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# Global dynamics of a diffusive competitive Lotka–Volterra model with advection term and more general nonlinear boundary condition

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## Abstract

We investigate a competitive diffusion–advection Lotka–Volterra model with more general nonlinear boundary condition. Based on some new ideas, techniques, and the theory of the principal spectral and monotone dynamical systems, we establish the influence of the following parameters on the dynamical behavior of system (1.2): advection rates  $\alpha_u$  and  $\alpha_v$ , interspecific competition intensities  $c_u$  and  $c_v$ , the resources functions  $r_u$  and  $r_v$  of the two competitive species, and nonlinear boundary functions  $g_1$  and  $g_2$ . The models of (Tang and Chen in *J. Differ. Equ.* 269(2):1465–1483, 2020; Zhou and Zhao in *J. Differ. Equ.* 264:4176–4198, 2018) are particular cases of our results when  $g_i \equiv \text{const}$  for  $i = 1, 2$ , and hence this paper extends some of the conclusions from (Tang and Chen in *J. Differ. Equ.* 269(2):1465–1483, 2020; Zhou and Zhao in *J. Differ. Equ.* 264:4176–4198, 2018).

**Keywords:** Diffusive competitive Lotka–Volterra model; Advection term; Principal spectral theory; Monotone dynamical system theory; Nonlinear boundary condition

It is well known that the global dynamic properties of biological systems is one of the hot and difficult issues studied by modern biologists and mathematicians. Especially, in the competitive species system of rivers, while direct competition among organisms directly captures our attention, indirect effects such as advection rates in a river, the resources functions (or the intrinsic growth rates)  $r_u$  and  $r_v$  of these two competitors and nonlinear boundary functions  $g_i$  ( $i = 1, 2$ ) are more indicative of the intrinsic patterns among organisms. Therefore in ecological research, it is more realistic and important to study global dynamical behavior of a competitive diffusion–advection Lotka–Volterra system under more general nonlinear boundary conditions. This paper is devoted to expanding some existing and relative results to more general scenarios, where resources are heterogeneous, and the downstream end  $x = \mathcal{D}$  possesses more general boundary conditions, including the classical boundary conditions such as Neumann, Dirichlet, and so on. Our main considerations include the existence and stability of nonnegative solutions corresponding to the steady-state system of a single species, as well as spectrum theory analysis by introducing some important definitions and lemmas. Simultaneously, we also take

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the properties of the single-species model into consideration in Sect. 2 and establish sufficient and necessary conditions for the existence of boundary equilibrium points  $(u^*, 0)$  and  $(0, v^*)$ . Finally, by using some new ideas, techniques, and monotone dynamical system theory we establish a relatively complete grasping of global dynamical behavior in system (1.2).

### 1 Introduction

In various environments, individuals face an advection term, which drives them out of the system and causes a decrease in population quantity. For example, it contains gut bacteria and benthic marine species [1–3, 12] and also includes oases in deserts blown away by wind [6]. However, the aquatic organisms living in rivers are the most significant example, since they are often affected by water movement. The natural question is why plants or animal community can still survive in streams when they face to be continuously washed downstream? To answer and solve it, Speirs and Gurney [26] raised the following mathematical model in an advective environment:

$$\begin{cases} \frac{\partial u}{\partial t} = d_u u_{xx} - \alpha_u u_x + u(r_u - u), & x \in (0, \mathcal{D}), t > 0, \\ d_u u_x(0, t) - \alpha_u u(0, t) = 0, & t > 0, \\ d_u u_x(\mathcal{D}, t) - \alpha_u u(\mathcal{D}, t) = -b_u \alpha_u u(\mathcal{D}, t), & t > 0, \\ u(x, 0) = u_0(x) \geq, \neq 0, & x \in (0, \mathcal{D}). \end{cases} \tag{1.1}$$

Here  $u(x, t)$  represents the species density at location  $x$  and time  $t$ . The upstream end (resp., downstream end) is denoted by  $x = 0$  (resp.,  $x = \mathcal{D}$ ),  $d_u$  and  $\alpha_u$  are the diffusion and effective advection rates, respectively, and  $r_u$  is a positive constant indicating the resource function. In system (1.1) the nonflux boundary condition is the applied upstream, which suggests that no individual passes through the boundary, whereas for the downstream, a new function  $-b_u \alpha_u$  appears to measure the individual’s loss rate relative to the flow velocity and is assumed to be nonnegative (detailed derivation can be found in [21]). Note that here  $d_u, r_u, \alpha_u, b_u,$  and  $L$  are all positive constants. Obviously, for  $b_u \equiv 0$ , this means that the upstream and downstream are assumed to satisfy the no-flux boundary condition, which can be used to describe the sinking phytoplankton model with effect (see, e.g., [9, 11, 13]). The case  $b_u = -1$  means that a single species satisfies the free flow condition, known as the Danckwerts condition, which can be used to describe the situation of flowing into the lake and can be referred to [29]. Especially, in the case where  $b_u$  becomes small enough, i.e.,  $b_u \rightarrow -\infty$ , which implies that a single species would undergo the hostile conditions, i.e., the zero Dirichlet boundary condition, which can be used in the situation of flowing into the ocean, we can refer to [26].

On the other hand, in the past few decades, many researchers propose various mathematical models to reveal the relationship among different species [17, 31]. It is well known that due to environmental heterogeneity [23, 27] and their survival instincts, species will exhibit random diffusion behavior. Therefore, motivated by the above research, we study a class of competitive diffusion–advection systems for two logistically growing with more

general nonlinear boundary condition

$$\begin{cases}
 \frac{\partial u}{\partial t} = d_u u_{xx} - \alpha_u u_x + u(r_u(x) - u - c_u v), & x \in (0, \mathcal{D}), t > 0, \\
 \frac{\partial v}{\partial t} = d_v v_{xx} - \alpha_v v_x + v(r_v(x) - c_v u - v), & x \in (0, \mathcal{D}), t > 0, \\
 d_u u_x(0, t) - \alpha_u u(0, t) = d_v v_x(0, t) - \alpha_v v(0, t) = 0, & t > 0, \\
 d_u u_x(\mathcal{D}, t) - \alpha_u u(\mathcal{D}, t) = \alpha_u u(\mathcal{D}, t) g_1(u(\mathcal{D}, t)), & t > 0, \\
 d_v v_x(\mathcal{D}, t) - \alpha_v v(\mathcal{D}, t) = \alpha_v v(\mathcal{D}, t) g_2(v(\mathcal{D}, t)), & t > 0, \\
 u(x, 0) = u_0(x) \geq, \neq 0, v(x, 0) = v_0(x) \geq, \neq 0.
 \end{cases} \tag{1.2}$$

Here  $u(x, t)$  and  $v(x, t)$  denote the species densities of the two competing species at location  $x$  and time  $t$ ,  $\mathcal{D}$  is the length of the river,  $d_u$  and  $d_v$  represent the diffusion rates,  $\alpha_u$  and  $\alpha_v$  are the advective intensity rates, and the functions  $r_u$  and  $r_v$  stand for the resources functions of these two competitive species. In our model, we assume that the upstream has no-flux boundary conditions, whereas for the downstream, new functions  $-g_i$  ( $i = 1, 2$ ) appear to measure the individuals' loss rates relative to the flow velocities.

Note that many researchers have studied system (1.2). For example, if  $\alpha_u = \alpha_v = 0$  ( $i = 1, 2$ ) or  $g_i = const$  ( $i = 1, 2$ ), we can refer to [16, 27, 28, 32]. If  $\alpha_u, \alpha_v \neq 0$ , Lou and Zhou [20] studied (1.2) when the two competitive species admit the same advection rate  $\alpha_u = \alpha_v = \alpha \geq 0$  but different diffusion rates  $d_u, d_v > 0$ ,  $r_u = r_v = r \equiv const$ , and  $g_1 = 0$ , and  $g_2 = -b \equiv const$ . They obtained the impact of  $b$  on the global dynamics of system (1.2). Later, Lou et al. [19] reconsidered (1.2) when the two competitive species possess the equivalent diffusion rate  $d_u = d_v = d > 0$  but different advection rates  $\alpha_u, \alpha_v \geq 0$ ,  $r_u = r_v = r \equiv const$ , and  $g_1 = g_2 \equiv 0$  in order that they can find out whether stronger or weaker advection is more advantageous in the competition. In biology, they [19] found that the weaker species will win the competition in the closed homogeneous advective environment. Considering the effects of environmental heterogeneity and the nonlinear boundary condition, Zhou and Zhao [32] focused on the dynamics of a advective competition–diffusion population model with  $g_i = -b \equiv const$ . By analyzing the properties of the single species model they described the global dynamical behavior. Due to influence of time delay on the nature of population dynamics, Ma and Feng [22] explored the dynamical behavior of a delayed and advective competition–diffusion models and explored the effect of advection on Hopf bifurcation; we can refer to other similar references such as [5, 30].

The main objective of this paper is to extend some existing and related results to more general scenarios, where resource functions may be highly dependent on spatial variables (spatially nonuniform environments), and the downstream boundary condition  $x = \mathcal{D}$  becomes very flexible, including the classical boundary conditions such as Neumann, Dirichlet, and so on. Since system (1.2) promotes similar models before, the dynamics of such systems with general nonlinear boundary conditions, to a large extent, will be more complex and determined by the eigenvalue theory and some analysis skills and their steady states. Previously, research methods similar to system (1.2) could not be directly used and required the use of new definitions, techniques, and methods.

