



Research article

Elimination, permanence, and exclusion in a competition model under Allee effects

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Abstract: In this paper, we study a system of nonlinear partial differential equations that models the population dynamics of two competitive species both under Allee effects. The consideration of the model includes Logistic growth with Allee effects, Lotka-Volterra competition, diffusion, initial density and boundary conditions on the habitat. In the reaction-diffusion system, we employ the method of upper and lower solutions to address questions on self-elimination or persistence, as well as permanence or competitive exclusion. Specific conditions on biological parameters are explicitly given for extinction, coexistence and competitive exclusion of the species under various boundary conditions. Numerical simulations for the model are demonstrated to illustrate our results from mathematical analysis.

Keywords: reaction-diffusion systems; competition with Allee effects; Permanence and competitive exclusion

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1. Introduction

In traditional methods of estimating population growth rates, people consider that most species reproduce and die proportionally to the current population size. A simple representation of this concept can be expressed with the exponential growth of the populations. There are at least two major reasons to further modify the system: 1) Infinite growth is impossible due to limitation of habitat and resources; 2) Competition between various species should be addressed. We can now introduce the Lotka-Volterra system to address inter-species competition, where $u(t)$ and $v(t)$ represent the population size of two biological species, b_u and b_v are intrinsic birth rates, d_u and d_v are death rates. Throughout this paper we will assume that for all species considered the intrinsic birth rate is larger than death rate. This type of competition, known as Lotka-Volterra competition [2,5], implies that species v diminishes resources

available to u by a factor of α , and u diminishes resources available to v by the factor β .

$$\frac{du}{dt} = u[b_u(1 - (u + \alpha v)) - d_u], \quad (1.1)$$

$$\frac{dv}{dt} = v[b_v(1 - (v + \beta u)) - d_v]. \quad (1.2)$$

Due to the possibility that small population size can make a species vulnerable to extinction, further modifications can be made to the above equations. The Allee effect (given as early as 1932, by Allee [1]) models this possibility and was introduced to the multi-species models in recent years [9, 14, 17, 18, 20, 21].

$$\frac{du}{dt} = u\left[b_u(1 - u - \alpha v)\left(\frac{u}{u + k_u}\right) - d_u\right], \quad (1.3)$$

$$\frac{dv}{dt} = v\left[b_v(1 - v - \beta u)\left(\frac{v}{v + k_v}\right) - d_v\right], \quad (1.4)$$

where k_u and k_v are called half-saturation constants. We see that, for large population sizes (u and v much larger than k_u and k_v respectively) the Allee term, $\left(\frac{u}{u+k_u}\right)$ or $\left(\frac{v}{v+k_v}\right)$, approaches 1 and has little effect on the modeled change in population. As population size u or v approaches 0, the Allee effect term gets near 0 and the death rate (d_u or d_v) dominates the differential equation, which drives a small population toward extinction.

We now have the above system of ordinary differential equations that addresses total population sizes, boundedness, and the vulnerability of species for sizes getting too small, as well as the competitive nature of the two species. Our final extension of the system (1.4) is to include the diffusion of both populations, local density and migration, as well as boundary conditions on the habitat. This leads to the following reaction-diffusion system for density functions $u(t, x)$ and $v(t, x)$ with respective diffusion rates $D_u, D_v > 0$ for both species:

$$\begin{aligned} \frac{\partial u}{\partial t} - D_u \nabla^2 u &= u\left[b_u(1 - u - \alpha v)\left(\frac{u}{u + k_u}\right) - d_u\right] \quad \text{in } (0, \infty) \times \Omega, \\ \frac{\partial v}{\partial t} - D_v \nabla^2 v &= v\left[b_v(1 - v - \beta u)\left(\frac{v}{v + k_v}\right) - d_v\right] \quad \text{in } (0, \infty) \times \Omega, \\ B_u[u] &= 0 \text{ and } B_v[v] = 0 \quad \text{on } (0, \infty) \times \partial\Omega, \\ u(0, x) &= u_0(x) \text{ and } v(0, x) = v_0(x) \quad \text{on } \bar{\Omega}. \end{aligned} \quad (1.5)$$

Here the boundary conditions are given as

$$B_u[u] = u \text{ or } B_u[u] = \frac{\partial u}{\partial \nu} + \gamma_u(x)u, \text{ and } B_v[v] = v \text{ or } B_v[v] = \frac{\partial v}{\partial \nu} + \gamma_v(x)v, \quad (1.6)$$

with ν as the normal vector on $\partial\Omega$, γ_u and $\gamma_v \in C^{1+\alpha}(\partial\Omega)$, and $\gamma_u(x), \gamma_v(x) \geq 0$ on $\partial\Omega$. This way, we include three commonly used types of boundary conditions: Dirichlet, Neumann, and Robin types.

The above reaction-diffusion system (with one-side Allee effect) on infinite spatial domain was recently studied in [9] where the asymptotic stability of the equilibria are given and the existence of traveling wave solutions are proven. In research studies on reaction-diffusion systems modeling multi-species population dynamics in bounded spatial domain (competition, predator-prey, food

chain, etc.), much attention has been given to extinction, permanence, and competition or predation caused exclusion [3, 6, 7, 10–13, 15, 17, 19]. These discussions are also extended to many variations of the Lotka-Volterra models under different boundary conditions [4, 8, 9]. In this paper, we apply the method of upper-lower solutions to the reaction-diffusion system 1.5 and find conditions for the competing species to self-eliminate (because of Allee effect), coexist (with balanced biological parameters and initial density functions), or competitively exclude (through resource competition and Allee effect). It is seen that the ultimate outcomes in the biological system also depend on the size of the habitat and boundary conditions for both species. According to the theoretical results on permanence and competitive exclusion, we will demonstrate numerical simulations under parameters satisfying conditions obtained.

Examining the reaction functions in system (1.5) by taking the partial derivative of

$$f(u, v) = u \left[b_u(1 - u - \alpha v) \left(\frac{u}{u + k_u} \right) - d_u \right]$$

with respect to v , and the partial derivative of

$$g(u, v) = v \left[b_v(1 - v - \beta u) \left(\frac{v}{v + k_v} \right) - d_v \right]$$

with respect to u , we find that (for u and $v \geq 0$):

$$\frac{\partial f}{\partial v} = \frac{-\alpha b_u u^2}{(u + k_u)} \leq 0 \quad \text{and} \quad \frac{\partial g}{\partial u} = \frac{-\beta b_v v^2}{(v + k_v)} \leq 0. \quad (1.7)$$

As defined in ([15], page 383), the system (1.5) is quasi-monotone non-increasing. The upper-lower solutions (\tilde{u}, \tilde{v}) and (\hat{u}, \hat{v}) defined as following ensure the existence-comparison result given in the below lemma.

