

# Competitive Exclusion in a Nonlocal Reaction-Diffusion-Advection Model of Phytoplankton Populations \*

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## Abstract

We continue our study on the global dynamics of a nonlocal reaction-diffusion-advection system modeling the population dynamics of two competing phytoplankton species in an eutrophic environment, where both populations depend solely on light for their metabolism. In our previous work [18], we proved that system (1.1) is a strongly monotone dynamical system with respect to a non-standard cone related to the cumulative distribution functions, and further determined the global dynamics when the species have either identical diffusion rate or identical advection rate. In this paper, we study the trade-off of diffusion and advection and their joint influence on the outcome of competition. Two critical curves for the local stability of two semi-trivial equilibria are analyzed, and some new competitive exclusion results are obtained. Our main tools, besides the theory of monotone dynamical system, include some new monotonicity results for the principal eigenvalues of elliptic operators in one-dimensional domains.

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## 1 Introduction

Phytoplankton is the generic name of microorganisms living in water columns, e.g. lakes and oceans, which constitute the basis of the aquatic food chain. Its importance for the proper functioning of the aquatic ecosystem has long been recognized, and its behavior has been widely studied. Nutrients and light are essential resources for the growth of phytoplankton. In oligotrophic ecosystems with ample supply of light, phytoplankton tend to compete only for nutrients, while in eutrophic environments with ample nutrient supply, they compete only for light. The distribution of phytoplankton in water columns is often highly heterogeneous, as they are not only diffused by water turbulence but can also be sinking or buoyant in the water column. To better understand the spatio-temporal dynamics of phytoplankton populations, a series of reaction-diffusion models including single and multiple phytoplankton species have been proposed and/or studied in [5, 6, 9, 14–16, 19, 20, 25, 31, 33] and the references therein.

In this article, we continue our investigation on the two-species nonlocal reaction-diffusion-advection system proposed by Huisman et al. [14, 16], which is used to describe the growth of phytoplankton species in a eutrophic vertical water column, where nutrients are in abundance and the species are limited by light only for their metabolism. The system describing the population dynamics of two phytoplankton species reads

$$\left\{ \begin{array}{ll} u_t = D_1 u_{xx} - \alpha_1 u_x + [g_1(I(x, t)) - d_1]u, & 0 < x < L, t > 0, \\ v_t = D_2 v_{xx} - \alpha_2 v_x + [g_2(I(x, t)) - d_2]v, & 0 < x < L, t > 0, \\ D_1 u_x(x, t) - \alpha_1 u(x, t) = 0, & x = 0, L, t > 0, \\ D_2 v_x(x, t) - \alpha_2 v(x, t) = 0, & x = 0, L, t > 0, \\ u(x, 0) = u_0(x) \geq, \neq 0, & 0 \leq x \leq L, \\ v(x, 0) = v_0(x) \geq, \neq 0, & 0 \leq x \leq L. \end{array} \right. \quad (1.1)$$

Here  $u(x, t), v(x, t)$  denote the population density of the phytoplankton species at depth  $x$  and time  $t$ , respectively. For  $i = 1, 2$ ,  $D_i > 0$  is the diffusion coefficient,  $\alpha_i \in \mathbb{R}$  is the sinking ( $\alpha_i > 0$ ) or buoyant ( $\alpha_i < 0$ ) velocity,  $d_i > 0$  is the death rate,  $g_i(I)$  represents the specific growth rate of phytoplankton species as a function of light intensity  $I(x, t)$ . By the Lambert-Beer law [21],

$$I(x, t) = I_0 \exp \left( -k_0 x - \int_0^x [k_1 u(s, t) + k_2 v(s, t)] ds \right), \quad (1.2)$$

where  $I_0 > 0$  is the incident light intensity,  $k_0 > 0$  is the background turbidity that summarizes light absorption by all non-phytoplankton components, and  $k_i$  is the absorption coefficient of the  $i$ -th phytoplankton species. We assume that  $g_i(I)$  is a smooth function satisfying

$$g_i(0) = 0 \quad \text{and} \quad g_i'(I) > 0 \quad \text{for} \quad I \geq 0. \quad (1.3)$$

The single species model, which can be obtained by setting  $v(x, t) \equiv 0$  in (1.1), has been well-studied. We refer to [7–9, 12, 17, 22, 27, 29–31] for further details regarding the background of single species. In contrast, very few results exist for two or more phytoplankton species, see [3, 7, 18, 28]. The main difficulty is that system (1.1) does not preserve the competitive order in the pointwise sense due to the nonlocal nature of the nonlinearity, and therefore the global dynamics of the resulting system is far from being completely understood. In [18], it is proved that the cumulative distribution functions

$$(U(x, t), V(x, t)) = \left( \int_0^x u(s, t) ds, \int_0^x v(s, t) ds \right)$$

satisfy a strong maximum principle, even though they do not satisfy a standard reaction-diffusion system. As a consequence, system (1.1) can be regarded as a strongly monotone dynamical system with respect to the order induced by a non-standard cone  $\mathcal{K} = \mathcal{K}_1 \times (-\mathcal{K}_1)$ , where

$$\mathcal{K}_1 = \left\{ \phi \in C([0, L], \mathbb{R}) : \int_0^x \phi(s) ds \geq 0 \quad \text{for} \quad x \in (0, L] \right\}. \quad (1.4)$$

This facilitates the application of the theory of strongly monotone dynamical system [2, 11, 13, 23, 32, 34], which provides a useful method to investigate the global dynamics of two-species system (1.1).

To analyze the effects of diffusion and advection on the global dynamics of (1.1), we henceforth assume that the two species have the same growth rates and death rates, i.e.

$$g_1(\cdot) = g_2(\cdot) \quad \text{and} \quad d_1 = d_2, \quad (1.5)$$

Furthermore, by replacing  $u(x, t)$  by  $\frac{1}{k_1}u(x, t)$ ,  $v(x, t)$  by  $\frac{1}{k_2}v(x, t)$ , and  $g(\cdot)$  by  $g(I_0 \cdot)$ , we may assume without loss of generality that  $k_1 = k_2 = I_0 = 1$ , so that

$$I(x, t) = \exp \left( -k_0 x - \int_0^x u(s, t) ds - \int_0^x v(s, t) ds \right).$$

In this case, the model under consideration reads as

$$\begin{cases} u_t = D_1 u_{xx} - \alpha_1 u_x + [g(I(x, t)) - d]u, & 0 < x < L, t > 0, \\ v_t = D_2 v_{xx} - \alpha_2 v_x + [g(I(x, t)) - d]v, & 0 < x < L, t > 0, \\ D_1 u_x(x, t) - \alpha_1 u(x, t) = 0, & x = 0, L, t > 0, \\ D_2 v_x(x, t) - \alpha_2 v(x, t) = 0, & x = 0, L, t > 0, \\ u(x, 0) = u_0(x) \geq, \neq 0, & 0 \leq x \leq L, \\ v(x, 0) = v_0(x) \geq, \neq 0, & 0 \leq x \leq L. \end{cases} \quad (1.6)$$