Throughout this paper, for convenience, we need to provide the following two assumptions: for  $i = 1, 2$ ,

- (H<sub>1</sub>)  $g_i(0) < 0$  and  $(g_i)_x < 0$  in  $[0, \infty)$ ;
- (H<sub>2</sub>)  $r_u, r_v \in C(0, \mathcal{D})$ , and  $\{x \in (0, \mathcal{D}) | r_u(x) > 0, r_v > 0\}$  is not empty.

We organize the rest of the paper as follows. In Sect. 2, we introduce some important results, which are used to describe the existence and linear stability of a single species. Section 3 is devoted to studying the linear stability of two boundary equilibrium points of system (1.2) and establishing the global dynamics of system (1.2) under some conditions and revealing the influence of the parameters: advection rates  $\alpha_u$  and  $\alpha_v$ , interspecific competition intensities  $c_u$  and  $c_v$ , the resources functions  $r_u$  and  $r_v$  of these two competitive species and more general nonlinear boundary functions  $g_i, i = 1, 2$ , on the global dynamical behavior of system (1.2).

### 2 Persistence of a single species

In this part, we focus on the existence, nonexistence, and attractiveness of positive solutions for single-species model

$$\begin{cases} u_t = d_u u_{xx} - \alpha_u u_x + u(r_u(x) - u), & x \in (0, \mathcal{D}), t > 0, \\ d_u u_x(0, t) - \alpha_u u(0, t) = 0, & t > 0, \\ d_u u_x(\mathcal{D}, t) - \alpha_u u(\mathcal{D}, t) = \alpha_u u(\mathcal{D}, t)g(u(\mathcal{D}, t)), & t > 0, \\ u(x, 0) = u_0(x) \geq, \neq 0, & x \in (0, \mathcal{D}), \end{cases} \tag{2.1}$$

where  $d_u > 0, \alpha_u > 0$ , and  $\mathcal{D} > 0, g(0) < 0$  and  $g_x(x) < 0$  in  $(0, \infty), r \in C(0, \mathcal{D})$ , and  $\{x \in (0, \mathcal{D}) | r_u(x) > 0\}$  is not empty.

**Definition 2.1** A function  $u \in C^{2,1}(\overline{\Omega} \times (0, \infty))$  is called a upper-solution (resp., lower-solution) of system (2.1) if  $u$  satisfies

$$\begin{cases} u_t \geq (\text{resp. } \leq) d_u u_{xx} - \alpha_u u_x + u(r_u(x) - u), & x \in (0, \mathcal{D}), t > 0, \\ d_u u_x(0, t) - \alpha_u u(0, t) \leq (\text{resp. } \geq) 0, & t > 0, \\ d_u u_x(\mathcal{D}, t) - \alpha_u u(\mathcal{D}, t) \geq (\text{resp. } \leq) \alpha_u u(\mathcal{D}, t)g(u(\mathcal{D}, t)), & t > 0, \\ u(x, 0) \geq u_0(x) \geq (\text{resp. } \leq), \neq 0, & 0 < x < \mathcal{D}. \end{cases} \tag{2.2}$$

Firstly, we study the steady states of system (2.1)

$$\begin{cases} d_u \theta_{xx} - \alpha_u \theta_x + \theta(r_u(x) - \theta) = 0, \\ d_u \theta_x(0) - \alpha_u \theta(0) = 0, \quad d_u \theta_x(\mathcal{D}) - \alpha_u \theta(\mathcal{D}) = \alpha_u \theta(\mathcal{D})g(\theta(\mathcal{D})), \end{cases} \tag{2.3}$$

where  $0 < x < \mathcal{D}$ . Assume that  $\theta$  is a nonnegative solution of system (2.3). Next, we will be interested in the local stability of  $\theta$ . To achieve this aim, by linearizing system (2.1) at  $\theta$  we describe the eigenvalue problem

$$\begin{cases} d_u \phi_{xx} - \alpha_u \phi_x + (r_u(x) - 2\theta)\phi = \lambda \phi, & x \in (0, \mathcal{D}), \\ d_u \phi_x(0) - \alpha_u \phi(0) = 0, \quad d_u \phi_x(\mathcal{D}) - \alpha_u \phi(\mathcal{D}) = \alpha_u \phi(\mathcal{D}) (g(\theta(\mathcal{D})) + \theta(\mathcal{D})g'(\theta(\mathcal{D}))). \end{cases} \tag{2.4}$$

We use  $\lambda_1(d_u, \alpha_u, r_u - 2\theta, g)$  and  $\phi_1(d_u, \alpha_u, r_u - 2\theta, g)$  to denote the principal eigenvalue and the eigenfunction of (2.4), respectively [14]. The following lemma shows the relation between the sign of  $\lambda_1(d_u, \alpha_u, r_u - 2\theta, g)$  of system (2.4) and the stability of steady state  $\theta$  to system (2.1).

**Lemma 2.2**

- (i) *Let  $\theta$  be a nonnegative steady-state solution of system (2.1). If  $\lambda_1(d_u, \alpha_u, r_u - 2\theta, g) < 0$ , then  $\theta$  is locally asymptotically stable, that is, there exist constants  $\delta > 0$  and  $\varrho > 0$  such that for any  $t > 0$  and  $x \in [0, \mathcal{D}]$ , there is a unique global solution  $u$  of system (2.1) satisfying*

$$|u(x, t) - \theta(x)| < \varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g)$$

with a not identically zero and nonnegative initial data  $u_0 \in C^2([0, \mathcal{D}])$  satisfying

$$|u_0 - \theta(x)| < \varrho \phi_1(d_u, \alpha_u, r_u - 2\theta, g)$$

for all  $x \in [0, \mathcal{D}]$ , where  $\phi_1(d_u, \alpha_u, r_u - 2\theta, g)$  is the principal eigenfunction corresponding to the principal eigenvalue  $\lambda_1(d_u, \alpha_u, r_u - 2\theta, g)$  of system (2.4).

- (ii) *Let  $\theta$  be a nonnegative steady state of system (2.1). If  $\lambda_1(d_u, \alpha_u, r_u - 2\theta, g) > 0$ , then  $\theta$  is unstable, that is, there exist constants  $0 < \gamma < 1$ ,  $\hat{\delta}(\gamma, \lambda_1) > 0$ , and  $\hat{\varrho}(\lambda_1) > 0$  such that if  $0 < \varrho \leq \hat{\varrho}_0$ , and the initial data  $u_0 \in C^2([0, \mathcal{D}])$  is nonnegative and not identically zero with*

$$u_0(x) \leq \theta(x) - \varrho(1 - \gamma)\phi_1(d_u, \alpha_u, r_u - 2\theta, g), \quad 0 < x < \mathcal{D},$$

then for all  $t > 0$  and  $x \in [0, \mathcal{D}]$ , any solution  $u$  of system (2.1) satisfies

$$u(x, t) \leq \theta(x) - \varrho(1 - \gamma e^{-\hat{\delta}t})\phi_1(d_u, \alpha_u, r_u - 2\theta, g). \tag{2.5}$$

Furthermore, there exist constants  $\tilde{\delta}(\gamma, \lambda_1) > 0$  and  $\tilde{\varrho}(\lambda_1) > 0$  such that if  $0 < \varrho \leq \tilde{\varrho}_0$  and the initial data  $u_0 \in C^2([0, \mathcal{D}])$  is nonnegative and not identically zero satisfying

$$u_0(x) \geq \theta(x) + \varrho(1 - \gamma)\phi_1(d_u, \alpha_u, r_u - 2\theta, g), \quad 0 < x < \mathcal{D},$$

then for all  $t > 0$  and  $x \in [0, \mathcal{D}]$ , any solution  $u$  of system (2.1) satisfies

$$u(x, t) \geq \theta(x) + \varrho(1 - \gamma e^{-\tilde{\delta}t})\phi_1(d_u, \alpha_u, r_u - 2\theta, g). \tag{2.6}$$

*Proof* The proof is motivated by [24, Theorem 5.3.3]. To prove (i), we set  $\tilde{v}(x, t) = \theta(x) + \varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g)$  with positive constants  $\varrho, \delta$ . By a series of simple computations we conclude that for any  $t > 0$  and  $x \in [0, \mathcal{D}]$ , there is a positive  $\varrho_1$  such that if  $\varrho \in (0, \varrho_1]$ , then

$$\tilde{v}_t - d_u \tilde{v}_{xx} + \alpha_u \tilde{v}_x - \tilde{v}(r_u(x) - \tilde{v}) \geq 0. \tag{2.7}$$

