Algal Competition in a water column with excessive dioxide in the atmosphere

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Abstract This paper deals with a resource competition model of two algal species in a water column with excessive dioxide in the atmosphere. First, the uniqueness of positive steady state solutions to the single-species model with two resources is established by the application of the degree theory and the strong maximum principle for the cooperative system. Second, some asymptotic behavior of the single-species model is given by comparison principle and uniform persistence theory. Third, the coexistence solutions to the competition system of two species with two substitutable resources are obtained by global bifurcation theory, various estimates and the strong maximum principle for the cooperative system. Numerical simulations are used to illustrate the outcomes of coexistence and competitive exclusion.

Keywords water column · steady state · uniqueness · maximum principle for cooperative system · global bifurcation

Mathematics Subject Classification (2000) 35K57 · 92D25

1 Introduction

Some of the most profound challenges in understanding the global environment involve the connection between phytoplankton and carbon. As photosynthetic organisms, the algae of oceans and lakes consume inorganic carbon and produce organic matter. Atmospheric carbon dioxide (CO_2) is the ultimate source of the carbon consumed by phytoplankton, and the organic matter they produce either fuels aquatic food webs (whence most of it is returned to the atmosphere as CO_2), or is transported to deep water and sediments by sinking algae. This sinking flux potentially influences whether the world's ocean can absorb enough of the CO_2 produced by burning fossil fuels to retard the expected warming of the earth (Siegenthaler and Sarmiento 1993; Sabine et al. 2004; Riebesell et al. 2007).

Understanding the role of phytoplankton in global carbon dynamics is complicated by many factors, including the biochemistry of carbon acquisition by algae and the geochemistry of inorganic carbon in aquatic systems. Algae acquire inorganic carbon from CO_2 dissolved in the water, assimilating it into photosynthesis via the Rubisco enzyme (Kaplan and Reihnold 1999; Badger et al. 2006). Many species possess various adaptations (called carbon concentrating mechanisms) to increase the concentration of CO_2 at the active site of this enzyme, including active transport of CO_2 and of bicarbonate, an ionic form of inorganic carbon, which is converted enzymatically to CO_2 (Raven 1970; Martin and Tortell 2008; Maberly et al. 2009). This biochemical capability to

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use bicarbonate can be important where, as in ocean water, the bicarbonate concentration greatly exceeds that of CO_2 (Rost et al. 2008). Geochemically, CO_2 diffuses across the air water interface, and is produced biochemically by the respiration and decomposition of organic matter. Once dissolved in water, CO_2 hydrates with water molecules to form carbonic acid. This acid can lose one proton to become the bicarbonate ion, which can in turn lose another to become the carbonate ion. Both of these ionic forms of inorganic carbon can enter aquatic systems through dissolution from sediments and surrounding rocks and soils, so that inland and coastal waters display greater variability of inorganic carbon concentrations than does the open ocean. The availability of CO_2 and bicarbonate to algae thus depends on multiple sources of supply and the kinetics of several chemical reactions, diffusive transport across the surface of the water, and on transport within the water by turbulent diffusion in deep or poorly mixed systems.

Two important quantities in aquatic chemistry strongly influence the kinetics of reactions involving inorganic carbon: pH and alkalinity. The pH is a measure of proton (or H^+ ion) concentration in water, on a negative $\log_{10}$ scale, and measures the difference between the concentration of ions that can absorb protons and the concentration of proton donors (Wolf-Gladrow et al. 2007). Although alkalinity potentially depends on the concentrations of many dissolved ions, it is strongly related to the concentrations of bicarbonate and carbonate ions. Both pH and alkalinity of the world's waters are influenced by human processes. The increasing CO_2 concentration of the atmosphere supplies inorganic carbon to water and lowers its pH, increasing its proton concentration (Orr et al. 2005). Atmospheric sulfur and nitrogen oxides, which are also produced by fossil fuel combustion, convert to acids, and when deposited in receiving waters they reduce both pH and alkalinity (Rice and Herman 2012). Alkalinity can also be altered by changes in erosion and weathering of rocks and soils accompanying various geological processes and human activities. Thus the relationship between inorganic carbon and the algae of oceans and lakes connects many environmental problems of global scale.

The goal of this paper is to construct a model of algal growth and competition between species in relation to the supply inorganic carbon, simplifying the complex processes involved to a point of analytical tractability. We begin with a simplification introduced by Van de Waal et al. (2011), who proposed to represent dissolved CO_2 and carbonic acid as one resource and bicarbonate and carbonate ions as another. For shorthand we denote the first resource as "CO_2" and the second as "CARB", denoting their concentrations ($\mu\mathrm{mol\,m^{-3}}$) as $R(x,t)$ and $S(x,t)$, respectively. These resources are substitutable (Tilman 1982) in their effects on algal growth. In a well-mixed system in contact with the atmosphere but containing no algae or additional external sources of inorganic carbon, the kinetics of R and S (taken independent of x), follow the linear system:

$$\begin{aligned} \tfrac{dR}{dt} &= -\alpha(R(t)-\hat{R}) + \omega_s S(t) - \omega_r R(t), \\ \tfrac{dS}{dt} &= -\omega_s S(t) + \omega_r R(t), \end{aligned} \tag{1}$$

where α is the rate of CO_2 gas exchange between air and water, $\hat{R}$ is the thermodynamic equilibrium concentration of CO_2 in water, ω_r is the rate at which carbonic acid loses a proton to become bicarbonate, and ω_s the rate of the reverse reaction. All of these parameters vary with the physical and chemical conditions of natural waters, including in particular temperature, pH and alkalinity. The parameter $\hat{R}$ also depends directly on the atmospheric CO_2 concentration, which is currently increasing due to fossil fuel combustion. If the parameters of the linear system are taken as constants, then it has a stable equilibrium in which $R(t)$ approaches $\hat{R}$, and $S(t)$ approaches a value $\hat{R}\omega_r/\omega_s$. Additional processes, such as consumption of CO_2 and CARB by algae, displace the system from this equilibrium. Van de Waal et al. (2011) introduced terms for this consumption, and additional computations of feedbacks that arise from changes in pH and alkalinity during algal growth and thus alter the parameters of the linear system. For the purposes of this study, we ignore these latter feedbacks, treating the parameters of the linear system as constant. An additional simplification used here is that the cellular carbon content (or quota) is constant.

These simplifications are intended to retain analytical tractability while coupling the assumed linear dynamics of CO_2 and CARB to consumption and growth of algae, and embedding these dynamics in a spatially extended system, representing the vertical water column of an ocean or lake. For this water column, atmospheric exchange occurs at the surface and is thus represented in the upper boundary conditions (depth $x = 0$). Additional sources of both CO_2 and CARB arise in the lower boundary (depth $x = L$), as a result of decomposition of organic matter and weathering of sediments, respectively. Turbulent diffusion transports all constituents between these boundary points, but produces only incomplete mixing.

Because algal species differ in their relative abilities to consume CO_2 and CARB (Badger et al. 2006; Martin and Tortell 2008; Maberly et al. 2009), we include two competing species, taking the first to be more proficient than the second at consuming CO_2, and the second to be more proficient at consuming CARB. Both resources are substitutable to both species. The conventional graphical analysis of competition between two species for two substitutable resources (Tilman 1982; Grover 1997) leads to the expectation that competition outcomes should depend on the relative supplies of CO_2 and CARB. Relatively high CO_2 supply should produce dominance by the better consumer of CO_2, relatively high CARB supply should produce dominance by the better consumer of CARB, and intermediate supplies could allow coexistence. Additional results are possible if one of the resources cannot support growth of one of the competitors (Ballyk and Wolkowicz 1993; Ballyk et al. 2005). In the model studied here there are further complications that have received little attention in the literature on substitutable resources: conversion between the resources such as represented by the linear system (1), recycling of one resource (CO_2) through respiration, and the spatial structure of a water column. Our goal is to address such resource conversion in a water-column model representing algal growth and competition in relation to inorganic carbon. Our model complements similar models representing competition for other inorganic nutrients and light in a water column (e.g. Huisman et al. 1999; Klausmeier and Litchman 2001; Yoshiyama et al. 2009; Grover 2009, 2011; Blasius and Ryabov 2011; Kerimoglu et al. 2012). From a practical standpoint, we wish to know whether different algal species win the competition, depending on the geochemical parameters governing inorganic carbon, which are currently impacted by human alteration. Because different algal species have different edibility to consumer animals, for example, such knowledge lays the foundation to understand the food web and ecosystem impacts of human alteration of the aquatic carbon cycle.

2 The Mathematical Model and Main Results

We consider a resource competition model of two species in a water column with excessive dioxide in the atmosphere

$$\begin{array}{ll} R_t = DR_{xx} + \omega_s S - \omega_r R + \frac{r_1}{Q_1^*} B_1 + \frac{r_2}{Q_2^*} B_2 - f_1(R)B_1 - f_2(R)B_2, & x \in (0,L), t > 0, \\ S_t = DS_{xx} - \omega_s S + \omega_r R - g_1(S)B_1 - g_2(S)B_2, & x \in (0,L), t > 0, \\ (B_1)_t = D(B_1)_{xx} - \nu_1 (B_1)_x + [f_1(R) + g_1(S) - \frac{r_1}{Q_1^*} - m_1]B_1, & x \in (0,L), t > 0, \\ (B_2)_t = D(B_2)_{xx} - \nu_2 (B_2)_x + [f_2(R) + g_2(S) - \frac{r_2}{Q_2^*} - m_2]B_2, & x \in (0,L), t > 0, \end{array} \tag{2}$$

with boundary conditions

$$\begin{array}{lll} R_x(0,t) = \alpha(R(0,t) - \hat{R}), & R(L,t) = R^0, & t > 0, \\ S_x(0,t) = 0, & S(L,t) = S^0, & t > 0, \\ D(B_i)_x(0,t) - \nu_i B_i(0,t) = 0, & D(B_i)_x(L,t) - \nu_i B_i(L,t) = 0, & i = 1,2,\ t > 0, \end{array} \tag{3}$$

and nonnegative initial conditions, where $R(x,t), S(x,t), B_1(x,t), B_2(x,t)$ are the concentrations of "CO_2", "CARB" and the two algal species. $\alpha, \hat{R}, \omega_s, \omega_r > 0$ are constants, whose biological meaning can be found in Introduction. $D > 0$ is the vertical turbulent diffusion coefficient, ν_i is the sinking velocity ($\nu_i > 0$) or the buoyant velocity ($\nu_i < 0$) of species $i (i = 1,2)$. m_i, r_i, Q_i^* are the death rate, respiration rate and Carbon quota of species $i (i = 1,2)$, respectively. $R^0, S^0 > 0$ are the source concentration of CO_2 and CARB at the bottom of the water column, respectively.

Here for $S, R \geq 0$,

$$f_i(R) = \frac{\mu_{ir} R}{a_{ir} + R} \quad \text{and} \quad g_i(S) = \frac{\mu_{is} S}{a_{is} + S}$$

with $i = 1, 2$, $\mu_{ir}, \mu_{is} > 0$ are the maximum growth/uptake rates of species $i(i = 1, 2)$ in relation to CO_2 and CARB respectively, and $a_{ir}, a_{is} > 0$ are the half-saturation constants for growth/uptake of species $i(i = 1, 2)$ in relation to CO_2 and CARB respectively. For $S, R \leq 0$, we take the response functions $f_i(R) = 0$ and $g_i(S) = 0$ with $i = 1, 2$.

For simplicity by suitable scaling, we may assume $L = 1$. Let $\bar{r}_i = \frac{r_i}{Q_i^*}$. Then the original system (2)-(3) becomes

$$\begin{array}{ll} R_t = DR_{xx} + \omega_s S - \omega_r R + r_1 B_1 + r_2 B_2 - f_1(R)B_1 - f_2(R)B_2, & x \in (0,1), t > 0, \\ S_t = DS_{xx} - \omega_s S + \omega_r R - g_1(S)B_1 - g_2(S)B_2, & x \in (0,1), t > 0, \\ (B_1)_t = D(B_1)_{xx} - \nu_1 (B_1)_x + [f_1(R) + g_1(S) - r_1 - m_1]B_1, & x \in (0,1), t > 0, \\ (B_2)_t = D(B_2)_{xx} - \nu_2 (B_2)_x + [f_2(R) + g_2(S) - r_2 - m_2]B_2, & x \in (0,1), t > 0, \end{array} \tag{4}$$

with the boundary conditions

$$\begin{array}{lll} R_x(0,t) = \alpha(R(0,t) - \hat{R}), & R(1,t) = R^0, & t > 0, \\ S_x(0,t) = 0, & S(1,t) = S^0, & t > 0, \\ D(B_i)_x(0,t) - \nu_i B_i(0,t) = 0, & D(B_i)_x(1,t) - \nu_i B_i(1,t) = 0, & i = 1,2,\ t > 0 \end{array} \tag{5}$$

and nonnegative initial conditions. Here we denote $\bar{r}_i$ by r_i $(i = 1, 2)$ for the sake of simplicity.

The steady-state system of (4)-(5) is

$$\begin{array}{ll} DR_{xx} + \omega_s S - \omega_r R + r_1 B_1 + r_2 B_2 - f_1(R)B_1 - f_2(R)B_2 = 0, & x \in (0,1), \\ DS_{xx} - \omega_s S + \omega_r R - g_1(S)B_1 - g_2(S)B_2 = 0, & x \in (0,1), \\ D(B_1)_{xx} - \nu_1 (B_1)_x + [f_1(R) + g_1(S) - r_1 - m_1]B_1 = 0, & x \in (0,1), \\ D(B_2)_{xx} - \nu_2 (B_2)_x + [f_2(R) + g_2(S) - r_2 - m_2]B_2 = 0, & x \in (0,1), \end{array} \tag{6}$$

with the boundary conditions

$$\begin{array}{ll} R_x(0) = \alpha(R(0) - \hat{R}), \quad R(1) = R^0, & S_x(0) = 0, \quad S(1) = S^0, \\ D(B_i)_x(0) - \nu_i B_i(0) = 0, & D(B_i)_x(1) - \nu_i B_i(1) = 0, \quad i = 1, 2, \end{array} \tag{7}$$

The nonnegative steady state solutions of (4)-(5) can be divided into three types:

(i) washout solutions (namely trivial solutions) $(R, S, 0, 0)$;

(ii) semi-trivial solutions $(R, S, B_1, 0)$ and $(R, S, 0, B_2)$;

(iii) positive solutions (R, S, B_1, B_2) with $B_1(x) > 0$ and $B_2(x) > 0$ on [0, 1].

We begin with determining the washout solutions to (4)-(5). If $B_1 = B_2 = 0$, we have

$$\begin{array}{l} R_t = DR_{xx} + \omega_s S - \omega_r R, \quad x \in (0,1), t > 0, \\ S_t = DS_{xx} - \omega_s S + \omega_r R, \quad x \in (0,1), t > 0, \\ R_x(0,t) = \alpha(R(0,t) - \hat{R}), \ R(1,t) = R^0, \\ S_x(0,t) = 0, \ S(1,t) = S^0, \\ R(x,0) = R_0(x) \geq 0, \quad S(x,0) = S_0(x) \geq 0. \end{array} \tag{8}$$

Theorem 2.1 *(8) has a unique steady state solution* $(R^*(x), S^*(x))$ *with* $R^*(x), S^*(x) > 0$ *on* $[0, 1]$. *Moreover, the solution* $(R(x,t), S(x,t))$ *of (8) satisfies* $(R(x,t), S(x,t)) \to (R^*, S^*)$ *as* $t \to +\infty$.

It follows from Theorem 2.1 that the steady-state system (6)-(7) has a unique washout equilibrium solution $(R^*, S^*, 0, 0)$. Here $R^* = R^*(x), S^* = S^*(x), 0 \leq x \leq 1$. Let

$$m_1^* := -\lambda_1(-f_1(R^*) - g_1(S^*), \nu_1) - r_1 \text{ and } m_2^* := -\lambda_1(-f_2(R^*) - g_2(S^*), \nu_2) - r_2,$$

where $\lambda_1(-f_i(R^*) - g_i(S^*), \nu_i)(i = 1, 2)$ is the smallest eigenvalue corresponding to the linear eigenvalue problem (39) (or (38) equivalently) with $q(x) = -f_i(R^*) - g_i(S^*)$ and $\nu = \nu_i$. Suppose $f_i(R^*) > r_i(i = 1, 2)$. Then $-f_i(R^*) - g_i(S^*) < -r_i$. It follows from Lemma D.1 that

$$\lambda_1(-f_i(R^*) - g_i(S^*), \nu_i) < \lambda_1(-r_i, \nu_i) = -r_i,$$

which implies $m_i^* > 0(i = 1, 2)$ provided that $f_i(R^*) > r_i(i = 1, 2)$.

Theorem 2.2 *Suppose $f_i(R^*) > r_i(i = 1, 2)$. Then the unique washout equilibrium solution $(R^*, S^*, 0, 0)$ of (6)-(7) is linearly stable provided $m_1 > m_1^*, m_2 > m_2^*$; and unstable provided $m_1 < m_1^*$ or $m_2 < m_2^*$.*

Next, we study the single population system

$$\begin{array}{ll}
R_t = DR_{xx} + \omega_s S - \omega_r R + rB - f(R)B, & x \in (0,1), t > 0,\\
S_t = DS_{xx} - \omega_s S + \omega_r R - g(S)B, & x \in (0,1), t > 0,\\
B_t = DB_{xx} - \nu B_x + [f(R) + g(S) - r - m]B, & x \in (0,1), t > 0,\\
R_x(0,t) = \alpha(R(0,t) - \hat{R}), \quad R(1,t) = R^0, & t > 0,\\
S_x(0,t) = 0, \quad S(1,t) = S^0, & t > 0,\\
DB_x(0,t) - \nu B(0,t) = 0,\ DB_x(1,t) - \nu B(1,t) = 0, & t > 0,\\
R(x,0) = R_0(x) \ge 0,\ S(x,0) = S_0(x) \ge 0,\ B(x,0) = B_0(x) \ge 0, \not\equiv 0, &
\end{array} \tag{9}$$

where $f(R), g(S), r, \nu$ have exactly the same meaning as the associated parameters or variables with subscript $i = 1$ or 2. The corresponding steady state problem is

$$\begin{array}{ll}
DR_{xx} + \omega_s S - \omega_r R + rB - f(R)B = 0, & x \in (0,1),\\
DS_{xx} - \omega_s S + \omega_r R - g(S)B = 0, & x \in (0,1),\\
DB_{xx} - \nu B_x + [f(R) + g(S) - r - m]B = 0, & x \in (0,1),
\end{array} \tag{10}$$

with the boundary conditions

$$\begin{array}{ll}
R_x(0) = \alpha(R(0) - \hat{R}), & R(1) = R^0,\\
S_x(0) = 0, & S(1) = S^0,\\
DB_x(0) - \nu B(0) = 0, & DB_x(1) - \nu B(1) = 0.
\end{array} \tag{11}$$

Theorem 2.3 *Let $m^* := -\lambda_1(-f(R^*) - g(S^*), \nu) - r$ and assume $f(R^*) > r$. Then (10)−(11) has a unique positive solution if $m \in (0, m^*)$ and it has no positive solution if $m \ge m^*$. Moreover, the unique positive solution (R, S, B) is continuous in $(0, m^*)$ with respect to m. Here $\lambda_1(-f(R^*) - g(S^*), \nu)$ is the smallest eigenvalue corresponding to the linear eigenvalue problem* (39) *(or* (38) *equivalently) with $q(x) = -f(R^*) - g(S^*)$.*

Theorem 2.4 *Let $m^* := -\lambda_1(-f(R^*) - g(S^*), \nu) - r$ and suppose $f(R^*) > r$. Then*

(i) *the solution $(R(x,t), S(x,t), B(x,t))$ of (9) converges to the washout steady state $(R^*, S^*, 0)$ as $t \to \infty$ uniformly on $[0, 1]$ provided $m > m^*$.*

(ii) *the system (9) is uniformly persistent (i.e. there exists $\epsilon_0 > 0$ such that the solution $(R(x,t), S(x,t), B(x,t))$ of (9) satisfies $\liminf_{t\to\infty} B(\cdot, t) \ge \epsilon_0$) provided $0 < m < m^*$.*

Remark 2.5 Theorems 2.3 and 2.4 indicate that m^* is a critical death rate. Namely, the species goes extinct if the death rate $m > m^*$; the species survives if the death rate $m < m^*$.

Now, we state the results on the two species system (4)-(5). It follows from Theorem 2.3 that the steady-state system (6)-(7) has two semi-trivial solutions, denoted by

$$(\bar{R}_1(m_1, \cdot), \bar{S}_1(m_1, \cdot), \bar{B}_1(m_1, \cdot), 0) \text{ and } (\bar{R}_2(m_2, \cdot), \bar{S}_2(m_2, \cdot), 0, \bar{B}_2(m_2, \cdot))$$

provided that $m_1 \in (0, m_1^*)$ and $m_2 \in (0, m_2^*)$. From now on, we denote the two semi-trivial solutions by omitting the spacial variable x or the parameters $m_i(i = 1, 2)$ for simplicity. Define the following two semi-trivial branches

$$\Gamma_1 = \{(m_2, \bar{R}_1(m_1), \bar{S}_1(m_1), \bar{B}_1(m_1), 0) : m_2 \in (0, +\infty)\}$$

and

$$\Gamma_2 = \{(m_2, \bar{R}_2(m_2), \bar{S}_2(m_2), 0, \bar{B}_2(m_2)) : m_2 \in (0, m_2^*)\}.$$

Next, we treat m_2 as the bifurcation parameter to construct positive solutions to (6)-(7) from the semi-trivial branch Γ_1. We assume $0 < m_1 < m_1^*, 0 < m_2 < m_2^*$ and use the global bifurcation theorem (see Theorem 2.1 of (Du 1996)) to find sufficient conditions for the existence of positive solutions to (6)-(7).

Theorem 2.6 *Suppose $f_i(\bar{R}_j) > r_i$ with $i = 1, 2, j = 1, 2$. Then for fixed $m_1 \in (0, m_1^*)$, (6)-(7) has a positive solution (R, S, B_1, B_2) if m_2 lies between $\hat{m}_2$ and $\tilde{m}_2$. Moreover, there exists a branch of positive solutions $\Gamma = \{(m_2, R, S, B_1, B_2)\} \subset (0, +\infty) \times C([0, 1], \mathbb{R}_+^4)$ which bifurcates from the semi-trivial solution branch Γ_1 at $(\hat{m}_2, \bar{R}_1, \bar{S}_1, \bar{B}_1, 0)$ and meets the other semi-trivial solution branch Γ_2 precisely at $(\tilde{m}_2, \bar{R}_2, \bar{S}_2, 0, \bar{B}_2)$. Here $\hat{m}_2 = -\lambda_1(-f_2(\bar{R}_1) - g_2(\bar{S}_1), \nu_2) - r_2$ and $\tilde{m}_2$ is determined by $m_1 = -\lambda_1(-f_1(\bar{R}_2(\tilde{m}_2)) - g_1(\bar{S}_2(\tilde{m}_2)), \nu_1) - r_1$.*

3 Numerical results

3.1 Competitive outcomes in relation to parameter values

To illustrate the dynamics of equation system (2)-(3) numerically, a default parameter set was assigned in Table 1. The biological parameters are similar to those used by Van de Waal et al. (2011), based on cyanobacteria that are common in inland waters. With the assigned values, both competing species consume CARB more effectively than CO_2, but species 1 is better than species 2 at consuming CO_2, while species 2 is better than species 1 at consuming CARB. The physical and geochemical parameters are assigned to represent CO_2 and CARB concentrations typical of thermally stratified inland waters of moderate to high alkalinity. If other nutrients are sufficient, lakes with these characteristics commonly contain cyanobacteria, and under these conditions CO_2 is at relatively low concentration, while CARB is relatively high. Under these default conditions, there is coexistence of the two competitors.