To facilitate the discussion, we also assume  $g(e^{-k_0 L}) - d > 0$  to guarantee that (1.6) has two semi-trivial equilibria  $(\tilde{u}, 0)$  and  $(0, \tilde{v})$  (see [12, Theorem 3.3]). Here  $\tilde{u}$  is the unique positive solution of

$$\begin{cases} D_1 \tilde{u}_{xx} - \alpha_1 \tilde{u}_x + [g(\exp(-k_0 x - \int_0^x \tilde{u}(s) ds)) - d]\tilde{u} = 0, & 0 < x < L, \\ D_1 \tilde{u}_x - \alpha_1 \tilde{u} = 0, & x = 0, L, \end{cases} \quad (1.7)$$

and  $\tilde{v}$  is the unique positive solution of

$$\begin{cases} D_2 \tilde{v}_{xx} - \alpha_2 \tilde{v}_x + [g(\exp(-k_0 x - \int_0^x \tilde{v}(s) ds)) - d]\tilde{v} = 0, & 0 < x < L, \\ D_2 \tilde{v}_x - \alpha_2 \tilde{v} = 0, & x = 0, L. \end{cases} \quad (1.8)$$

Assuming that the two species either have the same diffusion rates ( $D_1 = D_2$ ), or the same advection rates ( $\alpha_1 = \alpha_2$ ), the following results were obtained [18, Theorems 2.2-2.4]:

- (i) When  $D_1 = D_2$  and  $\alpha_1 < \alpha_2$ , the equilibrium  $(\tilde{u}, 0)$  is globally asymptotically stable.
- (ii) When  $D_1 < D_2$  and  $\alpha_1 = \alpha_2 \leq 0$ ,  $(\tilde{u}, 0)$  is globally asymptotically stable.
- (iii) When  $D_1 < D_2$  and  $\alpha_1 = \alpha_2 \geq [g(1) - d]L > 0$ , the equilibrium  $(0, \tilde{v})$  is globally asymptotically stable.

The biological mechanism behinds the above results is clear: whichever species has better access to the sunlight wins. For case (i), when diffusion rates are the same, the species that is more buoyant (or sinking more slowly) has the advantage. For case (ii), when both species are equally buoyant, the species with smaller diffusion rate wins since it is more likely to stay on the top of the water column to gain better access to sunlight. The reverse is true for case (iii), when both species are sinking with the same but large rate. In this case, the species which has a larger diffusion rate has better access to sunlight, in an average sense.

To explore the evolution of dispersal strategy, we will continue to enforce the simplifying assumption that the two species have the same growth rates and death rates, i.e.

(1.5) holds. Our main aim is to explore the joint influence of diffusion rate and advection rate, allowing for some form of trade-off between these two rates.

By the monotone dynamical system theory, the long-time dynamics of system (1.6) can largely be determined by (i) the local stability of the semi-trivial equilibria, and (ii) the existence and stability of co-existence equilibria.

We first discuss the local stability of the semi-trivial equilibria. The linear stability of the equilibrium  $(\tilde{u}, 0)$  is determined by the spectrum of the nonlocal eigenvalue problem

$$\begin{cases} D_1\phi_{xx} - \alpha_1\phi_x + [g(\sigma_1) - d]\phi - \tilde{u}g'(\sigma_1)\sigma_1 \int_0^x (\phi(s) + \psi(s)) ds + \lambda\phi = 0 & \text{in } (0, L), \\ D_2\psi_{xx} - \alpha_2\psi_x + [g(\sigma_1) - d]\psi + \lambda\psi = 0 & \text{in } (0, L), \end{cases} \quad (1.9)$$

where

$$\sigma_1(x) = \exp\left(-k_0x - \int_0^x \tilde{u}(s) ds\right). \quad (1.10)$$

Similarly, the linear stability of the equilibrium  $(0, \tilde{v})$  is determined by the spectrum of the following nonlocal eigenvalue problem

$$\begin{cases} D_1\phi_{xx} - \alpha_1\phi_x + [g(\sigma_2) - d]\phi + \lambda\phi = 0 & \text{in } (0, L), \\ D_2\psi_{xx} - \alpha_2\psi_x + [g(\sigma_2) - d]\psi - \tilde{v}g'(\sigma_2)\sigma_2 \int_0^x (\phi(s) + \psi(s)) ds + \lambda\psi = 0 & \text{in } (0, L), \end{cases} \quad (1.11)$$

where

$$\sigma_2(x) = \exp\left(-k_0x - \int_0^x \tilde{v}(s) ds\right). \quad (1.12)$$

The systems (1.9) and (1.11) are integro-PDEs, and their spectra can be hard to determine in general [24]. Nonetheless, it is proved in [18] that (1.9) (resp. (1.11)) has a principal eigenvalue. See Proposition 3.1 for details.

When  $D_1 = D_2$ , the previous result [18, Theorem 2.2] implies that  $(\tilde{u}, 0)$  is linearly stable if and only if  $\alpha_1 < \alpha_2$  and that  $(0, \tilde{v})$  is linearly stable if and only if  $\alpha_1 > \alpha_2$ . How would this change if we allow  $D_1 \neq D_2$ ?

Below, we will fix  $D_2 > D_1 > 0$  and characterize the local stability of semi-trivial equilibria  $(\tilde{u}, 0)$  and  $(0, \tilde{v})$  by the parameter  $(\alpha_1, \alpha_2) \in \mathbb{R}^2$ . Our first result is to show that decreasing  $\alpha_2$  (resp.  $\alpha_1$ ) destabilizes the equilibrium  $(\tilde{u}, 0)$  (resp.  $(0, \tilde{v})$ ). In fact, one can always define a critical value  $\alpha_i^*$  where the linear stability of the semi-trivial equilibria changes.

**Theorem 1.1** *Assume  $0 < d < g(e^{-k_0L})$  and fix  $0 < D_1 < D_2$ .*

- (a) For each  $\alpha_1 \in \mathbb{R}$ , there is a critical number  $\alpha_2^* = \alpha_2^*(\alpha_1, D_1, D_2) \in (-\infty, \frac{D_2}{D_1}\alpha_1)$  such that the equilibrium  $(\tilde{u}, 0)$  is linearly stable if and only if  $\alpha_2 > \alpha_2^*$ . If, in addition,  $\alpha_1 \geq (g(1) - d)L$ , then

$$\frac{D_2}{D_1}\alpha_1 - \left(\frac{D_2}{D_1} - 1\right)(g(1) - d)L < \alpha_2^* < \frac{D_2}{D_1}\alpha_1. \quad (1.13)$$

In particular,

$$\lim_{\alpha_1 \rightarrow +\infty} \frac{\alpha_2^*}{\alpha_1} = \frac{D_2}{D_1}.$$

- (b) For each  $\alpha_2 \in \mathbb{R}$ , there is a critical number  $\alpha_1^* = \alpha_1^*(\alpha_2, D_1, D_2) \in (\frac{D_1}{D_2}\alpha_2, \infty)$  such that the equilibrium  $(0, \tilde{v})$  is linearly stable if and only if  $\alpha_1 > \alpha_1^*$ . Moreover,

$$\begin{cases} \frac{D_1}{D_2}\alpha_2 < \alpha_1^*(\alpha_2) < (g(1) - d)L & \text{for } \alpha_2 < (g(1) - d)L, \\ \frac{D_1}{D_2}\alpha_2 < \alpha_1^*(\alpha_2) < \frac{D_1}{D_2}\alpha_2 + \left(1 - \frac{D_1}{D_2}\right)(g(1) - d)L & \text{for } \alpha_2 \geq (g(1) - d)L, \end{cases} \quad (1.14)$$

In particular,

$$\lim_{\alpha_2 \rightarrow +\infty} \frac{\alpha_2}{\alpha_1^*} = \frac{D_2}{D_1}.$$

Next, we consider the dependence of global dynamics of (1.6) on the parameters  $(\alpha_1, \alpha_2) \in \mathbb{R}^2$ .