As for the boundary condition, we have  $d_u \tilde{v}_x(0) - \alpha_u \tilde{v}(0) = 0$  and

$$\begin{aligned}
 & d_u \tilde{v}_x(\mathcal{D}) - \alpha_u \tilde{v}(\mathcal{D}) - \alpha_u \tilde{v}(\mathcal{D})g(\tilde{v}(\mathcal{D})) \\
 &= d_u \theta_x(\mathcal{D}) - \alpha_u \theta(\mathcal{D}) + \varrho e^{-\delta t} (d_u(\phi_1)_x(d_u, \alpha_u, r_u - 2\theta, g) - \alpha_u \phi_1(d_u, \alpha_u, r_u - 2\theta, g)) \\
 &\quad - \alpha_u \tilde{v}(\mathcal{D})g(\tilde{v}(\mathcal{D})) \\
 &= \alpha_u \theta(\mathcal{D})g(\theta(\mathcal{D})) + \alpha_u \varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g) (g(\theta(\mathcal{D})) + \theta(\mathcal{D})g'(\theta(\mathcal{D}))) \\
 &\quad - \alpha_u \theta(\mathcal{D}) [g(\theta(\mathcal{D})) + \varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g)g'(\theta(\mathcal{D})) + o(\varrho e^{-\delta t})] \\
 &\quad - \alpha_u \varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g) [g(\theta(\mathcal{D})) + \varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g)g'(\theta(\mathcal{D})) \\
 &\quad + o(\varrho e^{-\delta t})] \\
 &= -\alpha_u \varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g) [\varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g)g'(\theta(\mathcal{D})) + o(\varrho e^{-\delta t})].
 \end{aligned} \tag{2.8}$$

From (2.8), there is a positive constant  $\varrho_2$  such that for any  $\varrho \in (0, \varrho_2]$  and  $t > 0$ , we have

$$d_u \tilde{v}_x(\mathcal{D}) - \alpha_u \tilde{v}(\mathcal{D}) - \alpha_u \tilde{v}(\mathcal{D})g(\tilde{v}(\mathcal{D})) \geq 0 \tag{2.9}$$

due to  $g' < 0$ . Combining inequalities (2.7) and (2.9) and the initial data  $u_0 \leq \theta + \varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g)$  suggests that  $\tilde{v} = \theta + \varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g)$  is an upper-solution of system (2.1) if  $0 < \varrho \leq \min\{\varrho_1, \varrho_2\}$ .

Similarly, we can show that  $\tilde{v} = \theta - \varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g)$  is a lower-solution of (2.1), provided that  $u_0 \geq \theta - \varrho e^{-\delta t} \phi_1(d_u, \alpha_u, r_u - 2\theta, g)$ , where  $0 < \varrho \leq \varrho_3$  for some positive constant  $\varrho_3$ . Therefore we complete the proof of statement (i).

Next, we will show statement (ii). We set  $\hat{v}(x, t) = \theta(x) - \varrho(1 - \gamma e^{-\delta t})\phi_1(d_u, \alpha_u, r_u - 2\theta, g)$  with  $0 < \gamma < 1$  and positive constants  $\varrho$  and  $\delta$ . By a series of simple computations we can also show that there exist positive constants  $\varrho_1$  and  $\delta_1$  such that for any  $t > 0, x \in [0, \mathcal{D}]$ ,  $\varrho \in (0, \varrho_1]$ , and  $\delta = \delta_1$ ,

$$\hat{v}_t - d_u \hat{v}_{xx} + \alpha_u \hat{v}_x - \hat{v}(r_u(x) - \hat{v}) \geq 0. \tag{2.10}$$

As for the boundary condition, we have  $d_u \hat{v}_x(0) - \alpha_u \hat{v}(0) = 0$ , and for all  $t > 0$ , we have

$$d_u \hat{v}_x(\mathcal{D}) - \alpha_u \hat{v}(\mathcal{D}) - \alpha_u \hat{v}(\mathcal{D})g(\hat{v}(\mathcal{D})) \geq 0. \tag{2.11}$$

Inequalities (2.10) and (2.11) show that  $\hat{v}(x, t) = \theta(x) - \varrho(1 - \gamma e^{-\delta t})\phi_1(d_u, \alpha_u, r_u - 2\theta, g)$  is an upper-solution of (2.1) given that  $u_0 \leq \theta(x) - \varrho(1 - \gamma e^{-\delta t})\phi_1(d_u, \alpha_u, r_u - 2\theta, g)$ , where  $0 < \varrho \leq \min\{\varrho_1, \varrho_2\}$  and  $\delta = \delta_1$ . Consequently, (2.5) follows by the comparison argument.  $\square$

Next, we discuss a key element, the stability of the steady-state solution  $\theta = 0$  of (2.1). We investigate the more general eigenvalue problem

$$\begin{cases} d\phi_{xx} - \alpha\phi_x + m(x)\phi = \lambda\phi, & x \in (0, \mathcal{D}), \\ d\phi_x(0) - \alpha\phi(0) = 0, & d\phi_x(\mathcal{D}) - \alpha\phi(\mathcal{D}) = \alpha\phi(\mathcal{D})K, \end{cases} \tag{2.12}$$

where  $K < 0$  and  $m \in C(0, \mathcal{D})$ . By the Krein–Rutman theorem [14], (2.12) has a principal eigenvalue, denoted by  $\lambda_1(d, \alpha, m(x), K)$ , associated with principal eigenfunction

$\phi_1(d, \alpha, m(x), K) > 0$  on  $[0, \mathcal{D}]$ . In addition, through the variational method,  $\lambda_1(d, \alpha, m(x), K)$  is expressed by

$$\lambda_1(d, \alpha, m(x), K) = \sup_{0 \neq \psi \in H^1(0, \mathcal{D})} \frac{\int_0^{\mathcal{D}} (-d\psi_x^2 + m(x)\psi^2)e^{\frac{\alpha}{d}x} dx + \alpha e^{\frac{\alpha \mathcal{D}}{d}} \psi^2(\mathcal{D})K}{\int_0^{\mathcal{D}} e^{\frac{\alpha}{d}x} \psi^2 dx}.$$

**Lemma 2.3** *Let  $m \in C([0, \mathcal{D}])$  and  $K < 0$ . The following statements concerning  $\lambda_1(d, \alpha, m(x), K)$  and  $\phi_1(d, \alpha, m(x), K)$  of system (2.12) hold.*

- (i)  $\lambda_1(d, \alpha, m(x), K)$  and  $\phi_1(d, \alpha, m(x), K)$  of system (2.12) smoothly depend on  $d \in (0, +\infty)$  and  $\alpha \in [0, +\infty)$ .
- (ii) If  $m_i \in C([0, \mathcal{D}])$  ( $i = 1, 2$ ) and  $m_1 \geq, \neq m_2$  in  $(y_1, y_2)$ , then

$$\lambda_1(d, \alpha, m_1(x), K) > \lambda_1(d, \alpha, m_2(x), K).$$

- (iii) If  $m(x) \equiv m$ , then  $\lambda_1(d, 0, m, g(0)) = m$ ; if  $m(x)$  is not a constant function in  $(0, \mathcal{D})$ , then  $\lambda_1(d, 0, m(x), g(0))$  is strictly decreasing in  $d \in (0, \infty)$ .
- (iv)  $\lim_{d \rightarrow +\infty} \lambda_1(d, 0, m(x), K) = \frac{\int_0^{\mathcal{D}} m(x) dx}{\mathcal{D}}$  and  $\lim_{d \rightarrow 0^+} \lambda_1(d, 0, m(x), K) = \max_{x \in [0, \mathcal{D}]} m(x)$ .
- (v)  $\lim_{\alpha \rightarrow +\infty} \lambda_1(d, \alpha, m(x), K) = -\infty$ .
- (vi) We have that

$$\frac{\partial \lambda_1(d, \alpha, m(x), K)}{\partial \alpha} = \frac{(2K + 1)\phi_1^2(\mathcal{D})e^{-\frac{\alpha}{d}\mathcal{D}} - \phi_1^2(0) - \frac{\alpha}{d} \int_0^{\mathcal{D}} \phi_1^2 e^{-\frac{\alpha}{d}x} dx}{2 \int_0^{\mathcal{D}} \phi_1^2 e^{-\frac{\alpha}{d}x} dx}, \tag{2.13}$$

where  $\phi_1 = \phi_1(d, \alpha, m(x), K)$ . In particular, if  $K \leq -\frac{1}{2}$ , then  $\frac{\partial \lambda_1(d, \alpha, m(x), K)}{\partial \alpha} < 0$ .

*Proof* The proofs of statements (i)–(iii) can be found in [4, pp. 95 and 162] and [16]. Statement (iv) follows from [7, Proposition 2.2]. Following the approach in [20, Proposition 2.1], it is clear that statement (v) holds. Finally, we prove statement (vi). Similar proofs can be found in [18, Lemma 4.8] or [32, Proposition]. For the reader’s convenience, we provide the details. In the following proof, we use ‘ to denote  $\frac{\partial}{\partial \alpha}$ . For simplicity, we use  $\lambda$  and  $\phi$  to denote  $\lambda_1(d, \alpha, m(x), K)$  and  $\phi_1(d, \alpha, m(x), K)$ , respectively. Differentiating (2.12) with respect to  $\alpha$  yields

$$\begin{cases} d\phi'_{xx} - \alpha\phi'_x - \phi_x + m(x)\phi' = \lambda'\phi + \lambda\phi', & x \in (0, \mathcal{D}), \\ d\phi'_x(0) - \alpha\phi'(0) - \phi(0) = 0, \\ d\phi'_x(\mathcal{D}) - \alpha\phi'(\mathcal{D}) - \phi(\mathcal{D}) = \alpha\phi'(\mathcal{D})K + \phi(\mathcal{D})K. \end{cases} \tag{2.14}$$