Definition 1.1. *Upper and lower solutions [16].*

A pair of smooth functions in $\tilde{U} = (\tilde{u}, \tilde{v})$, and $\hat{U} = (\hat{u}, \hat{v})$ in $C((0, \infty) \times \bar{\Omega}) \cap C^{1,2}((0, \infty) \times \Omega)$ are ordered upper and lower solutions of system (1.5) if they satisfy the relation $\tilde{U} \geq \hat{U}$ and if:

$$\begin{aligned} \tilde{u}_t - D_u \nabla^2 \tilde{u} &\geq \tilde{u} \left[b_u(1 - \tilde{u} - \alpha \hat{v}) \left(\frac{\tilde{u}}{\tilde{u} + k_u} \right) - d_u \right] \text{ in } (0, \infty) \times \Omega, \\ \tilde{v}_t - D_v \nabla^2 \tilde{v} &\geq \tilde{v} \left[b_v(1 - \tilde{v} - \beta \hat{u}) \left(\frac{\tilde{v}}{\tilde{v} + k_v} \right) - d_v \right] \text{ in } (0, \infty) \times \Omega, \\ \hat{u}_t - D_u \nabla^2 \hat{u} &\leq \hat{u} \left[b_u(1 - \hat{u} - \alpha \tilde{v}) \left(\frac{\hat{u}}{\hat{u} + k_u} \right) - d_u \right] \text{ in } (0, \infty) \times \Omega, \\ \hat{v}_t - D_v \nabla^2 \hat{v} &\leq \hat{v} \left[b_v(1 - \hat{v} - \beta \tilde{u}) \left(\frac{\hat{v}}{\hat{v} + k_v} \right) - d_v \right] \text{ in } (0, \infty) \times \Omega, \end{aligned} \quad (1.8)$$

$$B_u[\tilde{u}] \geq 0 \geq B_u[\hat{u}] \quad \text{and} \quad B_v[\tilde{v}] \geq 0 \geq B_v[\hat{v}] \quad \text{on } (0, \infty) \times \partial\Omega,$$

$$\tilde{u}(0, x) \geq u_0(x) \geq \hat{u}(0, x) \quad \text{and} \quad \tilde{v}(0, x) \geq v_0(x) \geq \hat{v}(0, x) \quad \text{on } \bar{\Omega}.$$

Lemma 1.2. *Existence and comparison [16].*

If there are a pair of smooth functions $\tilde{U} = (\tilde{u}, \tilde{v})$ and $\hat{U} = (\hat{u}, \hat{v})$ as ordered upper and lower solutions of (1.5) (defined in Definition 1.1), then the reaction-diffusion system (1.5) has a unique solution $U = (u, v)$ with $(\tilde{u}, \tilde{v}) \geq (u, v) \geq (\hat{u}, \hat{v})$ on $(0, \infty) \times \bar{\Omega}$.

It can be easily verified that for any constants M_1 and M_2 satisfying the relations

$$M_1 = \max\{ \|u_0\|_\infty, \frac{b_u - d_u}{b_u} \}, M_2 = \max\{ \|v_0\|_\infty, \frac{b_v - d_v}{b_v} \}, \quad (1.9)$$

the constant functions (M_1, M_2) and $(0, 0)$ are a pair of ordered upper and lower solutions of (1.5) on $(0, \infty) \times \bar{\Omega}$ under any combination of the boundary conditions given in (1.6).

Theorem 1.3. Global existence and boundedness.

For any smooth function $u_0(x), v_0(x)$ on $\bar{\Omega}$ the reaction-diffusion system (1.5) has a unique solution $U = (u, v)$ with $(M_1, M_2) \geq (u, v) \geq (0, 0)$ on $(0, \infty) \times \bar{\Omega}$, with constants M_1 and M_2 given in (1.9).

2. Self-elimination by Allee effect

Throughout this paper, for each type of the boundary conditions in (1.6), say $B[\cdot]$, We let λ_0 and $\phi_0(x)$ (with $\|\phi_0\|_\infty = 1$) be the principal eigenvalue and associated eigenfunction of the eigenvalue problem

$$\nabla^2 \phi + \lambda \phi = 0 \text{ in } \Omega, B[\phi] = 0 \text{ on } \partial\Omega. \quad (2.1)$$

It is well-known that for Neumann Boundary condition, $\phi_0(x) = 1$ on $\bar{\Omega}$ with $\lambda_0 = 0$. Also, for Dirichlet or Robin boundary condition we have $\phi_0(x) > 0$ in Ω with $\lambda_0 > 0$. We demonstrate how the Allee effect, birth and death rates, as well as diffusion rates affect the long-term survival of each species with relatively small initial population size.

Theorem 2.1. Self-elimination by Allee effect (Neumann boundary condition).

Under the Neumann boundary conditions for the u -species

$$\frac{\partial u(t, x)}{\partial \nu} = 0 \text{ on } (0, \infty) \times \partial\Omega,$$

if $0 \leq u_0(x) < \frac{k_u d_u}{b_u - d_u}$ then $\lim_{t \rightarrow \infty} u(t, x) = 0$ uniformly on $\bar{\Omega}$.

Proof. For some $\sigma > 0$, let $\tilde{u} = Me^{-\sigma t}$ and $\hat{u} = 0$, $\tilde{v} = (b_v - d_v)/b_v$ and $\hat{v} = 0$. Since all the defined upper and lower solutions are independent of x , they satisfy the boundary condition inequalities in (1.8) with nonnegative function values and normal derivatives as 0. Also, $\tilde{u} \geq \hat{u}$ and $\tilde{v} \geq \hat{v}$ on $[0, \infty) \times \bar{\Omega}$. It is obvious that the differential inequalities for \hat{u}, \tilde{v} and \hat{v} are satisfied in (1.8).

To verify that $\tilde{u} = Me^{-\sigma t}$ satisfies the corresponding differential inequality in (1.8), we find that the following relation must be satisfied:

$$-\sigma Me^{-\sigma t} \geq Me^{-\sigma t} \left[b_u (1 - Me^{-\sigma t}) \left(\frac{Me^{-\sigma t}}{Me^{-\sigma t} + k_u} \right) - d_u \right].$$

After simplifying, the following must hold for all $t \in (0, \infty)$:

$$-\sigma \geq b_u (1 - Me^{-\sigma t}) \left(\frac{Me^{-\sigma t}}{Me^{-\sigma t} + k_u} \right) - d_u. \quad (2.2)$$

It suffices to have

$$-\sigma \geq b_u \left(\frac{M}{M + k_u} \right) - d_u. \quad (2.3)$$

Allowing for a small and positive σ , for \tilde{u} to function as an upper solution defined in (1.8) we just need:

$$M < \frac{k_u d_u}{b_u - d_u}. \quad (2.4)$$

By Definition 1.1 and Theorem 1.2, for any initial density function $u_0(x)$ with $0 \leq u_0(x) < \frac{k_u d_u}{b_u - d_u}$ on $\bar{\Omega}$, we have

$$0 \leq u(t, x) < M e^{-\sigma t} \text{ on } [0, \infty) \times \bar{\Omega},$$

with $M = \|u_0\|_\infty < \frac{k_u d_u}{b_u - d_u}$. Therefore, $\lim_{t \rightarrow \infty} u(t, x) = 0$ uniformly on $\bar{\Omega}$. \square

We now analyze the self-elimination by Allee effect of one species (say u) under Dirichlet or Robin boundary condition. For this case, the principal eigenvalue for $B_u[\cdot]$ is $\lambda_0 > 0$ and the corresponding eigenfunction $\phi_0(x) > 0$ in Ω (with $\|\phi_0\|_\infty = 1$).

Theorem 2.2. Self-elimination by Allee effect (Dirichlet or Robin boundary condition).

Under the Dirichlet or Robin (with non-trivial $\gamma_u(x)$) boundary condition for the u -species

$$u(t, x) = 0 \text{ or } \frac{\partial u(t, x)}{\partial \nu} + \gamma_u(x)u(t, x) = 0 \text{ on } \partial\Omega,$$

a) *If $D_u \lambda_0 \geq b_u - d_u$, then for any positive $M > 0$ with initial density $u_0(x) \leq M\phi_0(x)$, we have $\lim_{t \rightarrow \infty} u(t, x) = 0$ uniformly on $\bar{\Omega}$.*

b) *If $D_u \lambda_0 < b_u - d_u$ and $0 \leq u_0(x) \leq M\phi_0(x)$ for some $M < \frac{k_u(\lambda_0 D_u + d_u)}{b_u - d_u - \lambda_0 D_u}$, then $\lim_{t \rightarrow \infty} u(t, x) = 0$ uniformly on $\bar{\Omega}$.*

Proof. For some positive σ , Let $\tilde{u} = M\phi_0 e^{-\sigma t}$, and $\hat{u} = 0$, $\tilde{v} = (b_v - d_v)/b_v$ and $\hat{v} = 0$, so $(\tilde{u}, \tilde{v}) \geq (\hat{u}, \hat{v})$ on $[0, \infty) \times \bar{\Omega}$. Since $\phi_0(x) = 0$ on $\partial\Omega$, the boundary inequality in (1.8) for \tilde{u} is satisfied. As seen in the proof of the previous theorem, the differential and boundary inequalities in (1.8) for \hat{u} , \tilde{v} and \hat{v} are also satisfied.