**Theorem 1.2** Assume  $0 < d < g(e^{-k_0L})$  and fix  $0 < D_1 < D_2$ .

- (a) If  $\alpha_2 \geq \frac{D_2}{D_1}\alpha_1$ , then  $(\tilde{u}, 0)$  is globally asymptotically stable.
- (b) If  $\alpha_1 \geq (g(1) - d)L$  and  $\alpha_2 \leq \frac{D_2}{D_1}[\alpha_1 - (g(1) - d)L] + (g(1) - d)L$ , then  $(0, \tilde{v})$  is globally asymptotically stable.

We refer to Fig. 1 for the illustrations of Theorems 1.1 and 1.2. Based on Theorem 1.2, we conjecture that the curves of  $\alpha_2^*(\alpha_1)$  and  $\alpha_1^*(\alpha_2)$  in the entire  $\alpha_1 - \alpha_2$  plane do not intersect and they are ordered as illustrated. For the region between these two curves, we conjecture that there exists exactly one coexistence equilibrium. In the region above the curve  $\alpha_2 = \alpha_2^*(\alpha_1)$ , which includes  $\{(\alpha_1, \alpha_2) : \alpha_1 \in \mathbb{R}, \alpha_2 \geq \frac{D_2}{D_1}\alpha_1\}$ , we conjecture that  $(\tilde{u}, 0)$  is globally asymptotically stable; in the region below the curve  $\alpha_1 = \alpha_1^*(\alpha_2)$ , which includes  $\{(\alpha_1, \alpha_2) : \alpha_1 \geq (g(1) - d)L, \alpha_2 \leq \frac{D_2}{D_1}\alpha_1 - \left(\frac{D_2}{D_1} - 1\right)(g(1) - d)L\}$ ,  $(0, \tilde{v})$  is globally asymptotically stable.

Next, we fix the dispersal strategy  $(D_1, \alpha_1)$  of the first species and ask: What kind of dispersal strategies should the second species  $v$  adopt in order to drive the species  $u$  to

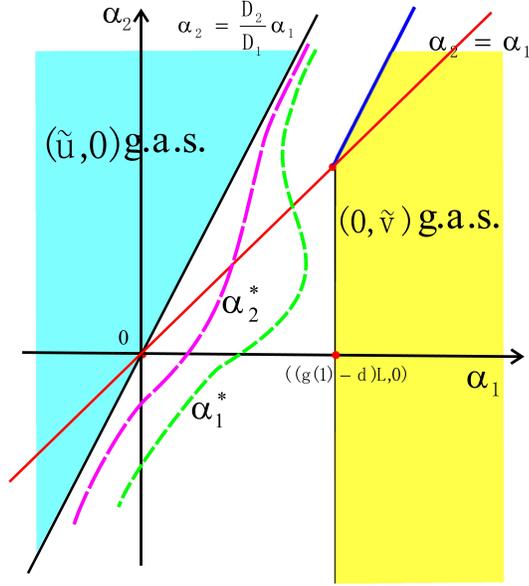


Figure 1: Illustrations of Theorems 1.1 and 1.2. For given  $0 < D_1 < D_2$ , we consider all possible choice of  $(\alpha_1, \alpha_2) \in \mathbb{R}^2$ : the blue region indicates the choice of parameters  $(\alpha_1, \alpha_2)$  such that  $(\tilde{u}, 0)$  is globally asymptotically stable, and the yellow region indicates the choice of parameters  $(\alpha_1, \alpha_2)$  such that  $(0, \tilde{v})$  is globally asymptotically stable. The curves  $\alpha_1 = \alpha_1^*(\alpha_2)$  and  $\alpha_2 = \alpha_2^*(\alpha_1)$  lie in the unshaded region, where the the global dynamics is unclear.

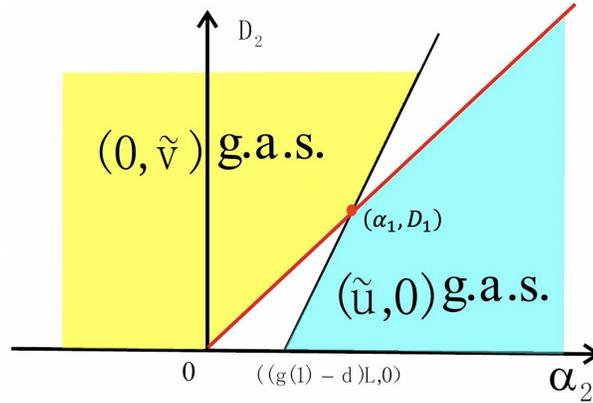


Figure 2: Illustration of Theorem 1.3. For given  $(D_1, \alpha_1) \in (0, \infty) \times [(g(1) - d)L, \infty)$ , the blue region indicates the choice of parameters  $(D_2, \alpha_2)$  such that  $(\tilde{u}, 0)$  is globally asymptotically stable, and the yellow region indicates the choice of parameters  $(D_2, \alpha_2)$  such that  $(0, \tilde{v})$  is globally asymptotically stable. The global dynamics is unclear in the unshaded region.

extinction? Previously, this point of view was adopted in [18] to study the evolutionary landscape by allowing only a single trait (i.e. diffusion rate or advection rate) to vary while fixing the other one. Here, we present our findings when the diffusion and advection rates are allowed to vary simultaneously. Theorems 1.3-1.4 below generalize and set the results in [18] in a broader biological context. They are illustrated in Fig. 2 and Fig. 3.

**Theorem 1.3** *Let  $(D_1, \alpha_1) \in (0, \infty) \times [(g(1) - d)L, \infty)$  be given.*

(a) *If  $(D_2, \alpha_2) \in (0, \infty) \times \mathbb{R} \setminus \{(D_1, \alpha_1)\}$  satisfies*

$$\frac{\alpha_2}{D_2} \leq \frac{\alpha_1}{D_1} \quad \text{and} \quad \frac{\alpha_2 - (g(1) - d)L}{D_2} \leq \frac{\alpha_1 - (g(1) - d)L}{D_1}, \quad (1.15)$$

*then  $(0, \tilde{v})$  is globally asymptotically stable.*

(b) *If  $(D_2, \alpha_2) \in (0, \infty) \times \mathbb{R} \setminus \{(D_1, \alpha_1)\}$  satisfies*

$$\frac{\alpha_2}{D_2} \geq \frac{\alpha_1}{D_1} \quad \text{and} \quad \frac{\alpha_2 - (g(1) - d)L}{D_2} \geq \frac{\alpha_1 - (g(1) - d)L}{D_1}, \quad (1.16)$$

*then  $(\tilde{u}, 0)$  is globally asymptotically stable.*

**Theorem 1.4** *Let  $(D_1, \alpha_1) \in (0, \infty) \times (-\infty, (g(1) - d)L)$  be given.*

(a) *If  $(D_2, \alpha_2) \in (0, \infty) \times \mathbb{R} \setminus \{(D_1, \alpha_1)\}$  satisfies*

$$\frac{\alpha_2}{D_2} \leq \frac{\alpha_1}{D_1} \quad \text{and} \quad D_2 \leq D_1, \quad (1.17)$$

*then  $(0, \tilde{v})$  is globally asymptotically stable.*

(b) *If  $(D_2, \alpha_2) \in (0, \infty) \times \mathbb{R}$  satisfies*

$$\alpha_2 \geq (g(1) - d)L \quad \text{and} \quad D_2 < D_1, \quad (1.18)$$

*then  $(\tilde{u}, 0)$  is globally asymptotically stable.*

(c) *If  $(D_2, \alpha_2) \in (0, \infty) \times \mathbb{R} \setminus \{(D_1, \alpha_1)\}$  satisfies*

$$\frac{\alpha_2}{D_2} \geq \frac{\alpha_1}{D_1} \quad \text{and} \quad D_2 \geq D_1 \quad (1.19)$$

*then  $(\tilde{u}, 0)$  is globally asymptotically stable.*

The rest of the paper is organized as follows: In Section 2, we establish some new monotonicity results for principal eigenvalues of elliptic problem in one-dimensional domains. In Section 3, we study the linear stability of two semi-trivial equilibria and the global dynamics of system (1.6). The conclusions are discussed in Section 4.

