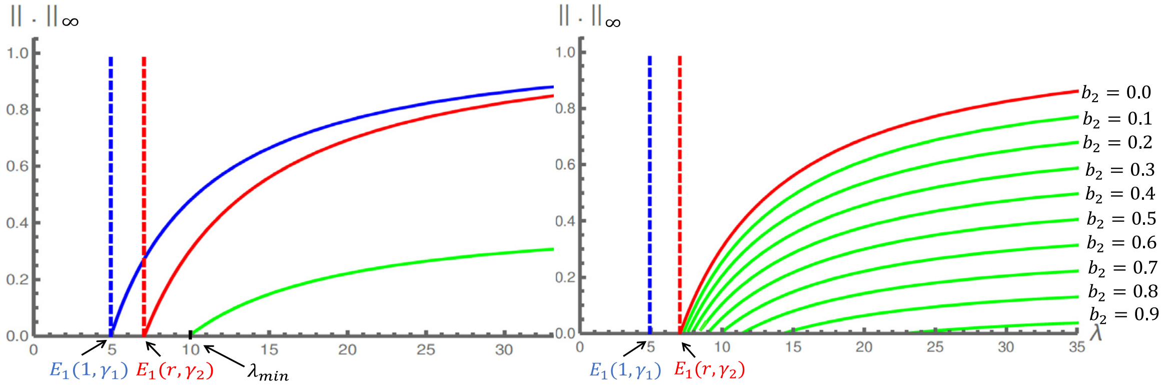


Fig. 10. Heatmap plot showing combined effects of r and γ_1 on λ_{max} for $b_2 = 1.1$ and $\gamma_2 = 2$.

shows $\lambda_{\min}$ decreases as r (G-D ratio, recall $r > 1$ implies an advantage for v) and γ_1 (u's matrix effect) increase, both of which promote increasing v density in the patch. The heatmap plots in Figs. 13 & 15 confirm that b_2 and γ_2 work in tandem to affect $\lambda_{\min}$, and similarly for r and γ_1.

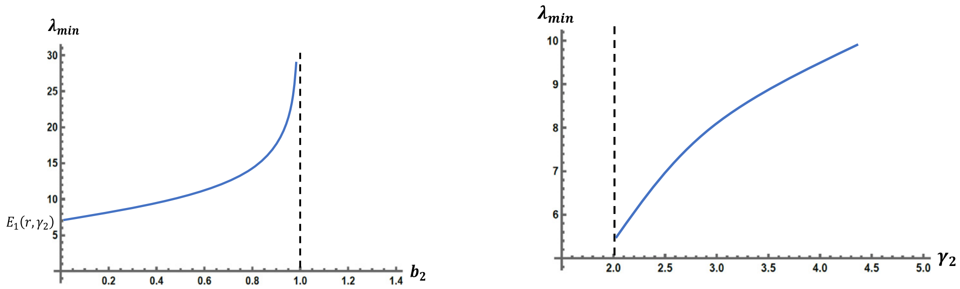
Computational Results 4.3 ($E_1(r,\gamma_2) = E_1(1,\gamma_1)$)**.** *If r, γ_1, and γ_2 are fixed such that $E_1(r,\gamma_2) = E_1(1,\gamma_1)$ and $b_2 \geq 0$ then the following hold:*

(a) If $b_2 < 1$ (weak competition) or $b_2 = 1$ (semistrong competition) then (4) has a positive solution for $\lambda > E_1(1,\gamma_1)$ and no positive solution for $\lambda \leq E_1(1,\gamma_1)$. Furthermore, $\|v\|_\infty \to 1 - b_2$ as $\lambda \to \infty$ (see Fig. 16).



(a) Fixed $b_2 = 0.6$. (b) Different values of $b_2 < 1$.

Fig. 11. Bifurcation diagrams for (4) with various b_2-values and $r = 1, \gamma_1 = 2$, and $\gamma_2 = 4$ implying that $E_1(r,\gamma_2) > E_1(1,\gamma_1)$. The blue curve represents the u-component of (u,v), as well as $(u,0)$, green represents the v-component of (u,v), and red represents $(0,v)$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



(a) Plot of b_2 versus $\lambda_{\min}$ (minimum patch size). (b) Plot of γ_2 versus $\lambda_{\min}$ (minimum patch size).