From  $d\phi_{xx} - \alpha\phi_x = d((\phi e^{-\frac{\alpha}{d}x})_x e^{\frac{\alpha}{d}x})_x$  it follows that we can rewrite (2.12) and (2.14), respectively, as

$$\begin{cases} d(e^{\frac{\alpha}{d}x} (e^{-\frac{\alpha}{d}x} \phi)_x)_x + m(x)\phi = \lambda\phi, & x \in (0, \mathcal{D}), \\ d\phi_x(0) - \alpha\phi(0) = 0, & d\phi_x(\mathcal{D}) - \alpha\phi(\mathcal{D}) = \alpha\phi(\mathcal{D})K, \end{cases} \tag{2.15}$$

and

$$\begin{cases} d(e^{\frac{\alpha}{d}x} (e^{-\frac{\alpha}{d}x} \phi')_x)_x - \phi_x + m(x)\phi' = \lambda'\phi + \lambda\phi', & x \in (0, \mathcal{D}), \\ d\phi'_x(0) - \alpha\phi'(0) = \phi(0), \\ d\phi'_x(\mathcal{D}) - \alpha\phi'(\mathcal{D}) = \phi(\mathcal{D}) + \alpha\phi'(\mathcal{D})K + \phi(\mathcal{D})K. \end{cases} \tag{2.16}$$

Multiplying the first equation of (2.15) by  $\phi' e^{-\frac{\alpha}{a}x}$  and then integrating on  $(0, \mathcal{D})$ , we obtain

$$\int_0^{\mathcal{D}} d((\phi e^{-\frac{\alpha}{a}x})_x e^{\frac{\alpha}{a}x})_x (\phi' e^{-\frac{\alpha}{a}x}) dx + \int_0^{\mathcal{D}} m(x) \phi \phi' e^{-\frac{\alpha}{a}x} dx = \int_0^{\mathcal{D}} \lambda \phi \phi' e^{-\frac{\alpha}{a}x} dx. \tag{2.17}$$

Multiplying the first equation of (2.16) by  $\phi e^{-\frac{\alpha}{a}x}$  and then integrating on  $(0, \mathcal{D})$  yield

$$\begin{aligned} & \int_0^{\mathcal{D}} d((\phi' e^{-\frac{\alpha}{a}x})_x e^{\frac{\alpha}{a}x})_x (\phi e^{-\frac{\alpha}{a}x}) dx - \int_0^{\mathcal{D}} \phi \phi_x e^{-\frac{\alpha}{a}x} dx + \int_0^{\mathcal{D}} m(x) \phi \phi' e^{-\frac{\alpha}{a}x} dx \\ &= \int_0^{\mathcal{D}} \lambda \phi \phi' e^{-\frac{\alpha}{a}x} dx + \int_0^{\mathcal{D}} \lambda' \phi^2 e^{-\frac{\alpha}{a}x} dx. \end{aligned} \tag{2.18}$$

Subtracting (2.17) from (2.18) and integrating by parts, we have

$$\begin{aligned} \lambda' \int_0^{\mathcal{D}} \phi^2 e^{-\frac{\alpha}{a}x} dx &= - \int_0^{\mathcal{D}} \phi \phi_x e^{-\frac{\alpha}{a}x} dx + d(e^{-\frac{\alpha}{a}x} \phi')_x \phi \Big|_0^{\mathcal{D}} - d(e^{-\frac{\alpha}{a}x} \phi)_x \phi' \Big|_0^{\mathcal{D}} \\ &= -\frac{1}{2} \int_0^{\mathcal{D}} (\phi^2)_x e^{-\frac{\alpha}{a}x} dx + [\alpha \phi'(\mathcal{D})K + \phi(\mathcal{D})K + \phi(\mathcal{D})] \phi(\mathcal{D}) e^{-\frac{\alpha}{a}\mathcal{D}} \\ &\quad - \phi^2(0) - \alpha K \phi'(\mathcal{D}) \phi(\mathcal{D}) e^{-\frac{\alpha}{a}\mathcal{D}} \\ &= \frac{(2K + 1) \phi^2(\mathcal{D}) e^{-\frac{\alpha}{a}\mathcal{D}} - \phi^2(0) - \frac{\alpha}{a} \int_0^{\mathcal{D}} \phi^2 e^{-\frac{\alpha}{a}x} dx}{2}, \end{aligned}$$

which immediately gives (2.13).

Therefore we complete the proof. □

Based on the above analysis, it is clear that if  $\lambda_1(d_u, \alpha_u, r_u(x), g(0)) > 0$  (resp.,  $\lambda_1(d_u, \alpha_u, r_u(x), g(0)) < 0$ ), then the zero solution is linearly unstable (resp., stable).

**Lemma 2.4** *Let  $K \leq -\frac{1}{2}$ , let  $\{x \in (0, \mathcal{D}) | r_u(x) > 0\}$  be nonempty, and let  $r \in C(0, \mathcal{D})$ .*

(i) *If  $\int_0^{\mathcal{D}} r_u(x) dx < 0$ , then there exists  $d^* > 0$  satisfying  $\lambda_1(d^*, 0, r_u(x), g(0)) = 0$  such that*

(i.1) *If  $d_u \geq d^*$ , then  $\lambda_1(d_u, \alpha_u, r_u(x), g(0)) < 0$  for any  $\alpha_u > 0$ ;*

(i.2) *If  $d_u < d^*$ , then there exists  $\alpha^* > 0$  satisfying  $\lambda_1(d_u, \alpha^*, r_u(x), g(0)) = 0$  such that*

$$\lambda_1(d_u, \alpha_u, r_u(x), g(0)) \begin{cases} < 0 & \text{for } \alpha_u > \alpha^*, \\ > 0 & \text{for } 0 < \alpha_u < \alpha^*; \end{cases}$$

(ii) *If  $\int_0^{\mathcal{D}} r_u(x) dx \geq 0$ , then for any given  $d_u > 0$ , there exists  $\alpha^* > 0$  satisfying*

$$\lambda_1(d_u, \alpha^*, r_u(x), g(0)) = 0$$

*such that*

$$\lambda_1(d_u, \alpha_u, r_u(x), g(0)) \begin{cases} < 0 & \text{for } \alpha_u > \alpha^*, \\ > 0 & \text{for } 0 < \alpha_u < \alpha^*. \end{cases}$$



*Proof* We only show statement (i), since since statement (ii) can be proved similarly. Firstly, by statement (iii) of Lemma 2.3 we have

$$\lim_{d_u \rightarrow +\infty} \lambda_1(d_u, 0, r_u(x), g(0)) = \frac{\int_0^{\mathcal{D}} r_u(x) dx}{\mathcal{D}} < 0$$

and

$$\lim_{d_u \rightarrow 0} \lambda_1(d_u, 0, r_u(x), K) = \max_{x \in [0, \mathcal{D}]} r_u(x) > 0,$$

which, together with statements (i) and (iv) of Lemma 2.3, implies that there exists  $d^* > 0$  satisfying  $\lambda_1(d^*, 0, r_u(x), g(0)) = 0$  such that

$$\text{if } d_u \begin{cases} \in (0, d^*), \\ \in (d^*, \infty), \end{cases} \text{ then } \lambda_1(d_u, 0, r_u(x), g(0)) \begin{cases} > 0, \\ < 0. \end{cases} \tag{2.19}$$

From statements (v) and (vi) of Lemma 2.3 it follows that

$$\lim_{\alpha_u \rightarrow +\infty} \lambda_1(d_u, \alpha_u, r_u(x), g(0)) = -\infty, \quad \frac{\partial \lambda_1(d_u, \alpha_u, r_u(x), g(0))}{\partial \alpha_u} < 0,$$

which, combined with statement (i) of Lemma 2.3 and (2.19), finishes the proof. □

We will show that the global dynamical behavior of system (2.1) is the linear stability of zero solution.

**Proposition 2.5** *For system (2.1), if the zero solution is linearly stable, then the zero solution is globally asymptotically stable (g.a.s); if the zero solution is linearly unstable, then there exists a unique positive steady-state solution  $\theta_{d,\alpha,m,g}$  of system (2.1) that is g.a.s.*

*Proof* We first assume that the zero solution is linearly stable ( $\lambda_1(d_u, \alpha_u, r_u(x), g(0)) < 0$ ). For simplicity, we denote  $\lambda_1(d_u, \alpha_u, r_u(x), g(0))$  and  $\phi_1(d_u, \alpha_u, r_u(x), g(0))$  by  $\lambda_1$  and  $\phi_1$ , respectively. Choose sufficiently large  $C > 0$  such that  $C\phi_1 \geq \theta_0$  in  $[0, \mathcal{D}]$ . Let  $\tilde{\theta}(x, t) = C\phi_1(x)e^{\lambda_1 t}$ . Then for  $x \in [0, \mathcal{D}]$  and  $t \geq 0$ ,  $\tilde{\theta}$  satisfies

$$\begin{cases} \tilde{\theta}_t \geq d_u \tilde{\theta}_{xx} - \alpha_u \tilde{\theta}_x + \tilde{\theta}(r_u(x) - \tilde{\theta}), \\ d_u \tilde{\theta}_x(0, t) - \alpha_u \tilde{\theta}(0, t) = 0, \\ d_u \tilde{\theta}_x(\mathcal{D}, t) - \alpha_u \tilde{\theta}(\mathcal{D}, t) \geq \alpha_u \tilde{\theta}(\mathcal{D}, t)g(\tilde{\theta}(\mathcal{D}, t)), \\ \tilde{\theta}(x, 0) \geq \theta_0(x). \end{cases}$$

By comparison principle, for  $x \in [0, \mathcal{D}]$  and  $t \geq 0$ , we get

$$0 \leq u(x, t) \leq \tilde{\theta}(x, t),$$

which further yields that

$$\lim_{t \rightarrow \infty} u(x, t) \equiv 0$$

due to  $\lambda_1 < 0$ .