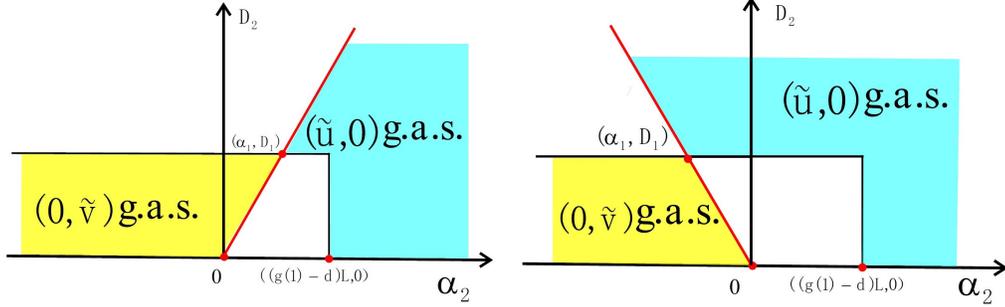


Figure 3: Illustration of Theorem 1.4. For given  $(D_1, \alpha_1) \in (0, \infty) \times (-\infty, (g(1) - d)L)$ , the blue region indicates the choice of parameters  $(D_2, \alpha_2)$  such that  $(\tilde{u}, 0)$  is globally asymptotically stable, and the yellow region indicates the choice of parameters  $(D_2, \alpha_2)$  such that  $(0, \tilde{v})$  is globally asymptotically stable. The global dynamics is unclear in the unshaded region.

## 2 Monotonicity results in an elliptic eigenvalue problem

In this subsection, we state or prove several useful lemmas concerning the principal eigenvalue  $\lambda_1(D, \alpha, h)$  of the eigenvalue problem

$$\begin{cases} D\phi_{xx} - \alpha\phi_x + h(x)\phi + \lambda_1\phi = 0, & 0 < x < L, \\ D\phi_x - \alpha\phi = 0, & x = 0, L, \end{cases} \quad (2.1)$$

where  $h$  satisfies

**(A)**  $h(x) \in C^1([0, L])$  such that  $h'(x) < 0$  in  $[0, L]$ .

By the transformation  $\psi = e^{-(\alpha/D)x}\phi$ ,  $\lambda_1(D, \alpha, h)$  is the principal eigenvalue, with positive eigenfunction  $\psi$ , of the following Neumann problem.

$$\begin{cases} D\psi_{xx} + \alpha\psi_x + h(x)\psi + \lambda_1\psi = 0, & 0 < x < L, \\ \psi_x(0) = \psi_x(L) = 0. \end{cases} \quad (2.2)$$

The main result of this section is

**Proposition 2.1** *Fix a function  $h(x)$  satisfying (A), and let  $\lambda_1(D, \alpha, h)$  be the principal eigenvalue of (2.1). Then*

(a)  $\frac{\partial \lambda_1}{\partial \alpha}(D, \alpha, h) > 0$  for  $(D, \alpha) \in (0, \infty) \times \mathbb{R}$ .

(b) For each  $(D_0, \alpha_0) \in (0, \infty) \times \mathbb{R}$ , we have

$$\frac{d}{ds} \lambda_1(sD_0, s\alpha_0, h) > 0 \quad \text{for any } s \in (0, \infty).$$

(c) For each  $(D_0, \alpha_0) \in (0, \infty) \times \mathbb{R}$  such that  $\alpha_0 \geq (h(0) + \lambda_1(D_0, \alpha_0, h))L$ , we have

$$\left. \frac{d}{ds} \lambda_1 \left( D_0 + s, \alpha_0 + \frac{\alpha_0 - (h(0) + \lambda_1(D_0, \alpha_0, h))L}{D_0} s, h \right) \right|_{s=0} < 0.$$

(d) For each  $(D_0, \alpha_0) \in (0, \infty) \times [h(0)L, \infty)$  such that  $\lambda_1(D_0, \alpha_0, h) \leq 0$ , we have

$$\frac{d}{ds} \lambda_1 \left( D_0 + s, \alpha_0 + \frac{\alpha_0 - h(0)L}{D_0} s, h \right) < 0 \quad \text{for all } s \geq 0.$$

**Remark 2.2** Assertion (a) was established in [18, Lemma 4.8] (see also [12, Lemma 5.2]). Assertion (b) is a consequence of the general reduction principle [1]. Assertions (c) – (d) are new.

We first recall the following result from [18, Lemma 4.7].

**Lemma 2.3** *If  $h(x)$  satisfies (A), then  $\psi_x < 0$  in  $(0, L)$ .*

**Proof.** Multiplying (2.2) by  $e^{\alpha x/D}$  and integrating the resulting equation over  $(0, L)$ , we deduce that  $\int_0^L e^{\alpha x/D} (h(x) + \lambda_1) \psi dx = 0$ , so that  $h(x) + \lambda_1$  changes sign. By (A), there is  $x_0 \in (0, L)$  such that  $h(x) + \lambda_1 > 0$  in  $[0, x_0)$  and  $h(x) + \lambda_1 < 0$  in  $(x_0, L]$ . Hence,

$$D(e^{\alpha x/D} \psi_x)_x = -e^{\alpha x/D} (h(x) + \lambda_1) \psi = \begin{cases} < 0 & \text{in } [0, x_0), \\ > 0 & \text{in } (x_0, L]. \end{cases}$$

Since  $\psi_x(0) = \psi_x(L) = 0$ , we deduce that  $\psi_x < 0$  in  $(0, L)$ . □

**Lemma 2.4** *If  $h(x)$  satisfies (A), then*

$$D\psi_x + \alpha\psi(x) > [\alpha - (h(0) + \lambda_1)L]\psi(0) \quad \text{in } (0, L).$$

**Proof.** By assumption (A),  $\psi(x) > 0$  and  $\psi_x < 0$  we have

$$\begin{aligned} \int_0^x [h(s) + \lambda_1] \psi(s) ds &< \int_0^x [h(0) + \lambda_1] \psi(s) ds \\ &< [h(0) + \lambda_1] \int_0^x \psi(0) ds \\ &\leq [h(0) + \lambda_1] \psi(0) L. \end{aligned}$$

Next, we integrate (2.2) in  $(0, x)$ , to get

$$\begin{aligned} D\psi_x(x) + \alpha\psi(x) &= \alpha\psi(0) - \int_0^x [h(s) + \lambda_1] \psi(s) ds \\ &> [\alpha - (h(0) + \lambda_1)L]\psi(0) \end{aligned}$$

for all  $x \in (0, L)$ .  $\square$

**Proof of Proposition 2.1.** Assertion (a) follows from [18, Lemma 4.8] (see also [12, Lemma 5.2]).

For assertion (b), we fix  $D_0, \alpha_0, h$ , set  $(D, \alpha) = (sD_0, s\alpha_0)$  and denote  $\Lambda_b(s) = \lambda_1(sD_0, s\alpha_0, h)$ . Then (2.2) becomes

$$\begin{cases} sD_0\psi_{xx} + s\alpha_0\psi_x + h(x)\psi + \Lambda_b\psi = 0 & \text{for } 0 < x < L, \\ \psi_x(0) = \psi_x(L) = 0. \end{cases}$$