Table 1: Default Parameters

Quantity	Value	Quantity	Value
D	$3\,\mathrm{m^2\,d^{-1}}$	L	$10\,\mathrm{m}$
α	$0.05\,\mathrm{d^{-1}}$	$\hat{R}$	$10^4\,\mu\mathrm{mol\,C\,m^{-3}}$
R^0	$10^4\,\mu\mathrm{mol\,C\,m^{-3}}$	S^0	$10^4\,\mu\mathrm{mol\,C\,m^{-3}}$
ω_r	$3000\,\mathrm{d^{-1}}$	ω_s	$20\,\mathrm{d^{-1}}$
ν_1	$0.5\,\mathrm{m\,d^{-1}}$	ν_2	$0.2\,\mathrm{m\,d^{-1}}$
μ_{1r}	$0.2\,\mathrm{d^{-1}}$	μ_{2r}	$0.18\,\mathrm{d^{-1}}$
μ_{1s}	$1.6\,\mathrm{d^{-1}}$	μ_{2s}	$3\,\mathrm{d^{-1}}$
a_{1r}	$1000\,\mu\mathrm{mol\,C\,m^{-3}}$	a_{2r}	$2000\,\mu\mathrm{mol\,C\,m^{-3}}$
a_{1s}	$2 \times 10^5\,\mu\mathrm{mol\,C\,m^{-3}}$	a_{2s}	$7.5 \times 10^4\,\mu\mathrm{mol\,C\,m^{-3}}$
r_1	$50 \times 10^{-9}\,\mu\mathrm{mol\,C\,cell^{-1}\,d^{-1}}$	r_2	$50 \times 10^{-9}\,\mu\mathrm{mol\,C\,cell^{-1}\,d^{-1}}$
Q_1^*	$2500 \times 10^{-9}\,\mu\mathrm{mol\,C\,cell^{-1}}$	Q_2^*	$3000 \times 10^{-9}\,\mu\mathrm{mol\,C\,cell^{-1}}$
m_1	$0.1\,\mathrm{d^{-1}}$	m_2	$0.44\,\mathrm{d^{-1}}$

With the other parameters fixed at their default values, selected parameters were varied though biologically realistic ranges, and bifurcations related to competitive exclusion and coexistence were summarized by calculating the total biomasses of each species (as L^1 norms), and then the proportion of biomass represented by species 2, the CARB specialist. These calculations were done after the system reached its asymptotic state. Thus competitive exclusion of species 1 is associated with a biomass proportion of one, competitive exclusion of species 2 with a biomass proportion of zero, and coexistence by values between zero and one.

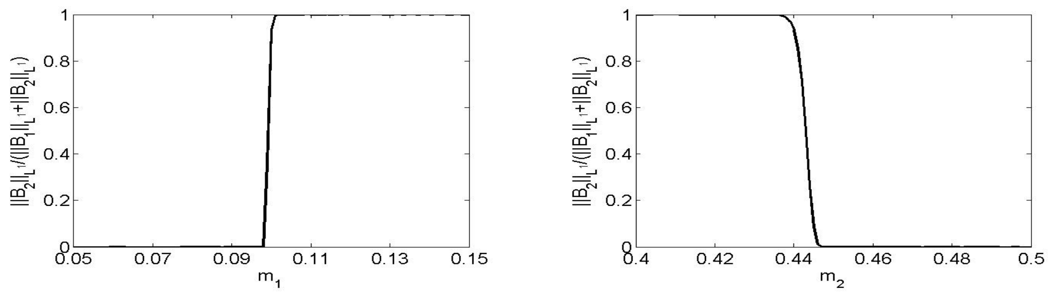
The theorems in section 2 address how the competitive outcomes of exclusion and coexistence are related to the semitrivial and positive solutions of the system (2)-(3), when mortality rates are taken as bifurcation parameters. As expected from these theorems, and in agreement with biological intuition, low values for the mortality rate of species 1 (m_1) enable it to exclude species 2, intermediate values allow coexistence, while high values produce exclusion of species 1 (Fig. 1a). Similarly, low values for the mortality rate of species 2 (m_2) enable it to exclude species 1, intermediate values allow coexistence, while high values produce exclusion of species 2 (Fig. 1b).

Sinking out of the water column can represent a loss process for planktonic algae, and thus variations in sinking rate might intuitively be expected to produce competitive outcomes similar to those seen in relation to mortality rate. This is not the case, however. For the default values of $\nu_1 = 0.5\,\mathrm{m\,d^{-1}}$ and $\nu_2 = 0.2\,\mathrm{m\,d^{-1}}$ there is coexistence. Reducing the sinking rate for one species alone leads to its competitive exclusion. That is, reducing ν_1 produces exclusion for species 1 (Fig. 2a), and reducing ν_2 leads to exclusion of species 2 (Fig. 2b). Conversely, raising the sinking rate for one species alone leads to its dominance and exclusion of the other species (species 1 - Fig. 2a; species 2 - Fig. 2b). Throughout most of the water column, CO_2 is depleted to near zero (some illustrations are presented in section 3.3), but it rises sharply near the bottom due to the non-zero value of R^0. Apparently, both species can benefit from the supply of CO_2 at the bottom of the water column and within the range of sinking rates explored, higher rates bring a larger proportion of their populations into the vicinity of this source.

Another counterintuitive result arises from bifurcations in relation to $\hat{R}$, the thermodynamic equilibrium concentration of CO_2. This parameter depends directly on the atmospheric CO_2 concentration, which is currently rising. Although the increased supply of CO_2 from the atmosphere might be expected to favor the CO_2 specialist (species 1), the result instead is that an increase of $\hat{R}$ favors dominance by species 2 (the CARB specialist), and eventually the exclusion of species 1 (Fig. 3). For the parameters assigned, the conversion of CO_2 to CARB is very rapid, so that as the atmospheric supply of CO_2 increases, the water column experiences an effective increase in CARB.

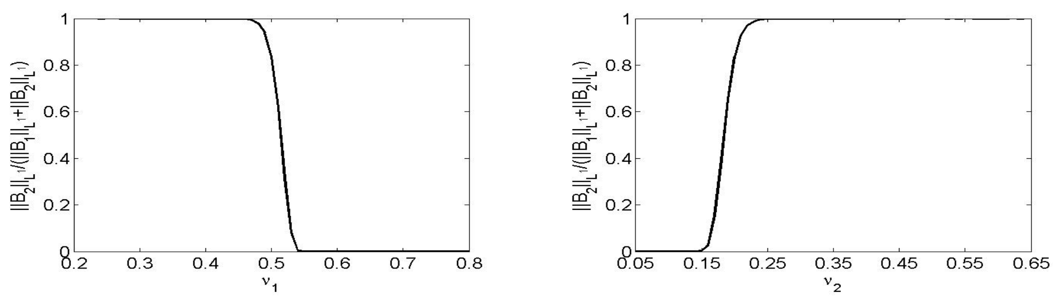
The parameters governing conversion between CO_2 and CARB also affect competitive outcomes, though more intuitively. As ω_r increases, conversion of CO_2 to CARB becomes more rapid, increasing the effective supply of CARB relative to CO_2. Accordingly, low values of ω_r produce exclusion of the CARB specialist (species 2), intermediate values produce coexistence, and high values produce exclusion of the CO_2 specialist (species 1) (Fig. 4a). Similarly, as ω_s increases, conversion of CARB to CO_2 becomes more rapid, increasing the effective supply of CO_2 relative to CARB. Low values of ω_s produce exclusion of the CO_2 specialist (species 1), intermediate values produce coexistence, and high values produce exclusion of the CARB specialist (species 2) (Fig. 4b).

The parameters representing sources of CO_2 and CARB at the bottom of the water column (R^0 and S^0) also affect competitive outcomes, although in counterintuitive ways. The default value of R^0, produces coexistence. But, both higher and lower values produce exclusion of species 1, the CO_2 specialist when other parameters are at their default settings (Fig. 5a). Both species consume CARB more effectively than CO_2, and the CO_2 introduced at the bottom of the water column when R^0 is high is mostly converted geochemically to CARB. This conversion benefits species 2 because it is a better competitor for CARB. A wide range of values for S^0 was explored because natural waters vary greatly in geochemical sources of CARB. Against intuition, raising S^0 to high values above the default value produces exclusion of species 2, the CARB specialist (Fig. 5b). For sufficiently low values of $S^0 (<$ about $400\,\mu\mathrm{mol\,C\,m^{-3}}$, not displayed on Fig. 5b), species 1 is excluded. Increasing S^0 through this very low range appears to produce coexistence and then exclusion of species 2, but for these lower values of S^0 dynamics are complex and do not approach equilibrium quickly.



(a) (b)

Figure 1: Bifurcation diagrams of positive steady state solutions to (2)-(3) with the bifurcation parameters m_1 and m_2, respectively. For (a), m_1 ranges from $0.05\,\mathrm{d}^{-1}$ to $0.15\,\mathrm{d}^{-1}$, and for (b) m_2 ranges from $0.4\,\mathrm{d}^{-1}$ to $0.5\,\mathrm{d}^{-1}$. The other parameters are fixed as above. In this figure, the vertical axis is $\frac{\|B_2(\cdot,t)\|_{L^1}}{\|B_1(\cdot,t)\|_{L^1}+\|B_2(\cdot,t)\|_{L^1}}$, where $\|\cdot\|_{L^1}$ is the L^1 norm and $t = 1000\,\mathrm{d}$. This appears to be long enough to allow the solutions to be very close to steady state. Moreover, it is easy to see that $\frac{\|B_2(\cdot,t)\|_{L^1}}{\|B_1(\cdot,t)\|_{L^1}+\|B_2(\cdot,t)\|_{L^1}} \in (0,1)$ implies coexistence, and $\frac{\|B_2(\cdot,t)\|_{L^1}}{\|B_1(\cdot,t)\|_{L^1}+\|B_2(\cdot,t)\|_{L^1}} = 0$ or 1 implies competitive exclusion.



(a) (b)

Figure 2: Bifurcation diagram of positive steady state solutions to (2)-(3). For (a), the bifurcation parameter ν_1 ranging from $0.2\,\mathrm{m\,d}^{-1}$ to $0.8\,\mathrm{m\,d}^{-1}$, and the other parameters are fixed as above. For (b), the bifurcation parameter ν_2 ranging from $0.05\,\mathrm{m\,d}^{-1}$ to $0.65\,\mathrm{m\,d}^{-1}$, and the other parameters are fixed as above. The vertical axis is still $\frac{\|B_2(\cdot,t)\|_{L^1}}{\|B_1(\cdot,t)\|_{L^1}+\|B_2(\cdot,t)\|_{L^1}}$, where $\|\cdot\|_{L^1}$ is the L^1 norm and $t = 1000\,\mathrm{d}$.

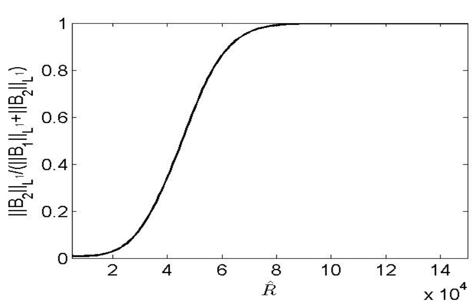
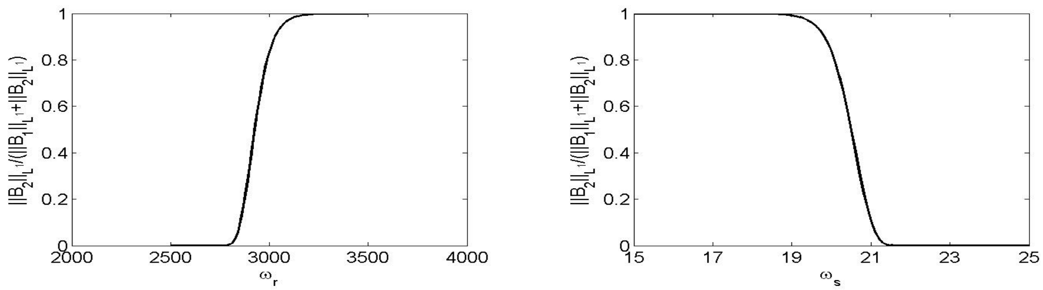
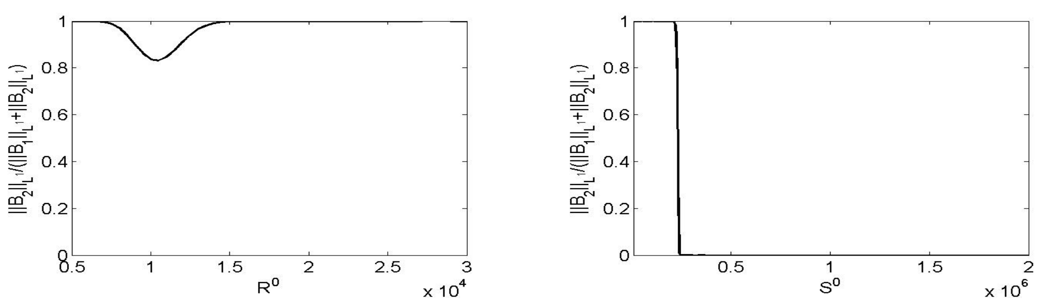


Figure 3: Bifurcation diagram of positive steady state solutions to (2)-(3) with the bifurcation parameter $\hat{R}$ ranging from $0.5 \times 10^4\,\mu\mathrm{mol\,C\,m}^{-3}$ to $1.5 \times 10^5\,\mu\mathrm{mol\,C\,m}^{-3}$. The other parameters are fixed as above. The vertical axis is also $\frac{\|B_2(\cdot,t)\|_{L^1}}{\|B_1(\cdot,t)\|_{L^1}+\|B_2(\cdot,t)\|_{L^1}}$, where $\|\cdot\|_{L^1}$ is the L^1 norm and $t = 1000\,\mathrm{d}$.



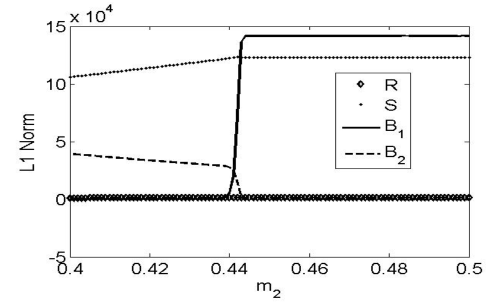
(a) (b)

Figure 4: Bifurcation diagram of positive steady state solutions to (2)-(3). For (a), the bifurcation parameter ω_r ranging from $2000\,\mathrm{d}^{-1}$ to $4000\,\mathrm{d}^{-1}$, and the other parameters are fixed as above. For (b), the bifurcation parameter ω_s ranging from $15\,\mathrm{d}^{-1}$ to $25\,\mathrm{d}^{-1}$, and the other parameters are fixed as above. The vertical axis is also $\frac{\|B_2(\cdot,t)\|_{L^1}}{\|B_1(\cdot,t)\|_{L^1}+\|B_2(\cdot,t)\|_{L^1}}$, where $\|\cdot\|_{L^1}$ is the L^1 norm and $t = 1000\,\mathrm{d}$.

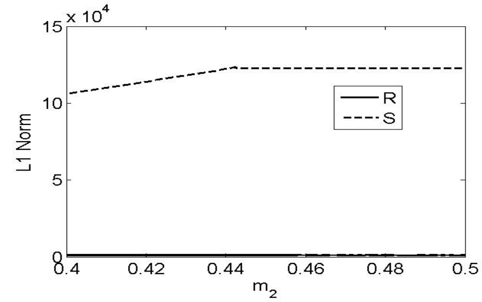


(a) (b)

Figure 5: Bifurcation diagram of positive steady state solutions to (2)-(3). For (a), the bifurcation parameter R^0 ranging from $5000\,\mu\mathrm{mol\,C\,m}^{-3}$ to $3\times10^4\,\mu\mathrm{mol\,C\,m}^{-3}$, and the other parameters are fixed as above. For (b), the bifurcation parameter S^0 ranging from $1\times10^4\,\mu\mathrm{mol\,C\,m}^{-3}$ to $2\times10^6\,\mu\mathrm{mol\,C\,m}^{-3}$, and the other parameters are fixed as above. The vertical axis is also $\frac{\|B_2(\cdot,t)\|_{L^1}}{\|B_1(\cdot,t)\|_{L^1}+\|B_2(\cdot,t)\|_{L^1}}$, where $\|\cdot\|_{L^1}$ is the L^1 norm and $t = 1000\,\mathrm{d}$.



(a)



(b)

Figure 6: Bifurcation diagrams of positive steady state solutions to (2)-(3) with the bifurcation parameters m_2 ranging from $0.4\,\mathrm{d}^{-1}$ to $0.5\,\mathrm{d}^{-1}$. In these figures, the vertical axis denote the L^1 norm of $R(\cdot,t), S(\cdot,t), B_1(\cdot,t), B_2(\cdot,t)$ at $t = 1000\,\mathrm{d}$, respectively.

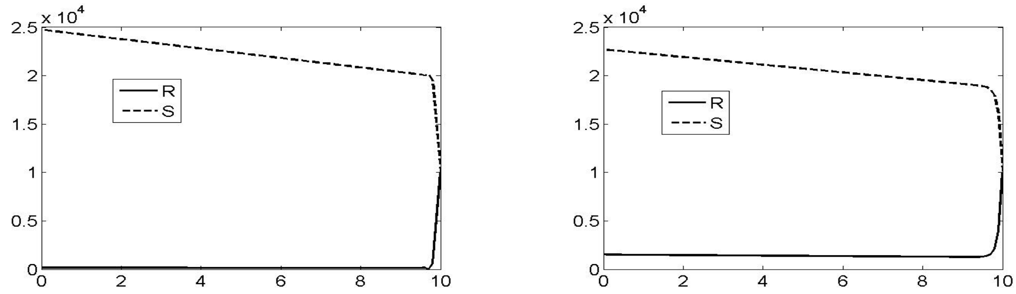
3.2 Carbon stocks in relation to mortality

By varying the mortality rate of species 2, competitive outcomes vary from dominance by species 2, to coexistence, to dominance by species 1, when other parameters are at default values (Fig. 1b). Throughout these changes, the depth-integrated stock of CARB greatly exceeds that of CO_2 (Fig. 6a, b). As m_2 increases through the low range where species 2 is dominant, stocks of both CO_2 and CARB rise, as expected from Theorem 2.6 (Fig. 6b). When m_2 is low and the CARB specialist (species 2) dominates, its depth-integrated biomass is lower than the CARB stock (Fig. 6a), and its biomass decreases with m_2 as expected from Theorem 2.6. As m_2 increases to the point where the CO_2 specialist (species 1) dominates, the depth-integrated biomass of species 1 is higher than that attained by species 2, and higher than the CARB stock (Fig. 6a). Through this high range of m_2, stocks of CO_2 and CARB are independent of variations in m_2, because species 2 is excluded. More generally, for the parameter space explored in this study, CARB is a dominant carbon stock, although algal biomass can attain similar levels, while CO_2 is generally at much lower levels.

3.3 Depth distributions

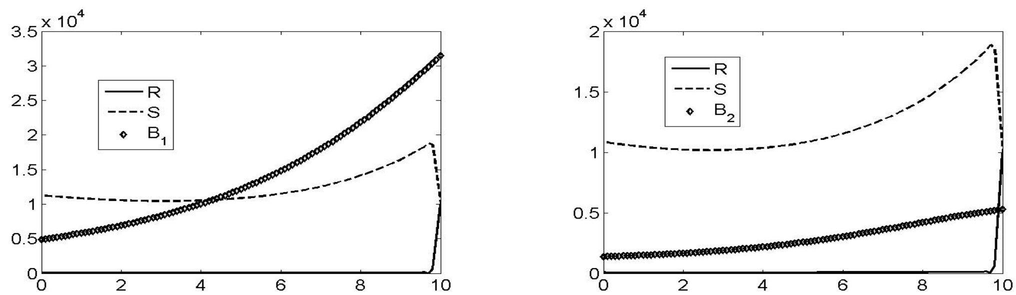
Although consumption by algae is partially responsible for low levels of CO_2, the depth distributions characterizing the washout, semitrivial and coexistence equilibria (Figs. 7-9) under the default parameters (except as noted) suggest that rapid conversion to CARB has a strong influence on CO_2 dynamics. When no algae are present (washout solution), the CARB concentration greatly exceeds that of CO_2 at all depths (Fig. 7), due to the very rapid conversion of CO_2 to CARB dictated by parameter values ($\omega_r \gg \omega_s \gg 1$). If the water column was well mixed, CO_2 would dissolve from the atmosphere into the water and be distributed over depth, with its concentration approaching the thermodynamic equilibrium value, $\hat{R}$, independent of the parameters ω_r and ω_s, whose ratio would determine the concentration of CARB. Instead, concentrations of both CO_2 and CARB vary with depth and depend on the parameters ω_r and ω_s (e.g. compare Figs. 7a, b). Most of the CO_2 that enters from the atmosphere at the surface is rapidly converted to CARB, and then distributed downward by mixing, producing decreasing depth distributions in the absence of algae (Figs. 7a, b). Toward the very bottom of the water column, CARB decreases sharply and CO_2 rises sharply, as both converge to the source concentrations R^0 and S^0, respectively.

For most depths, consumption by algae reduces CO_2 and CARB below the concentrations seen in the washout solution (Figs. 8, 9a). In the semitrivial equilibria where each species grows alone, each displays increasing biomass distributions with depth, as a result accumulation from sinking out of shallower water and growth on the CO_2 and CARB sources at the bottom (Fig. 8). The distribution of CARB is modified from the washout equilibrium, with a peak concentration near



(a) (b)

Figure 7: The washout solutions to (2)-(3) with $w_r = 3000\,\mathrm{d}^{-1}$ for (a) and $w_r = 300\,\mathrm{d}^{-1}$ for (b). In these figures, the concentrations $R(x,t), S(x,t)$ at $t = 1000\,\mathrm{d}$ are plotted versus the spatial variable x on $[0, L]$, respectively.



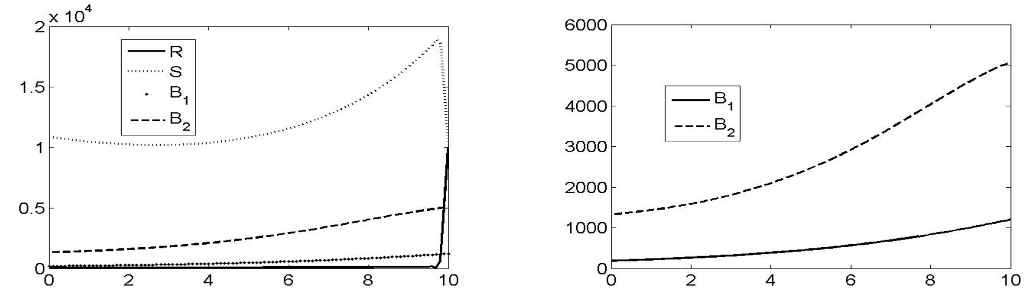
(a) (b)

Figure 8: The semitrivial solutions to (2)-(3) with all parameters fixed as above. In these figures, the concentrations $R(x,t), S(x,t), B_1(x,t), B_2(x,t)$ at $t = 1000\,\mathrm{d}$ are plotted versus the spatial variable x on $[0, L]$, respectively.

the bottom source, a minimum at intermediate depths owing to consumption by algae, and an increase towards the surface resulting from atmospheric input of CO_2 and conversion to CARB (Fig. 8). Qualitatively similar depth distributions are observed for the coexistence equilibrium (Fig. 9).

4 Discussion

We have shown that when two species compete for inorganic carbon (consisting of CO_2 and CARB) in a water column, the competitive outcomes can include competitive exclusion of one or the other species independent of initial conditions, and coexistence of the two species, depending on parameter values. It is likely that for some parameter values another outcome, competitive exclusion dependent on initial conditions arises, though we have not explicitly analyzed this possibility. This range of outcomes is expected for competition models (Ballyk and Wolkowicz 2011), and biologically intuitive relationships between the competitors' mortality rates and competitive outcomes were illustrated. The relationship of competitive outcomes to several other parameters was less intuitive, at least from the perspective of the conventional analysis of substitutable resources found in the ecological literature (Tilman 1982; Grover 1997). According to this conventional analysis, high CO_2 supply should produce dominance by the better consumer of CO_2, high CARB supply should produce dominance by the better consumer of CARB, and intermediate supplies could allow coexistence. Variations of parameters that influence relative supplies of CO_2 and CARB did not always have this expected effect.