For part a), assume that $D_u \lambda_0 > b_u - d_u$. To satisfy the differential inequality in (1.8) for \tilde{u} we need:

$$-\sigma M\phi_0 e^{-\sigma t} + D_u \lambda_0 M\phi_0 e^{-\sigma t} \geq M\phi_0 e^{-\sigma t} \left[b_u (1 - M\phi_0 e^{-\sigma t}) \left(\frac{M\phi_0 e^{-\sigma t}}{M\phi_0 e^{-\sigma t} + k_u} \right) - d_u \right]. \quad (2.5)$$

Simplifying above and allowing for a small positive σ , it is suffice to have the following hold for any $t > 0$:

$$D_u \lambda_0 > b_u (1 - M\phi_0 e^{-\sigma t}) \left(\frac{M\phi_0 e^{-\sigma t}}{M\phi_0 e^{-\sigma t} + k_u} \right) - d_u. \quad (2.6)$$

We recognize that $1 - M\phi_0 e^{-\sigma t} < 1$ and $0 < \frac{M\phi_0 e^{-\sigma t}}{M\phi_0 e^{-\sigma t} + k_u} < 1$, so we can ensure that:

$$D_u \lambda_0 > b_u - d_u > b_u (1 - M\phi_0 e^{-\sigma t}) \left(\frac{M\phi_0 e^{-\sigma t}}{M\phi_0 e^{-\sigma t} + k_u} \right) - d_u. \quad (2.7)$$

Hence the differential inequality for the upper solution is satisfied by any $\tilde{u} = M\phi_0 e^{-\sigma t}$ with any $M > 0$. This proves part a).

For part b), assume that $D_u\lambda_0 < b_u - d_u$. As in part a), the differential inequality for \tilde{u} in (1.8) needs to be satisfied for all $t > 0$:

$$D_u\lambda_0 - \sigma \geq \left[b_u(1 - M\phi_0 e^{-\sigma t}) \left(\frac{M\phi_0 e^{-\sigma t}}{M\phi_0 e^{-\sigma t} + k_u} \right) - d_u \right], \quad (2.8)$$

which can be ensured by

$$D_u\lambda_0 - \sigma \geq b_u \left(\frac{M}{M + k_u} \right) - d_u. \quad (2.9)$$

The above relation holds for a small and positive σ , and constant M :

$$M < \frac{k_u(\lambda_0 D_u + d_u)}{b_u - d_u - \lambda_0 D_u}. \quad (2.10)$$

By Definition 1.1 and Theorem 1.2, for any initial density function $u_0(x)$ with $0 \leq u_0(x) \leq M\phi_0(x)$ on $\bar{\Omega}$, we have $0 \leq u(t, x) \leq M\phi_0 e^{-\sigma t}$ and $\lim_{t \rightarrow \infty} u(t, x) = 0$ uniformly on $\bar{\Omega}$. \square

Theorems 2.1 and 2.2 shows that larger Allee effect coefficient, higher death rate, and faster diffusion will drive a population to extinction as long as the initial density is within the given ranges for self-elimination.

In the next theorem, we give a result of global extinction under the significance of the Allee effect, for one of the competing species (say u) with any initial density size and boundary condition.

Theorem 2.3. Global extinction of u -species under Allee effect (any boundary condition).

For the boundary condition $B_u[\cdot] = 0$, let $\lambda_0 \geq 0$ be the principal eigenvalue with the corresponding eigenfunction $\phi_0(x) > 0$ in Ω . If

$$d_u + D_u\lambda_0 > \frac{b_u(1 + k_u - \sqrt{k_u(1 + k_u)})(\sqrt{k_u(1 + k_u)} - k_u)}{\sqrt{k_u(k_u + 1)}}, \quad (2.11)$$

then $\lim_{t \rightarrow \infty} u(t, x) = 0$ uniformly on $\bar{\Omega}$ with all initial density $0 \leq u_0(x) \leq N\phi_0(x)$ for any $N > 0$.

Proof. Again, for any $N > 0$ and some small $\sigma > 0$, Let $\tilde{u} = N\phi_0 e^{-\sigma t}$, and $\hat{u} = 0$, $\tilde{v} = (b_v - d_v)/b_v$ and $\hat{v} = 0$, so $(\tilde{u}, \tilde{v}) \geq (\hat{u}, \hat{v})$ on $[0, \infty) \times \bar{\Omega}$. We can show see that the differential and boundary inequalities are satisfied are all satisfied for \hat{u} , \tilde{v} , and \hat{v} under any boundary conditions for u and v , as in the proofs for previous theorems.

Also, as seen in (2.6), for the upper solution \tilde{u} to satisfy the required differential inequality given in (1.8), we need to ensure that for all $t > 0$,

$$\frac{b_u(1 - N\phi_0 e^{-\sigma t})N\phi_0 e^{-\sigma t}}{N\phi_0 e^{-\sigma t} + k_u} < d_u + D_u\lambda_0.$$

We now examine the positive maximum of $G(X) = \frac{b_u(1-X)X}{X+k_u}$ for $X \in [0, \infty)$. Note that $G(0) = G(1) = 0$, and $G(X) < 0$ for $X > 1$.

$$G'(X) = \frac{b_u(-X^2 - 2k_u X + k_u)}{(X + k_u)^2},$$

so $G'(X) = 0$ when $X = -k_u \pm \sqrt{k_u(k_u + 1)}$. We then allocate the only positive maximum point of $G(X)$, at $X = \sqrt{k_u(k_u + 1)} - k_u \in (0, 1)$. This implies that for all $t > 0$,

$$\begin{aligned} \frac{b_u(1 - N\phi_0 e^{-\sigma t})N\phi_0 e^{-\sigma t}}{N\phi_0 e^{-\sigma t} + k_u} &\leq G(\sqrt{k_u(k_u + 1)} - k_u) \\ &= \frac{b_u(1 + k_u - \sqrt{k_u(1 + k_u)})(\sqrt{k_u(1 + k_u)} - k_u)}{\sqrt{k_u(k_u + 1)}}. \end{aligned} \quad (2.12)$$

We can now conclude that if

$$d_u + D_u \lambda_0 > \frac{b_u(1 + k_u - \sqrt{k_u(1 + k_u)})(\sqrt{k_u(1 + k_u)} - k_u)}{\sqrt{k_u(k_u + 1)}},$$

then for any positive N and some small positive σ , $0 \leq u(t, x) \leq N\phi_0 e^{-\sigma t}$ on $[0, \infty) \times \bar{\Omega}$ as long as $0 \leq u_0(x) \leq N\phi_0(x)$ on $\bar{\Omega}$. The global extinction of u -species given in the theorem then follows. \square

3. Permanence

In this section, we explore on conditions for permanence (long-term survival of both species) in the competition model (1.5). Our approach is to find the possibility of a pair of upper-lower solutions given in Definition 1.1 with nontrivial lower solutions for both u and v .

Theorem 3.1. Permanence of both species (Neumann boundary condition).