Next, we suppose that the zero solution is linearly unstable ( $\lambda_1(d_u, \alpha_u, r_u(x), g(0)) > 0$ ).

*Claim 1:* There is a unique positive solution  $\theta_{d_u, \alpha_u, r_u, g}$  of system (2.3). For small  $\epsilon$ , we have

$$\begin{cases} d_u \epsilon (\phi_1)_{xx} - \alpha_u \epsilon (\phi_1)_x + \epsilon \phi_1 (r_u(x) - \epsilon \phi_1) = \epsilon \phi_1 (1 - \epsilon \phi_1) > 0, & x \in (0, D), \\ d_u \epsilon (\phi_1)_x(0) - \alpha_u \epsilon \phi_1(0) = 0, \\ d_u \epsilon (\phi_1)_x(D) - \alpha_u \epsilon \phi_1(D) = \alpha_u \epsilon \phi_1(D) g(\epsilon \phi_1(D)). \end{cases}$$

Hence, for any small  $\epsilon > 0$ ,  $\epsilon \phi_1$  is a lower-solution for system (2.3). On the other hand, for large  $C$ , we observe that  $Ce^{\frac{\alpha_u}{d_u}x}$  for any  $x \in (0, D)$  satisfies

$$\begin{cases} d_u (Ce^{\frac{\alpha_u}{d_u}x})_{xx} - \alpha_u (C\phi_1)_x + Ce^{\frac{\alpha_u}{d_u}x} (r_u(x) - Ce^{\frac{\alpha_u}{d_u}x}) < 0, \\ d_u (Ce^{\frac{\alpha_u}{d_u}x})_x(0) - \alpha_u Ce^{\frac{\alpha_u}{d_u}x}|_{x=0} = 0, \\ d_u (Ce^{\frac{\alpha_u}{d_u}x})_x(D) - \alpha_u Ce^{\frac{\alpha_u}{d_u}x}|_{x=D} = 0 > \alpha_u Ce^{\frac{\alpha_u}{d_u}D} g(Ce^{\frac{\alpha_u}{d_u}D}), \end{cases}$$

and  $Ce^{\frac{\alpha_u}{d_u}x} > \epsilon \phi_1$  for small  $\epsilon$ . Hence, by the method of lower-upper solutions, (2.3) has at least one positive solution. Next, for system (2.3), we will show the positive solution is unique. If not, then we assume that there are at least two positive solutions  $\theta_1$  and  $\theta_2$  of system (2.3). Since we can choose large  $C$  and small  $\epsilon$  such that  $Ce^{\frac{\alpha_u}{d_u}x}$  and  $\epsilon \phi_1$  are the upper- and lower-solutions of system (2.3), respectively. We may assume that

$$\theta_2 \geq, \neq \theta_1. \tag{2.20}$$

Multiplying the equations by  $\theta_2 e^{-\frac{\alpha_u}{d_u}x}$  and  $\theta_1 e^{-\frac{\alpha_u}{d_u}x}$ , respectively, subtracting the resulting equations, and then integrating on  $(0, D)$ , we have

$$\begin{aligned} \int_0^D \theta_1 \theta_2 (\theta_1 - \theta_2) e^{-\frac{\alpha_u}{d_u}x} dx &= \int_0^D d_u \left( \left( e^{-\frac{\alpha_u}{d_u}x} \theta_1 \right)_x e^{\frac{\alpha_u}{d_u}x} \right)_x \left( \theta_2 e^{-\frac{\alpha_u}{d_u}x} \right) dx \\ &\quad - \int_0^D d_u \left( \left( e^{-\frac{\alpha_u}{d_u}x} \theta_2 \right)_x e^{\frac{\alpha_u}{d_u}x} \right)_x \left( \theta_1 e^{-\frac{\alpha_u}{d_u}x} \right) dx \\ &= d_u \left( e^{-\frac{\alpha_u}{d_u}x} \theta_1 \right)_x \theta_2 \Big|_0^D - d_u \left( e^{-\frac{\alpha_u}{d_u}x} \theta_2 \right)_x \theta_1 \Big|_0^D \\ &= \alpha_u \theta_1(D) \theta_2(D) (g(\theta_1(D)) - g(\theta_2(D))) e^{-\frac{\alpha_u}{d_u}D} \\ &\geq 0, \end{aligned}$$

which contradicts (2.20). Thus Claim 1 holds.

Finally, we prove that  $\lim_{t \rightarrow \infty} u(x, t) = \theta_{d_u, \alpha_u, r_u, g}$ . Indeed, for any  $t_0 > 0$ , by the maximum principle we obtain  $u(x, t_0) > 0$  for  $x \in [0, D]$ . Choose small  $\epsilon$  and large  $C$  such that

$$\epsilon \phi_1 < u(x, t_0) \quad \text{and} \quad Ce^{\frac{\alpha_u}{d_u}x} > u(x, t_0).$$

Let  $u_*(x, t)$  and  $u^*(x, t)$  be the solutions of (2.1) with  $u_*(x, 0) = \epsilon \phi_1$  and  $u^*(x, 0) = Ce^{\frac{\alpha_u}{d_u}x}$ . Then  $\frac{\partial u_*}{\partial t}(x, 0) > 0$  and  $\frac{\partial u^*}{\partial t}(x, 0) < 0$  in  $(0, D)$ , which further yields that  $u_*(x, t)$  is increasing in  $t \in (0, \infty)$  and  $u^*(x, t)$  is decreasing in  $t \in (0, \infty)$ . So we obtain

$$\epsilon \phi_1 \leq u_*(x, t) \leq u^*(x, t) \leq Ce^{\frac{\alpha_u}{d_u}x}.$$

Moreover,  $u_*(x, t)$  (resp.,  $u^*(x, t)$ ) will converge to some positive steady state. By Claim 1 we have that

$$\lim_{t \rightarrow \infty} u_*(x, t) = \theta_{d_u, \alpha_u, r_u, g} = \lim_{t \rightarrow \infty} u^*(x, t). \tag{2.21}$$

Using the comparison principle, we have

$$u^*(x, t) \geq u(x, t + t_0) \geq u_*(x, t) \quad \text{for all } x \in [0, \mathcal{D}], t \geq 0,$$

which, combined with (2.21), yields that  $u(x, t) \rightarrow \theta_{d_u, \alpha_u, r_u, g}$  as  $t \rightarrow \infty$ . □

Based on Proposition 2.5, we establish the existence/nonexistence of semitrivial steady-state solution of system (1.2).

**Proposition 2.6** *Assume that  $g_1(0) \leq -\frac{1}{2}$  and  $g_2(0) \leq -\frac{1}{2}$ .*

- (i) *If  $\int_0^{\mathcal{D}} r_u(x) dx < 0$  (resp.,  $\int_0^{\mathcal{D}} r_v(x) dx < 0$ ), then there exists  $d_u^* > 0$  (resp.,  $d_v^* > 0$ ) satisfying  $\lambda_1(d_u^*, 0, r_u(x), g_1(0)) = 0$  (resp.,  $\lambda_1(d_v^*, 0, r_v(x), g_2(0)) = 0$ ) such that:*
  - (i.1) *If  $d_u \geq d_u^*$  (resp.,  $d_v \geq d_v^*$ ), then system (1.2) does not admit a semitrivial steady-state solution  $(u^*, 0)$  (reps.,  $(0, v^*)$ ) for any  $\alpha_u > 0$  (resp.,  $\alpha_v > 0$ ).*
  - (i.2) *If  $d_u < d_u^*$  (resp.,  $d_v < d_v^*$ ), then there exists  $\alpha_u^* > 0$  (resp.,  $\alpha_v^* > 0$ ) satisfying  $\lambda_1(d_u, \alpha_u^*, r_u(x), g_1(0)) = 0$  (resp.,  $\lambda_1(d_v, \alpha_v^*, r_v(x), g_2(0)) = 0$ ) such that if  $\alpha_u > \alpha_u^*$  (resp.,  $\alpha_v > \alpha_v^*$ ), then there is no semitrivial steady-state solution  $(u^*, 0)$  (reps.,  $(0, v^*)$ ) of system (1.2); if  $\alpha_u < \alpha_u^*$  (resp.,  $\alpha_v < \alpha_v^*$ ), then system (1.2) admits a semitrivial steady-state solution  $(u^*, 0)$  (resp.,  $(0, v^*)$ ).*
- (ii) *If  $\int_0^{\mathcal{D}} r_u(x) dx \geq 0$  (resp.,  $\int_0^{\mathcal{D}} r_v(x) dx \geq 0$ ), then there exists  $\alpha_u^* > 0$  (resp.,  $\alpha_v^* > 0$ ) satisfying  $\lambda_1(d_u, \alpha_u^*, r_u(x), g_1(0)) = 0$  (resp.,  $\lambda_1(d_v, \alpha_v^*, r_v(x), g_2(0)) = 0$ ) such that if  $\alpha_u > \alpha_u^*$  (resp.,  $\alpha_v > \alpha_v^*$ ), then there is no semitrivial steady-state solution  $(u^*, 0)$  (resp.,  $(0, v^*)$ ) of system (1.2); if  $\alpha_u < \alpha_u^*$  (resp.,  $\alpha_v < \alpha_v^*$ ), then there exists a semitrivial steady-state solution  $(u^*, 0)$  (resp.,  $(0, v^*)$ ) of system (1.2).*

*Remark 2.7* Note that  $u^* = \theta_{d_u, \alpha_u, r_u, g_1}$  and  $v^* = \theta_{d_v, \alpha_v, r_v, g_2}$ .