(a) (b)

Figure 9: The coexistence solutions to (2)-(3) with all parameters fixed as above. In these figures, the concentrations $R(x,t), S(x,t), B_1(x,t), B_2(x,t)$ at $t = 1000\,\mathrm{d}$ are plotted versus the spatial variable x on $[0, L]$, respectively.

The conventional graphical analysis of competition for substitutable resources focuses on the set of resource concentrations (R, S) where growth balances mortality, called the Zero Net Growth Isocline (ZNGI). Usually, the ZNGI is defined by $f_i(R) + g_i(S) - m_i = 0$, neglecting respiratory losses, and ZNGIs are drawn as decreasing functions of R in the RS-plane. Such graphs assume that each resource can support the growth of each species when the other resource is unavailable. Large disparities in the ability of each resource to support growth could produce violations of this assumption (Ballyk and Wolkowicz 1993). In the parameterized model presented here, CO_2 supports growth at much lower rates than CARB ($\mu_{ir} < \mu_{is}$). For the mortality rates explored here there are conditions where CO_2 cannot alone support positive growth by species 2. In such cases, the ZNGI graphed on the RS-plane is an increasing function of R, indicating that higher CO_2 concentrations inhibit rather than promote growth, and the conventionally expected competitive outcomes might not be observed (Ballyk and Wolkowicz 1993). Ecologically, the relationship between such species is not necessarily one of pure and simple competition. If increased CO_2 inhibits growth of one competitor (e.g. species 2), then consumption by the other competitor (species 1) facilitates the growth of the inhibited species.

Additional complications in the model presented here depart further from the conventional representation of competition for substitutable resources. The consumption of CO_2 is relatively slow, i.e. $f_i(R)$ is relatively small due to the low value of μ_{ir}. Therefore, under conditions where CO_2 is low, which is common in the upper part of the water column (Figs. 7-9), the respiration rate r_i/Q_i^* is higher than the consumption rate, and instead of consuming CO_2, species are net producers of CO_2. Both species primarily consume CARB to meet their needs for growth and respiration, and the latter process converts some of the consumed CARB to CO_2. Towards the bottom of the water column, CO_2 is high enough so that consumption exceeds respiratory recycling, and both species are net consumers of CO_2. Both the respiratory recycling of CO_2 and depth-related changes in consumption versus recycling are factors not considered by the conventional analysis of competition for substitutable resources.

A final complication in the model presented here is the abiotic inter-conversion between CO_2 and CARB. Such inter-conversion is not a part of conventional analyses, and indeed may only arise for resources that are reactive chemical forms of the same nutrient element. Due to this inter-conversion, changes in a parameter governing resource supply do not independently affect the supply of only one resource. The conversion favors CARB over CO_2 for parameters used here, thus increasing the supply of either resource through changes in $\hat{R}$, R^0, or S^0, tends predominantly to increase the availability of CARB. Changing the parameters that govern conversion between CO_2 and CARB (ω_r and ω_s) has a strong influence on competitive outcomes. Altering these parameters to produce relatively high CO_2 supply produces dominance by the better consumer of CO_2, and altering them to produce high CARB supply produces dominance by the better consumer of CARB, and with intermediate values producing coexistence.

Indeed one potentially important prediction of this analysis is the strong effect of varying ω_r and ω_s(Figs. 4) compared to the weak influence of $\hat{R}$(Fig. 3). The latter parameter represents the influence of atmospheric CO_2 concentration, and our analysis suggests that ongoing increases (Siegenthaler and Sarmiento 1993; Sabine et al. 2004) would have only weak direct effects on competition between algae for inorganic carbon through changes in $\hat{R}$. However, increased atmospheric CO_2 concentration also acidifies aquatic ecosystems (Orr et al. 2005; Riebesell et al. 2007), which effectively reduces ω_r relative to ω_s. Anthropogenic emissions of sulfur and nitrogen oxides, which accompany combustion emissions of CO_2, also acidify aquatic ecosystems, especially inland waters, and reduce alkalinity (Rice and Herman 2012). Strong acidification can dramatically reduce the effective values of ω_r relative to ω_s. Our model thus suggests that acidification and alkalinity reduction from human impacts could more strongly affect algal competition for inorganic carbon than the direct increase in CO_2 availability.

These predictions are based on a parameterized model, and might not hold in regions of parameter space not yet explored. However, we argue that essential aspects of our parameterization are biologically and geochemically reasonable. Biologically, we have represented algae that consume CARB more rapidly at high concentration than they consume CO_2. While this parameterization is inspired by observations on strains of a particular species of freshwater cyanobacteria (Van de Waal et al. 2011), it might apply more broadly for other algae in aquatic environments of relatively high pH and alkalinity, where CARB concentrations greatly exceed that of CO_2. However, we acknowledge that there is wide variation among species in their kinetics of inorganic carbon uptake and relative capabilities to use CO_2 and CARB (Rost et al. 2003; Martin and Tortell 2008; Maberly et al. 2009). Our model represents the geochemistry of inorganic carbon in a highly simplified manner, through the linear system (1) and the parameters $\hat{R}$, ω_r, and ω_s. We assigned values to these parameters so that in a well mixed system open to the atmosphere but containing no algae, CO_2 and CARB concentrations would approach a realistic thermodynamic equilibrium. In this state, the assigned parameters lead to CARB concentrations much higher than those of CO_2, which is realistic for seawater and for inland waters with pH above neutral and moderate to high alkalinity. For inland waters with lower pH and alkalinity, especially those impacted by acidification, smaller values of ω_r, relative to ω_s would be appropriate.

Historically, the possibility of competition among algae for different sources of inorganic carbon has been somewhat neglected. Some influential, early studies established that the kinetics of conversion between CO_2 and CARB are very rapid compared to the kinetics of algal uptake and growth (Goldman et al. 1974). These early studies implied that rapid kinetic equilibration between CO_2 and CARB would effectively make them a single resource, instead of two substitutable resources, and an early observation of competitive outcomes was consistent with this interpretation (Williams and Turpin 1987). Since then, observations have accumulated suggesting that algae differ in their capabilities to use CO_2 and CARB, and that such differences affect their competitive fitness (Chen and Durbin 1998; Caraco and Miller 1998; Van de Waal et al. 2011). Notwithstanding the rapid kinetics of conversion between CO_2 and CARB, our theory predicts that at high biomass, algal growth and consumption deplete the availabilities and alter the spatial distributions of these two resources, leading to the classical competitive outcomes of exclusion or coexistence depending on parameters. In addition to these consumption-mediated competitive feedbacks, algal alteration of pH and alkalinity (Brewer and Goldman 1976; Van de Waal et al. 2011), which we neglected here for simplicity, could further complicate interactions among algal species in habitats with low availability of inorganic carbon.

Algae require inorganic nutrients other than carbon, and it is well known that nitrogen, phosphorus, iron and other elements can limit algal growth, with inorganic carbon regarded as less likely to be limiting in most aquatic habitats. We neglected the influence of other nutrients in this study in the interest of simplicity, but acknowledge that examining the joint dynamics of competition for carbon and other nutrients will be important. Among the widespread environmental changes now taking place under human influence, increased supplies of nitrogen and phosphorus in aquatic habitats are often accompanied by acidification and reduction of alkalinity. The latter changes effectively reduce the supply of CARB, potentially setting the stage for one of the outcomes sketched here - competitive elimination of algae better adapted to using CARB than CO_2.

5 Appendix: Some mathematical proofs

A. The washout solution

The purpose of this subsection is to study the washout solution of (4)-(5). Noting that (8) is a cooperative system, we first introduce the maximum principle for cooperative weakly coupled elliptic systems, which is adapted from (Amann 2004) and (López-Gómez and Molina-Meyer 1994) and plays a crucial role throughout this paper. This maximum principle helps us to decouple the full elliptic system into some scalar systems or some lower dimensional systems.

Let $E_1 = C^{2+\sigma}([0,1],\mathbb{R}^2)$, $E_2 = C^{\sigma}([0,1],\mathbb{R}^2)$, and $\mathcal{L}_0 : E_1 \to E_2$ be given by

$$\mathcal{L}_0 = \begin{pmatrix} D\frac{d^2}{dx^2} - \omega_r & \omega_s \\ \omega_r & D\frac{d^2}{dx^2} - \omega_s \end{pmatrix}.$$

Consider the eigenvalue problem

$$\begin{aligned} &-\mathcal{L}_0(\phi_1,\phi_2)^\intercal = \lambda(\phi_1,\phi_2)^\intercal, \quad x \in (0,1), \\ &-(\phi_1)_x(0) + \alpha\phi_1(0) = 0, \phi_1(1) = 0, \quad (\phi_2)_x(0) = 0, \phi_2(1) = 0. \end{aligned} \tag{12}$$

It follows from Theorem 2.6 or Remark 2.4 of (López-Gómez and Molina-Meyer 1994) that the operator $(-\mathcal{L}_0)^{-1} : E_2 \to E_1$ with the above boundary conditions is well defined and it is compact and strongly order preserving, and the principal eigenvalue of $-\mathcal{L}_0$, denoted by $\lambda_1(-\mathcal{L}_0)$, is strictly positive and has a positive eigenfunction. That is, $-\mathcal{L}_0$ subject to the boundary conditions: $-(\phi_1)_x(0)+\alpha\phi_1(0) = 0, \phi_1(1) = 0,\ (\phi_2)_x(0) = 0, \phi_2(1) = 0$ satisfies the strong maximum principle (cf. Theorem 13 of (Amann 2004)).

Proof of Theorem 2.1. The steady-state system corresponding to (8) is

$$\begin{aligned} &DR_{xx} + \omega_s S - \omega_r R = 0, \quad x \in (0,1), \\ &DS_{xx} - \omega_s S + \omega_r R = 0, \quad x \in (0,1), \\ &R_x(0) = \alpha(R(0) - \hat{R}),\ R(1) = R^0, \quad S_x(0) = 0,\ S(1) = S^0. \end{aligned} \tag{13}$$

It follows from Theorem 13 of (Amann 2004) or Theorem 2.6 and Remark 2.4 of (López-Gómez and Molina-Meyer 1994) that the principle eigenvalue of $-\mathcal{L}_0$ is positive, and hence the strong maximum principle holds for (13). In view of Theorem 15 of (Amann 2004), (13) has a unique solution, which is positive and denoted by (R^*, S^*).

Note that the solutions of (8) generate a monotone semi-dynamical system on $C([0,1],\mathbb{R}^2_+)$. Hence, (ii) is a direct result of (i) and Theorem 2.2.6 of (Zhao 2003).

Proof of Theorem 2.2. The linearized eigenvalue problem of (6)-(7) with respect to the washout solution $(R^*, S^*, 0, 0)$ is

$$\begin{aligned} &D\phi_{1xx} + \omega_s\phi_2 - \omega_r\phi_1 - (f_1(R^*) - r_1)\psi_1 - (f_2(R^*) - r_2)\psi_2 = -\lambda\phi_1, \\ &D\phi_{2xx} - \omega_s\phi_2 + \omega_r\phi_1 - g_1(S^*)\psi_1 - g_2(S^*)\psi_2 = -\lambda\phi_2, \\ &D\psi_{1xx} - \nu_1\psi_{1x} + [f_1(R^*) + g_1(S^*) - r_1 - m_1]\psi_1 = -\lambda\psi_1, \\ &D\psi_{2xx} - \nu_2\psi_{2x} + [f_2(R^*) + g_2(S^*) - r_2 - m_2]\psi_2 = -\lambda\psi_2, \end{aligned} \tag{14}$$

with boundary conditions

$$\begin{aligned} &-\phi_{1x}(0) + \alpha\phi_1(0) = 0, \quad \phi_1(1) = 0, \\ &\phi_{2x}(0) = 0, \quad \phi_2(1) = 0, \\ &D\psi_{ix}(0) - \nu_i\psi_i(0) = 0, \quad D\psi_{ix}(1) - \nu_i\psi_i(1) = 0, \quad i = 1, 2. \end{aligned} \tag{15}$$

Clearly, the eigenvalues of the linearized eigenvalue problem (14)-(15) consist of the eigenvalues of the following three operators: $-\mathcal{L}_0$, $L_1 = -D\frac{d^2}{dx^2} + \nu_1\frac{d}{dx} - (f_1(R^*) + g_1(S^*) - r_1 - m_1)$ and $L_2 = -D\frac{d^2}{dx^2} + \nu_2\frac{d}{dx} - (f_2(R^*) + g_2(S^*) - r_2 - m_2)$. Recall that the smallest eigenvalue $\lambda_1(-\mathcal{L}_0) > 0$ of $-\mathcal{L}_0$. Meanwhile, the smallest eigenvalue of $L_i (i = 1, 2)$ is larger than 0 provided $m_i > m_i^*$, and less than 0 provided $m_i < m_i^*$. Hence, all eigenvalues of the linearized eigenvalue problem (14)-(15) are larger than zero provided $m_1 > m_1^*, m_2 > m_2^*$, and the linearized eigenvalue problem (14)-(15) has an eigenvalue less than zero provided $m_1 < m_1^*$ or $m_2 < m_2^*$. That is, the washout equilibrium solution $(R^*, S^*, 0, 0)$ is linearly stable provided $m_1 > m_1^*, m_2 > m_2^*$; and unstable provided $m_1 < m_1^*$ or $m_2 < m_2^*$.

B. Single population system

The purpose of this subsection is to study the dynamical behavior of the single population system (9) and to establish Theorems 2.3–2.4.

First, we study the well-posedness of the initial boundary value problem (9). Let $X^+ = C([0, 1], \mathbb{R}^3_+)$ be the positive cone in the Banach space $X = C([0, 1], \mathbb{R}^3)$ with the usual supremum norm. To simplify notations, we set

$$\Phi_1 = R,\ \Phi_2 = S,\ \Phi_3 = e^{-\frac{\nu}{D}x}B \text{ and } \Phi = (\Phi_1, \Phi_2, \Phi_3).$$

Note that the initial conditions in (9) satisfying $(\Phi_1^0, \Phi_2^0, \Phi_3^0) = (R_0(x), S_0(x), e^{-\frac{\nu}{D}x}B_0(x)) \in X^+$. For the local existence and positivity of solutions, we appeal to the theory developed by Martin and Smith (1990) where existence, uniqueness and positivity are treated simultaneously. The idea is to view the system (9) as the abstract ordinary differential equation in X^+ and the so-called mild solutions can be obtained for any given initial data. More precisely,

$$\begin{aligned}
&\begin{pmatrix} \Phi_1(t) \\ \Phi_2(t) \end{pmatrix} = H_0(t) \cdot \begin{pmatrix} \Phi_1^0 \\ \Phi_2^0 \end{pmatrix} + \int_0^t G_0(t-s) \cdot \begin{pmatrix} F_1(\Phi(s)) \\ F_2(\Phi(s)) \end{pmatrix} \mathrm{d}s, \\
&\Phi_3(t) = G_1(t)\Phi_3^0 + \int_0^t G_1(t-s)F_3(\Phi(s))\mathrm{d}s,
\end{aligned}$$

where $G_0(t)$ is the positive, non-expansive, analytic semigroup on $C([0, 1], \mathbb{R}^2)$ (see, e.g., Chapter 7 in the book by Smith (1995)) such that $(u, v)^\intercal = G_0(t) \cdot (\Phi_1^0, \Phi_2^0)^\intercal$ satisfies the linear initial value problem

$$\begin{aligned}
&\begin{pmatrix} u \\ v \end{pmatrix}_t = \mathcal{L}_0 \begin{pmatrix} u \\ v \end{pmatrix}, \quad 0 < x < 1, t > 0, \\
&-u_x(0, t) + \alpha u(0, t) = 0,\ u(1, t) = 0,\ \ v_x(0, t) = 0,\ v(1, t) = 0, \quad t > 0, \\
&u(x, 0) = \Phi_1^0(x), \quad v(x, 0) = \Phi_2^0(x), \quad 0 \le x \le 1,
\end{aligned}$$

and $G_1(t)$ is the positive, non-expansive, analytic semigroup on $C[0, 1]$ (see, e.g., Chapter 7 in the book by Smith (1995)) such that $u = G_1(t)\Phi_3^0$ satisfies the linear initial value problem

$$\begin{aligned}
&u_t = Du_{xx} + \nu u_x - (r + m)u, && 0 < x < 1, t > 0, \\
&u_x(0, t) = 0,\ \ u_x(1, t) = 0, && t > 0, \\
&u(x, 0) = e^{-\frac{\nu}{D}x}\Phi_3^0(x), && 0 \le x \le 1.
\end{aligned}$$

$H_0(t)$, $t > 0$, is the family of affine operators on $C([0, 1], \mathbb{R}^2)$ (see, e.g., Chapter 5 in the book by Pazy (1983)) such that $(u, v)^\intercal = H_0(t) \cdot (\Phi_1^0, \Phi_2^0)^\intercal$ satisfies the linear systems with nonhomogeneous boundary condition given by

$$\begin{aligned}
&\begin{pmatrix} u \\ v \end{pmatrix}_t = \mathcal{L}_0 \begin{pmatrix} u \\ v \end{pmatrix}, \quad t > 0, 0 < x < 1, \\
&-u_x(0, t) + \alpha u(0, t) = \alpha\hat{R},\ u(1, t) = R^0,\ \ v_x(0, t) = 0, \quad v(1, t) = S^0, \quad t > 0, \\
&u(x, 0) = \Phi_1^0(x), \quad v(x, 0) = \Phi_2^0(x), \quad 0 \le x \le 1.
\end{aligned}$$

The nonlinear operators $F_i : C([0,1], \mathbb{R}_+) \to C[0,1]$ are defined by

$$\begin{aligned} &F_1(\Phi) = -(f(\Phi_1) - r)\Phi_3, \\ &F_2(\Phi) = -g(\Phi_2)\Phi_3, \\ &F_3(\Phi) = [f(\Phi_1) + g(\Phi_2)]\Phi_3. \end{aligned}$$

By the maximum principle arguments, it follows that

$$\begin{aligned} &G_0(t) \cdot C([0,1], \mathbb{R}^2_+) \subset C([0,1], \mathbb{R}^2_+),\ \forall\ t > 0, \\ &H_0(t) \cdot C([0,1], \mathbb{R}^2_+) \subset C([0,1], \mathbb{R}^2_+),\ \forall\ t > 0, \\ &G_1(t) C([0,1], \mathbb{R}_+) \subset C([0,1], \mathbb{R}_+),\ \forall\ t > 0. \end{aligned}$$

Since $f(0) = 0, g(0) = 0$, it follows that $F_i(\Phi) \geq 0$ whenever $\Phi_i \equiv 0$, $\forall\ 1 \leq i \leq 3$, and hence, $\mathbf{F} := (F_1, F_2, F_3)$ is quasipositive (see, e.g., Remark 1.1 of (Martin and Smith 1990)). By Theorem 1 and Remark 1.1 of (Martin and Smith 1990), it follows that the system (9) has a unique solution and the solutions to (9) remain non-negative on their interval of existence if they are non-negative initially. In other words, the following results hold:

Lemma B.1 *For every initial value function $\Phi^0 = (\Phi_1^0, \Phi_2^0, \Phi_3^0) \in X^+$, the system (9) has a unique mild solution $\Phi(x,t,\Phi^0)$ on $(0, \delta_{\Phi^0})$ with $\Phi(\cdot, 0, \Phi^0) = \Phi^0$, where $\delta_{\Phi^0} \leq \infty$. Furthermore, $\Phi(\cdot, t, \Phi^0) \in X^+$, $\forall\ t \in (0, \delta_{\Phi^0})$ and $\Phi(x,t,\Phi^0)$ is a classical solution of (9) for $t > 0$.*

Next, we are ready to show the solutions of (9) exist globally on $(0, +\infty)$ and converge to a compact attractor in X^+. At first, we show solutions are ultimately bounded and uniformly bounded in X^+.

Lemma B.2 *Suppose $f(R^*) > r$ and $m > 0$. Then for every initial value function $\Phi^0 = (\Phi_1^0, \Phi_2^0, \Phi_3^0) \in X^+$, the system (9) has a unique solution $\Phi(x,t,\Phi^0)$ on $[0,\infty)$ with $\Phi(\cdot,0,\Phi^0) = \Phi^0$, and the solutions of (9) are ultimately bounded and uniformly bounded in X^+.*

Proof. Let $W = e^{-\frac{\nu}{D}x} B$. Then (9) becomes

$$\begin{aligned} &R_t = DR_{xx} + \omega_s S - \omega_r R - (f(R) - r)e^{\frac{\nu}{D}x} W, \quad x \in (0,1), t > 0, \\ &S_t = DS_{xx} - \omega_s S + \omega_r R - g(S) e^{\frac{\nu}{D}x} W, \quad x \in (0,1), t > 0, \\ &e^{\frac{\nu}{D}x} W_t = D\left(e^{\frac{\nu}{D}x} W_x\right)_x + (f(R) + g(S) - r - m) e^{\frac{\nu}{D}x} W, \quad x \in (0,1), t > 0, \\ &R_x(0,t) = \alpha(R(0,t) - \hat{R}), \quad R(1,t) = R^0, \quad t > 0, \\ &S_x(0,t) = 0, \quad S(1,t) = S^0, \quad W_x(0,t) = W_x(1,t) = 0, \quad t > 0, \\ &R(x,0) = R_0(x) \geq 0, \quad S(x,0) = S_0(x) \geq 0, \quad W(x,0) = e^{-\frac{\nu}{D}x} B_0(x) \geq 0, \not\equiv 0. \end{aligned} \tag{16}$$

By Lemma B.1, any solution (R,S,W) to (16) satisfies $R(x,t) > 0, S(x,t) > 0, W(x,t) > 0$. Note that there exists a constant $\rho > 1$ large enough such that $R_0(x) \leq \rho R^*, S_0(x) \leq \rho S^*$. For given $W(x,t) \geq 0$, consider the following system

$$\begin{aligned} &R_t = DR_{xx} + \omega_s S - \omega_r R - (f(R) - r)e^{\frac{\nu}{D}x} W, \quad x \in (0,1), t > 0, \\ &S_t = DS_{xx} - \omega_s S + \omega_r R - g(S) e^{\frac{\nu}{D}x} W, \quad x \in (0,1), t > 0, \\ &R_x(0,t) = \alpha(R(0,t) - \hat{R}), \quad R(1,t) = R^0, \quad t > 0, \\ &S_x(0,t) = 0, \quad S(1,t) = S^0, \quad t > 0, \\ &R(x,0) = R_0(x) \geq 0, \quad S(x,0) = S_0(x) \geq 0. \end{aligned} \tag{17}$$

Clearly, $(0,0)$ and $\rho(R^*, S^*)$ are the ordered lower and upper solutions of (17) by Definition 8.1.2 in the book by Pao (1992). It follows from the iteration process of Chapter 8.2 in the book by Pao (1992) and Theorem 8.3.1 in the book by Pao (1992) that (17) has a unique solution $(R(x,t), S(x,t))$ satisfies $0 \leq R(x,t) \leq \rho R^*, 0 \leq S(x,t) \leq \rho S^*$ for all $x \in [0,1], t > 0$. Namely, $\Lambda = \{(R,S) : 0 \leq R \leq \rho R^*, 0 \leq S \leq \rho S^*\}$ is an invariant set(cf. Definition 5.4.1 in the book by Pao (1992)) of the system (17), which implies $R(x,t), S(x,t)$ are ultimately bounded and uniformly bounded in X^+.