Fig. 12. Variations of $\lambda_{\min}$ with respect to b_2 and γ_2 for $r = 1$ and $\gamma_1 = 2$. In (a), $b_2 < 1$ and $\gamma_2 = 4$, while $b_2 = 0.6$ and $\gamma_2 > 2$ in (b) are taken to maintain $E_1(1,\gamma_1) < E_1(r,\gamma_2)$.

(b) For $b_2 > 1$, (semistrong competition) there exists $\lambda_{\max} > E_1(1,\gamma_1)$, a maximum patch size, such that (4) has no positive solution for $\lambda > \lambda_{\max}$. Moreover $\lambda_{\max}$ is decreasing in b_2 (see Figs. 17–18).

Figs. 16–18 illustrate Computational Result 4.3. This case gives similar conclusions as those in Computational Result 4.1.

We close this section with a proof of Theorem 4.1.

Proof of Theorem 4.1. Assume that v_1, v_2 are two distinct positive solutions of (121) for $\lambda > E_1(1,\gamma_1)$ and let $u_\lambda = W_{1,\gamma_1}$ be the unique positive solution of (120). Since $z \equiv 1$ is a global supersolution of (121), without loss of generality we can assume $v_2 \leq v_1$; $\overline{\Omega}$ and there exists an $x_0 \in \Omega$ such that $v_2(x_0) < v_1(x_0)$.

Now, employing Green's Identity we have

$$\int_\Omega -\Delta v_1 v_2 + \Delta v_2 v_1 dx = \int_{\partial\Omega} -\frac{\partial v_1}{\partial \eta} v_2 + \frac{\partial v_2}{\partial \eta} v_1 ds, \tag{122}$$

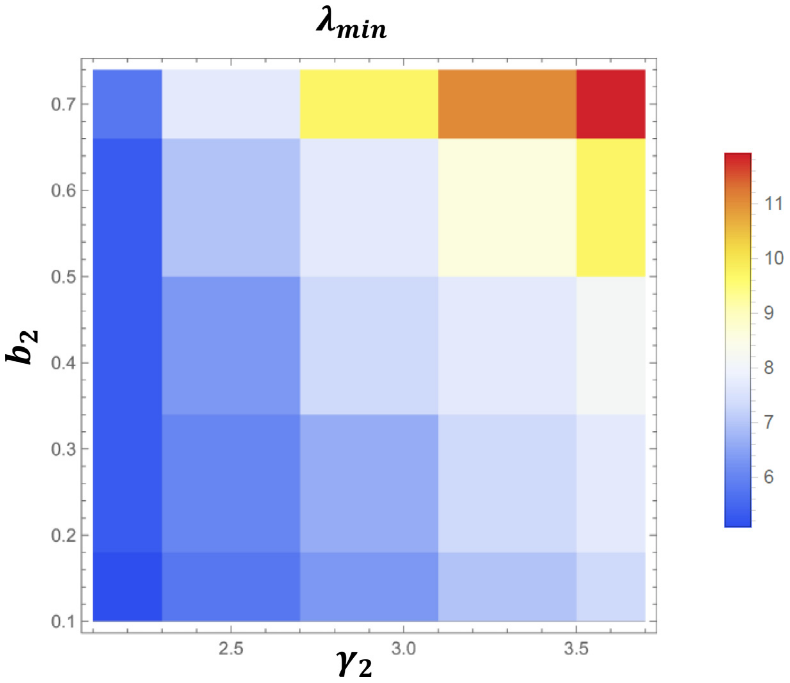
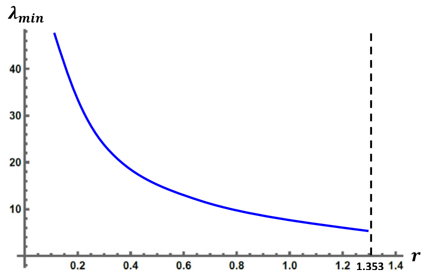
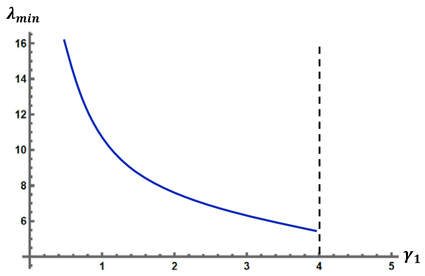


Fig. 13. Heatmap plot showing combined effects of b_2 and γ_2 on $\lambda_{\min}$ for $r = 1$ and $\gamma_1 = 2$.



(a) Plot of r versus $\lambda_{\min}$ (minimum patch size).



(b) Plot of γ_1 versus $\lambda_{\min}$ (minimum patch size).