Let u and v both satisfy the no-flux boundary condition $\frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0$ on $\partial\Omega$. If

$$\begin{aligned} 0 < \alpha < \frac{b_v(b_u - d_u)}{b_u(b_v - d_v)} \text{ and } 0 < \beta < \frac{b_u(b_v - d_v)}{b_v(b_u - d_u)}, \\ k_u \leq \frac{b_u}{4d_u} \left(\frac{b_u - d_u}{b_u} - \alpha \frac{b_v - d_v}{b_v} \right)^2 \text{ and } k_v \leq \frac{b_v}{4d_v} \left(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u} \right)^2, \end{aligned} \quad (3.1)$$

then the competition model (1.5) is permanent as long as the initial density functions satisfy

$$\frac{1}{2} \left(\frac{b_u - d_u}{b_u} - \alpha \frac{b_v - d_v}{b_v} \right) < u_0(x) < \frac{b_u - d_u}{b_u} \quad \text{on } \bar{\Omega}, \quad (3.2)$$

and

$$\frac{1}{2} \left(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u} \right) < v_0(x) < \frac{b_v - d_v}{b_v} \quad \text{on } \bar{\Omega}. \quad (3.3)$$

Proof. Let the conditions in (3.1) and (3.2) hold. We will show that $(\tilde{u}, \tilde{v}) = (\frac{b_u - d_u}{b_u}, \frac{b_v - d_v}{b_v})$ and $(\hat{u}, \hat{v}) = (\epsilon_u, \epsilon_v)$, where $\frac{b_u - d_u}{b_u} > \epsilon_u > 0$ and $\frac{b_v - d_v}{b_v} > \epsilon_v > 0$, are a pair of ordered upper and lower solutions given in Definition 1.1. It is clear that $(\tilde{u}, \tilde{v}) \geq (\hat{u}, \hat{v})$. Since \tilde{u} , \hat{u} , \tilde{v} , and \hat{v} are all independent of x , so they satisfy the boundary condition inequalities in (1.8).

In order to satisfy the differential inequalities in (1.8), we need the following relations to hold:

$$0 \geq \frac{b_u - d_u}{b_u} \left[b_u \left(1 - \frac{b_u - d_u}{b_u} - \alpha \epsilon_v \right) \left(\frac{\frac{b_u - d_u}{b_u}}{\frac{b_u - d_u}{b_u} + k_u} \right) - d_u \right],$$

$$\begin{aligned}
0 &\geq \frac{b_v - d_v}{b_v} \left[b_v \left(1 - \frac{b_v - d_v}{b_v} - \beta \epsilon_u \right) \left(\frac{\frac{b_v - d_v}{b_v}}{\frac{b_v - d_v}{b_v} + k_v} \right) - d_v \right], \\
0 &\leq \epsilon_u \left[b_u \left(1 - \epsilon_u - \alpha \frac{b_v - d_v}{b_v} \right) \left(\frac{\epsilon_u}{\epsilon_u + k_u} \right) - d_u \right], \\
0 &\leq \epsilon_v \left[b_v \left(1 - \epsilon_v - \beta \frac{b_u - d_u}{b_u} \right) \left(\frac{\epsilon_v}{\epsilon_v + k_v} \right) - d_v \right].
\end{aligned}$$

Consider the following factors in the first two inequalities for upper solutions:

$$b_u \left(1 - \frac{b_u - d_u}{b_u} - \alpha \epsilon_v \right) \frac{b_u - d_u}{(1 + k_u)b_u - d_u} < d_u - \alpha \epsilon_v b_u < d_u,$$

and

$$b_v \left(1 - \frac{b_v - d_v}{b_v} - \alpha \epsilon_u \right) \frac{b_v - d_v}{(1 + k_v)b_v - d_v} < d_v - \alpha \epsilon_u b_v < d_v.$$

It's clear to see that the right-hand sides of the first two inequalities are strictly negative, so the differential inequalities for the upper solutions are satisfied.

According to the required differential inequalities for the lower solutions, we need the following to hold:

$$\begin{aligned}
b_u \left(1 - \epsilon_u - \alpha \frac{b_v - d_v}{b_v} \right) \left(\frac{\epsilon_u}{\epsilon_u + k_u} \right) - d_u &\geq 0, \\
b_v \left(1 - \epsilon_v - \beta \frac{b_u - d_u}{b_u} \right) \left(\frac{\epsilon_v}{\epsilon_v + k_v} \right) - d_v &\geq 0.
\end{aligned} \tag{3.4}$$

Multiplying the inequalities in (3.4) by $-\frac{\epsilon_u + k_u}{b_u}$ and $-\frac{\epsilon_v + k_v}{b_v}$ respectively, we now need to analyze the following functions to find $\epsilon_u > 0$ and $\epsilon_v > 0$ to ensure

$$\begin{aligned}
F_1(\epsilon_u) &= \epsilon_u^2 + \left(\alpha \frac{b_v - d_v}{b_v} + \frac{d_u}{b_u} - 1 \right) \epsilon_u + \frac{k_u d_u}{b_u} \leq 0, \\
F_2(\epsilon_v) &= \epsilon_v^2 + \left(\beta \frac{b_u - d_u}{b_u} + \frac{d_v}{b_v} - 1 \right) \epsilon_v + \frac{k_v d_v}{b_v} \leq 0.
\end{aligned} \tag{3.5}$$

The functions F_1 and F_2 (as parabolas opening upward and with $F_1(0), F_2(0) > 0$) have their respective vertices at:

$$\begin{aligned}
\epsilon_u^* &= \frac{1}{2} \left(\frac{b_u - d_u}{b_u} - \alpha \frac{b_v - d_v}{b_v} \right) < \frac{b_u - d_u}{b_u}, \\
\epsilon_v^* &= \frac{1}{2} \left(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u} \right) < \frac{b_v - d_v}{b_v}.
\end{aligned} \tag{3.6}$$

We then see that the following conditions on competition coefficients α and β ensure that ϵ_u^* and $\epsilon_v^* > 0$ in (3.6):

$$0 < \alpha < \frac{b_v(b_u - d_u)}{b_u(b_v - d_v)}, \text{ and } 0 < \beta < \frac{b_u(b_v - d_v)}{b_v(b_u - d_u)}. \tag{3.7}$$

Finally, we place a constraint on F_1 and F_2 for the function values at the vertices to be negative. For

$$F_1(\epsilon_u^*) = \frac{1}{4} \left(\frac{b_u - d_u}{b_u} - \alpha \frac{b_v - d_v}{b_v} \right)^2 - \frac{1}{2} \left(\frac{b_u - d_u}{b_u} - \alpha \frac{b_v - d_v}{b_v} \right)^2 + \frac{k_u d_u}{b_u} < 0,$$

and doing the same computation for $F_2(\epsilon_v^*) < 0$, we can now find the permanence conditions with respect to the Allee effect coefficients k_u and k_v :

$$k_u < \frac{b_u}{4d_u} \left(\frac{b_u - d_u}{b_u} - \alpha \frac{b_v - d_v}{b_v} \right)^2 \text{ and } k_v < \frac{b_v}{4d_v} \left(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u} \right)^2. \quad (3.8)$$

Given constraints (3.7) and (3.8), by Definition 1.1 and Lemma 1.2, for any initial density functions $u_0(x)$ and $v_0(x)$ with $\epsilon_u^* \leq u_0(x) \leq \frac{b_u - d_u}{b_u}$ and $\epsilon_v^* \leq v_0(x) \leq \frac{b_v - d_v}{b_v}$, the unique solution of (1.5) exists in $\langle (\hat{u}, \hat{v}), (\tilde{u}, \tilde{v}) \rangle$. This implies permanence in the ecological system and proves the theorem. \square