Next, we claim $W(1,t)$ is bounded in $t \in (0,+\infty)$. If not, we can find $t_n \to \infty$ such that $W(1,t_n) \to \infty$ as $t_n \to \infty$. Let $\widehat{W}_n(x,t) = \frac{W(x,t+t_n)}{W(1,t_n)}$. Then $\widehat{W}_n(x,t)$ satisfies

$$\begin{aligned}
&(e^{\frac{\nu}{D}x}\widehat{W}_n)_t = D(e^{\frac{\nu}{D}x}(\widehat{W}_n)_x)_x + (f(R(x,t+t_n)) + g(S(x,t+t_n)) - r - m)e^{\frac{\nu}{D}x}\widehat{W}_n,\\
&(\widehat{W}_n)_x(0,t) = (\widehat{W}_n)_x(1,t) = 0,\\
&\widehat{W}_n(x,0) \geq 0, \widehat{W}_n(1,0) = 1.
\end{aligned}$$

Note that $|f(R(x,t+t_n)) + g(S(x,t+t_n)) - r - m| \leq |f(\rho R^*) + g(\rho S^*) - r - m|$ is bounded. It follows from Lemma D.2 that $\widehat{W}_n(x,t) > \delta > 0$ for all $x \in [0,1]$ and $t > 0$, which implies $W(x,t+t_n) > \delta W(1,t_n)$. Thus, $W(x,t) \to \infty$ as $t \to \infty$ uniformly in $[0,1]$. Hence, for any $M > 0$, there exists $t_0 > 0$ large enough such that $W(x,t) > M$ on [0, 1] for $t \geq t_0$, which implies

$$S_t \leq DS_{xx} - \omega_s S - g(S)e^{\frac{\nu}{D}x}M + \omega_r \rho R^*.$$

Namely, $S(x,t)$ is a lower solution of the parabolic problem

$$\begin{aligned}
&\tilde{S}_t = D\tilde{S}_{xx} - \omega_s\tilde{S} - g(\tilde{S})e^{\frac{\nu}{D}x}M + \omega_r\rho R^*, && x \in (0,1), t > t_0,\\
&\tilde{S}_x(0,t) = 0, \quad \tilde{S}(1,t) = S^0, && t > t_0,\\
&\tilde{S}(x,t_0) = S(x,t_0), && x \in [0,1].
\end{aligned} \tag{18}$$

It follows from the comparison principle for parabolic equation that $S(x,t) \leq \tilde{S}(x,t)$ for $t \geq t_0$. Note that the steady state system of (18) satisfies

$$\begin{aligned}
&-D\tilde{S}_{xx} + (\omega_s + \textstyle\int_0^1 g'(\tau\tilde{S})d\tau e^{\frac{\nu}{D}x}M)\tilde{S} = \omega_r\rho R^* > 0, \quad x \in (0,1),\\
&\tilde{S}_x(0) = 0, \quad \tilde{S}(1) = S^0.
\end{aligned} \tag{19}$$

It follows from the maximum principle that the steady state solution $\tilde{S} > 0$ on [0, 1]. Let $\chi = S^0 - \tilde{S}$. Then

$$\begin{aligned}
&D\chi_{xx} - \omega_s\chi + g(S^0 - \chi)e^{\frac{\nu}{D}x}M + \omega_s S^0 - \omega_r\rho R^* = 0, \quad x \in (0,1),\\
&\chi_x(0) = 0, \quad \chi(1) = 0.
\end{aligned} \tag{20}$$

Suppose $\inf\limits_{[0,1]} \chi = \chi(x_0) < 0$. Then $-\omega_s\chi(x_0) + g(S^0 - \chi(x_0))e^{\frac{\nu}{D}x_0}M + \omega_s S^0 - \omega_r\rho R^*(x_0) \leq 0$, which implies $g(S^0)M + \omega_s S^0 < \omega_r\rho \max\limits_{[0,1]} R^*$. Choosing M such that $\omega_s S^0 + g(S^0)M \geq \omega_r\rho\max\limits_{[0,1]} R^*$, we get a contradiction. Hence, $\chi \geq 0$ on [0, 1], which means $0 < \tilde{S} \leq S^0$ on [0, 1]. Moreover, in view of $\omega_s S^0 + g(S^0)M \geq \omega_r\rho\max\limits_{[0,1]} R^*$, it is easy to see that 0 is a strictly lower solution to the steady state system of (18), and S^0 is a strictly upper solution to the steady state system of (18). It follows from monotone iteration process that there exists a pair $\tilde{S}^+$ and $\tilde{S}^-$, which are the maximal and minimal solutions to the steady state system of (18), and satisfy the relation $0 < \tilde{S}^- \leq \tilde{S}^+ \leq S^0$. Next, we show $\tilde{S}^- \equiv \tilde{S}^+$. Obviously,

$$D(\tilde{S}^+ - \tilde{S}^-)_{xx} - \omega_s(\tilde{S}^+ - \tilde{S}^-) - (g(\tilde{S}^+) - g(\tilde{S}^-))e^{\frac{\nu}{D}x}M = 0.$$

Integrating over $[0,x]$, and integrating over $[0,1]$ again, we have

$$-D(\tilde{S}^+(0) - \tilde{S}^-(0)) - \omega_s\int_0^1\int_0^x(\tilde{S}^+(\xi) - \tilde{S}^-(\xi))\mathrm{d}\xi\mathrm{d}x - M\int_0^1\int_0^x(g(\tilde{S}^+(\xi)) - g(\tilde{S}^-(\xi)))e^{\frac{\nu}{D}\xi}M\mathrm{d}\xi\mathrm{d}x = 0.$$

Noting that $\tilde{S}^+ \geq \tilde{S}^-$ on $[0,1]$, and $g(S)$ is strictly increasing with respect to S, we must have $\tilde{S}^+ \equiv \tilde{S}^-$. Hence, if $\omega_s S^0 + g(S^0)M \geq \omega_r\rho\max\limits_{[0,1]} R^*$, (18) has a unique positive steady state solution, denoted by $\tilde{S}^*_M(x)$, which satisfies $0 < \tilde{S}^*_M(x) \leq S^0$.

Meanwhile, it follows from (20) that $\chi = a\int_0^1 G(x,\xi)\left(g(\tilde{S}(\xi))e^{\frac{\nu}{D}\xi}M + \omega_s S^0 - \omega_r\rho R^*(\xi)\right)\mathrm{d}\xi$, where $G(x,\xi)$ is the Green's function corresponding to

$$-DG_{xx} + \omega_s G = \delta(x-\xi),\, x \in (0,1), \quad G_x(0) = 0, \quad G(1) = 0.$$

Letting $M \to \infty$, we obtain $g(\tilde{S}(\xi)) \to 0$ in (0, 1), that is, $\lim_{M\to\infty} g(\tilde{S}^*_M(x)) = 0$ in (0, 1).

On the other hand, it is easy to see that the solutions of (18) generate a monotone semi-dynamical system on $C([0,1],\mathbb{R}_+)$. Hence, it follows from Theorem 2.2.6 of (Zhao 2003) that the solution $\tilde{S}(x,t)$ of (18) converges to the unique positive steady-state solution $\tilde{S}^*_M(x)$ of (19) as $t \to \infty$, and $g(\tilde{S}^*_M(x)) \to 0$ in (0, 1) as $M \to \infty$. Hence, for any $\epsilon > 0$, there exist $M_1 > 0$ and $t_1 > t_0$ large enough such that for $M \geq M_1$ and $t \geq t_1$, we have $0 < g(S(x,t)) \leq g(\tilde{S}(x,t)) < \epsilon$ in (0, 1). Similarly, we can show that for any $\epsilon > 0$, there exist $M_2 > 0$ and $t_2 > 0$ large enough such that for $M \geq M_2$ and $t \geq t_2$, we have $f(R) - r < \epsilon$ in (0, 1). Take $M_0 = \max\{M_1, M_2\}$ and $T_0 = \max\{t_1, t_2\}$. Thus for $M \geq M_0, t \geq T_0$ and $m \geq \delta_0$, we have $f(S)+g(S)-r-m < 2\epsilon-\delta_0 < 0$ in (0, 1) as long as $0 < \epsilon < \delta_0/2$. Take $\epsilon = \frac{\delta_0}{4}$. Then $e^{\frac{\nu}{D}x}W_t \leq D\left(e^{\frac{\nu}{D}x}W_x\right)_x - \frac{\delta_0}{2}e^{\frac{\nu_1}{D}x}W$ for $M \geq M_0$, $t \geq T_0$ and $m \geq \delta_0$, which implies $W(x,t) \to 0$ in (0,1) as $t \to \infty$, a contradiction. Hence, $W(1,t)$ is bounded in $t \in (0,+\infty)$.

Let ϕ be the principal eigenfunction of

$$-\phi_{xx} = \mu\phi, \quad x \in (0,1), \quad \phi_x(0) = 0, \phi(1) = 0.$$

Then the principal eigenvalue $\mu_1 = \frac{\pi^2}{4}$, and the associated eigenfunction $\phi = \cos(\frac{\pi}{2}x)$, and $\phi(0) = 1, \phi_x(1) = -\frac{\pi}{2}$. Let $Q(x,t) = R + S + e^{\frac{\nu}{D}x}W$. By direct computation, we obtain

$$\begin{aligned}
&\tfrac{\mathrm{d}}{\mathrm{d}t}\textstyle\int_0^1 Q(x,t)\phi \mathrm{d}x \\
&= D\textstyle\int_0^1 [R_{xx}\phi + S_{xx}\phi + (e^{\frac{\nu}{D}x}W_x)_x\phi \mathrm{d}x] - m\int_0^1 e^{\frac{\nu}{D}x}W\phi \mathrm{d}x \\
&= D(\alpha(\hat{R} - R(0,t)) + \tfrac{\pi}{2}R^0 + \tfrac{\pi}{2}S^0) - \tfrac{\pi^2}{4}D\textstyle\int_0^1 (R+S)\phi \mathrm{d}x \\
&\quad + D\textstyle\int_0^1 (e^{\frac{\nu}{D}x}W_x)_x\phi \mathrm{d}x - m\int_0^1 e^{\frac{\nu}{D}x}W\phi \mathrm{d}x,
\end{aligned}$$

where

$$\begin{aligned}
&D\textstyle\int_0^1 (e^{\frac{\nu}{D}x}W_x)_x\phi \mathrm{d}x = -D\int_0^1 \phi_x e^{\frac{\nu}{D}x}W_x \mathrm{d}x \\
&= -D\textstyle\int_0^1 \phi_x \mathrm{d}(e^{\frac{\nu}{D}x}W_x - \int_0^x \frac{\nu}{D}W(\xi,t)e^{\frac{\nu}{D}\xi}\mathrm{d}\xi) \\
&= \tfrac{\pi}{2}De^{\frac{\nu}{D}}W(1,t) - \tfrac{\pi}{2}\nu\textstyle\int_0^1 We^{\frac{\nu}{D}x}\mathrm{d}x - \tfrac{\pi^2}{4}D\int_0^1 We^{\frac{\nu}{D}x}\phi \mathrm{d}x + \tfrac{\pi^2}{4}\nu\int_0^1(\int_0^x W(\xi,t)e^{\frac{\nu}{D}\xi}\mathrm{d}\xi)\phi \mathrm{d}x.
\end{aligned}$$

Note that $\int_0^1 \phi \mathrm{d}x = \frac{2}{\pi}$, and

$$\begin{aligned}
&\tfrac{\pi^2}{4}\nu\textstyle\int_0^1(\int_0^x W(\xi,t)e^{\frac{\nu}{D}\xi}\mathrm{d}\xi)\phi \mathrm{d}x - \tfrac{\pi}{2}\nu\int_0^1 We^{\frac{\nu}{D}x}\mathrm{d}x \\
&\leq \tfrac{\pi^2}{4}\nu\textstyle\int_0^1 W(\xi,t)e^{\frac{\nu}{D}x}\mathrm{d}x\int_0^1 \phi \mathrm{d}x - \tfrac{\pi}{2}\nu\int_0^1 We^{\frac{\nu}{D}x}\mathrm{d}x \\
&= 0.
\end{aligned}$$

Hence,

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_0^1 Q(x,t)\phi \mathrm{d}x + \frac{\pi^2}{4}D\int_0^1 Q\phi \mathrm{d}x \leq D(\alpha\hat{R} + \frac{\pi}{2}R^0 + \frac{\pi}{2}S^0) + \frac{\pi}{2}De^{\frac{\nu}{D}}W(1,t) - m\int_0^1 e^{\frac{\nu}{D}x}W\phi \mathrm{d}x,$$

that is,

$$\frac{\mathrm{d}}{\mathrm{d}t}\left(e^{\frac{\pi^2}{4}Dt}\int_0^1 Q(x,t)\phi \mathrm{d}x\right) \leq D(\alpha\hat{R}+\frac{\pi}{2}R^0+\frac{\pi}{2}S^0)e^{\frac{\pi^2}{4}Dt}+\frac{\pi}{2}De^{\frac{\nu}{D}}W(1,t)e^{\frac{\pi^2}{4}Dt}-me^{\frac{\pi^2}{4}Dt}\int_0^1 e^{\frac{\nu}{D}x}W\phi \mathrm{d}x.$$

Since $W(1,t)$ is bounded, by Gronwall inequality we get

$$\begin{aligned}
\textstyle\int_0^1 Q(x,t)\phi \mathrm{d}x \quad &\leq e^{-\frac{\pi^2}{4}Dt}\textstyle\int_0^1 Q(x,0)\phi \mathrm{d}x + D(\alpha\hat{R} + \frac{\pi}{2}R^0 + \frac{\pi}{2}S^0)\frac{4}{\pi^2 D}(1 - e^{-\frac{\pi^2}{4}Dt}) \\
&\quad + \tfrac{\pi}{2}De^{\frac{\nu}{D}}\textstyle\int_0^t W(1,\tau)e^{-\frac{\pi^2}{4}D(t-\tau)}\mathrm{d}\tau - m\int_0^t(\int_0^1 e^{\frac{\nu}{D}x}W(x,\tau)\phi \mathrm{d}x)e^{-\frac{\pi^2}{4}D(t-\tau)}\mathrm{d}\tau \\
&\leq e^{-\frac{\pi^2}{4}Dt}\textstyle\int_0^1 Q(x,0)\phi \mathrm{d}x + D(\alpha\hat{R} + \frac{\pi}{2}R^0 + \frac{\pi}{2}S^0)\frac{4}{\pi^2 D}(1 - e^{-\frac{\pi^2}{4}Dt}) \\
&\quad + \tfrac{\pi}{2}De^{\frac{\nu}{D}}\textstyle\int_0^t W(1,\tau)e^{-\frac{\pi^2}{4}D(t-\tau)}\mathrm{d}\tau \\
&\leq e^{-\frac{\pi^2}{4}Dt}\textstyle\int_0^1 Q(x,0)\phi \mathrm{d}x + D(\alpha\hat{R} + \frac{\pi}{2}R^0 + \frac{\pi}{2}S^0)\frac{4}{\pi^2 D}(1 - e^{-\frac{\pi^2}{4}Dt}) \\
&\quad + \tfrac{2}{\pi}De^{\frac{\nu}{D}}C(1 - e^{-\frac{\pi^2}{4}Dt})
\end{aligned} \tag{21}$$

Next, we show $W(x,t)$ is bounded for all $x\in[0,1]$ and $t>0$. Let $\mathbf{W}(t)=\max_{x\in[0,1],\tau\in[0,t]}W(x,\tau)$. Clearly, $\mathbf{W}(t)$ is nondecreasing. Suppose for contradiction that $\mathbf{W}(t)\to\infty$ as $t\to\infty$. Then we can find $t_n\to\infty$ such that $\mathbf{W}(t_n)=\max_{x\in[0,1]}W(x,t_n)$. We may assume that $t_n>1$ for all $n\geq 1$. Define $\widetilde{W}_n(x,t)=\frac{W(x,t+t_n-1)}{\mathbf{W}(t_n)}$. Then $\widetilde{W}_n(x,t)$ satisfies

$$\begin{aligned}
&(e^{\frac{\nu}{D}x}\widetilde{W}_n)_t=D(e^{\frac{\nu}{D}x}(\widetilde{W}_n)_x)_x+(f(R(x,t+t_n-1))+g(S(x,t+t_n-1))-r-m)e^{\frac{\nu}{D}x}\widetilde{W}_n,\\
&(\widetilde{W}_n)_x(0,t)=(\widetilde{W}_n)_x(1,t)=0,\\
&0\leq\widetilde{W}_n(x,0)\leq 1.
\end{aligned}$$

Noting that $|f(R(x,t+t_n-1))+g(S(x,t+t_n-1))-r-m|\leq|f(\rho R^*)+g(\rho S^*)-r-m|:=\Lambda_0$, the comparison principle for parabolic system leads to $0\leq\widetilde{W}_n(x,t)\leq e^{\Lambda_0 t}$ for $x\in[0,1]$ and $t\geq 0$. Hence by the application of standard parabolic regularity, we can conclude that $\{\widetilde{W}_n\}$ is bounded in $C^{1+\gamma,\gamma}([0,1]\times[\frac{1}{2},2])$ for any $\gamma\in(0,1)$. Hence, by passing to a subsequence if necessary we get $\widetilde{W}_n(x,t)\to\widetilde{W}$ in $C^{1,0}([0,1]\times[\frac{1}{2},2])$. Since $|f(R(x,t+t_n-1))+g(S(x,t+t_n-1))-r-m|\leq\Lambda_0$, we may assume that $f(R(x,t+t_n-1))+g(S(x,t+t_n-1))-r-m\to h(x,t)$ weakly in $L^2([0,1]\times[\frac{1}{2},2])$ by passing to a further subsequence if necessary. Moreover, $|h(x,t)|\leq\Lambda_0$, and $\widetilde{W}$ is a weak solution to

$$\begin{aligned}
&(e^{\frac{\nu}{D}x}\widetilde{W})_t=D(e^{\frac{\nu}{D}x}\widetilde{W}_x)_x+h(x,t)e^{\frac{\nu}{D}x}\widetilde{W},\quad x\in(0,1),t\in[\tfrac{1}{2},2],\\
&\widetilde{W}_x(0,t)=\widetilde{W}_x(1,t)=0,\quad t\in[\tfrac{1}{2},2],\\
&0\leq\widetilde{W}(x,t)\leq e^{\Lambda_0 t},\quad x\in[0,1],t\in[\tfrac{1}{2},2].
\end{aligned}$$

It follows from $\max_{x\in[0,1]}\widetilde{W}_n(x,1)=1$ that $\max_{x\in[0,1]}\widetilde{W}(x,1)=1$, which implies $\widetilde{W}\not\equiv 0$. By the strong maximum principle, we deduce that $\widetilde{W}(x,1)\geq\delta_1>0$ in [0,1]. Hence, $\widetilde{W}_n(x,1)\geq\frac{\delta_1}{2}$ for all large n and $x\in[0,1]$, which leads to

$$W(x,t_n)=\widetilde{W}_n(x,1)\mathbf{W}(t_n)\geq\frac{\delta_1}{2}\mathbf{W}(t_n)\text{ for all large } n \text{ and } x\in[0,1].$$

It follows that

$$\int_0^1 Q(x,t_n)\phi\mathrm{d}x>\int_0^1 W(x,t_n)\phi\mathrm{d}x\geq\int_0^1\frac{\delta_1}{2}\mathbf{W}(t_n)\phi\mathrm{d}x\to\infty$$

as $n\to\infty$, a contradiction to (21). That is, $W(x,t)$ is bounded for all $x\in[0,1]$ and $t>0$. In view of $W(x,t)>0$ for all $x\in[0,1]$ and $t>0$, we obtain that there exists a positive constant $C_1>0$ such that $0<B(x,t)\leq C_1$ for all $x\in[0,1]$ and $t>0$. Namely, $B(x,t)$ is ultimately bounded and uniformly bounded in X^+. The proof is completed. □

Next, we derive a priori estimates for positive solutions of the steady-state system (10)-(11).

Lemma B.3 *Suppose $f(R^*)>r$ and (R,S,B) is a nonnegative solution of (10)-(11) with $B\not\equiv 0$. Then*

(i) $0<R<R^*$, $0<S<S^*$, $B>0$ *in* $(0,1)$*;*

(ii) $0<m<m^*$, *where* $m^*=-\lambda_1(-f(R^*)-g(S^*),\nu)-r$*;*

(iii) *for any given $\delta_0>0$, there exists a positive constant $M_0(\delta_0)$ such that $\|B\|_\infty\leq M_0$ provided that $m\in[\delta_0,m^*)$.*

Proof. (i) Note that

$$\begin{aligned}
&-DS_{xx}+[\omega_s+B\textstyle\int_0^1 g'(\tau S)d\tau]S=\omega_r R\geq 0,\quad x\in(0,1),\\
&-DR_{xx}+[\omega_r+B\textstyle\int_0^1 f'(\tau R)d\tau]R=\omega_s S+rB\geq 0,\quad x\in(0,1),\\
&S_x(0)=0,\quad S(1)=S^0>0,\quad -R_x(0)+\alpha R(0)=\alpha\hat{R}>0,\quad R(1)=R^0>0.
\end{aligned}$$

By the strong maximum principle, it is easy to see that $R > 0,\ S > 0$ on $[0, 1]$. Let $W = e^{-\frac{\nu}{D}x}B$. Then

$$\begin{array}{l} -DW_{xx} - \nu W_x + (r+m)W = [f(R) + g(S)]W \geq 0, \not\equiv 0, \quad x \in (0,1), \\ W_x(0) = 0, \quad W_x(1) = 0. \end{array}$$

It follows from the strong maximum principle that $W > 0$ on $[0, 1]$, and hence $B > 0$ on $[0, 1]$.

Now, we begin to prove $R < R^*, S < S^*$. To this end, let $U = R^* - R, V = S^* - S$. Then $U < R^*, V < S^*$, and

$$\begin{array}{l} -DU_{xx} + \omega_r U - \omega_s V = (f(R^* - U) - r)B, \quad x \in (0,1), \\ -DV_{xx} + \omega_s V - \omega_r U = g(S^* - V)B, \quad x \in (0,1), \\ -U_x(0) + \alpha U(0) = 0,\ U(1) = 0, \quad V_x(0) = 0,\ V(1) = 0. \end{array} \tag{22}$$

At first, it is easy to see that there exists some $x_0 \in (0, 1)$ such that $U(x_0) > 0$. Otherwise, $U(x) \leq 0$ on [0, 1]. Then $-\mathcal{L}_0(U, V)^T > 0$ based on $f(R^*) > r$ and $V < S^*, B > 0$. Hence, we have $(U, V) > 0$ on [0, 1] by using Theorem 15 of (Amann 2004), a contradiction. Noting that $U(1) = 0, V(1) = 0$ and $f(R^*) > r$, one can show that there exists $\epsilon > 0$ small enough such that $U_{xx} < 0$ and $V_{xx} < 0$ for any $x \in (1 - \epsilon, 1)$. Furthermore, we claim that $U_x(1) < 0, V_x(1) < 0$. If not, we have $U_x(1) \geq 0$ or $V_x(1) \geq 0$. Thus we have three cases: (1) $U_x(1) \geq 0, V_x(1) \geq 0$; (2) $U_x(1) \geq 0, V_x(1) < 0$; (3) $U_x(1) < 0, V_x(1) \geq 0$.