### 3 Two-species competition model

In this section, we focus on the global dynamical behavior of system (1.2).

#### 3.1 Monotone dynamical system

**Lemma 3.1** *Let  $(u_i(x, t), v_i(x, t))$  be the solutions of model (1.2) with initial value  $(u_i^0, v_i^0)$  for  $i = 1, 2$ . Suppose that  $u_1^0(x) \geq u_2^0(x) \geq 0$  for  $x \in (0, \mathcal{D})$ ,  $0 \leq v_1^0(x) \leq v_2^0(x)$  for  $x \in (0, \mathcal{D})$ ,  $(u_1^0, v_1^0) \not\equiv (u_2^0, v_2^0)$ , and  $u_2^0 + v_1^0 \not\equiv 0$ . Then for all  $x \in (0, \mathcal{D})$  and  $t > 0$ , we have  $u_1(x, t) > u_2(x, t)$  and  $v_1(x, t) < v_2(x, t)$ .*

*Proof* Let  $w(x, t) = u_1(x, t) - u_2(x, t)$ ,  $w^0(x) = u_1^0(x) - u_2^0(x)$ ,  $z(x, t) = v_2(x, t) - v_1(x, t)$ , and  $z^0(x) = v_2^0(x) - v_1^0(x)$ . Then for all  $t > 0$ ,  $(w, z)$  satisfies

$$\begin{cases} \frac{\partial w}{\partial t} = d_u w_{xx} - \alpha_u w_x + w(r_1 - u_1 - u_2 - c_u v_1) + c_u u_2 z, & 0 < x < \mathcal{D}, \\ \frac{\partial z}{\partial t} = d_v z_{xx} - \alpha_v z_x + z(r_2 - v_1 - v_2 - c_v u_2) + c_v v_1 w, & 0 < x < \mathcal{D}, \\ d_u w_x(0, \cdot) - \alpha_u w(0, \cdot) = d_v z_x(0, \cdot) - \alpha_v z(\mathcal{D}, \cdot) = 0, \\ d_u w_x(\mathcal{D}, \cdot) - \alpha_u w(\mathcal{D}, \cdot) = \alpha_u u_1(\mathcal{D}, t) g_1(u_1(\mathcal{D}, \cdot)) - \alpha_u u_2(\mathcal{D}, t) g_1(u_2(\mathcal{D}, \cdot)), \\ d_v z_x(\mathcal{D}, \cdot) - \alpha_v z(\mathcal{D}, \cdot) = \alpha_v v_2(\mathcal{D}, t) g_2(v_2(\mathcal{D}, \cdot)) - \alpha_v v_1(\mathcal{D}, t) g_2(v_1(\mathcal{D}, \cdot)), \\ w(x, 0) = w^0(x), \quad z(x, 0) = z^0(x), \quad 0 < x < \mathcal{D}. \end{cases}$$

For any  $t > 0$ , observe that

$$\begin{aligned} & d_u w_x(\mathcal{D}, \cdot) - \alpha_u w(\mathcal{D}, \cdot) \\ &= \alpha_u [u_1(\mathcal{D}, \cdot) g_1(u_1(\mathcal{D}, \cdot)) - u_2(\mathcal{D}, \cdot) g_1(u_1(\mathcal{D}, \cdot))] \\ &\quad + \alpha_u [u_2(\mathcal{D}, \cdot) g_1(u_1(\mathcal{D}, \cdot)) - u_2(\mathcal{D}, \cdot) g_1(u_2(\mathcal{D}, \cdot))] \\ &= \alpha_u [w(\mathcal{D}, \cdot) g_1(u_1(\mathcal{D}, \cdot)) + u_2 (g_1(u_1(\mathcal{D}, \cdot)) - g_1(u_2(\mathcal{D}, \cdot)))] \\ &= \alpha_u w(\mathcal{D}, \cdot) [g_1(u_1(\mathcal{D}, \cdot)) + u_2 g_1'(u_1(\mathcal{D}, \cdot) + \sigma_1 w(\mathcal{D}, \cdot))], \quad \sigma_1 \in (0, 1), \end{aligned}$$

and

$$d_v z_x(\mathcal{D}, \cdot) - \alpha_v z(\mathcal{D}, \cdot) = \alpha_v z(\mathcal{D}, \cdot) [g_2(v_2(\mathcal{D}, \cdot)) + v_1 g_2'(v_1(\mathcal{D}, \cdot) + \sigma_2 z(\mathcal{D}, \cdot))], \quad \sigma_2 \in (0, 1).$$

Let  $\tilde{w} = e^{-\frac{\alpha_u}{d_u} x} w$  and  $\tilde{z} = e^{-\frac{\alpha_v}{d_v} x} z$ . Then for all  $t > 0$ ,  $(\tilde{w}, \tilde{z})$  satisfies

$$\begin{cases} \frac{\partial \tilde{w}}{\partial t} = d_u \tilde{w}_{xx} + \alpha_u \tilde{w}_x + \tilde{w}(r_u - u_1 - u_2 - c_u v_1) + c_u u_2 \tilde{z} e^{(\frac{\alpha_v}{d_v} - \frac{\alpha_u}{d_u})x}, & 0 < x < \mathcal{D}, \\ \frac{\partial \tilde{z}}{\partial t} = d_v \tilde{z}_{xx} + \alpha_v \tilde{z}_x + \tilde{z}(r_v - v_1 - v_2 - c_v u_2) + c_v v_1 \tilde{w} e^{(\frac{\alpha_u}{d_u} - \frac{\alpha_v}{d_v})x}, & 0 < x < \mathcal{D}, \\ \tilde{w}_x(0, \cdot) = \tilde{z}_x(0, \cdot) = 0, \\ d_u \tilde{w}_x(\mathcal{D}, \cdot) - \alpha_u \tilde{w}(\mathcal{D}, \cdot) [g_1(u_1(\mathcal{D}, \cdot)) + u_2 g_1'(u_1(\mathcal{D}, \cdot) + \sigma_1 w(\mathcal{D}, \cdot))] = 0, \\ d_v \tilde{z}_x(\mathcal{D}, \cdot) - \alpha_v \tilde{z}(\mathcal{D}, \cdot) [g_2(v_2(\mathcal{D}, \cdot)) + v_1 g_2'(v_1(\mathcal{D}, \cdot) + \sigma_2 z(\mathcal{D}, \cdot))] = 0, \\ \tilde{w}(x, 0) = w^0(x), \quad \tilde{z}(x, 0) = z^0(x), \quad 0 < x < \mathcal{D}. \end{cases}$$

Since  $g_1(u_1(\mathcal{D}, \cdot)) + u_2 g_1'(u_1(\mathcal{D}, \cdot) + \sigma_1 w(\mathcal{D}, \cdot)) < 0$  and  $g_2(v_2(\mathcal{D}, \cdot)) + v_1 g_2'(v_1(\mathcal{D}, \cdot) + \sigma_2 z(\mathcal{D}, \cdot)) < 0$  for all  $t > 0$ , from [15, Theorem 3.1.2 or Lemma 7.1.3] it follows that the theorem holds.  $\square$

### 3.2 Spectral analysis

In this subsection, we first investigate the linear stability of two boundary equilibrium points of system (1.2).

**Lemma 3.2** Fix all the parameters except  $c_u$  and  $c_v$  and assume that system (1.2) has two boundary equilibrium points  $(u^*, 0)$  and  $(0, v^*)$ .

- (i) There exists  $c_v^* > 0$  satisfying  $\lambda_1(d_v, \alpha_v, r_v - c_v^* u^*, g_2(0)) = 0$  such that  $(u^*, 0)$  is linearly stable for  $c_v > c_v^*$  and  $(u^*, 0)$  is linearly unstable for  $c_v < c_v^*$ .
- (ii) There exists  $c_u^* > 0$  satisfying  $\lambda_1(d_u, \alpha_u, r_u - c_u^* v^*, g_1(0)) = 0$  such that  $(0, v^*)$  is linearly stable for  $c_u > c_u^*$  and  $(0, v^*)$  is linearly unstable for  $c_u < c_u^*$ .