In model (1.5), to secure long-term survival of both species we have obtained constraints (3.1) on α , β (the Lotka-Volterra competition coefficients from one species to another) and k_u , k_v (the Allee effect coefficients for each species) in relation with the birth and death rates. Also, the initial density functions need to be balanced in ranges given in (3.3). To demonstrate a numerical example (in Figure 1), we make the following choices on the biological parameters which satisfy all conditions for permanence in (3.1):

$$b_u = 0.8, \quad b_v = 0.6, \quad d_u = 0.4, \quad d_v = 0.2, \quad k_u = 0.045, \quad k_v = 0.12, \quad \alpha = 0.3, \quad \beta = 0.5,$$

$$D_1 = 0.08, \quad D_2 = 0.03.$$

Also, we set the initial density functions as follows to satisfy the permanence conditions (3.3) on $\bar{\Omega} = [0, 1]$ and the no-flux boundary condition on $\partial\Omega$:

$$u_0(x) = 0.2 - 0.05 \cos(2\pi x), \quad v_0(x) = 0.26 - 0.05 \cos(2\pi x).$$

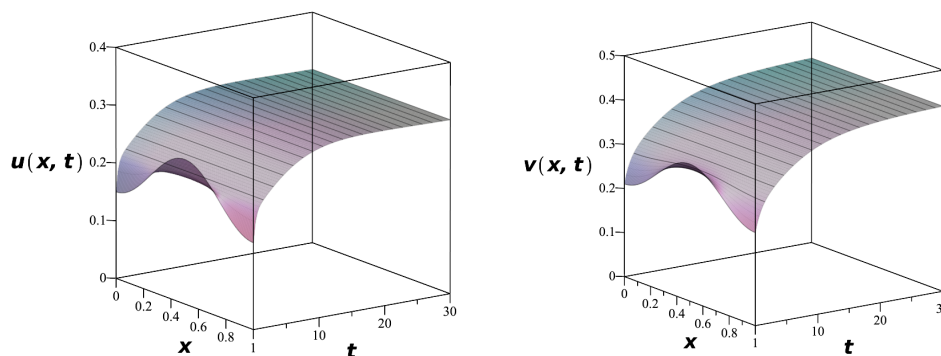


Figure 1. Theorem 3.1, permanence under Neumann boundary condition.

4. Competitive exclusion

In previous sections, we have studied criteria for self-elimination of each species and long-term survival of both species. Now in this section, we examine conditions for competitive exclusion, that is, one species survives and forces the other species into extinction in (1.5). Various competitive exclusion results can be derived from different combinations of boundary conditions for the two species.

Theorem 4.1. Competitive exclusion of one species (u) (Neumann boundary condition).

Let u and v both satisfy the no-flux boundary condition $\frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0$ on $\partial\Omega$. Assume that the following inequalities are satisfied

$$0 < \beta < \frac{b_u(b_v - d_v)}{b_v(b_u - d_u)} \text{ and } k_v \leq \frac{b_v}{4d_v} \left(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u} \right)^2. \quad (4.1)$$

If

$$v_0(x) \geq \epsilon_v^* = \frac{1}{2} \left(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u} \right) \text{ and } \bar{\Omega},$$

then

$$\lim_{t \rightarrow \infty} u(t, x) = 0 \text{ and } u_0(x) < \min \left\{ \frac{b_u - d_u}{b_u}, \frac{k_u d_u}{b_u - d_u - \alpha b_u \epsilon_v^*} \right\} \text{ on } \bar{\Omega},$$

then

$$\lim_{t \rightarrow \infty} u(t, x) = 0 \text{ and } \liminf_{t \rightarrow \infty} v(t, x) \geq \frac{1}{2} \left(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u} \right)$$

uniformly on $\bar{\Omega}$.

Proof. Let inequalities in (4.1) be satisfied. We have

$$M_1 < \min \left\{ \frac{b_u - d_u}{b_u}, \frac{k_u d_u}{b_u - d_u - \alpha b_u \epsilon_v^*} \right\},$$

where M_1 is the maximum value of $u_0(x)$ on $\bar{\Omega}$. We are going to verify that for some $\sigma_1 > 0$ (to be determined), $(\tilde{u}, \tilde{v}) = (M_1 e^{-\sigma_1 t}, \frac{b_v - d_v}{b_v})$, and $(\hat{u}, \hat{v}) = (0, \epsilon_v^*)$ are a pair of ordered upper-lower solutions. It is obvious that $(\tilde{u}, \tilde{v}) \geq (\hat{u}, \hat{v})$ in $[0, \infty) \times \bar{\Omega}$. \tilde{u} , \hat{u} , \tilde{v} , and \hat{v} are all independent of x , so their normal derivatives are equal to 0 on $\partial\Omega$ and the boundary inequalities in (1.8) are satisfied.

In order to satisfy the differential inequalities in (1.8), first notice that the differential inequality for $\hat{u} = 0$ trivially holds. For the rest, we need the following relations to hold:

$$\begin{aligned} -\sigma_1 M_1 e^{-\sigma_1 t} &\geq M_1 e^{-\sigma_1 t} \left[b_u (1 - M_1 e^{-\sigma_1 t} - \alpha \epsilon_v^*) \left(\frac{M_1 e^{-\sigma_1 t}}{M_1 e^{-\sigma_1 t} + k_u} \right) - d_u \right], \\ 0 &\geq \frac{b_v - d_v}{b_v} \left[b_v \left(1 - \frac{b_v - d_v}{b_v} \right) \left(\frac{\frac{b_v - d_v}{b_v}}{\frac{b_v - d_v}{b_v} + k_v} \right) - d_v \right], \\ 0 &\leq \epsilon_v^* \left[b_v (1 - \epsilon_v^* - \beta M_1 e^{-\sigma_1 t}) \left(\frac{\epsilon_v^*}{\epsilon_v^* + k_v} \right) - d_v \right]. \end{aligned} \quad (4.2)$$

We now analyze the differential inequalities in (4.2). The second of these inequalities is clearly satisfied by the fact that

$$b_v \left(1 - \frac{b_v - d_v}{b_v} \right) \left(\frac{\frac{b_v - d_v}{b_v}}{\frac{b_v - d_v}{b_v} + k_v} \right) - d_v = d_v \left(\frac{\frac{b_v - d_v}{b_v}}{\frac{b_v - d_v}{b_v} + k_v} \right) - d_v \leq 0.$$

Also, by the fact that $M_1 e^{-\sigma_1 t} \leq \frac{b_u - d_u}{b_u}$ and the argument related to ϵ_v^* in the proof of Theorem 3, we can conclude that the condition $k_v \leq \frac{b_v}{4d_v} \left(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u} \right)^2$ ensures the third inequality in (4.2).

We further analyze the first inequality in (4.2). By the fact that $0 \leq e^{-\sigma_1 t} \leq 1$, it suffices to have the following holds and allow a small $\sigma_1 > 0$:

$$b_u(1 - \alpha\epsilon_v^*)\left(\frac{M_1}{M_1 + k_u}\right) < d_u.$$

Solving for M from above, we conclude that for $M_1 < \frac{k_u d_u}{b_u - d_u - \alpha b_u \epsilon_v^*}$ and a positive number σ_1 which is small enough, the first inequality in (4.2) will also be satisfied. Hence we have verified all required inequalities for the coupled upper-lower solutions.

By Definition 1.1 and Lemma 1.2, for any smooth initial density function $u_0(x)$ and $v_0(x)$ with $u_0(x) < M_1$ and $v_0(x) \geq \epsilon_v^*$, there is a unique solution of (1.5) with

$$(0, \epsilon_v^*) \leq (u(t, x), v(t, x)) \leq (M_1 e^{-\sigma_1 t}, \frac{b_v - d_v}{b_v}).$$

This implies that: $\lim_{t \rightarrow \infty} u(t, x) = 0$ uniformly on $\bar{\Omega}$ and $v(t, x) \geq \frac{1}{2}(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u})$ in $[0, \infty) \times \bar{\Omega}$. \square