Case (1): Suppose $U_x(1) \geq 0, V_x(1) \geq 0$. Since $U(1) = 0$ and $U_{xx} < 0$ for any $x \in (1-\epsilon, 1)$, we have $U(1 - \epsilon) < 0$. Let

$$x_1 = \sup\{x \in (0,1) | U_x(x) = 0, U(x) < 0\}.$$

Then $0 < x_1 < 1$ because there exists some $x_0 \in (0, 1)$ such that $U(x_0) > 0$. Moreover, $U(x) < 0$ for $x \in [x_1, 1)$, $U_x(x_1) = 0$ and $U_{xx}(x_1) \geq 0$. It follows from the first equation of (22) that

$$\omega_s V(x_1) = -DU_{xx}(x_1) + \omega_r U(x_1) - (f(R^*(x_1) - U(x_1)) - r)B(x_1) < 0,$$

which leads to $V(x_1) < 0$. Adding the equations for U and V, we obtain

$$-D(U+V)_{xx} = (f(R^* - U) - r)B + g(S^* - V)B > 0$$

for any $x \in [x_1, 1)$ since $f(R^*) > r$, $U < 0$ in $[x_1, 1)$ and $V < S^*, B > 0$ in [0, 1]. Hence, $V_{xx}(x_1) < 0$. Integrating this equation over $[x_1, 1]$, we obtain $V_x(x_1) > U_x(1) + V_x(1) \geq 0$. Define

$$y_1 = \sup\{x \in (0, x_1) | V_x(x) = 0, V(x) < 0\}.$$

Noting that $V(x_1) < 0$, $V_x(x_1) > 0$ and $V_{xx}(x_1) < 0$, we can show that $0 \leq y_1 < x_1$, $v(y) < 0$ on $[y_1, x_1]$, $V_x(y_1) = 0$, $V_x \geq 0$ on $[y_1, x_1]$, and $V_{xx}(y_1) \geq 0$. It follows from the second equation of (22) that

$$\omega_r U(y_1) = -DV_{xx}(y_1) + \omega_s V(y_1) - g(S^*(y_1) - V(y_1))B(y_1) < 0,$$

which leads to $U(y_1) < 0$. If $y_1 = 0$. Then $U(0) < 0$ and $U_x(0) = \alpha U(0) < 0$. Let $z_1 = \inf\{x \in (0, x_1) | U(x) = 0\}$. Then $0 < z_1 < 1$ since there exists some $x_0 \in (0, 1)$ such that $U(x_0) > 0$. Moreover, we have $U(x) < 0$ in $(0, z_1)$ and $U_x(z_1) \geq 0$. Now, consider the following elliptic problem on $[0, z_1]$

$$\begin{array}{l} -DU_{xx} + \omega_r U - \omega_s V = (f(R^* - U) - r)B > 0, \quad x \in (0, z_1), \\ -DV_{xx} + \omega_s V - \omega_r U = g(S^* - V)B > 0, \quad x \in (0, z_1), \\ -U_x(0) + \alpha U(0) = 0,\ U_x(z_1) \geq 0, \quad V_x(0) = 0,\ V_x(z_1) \geq 0. \end{array}$$

It follows from Theorem 15 of (Amann 2004) that $(U, V) > 0$ on $[0, z_1]$, a contradiction. Hence $0 < y_1 < x_1$.

Now, we have two cases: (a) $U(x) < 0$ on $[y_1, 1]$; (b) $U(x_0) > 0$ for some $x_0 \in (y_1, x_1)$. If $U(x) < 0$ on $[y_1, 1]$, by adding the equations for U and V, we obtain $-D(U + V)_{xx} = (f(R^* -$

$U) - r)B + g(S^* - V)B > 0$ for any $x \in (y_1, 1)$. Hence, $U_{xx}(y_1) < 0$. Integrating this equation over $[y_1, 1]$, we obtain $U_x(y_1) > U_x(1) + V_x(1) \geq 0$. Define

$$x_2 = \sup\{x \in (0, y_1) | U_x(x) = 0, U(x) < 0\}.$$

Then we can assert that $0 < x_2 < x_1$, $U(x_2) < 0$ in $(x_2, 1)$, $U_x(x_2) = 0$, $U_x \geq 0$ on $[x_2, y_1]$, and $U_{xx}(x_2) \geq 0$ similarly. The same arguments lead to $V(x_2) < 0$, $V_x(x_2) > 0$ and $V_{xx}(x_2) < 0$. Hence, similarly, we can define

$$y_2 = \sup\{x \in (0, x_2) | V_x(x) = 0, V(x) < 0\}.$$

Moreover, $0 < y_2 < x_2$ by the above arguments. Continuing the above process, we can show that there must exist positive integer i such that $U(x_0) > 0$ for some $x_0 \in (y_i, x_i)$. Moreover,

$$U(y_i) < 0, U_{xx}(y_i) < 0, U(x_i) < 0, U_x(x_i) = 0, U_{xx}(x_i) \geq 0,$$

and

$$V(x_i) < 0, V_{xx}(x_i) < 0, V(y_i) < 0, V_x(y_i) = 0, V_{xx}(y_i) \geq 0, V_x \geq 0 \text{ on } [y_i, x_i].$$

Let $z_i = \inf\{x \in (y_i, x_i) | U(x) = 0\}$. Then $y_i < z_i < x_i$, $U_x(z_i) \geq 0$ and $U < 0$ in (y_i, z_i). Adding the equations for U and V, we obtain $-D(U + V)_{xx} = (f(R^* - U) - r)B + g(S^* - V)B > 0$ for any $x \in (y_i, z_i)$. Integrating this equation over $[y_i, z_i]$, we obtain $U_x(y_i) > U_x(z_i) + V_x(z_i) \geq 0$. Hence, we can define

$$x_{i+1} = \sup\{x \in (0, y_i) | U_x(x) = 0, U(x) < 0\} \text{ and } y_{i+1} = \sup\{x \in (0, x_{i+1}) | V_x(x) = 0, V(x) < 0\}.$$

This process will be terminated if $y_{i+1} = 0$ or $V_x < 0$ for any $x \in (0, y_{i+1})$. If $y_{i+1} = 0$. Then $U(0) < 0$. Noting that $U < 0$ in (x_{i+1}, z_i), we can prove that there exists some $\hat{x}_0 \in (0, x_{i+1})$ such that $U(\hat{x}_0) > 0$. Otherwise, $U \leq 0$ on $[0, z_i]$. On the other hand, considering the equations for U and V on $[0, z_i]$, we have $(U, V) > 0$ on $[0, z_i]$, a contradiction. Let $z_{i+1} = \inf\{x \in (0, x_{i+1}) | U(x) = 0\}$. Considering the equations for U and V on $[0, z_{i+1}]$, we have $(U, V) > 0$ on $[0, z_{i+1}]$, a contradiction. If $V_x < 0$ for any $x \in (0, y_{i+1})$, we define $x_{i+2} = \sup\{x \in (0, y_{i+1}) | U_x(x) = 0, U(x) < 0\}$. Then $0 < x_{i+2} < y_{i+1}$. Considering the equations for U and V on $[x_{i+2}, y_{i+1}]$, we get

$$\begin{aligned}
&-DU_{xx} + \omega_r U - \omega_s V = (f(R^* - U) - r)B > 0, \quad x \in (x_{i+2}, y_{i+1}), \\
&-DV_{xx} + \omega_s V - \omega_r U = g(S^* - V)B > 0, \quad x \in (x_{i+2}, y_{i+1}), \\
&U_x(x_{i+2}) = 0, \ U_x(y_{i+1}) \geq 0, \quad -V_x(x_{i+2}) \geq 0, \ V_x(y_{i+1}) = 0.
\end{aligned}$$

It follows from Theorem 15 of (Amann 2004) that $(U, V) > 0$ on $[x_{i+2}, y_{i+1}]$, a contradiction.

Case (2): $U_x(1) \geq 0, V_x(1) < 0$. Noting that $U(1) = 0, V(1) = 0$ and $U_{xx} < 0, V_{xx} < 0$ for any $x \in (1 - \epsilon, 1)$, we have $U(1 - \epsilon) < 0$ and $V(1 - \epsilon) > 0$. Let $x_1 = \sup\{x \in (0, 1) | U_x = 0, U(x) < 0\}$. Then $U(x) < 0$ for $x \in [x_1, 1)$, $U_x(x_1) = 0$, $U_x \geq 0$ on $[x_1, 1]$, and $U_{xx}(x_1) \geq 0$. It follows from the first equation of (22) that $\omega_s V(x_1) = -DU_{xx}(x_1) + \omega_r U(x_1) - (f(R^*(x_1) - U(x_1)) - r)B(x_1) < 0$ since $f(R^*) > r$, which leads to $V(x_1) < 0$. In view of $V(x_1) < 0, V(1 - \epsilon) > 0$, we define $z_1 = \inf\{x \in (x_1, 1) | V(x) = 0\}$. Then $x_1 < z_1 < 1$ and $V_x(z_1) \geq 0$. On the other hand, we have $U_x(z_1) \geq 0$. Hence, we obtain a contradiction as Case (1) on $[0, z_1]$ by the same arguments.

Case (3): $U_x(1) < 0, V_x(1) \geq 0$. Noting that $U(1) = 0, V(1) = 0$ and $U_{xx} < 0, V_{xx} < 0$ for any $x \in (1 - \epsilon, 1)$, we have $U(1 - \epsilon) > 0$ and $V(1 - \epsilon) < 0$. Let $y_1 = \sup\{x \in (0, 1) | V_x = 0, V(x) < 0\}$. Then $V(x) < 0$ for $x \in [y_1, 1)$, $V_x(y_1) = 0$, $V_{xx}(y_1) \geq 0$ and $V_x \geq 0$ for any $x \in (y_1, 1)$. It follows from the second equation of (22) that $\omega_r U(y_1) = -DV_{xx}(y_1) + \omega_s V(y_1) - g(S^*(y_1) - V(y_1))B(y_1) < 0$, which leads to $U(y_1) < 0$. In view of $U(y_1) < 0, U(1 - \epsilon) > 0$, we define $z_1 = \inf\{x \in (y_1, 1) | U(x) = 0\}$. Then $y_1 < z_1 < 1$ and $U_x(z_1) \geq 0$. On the other hand, we have $V_x(z_1) \geq 0$. Similarly, we obtain a contradiction as Case (1) on $[0, z_1]$.

Thus, $U_x(1) < 0, V_x(1) < 0$. Hence, there exists $\epsilon > 0$ small such that $U(1-\epsilon) > 0, V(1-\epsilon) > 0$. Next, we show $U > 0, V > 0$ in [0, 1). Suppose $U(x_0) < 0$ for some point $x_0 \in [0, 1)$. Define

$$x_1 = \sup\{x \in (0, 1) | U_x = 0, U(x) < 0\} \text{ and } z_1 = \inf\{x \in (x_1, 1) | U(x) = 0\}.$$

Then $U \geq 0$ on $[z_1, 1]$. By virtue of $U(1-\epsilon) > 0$, it is easy to check that $U(x) < 0$ in $[x_1, z_1)$, $U_x(x_1) = 0$, $U_x \geq 0$ on $[x_1, z_1]$, $U_{xx}(x_1) \geq 0$. It follows from the first equation of (22) that

$$\omega_s V(x_1) = -DU_{xx}(x_1) + \omega_r U(x_1) - (f(R^*(x_1) - U(x_1)) - r)B(x_1) < 0$$

based on $f(R^*) > r$, which leads to $V(x_1) < 0$. Define

$$y_1 = \sup\{x \in (0,1) | V_x = 0, V(x) < 0\} \text{ and } z_2 = \inf\{x \in (y_1, 1) | V(x) = 0\}.$$

In view of $V(1-\epsilon) > 0$, it is easy to check that $V(x) < 0$ in $[y_1, z_2)$, $V_x(y_1) = 0$, $V_x \geq 0$ on $[y_1, z_2]$, $V_{xx}(y_1) \geq 0$. It follows from the second equation of (22) that

$$\omega_r U(y_1) = -DV_{xx}(y_1) + \omega_s V(y_1) - g(S^*(y_1) - V(y_1))B(y_1) < 0,$$

which leads to $U(y_1) < 0$. Hence $y_1 < z_1$ based on $U \geq 0$ on $[z_1, 1]$. Let $z_0 = \min\{z_1, z_2\}$. Then $U_x(z_0) \geq 0$ and $V_x(z_0) \geq 0$. Hence, we can derive a contradiction as Case (1) on $[0, z_0]$ by similar arguments. Thus we have $U \geq 0$ on [0, 1]. By the application of strong maximum principle to the equations (22), we can find immediately that $U, V > 0$ in (0, 1). That is, $0 < R < R^*, 0 < S < S^*$ in (0, 1).

(ii) It follows from the equation for B that $m = -\lambda_1(-f(R) - g(S), \nu) - r$. Noting that $0 < R < R^*$, $0 < S < S^*$ and the properties of eigenvalue $\lambda_1(q(x), \nu)$, it is easy to see that $0 < m < m^* = -\lambda_1(-f(R^*) - g(S^*), \nu) - r$.

(iii) We argue by contradiction. Suppose there exists a sequence $m_n \in (\delta, m^*)(n = 1, 2, \cdots)$, and positive solution (R_n, S_n, B_n) of (10)-(11) with $m = m_n$ such that $\|B_n\|_\infty \to \infty$ as $n \to \infty$. Passing to a subsequence if necessary we may assume that $m_n \to m_0 \in [\delta, m^*]$. Set $\hat{B}_n = \frac{B_n}{\|B_n\|_\infty}$. Then

$$\begin{aligned} &D(\hat{B}_n)_{xx} - \nu(\hat{B}_n)_x + (f(R_n) + g(S_n) - r - m_n)\hat{B}_n = 0, x \in (0,1), \\ &D(\hat{B}_n)_x(0) - \nu(\hat{B}_n)(0) = 0, \quad D(\hat{B}_n)_x(1) - \nu(\hat{B}_n)(1) = 0. \end{aligned}$$

Integrating the above equation from 0 to x, we obtain

$$D(\hat{B}_n)_x(x) - \nu(\hat{B}_n)(x) + \int_0^x (f(R_n) + g(S_n) - r - m_n)\hat{B}_n dx = 0,$$

which indicates $(\hat{B}_n)_x(x)$ is uniformly bounded since $0 < R_n < R^*$, $0 < S_n < S^*$ and $\|\hat{B}_n\|_\infty = 1$. Hence, $(\hat{B}_n)_{xx}$ is uniformly bounded. Passing to a subsequence if necessary, we may assume $\hat{B}_n \to \hat{B}$ in $C^1[0,1]$, and $\hat{B} \geq 0, \|\hat{B}\|_\infty = 1$. Let $F_n(x) = f(R_n) + g(S_n) - r$. Then $-r \leq F_n(x) \leq f(R^*) + g(S^*) - r$ on [0, 1], and hence we may assume $F_n(x) \to F_0(x)$ weakly in $L^2(0,1)$ for some function $F_0(x)$ satisfy $-r \leq F_0(x) \leq f(R^*) + g(S^*) - r$. Hence, $\hat{B}$ is a weak solution to

$$\begin{aligned} &D\hat{B}_{xx} - \nu\hat{B}_x + (F_0(x) - m_0)\hat{B} = 0, x \in (0,1), \\ &D\hat{B}_x(0) - \nu\hat{B}(0) = 0, \quad D\hat{B}(1) - \nu\hat{B}(1) = 0. \end{aligned} \tag{23}$$

It follows from the strong maximum principle that $\hat{B} > 0$ on [0, 1]. Let $U_n = R^* - R_n, V_n = S^* - S_n$. Then $0 < U_n < R^*, 0 < V_n < S^*$, and (U_n, V_n) satisfies

$$\begin{aligned} &D(U_n)_{xx} - \omega_r U_n + \omega_s V_n + (f(R_n) - r)\|B_n\|_\infty \hat{B}_n = 0, \quad x \in (0,1), \\ &D(V_n)_{xx} - \omega_s V_n + \omega_r U_n + g(S_n)\|B_n\|_\infty \hat{B}_n = 0, \quad x \in (0,1), \\ &-(U_n)_x(0) + \alpha U_n(0) = 0, \ U_n(1) = 0, \quad (V_n)_x(0) = 0, \ V_n(1) = 0. \end{aligned}$$

Hence, we have

$$D(U_n)_{xx} + D(V_n)_{xx} + F_n(x)\|B_n\|_\infty \hat{B}_n = 0.$$

Multiplying this equation by any smooth function $\varphi \in C^\infty[0,1]$ whose support is in (0, 1), we obtain

$$D\frac{U_n(0) + V_n(0)}{\|B_n\|_\infty}\varphi_x(0) + D\int_0^1 \frac{U_n + V_n}{\|B_n\|_\infty}\varphi_{xx} dx + \int_0^1 F_n(x)\hat{B}_n \varphi dx = 0.$$

Taking the weak limits, we get $\int_0^1 F_0(x)\hat{B}\varphi dx = 0$. The arbitrariness of φ leads to $F_0(x)\hat{B} = 0$ a.e. in (0, 1). Integrating (23) over (0, 1), we get $m_0 = 0$, a contradiction to $m_0 \in [\delta, m^*]$. □

Remark B.4 It is easy to check that $m^* = -\lambda_1(-f(R^*)-g(S^*),\nu)-r > 0$ based on the hypothesis $f(R^*) > r$. Moreover, it follows from Lemma B.3 that (10)-(11) has no positive solution when $m \geq m^*$.

Now we are ready to prove Theorem 2.3. Since the proof is complicated, we divided it into the following three lemmas.

Lemma B.5 *Assume $f(R^*) > r$. Then given $B \in X_1^+ := C([0,1],\mathbb{R}_+)$, the problem*

$$\begin{aligned}&\mathcal{L}_0\begin{pmatrix} R \\ S \end{pmatrix} - \begin{pmatrix} f(R)-r \\ g(S) \end{pmatrix} B(x) = 0,\\ &-R_x(0)+\alpha R(0) = \alpha\hat{R},\ R(1) = R^0,\quad S_x(0) = 0,\ S(1) = S^0\end{aligned} \tag{24}$$

has a unique solution $(R(\cdot,B),S(\cdot,B))$, which satisfies $0 < R(\cdot,B) \leq R^*, 0 < S(\cdot,B) \leq S^*$ and $(R(\cdot,0),S(\cdot,0)) = (R^*,S^*)$. Moreover, for any $0 \leq B \leq M_0$, the maps $B \mapsto R(\cdot,B)$ and $B \mapsto S(\cdot,B)$ are Lipschitz continuous from $X_1^+ \to X_1^+$ and C^1 continuous from $\dot{X}_1^+ \to X_1^+$, where M_0 is given in Lemma B.3 and $\dot{X}_1^+ = \{u(x) \in X_1^+ : u(x) > 0$ on $[0,1]\}$.

Proof. From Lemma B.3, one can find that any nonnegative solution to (24) satisfies $0 < R \leq R^*, 0 < S < S^*$ provided $B(x) \geq 0$. Note that (24) is a cooperative system, and the reaction terms are C^1 continuous. According to Definition 8.4.1 of (Pao 1992), it is easy to see that $(0,0)$ is a strictly lower solution to (24), and (R^*,S^*) is a strictly upper solution to (24) provided $f(R^*) > r$. It follows from monotone iteration process in Chapter 8.4 of (Pao 1992) that there exists a pair (R^+,S^+) and (R^-,S^-), which are the maximal and minimal solutions to (24), and satisfy the relation $0 < R^- \leq R^+ \leq R^*,\ 0 < S^- \leq S^+ \leq S^*$. The detailed proof can be found in Lemma 8.4.1 and Theorem 8.4.1 of (Pao 1992). Next, we show $R^- \equiv R^+, S^- \equiv S^+$. Obviously,

$$\mathcal{L}_0\begin{pmatrix} R^+-R^- \\ S^+-S^- \end{pmatrix} + \begin{pmatrix} f(R^-)-f(R^+) \\ g(S^-)-g(S^+) \end{pmatrix} B(x) = 0.$$

Hence, we have

$$D(R^+-R^-)_{xx} + D(S^+-S^-)_{xx} + [f(R^-)-f(R^+)+g(S^-)-g(S^+)]B(x) = 0.$$

Integrating over $[0,x]$, and integrating over $[0,1]$ again, we have

$$-(D+\alpha D)(R^+(0)-R^-(0))-D(S^+(0)-S^-(0))+\int_0^1\int_0^x [f(R^-)-f(R^+)+g(S^-)-g(S^+)]B(\xi)d\xi dx = 0.$$

Noting that $R^+ \geq R^-, S^+ \geq S^-$ on $[0,1]$, and $f(R), g(S)$ are strictly increasing, we must have $R^+ \equiv R^-, S^+ \equiv S^-$. Hence, (24) has a unique solution, denoted by $(R(\cdot,B),S(\cdot,B))$, satisfying $0 < R(\cdot,B) \leq R^*, 0 < S(\cdot,B) \leq S^*$. It follows from Theorem 2.1 that $(R(\cdot,0),S(\cdot,0)) = (R^*,S^*)$.

Next, we prove the Lipschitz continuity of the maps $R(\cdot,B)$ and $S(\cdot,B)$ with respect to B. To this end, let $(R_1,S_1) = (R(\cdot,B_1),S(\cdot,B_1))$ and $(R_2,S_2) = (R(\cdot,B_2),S(\cdot,B_2))$ be the unique solution to (24) with $B = B_1$ and $B = B_2$ respectively. Here $0 \leq B_1(x) \leq B_2(x) \leq M_0$ with $B_1(x), B_2(x) \in C[0,1]$ and $B_1(x) \not\equiv B_2(x)$. Then

$$\mathcal{L}_0\begin{pmatrix} R_1-R_2 \\ S_1-S_2 \end{pmatrix} - \begin{pmatrix} f(R_1)B_1-f(R_2)B_2-r(B_1-B_2) \\ g(S_1)B_1-g(S_2)B_2 \end{pmatrix} = 0.$$

It follows from mean value theorem that

$$\left[\mathcal{L}_0 - \begin{pmatrix} f'(\xi_1)B_1 & 0 \\ 0 & g'(\xi_2)B_1 \end{pmatrix}\right]\begin{pmatrix} R_1-R_2 \\ S_1-S_2 \end{pmatrix} = \begin{pmatrix} (f(R_2)-r)(B_1-B_2) \\ g(S_2)(B_1-B_2) \end{pmatrix},$$

where ξ_1 lies between R_1 and R_2, and ξ_2 lies between S_1 and S_2. Hence, $0 < \xi_1 \leq R^*,\ 0 < \xi_2 \leq S^*$. Recalling that $f'(R), g'(S) > 0$, we can find that the operator

$$\hat{\mathcal{L}}_0 = \mathcal{L}_0 - \begin{pmatrix} f'(\xi_1)B_1 & 0 \\ 0 & g'(\xi_2)B_1 \end{pmatrix}$$

is invertible, and its inverse operator is a bounded negative operator by Theorem 2.6 or Remark 2.4 of (López-Gómez and Molina-Meyer 1994). Therefore,

$$\begin{pmatrix} R_1 - R_2 \\ S_1 - S_2 \end{pmatrix} = (\hat{\mathcal{L}}_0)^{-1} \begin{pmatrix} (f(R_2) - r)(B_1 - B_2) \\ g(S_2)(B_1 - B_2) \end{pmatrix}.$$

The boundedness of the operator $(\hat{\mathcal{L}}_0)^{-1}$ and $(R_i, S_i)(i = 1, 2)$ leads to the Lipschitz continuity of the maps $B \mapsto R(\cdot, B)$ and $B \mapsto S(\cdot, B)$.