Differentiating with respect to  $s$ , and denoting  $\frac{d}{ds} = '$ , we have

$$\begin{cases} sD_0\psi'_{xx} + s\alpha_0\psi'_x + h(x)\psi' + \Lambda_b\psi' = -D_0\psi_{xx} - \alpha_0\psi_x - \Lambda'_b\psi & \text{for } x \in (0, L), \\ \psi'_x(0) = \psi'_x(L) = 0 \end{cases}$$

Multiply the above by  $e^{\alpha_0 x/D_0}\psi(x)$  and integrating by parts, we have

$$0 = -D_0 \int_0^L (e^{\alpha_0 x/D_0}\psi_x)_x \psi \, dx - \Lambda'_b \int_0^L e^{\alpha_0 x/D_0} |\psi|^2 \, dx.$$

Integrating by parts once more, we have

$$\Lambda'_b \int_0^L e^{\alpha_0 x/D_0} |\psi|^2 \, dx = -D_0 \int_0^L (e^{\alpha_0 x/D_0}\psi_x)_x \psi \, dx = D_0 \int_0^L e^{\alpha_0 x/D_0} |\psi_x|^2 \, dx > 0,$$

where the last strict inequality holds since  $h(x)$ , and hence  $\psi$ , are non-constant. Thus  $\Lambda'_b(s) > 0$  for  $s > 0$ . This proves assertion (b).

For assertion (c), we fix  $D_0, \alpha_0, h$ , and define

$$\Lambda_c(s) = \lambda_1 \left( D_0 + s, \alpha_0 + \frac{\alpha_0 - (h(0) + \lambda_1(D_0, \alpha_0, h))L}{D_0} s, h \right).$$

We need to show  $\Lambda'_c(0) < 0$ . To this end, we set

$$(D, \alpha) = \left( D_0 + s, \alpha_0 + \frac{\alpha_0 - (h(0) + \lambda_1(D_0, \alpha_0, h))L}{D_0} s \right)$$

in (2.2), differentiate in  $s$  and then set  $s = 0$  to get

$$\begin{cases} D_0\psi'_{xx} + \alpha_0\psi'_x + h(x)\psi' + \Lambda_c(0)\psi' = -\psi_{xx} - m_0\psi_x - \Lambda'_c(0)\psi & \text{for } x \in (0, L), \\ \psi'_x(0) = \psi'_x(L) = 0, \end{cases}$$

where  $m_0 := [\alpha_0 - (h(0) + \lambda_1(D_0, \alpha_0, h))L]/D_0$  is a nonnegative constant by assumption. Multiplying the equation of  $\psi'$  by  $e^{\alpha_0 x/D_0} \psi$ , integrating by parts and applying the equation of  $\psi$ , we have

$$\begin{aligned} 0 &= - \int_0^L e^{\alpha_0 x/D_0} \psi_{xx} \psi \, dx - m_0 \int_0^L e^{\alpha_0 x/D_0} \psi_x \psi \, dx - \Lambda'_c(0) \int_0^L e^{\alpha_0 x/D_0} |\psi|^2 \, dx \\ &= - \int_0^L (e^{\alpha_0 x/D_0} \psi_x)_x \psi \, dx - \left(m_0 - \frac{\alpha_0}{D_0}\right) \int_0^L e^{\alpha_0 x/D_0} \psi_x \psi \, dx - \Lambda'_c(0) \int_0^L e^{\alpha_0 x/D_0} |\psi|^2 \, dx. \end{aligned}$$

Integrating by parts the first term, and rearranging, we have

$$\begin{aligned} &\Lambda'_c(0) \int_0^L e^{\alpha_0 x/D_0} |\psi|^2 \, dx \\ &= \int_0^L e^{\alpha_0 x/D_0} |\psi_x|^2 \, dx - \left(m_0 - \frac{\alpha_0}{D_0}\right) \int_0^L e^{\alpha_0 x/D_0} \psi_x \psi \, dx \\ &= \int_0^L e^{\alpha_0 x/D_0} \psi_x \left[ \psi_x - \left(m_0 - \frac{\alpha_0}{D_0}\right) \psi \right] \, dx \\ &< \int_0^L e^{\alpha_0 x/D_0} \psi_x \left[ \frac{\alpha_0 - (h(0) + \lambda_1(D_0, \alpha_0, h))L}{D_0} \psi(0) - m_0 \psi(x) \right] \, dx \\ &\leq \int_0^L e^{\alpha_0 x/D_0} \psi_x \left[ \frac{\alpha_0 - (h(0) + \lambda_1(D_0, \alpha_0, h))L}{D_0} - m_0 \right] \psi(0) \, dx = 0, \end{aligned}$$

where we used Lemma 2.4 for the first inequality,  $m_0 \geq 0$  and  $\psi_x < 0$  for the second inequality, and the definition of  $m_0$  in the final equality. This shows  $\Lambda'_c(0) < 0$ , and completes the proof of (c).

To show assertion (d), define

$$\Lambda_d(s) = \lambda_1 \left( D_0 + s, \alpha_0 + \frac{\alpha_0 - h(0)L}{D_0} s, h \right).$$

Notice that

$$\Lambda'_d(0) = \Lambda'_c(0) + \frac{\lambda_1(D_0, \alpha_0, h)L}{D_0} \frac{\partial}{\partial \alpha} \lambda_1(D_0, \alpha_0, h) < 0,$$

by assertions (a) and (c). This together with the assumption  $\lambda_1(D_0, \alpha_0, h) \leq 0$  shows that  $\Lambda'_d(s) < 0$  for  $0 < s \ll 1$ . Define  $\tilde{s} := \sup\{s_0 > 0 : \Lambda'(s) < 0 \text{ in } (0, s_0)\}$ , then  $\tilde{s} > 0$ . If  $\tilde{s} = \infty$ , then we are done. Suppose  $\tilde{s} < +\infty$ , then  $\Lambda_d(\tilde{s}) < 0$  and  $\Lambda'_d(\tilde{s}) = 0$ . But one can apply Proposition 2.1(c) to derive a contradiction as follows: Set

$$(\tilde{D}_0, \tilde{\alpha}_0) = \left( D_0 + \tilde{s}, \alpha_0 + \frac{\alpha_0 - h(0)L}{D_0} \tilde{s} \right)$$

so that

$$\frac{\tilde{\alpha}_0 - h(0)L}{\tilde{D}_0} = \frac{\alpha_0 - h(0)L}{D_0}. \quad (2.3)$$

Then  $\Lambda_d(\tilde{s}) < 0$  implies  $\lambda_1(\tilde{D}_0, \tilde{\alpha}_0, h) < 0$ . Therefore,

$$\tilde{\alpha}_0 \geq \alpha_0 \geq h(0)L > (h(0) + \lambda_1(\tilde{D}_0, \tilde{\alpha}_0, h))L.$$