To demonstrate a numerical example (in Figure 2) for competitive exclusion of u -species given above, we make the following choices on the biological parameters which satisfy all conditions given in (4.1):

$$b_u = 0.5, b_v = 0.8, d_u = 0.1, d_v = 0.2, k_u = 0.7, k_v = 0.25, \alpha = 0.5, \beta = 0.3,$$

$$D_1 = 0.06, D_2 = 0.04.$$

Also, we set the initial density functions as follows to satisfy the conditions given in Theorem 4.1 on $\bar{\Omega} = [0, 1]$ and the no-flux boundary condition on $\partial\Omega$:

$$u_0(x) = 0.178 - 0.03 \cos(2\pi x), v_0(x) = 0.27 - 0.015 \cos(2\pi x).$$

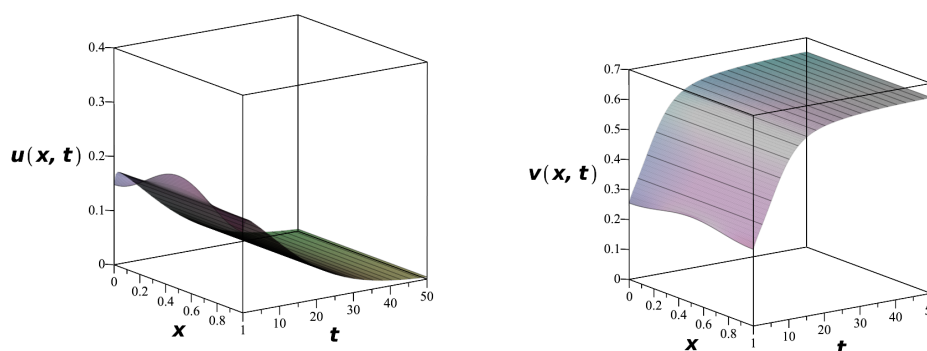


Figure 2. Theorem 4.1, competitive exclusion of u under Neumann boundary condition.

As seen in the theorem above, from the Allee coefficient k_u and death rate b_u for u -species and the persistence strength ϵ_v^* for v -species, we can determine the magnitude M_1 of $\|u_0(\cdot)\|_\infty$ which will drive the u population to extinction. Moreover, with the presence of a competitor, large competition coefficient (α) and small difference between the birth and death rates (ratio $\frac{d_u}{b_u}$ being close to 1) also

will drive the population (u) with larger initial size to extinction. The following theorem shows those detrimental effects to the survival of u -species under reasonably large initial population size. We now examine conditions for competitive exclusion of u -species globally for $0 \leq u_0(x) \leq \frac{b_u - d_u}{b_u}$.

Theorem 4.2. Global exclusion of one species (u) under stronger competitor (v) (Neumann boundary condition).

Let u and v both satisfy the no-flux boundary condition $\frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0$ on $\partial\Omega$. Assume that the inequalities in (4.1) hold. If

$$d_u > \frac{b_u(1 - \alpha\epsilon_v^* - \sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u + k_u})(\sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u} - k_u)}{\sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u}}, \quad (4.3)$$

with $\epsilon_v^* = \frac{1}{2}(\frac{b_v - d_v}{b_v} - \beta\frac{b_u - d_u}{b_u})$, and the initial population functions satisfy $v_0(x) \geq \epsilon_v^*$ and $u_0(x) < \frac{b_u - d_u}{b_u}$, then $\lim_{t \rightarrow \infty} u(t, x) = 0$ and $\liminf_{t \rightarrow \infty} v(t, x) \geq \frac{1}{2}(\frac{b_v - d_v}{b_v} - \beta\frac{b_u - d_u}{b_u})$ uniformly on $\bar{\Omega}$.

Proof. As in the proof of Theorem 4.1, we will verify that for some small $\sigma_1 > 0$ and the maximum of $u_0(x)$ $M_1 < \frac{b_u - d_u}{b_u}$, $(\tilde{u}, \tilde{v}) = (M_1 e^{-\sigma_1 t}, \frac{b_v - d_v}{b_v})$, and $(\hat{u}, \hat{v}) = (0, \epsilon_v^*)$ are a pair of ordered upper-lower solutions. It is already known that $(\tilde{u}, \tilde{v}) \geq (\hat{u}, \hat{v})$ in $[0, \infty) \times \bar{\Omega}$, and all the boundary inequalities in (1.8) are satisfied. Among the four differential inequalities for upper-lower solution given in (4.2), we also know from the previous proof that the second, third, and fourth inequalities already hold.

We now focus on analyzing the first differential inequality in (4.2). Let $M_1 e^{-\sigma_1 t} = X$, we need to find a condition for

$$d_u - \sigma_1 \geq b_u(1 - X - \alpha\epsilon_v^*)\left(\frac{X}{X + k_u}\right)$$

with all $X > 0$ and some $\sigma_1 > 0$. Define the function

$$H(X) = \frac{b_u[(1 - \alpha\epsilon_v^*) - X]X}{X + k_u},$$

and note that $H(0) = H(1 - \alpha\epsilon_v^*) = 0$, and $H(X) < 0$ for $X > 1 - \alpha\epsilon_v^*$. Since $H(x) > 0$ in the interval $(0, 1 - \alpha\epsilon_v^*)$, we look for the maximum value of $H(X)$ there. Setting

$$H'(X) = \frac{[b_u[(1 - \alpha\epsilon_v^*) - 2X](X + k_u) - b_u(1 - \alpha\epsilon_v^* - X)X]}{(X + k_u)^2} = 0,$$

we find the local extremum at $\sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u} - k_u$ in the interval $[0, 1 - \alpha\epsilon_v^*]$.

Since

$$\begin{aligned} & H(\sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u} - k_u) \\ &= \frac{b_u(1 - \alpha\epsilon_v^* - \sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u} + k_u)(\sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u} - k_u)}{\sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u}}, \end{aligned} \quad (4.4)$$

allowing for a small $\sigma_1 > 0$, the first differential inequality (4.2) is satisfied if

$$\frac{b_u(1 - \alpha\epsilon_v^* - \sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u} + k_u)(\sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u} - k_u)}{\sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u}} < d_u.$$

By Definition 1.1 and Lemma 1.2, for any smooth initial density function $u_0(x)$ and $v_0(x)$ with $u_0(x) < \frac{b_u - d_u}{b_u}$ and $v_0(x) \geq \epsilon_v^*$, there is a unique solution of (1.5) with $(0, \epsilon_v^*) \leq (u(t, x), v(t, x)) \leq (M_1 e^{-\sigma_1 t}, \frac{b_v - d_v}{b_v})$. This implies that: $\lim_{t \rightarrow \infty} u(t, x) = 0$ uniformly on $\bar{\Omega}$ and $v(t, x) \geq \frac{1}{2}(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u})$ on $[0, \infty) \times \bar{\Omega}$. \square

We now examine an numerical example (in Figure 3) for the above global exclusion result, which shows competitive exclusion of u -species with any initial density $u_0(x) < (b_u - d_u)/b_u$. We choose the following biological parameters that satisfy all the conditions in (4.1) and (4.3). Also, we use initial density functions with relatively larger $u_0(x)$ which satisfy the conditions given in Theorem 4.2 on $\bar{\Omega} = [0, 1]$ and the no-flux boundary condition on $\partial\Omega$.

$$b_u = 0.8, b_v = 0.6, d_u = 0.18, d_v = 0.2, k_u = 0.5, k_v = 0.12, \alpha = 0.5, \beta = 0.2,$$

$$D_1 = 0.03, D_2 = 0.08. u_0(x) = 0.5 - 0.27 \cos(2\pi x), v_0(x) = 0.3 - 0.044 \cos(2\pi x).$$

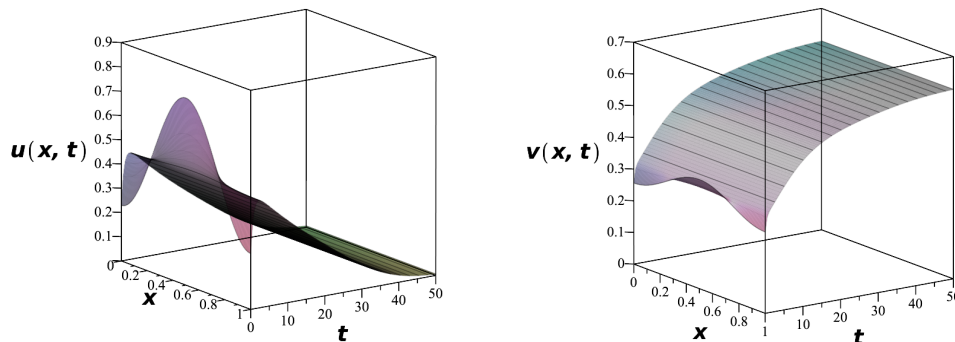


Figure 3. Theorem 4.2, global exclusion of u under Neumann boundary condition.