At last, we show the C^1 continuity of the maps $B \mapsto R(\cdot, B)$ and $B \mapsto S(\cdot, B)$ by the implicit function theorem. Define $\mathbf{H} : \dot{X}_1^+ \times C^{2+\gamma}[0, 1] \times C^{2+\gamma}[0, 1] \to C^\gamma[0, 1]$ by

$$\mathbf{H}(B, R, S) = \mathcal{L}_0 \begin{pmatrix} R \\ S \end{pmatrix} - \begin{pmatrix} f(R) - r \\ g(S) \end{pmatrix} B(x),$$

subject to the boundary conditions $-R_x(0) + \alpha R(0) = \alpha \hat{R},\ R(1) = R^0,\ \ S_x(0) = 0,\ S(1) = S^0$. Clearly, $\mathbf{H}$ is a C^1 function. Given $B_0(x) \in \dot{X}_1^+$, $\mathbf{H}(B_0, R(\cdot, B_0), S(\cdot, B_0)) \equiv 0$, and the Fréchet derivative

$$\mathrm{D}_{(R,S)}\mathbf{H}(B_0, R(\cdot, B_0), S(\cdot, B_0)) = \mathcal{L}_0 - \begin{pmatrix} f'(R(\cdot, B_0))B_1 & 0 \\ 0 & g'(S(\cdot, B_0))B_1 \end{pmatrix}$$

is a non-degenerate negative operator subject to the boundary conditions $-R_x(0) + \alpha R(0) = 0,\ R(1) = 0,\ \ S_x(0) = 0,\ S(1) = 0$. It follows from the implicit function theorem that there exists a C^1 map $(R(\cdot, B), S(\cdot, B)) : \dot{X}_1^+ \to C^{2+\gamma}[0, 1] \times C^{2+\gamma}[0, 1]$ defined in a neighborhood of B_0 such that $(R(\cdot, B), S(\cdot, B))|_{B=B_0} = (R(\cdot, B_0), S(\cdot, B_0))$, and $\mathbf{H}(B, R(\cdot, B), S(\cdot, B)) = 0$. It follows from the uniqueness of the solution $(B, R(\cdot, B), S(\cdot, B))$ close to $(B_0, R(\cdot, B_0), S(\cdot, B_0))$ that $R(\cdot, B), S(\cdot, B)$ are continuously differentiable with respect to B respectively. □

Lemma B.6 *Suppose $f(R^*) > r$. Then for any given $\delta_0 > 0$, the following problem has a unique positive solution provided $m \in [\delta_0, m^*)$*

$$\begin{aligned} &DB_{xx} - \nu B_x + (f(R(\cdot, B)) + g(S(\cdot, B)) - r - m)B = 0, \\ &DB_x(0) = \nu B(0), \quad DB_x(1) = \nu B(1). \end{aligned} \tag{25}$$

Proof. At first, by Lemma B.3, if B is a nonnegative solution, we must have $0 < B < M_0$ provided $m \in [\delta_0, m^*)$. Next, we show (25) has exactly only one positive solution $B \in (0, M_0)$. Let $W = e^{-\frac{\nu}{D}x}B(x)$. Then

$$\begin{aligned} &D(e^{\frac{\nu}{D}x}W_x)_x + (f(R(\cdot, e^{\frac{\nu}{D}x}W)) + g(S(\cdot, e^{\frac{\nu}{D}x}W)) - r - m)e^{\frac{\nu}{D}x}W = 0, \\ &W_x(0) = W_x(1) = 0. \end{aligned} \tag{26}$$

Let $\Omega = \{W \in X_1^+ : W < M_0 + 1\}$, and define a differential operator $T_\tau : [0, 1] \times \Omega \to X_1^+$ by

$$T_\tau(W) = K_P\left((\tau f(R(\cdot, e^{\frac{\nu}{D}x}W)) + \tau g(S(\cdot, e^{\frac{\nu}{D}x}W)) - r - m)e^{\frac{\nu}{D}x}W + PW\right)$$

where P is large enough such that $(\tau f(R(\cdot, e^{\frac{\nu}{D}x}W)) + \tau g(S(\cdot, e^{\frac{\nu}{D}x}W)) - r - m)e^{\frac{\nu}{D}x} + P > 0$ for all $W \in \Omega$ and $\tau \in [0, 1]$, and K_P is the solution operator $W = K_P(h(x))$ for the problem

$$-D(e^{\frac{\nu}{D}x}W_x)_x + PW = h(x),\ x \in (0, 1), \quad W_x(0) = W_x(1) = 0.$$

Let $T = T_1$. Then $T : \Omega \to X_1^+$ is compact and continuously differentiable, and (26) has nonnegative solutions if and only if the operator T has a fixed point in Ω. Moreover, T_τ has no fixed point on $\partial\Omega$. By the homotopic invariance of the degree, it is easy to see that

$$\mathrm{index}(T, \Omega, X_1^+) = \mathrm{index}(T_\tau, \Omega, X_1^+) = \mathrm{index}(T_0, \Omega, X_1^+) = \mathrm{index}(T_0, 0, X_1^+) = 1.$$

By Lemma D.3, it is easy to check that $\mathrm{index}(T, 0, X_1^+) = 0$ provided that $m < m_*$. The additivity of index implies that T has at least one positive fixed point in Ω.

It remains to prove the uniqueness of positive fixed points. To this end, we first claim that any positive fixed point W_0 of T is non-degenerative, and $\mathrm{index}(T, W_0, X_1^+) = 1$. It follows from Leray-Schauder degree theory that $\mathrm{index}(T, W_0, X_1^+) = (-1)^p$, where p is the sum of the multiplicities of all the eigenvalue of T which are greater than one. Hence it suffices to show T has no eigenvalue greater than or equal to 1. Suppose $\lambda \geq 1$ is an eigenvalue of the Fréchet derivative operator of T at W_0 with the associated eigenfunction ψ. Then

$$\begin{aligned} &-\lambda D(e^{\frac{\nu}{D}x}\psi_x)_x + (\lambda - 1)P\psi - (f(R(\cdot, B_0)) + g(S(\cdot, B_0)) - r - m)e^{\frac{\nu}{D}x}\psi \\ &\qquad -B_0 f'(R(\cdot, B_0)) \cdot \partial_B R(\cdot, B_0)e^{\frac{\nu}{D}x}\psi - B_0 g'(S(\cdot, B_0)) \cdot \partial_B S(\cdot, B_0)e^{\frac{\nu}{D}x}\psi = 0, \\ &\psi_x(0) = \psi_x(1) = 0, \end{aligned} \tag{27}$$

where $B_0 = e^{\frac{\nu}{D}x}W_0$. Let $\phi_1 = \partial_B R(\cdot, B_0)e^{\frac{\nu}{D}x}\psi$, $\phi_2 = \partial_B S(\cdot, B_0)e^{\frac{\nu}{D}x}\psi$. It follows from $(R(\cdot, B_0), S(\cdot, B_0))$ is the unique solution to (24) with $B = B_0$ that

$$\begin{aligned} &\mathcal{L}_0 \begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} - \begin{pmatrix} B_0 f'(R(\cdot, B_0))\phi_1 \\ B_0 g'(S(\cdot, B_0))\phi_2 \end{pmatrix} = \begin{pmatrix} f(R(\cdot, B_0)) - r \\ g(S(\cdot, B_0)) \end{pmatrix} e^{\frac{\nu}{D}x}\psi, \\ &L_\lambda \psi = B_0 f'(R(\cdot, B_0))\phi_1 + B_0 g'(S(\cdot, B_0))\phi_2, \end{aligned}$$

where $L_\lambda \psi = -\lambda D(e^{\frac{\nu}{D}x}\psi_x)_x + (\lambda - 1)P\psi - (f(R(\cdot, B_0)) + g(S(\cdot, B_0)) - r - m)e^{\frac{\nu}{D}x}\psi$. It follows from Theorem 13 of (Amann 2004) that

$$\tilde{\mathcal{L}}_0 = \mathcal{L}_0 - \begin{pmatrix} B_0 f'(R(\cdot, B_0)) & 0 \\ 0 & B_0 g'(S(\cdot, B_0)) \end{pmatrix}$$

is invertible subject to the boundary conditions: $-(\phi_1)_x(0) + \alpha\phi_1(0) = 0, \phi_1(1) = 0,\ (\phi_2)_x(0) = 0, \phi_2(1) = 0$, and all eigenvalues of $\tilde{\mathcal{L}}_0$ are negative.

Let L_1 be the linear operator L_λ with $\lambda = 1$. Then $L_1 = -D(e^{\frac{\nu}{D}x}\psi_x)_x - (f(R(\cdot, B_0)) + g(S(\cdot, B_0)) - r - m)e^{\frac{\nu}{D}x}\psi$. Noting that W_0 is a positive solution to (26), that is $L_1 W_0 = 0$ in $(0, 1)$, we can find that for $\lambda > 1$, L_λ is invertible subject to the boundary conditions: $\psi_x(0) = \psi_x(1) = 0$, and all eigenvalues of L_λ are positive, which implies the strong maximum principle can be applied to the operator L_λ. Meanwhile, since $L_1 W_0 = 0$ in $(0,\ 1)$, we conclude that $\lambda_1(L_1) = 0$ and all of other eigenvalue of L_1 are positive. Hence, the general maximum principle can be applied to the operator L_1 for the function ψ/W_0. By the similar arguments as in Lemma 3.3 of (Nie et al. 2015) and Theorem 3.1 of (López-Gómez and Pardo 1994), one can deduce that $\psi \equiv 0$. That is, the Fréchet derivative operator of T at W_0 has no eigenvalue greater than or equal to 1. Hence, $\mathrm{index}(T, W_0, X_1^+) = (-1)^0 = 1$.

Since T is compact and any positive fixed point of T is non-degenerative, and the only trivial non-negative fixed point 0 is also non-degenerative, we see that T has finitely many positive fixed points in Ω. Let them be $W_i (i = 1, 2, \cdots, l)$. By the additivity of the fixed-point index, we obtain

$$1 = \mathrm{index}(T, \Omega, X_1^+) = \mathrm{index}(T, 0, X_1^+) + \sum_{i=1}^{l} \mathrm{index}(T, W_i, X_1^+) = l.$$

Hence $l = 1$ and T has a unique positive fixed point. Namely, (25) has a unique positive solution provided $m \in [\delta_0, m^*)$. □

It follows from Lemmas B.5–B.6 that for $m \in (0, m^*)$, (10)-(11) has a unique positive solution $(R_m(x), S_m(x), B_m(x))$ provided $f(R^*) > r$. Next, we turn to show the continuity of the unique positive solution $(R_m(x), S_m(x), B_m(x))$ with respect to m.

Lemma B.7 *Suppose $f(R^*) > r$, and let $(R_m(x), S_m(x), B_m(x))$ be the unique positive solution to (10)-(11) when $m \in (0, m^*)$. Then $(R_m(x), S_m(x), B_m(x))$ is continuous from $(0, m^*)$ to $(C^1[0, 1])^3$.*

Proof. The continuity of the unique positive solution $(R_m(x), S_m(x), B_m(x))$ with respect to m follows from a standard compactness and uniqueness consideration. Indeed, if $m_n \to m_0 \in (0, m^*)$, then there exists a subsequence of $(R_{m_n}(x), S_{m_n}(x), B_{m_n}(x))$ converges in $C^1([0,1], \mathbb{R}^3)$ to a positive solution of (10)-(11) with $m = m_0$. By the uniqueness, this positive solution must be $(R_{m_0}(x), S_{m_0}(x), B_{m_0}(x))$. Therefore the entire sequence converges to $(R_{m_0}(x), S_{m_0}(x), B_{m_0}(x))$. □

Remark B.8 It follows from Remark B.4 and Lemmas B.5–B.7 that Theorem 2.3 holds.

Remark B.9 By application of a standard bifurcation argument, $(m^*; R^*, S^*, 0)$ is a simple bifurcation point, and (10)-(11) has an unbounded connected branch of positive solution bifurcating from $(m^*; R^*, S^*, 0)$. Moreover, we can show the branch of positive solution can only become unbounded through $(m; R_m, S_m, B_m)$ belongs to the branch and satisfies $m \to 0$, and $\|B_m\|_\infty \to \infty$, which leads to $f(R_n) + g(S_n) - r \to 0$ a.e. in $(0,1)$.

Proof of Theorem 2.4. (i) By Lemma B.1, any solution (R, S, B) to (9) satisfies $R(x,t) > 0, S(x,t) > 0, B(x,t) > 0$. In order to show $(R(x,t), S(x,t), B(x,t))$ converges to $(R^*, S^*, 0)$, we first consider the following system

$$\begin{array}{ll} R_t = DR_{xx} + \omega_s S - \omega_r R + rB - f(R)B, & x \in (0,1), \\ S_t = DS_{xx} - \omega_s S + \omega_r R - g(S)B, & x \in (0,1), \\ -R_x(0,t) + \alpha R(0,t) = \alpha \hat{R}, & R(1,t) = R^0, \\ S_x(0,t) = 0, \quad S(1,t) = S^0, & \\ R(x,0) = R_0(x) \geq 0, & S(x,0) = S_0(x) \geq 0, \end{array} \tag{28}$$

where $B(x,t) > 0$ fixed. Clearly, there exists $\rho > 1$ large enough such that $\rho(R^*, S^*) \geq (R_0(x), S_0(x))$. Hence $(0,0)$ and $\rho(R^*, S^*)$ are the ordered lower and upper solutions of (28) by Definition 8.1.2 of (Pao 1992). It follows from the iteration process of Chapter 8.2 in the book by Pao (1992) and Theorem 8.3.1 of (Pao 1992) that (28) has a unique solution $(R(x,t,B), S(x,t,B))$ satisfies $0 < R(x,t,B) < \rho R^*, 0 < S(x,t,B) < \rho S^*$. Let $\Lambda = \{(R,S) : 0 \leq R \leq \rho R^*, 0 \leq S \leq \rho S^*\}$. Then Λ is an invariant set of the semi-dynamical system generated by the solutions of (28). Since (28) is a cooperative system, the semi-dynamical system generated by the solutions of (28) is strictly monotone. By Lemma B.5, the corresponding steady state system (24) has a unique solution $(R(x,B), S(x,B))$, which satisfies $0 < R(x,B) \leq R^*, 0 < S(x,B) \leq S^*$. Hence, $\limsup_{t\to\infty} R \leq R^*, \limsup_{t\to\infty} S \leq S^*$ by Theorem 2.2.6 of (Zhao 2003). This implies there exists $\epsilon > 0$ small such that $R \leq R^* + \epsilon,\ S \leq S^* + \epsilon$. Let $W = e^{-\frac{\nu}{D}x}B$. Then

$$\begin{aligned} e^{\frac{\nu}{D}x}W_t &= D(e^{\frac{\nu}{D}x}W_x)_x + (f(R) + g(S) - r - m)We^{\frac{\nu}{D}x} \\ &\leq D(e^{\frac{\nu}{D}x}W_x)_x + (f(R^*+\epsilon) + g(S^*+\epsilon) - r - m)We^{\frac{\nu}{D}x}. \end{aligned}$$

Noting that $m > m^* = -\lambda_1(-(f(R^*) + g(S^*)), \nu) - r$, there is ϵ small enough such that $r + m > -\lambda_1(-(f(R^*+\epsilon) + g(S^*+\epsilon)), \nu)$. Hence the comparison principle leads to $W(x,t) \to 0$ as $t \to \infty$ uniformly in $x \in [0,1]$. Thus $\lim_{t\to\infty} B(x,t) = 0$ uniformly for $x \in [0,1]$ provided $m > m_*$, which leads to $0 < B(x,t) \leq \epsilon$ for some $\epsilon > 0$. Therefore,

$$\begin{pmatrix} R \\ S \end{pmatrix}_t \geq \mathcal{L}_0 \begin{pmatrix} R \\ S \end{pmatrix} - \begin{pmatrix} f(R) - r \\ g(S) \end{pmatrix} \epsilon \geq \mathcal{L}_0 \begin{pmatrix} R \\ S \end{pmatrix} - \begin{pmatrix} f(R^*+\epsilon) - r \\ g(S^*+\epsilon) \end{pmatrix} \epsilon.$$

The comparison principle implies $(R, S) \geq (R_\epsilon, S_\epsilon)$, where (R_ϵ, S_ϵ) is the solution of

$$\begin{pmatrix} R_\epsilon \\ S_\epsilon \end{pmatrix}_t = \mathcal{L}_0 \begin{pmatrix} R_\epsilon \\ S_\epsilon \end{pmatrix} - \begin{pmatrix} f(R^*+\epsilon) - r \\ g(S^*+\epsilon) \end{pmatrix} \epsilon.$$

Obviously, $(R_\epsilon, S_\epsilon) \to (R^*, S^*)$. Hence, $(R(x,t), S(x,t), B(x,t))$ converges to $(R^*, S^*, 0)$.

We prove (ii) by making use of the abstract persistence theory (Smith and Zhao 2001). Let $\Psi(t)$ be the solution semiflow generated by the system (9) on the state space X^+. Set $X_0 := \{(R, S, B) \in X^+ : B(x) \not\equiv 0\}$ and $\partial X_0 := X^+ \backslash X_0$. Let $M_\partial := \{\Phi \in \partial X_0 : \Psi(t)\Phi \in \partial X_0, \forall t \geq 0\}$ and $\omega(\Phi)$ be the omega limit set of the forward orbit $\gamma^+(\Phi) := \{\Psi(t)\Phi : t \geq 0\}$. Then X_0 is open in X^+ and forward invariant under the dynamics generated by (9) and ∂X_0 contains the washout equilibrium $(R^*, S^*, 0)$.

We first claim that $\cup_{\Phi \in M_\partial}\omega(\Phi) \subset \{(R^*, S^*, 0)\}$. For any given $\Phi \in M_\partial$, we have $\Psi(t)\Phi \in M_\partial, \forall t \geq 0$, which implies for each $t \geq 0$, we have $B(\cdot, t, \Phi) \equiv 0$. Thus (R, S) satisfies (8). It follows from Theorem 2.1 that $\lim_{t\to\infty}(R, S) = (R^*, S^*)$ uniformly for $x \in [0, 1]$. Hence, the claim is proved.

Next, we claim that $(R^*, S^*, 0)$ is uniform weak repeller in the sense that $\limsup_{t\to\infty} \|\Psi(t)\Phi - (R^*, S^*, 0)\| \geq \delta$ for all $\Phi \in X_0$. Assume to the contrary that $(R^*, S^*, 0)$ is not a weak repeller. Then there exists such a solution satisfying $(R(x,t), S(x,t), B(x,t)) \to (R^*, S^*, 0)$ uniformly in $x \in [0, 1]$ as $t \to \infty$. Note that for $(R(x, 0), S(x, 0), B(x, 0)) \in X_0$, we have $B(x, t) > 0$ for all $t > 0$ by change of variable. Since $m < m^* = -\lambda_1(-f(R^*) - g(S^*), \nu) - r$, there is an $\epsilon > 0$ small such that $r + m < -\lambda_1(-f(R^* - \epsilon) - g(S^* - \epsilon), \nu)$. Recalling the hypothesis $(R, S, B) \to (R^*, S^*, 0)$, there exists $t_0 > 0$ such that $R^* - \epsilon < R(x, t) < R^* + \epsilon, S^* - \epsilon < S(x, t) < S^* + \epsilon, 0 < B < \epsilon$ for $t \geq t_0$. Consequently, for $t \geq t_0$, $B_t \geq DB_{xx} - \nu B_x + [f(R^* - \epsilon) + g(S^* - \epsilon) - r - m]B$. Let $W = e^{-\frac{\nu}{D}x}B$. Then for $t \geq t_0$,

$$e^{\frac{\nu}{D}x}W_t \geq D(e^{\frac{\nu}{D}x}W_x)_x + [f(R^* - \epsilon) + g(S^* - \epsilon) - r - m]We^{\frac{\nu}{D}x}, \quad W_x(0, t) = W_x(1, t) = 0.$$

Choosing $W(x, t_0) \geq \delta_1\psi^*(x, \epsilon)$, by comparison principle, $W \geq \delta_1\psi^*(x, \epsilon)e^{\lambda_\epsilon(t-t_0)}$ for $t > t_0$, where $\lambda_\epsilon = -\lambda_1(-f(R^*-\epsilon)-g(S^*-\epsilon), \nu)-r-m > 0$, and $\psi^*(x, \epsilon)$ is the associate positive eigenfunction to the eigenvalue problem (39) with $q(x) = -f(R^* - \epsilon) - g(S^* - \epsilon)$. This is a contradiction to $e^{\frac{\nu}{D}x}W(x, t) < \epsilon$. Hence, we conclude that $(R^*, S^*, 0)$ is a uniform weak repeller and $\{(R^*, S^*, 0)\}$ is an isolated invariant set in X^+.

Define a continuous function $\mathbf{p} : X^+ \to [0, \infty)$ by $\mathbf{p}(\Phi) := \min_{x\in[0,1]} \Phi_3(x)$ for any $\Phi = (\Phi_1, \Phi_2, \Phi_3) \in X^+$. It follows from the standard comparison principle that $\mathbf{p}^{-1}(0, \infty) \subseteq X_0$ and $\mathbf{p}$ satisfies that if $\mathbf{p}(\Phi) > 0$ or $\Phi \in X_0$ with $\mathbf{p}(\Phi) = 0$, then $\mathbf{p}(\Psi(t)\Phi) > 0$ for all $t > 0$. That is, $\mathbf{p}$ is a generalized distance function for the semiflow $\Psi(t) : X^+ \to X^+$ (Smith and Zhao 2001). It follows from $\cup_{\Phi\in M_\partial}\omega(\Phi) \subset \{(R^*, S^*, 0)\}$ that any forward orbit of $\Psi(t)$ in M_∂ converges to $(R^*, S^*, 0)$. Note that $\{(R^*, S^*, 0)\}$ is an isolated invariant set in X^+, and the stable set $W^s(\{(R^*, S^*, 0)\}) \cap X_0 = \emptyset$. Hence,there is no subsets of $\{(R^*, S^*, 0)\}$ forms a cycle in M_∂. Meanwhile, it follows from Lemma B.2 that $\Psi(t)$ is point dissipative on X^+, and forward orbits of bounded subsets of X^+ for $\Psi(t)$ are bounded. By Theorem 2.6 of (Magal and Zhao 2005), $\Psi(t)$ has a global attractor that attracts each bounded set in X^+. It follows from Theorem 3 of (Smith and Zhao 2001) that there exists a ϵ_0 such that for any $\Phi \in X_0$, $\min_{\Phi^0\in\omega(\Phi)} \mathbf{p}(\Phi^0) > \epsilon_0$, which implies that for any $\Phi \in X_0$, $\liminf_{t\to\infty} B(\cdot, t) \geq \epsilon_0$. The proof is completed.

C. Coexistence Results

The aim of this subsection is devoted to study coexistence solutions of the two species system (6)-(7), and to establish Theorem 2.6 by the global bifurcation theory (Crandall and Rabinowitz 1971; Du 1996). Let

$$m_1^* = -\lambda_1(-f_1(R^*) - g_1(S^*), \nu_1) - r_1, \; m_2^* = -\lambda_1(-f_2(R^*) - g_2(S^*), \nu_2) - r_2,$$

where $\lambda_1(-f_i(R^*) - g_i(S^*), \nu_i)(i = 1, 2)$ is the smallest eigenvalue corresponding to the linear eigenvalue problem (39) (or (38) equivalently) with $q(x) = -f_i(R^*) - g_i(S^*)$ and $\nu = \nu_i$. It follows from Theorem 2.3 that there are three types of nonnegative steady-state solutions to (6)-(7):

(i) washout solution $(R^*, S^*, 0, 0)$;

(ii) semi-trivial solutions: $(\bar{R}_1, \bar{S}_1, \bar{B}_1, 0)$ provided $0 < m_1 < m_1^*$; $(\bar{R}_2, \bar{S}_2, 0, \bar{B}_2)$ provided $0 < m_2 < m_2^*$;

(iii) positive solutions (R, S, B_1, B_2) with $B_1(x) > 0$ and $B_2(x) > 0$ on $[0, 1]$.

Repeating the same arguments in Lemma B.3, we obtain a priori estimates for positive solutions of (6)-(7).

Lemma C.1 *Assume $f_i(R^*) > r_i (i = 1, 2)$ and (R, S, B_1, B_2) is a nonnegative solution of (6)-(7) with $B_1 \not\equiv 0$ and $B_2 \not\equiv 0$. Then*

(i) $0 < R < R^*, 0 < S < S^*, B_1 > 0, B_2 > 0$ *in* $(0, 1)$*;*

(ii) $0 < m_1 < m_1^*, 0 < m_2 < m_2^*$*;*

(iii) *for any given $\delta > 0$, there exists a positive constant $M(\delta)$ such that every positive solution (R, S, B_1, B_2) of (6)-(7) with $m_1 \in [\delta, m_1^*), m_2 \in [\delta, m_2^*)$ satisfies $\|B_1\|_\infty + \|B_2\|_\infty \le M(\delta)$.*

It follows from Lemma C.1 that the necessary conditions for the existence of a positive solution of (6)-(7) are

$$0 < m_1 < m_1^*, 0 < m < m_2^*.$$

Next, we assume $0 < m_1 < m_1^*, 0 < m_2 < m_2^*$, and construct a positive solution of (6)-(7) by the global bifurcation theorem. Thus we need to rewrite (6)-(7) as an abstract equation related to a completely continuous operator. Let $\mathbb{X} = C([0, 1], \mathbb{R}^4)$, and $\mathbb{X}^+ = C([0, 1], \mathbb{R}^4_+)$ be the positive cone of the ordered Banach space $\mathbb{X}$.