Next, we will show that every coexistence steady state (if it exists) of system (1.2) is linearly stable under the following assumption:

$$(H_3) \quad c_u c_v \leq e^{-1 \left( \frac{\alpha_u}{d_u} - \frac{\alpha_v}{d_v} \right) \mathcal{D}}.$$

Assume that  $(u, v)$  is a positive steady state of system (1.2). Then for any  $x \in (0, \mathcal{D})$ ,  $(u, v)$  satisfies

$$\begin{cases} d_u u_{xx} - \alpha_u u_x + u(r_u(x) - u - c_u v) = 0, \\ d_v v_{xx} - \alpha_v v_x + v(r_v(x) - c_v u - v) = 0, \\ d_u u_x(0) - \alpha_u u(0) = d_v v_x(0) - \alpha_v v(0) = 0, \\ d_u u_x(\mathcal{D}) - \alpha_u u(\mathcal{D}) = \alpha_u u(\mathcal{D}) g_1(u(\mathcal{D})), \\ d_v v_x(\mathcal{D}) - \alpha_v v(\mathcal{D}) = \alpha_v v(\mathcal{D}) g_2(v(\mathcal{D})). \end{cases} \tag{3.1}$$

Linearizing system (1.2) at  $(u, v)$ , we obtain

$$\begin{cases} d_u \phi_{xx} - \alpha_u \phi_x + \phi(r_u(x) - u - c_u v) - u(\phi + c_u \psi) = \tau \phi, & x \in (0, \mathcal{D}), \\ d_v \psi_{xx} - \alpha_v \psi_x + \psi(r_v(x) - c_v u - v) - v(c_v \phi + \psi) = \tau \psi, & x \in (0, \mathcal{D}), \\ d_u \phi_x(0) - \alpha_u \phi(0) = d_v \psi_x(0) - \alpha_v \psi(0) = 0, \\ d_u \phi_x(\mathcal{D}) - \alpha_u \phi(\mathcal{D}) = \alpha_u \phi(\mathcal{D})(g_1(u(\mathcal{D})) + u(\mathcal{D})g'_1(u(\mathcal{D}))), \\ d_v \psi_x(\mathcal{D}) - \alpha_v \psi(\mathcal{D}) = \alpha_v \psi(\mathcal{D})(g_2(v(\mathcal{D})) + v(\mathcal{D})g'_2(v(\mathcal{D}))). \end{cases} \tag{3.2}$$

Based on the Krein–Rutman theorem [14], we obtain that system (3.2) has a principal eigenvalue  $\tau_1$  and its corresponding eigenfunction  $(\phi_1, \psi_1)$  can be chosen to satisfy  $\phi_1 > 0 > \psi_1$  in  $[0, \mathcal{D}]$ .

**Lemma 3.3** Assume that  $(H_3)$  holds. If system (1.2) admits a positive steady-state solution  $(u, v)$ , then it is linearly stable, that is,  $\tau_1 < 0$ .

*Proof* For simplicity, we use  $\tau$  and  $(\phi, \psi)$  to denote the principal eigenvalue  $\tau_1$  and principal eigenfunction  $(\phi_1, \psi_1)$ , respectively. Multiplying the first equations in (3.2) and (3.1) by  $ue^{-\frac{\alpha_u}{d_u}x}$  and  $e^{-\frac{\alpha_u}{d_u}x}$ , respectively, and subtracting the resulting equations, we obtain

$$\tau \phi u e^{-\frac{\alpha_u}{d_u}x} = [d_u \phi_{xx} - \alpha_u \phi_x] u e^{-\frac{\alpha_u}{d_u}x} - [d_u u_{xx} - \alpha_u u_x] \phi e^{-\frac{\alpha_u}{d_u}x} - u^2 (\phi + c_u \psi) e^{-\frac{\alpha_u}{d_u}x}. \tag{3.3}$$

Multiplying (3.3) by  $\frac{\phi^2}{u^2}$  and integrating over  $(0, \mathcal{D})$ , we have

$$\begin{aligned}
 & \tau \int_0^{\mathcal{D}} \frac{\phi^3}{u} e^{-\frac{\alpha u}{d_u} x} dx \\
 &= \int_0^{\mathcal{D}} \left[ [d_u \phi_x - \alpha_u \phi]_x u e^{-\frac{\alpha u}{d_u} x} \left(\frac{\phi}{u}\right)^2 - [d_u u_x - \alpha_u u]_x \phi e^{-\frac{\alpha u}{d_u} x} \left(\frac{\phi}{u}\right)^2 \right] dx \\
 &\quad - \int_0^{\mathcal{D}} (\phi^3 + c_u \phi^2 \psi) e^{-\frac{\alpha u}{d_u} x} dx \\
 &= [d_u \phi_x - \alpha_u \phi] u e^{-\frac{\alpha u}{d_u} x} \left(\frac{\phi}{u}\right)^2 \Big|_0^{\mathcal{D}} - [d_u u_x - \alpha_u u] \phi e^{-\frac{\alpha u}{d_u} x} \left(\frac{\phi}{u}\right)^2 \Big|_0^{\mathcal{D}} \\
 &\quad - 2 \int_0^{\mathcal{D}} \left[ [d_u \phi_x - \alpha_u \phi] \phi \left(\frac{\phi}{u}\right)_x e^{-\frac{\alpha u}{d_u} x} - [d_u u_x - \alpha_u u] \frac{\phi^2}{u} \left(\frac{\phi}{u}\right)_x e^{-\frac{\alpha u}{d_u} x} \right] dx \\
 &\quad - \int_0^{\mathcal{D}} (\phi^3 + c_u \phi^2 \psi) e^{-\frac{\alpha u}{d_u} x} dx \tag{3.4} \\
 &= \alpha_u \phi^3(\mathcal{D}) g'_1(u(\mathcal{D})) e^{-\frac{\alpha u}{d_u} \mathcal{D}} - \int_0^{\mathcal{D}} (\phi^3 + c_u \phi^2 \psi) e^{-\frac{\alpha u}{d_u} x} dx \\
 &\quad - 2 d_u \int_0^{\mathcal{D}} u \phi \frac{\phi_x u - u_x \phi}{u^2} \left(\frac{\phi}{u}\right)_x e^{-\frac{\alpha u}{d_u} x} dx \\
 &= \alpha_u \phi^3(\mathcal{D}) g'_1(u(\mathcal{D})) e^{-\frac{\alpha u}{d_u} \mathcal{D}} - \int_0^{\mathcal{D}} (\phi^3 + c_u \phi^2 \psi) e^{-\frac{\alpha u}{d_u} x} dx \\
 &\quad - 2 d_u \int_0^{\mathcal{D}} u \phi \left[\left(\frac{\phi}{u}\right)_x\right]^2 e^{-\frac{\alpha u}{d_u} x} dx \\
 &< - \int_0^{\mathcal{D}} (\phi^3 + c_u \phi^2 \psi) e^{-\frac{\alpha u}{d_u} x} dx,
 \end{aligned}$$

where we have used  $(H_1)$  and  $\phi > 0$  in  $[0, \mathcal{D}]$ . Similarly, multiplying the second equations in (3.2) and (3.1) by  $v e^{-\frac{\alpha v}{d_v} x}$  and  $\psi e^{-\frac{\alpha v}{d_v} x}$  respectively, and subtracting the resulting equations, we arrive at

$$\tau \psi v e^{-\frac{\alpha v}{d_v} x} = [d_v \psi_{xx} - \alpha_v \psi_x] v e^{-\frac{\alpha v}{d_v} x} - [d_v v_{xx} - \alpha_v v_x] \psi e^{-\frac{\alpha v}{d_v} x} - v^2 (c_v \phi + \psi) e^{-\frac{\alpha v}{d_v} x}. \tag{3.5}$$

Multiplying (3.5) by  $\frac{\psi^2}{v^2}$  and integrating over  $(0, \mathcal{D})$ , we have

$$\begin{aligned}
 & \tau \int_0^{\mathcal{D}} \frac{\psi^3}{v} e^{-\frac{\alpha v}{d_v} x} dx \\
 &= \int_0^{\mathcal{D}} \left[ [d_v \psi_x - \alpha_v \psi]_x v e^{-\frac{\alpha v}{d_v} x} \left(\frac{\psi}{v}\right)^2 - [d_v v_x - \alpha_v v]_x \psi e^{-\frac{\alpha v}{d_v} x} \left(\frac{\psi}{v}\right)^2 \right] dx \\
 &\quad - \int_0^{\mathcal{D}} (c_v \phi \psi^2 + \psi^3) e^{-\frac{\alpha v}{d_v} x} dx \\
 &= [d_v \psi_x - \alpha_v \psi] v e^{-\frac{\alpha v}{d_v} x} \left(\frac{\psi}{v}\right)^2 \Big|_0^{\mathcal{D}} - [d_v v_x - \alpha_v v] \psi e^{-\frac{\alpha v}{d_v} x} \left(\frac{\psi}{v}\right)^2 \Big|_0^{\mathcal{D}} \\
 &\quad - 2 \int_0^{\mathcal{D}} \left[ [d_u \phi_x - \alpha_u \phi] \phi \left(\frac{\phi}{u}\right)_x e^{-\frac{\alpha u}{d_u} x} - [d_u u_x - \alpha_u u] \frac{\phi^2}{u} \left(\frac{\phi}{u}\right)_x e^{-\frac{\alpha u}{d_u} x} \right] dx
 \end{aligned}$$

$$\begin{aligned}
 & - \int_0^D (c_v \phi \psi^2 + \psi^3) e^{-\frac{\alpha_v}{d_v} x} dx & (3.6) \\
 & = \alpha_v \psi^3(D) g_2'(v(D)) e^{-\frac{\alpha_v}{d_v} D} - 2d_v \int_0^D v \psi \frac{\psi_x v - v_x \psi}{v^2} \left(\frac{\psi}{v}\right)_x e^{-\frac{\alpha_v}{d_v} x} dx \\
 & \quad - \int_0^D (c_v \phi \psi^2 + \psi^3) e^{-\frac{\alpha_v}{d_v} x} dx \\
 & = \alpha_v \psi^3(D) g_2'(v(D)) e^{-\frac{\alpha_v}{d_v} D} - 2d_v \int_0^D v \psi \left[\left(\frac{\psi}{v}\right)_x\right]^2 e^{-\frac{\alpha_v}{d_v} x} dx \\
 & \quad - \int_0^D (c_v \phi \psi^2 + \psi^3) e^{-\frac{\alpha_v}{d_v} x} dx \\
 & > - \int_0^D (c_v \phi \psi^2 + \psi^3) e^{-\frac{\alpha_v}{d_v} x} dx,
 \end{aligned}$$

where we have used  $(H_1)$  and  $\psi < 0$  in  $[0, D]$ .