Hence, we can apply Proposition 2.1(c), with  $(D_0, \alpha_0)$  replaced by  $(\tilde{D}_0, \tilde{\alpha}_0)$ , to get

$$\frac{\partial \lambda_1}{\partial D}(\tilde{D}_0, \tilde{\alpha}_0) + \frac{\partial \lambda_1}{\partial \alpha}(\tilde{D}_0, \tilde{\alpha}_0) \cdot \frac{\tilde{\alpha}_0 - (h(0) + \lambda_1(\tilde{D}_0, \tilde{\alpha}_0, h))L}{\tilde{D}_0} < 0. \quad (2.4)$$

Note that  $\Lambda'_d(\tilde{s}) = 0$  can be written as

$$\frac{\partial \lambda_1}{\partial D}(\tilde{D}_0, \tilde{\alpha}_0) + \frac{\partial \lambda_1}{\partial \alpha}(\tilde{D}_0, \tilde{\alpha}_0) \cdot \frac{\alpha_0 - h(0)L}{D_0} = 0. \quad (2.5)$$

Combining equations (2.4)-(2.5) and  $\frac{\partial \lambda_1}{\partial \alpha} > 0$  (Proposition 2.1(a)) we get

$$\frac{\tilde{\alpha}_0 - (h(0) + \lambda_1(\tilde{D}_0, \tilde{\alpha}_0, h))L}{\tilde{D}_0} < \frac{\alpha_0 - h(0)L}{D_0},$$

which, in view of (2.3), leads to  $\lambda_1(\tilde{D}_0, \tilde{\alpha}_0, h) > 0$ . This is in contradiction with the non-positivity of  $\lambda_1(\tilde{D}_0, \tilde{\alpha}_0, h)$ .  $\square$

### 3 Linear stability of the semi-trivial equilibria

Recall that the linear stability of  $(\tilde{u}, 0)$  is determined by the spectrum of (1.9), which is a system of two nonlocal PDEs. Proposition 4.5 of [18] says that it is equivalent to determining the sign of the principal eigenvalue  $\lambda_u$  of a problem involving a single equation.

**Proposition 3.1** *Denote*

$$\lambda_u = \lambda_1(D_2, \alpha_2, g(\sigma_1(x)) - d) \quad \text{and} \quad \lambda_v = \lambda_1(D_1, \alpha_1, g(\sigma_2(x)) - d) \quad (3.1)$$

where  $\sigma_1$  and  $\sigma_2$  are given in (1.10) and (1.12). Namely,

$$\sigma_1(x) = \exp\left(-k_0x - \int_0^x \tilde{u}(s) ds\right) \quad \text{and} \quad \sigma_2(x) = \exp\left(-k_0x - \int_0^x \tilde{v}(s) ds\right).$$

Then

- (a) *The equilibrium  $(\tilde{u}, 0)$  is linearly stable if  $\lambda_u > 0$  and is linearly unstable if  $\lambda_u < 0$ ;*

(b) *The equilibrium  $(0, \tilde{v})$  is linearly stable if  $\lambda_v > 0$  and is linearly unstable if  $\lambda_v < 0$ .*

**Proof.** By [18, Proposition 4.5], the problem (1.9), which determines the stability of  $(\tilde{u}, 0)$ , has a principal eigenvalue  $\Lambda_u \in \mathbb{R}$ , in the sense that  $\Lambda_u \leq \operatorname{Re} \Lambda$  for all eigenvalues  $\Lambda$  of (1.9). Furthermore, the sign of  $\Lambda_u$  is identical with the sign of the principal eigenvalue  $\lambda_u$  of

$$\begin{cases} D_2 \varphi_{xx} - \alpha_2 \varphi_x + [g(\sigma_1(x)) - d] \varphi + \lambda_1 \varphi = 0, & 0 < x < L, \\ D_2 \varphi_x - \alpha_2 \varphi = 0, & x = 0, L, \end{cases} \quad (3.2)$$

where  $\sigma_1$  is given in (1.10). Since  $\lambda_u = \lambda_1(D_2, \alpha_2, g(\sigma_1(x)) - d)$  by definition, the assertion (a) holds. Assertion (b) follows from [18, Proposition 4.6] in a similar fashion.  $\square$

Next, we prove that  $\alpha_1^*(\alpha_2)$  and  $\alpha_2^*(\alpha_1)$ , which were given in the statement of Theorem 1.1, are well defined.

**Lemma 3.2** *For each  $\alpha_1 \in \mathbb{R}$ , there is a critical number  $\alpha_2^* \in \mathbb{R}$  such that  $(\tilde{u}, 0)$  is linearly stable if and only if  $\alpha_2 > \alpha_2^*$ .*

**Proof.** Let  $(\tilde{u}, 0)$  be the semi-trivial equilibrium of (1.6), where  $\tilde{u}$  is the unique positive solution of (1.7). Integrate the equation (1.7) to get  $\int_0^L (g(\sigma_1(x)) - d) \tilde{u} dx = 0$ . Since  $\tilde{u} > 0$  in  $[0, L]$ , the function  $g(\sigma_1(x)) - d$  must change sign in  $[0, L]$ . Since  $x \mapsto \sigma_1(x)$ , and thus  $x \mapsto g(\sigma_1(x))$ , are strictly decreasing in  $x$ , we deduce

$$g(\sigma_1(0)) - d > 0 > g(\sigma_1(L)) - d. \quad (3.3)$$

We claim that  $(\tilde{u}, 0)$  is linearly stable for  $\alpha_2 > 0$  large, and linearly unstable for  $\alpha_2 < 0$  large. By Proposition 3.1, it suffices to show that  $\lambda_u > 0$  for  $\alpha_2 \rightarrow \infty$  large, and that  $\lambda_u < 0$  for  $\alpha_2 \rightarrow -\infty$ . Here  $\lambda_u$  is the principal eigenvalue of (2.2) with  $(D, \alpha, h) = (D_2, \alpha_2, g(\exp(-k_0 x - \int_0^x \tilde{u}(s) ds)) - d)$ . It then follows from [4, Theorem 1.1] and (3.3) that

$$\lambda_1(D_2, \alpha_2, g(\sigma_1(x)) - d) \rightarrow d - g(\sigma_1(L)) > 0 \quad \text{as } \alpha_2 \rightarrow +\infty.$$

Thus  $(\tilde{u}, 0)$  is linearly stable for  $\alpha_2 > 0$  large. Whereas, by [4, Theorem 1.1] and (3.3), we have

$$\lambda_1(D_2, \alpha_2, g(\sigma_1(x)) - d) \rightarrow d - g(\sigma_1(0)) < 0 \quad \text{as } \alpha_2 \rightarrow -\infty.$$

Hence,  $(\tilde{u}, 0)$  is linearly unstable for  $\alpha_2 < 0$  large.

Since  $\lambda_1$  is strictly increasing in  $\alpha_2 \in \mathbb{R}$  (Proposition 2.1(a)), there is a unique  $\alpha_2^*$  such that  $\lambda_u = \lambda_1(D_2, \alpha_2^*, g(\sigma_1(x)) - d) = 0$ ,  $\lambda_u > 0$  for  $\alpha_2 > \alpha_2^*$  and  $\lambda_u < 0$  for  $\alpha_2 < \alpha_2^*$ . This completes the proof.  $\square$

**Lemma 3.3** *For each  $\alpha_2 \in \mathbb{R}$ , there is a critical number  $\alpha_1^* \in \mathbb{R}$  such that  $(0, \tilde{v})$  is linearly stable if and only if  $\alpha_1 > \alpha_1^*$ .*

**Proof.** The proof is completely analogous with that of Lemma 3.2, and is omitted.  $\square$

**Proposition 3.4** *Suppose  $0 < D_1 < D_2$ , and one of the following holds:*

- (i)  $\alpha_1 < (g(1) - d)L$  and  $\alpha_2 \in \left[ \frac{D_2}{D_1} \alpha_1, \infty \right)$ ;
- (ii)  $\alpha_1 \geq (g(1) - d)L$  and  $\alpha_2 \in \left( -\infty, \frac{D_2}{D_1} \alpha_1 - \left( \frac{D_2}{D_1} - 1 \right) (g(1) - d)L \right] \cup \left[ \frac{D_2}{D_1} \alpha_1, \infty \right)$ .