Let $u = R^* - R, v = S^* - S, w_1 = e^{-\frac{\nu_1}{D}x} B_1, w_2 = e^{-\frac{\nu_2}{D}x} B_2$. Then the steady state system (6)-(7) is equivalent to

$$\begin{aligned}
&-(Du_{xx} + \omega_s v - \omega_r u) = (f_1(R^* - u) - r_1)e^{\frac{\nu_1}{D}x} w_1 + (f_2(R^* - u) - r_2)e^{\frac{\nu_2}{D}x} w_2, \\
&-(Dv_{xx} - \omega_s v + \omega_r u) = g_1(S^* - v)e^{\frac{\nu_1}{D}x} w_1 + g_2(S^* - v)e^{\frac{\nu_2}{D}x} w_2, \\
&-D\left(e^{\frac{\nu_1}{D}x}(w_1)_x\right)_x = [f_1(R^* - u) + g_1(S^* - v) - r_1 - m_1]e^{\frac{\nu_1}{D}x} w_1, \\
&-D\left(e^{\frac{\nu_2}{D}x}(w_2)_x\right)_x = [f_2(R^* - u) + g_2(S^* - v) - r_2 - m_2]e^{\frac{\nu_2}{D}x} w_2,
\end{aligned} \tag{29}$$

with the boundary conditions

$$-u_x(0) + \alpha u(0) = 0,\ u(1) = 0, \quad v_x(0) = 0,\ v(1) = 0, \quad (w_i)_x(0) = (w_i)_x(1) = 0, \quad i = 1, 2, \tag{30}$$

We define $\mathbb{A} : (0, +\infty) \times \mathbb{X} \to \mathbb{X}$ by

$$\mathbb{A}(m_2; u, v, w_1, w_2) = (\mathbb{A}_0(u, v, w_1, w_2), \mathbb{A}_1(u, v, w_1, w_2), \mathbb{A}_2(u, v, w_1, w_2)),$$

where

$$\begin{aligned}
\mathbb{A}_0(u, v, w_1, w_2) &= \mathbb{K}_0 \begin{pmatrix} (f_1(R^* - u) - r_1)e^{\frac{\nu_1}{D}x} w_1 + (f_2(R^* - u) - r_2)e^{\frac{\nu_2}{D}x} w_2 \\ g_1(S^* - v)e^{\frac{\nu_1}{D}x} w_1 + g_2(S^* - v)e^{\frac{\nu_2}{D}x} w_2 \end{pmatrix} \\
\mathbb{A}_1(u, v, w_1, w_2) &= \mathbb{K}_1 \left([f_1(R^* - u) + g_1(S^* - v) - r_1 - m_1]e^{\frac{\nu_1}{D}x} w_1 + M_1 w_1\right) \\
\mathbb{A}_2(u, v, w_1, w_2) &= \mathbb{K}_2 \left([f_2(R^* - u) + g_2(S^* - v) - r_2 - m_2]e^{\frac{\nu_1}{D}x} w_2 + M_2 w_2\right)
\end{aligned}$$

and $\mathbb{K}_0, \mathbb{K}_i (i = 1, 2)$ are the solution operators for the problems, respectively,

$$\begin{aligned}
&-\mathcal{L}_0(\phi_1, \phi_2)^\intercal = (h_1(x), h_2(x))^\intercal, \quad x \in (0, 1), \\
&-(\phi_1)_x(0) + \alpha\phi_1(0) = 0, \phi_1(1) = 0, \quad (\phi_2)_x(0) = 0, \phi_2(1) = 0;
\end{aligned} \tag{31}$$

$$-D\left(e^{\frac{\nu_i}{D}x} w_x\right)_x + M_i w = h(x),\ x \in (0, 1), \quad w_x(0) = w_x(1) = 0. \tag{32}$$

That is, for any given $h_1(x), h_2(x) \in C[0,1]$ and $h(x) \in C[0,1]$, $(\phi_1, \phi_2)^\intercal = \mathbb{K}_0(h_1(x), h_2(x))^\intercal$ and $w = \mathbb{K}_i(h(x))$. Here, $M_i (i = 1, 2)$ is large enough such that $(f_i(R^* - u) + g_i(S^* - v) - r_i - m_i)e^{\frac{\nu_i}{D}x} + M_i > 0$. By the application of Theorem 2.6 of (López-Gómez and Molina-Meyer 1994), we obtain that $\mathbb{K}_0$ is strongly positive compact operator when seen as an operator from $C^1([0,1], \mathbb{R}^2)$ to $C^1([0,1], \mathbb{R}^2)$ and from $L^2((0,1), \mathbb{R}^2)$ to $L^2((0,1), \mathbb{R}^2)$. Similarly, $\mathbb{K}_i (i = 1, 2)$ is strongly positive compact operator when seen as an operator from $C^1[0,1]$ to $C^1[0,1]$ and from $L^2(0,1)$ to $L^2(0,1)$. By standard elliptic regularity theory we know that $\mathbb{A} : (0, +\infty) \times \mathbb{X} \to \mathbb{X}$ is completely continuous. Let $\mathbf{U} = (u, v, w_1, w_2)^\intercal$ and $\mathbb{G}(m_2; \mathbf{U}) = \mathbf{U} - \mathbb{A}(m_2, \mathbf{U})$. Then the zeros of $\mathbb{G}(m_2; \mathbf{U}) = 0$ with $0 \le u \le R^*, 0 \le v \le S^*, w_1 \ge 0, w_2 \ge 0$ correspond to the nonnegative solutions of (29)-(30).

It follows from Theorem 2.3 that (29)-(30) have two semi-trivial solutions

$$\mathbf{U}_1 = (R^* - \bar{R}_1, S^* - \bar{S}_1, e^{-\frac{\nu_1}{D}x}\bar{B}_1, 0) \text{ and } \mathbf{U}_2 = (R^* - \bar{R}_2, S^* - \bar{S}_2, 0, e^{-\frac{\nu_2}{D}x}\bar{B}_2)$$

when $0 < m_1 < m_1^*, 0 < m_2 < m_2^*$. Next, we construct a positive solution branch $\Gamma' = \{m_2; \mathbf{U}\} \subset (0, +\infty) \times \mathbb{X}^+$ bifurcating from the semi-trivial solution branches $\Gamma_1' = \{(m_2; \mathbf{U}_1) \subset (0, +\infty) \times \mathbb{X}^+ : m_2 \in (0, +\infty)\}$ and $\Gamma_2' = \{(m_2; \mathbf{U}_2) \subset (0, +\infty) \times \mathbb{X}^+ : m_2 \in (0, +\infty)\}$. To this end, we fix $m_1 \in (0, m_1^*)$ and take m_2 as the bifurcation parameter. Introduce

$$\hat{m}_1(m_2) = -\lambda_1(-f_1(\bar{R}_2(\cdot, m_2)) - g_1(\bar{S}_2(\cdot, m_2)), \nu_1) - r_1,$$
$$\hat{m}_2(m_1) = -\lambda_1(-f_2(\bar{R}_1(\cdot, m_1)) - g_2(\bar{S}_1(\cdot, m_1)), \nu_2) - r_2,$$

where $\lambda_1(-f_1(\bar{R}_2(\cdot, m_2)) - g_1(\bar{S}_2(\cdot, m_2)), \nu_1)$ and $\lambda_1(-f_2(\bar{R}_1(\cdot, m_1)) - g_2(\bar{S}_1(\cdot, m_1)), \nu_2)$ are the smallest eigenvalues corresponding to the linear eigenvalue problem (39) (or (38) equivalently) with $q(x) = -f_1(\bar{R}_2(\cdot, m_2)) - g_1(\bar{S}_2(\cdot, m_2)), \nu = \nu_1$ and $q(x) = -f_2(\bar{R}_1(\cdot, m_1)) - g_2(\bar{S}_1(\cdot, m_1)), \nu = \nu_2$. In view of $0 < \bar{R}_1 < R^*, 0 < \bar{S}_1 < S^*$, it follows from Lemma D.1 that $0 < \hat{m}_1(m_2) < m_1^*$, $0 < \hat{m}_2(m_1) < m_2^*$.

Proof of Theorem 2.6. For any $\delta > 0$ and $m_1 \in [\delta, m_1^*)$ fixed, we construct the global bifurcation which corresponds to positive solutions by treating m_2 as a bifurcation parameter. The Fréchet derivative of $\mathbb{G}(m_2; \mathbf{U})$ with respect to $\mathbf{U}$ at $\mathbf{U}_1$ is denoted by $\mathrm{D}_{\mathbf{U}}G(m_2; \mathbf{U}_1)$. In order to apply Crandall-Rabinowitz Theorem of bifurcation from simple eigenvalue (Crandall and Rabinowitz 1971), we first show that the dimension of the null space of $\mathrm{D}_{\mathbf{U}}G(m_2; \mathbf{U}_1)$ is 1. Let $\mathrm{D}_{\mathbf{U}}G(m_2; \mathbf{U}_1)(\phi_1, \phi_2, \psi_1, \psi_2) = 0$. Then direct computation gives

$$\begin{aligned}
&\mathcal{L}_0 \begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} - \begin{pmatrix} f_1'(\bar{R}_1)\bar{B}_1\phi_1 \\ g_1'(\bar{S}_1)\bar{B}_1\phi_2 \end{pmatrix} + \begin{pmatrix} (f_1(\bar{R}_1) - r_1)e^{\frac{\nu_1}{D}x}\psi_1 + (f_2(\bar{R}_1) - r_2)e^{\frac{\nu_2}{D}x}\psi_2 \\ g_1(\bar{S}_1)e^{\frac{\nu_1}{D}x}\psi_1 + g_2(\bar{S}_1)e^{\frac{\nu_2}{D}x}\psi_2 \end{pmatrix} = 0 \\
&D(e^{\frac{\nu_1}{D}x}\psi_{1x})_x + [f_1(\bar{R}_1) + g_1(\bar{S}_1) - r_1 - m_1]e^{\frac{\nu_1}{D}x}\psi_1 - f_1'(\bar{R}_1)\bar{B}_1\phi_1 - g_1'(\bar{S}_1)\bar{B}_1\phi_2 = 0 \\
&D(e^{\frac{\nu_2}{D}x}\psi_{2x})_x + [f_2(\bar{R}_1) + g_2(\bar{S}_1) - r_2 - m_2]e^{\frac{\nu_2}{D}x}\psi_2 = 0
\end{aligned}$$

with the corresponding boundary conditions. Take $m_2 = \hat{m}_2$, $\psi_2 = \hat{\psi}_2$, which is the associated positive eigenfunction to the eigenvalue $\lambda_1(-f_2(\bar{R}_1) - g_2(\bar{S}_1), \nu_2)$. It follows from Theorem 13 of (Amann 2004) that

$$\bar{\mathcal{L}}_0 = \mathcal{L}_0 - \begin{pmatrix} f_1'(\bar{R}_1)\bar{B}_1 & 0 \\ 0 & g_1'(\bar{S}_1)\bar{B}_1 \end{pmatrix}$$

is invertible subject to the boundary conditions: $-(\phi_1)_x(0) + \alpha\phi_1(0) = 0, \phi_1(1) = 0$, $(\phi_2)_x(0) = 0, \phi_2(1) = 0$, and all eigenvalues of $\bar{\mathcal{L}}_0$ are negative. Hence

$$\begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} = -\bar{\mathcal{L}}_0^{-1}\left[\begin{pmatrix} f_1(\bar{R}_1) - r_1 \\ g_1(\bar{S}_1) \end{pmatrix} e^{\frac{\nu_1}{D}x}\psi_1\right] - \bar{\mathcal{L}}_0^{-1}\left[\begin{pmatrix} f_2(\bar{R}_1) - r_2 \\ g_2(\bar{S}_1) \end{pmatrix} e^{\frac{\nu_2}{D}x}\hat{\psi}_2\right].$$

Here $\bar{\mathcal{L}}_0^{-1}$ is the inverse operator of $\bar{\mathcal{L}}_0$ subject to the boundary conditions $-(\phi_1)_x(0) + \alpha\phi_1(0) = 0, \phi_1(1) = 0$, $(\phi_2)_x(0) = 0, \phi_2(1) = 0$. Let

$$\begin{pmatrix} \bar{\phi}_1(\psi_1) \\ \bar{\phi}_2(\psi_1) \end{pmatrix} = \bar{\mathcal{L}}_0^{-1}\left[\begin{pmatrix} f_1(\bar{R}_1) - r_1 \\ g_1(\bar{S}_1) \end{pmatrix} e^{\frac{\nu_1}{D}x}\psi_1\right]$$

and

$$\begin{pmatrix} \tilde{\phi}_1(\hat{\psi}_2) \\ \tilde{\phi}_2(\hat{\psi}_2) \end{pmatrix} = \bar{\mathcal{L}}_0^{-1}\left[\begin{pmatrix} f_2(\bar{R}_1) - r_2 \\ g_2(\bar{S}_1) \end{pmatrix} e^{\frac{\nu_2}{D}x}\hat{\psi}_2\right]$$

Putting them into the equation for ψ_1, we have

$$\begin{array}{l} D(e^{\frac{\nu_1}{D}x}\psi_{1x})_x + [f_1(\bar{R}_1) + g_1(\bar{S}_1) - r_1 - m_1]e^{\frac{\nu_1}{D}x}\psi_1 \\ \quad +(f_1'(\bar{R}_1)\bar{\phi}_1(\psi_1) + g_1'(\bar{S}_1)\bar{\phi}_2(\psi_1))\bar{B}_1 + (f_1'(\bar{R}_1)\tilde{\phi}_1(\hat{\psi}_2) + g_1'(\bar{S}_1)\tilde{\phi}_2(\hat{\psi}_2))\bar{B}_1 = 0. \end{array} \tag{33}$$

Clearly, $\bar{\phi}_1(\psi_1), \bar{\phi}_2(\psi_1)$ are differentiable with respect to ψ. Note that $\bar{\phi}_1(0) = \bar{\phi}_2(0) = 0$. Take $\|\psi_1\| = \varepsilon$ by re-scaling. Then $\bar{B}_1(f_1'(\bar{R}_1)\bar{\phi}_1(\psi_1) + g_1'(\bar{S}_1)\bar{\phi}_2(\psi_1)) = \bar{B}_1[f_1'(\bar{R}_1)((\partial_{\psi_1}\bar{\phi}_1)\psi_1 + o(\varepsilon)\psi_1) + g_1'(\bar{S}_1)((\partial_{\psi_1}\bar{\phi}_2)\psi_1 + o(\varepsilon)\psi_1)] = \bar{B}_1[f_1'(\bar{R}_1)\partial_{\psi_1}\bar{\phi}_1 + g_1'(\bar{S}_1)\partial_{\psi_1}\bar{\phi}_2 + o(\epsilon)]\psi_1$. Note that $\mathcal{L}_1 = D\frac{d}{dx}(e^{\frac{\nu_1}{D}x}\frac{d}{dx}) + [f_1(\bar{R}_1) + g_1(\bar{S}_1) - r_1 - m_1]e^{\frac{\nu_1}{D}x} + \bar{B}_1 f_1'(\bar{R}_1)\partial_{\psi_1}\bar{\phi}_1 + g_1'(\bar{S}_1)\partial_{\psi_1}\bar{\phi}_2)$ is invertible. Hence $\psi_1 = \hat{\psi}_1$ can be solved by (33) uniquely, which implies the null space of $\mathrm{D}_{\mathbf{U}}G(\hat{m}_2; \mathbf{U}_1)$ is spanned by $(\hat{\phi}_1, \hat{\phi}_2, \hat{\psi}_1, \hat{\psi}_2)$. Here

$$\begin{pmatrix} \hat{\phi}_1 \\ \hat{\phi}_2 \end{pmatrix} = -\bar{\mathcal{L}}_0^{-1}\left[\begin{pmatrix} f_1(\bar{R}_1) - r_1 \\ g_1(\bar{S}_1) \end{pmatrix} e^{\frac{\nu_1}{D}x}\hat{\psi}_1\right] - \bar{\mathcal{L}}_0^{-1}\left[\begin{pmatrix} f_2(\bar{R}_1) - r_2 \\ g_2(\bar{S}_1) \end{pmatrix} e^{\frac{\nu_2}{D}x}\hat{\psi}_2\right].$$

Direct computation leads to that the range of $\mathrm{D}_{\mathbf{U}}G(\hat{m}_2; \mathbf{U}_1)$ is

$$\{\mathbf{U} = (u, v, w_1, w_2) \in \mathbb{X} : \int_0^1 [(f_2(\bar{R}_1) + g_2(\bar{S}_1) - r_2 - \hat{m}_2)e^{\frac{\nu_2}{D}x} + M_2]\hat{\psi}_2 w_2 dx = 0\}.$$

By virtue of $\mathbb{K}_2(e^{\frac{\nu_2}{D}x}\hat{\psi}_2) > 0$, we have

$$\int_0^1 \mathbb{K}_2(e^{\frac{\nu_2}{D}x}\hat{\psi}_2)[(f_2(\bar{R}_1) + g_2(\bar{S}_1) - r_2 - \hat{m}_2)e^{\frac{\nu_2}{D}x} + M_2]\hat{\psi}_2 dx > 0$$

Hence, $\mathrm{D}^2_{m_2\mathbf{U}}G(\hat{m}_2; \mathbf{U}_1)(\hat{\phi}_1, \hat{\phi}_2, \hat{\psi}_1, \hat{\psi}_2) = (0, 0, 0, \mathbb{K}_2(e^{\frac{\nu_2}{D}x}\hat{\psi}_2))$ does not belong to the range of $\mathrm{D}_{\mathbf{U}}G(\hat{m}_2; \mathbf{U}_1)$. By application of the bifurcation theorem from a simple eigenvalue (Crandall and Rabinowitz 1971), there exists a $\tau_0 > 0$ and C^1 function $(m_2(\tau), R(\tau), S(\tau), B_1(\tau), B_2(\tau))$: $(-\tau_0, \tau_0) \mapsto (-\infty, +\infty) \times \mathbb{X}$ such that $m(0) = \hat{m}_2, R(0) = \bar{R}_1, S(0) = \bar{S}_1, B_1(0) = \bar{B}_1, B_2(0) = 0$ and $(m_2, R(\tau), S(\tau), B_1(\tau), B_2(\tau)) = (m_2(\tau), \bar{R}_1 + \tau(\hat{\phi}_1 + U(\tau)), \bar{S}_1 + \tau(\hat{\phi}_2 + V(\tau)), \bar{B}_1 + \tau(\hat{\psi}_1 + \omega_1(\tau)), \tau(\hat{\psi}_2 + \omega_2(\tau)))(|\tau| < \tau_0)$, which is the solution of the steady state system (6)-(7). If we take $0 < \tau < \tau_0$, this bifurcation branch is just the positive solution of the steady state system (6)-(7).

Next, we extend the local bifurcation to the global one. Suppose $\lambda \geq 1$ is an eigenvalue of $\mathrm{D}_{\mathbf{U}}\mathbb{A}(m_2; \mathbf{U}_1)$ with the corresponding eigenfunction $(\phi_1, \phi_2, \psi_1, \psi_2)$. Then

$$\begin{array}{l} \lambda\mathcal{L}_0\begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} + \begin{pmatrix} -f_1'(\bar{R}_1)\bar{B}_1\phi_1 + (f_1(\bar{R}_1) - r_1)e^{\frac{\nu_1}{D}x}\psi_1 + (f_2(\bar{R}_1) - r_2)e^{\frac{\nu_2}{D}x}\psi_2 \\ -g_1'(\bar{S}_1)\bar{B}_1\phi_2 + g_1(\bar{S}_1)e^{\frac{\nu_1}{D}x}\psi_1 + g_2(\bar{S}_1)e^{\frac{\nu_2}{D}x}\psi_2 \end{pmatrix} = 0, \\ \lambda D(e^{\frac{\nu_1}{D}x}\psi_{1x})_x + (1-\lambda)M_1\psi_1 + [f_1(\bar{R}_1) + g_1(\bar{S}_1) - r_1 - m_1]e^{\frac{\nu_1}{D}x}\psi_1 \\ \qquad -f_1'(\bar{R}_1)\bar{B}_1\phi_1 - g_1'(\bar{S}_1)\bar{B}_1\phi_2 = 0, \\ D(e^{\frac{\nu_2}{D}x}\psi_{2x})_x + M_2(-1 + \frac{1}{\lambda})\psi_2 + \frac{1}{\lambda}(f_2(\bar{R}_1) + g_2(\bar{S}_1) - r_2 - m_2)e^{\frac{\nu_2}{D}x}\psi_2 = 0 \end{array} \tag{34}$$

with the boundary conditions (30). Claim that $\psi_2 \not\equiv 0$. If not, then $\psi_2 \equiv 0$, similar arguments lead to

$$\bar{\mathcal{L}}_\lambda = \mathcal{L}_0 - \frac{1}{\lambda}\begin{pmatrix} f_1'(\bar{R}_1)\bar{B}_1 & 0 \\ 0 & g_1'(\bar{S}_1)\bar{B}_1 \end{pmatrix}$$

is invertible subject to the boundary conditions: $-(\phi_1)_x(0) + \alpha\phi_1(0) = 0, \phi_1(1) = 0,\ (\phi_2)_x(0) = 0, \phi_2(1) = 0$, and all eigenvalues of $\bar{\mathcal{L}}_\lambda$ are negative. Hence

$$\begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} = -\bar{\mathcal{L}}_\lambda^{-1}\left[\frac{1}{\lambda}\begin{pmatrix} f_1(\bar{R}_1) - r_1 \\ g_1(\bar{S}_1) \end{pmatrix} e^{\frac{\nu_1}{D}x}\psi_1\right].$$

Substituting (ϕ_1, ϕ_2) into the equation for ψ_1 in (34), we have $\psi_1 \equiv 0$ by similar arguments as above, which leads to $\phi_1 = \phi_2 \equiv 0$. This is a contradiction. Hence $\psi_2 \not\equiv 0$. Noting that $\bar{\mathcal{L}}_\lambda$ is invertible, similar arguments as above deduce that ϕ_1, ϕ_2 and ψ_1 can be determined by (34) uniquely. Hence, $\lambda \geq 1$ is an eigenvalue of $\mathrm{D}_{\mathbf{U}}\mathbb{A}(m_2; \mathbf{U}_1)$ if and only if $\lambda \geq 1$ satisfies

$$\begin{aligned}
&D(e^{\frac{\nu_2}{D}x}\psi_{2x})_x + M_2(-1 + \tfrac{1}{\lambda})\psi_2 + \tfrac{1}{\lambda}(f_2(\bar{R}_1) + g_2(\bar{S}_1) - r_2 - m_2)e^{\frac{\nu_2}{D}x}\psi_2 = 0,\\
&\psi_{2x}(0) = \psi_{2x}(1) = 0.
\end{aligned}$$

That is, $\lambda \geq 1$ is an eigenvalue of $\mathrm{D}_{\mathbf{U}}\mathbb{A}(m_2; \mathbf{U}_1)$ if and only if $\frac{1}{\lambda}(0 < \frac{1}{\lambda} \leq 1)$ is an eigenvalue of

$$\begin{aligned}
&-D(e^{\frac{\nu_2}{D}x}\psi_{2x})_x + M_2\psi_2 = \sigma[(f_2(\bar{R}_1) + g_2(\bar{S}_1) - r_2 - m_2)e^{\frac{\nu_2}{D}x} + M_2]\psi_2,\\
&\psi_{2x}(0) = \psi_{2x}(1) = 0.
\end{aligned} \tag{35}$$

If $m_2 > \hat{m}_2$, then $\lambda_1(-f_2(\bar{R}_1) - g_2(\bar{S}_1) + r_2 + m_2, \nu_2) > 0$. It follows from Lemma D.4 that the eigenvalue problem (35) has no eigenvalue less than or equal to 1, which leads to $\mathrm{D}_{\mathbf{U}}\mathbb{A}(m_2; \mathbf{U}_1)$ has no eigenvalue $\lambda > 1$. Thus index$(\mathbb{A}(m_2; \mathbf{U}), \mathbf{U}_1) = 1$.