At last, we consider the case that the population density function $u(t, x)$ is subject to the Dirichlet or Robin boundary condition (with $\lambda_0 > 0$) and the population density function $v(t, x)$ is subject to the Neumann boundary condition. This way, the u -species will be under greater strain at the boundary, so we study the conditions that will drive u -species to extinction under Allee effect and competition from v -species.

Theorem 4.3. Competitive exclusion of one species (mixed boundary conditions).

Let u and v satisfy the boundary condition

$$\frac{\partial v(t, x)}{\partial \nu} = 0, u(t, x) = 0 \text{ or } \frac{\partial u(t, x)}{\partial \nu} + \gamma_u(x)u(t, x) = 0 \text{ on } \partial\Omega,$$

with nontrivial $\gamma_u(x)$ on $\partial\Omega$.

Assume that the inequalities in (4.1) hold and $v_0(x) \geq \epsilon_v^* = \frac{1}{2}(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u})$, $u_0(x) \leq M\phi_0(x)$ on $\bar{\Omega}$ for some $M > 0$, with eigenfunction $\phi_0(x)$ and eigenvalue λ_0 for $B_u[\cdot]$ given in (2.1). If one of the following conditions holds:

a)

$$b_u(1 - \alpha\epsilon_v^*) \leq D_u\lambda_0 + d_u$$

and $M \leq \frac{b_u - d_u}{b_u}$, or
b)

$$b_u(1 - \alpha\epsilon_v^*) > D_u\lambda_0 + d_u$$

and $M < \frac{k_u(D_u\lambda_0 + d_u)}{b_u(1 - \alpha\epsilon_v^*) - D_u\lambda_0 - d_u}$, or
c)

$$D_u\lambda_0 + d_u > k_u \frac{b_u(1 - \alpha\epsilon_v^* - \sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u + k_u})(\sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u - k_u})}{\sqrt{k_u^2 + k_u - \alpha\epsilon_v^*k_u}}$$

and $M \leq \frac{b_u - d_u}{b_u}$, then $\lim_{t \rightarrow \infty} u(t, x) = 0$ uniformly on $\bar{\Omega}$ and $v(t, x) > \frac{1}{2}(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u})$ in $[0, \infty) \times \bar{\Omega}$.

Proof. Once again, for M and $\sigma > 0$, we set up the ordered upper and lower solutions $(\tilde{u}, \tilde{v}) = (M\phi_0 e^{-\sigma t}, \frac{b_v - d_v}{b_v})$, and $(\hat{u}, \hat{v}) = (0, \epsilon_v^*)$. Noting that \tilde{v} and \hat{v} are independent of x , with respective normal derivatives = 0 on $\partial\Omega$. $\hat{u} = 0$ on $\bar{\Omega}$ and $B_u[\phi_0] = 0$ on $\partial\Omega$. Therefore all boundary inequalities in (1.8) are satisfied.

As seen in the proofs of previous theorems, the differential inequalities in (1.8) for \tilde{v} , \hat{u} and \hat{v} also hold as long as $M \leq \frac{b_u - d_u}{b_u}$.

We now analyze the differential inequality (1.8) for $\tilde{u} = M\phi_0 e^{-\sigma t}$:

$$\begin{aligned} & -\sigma M e^{-\sigma t} + D_u\lambda_0 M\phi_0 e^{-\sigma t} \\ & \geq M\phi_0 e^{-\sigma t} \left[b_u(1 - M\phi_0 e^{-\sigma t} - \alpha\epsilon_v^*) \left(\frac{M\phi_0 e^{-\sigma t}}{M\phi_0 e^{-\sigma t} + k_u} \right) - d_u \right]. \end{aligned} \quad (4.5)$$

To satisfy (4.5), it suffices to have the following relation hold which allows a small $\sigma > 0$:

$$D_u\lambda_0 + d_u > b_u(1 - \alpha\epsilon_v^*) \left(\frac{M}{M + k_u} \right). \quad (4.6)$$

If $b_u(1 - \alpha\epsilon_v^*) \leq D_u\lambda_0 + d_u$, the first differential inequality (4.5) is satisfied for all $M > 0$. Therefore the condition a) will ensure that $(\tilde{u}, \tilde{v}) = (M\phi_0 e^{-\sigma t}, \frac{b_v - d_v}{b_v})$ and $(\hat{u}, \hat{v}) = (0, \epsilon_v^*)$ are a pair of ordered upper-lower solutions under the mixed boundary conditions.

On the other hand, if $b_u(1 - \alpha\epsilon_v^*) > D_u\lambda_0 + d_u$, solving for M from the inequality (4.6) leads to $M < \frac{k_u(D_u\lambda_0 + d_u)}{b_u(1 - \alpha\epsilon_v^*) - D_u\lambda_0 - d_u}$. Hence the condition b) also ensures the ordered upper-lower solutions as designed.

Furthermore, the first differential inequality (4.5) is satisfied if the following holds for any $X > 0$:

$$D_u\lambda_0 + d_u > b_u(1 - X - \alpha\epsilon_v^*) \left(\frac{X}{X + k_u} \right). \quad (4.7)$$

Maximizing the right side of the inequality as in the proof of Theorem 4.2, we can conclude that condition c) and a small $\sigma > 0$ ensures the first differential inequality in (4.5) and verifies the ordered upper-lower solutions as designed.

By Definition 1.1 and Lemma 1.2, under the assumptions given and with one condition from a), b), or c), there exists a unique solution of (1.5) with $(0, \epsilon_v^*) \leq (u(t, x), v(t, x)) \leq (M\phi_0 e^{-\sigma t}, \frac{b_v - d_v}{b_v})$. This concludes that: $\lim_{t \rightarrow \infty} u(t, x) = 0$ uniformly on $\bar{\Omega}$ and $v(t, x) \geq \frac{1}{2}(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u})$ in $[0, \infty) \times \bar{\Omega}$. \square

We will end this section with two numerical examples for Theorem 4.3 on competitive exclusion of one species (u) which is under Dirichlet or Robin boundary condition. Setting $\Omega = (0, 1)$, we let $u(t, x)$ be under the Dirichlet boundary condition $u(t, 0) = u(t, 1) = 0$. This way, the principal eigenvalue $\lambda_0 = \pi^2$ with corresponding eigenfunction $\phi_0(x) = \sin(\pi x)$. For condition b) to be satisfied, we choose the following biological parameters and initial functions to demonstrate our numerical simulation (in Figure 4):

$$b_u = 0.8, b_v = 0.6, d_u = 0.3, d_v = 0.2, k_u = 0.3, k_v = 0.1, \alpha = 0.5, \beta = 0.3,$$

$$D_1 = 0.04, D_2 = 0.1. u_0(x) = 0.9 \sin(\pi x), v_0(x) = 0.3 - 0.06 \cos(2\pi x).$$

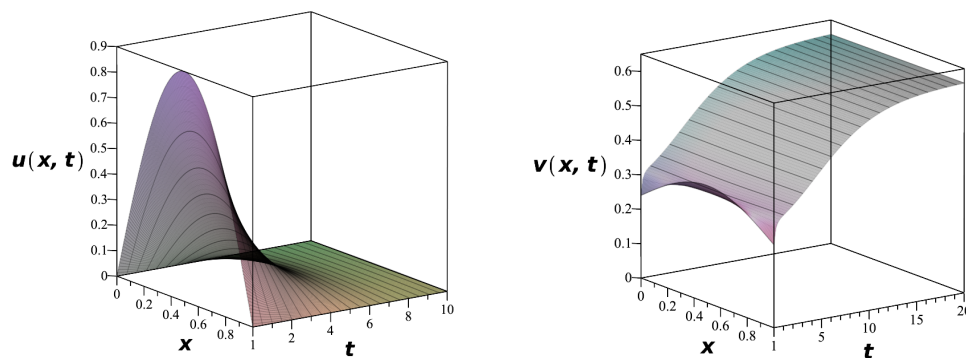


Figure 4. Theorem 4.3 b), competitive exclusion of u under mixed boundary condition.