*Then system (1.6) has no co-existence equilibria.*

**Proof.** Suppose to the contrary that (1.6) has a co-existence equilibrium  $(\hat{u}, \hat{v})$ , then by the strong maximum principle,  $\hat{u} > 0$  and  $\hat{v} > 0$  in  $[0, L]$ . By definition of  $\lambda_1(D, \alpha, h)$  of Section 2, we deduce that

$$\lambda_1(D_1, \alpha_1, \hat{h}) = \lambda_1(D_2, \alpha_2, \hat{h}) = 0, \quad (3.4)$$

where  $\hat{h} = g(\exp(-k_0 x - \int_0^x \hat{u}(s) ds - \int_0^x \hat{v}(s) ds)) - d$  satisfies **(A)**. First, we assume that  $0 < D_1 < D_2$  and  $\alpha_2 \geq \frac{D_2}{D_1} \alpha_1$ . In this case, we have

$$\lambda_1(D_1, \alpha_1, \hat{h}) < \lambda_1 \left( D_2, \frac{D_2}{D_1} \alpha_1, \hat{h} \right) \leq \lambda_1(D_2, \alpha_2, \hat{h}),$$

where the first inequality follows from Proposition 2.1(b) and the second one from Proposition 2.1(a). This is a contradiction with (3.4). Assertion (i) is proved.

Next, we prove (ii). Since the case  $\alpha_2 \geq \frac{D_2}{D_1} \alpha_1$  is included in the above, it remains to consider the case

$$0 < D_1 < D_2, \quad \alpha_1 \geq (g(1) - d)L \quad \text{and} \quad \alpha_2 \leq \frac{D_2}{D_1} \alpha_1 - \left( \frac{D_2}{D_1} - 1 \right) (g(1) - d)L,$$

which implies

$$\lambda_1(D_1, \alpha_1, \hat{h}) > \lambda_1 \left( D_2, \alpha_1 + \frac{\alpha_1 - (g(1) - d)L}{D_1} (D_2 - D_1), \hat{h} \right) \geq \lambda_1(D_2, \alpha_2, \hat{h}),$$

where the first and second inequalities follow from Proposition 2.1(d) and (a), respectively. This is a contradiction with (3.4). Assertion (ii) is proved.  $\square$

**Proof of Theorem 1.2.** First, we prove assertion (a). We claim that  $(0, \tilde{v})$  is linearly unstable, i.e.  $\lambda_1(D_1, \alpha_1, g(\sigma_2(x)) - d) < 0$ , where  $\sigma_2(x) = \exp(-k_0 x - \int_0^x \tilde{v}(s) ds)$ . Now,

observe that  $\lambda_1(D_2, \alpha_2, g(\sigma_2(x)) - d) = 0$  with  $\tilde{v} > 0$  being the corresponding positive eigenfunction. It then follows that

$$\lambda_1(D_1, \alpha_1, g(\sigma_2(x)) - d) < \lambda_1\left(D_2, \frac{D_2}{D_1}\alpha_1, g(\sigma_2(x)) - d\right) \leq \lambda_1(D_2, \alpha_2, g(\sigma_2(x)) - d) = 0,$$

where the first and second inequalities follow from Proposition 2.1(b) and (a), respectively. This shows that  $(0, \tilde{v})$  is linearly unstable.

Recall that by [18, Theorem 2.1], the system (1.6) generates a strongly monotone dynamical system. Since  $(0, \tilde{v})$  is linearly unstable and, by Proposition 3.4, (1.6) has no co-existence equilibria, it follows from [13, Theorem B] and the proof of [23, Theorem 1.3] that  $(\tilde{u}, 0)$  is globally asymptotically stable. This establishes assertion (a).

Next, we prove assertion (b). We claim that  $(\tilde{u}, 0)$  is linearly unstable, i.e.  $\lambda_1(D_2, \alpha_2, g(\sigma_1(x)) - d) < 0$ , where  $\sigma_1(x) = \exp(-k_0x - \int_0^x \tilde{u}(s) ds)$ . We see that  $\lambda_1(D_1, \alpha_1, g(\sigma_1(x)) - d) = 0$  with  $\tilde{u} > 0$  being the corresponding positive eigenfunction. It then follows from Proposition 2.1(d) that  $s \mapsto \lambda_1\left(D_1 + s, \alpha_1 + \frac{\alpha_1 - (g(1) - d)L}{D_1}s\right)$  is strictly decreasing in  $[0, \infty)$ . (Note that  $g(\sigma_1(0)) - d = g(1) - d$ .) Hence,

$$\begin{aligned} \lambda_1(D_2, \alpha_2, g(\sigma_1(x)) - d) &\leq \lambda_1\left(D_2, \frac{D_2}{D_1}[\alpha_1 - (g(1) - d)L] + (g(1) - d)L, g(\sigma_1(x)) - d\right) \\ &< \lambda_1(D_1, \alpha_1, g(\sigma_1(x)) - d) = 0, \end{aligned}$$

where the first and second inequalities follow from Proposition 2.1(a) and (d), respectively. This shows that  $(\tilde{u}, 0)$  is linearly unstable. Arguing similarly as in the proof of Theorem 1.2(a), we can conclude that  $(0, \tilde{v})$  is globally asymptotically stable. This establishes assertion (b).  $\square$

**Proof of Theorem 1.1.** First, we prove assertion (a). Let  $D_2 > D_1 > 0$  and  $\alpha_1 \in \mathbb{R}$  be given. By Lemma 3.2,  $\alpha_2^*$  is well-defined. By Theorem 1.2(a),  $(\tilde{u}, 0)$  is globally asymptotically stable if  $\alpha_2 \geq \frac{D_2}{D_1}\alpha_1$ . By the definition of  $\alpha_2^*$ , this implies that  $\alpha_2^* < \frac{D_2}{D_1}\alpha_1$ . If, in addition,  $\alpha_1 \geq (g(1) - d)L$ , then Theorem 1.2(b) is applicable, i.e. if  $\alpha_2 \leq \frac{D_2}{D_1}(\alpha_1 - (g(1) - d)L) + (g(1) - d)L$ , then  $(0, \tilde{v})$  is globally asymptotically stable and  $(\tilde{u}, 0)$  is unstable. This implies that  $\alpha_2^* \geq \frac{D_2}{D_1}(\alpha_1 - (g(1) - d)L) + (g(1) - d)L$ . Summarizing the above, we obtain (1.13). This proves assertion (a).

Next, we prove assertion (b). Again,  $\alpha_1^* > \frac{D_1}{D_2}\alpha_2$  follows as a consequence of Theorem 1.2(a). It remains to show the upper bounds of  $\alpha_1^*$  in (1.14) by considering the following two cases:

- (i)  $\alpha_2 < (g(1) - d)L$ ;
- (ii)  $\alpha_2 \geq (g(1) - d)L$ .