On the other hand, in view of $f_2(\bar{R}_1) + g_2(\bar{S}_1) - r_2 - m_2 + M_2 > 0$, it is easy to check that all eigenvalues $\sigma_i(m_2)$ of (35) are real and strictly increasing with respect to m_2, and can be ordered as $0 < \sigma_1(m_2) < \sigma_2(m_2) \leq \sigma_3(m_2) \leq \cdots$ with $\sigma_1(\hat{m}_2) = 1$(cf. Courant and Hilbert 1953). Hence, for $\hat{m}_2 - \epsilon < m_2 < \hat{m}_2$, one can find that $0 < \sigma_1(m_2) < \sigma_1(\hat{m}_2) = 1$ and $\sigma_2(\hat{m}_2) > \sigma_1(\hat{m}_2) = 1$. The continuity of $\sigma_2(m_2)$ leads to $\sigma_2(m_2) > \sigma_2(\hat{m}_2 - \epsilon) > 1$ as long as ϵ is small enough. Thus $\sigma_1(m_2)$ is the unique eigenvalue of (35), which is less than 1, and (35) has exactly one nontrivial solution (up to a multiplicative constant), denoted by $\tilde{\psi}_2$, whenever $m_2 < \hat{m}_2$ is close enough to $\hat{m}_2$. This establishes that $\mathrm{D}_{\mathbf{U}}\mathbb{A}(m_2; \mathbf{U}_1)$ has a unique eigenvalue $\lambda_0 = \frac{1}{\sigma_1(m_2)} > 1$.

Next, we can show that

$$N(\lambda_0 I - \mathrm{D}_{\mathbf{U}}\mathbb{A}(m_2; \mathbf{U}_1)) \cap R(\lambda_0 I - \mathrm{D}_{\mathbf{U}}\mathbb{A}(m_2; \mathbf{U}_1)) = \{0\},$$

which implies the algebraic multiplicity of the eigenvalue λ_0 is one. If not, without loss of generality, we may assume that $(\phi_1, \phi_2, \psi_1, \tilde{\psi}_2) \in R(\lambda_0 I - \mathrm{D}_{\mathbf{U}}\mathbb{A}(m_2; \mathbf{U}_1))$, where $(\phi_1, \phi_2, \psi_1, \tilde{\psi}_2)$ satisfies (34) with $\lambda = \lambda_0$. Then there exists $(\Phi_1, \Phi_2, \Psi_1, \Psi_2) \in \mathbb{X}$ such that

$$\begin{aligned}
&\lambda_0 D(e^{\frac{\nu_2}{D}x}\Psi_{2x})_x - M_2(\lambda_0 - 1)\Psi_2 + (f_2(\bar{R}_1) + g_2(\bar{S}_1) - r_2 - m_2)e^{\frac{\nu_2}{D}x}\Psi_2\\
&\qquad = D(e^{\frac{\nu_2}{D}x}\tilde{\psi}_{2x})_x - M_2\tilde{\psi}_2,\\
&\Psi_{2x}(0) = \Psi_{2x}(1) = 0.
\end{aligned} \tag{36}$$

Meanwhile, note that $\lambda_0 = \frac{1}{\sigma_1(m_2)}$, $\tilde{\psi}_2 \neq 0$ and

$$\begin{aligned}
&-D(e^{\frac{\nu_2}{D}x}\tilde{\psi}_{2x})_x + M_2\tilde{\psi}_2 = \sigma_1(m_2)[(f_2(\bar{R}_1) + g_2(\bar{S}_1) - r_2 - m_2)e^{\frac{\nu_2}{D}x} + M_2]\tilde{\psi}_2,\\
&\tilde{\psi}_{2x}(0) = \tilde{\psi}_{2x}(1) = 0.
\end{aligned} \tag{37}$$

Multiplying (36) by $\tilde{\psi}_2$ and (37) by Ψ_2, and integrating over (0, 1) by parts, we obtain

$$-D\int_0^1 e^{\frac{\nu_2}{D}x}\tilde{\psi}_{2x}^2 dx - M_2\int_0^1 \tilde{\psi}_2^2 dx = 0,$$

a contradiction. Hence, λ_0 is the unique eigenvalue of $\mathrm{D}_{\mathbf{U}}\mathbb{A}(m_2; \mathbf{U}_1)$ greater than 1. Moreover, its algebraic multiplicity is one. This gives index$(\mathbb{A}(m_2; \mathbf{U}), \mathbf{U}_1) = -1$.

By the global bifurcation theorem (see Theorem 2.1 of (Du 1996)), the local bifurcation given as above can be extended to a continuum Γ, satisfying one of the alternative: (i) meets $(\bar{m}_2, \bar{R}_1, \bar{S}_1, \bar{B}_1, 0)$ at $\bar{m}_2 \neq \hat{m}_2$; (ii) joins $(\hat{m}_2, \bar{R}_1, \bar{S}_1, \bar{B}_1, 0)$ to ∞ in $(-\infty, +\infty) \times \mathbb{X}$.

Suppose (i) holds. Then we can find a sequence of points $(m_2^{(n)}, R_n, S_n, B_1^{(n)}, B_2^{(n)}) \in (0, m_2^*) \times \mathbb{X}^+$ with $R_n, S_n, B_1^{(n)}, B_2^{(n)} > 0$ on $[0, 1]$, which converges to $(\bar{m}_2, \bar{R}_1, \bar{S}_1, \bar{B}_1, 0)$ in $(0, +\infty) \times \mathbb{X}$. It follows from the equation for $B_2^{(n)}$, we have

$$-m_2^{(n)} = \lambda_1(-f_2(R_n) - g_2(S_n), \nu_2) + r_2 \to \lambda_1(-f_2(\bar{R}_1) - g_2(\bar{S}_1), \nu_2) + r_2 = -\hat{m}_2.$$

Hence, $\bar{m}_2 = \hat{m}_2$, a contradiction. Thus (i) can not occur.

It follows from Lemma B.3 that $0 < R < R^*, 0 < S < S^*, B_1 > 0, B_2 > 0$, and $\|B_1\|_\infty + \|B_2\|_\infty \le M$ for $m_1 \in [\delta, m_1^*), m_2 \in [\delta, m_2^*)$ and any $\delta > 0$. By L^p estimate and Sobolev embedding theorem, we can claim that $\|R\|, \|S\|, \|B_1\|, \|B_2\|$ are bounded. So Γ is bounded in $[\delta, m_2^*) \times \mathbb{X}^+$. Since (ii) holds, one can claim that the global bifurcation branch Γ must meet the boundary of $[\delta, m_2^*) \times \mathbb{X}^+$. Thus $\Gamma - \{(\hat{m}_2, \bar{R}_1, \bar{S}_1, \bar{B}_1, 0)\} \not\subseteq \mathbb{X}^+$ or Γ contains a point $(m_2, R, S, B_1, B_2) \in [\delta, m_2^*) \times \mathbb{X}^+$ with $m_2 = \delta$, or $m_2 = m_2^*$.

Suppose there exist $m_2^{(n)} \to m_2^*-$ and positive solution $(R_n, S_n, B_1^{(n)}, B_2^{(n)})$ of (6)-(7) with $m_2 = m_2^{(n)}$. Let $\hat{B}_i^{(n)} = \frac{B_i^n}{\|B_i^n\|_\infty}$. Since $0 \le f_i(R_n) + g_i(S_n) \le f_i(R^*) + g_i(S^*)(i = 1, 2)$, we can assume $f_i(R_n) + g_i(S_n) \to F_i(x)$ weakly in $L^2(0, 1)$. Here $0 \le F_i(x) \le f_i(R^*) + g_i(S^*)$. Then

$$\begin{aligned} &D(\hat{B}_2^{(n)})_{xx} - \nu_2(\hat{B}_2^{(n)})_x + [f_2(R_n) + g_2(S_n) - r_2 - m_2^{(n)}]\hat{B}_2^{(n)} = 0, \quad x \in (0, 1),\\ &D(\hat{B}_2^{(n)})_x(0) - \nu_2\hat{B}_2^{(n)}(0) = 0, \quad D(\hat{B}_2^{(n)})_x(1) - \nu_2\hat{B}_2^{(n)}(1) = 0. \end{aligned}$$

Integrating the above equation from 0 to x, we obtain

$$D(\hat{B}_2^{(n)})_x(x) - \nu_2\hat{B}_2^{(n)}(x) + \int_0^x (f_2(R_n) + g_2(S_n) - r_2 - m_2^{(n)})\hat{B}_2^{(n)}dx = 0,$$

which indicates $(\hat{B}_2^{(n)})_x(x)$ is uniformly bounded since $0 < R_n < R^*, 0 < S_n < S^*$ and $\|\hat{B}_2^{(n)}\|_\infty = 1$. Hence, $(\hat{B}_2^{(n)})_{xx}$ is uniformly bounded. Passing to a sequence if necessary, we may assume $\hat{B}_2^{(n)} \to \hat{B}_2$ in $C^1[0, 1]$, and $\hat{B}_2$ is a weak solution to

$$\begin{aligned} &D(\hat{B}_2)_{xx} - \nu_2(\hat{B}_2)_x + (F_2(x) - r_2 - m_2^*)\hat{B}_2 = 0, \quad x \in (0, 1),\\ &D(\hat{B}_2)_x(0) - \nu_2\hat{B}_2(0) = 0, \quad D(\hat{B}_2)_x(1) - \nu_2\hat{B}_2(1) = 0. \end{aligned}$$

Here $0 \le F_2(x) \le f_2(R^*) + g_2(S^*)$. It follows from the strong maximum principle that $\hat{B}_2 > 0$. Moreover, $r_2 + m_2^* = -\lambda_1(-F_2(x), \nu_2) \le -\lambda_1(-f_2(R^*) - g_2(S^*), \nu_2) = m_2^* + r_2$. The equality holds if and only if $F_2(x) = f_2(R^*) + g_2(S^*)$. Similar arguments lead to $\hat{B}_1^{(n)} \to \hat{B}_1$ in $C^1[0, 1]$, and $\hat{B}_1$ satisfies

$$\begin{aligned} &D(\hat{B}_1)_{xx} - \nu_1(\hat{B}_1)_x + \hat{B}_1(F_1(x) - r_1 - m_1) = 0, \quad x \in (0, 1),\\ &D(\hat{B}_1)_x(0) - \nu_1\hat{B}_1(0) = 0, \; D(\hat{B}_1)_x(1) - \nu_1\hat{B}_1(1) = 0, \end{aligned}$$

where $0 \le F_1(x) \le f_1(R^*) + g_1(S^*)$. By the strong maximum principle, we have $\hat{B}_1 > 0$. Hence, $r_1 + m_1 = -\lambda_1(-F_1(x), \nu_1) \le -\lambda_1(-f_1(R^*) - g_1(S^*), \nu_1) = m_1^* + r_1$. Note that $f_i(R_n) + g_i(S_n) \to F_i(x)$ weakly in $L^2(0, 1)$, $F_2(x) = f_2(R^*) + g_2(S^*)$, and a priori estimates $0 \le R_n \le R^*, \; 0 \le S_n \le S^*$. It follows from the monotonicity of $f_i(R), g_i(S)$ that $F_1(x) = f_1(R^*) + g_1(S^*)$, which deduce $m_1 = m_1^*$, a contradiction.

Suppose there exist $m_2^{(n)} \to 0+$ and positive solution $(R_n, S_n, B_1^{(n)}, B_2^{(n)})$ of (6)-(7) with $m_2 = m_2^{(n)}$. At first, we show $\|B_2^{(n)}\|_\infty \to \infty$. If not, it follows from Lemma C.1 and (6)-(7) with $(R, S, B_1, B_2) = (R_n, S_n, B_1^{(n)}, B_2^{(n)})$ and $m_2 = m_2^{(n)}$ that $(R_n)_{xx}, (S_n)_{xx}, (B_1^{(n)})_{xx}, (B_2^{(n)})_{xx}$ are uniformly bounded. By L^p estimates and Sobolev embedding theorem, we may assume by passing to a subsequence that $R_n \to R$, $S_n \to S$, $B_1^{(n)} \to B_1$, $B_2^{(n)} \to B_2$ in $C^1[0, 1]$, and (R, S, B_1, B_2) is a weak solution to (6)-(7) with $m_2 = 0$. Let $\hat{B}_2^{(n)} = \frac{B_2^n}{\|B_2^n\|_\infty}$. Similar arguments lead to $\hat{B}_2^{(n)} \to \hat{B}_2$ in $C^1[0, 1]$, and $\hat{B}_2$ satisfies

$$\begin{aligned} &D(\hat{B}_2)_{xx} - \nu_2(\hat{B}_2)_x + \hat{B}_2(f_2(R) + g_2(S) - r_2) = 0,\\ &D(\hat{B}_2)_x(0) - \nu_2\hat{B}_2(0) = 0, \; D(\hat{B}_2)_x(1) - \nu_2\hat{B}_2(1) = 0. \end{aligned}$$

respectively. It follows from the strong maximum principle that $\hat{B}_2 > 0$. Integrating the equation for $\hat{B}_2$ over $[0, 1]$, we deduce $\int_0^1 (f_2(R) - r_2 + g_2(S))\hat{B}_2 dx = 0$, which implies $f_2(R) - r_2 + g_2(S) = 0$

a.e in $(0,1)$ by Lemma C.1. It follows that $S \equiv 0$ in $[0,1]$, a contradiction. Hence, $\|B_2^{(n)}\|_\infty \to \infty$. By the same reasoning as in the proof of Lemma B.3, for given $B_1^{(n)}, B_2^{(n)} > 0$, we can show that the following problem

$$\begin{aligned}
&D(R_n)_{xx} + \omega_s S_n - \omega_r R_n - (f_1(R_n) - r_1)B_1^{(n)} - (f_2(R_n) - r_2)B_2^{(n)} = 0,\\
&D(S_n)_{xx} - \omega_s S_n + \omega_r R_n - g_1(S_n)B_1^{(n)} - g_2(S_n)B_2^{(n)} = 0,\\
&-(R_n)_x(0) + \alpha R_n(0) = \alpha \hat{R},\ R_n(1) = R^0, \quad (S_n)_x(0) = 0,\ S_n(1) = S^0.
\end{aligned}$$

has a unique solution $(R_n(x, B_1, B_2), S_n(x, B_1, B_2))$, which satisfies $f_i(R_n) - r_i \to 0$ and $g_i(S_n) \to 0$ a.e. in (0, 1) by similar arguments as in Lemma B.3. Noting that the equation for $B_1^{(n)}$, we have $-m_1 = \lambda_1(-f_1(R_n) + r_1 - g_1(S_n))$. Letting $n \to \infty$, we get $m_1 = 0$, a contradiction.

Suppose $\Gamma - \{(\hat{m}_2, \bar{R}_1, \bar{S}_1, \bar{B}_1, 0)\} \not\subseteq \mathbb{X}^+$. Then we can find a sequence of points

$$(m_2^{(n)}, R_n, S_n, B_1^{(n)}, B_2^{(n)}) \in \Gamma \cap \mathbb{X}^+ \text{ with } R_n, S_n, B_1^{(n)}, B_2^{(n)} > 0 \text{ on } [0,1],$$

which converges to $(\underline{m}_2, \underline{R}, \underline{S}, \underline{B}_1, \underline{B}_2) \in (\Gamma - \{(\hat{m}_2, \bar{R}_1, \bar{S}_1, \bar{B}_1, 0)\}) \cap \partial\mathbb{X}^+$ in $(0, +\infty) \times \mathbb{X}$. Since $(\underline{R}, \underline{S}, \underline{B}_1, \underline{B}_2) \in \partial\mathbb{X}^+$ and $\underline{R}, \underline{S} > 0$, we obtain that either $\underline{B}_1 \geq 0, \underline{B}_1(x_0) = 0$ for some point $x_0 \in [0,1]$ or $\underline{B}_2 \geq 0, \underline{B}_2(x_0) = 0$ for some point $x_0 \in [0,1]$. By the maximum principle, we have $\underline{B}_1 \equiv 0$ if $\underline{B}_1(x_0) = 0$ for some point $x_0 \in [0,1]$. Similarly, we can show $\underline{B}_2 \equiv 0$ for the other case. Therefore, we have the following alternatives: (a)$(\underline{R}, \underline{S}, \underline{B}_1, \underline{B}_2) \equiv (R^*, S^*, 0, 0)$; (b)$(\underline{R}, \underline{S}, \underline{B}_1, \underline{B}_2) \equiv (\bar{R}_1, \bar{S}_1, \bar{B}_1, 0)$; (c)$(\underline{R}, \underline{S}, \underline{B}_1, \underline{B}_2) \equiv (\bar{R}_2, \bar{S}_2, 0, \bar{B}_2)$.

If $(m_2^{(n)}, R_n, S_n, B_1^{(n)}, B_2^{(n)}) \to (\bar{m}_2, R^*, S^*, 0, 0)$, then $m_1 = -\lambda_1(-f_1(R_n) - g_1(S_n)) - r_1 \to m_1^*$, contradicting $m_1 \in [\delta, m_1^*)$. If $(m_2^{(n)}, R_n, S_n, B_1^{(n)}, B_2^{(n)}) \to (\bar{m}_2, \bar{R}_1, \bar{S}_1, \bar{B}_1, 0)$, $-m_2^{(n)} = \lambda_1(-f_2(R_n) - g_2(S_n), \nu_2) + r_2 \to \lambda_1(-f_2(\bar{R}_1) - g_2(\bar{S}_1), \nu_2) + r_2 = -\hat{m}_2$. Hence, $\bar{m}_2 = \hat{m}_2$, a contradiction. Therefore, (c) necessarily happens and the global bifurcation Γ must meet the semi-trivial branch Γ_2 at the point $(\tilde{m}_2, \bar{R}_2, \bar{S}_2, 0, \bar{B}_2)$, that is, $\Gamma \cap \Gamma_2 = \{(\tilde{m}_2, \bar{R}_2, \bar{S}_2, 0, \bar{B}_2)\}$. Hence there exists a sequence $(m_2^{(n)}, R_n, S_n, B_1^{(n)}, B_2^{(n)}) \to (\tilde{m}_2, \bar{R}_2, \bar{S}_2, 0, \bar{B}_2)$. By the equation for $B_1^{(n)}$, we have $m_1 = -\lambda_1(-f_1(R_n) - g_1(S_n), \nu_1) - r_1$. Taking the limit, we get $m_1 = -\lambda_1(-f_1(\bar{R}_2(\tilde{m}_2)) - g_1(\bar{S}_2(\tilde{m}_2)), \nu_1) - r_1$. Namely, $\tilde{m}_2$ is determined by $m_1 = -\lambda_1(-f_1(\bar{R}_2(\tilde{m}_2)) - g_1(\bar{S}_2(\tilde{m}_2)), \nu_1) - r_1$. The proof is completed.

D. Some Well-known Lemmas

Finally, we state some well-known lemmas as appendix without proof, which is useful for obtaining the main results in this paper.

Consider the linear eigenvalue problem

$$\begin{aligned}
&-D\varphi_{xx} + \nu\varphi_x + q(x)\varphi = \lambda\varphi, \quad 0 < x < 1\\
&D\varphi_x(0) - \nu\varphi(0) = 0, \quad D\varphi_x(1) - \nu\varphi(1) = 0,
\end{aligned} \tag{38}$$

where $q(x)$ is a continuous function in [0, 1], D, ν are positive constants. Let $\psi = e^{-\frac{\nu}{D}x}\varphi(x)$. Then ψ satisfies

$$\begin{aligned}
&-D\left(e^{\frac{\nu}{D}x}\psi_x\right)_x + q(x)e^{\frac{\nu}{D}x}\psi = \lambda e^{\frac{\nu}{D}x}\psi, \quad 0 < x < 1\\
&\psi_x(0) = \psi_x(1) = 0.
\end{aligned} \tag{39}$$

Lemma D.1 (Courant and Hilbert 1953; Hsu and Lou 2010) *All eigenvalues of (39) are real, and the smallest eigenvalue $\lambda_1(q(x), \nu)$ can be characterized as*

$$\lambda_1(q(x), \nu) = \inf_{\psi \neq 0, \psi \in H^1(0,1)} \frac{\int_0^1 e^{\frac{\nu}{D}x}(D\psi_x^2 + q(x)\psi^2)dx}{\int_0^1 e^{\frac{\nu}{D}x}\psi^2 dx},$$

which corresponds to a positive eigenfunction ψ_1, and $\lambda_1(q(x), \nu)$ is the only eigenvalue whose corresponding eigenfunction does not change sign. Moreover,

(i) $q_1(x) \geq q_2(x)$ *implies* $\lambda_1(q_1(x),\nu) \geq \lambda_1(q_2(x),\nu)$, *and the equality holds only if* $q_1(x) \equiv q_2(x)$*;*

(ii) $q_n(x) \to q(x)$ *in* $C[0,1]$ *implies* $\lambda_1(q_n(x),\nu) \to \lambda_1(q(x),\nu)$.

Lemma D.2 (Parabolic Harnack inequality) (Evans 1998). *Let* $\Omega \subset \mathbb{R}^n$ *be an open set,* $Q_T = \Omega \times (0,T]$ *and*

$$Lu = -\sum_{i,j=1}^{n} a_{ij}(x)u_{x_ix_j} + \sum_{i=1}^{n} b_i(x)u_{x_i} + c(x)u,$$

where the coefficients $a_{ij}(x), b_i(x), c(x)$ *are continuous, and* $-L$ *is uniformly elliptic in* Ω. *Assume* $u \in C^{2,1}(Q_T)$ *solves* $u_t + Lu = 0$ *in* Q_T, *and* $u \geq 0$ *in* Q_T. *Suppose* $K \subset\subset \Omega$ *is connected. Then for each* $0 < t_1 < t_2 \leq T$, *there exists a constants* C *such that*

$$\sup_K u(\cdot,t_1) \leq C \inf_K u(\cdot,t_2).$$

The constant C *depends only on* K, t_1, t_2, *and the coefficients* $a_{ij}(x), b_i(x), c(x)$.

Lemma D.3 (Dancer 1983; Dancer 1984) *Let* $F: W \to W$ *be a compact, continuously differentiable operator,* W *be a cone in the Banach space* E *with zero* Θ. *Suppose that* $W - W$ *is dense in* E *and that* $\Theta \in W$ *is a fixed point of* F *and* $A_0 = F'(\Theta)$. *Then the following results hold:*

(i) $\mathrm{index}_W(F,\Theta) = 1$ *if* $r(A_0) < 1$*;*

(ii) $\mathrm{index}_W(F,\Theta) = 0$ *if* A_0 *has eigenvalue greater than 1 and* Θ *is an isolated solution of* $x = F(x)$, *that is* $h \neq A_0 h$ *if* $h \in \overline{W} - \Theta$.

Lemma D.4 (Wang 2010) *Let* Ω *is a bounded domain in* $\mathbb{R}^n$ *with boundary surface* $\partial\Omega \in C^{2+\gamma}$, $q(x) \in C(\overline{\Omega})$ *and* P *be a positive constant such that* $P - q(x) > 0$ *on* $\overline{\Omega}$. *Let* $\lambda_1(q(x))$ *be the principal eigenvalue of the eigenvalue problem*

$$-\sum_{i,j=1}^{n} \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i\varphi) + q(x)\varphi = \lambda\varphi, x \in \Omega, \quad \sum_{i,j=1}^{n} a_{ij}(x)\mathrm{D}_i\varphi\cos(\varpi, x_j) + b(x)\varphi = 0, x \in \partial\Omega,$$

where $a_{i,j}(x), b(x) \in C(\partial\Omega)$, $b(x) \geq 0$, *and* ϖ *is the outward unit normal vector on* $\partial\Omega$. *Then the following conclusions hold*

(i) if $\lambda_1(q(x)) < 0$ then the spectral radius $r[(P - \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i))^{-1}(P - q(x))] > 1$;

(ii) if $\lambda_1(q(x)) > 0$ then the spectral radius $r[(P - \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i))^{-1}(P - q(x))] < 1$;

(iii) if $\lambda_1(q(x)) = 0$ then the spectral radius $r[(P - \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i))^{-1}(P - q(x))] = 1$.

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