Fig. 14. Variations of $\lambda_{\min}$ with respect to r and γ_1 for $\gamma_2 = 4$ and $b_2 = 0.6$. In (a), $\gamma_1 = 2$ and $r < 1.353$, while $\gamma_1 < 4$ and $r = 1$ in (b) are taken to maintain $E_1(1, \gamma_1) < E_1(r, \gamma_2)$.

where the right-hand-side of (122) is clearly equal to zero. But, we also have

$$\begin{aligned}\int_\Omega -\Delta v_1 v_2 + \Delta v_2 v_1 dx &= \int_\Omega -\lambda r v_1(1 - v_1 - b_2 u_\lambda) v_2 + \lambda r v_2 (1 - v_2 - b_2 u_\lambda) v_1 dx \\ &= \lambda r \int_\Omega v_1 v_2 \left[1 - v_2 - b_2 u_\lambda - 1 + v_1 + b_2 u_\lambda\right] dx \\ &= \lambda r \int_\Omega v_1 v_2 \left[v_1 - v_2\right] dx > 0. \end{aligned} \tag{123}$$

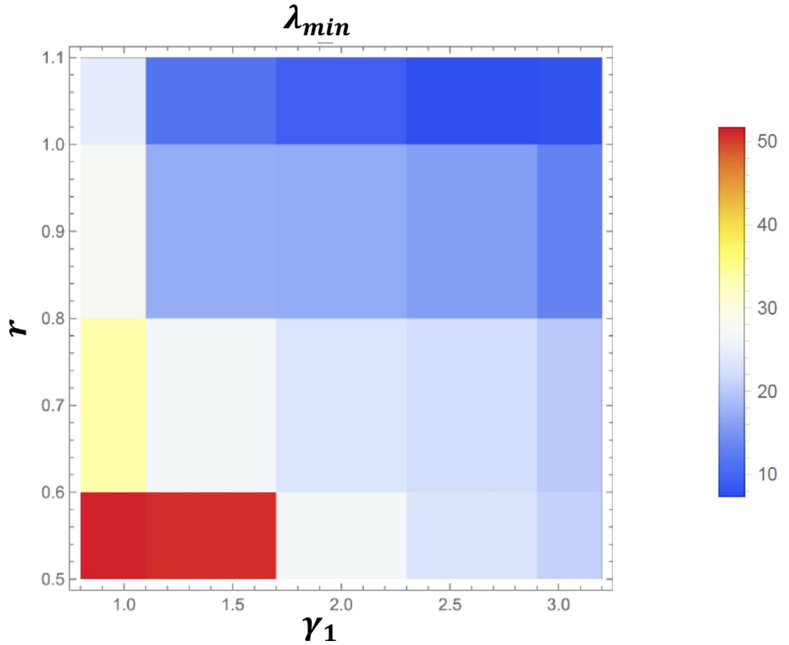
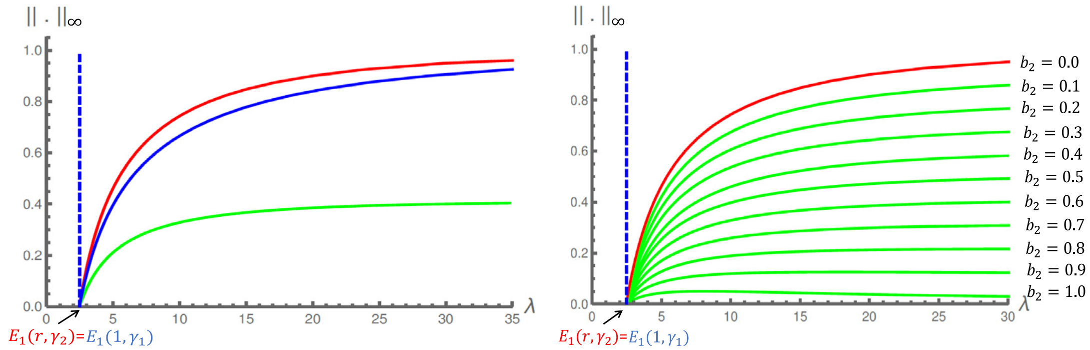


Fig. 15. Heatmap plot showing combined effects of r and γ_1 on $\lambda_{\min}$ for $b_2 = 0.6$ and $\gamma_2 = 4$.



(a) Fixed $b_2 = 0.6$.

(b) Different values of $b_2 \leq 1$.