For condition c) to be satisfied, we choose the following biological parameters and initial functions to demonstrate our numerical simulation (in Figure 5):

$$b_u = 0.5, b_v = 0.8, d_u = 0.2, d_v = 0.2, k_u = 0.5, k_v = 0.2, \alpha = 0.3, \beta = 0.5,$$

$$D_1 = 0.3, D_2 = 0.1. u_0(x) = 0.6 \sin(\pi x), v_0(x) = 0.28 - 0.04 \cos(2\pi x).$$

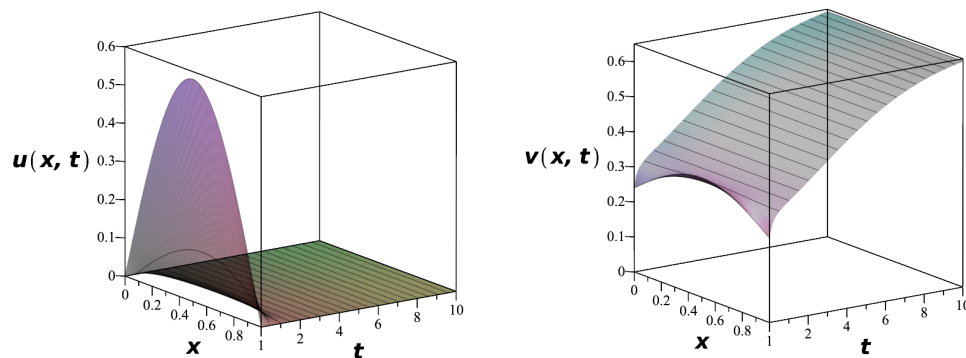


Figure 5. Theorem 4.3 c), competitive exclusion of u under mixed boundary condition.

5. Conclusions and discussion

The results shown in this article demonstrate how all the biological parameters in the model, especially the coefficients representing Allee effects, ultimately determine the long-term survival of each competing species. We also pay special attention to the impacts of the dimensions of the habitat Ω and boundary conditions for both species on $\partial\Omega$. As we know, Dirichlet boundary condition ($u = 0$ on $\partial\Omega$) indicates the biological species diminishes on the boundary of the habitat, while Neumann boundary condition ($\frac{\partial u}{\partial \nu} = 0$ on $\partial\Omega$) indicates no flux on the boundary of the habitat as the advection and diffusion fluxes of the population are exactly balanced. And, the Robin boundary condition in (1.6) is a linear combination of those two.

In Section 2, we give several results on self-elimination by Allee effect of one species despite the behavior of other. In Theorem 2.1 (Neumann boundary condition) and Theorem 2.2 (Dirichlet or Robin boundary condition), we find ranges for initial density function u_0

$$0 \leq u_0(x) < \frac{k_u d_u}{b_u - d_u} \quad \text{or} \quad 0 \leq u_0(x) < \frac{k_u(\lambda_0 D_u + d_u)}{b_u - d_u - \lambda_0 D_u} \Phi_0(x)$$

which ensure extinction of species u . And, in Theorem 2.3, the following self-elimination condition on all the biological parameters is obtained under all boundary conditions and any feasible initial density (global elimination):

$$d_u + D_u \lambda_0 > \frac{b_u(1 + k_u - \sqrt{k_u(1 + k_u)})(\sqrt{k_u(1 + k_u)} - k_u)}{\sqrt{k_u(k_u + 1)}}.$$

We note that

$$\lim_{k_u \rightarrow \infty} \frac{b_u(1 - (\sqrt{k_u(k_u + 1)} - k_u))(\sqrt{k_u(k_u + 1)} - k_u)}{\sqrt{k_u(k_u + 1)}} = 0.$$

Therefore, for sufficiently large Allee effect coefficient k_u , relatively large death rate and limited birth rate, as well as faster diffusion that makes the global elimination condition hold, a species with any nonnegative initial density will be driven to extinction under all three boundary conditions.

In section 3, we explore the possibility of permanence for both species under Neumann (no flux) boundary conditions. This requires balanced constraints on birth, death, and competition rates, as well as the Allee effect coefficients:

$$0 < \alpha < \frac{b_v(b_u - d_u)}{b_u(b_v - d_v)} \quad \text{and} \quad 0 < \beta < \frac{b_u(b_v - d_v)}{b_v(b_u - d_u)},$$

$$k_u \leq \frac{b_u}{4d_u} \left(\frac{b_u - d_u}{b_u} - \alpha \frac{b_v - d_v}{b_v} \right)^2 \quad \text{and} \quad k_v \leq \frac{b_v}{4d_v} \left(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u} \right)^2.$$

Also, the initial density functions are required to be above some minimum thresholds:

$$\frac{1}{2} \left(\frac{b_u - d_u}{b_u} - \alpha \frac{b_v - d_v}{b_v} \right) < u_0(x) < \frac{b_u - d_u}{b_u} \quad \text{on } \bar{\Omega},$$

and

$$\frac{1}{2} \left(\frac{b_v - d_v}{b_v} - \beta \frac{b_u - d_u}{b_u} \right) < v_0(x) < \frac{b_v - d_v}{b_v} \quad \text{on } \bar{\Omega}.$$

In Section 4, conditions for competitive exclusion are investigated under various boundary conditions. Under Neumann boundary conditions for both species and with the persistence constraints for v -species hold, we give the range for initial density u_0 ensuring extinction of u -species and survival of v species in Theorem 4.1:

$$u_0(x) < \min \left\{ \frac{b_u - d_u}{b_u}, \frac{k_u d_u}{b_u - d_u - \alpha b_u \epsilon_v^*} \right\}.$$

In Theorems 4.2 and 4.3, under Neumann boundary condition for v -species and any boundary condition for u -species, global exclusion of u -species are ensured by the following condition for all feasible initial density u_0 :

$$D_u \lambda_0 + d_u > k_u \frac{b_u(1 - \alpha \epsilon_v^* - \sqrt{k_u^2 + k_u - \alpha \epsilon_v^* k_u + k_u})(\sqrt{k_u^2 + k_u - \alpha \epsilon_v^* k_u - k_u})}{\sqrt{k_u^2 + k_u - \alpha \epsilon_v^*}}.$$

Here for the u -species, $\lambda_0 = 0$ under Neumann boundary condition and $\lambda_0 > 0$ under Dirichlet or Robin boundary condition. Specifically, with Dirichlet or Robin boundary condition, limited habitat size can also be detrimental to the persistence of the u -species. Examining a special case of the eigenvalue problem with Dirichlet boundary condition on a 1-dimensional habitat $\Omega = (0, L)$:

$$\nabla^2 \phi_0 + \lambda_0 \phi_0 = 0 \text{ in } (0, L), \quad \phi_0(0) = \phi_0(L) = 0,$$

we see that

$$\lambda_0 = \frac{\pi^2}{L^2} \text{ and } \phi_0(x) = \sin(\pi x/L).$$

This shows that smaller habitat size (L) makes much bigger λ_0 which validates the above competitive exclusion condition while all other biological parameters remaining unchanged. In addition to the self-elimination and competitive exclusion constraints on all biological parameters mentioned in Sections 2 and 4, this example illustrates that limited habitat size can also drive a biological population into extinction under Dirichlet or Robin boundary condition.

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Conflict of interest

The authors declare no conflicts of interest.

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