In the case (i) (i.e.  $\alpha_2 < (g(1) - d)L$ ), observe that for any  $\alpha_1 \in [(g(1) - d)L, \infty)$ , we have

$$\alpha_2 < (g(1) - d)L \leq \frac{D_2}{D_1}(\alpha_1 - (g(1) - d)L) + (g(1) - d)L.$$

Thus Theorem 1.2(b) can be applied to yield that  $(0, \tilde{v})$  is globally asymptotically stable. This shows that  $\alpha_1^* < (g(1) - d)L$ .

In the case (ii) (i.e.  $\alpha_2 \geq (g(1) - d)L$ ), observe that for every

$$\alpha_1 \in \left[ \frac{D_1}{D_2}(\alpha_2 - (g(1) - d)L) + (g(1) - d)L, +\infty \right),$$

it holds that

$$\alpha_1 \geq (g(1) - d)L \quad \text{and} \quad \alpha_2 \leq \frac{D_2}{D_1}(\alpha_1 - (g(1) - d)L) + (g(1) - d)L.$$

Thus Theorem 1.2(b) can be applied to yield that  $(0, \tilde{v})$  is globally asymptotically stable for  $\alpha_1 \in \left[ \frac{D_1}{D_2}(\alpha_2 - (g(1) - d)L) + (g(1) - d)L, \infty \right)$ . By definition of  $\alpha_1^*$ , this means  $\alpha_1^* < \frac{D_1}{D_2}(\alpha_2 - (g(1) - d)L) + (g(1) - d)L$ . This completes the proof.  $\square$

**Proof of Theorem 1.3.** Let  $D_1 > 0$  and  $\alpha_1 \geq (g(1) - d)L$  be given. For the convenience of the reader, the parameter regions where  $(0, \tilde{v})$  (resp.  $(\tilde{u}, 0)$ ) is globally asymptotically stable are illustrated in Fig. 2. First, we prove assertion (a). To this end, we assume (1.15) and divide the proof into the following three cases:

$$(i) \quad D_1 < D_2; \quad (ii) \quad D_1 = D_2; \quad (iii) \quad D_1 > D_2. \quad (3.5)$$

In case (i), we apply Theorem 1.2(b) to deduce that  $(0, \tilde{v})$  is globally stable. In case (ii), we apply [18, Theorem 2.2] to deduce that  $(0, \tilde{v})$  is globally stable. In case (iii) (i.e.  $D_1 > D_2$ ), by re-ordering the two species, Theorem 1.2(a) says that  $(0, \tilde{v})$  is globally stable if  $\alpha_1 \geq \frac{D_1}{D_2}\alpha_2$ . This proves assertion (a).

Next, we prove assertion (b). To this end, we assume (1.16) and divide into the three cases as in (3.5). In case (i), Theorem 1.2(a) implies that  $(\tilde{u}, 0)$  is globally asymptotically stable. In case (ii), we use [18, Theorem 2.2]. In case (iii), observe that  $\alpha_1 \geq (g(1) - d)L$  and the second part of (1.16) implies

$$\alpha_2 \geq (g(1) - d)L \quad \text{and} \quad \alpha_1 \leq \frac{D_1}{D_2}(\alpha_2 - (g(1) - d)L) + (g(1) - d)L.$$

Hence, by re-ordering the two species, and we can apply Theorem 1.2(b) to conclude that  $(\tilde{u}, 0)$  is globally stable. This proves assertion (b).  $\square$

**Proof of Theorem 1.4.** Let  $D_1 > 0$  and  $\alpha_1 < (g(1) - d)L$  be given. For the convenience of the reader, the parameter regions where  $(0, \tilde{v})$  (resp.  $(\tilde{u}, 0)$ ) is globally asymptotically stable are illustrated in Fig. 3. First, we prove assertion (a). To this end, we assume (1.17) and divide into the following cases:

$$(i) \quad D_1 = D_2; \quad (ii) \quad D_1 > D_2. \quad (3.6)$$

For case (i), we use [18, Theorem 2.2]. For case (ii), observe that we have  $\alpha_1 \geq \frac{D_1}{D_2}\alpha_2$  and  $D_2 < D_1$ , so that we can re-label the two species and apply Theorem 1.2(a) to establish the global stability of  $(0, \tilde{v})$ .

Next, we prove assertion (b). In this case,  $\alpha_1 < (g(1) - d)L$  and (1.18) hold. These imply that  $D_2 < D_1$ , and that

$$\alpha_2 \geq (g(1) - d)L \quad \text{and} \quad \alpha_1 \leq \frac{D_1}{D_2}(\alpha_2 - (g(1) - d)L) + (g(1) - d)L.$$

We can re-label the two species and apply Theorem 1.2(b) to establish the global stability of  $(\tilde{u}, 0)$ .

Finally, we prove assertion (c). In view of [18, Theorem 2.2], which treats the case  $D_1 = D_2$ , it remains to consider the case  $\alpha_2 \geq \frac{D_2}{D_1}\alpha_1$  and  $D_2 > D_1$ . In this case Theorem 1.2(a) implies that  $(\tilde{u}, 0)$  is globally stable. This completes the proof.  $\square$

## 4 Discussion

In this paper, we further study a nonlocal reaction-diffusion-advection system, which arises in the mathematical modeling of two competing phytoplankton species in a water column, where the species depend solely on light for their metabolism. In our previous work [18], we proved that system (1.1) is a strongly monotone dynamical system with respect to the order generated by the positive cone of the cumulative distribution functions, which enables the application of the various tools in the theory of monotone dynamical systems.

For fixed  $D_2 > D_1 > 0$ , we studied the local and global stability of the semi-trivial equilibria of system (1.6) in Theorems 1.1 and 1.2. First, we showed that the local stability of the semi-trivial equilibria changes at two critical parameters  $\alpha_2^*$  and  $\alpha_1^*$ , and showed that

$$\lim_{\alpha_1 \rightarrow \infty} \frac{\alpha_2^*(\alpha_1)}{\alpha_1} = \frac{D_2}{D_1} = \lim_{\alpha_2 \rightarrow \infty} \frac{\alpha_2}{\alpha_1^*(\alpha_2)}.$$

These limits suggest that two phytoplankton populations can only coexist in fairly narrow regions of large sinking rates. Biologically this is meaningful, as large sinking rates push

both phytoplankton populations to the bottom of the water column where the competitive exclusion occurs in most, if not all, situations.

We also explored the global dynamics of (1.6), from the perspective of evolution dispersal, in Theorems 1.3 and 1.4. By varying both the dispersal traits  $D_i$  and  $\alpha_i$ , we generalized and extended our previous results in [18], and give various sufficient conditions in which one of the semi-trivial equilibria attracts all positive solutions of (1.6). Besides the theory of monotone dynamical systems, another key tool is a monotonicity result concerning the principal eigenvalue of an elliptic problem in one-dimensional domains, where the coefficient of the zero-th order term is monotone decreasing. This is relevant in our situation since the growth rates of either species depend only on the availability of sunlight, which is always monotonically decreasing in the water depth. However, we have mostly focused on the role of the dispersal parameters  $D_i$  and  $\alpha_i$ , and assumed that the growth function  $g$  and death rate are the same with the two species.

The stability and uniqueness of the coexistence equilibria is another interesting problem that is left open. For system (1.6), the associated linearized eigenvalue problem at the coexistence equilibrium is a strongly coupled, nonlocal reaction-diffusion-advection system, and its dependence on the diffusion, advection and nonlocal terms is likely different from that of the Lotka-Volterra competition system [10, 26, 35]. It will also be of interest to determine the asymptotic profiles of coexistence states for small diffusion rates or large drift rates.

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