Fig. 16. Bifurcation diagrams for (4) with various b_2-values and $r = \frac{16}{9}, \gamma_1 = 1$, and $\gamma_2 = \frac{4}{\sqrt{3}}$ implying that $E_1(r, \gamma_2) = E_1(1, \gamma_1)$. The blue curve represents the u-component of (u, v), as well as $(u, 0)$, green represents the v-component of (u, v), and red represents $(0, v)$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

This is a contradiction, giving that (121) has at most one positive solution. This completes the proof. □

5. Summary and conclusion

In this paper, we have explored structure of coexistence states of the diffusive Lotka–Volterra competition model in a fragmented landscape. The model is built upon the reaction diffusion framework and includes a boundary condition designed to model effects of differential matrix hostility and behavior response to habitat edges between species. Our results are based on study of certain eigenvalue problems and sub-supersolutions in the general case and time map analysis and shooting methods in the one-dimensional asymmetric competition case. Since our coexistence results follow from instability of the trivial and semi-trivial steady states, statements of coexistence here will always imply that both species are able to invade the patch when rare with their competitor near equilibrium in the patch, and persist. In the literature, the

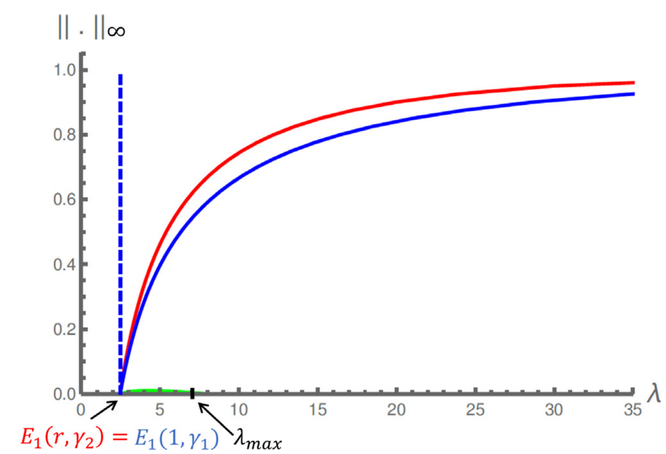


Fig. 17. Bifurcation diagram for (4) showing existence of a maximum patch size, $\lambda_{\max}$, when $r = \frac{16}{9}, \gamma_1 = 1$, $\gamma_2 = \frac{4}{\sqrt{3}}$, and $b_2 = 1.1$ imply that $E_1(r,\gamma_2) = E_1(1,\gamma_1)$. The blue curve represents the u-component of (u,v), as well as $(u,0)$, green represents the v-component of (u,v), and red represents $(0,v)$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

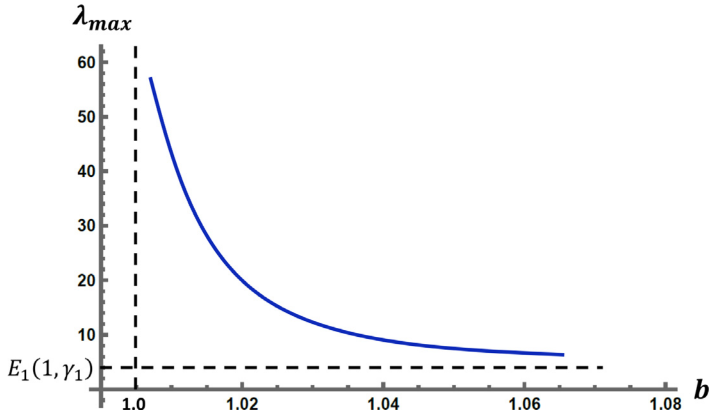


Fig. 18. Plot of b_2 versus $\lambda_{\max}$ (maximum patch size) for $r = \frac{16}{9}, \gamma_1 = 1$, and $\gamma_2 = \frac{4}{\sqrt{3}}$.

diffusive L–V model has been extensively studied in the case of a closed patch (reflecting boundary) and to a somewhat lesser degree in the case of an immediately lethal matrix (absorbing boundary). However, little attention has been paid to the diffusive L–V model in a fragmented landscape with a framework that allows for more realistic modeling of organismal behavior at the patch/matrix interface.