Since the proofs are similar, we may assume that  $\frac{\alpha_u}{d_u} \geq \frac{\alpha_v}{d_v}$ . By (3.6) and  $\psi < 0$  we have

$$\tau \int_0^D \frac{\psi^3}{v} e^{-\frac{\alpha_v}{d_v} x} dx > - \int_0^D c_v \phi \psi^2 e^{-\frac{\alpha_v}{d_v} x} dx - \int_0^D \psi^3 e^{-\frac{\alpha_u}{d_u} x} dx. \tag{3.7}$$

Multiplying (3.7) by  $c_u^3$  and using assumption  $(H_3)$ , we get

$$\begin{aligned}
 \tau \int_0^D c_u^3 \frac{\psi^3}{v} e^{-\frac{\alpha_u}{d_u} x} dx & > - \int_0^D c_u c_v \phi (c_u \psi)^2 e^{-\frac{\alpha_v}{d_v} x} dx - \int_0^D (c_u \psi)^3 e^{-\frac{\alpha_u}{d_u} x} dx \\
 & > - \int_0^D \phi (c_u \psi)^2 e^{-\frac{\alpha_u}{d_u} x} dx - \int_0^D (c_u \psi)^3 e^{-\frac{\alpha_u}{d_u} x} dx,
 \end{aligned}$$

which, combined with (3.4) and  $\phi > 0 > \psi$ , yields that

$$\begin{aligned}
 & \tau \left[ \int_0^D \frac{\phi^3}{u} e^{-\frac{\alpha_u}{d_u} x} dx - \int_0^D c_u^3 \frac{\psi^3}{v} e^{-\frac{\alpha_v}{d_v} x} dx \right] \\
 & < - \int_0^D \phi^3 e^{-\frac{\alpha_u}{d_u} x} dx - \int_0^D c_u \phi^2 \psi e^{-\frac{\alpha_u}{d_u} x} dx \\
 & \quad + \int_0^D \phi (c_u \psi)^2 e^{-\frac{\alpha_u}{d_u} x} dx + \int_0^D (c_u \psi)^3 e^{-\frac{\alpha_u}{d_u} x} dx \\
 & = \int_0^D (c_u \psi + \phi)^2 (c_u \psi - \phi) e^{-\frac{\alpha_u}{d_u} x} dx \\
 & \leq 0.
 \end{aligned}$$

This fact implies that  $\tau < 0$ . □

### 3.3 Global dynamics of system (1.2)

In this subsection, we establish the global dynamical behavior of system (1.2).

**Theorem 3.4** *Assume that  $K \leq -\frac{1}{2}$  and  $(H_3)$  holds.*

- (i) *If  $\int_0^D r_u(x) dx < 0$  and  $\int_0^D r_v(x) dx < 0$ , then:*

- (i.1) If  $d_u \geq d_u^*$  or  $d_u < d_u^*$  and  $\alpha_u > \alpha_u^*$  and if  $d_v \geq d_v^*$  or  $d_v < d_v^*$  and  $\alpha_v > \alpha_v^*$ , then  $(0, 0)$  is g.a.s.
- (i.2) If either  $d_u < d_u^*$ ,  $\alpha_u < \alpha_u^*$ , and  $d_v > d_v^*$  or  $d_v < d_v^*$  and  $\alpha_v > \alpha_v^*$ , then  $(u^*, 0)$  is g.a.s.
- (i.3) If either  $d_v < d_v^*$ ,  $\alpha_v < \alpha_v^*$ , and  $d_u > d_u^*$  or  $d_u < d_u^*$  and  $\alpha_u > \alpha_u^*$ , then  $(0, v^*)$  is g.a.s.
- (i.4) If  $d_u < d_u^*$ ,  $\alpha_u < \alpha_u^*$ ,  $d_v < d_v^*$ , and  $\alpha_v < \alpha_v^*$ , then  $(u^*, 0)$  is g.a.s for  $c_v > c_v^*$ ;  $(0, v^*)$  is g.a.s for  $c_u > c_u^*$ , and system (1.2) admits a unique coexistence steady state, which is g.a.s for  $c_u < c_u^*$  and  $c_v < c_v^*$ .
- (ii) If  $\int_0^D r_u(x)dx \geq 0$  and  $\int_0^D r_v(x)dx < 0$ , then:
  - (ii.1) If either  $\alpha_u > \alpha_u^*$  and  $d_v \geq d_v^*$  or  $d_v < d_v^*$  and  $\alpha_v > \alpha_v^*$ , then  $(0, 0)$  is g.a.s.
  - (ii.2) If either  $\alpha_u < \alpha_u^*$  and  $d_v > d_v^*$  or  $d_v < d_v^*$  and  $\alpha_v > \alpha_v^*$ , then  $(u^*, 0)$  is g.a.s.
  - (ii.3) If  $d_v < d_v^*$ ,  $\alpha_v < \alpha_v^*$ , and  $\alpha_u > \alpha_u^*$ , then  $(0, v^*)$  is g.a.s.
  - (ii.4) If  $\alpha_u < \alpha_u^*$ ,  $d_v < d_v^*$ , and  $\alpha_v < \alpha_v^*$ , then  $(u^*, 0)$  is g.a.s for  $c_v > c_v^*$ ;  $(0, v^*)$  is g.a.s for  $c_u > c_u^*$ , and system (1.2) admits a unique coexistence steady state, which is g.a.s for  $c_u < c_u^*$  and  $c_v < c_v^*$ .
- (iii) If  $\int_0^D r_u(x)dx < 0$  and  $\int_0^D r_v(x)dx \geq 0$ , then:
  - (iii.1) If either  $\alpha_v > \alpha_v^*$  and  $d_u \geq d_u^*$  or  $d_u < d_u^*$  and  $\alpha_u > \alpha_u^*$ , then  $(0, 0)$  is g.a.s.
  - (iii.2) If  $d_u < d_u^*$ ,  $\alpha_u < \alpha_u^*$ , and  $\alpha_v > \alpha_v^*$ , then  $(u^*, 0)$  is g.a.s.
  - (iii.3) If either  $\alpha_v < \alpha_v^*$  and  $d_u \geq d_u^*$  or  $d_u < d_u^*$  and  $\alpha_u > \alpha_u^*$ , then  $(0, v^*)$  is g.a.s.
  - (iii.4) If  $\alpha_v < \alpha_v^*$ ,  $d_u < d_u^*$ , and  $\alpha_u < \alpha_u^*$ , then  $(u^*, 0)$  is g.a.s for  $c_v > c_v^*$ ;  $(0, v^*)$  is g.a.s for  $c_u > c_u^*$ ; and system (1.2) admits a unique coexistence steady state, which is g.a.s for  $c_u < c_u^*$  and  $c_v < c_v^*$ .
- (iv) If  $\int_0^D r_u(x)dx \geq 0$  and  $\int_0^D r_v(x)dx \geq 0$ , then:
  - (iv.1) If  $\alpha_v > \alpha_v^*$  and  $\alpha_u > \alpha_u^*$ , then  $(0, 0)$  is g.a.s.
  - (iv.2) If  $\alpha_u < \alpha_u^*$  and  $\alpha_v > \alpha_v^*$ , then  $(u^*, 0)$  is g.a.s.
  - (iv.3) If  $\alpha_v < \alpha_v^*$  and  $\alpha_u > \alpha_u^*$ , then  $(0, v^*)$  is g.a.s.
  - (iv.4) If  $\alpha_v < \alpha_v^*$  and  $\alpha_u < \alpha_u^*$ , then  $(u^*, 0)$  is g.a.s for  $c_v > c_v^*$ ;  $(0, v^*)$  is g.a.s for  $c_u > c_u^*$ ; and system (1.2) admits a unique coexistence steady state, which is g.a.s for  $c_u < c_u^*$  and  $c_v < c_v^*$ .

*Proof* Since the proofs are similar, we only prove statement (iv). Statements (iv.1)–(iv.3) follow directly from Proposition 2.6 and monotone dynamical systems theory [8, 10, 25, 32]. By Lemmas 3.2, 3.3, Proposition 2.6, and monotone dynamical systems theory [8, 10, 25, 32] we have that statement (iv.4) holds, which completes the proof. □

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**Author contributions**

GZ: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing – original draft (equal). LM: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). All authors read and approved the final manuscript.

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**Data availability**

Data sharing is not applicable to this paper as no new data were created or analyzed in this study.



## Declarations

### Competing interests

The authors declare no competing interests.

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