Our results show that in all levels of competition a necessary condition for coexistence is a large enough patch size such that each organism is able to invade and colonize the patch when rare in the absence of its competitor. In the weak competition case, a sufficiently large patch size guarantees coexistence with the coexistence state bounded from below away from zero. For b_1, b_2 sufficiently small, our results guarantee uniqueness of this coexistence state, however, beyond our given sufficient condition, uniqueness in general remains an open question. In the special case that both species' growth-to-diffusion rates are equal (i.e. $r = 1$) and matrix effects are comparable between species (i.e. $\gamma_1 = \gamma_2$), we actually have a closed form solution which approaches the solution of the spatially homogeneous L–V model when patch size approaches infinity. Considering neutral competition in this case, our results show existence of infinitely many coexistence states for sufficiently large patch size, again with a closed form solution. Coexistence for strong competition is also guaranteed for sufficiently large patch sizes with a closed form solution, though uniqueness of the coexistence state is an open problem. Also, Theorem 1.4(A)(i) guarantees that for any level of competition, i.e., either

$b_1 > 0$ or $b_2 > 0$, the coexistence state will occur at a lower density than the density of individuals inhabiting the patch without competition. These results are qualitatively similar to those in previous studies where either a closed patch (i.e. reflecting boundary: $\gamma_1 = 0 = \gamma_2$ in our framework) or a patch surrounded by an immediately hostile matrix (i.e. absorbing boundary: $\gamma_1, \gamma_2 \to \infty$ in our framework) were considered (see, e.g., [22,23,41]).

Perhaps the most interesting aspect of our results is finding coexistence for intermediate ranges of patch size in the semistrong competition case. Recall that when a patch is completely isolated from its surrounding matrix (i.e., a reflecting boundary), coexistence is not possible in the semistrong case. Though it is somewhat intuitive to expect prediction of a minimum patch from a model such as (3) when some level of mortality is induced at the patch/matrix interface (see, e.g., [29]), existence of a maximum patch size in this case is remarkable. Thus, for a semistrong competition system inhabiting a fragmented landscape, we could potentially observe sufficiently large and sufficiently small patches not being able to sustain coexistence, but an intermediate sized patch where coexistence is possible. Though not comprehensive, our results as summarized in Table 1 suggest that coexistence in this case arises from a situation where one species has an advantage in being able to invade and colonize smaller patches in the absence of its competition, while the other species has an advantage in being less affected by direct competition for resources. In the converse, if all mechanisms (patch intrinsic growth rate, patch diffusion rate, behaviorial response to habitat edge, matrix hostility, matrix diffusion rate, and direct competition for patch resources) either do not favor one species over the other or confer advantage from one or all of them to the same species then coexistence is not possible. In fact, we conjecture that such a counterbalancing of advantage (i.e., a tradeoff) is actually necessary for coexistence in the semistrong competition case. Ecologists have theorized that a key mechanism promoting the coexistence among competing species is a tradeoff between dispersal and competitive ability [7]. Here, poorly competitive but highly dispersive species can coexist with highly competitive but poorly dispersive species at the regional scale because of the spatial variation that arises in their distributions (e.g., [7,42–45]). Our models suggest that poor competitive ability could be offset by either a high diffusion rate, low matrix hostility, or some combination of the two. Whether the effect of dispersal-competition tradeoffs on coexistence are modulated by patch size has never been tested empirically.

These results also have implications for conservation. A scenario could arise in which one species (say u) of an endangered semistrong competition system inhabiting a fragmented landscape could have a significant advantage in competition for resources over the other species (say v). If v has an advantage in being able to invade and colonize smaller patches than u then we could have a counterintuitive scenario where coexistence is not possible in large patches. In fact, coexistence would only be possible in an intermediate range of patches where the different mechanisms giving favor to one or the other species is counterbalanced. Although there are numerous empirical and theoretical studies of minimum patch size (e.g., [33,46,47]), studies of a maximum patch size and, by extension, the possibility that an intermediate patch size is necessary for coexistence, has not been investigated beyond the current study. However, if realistic conditions involving competition and dispersal do favor coexistence in patches of intermediate size, it could upend the longstanding SLOSS debate among conservation biologists [48,49] about whether a Single-Large Or Several Small patches is best for the design of wildlife reserves.

If u had both advantage in competition for resources and the ability to invade and colonize smaller patches than v then coexistence would never be possible for any patch size. In fact, experimentation in a lab setting with closed patches would not be sufficient to fully understand coexistence in a more realistic fragmented landscape. Also, focusing empirical research only on one of these mechanisms (direct competition for resources or invasibility of a patch in the absence of competition when rare) alone may prohibit a full understanding of when coexistence is possible. Our results suggest that more study, both theoretical and empirical, is needed in more realistic scenarios where a patch is not completely isolated from its surrounding matrix.

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