ON A NONLOCAL REACTION-DIFFUSION PROBLEM ARISING FROM THE MODELING OF PHYTOPLANKTON GROWTH

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ABSTRACT. In this paper we analyze a nonlocal reaction-diffusion model which arises from the modeling of competition of phytoplankton species with incomplete mixing in a water column. The nonlocal nonlinearity in the model describes the light limitation for the growth of the phytoplankton species. We first consider the single species case and obtain a complete description of the long-time dynamical behavior of the model. Then we study the two species competition model and obtain sufficient conditions for the existence of positive steady states and uniform persistence of the dynamical system. Our approach is based on a new modified comparison principle, fixed point index theory, global bifurcation arguments, elliptic and parabolic estimates, and various analytical techniques.

1. INTRODUCTION

In this paper we analyze a reaction-diffusion model which describes the growth of phytoplankton species in a eutrophic environment. In such environments there are ample nutrients and the phytoplankton species typically compete for light. In [16, 17, 25] Huisman and Weissing developed a theory of interspecific competition for light that assumes complete mixing of phytoplankton species. This theory is based on a system of ordinary differential equations and predicts that complete mixing leads to competitive exclusion similar to that in [13, 1, 23], namely the species with the lowest "critical light intensity" wins the competition.

However, in many aquatic environments, phytoplankton species are not thoroughly mixed. To understand the effect of incomplete mixing on the growth of phytoplankton species in a eutrophic environment, Huisman et al. [18] introduced a reaction-diffusion model, and analyzed the model through numerical simulations. But a thorough mathematical treatment of the model has been lacking. The purpose of this paper is to prove some basic mathematical facts for this

model, which provide a basis for further rigorous mathematical analysis of the involved reaction-diffusion system. Our uniform persistence result indicates that with incomplete mixing of the phytoplankton species, competitive exclusion does not always happen, and coexistence can occur in some parameter ranges.

The model of [18] is one among many mathematical models of phytoplankton proposed and investigated in recent years, see [20, 9, 14, 10, 15, 21, 26] and the references therein for related study on the formation of phytoplankton blooms from the mathematical, experimental and numerical viewpoints. It is our hope that some of the mathematical theory and techniques developed here for treating the model of [18] can also find applications in the study of other phytoplankton models. Some closely related mathematical research to this paper is mentioned at the end of this section with more detail.

We now briefly describe the model of [18]. Consider a water column with a cross section of one unit area and with n phytoplankton species. Let x denote the depth within the water column where x runs from 0 (top) to L (bottom). And let $u_i(x,t)$ denote the population density (numbers per unit volume) of a phytoplankton species i at depth x and time t. The rate of changes in phytoplankton densities is described by the following system of reaction-diffusion equations:

$$(1.1) \qquad (u_i)_t = D_i(u_i)_{xx} + (g_i(I(x,t)) - d_i)u_i, \ i = 1, 2, ..., n,$$

where $g_i(I(x,t))$ is the specific growth rate of phytoplankton species i as a function of light intensity $I(x,t)$, D_i is the diffusion coefficient and d_i is the loss rate of the phytoplankton species i. Assume that the water column is closed, with no phytoplankton species entering or leaving the column at the top or the bottom. Thus the following boundary conditions are satisfied:

$$(1.2) \qquad (u_i)_x(0,t) = (u_i)_x(L,t) = 0, \ i = 1, 2, ..., n.$$

The initial conditions are

$$(1.3) \qquad u_i(x,0) = u_i^0(x) \geq 0, \ 0 \leq x \leq L, \ i = 1, 2, ..., n.$$

The specific growth rate $g_i(I)$ satisfies

$$(1.4) \qquad g_i(0) = 0, \ g_i'(I) > 0 \text{ for } I \geq 0.$$

A typical example of $g_i(I)$ takes the Michaelis-Menten form, $g_i(I) = m_i I/(a_i + I)$, where m_i is the maximal growth rate and a_i is the half saturation constant. The light intensity $I(x,t)$ takes the form

$$(1.5) \qquad I(x,t) = I_0 e^{-k_0 x} \exp\Big(-\int_0^x [k_1 u_1(s,t) + ... + k_n u_n(s,t)]ds\Big),$$

where I_0 is the incident light intensity, k_0 is the background turbidity that summarizes light absorption by all non-phytoplankton components, and k_i is the specific light attenuation coefficient of the phytoplankton species i.

In this paper we only consider the single species case ($n = 1$) and the two species case ($n = 2$). For a single species we obtain a complete understanding of the dynamical behavior of the reaction-diffusion problem. We show the existence of a critical loss rate $d_* > 0$, determined by an eigenvalue problem, such that when the loss rate d lies in $(0, d_*)$, the population density $u(x, t)$ of the species stabilizes at a unique positive steady state as time t goes to infinity, and $u(x, t)$ goes to 0 as $t \to \infty$ when $d \geq d_*$. Moreover, we obtain qualitative properties of the unique positive steady-state solution, which are crucial for the study of the multi-species model. For the two species model, our results are partial; we obtain some existence results for positive steady states and prove uniform persistence of the system under suitable conditions.

A main technical difficulty in our analysis is the lack of an "order preserving property" of the single species equation, caused by the nonlocal nature of the nonlinearity. Many key techniques for handling similar problems collapse for the model here because of this. In section 2, we study the steady state for the single species equation based on a bifurcation approach (for existence) and various subtle analytical techniques (for uniqueness and other properties of the solution). Section 3 is devoted to the global dynamical behavior of the single species equation, which relies on a comparison lemma and a boundedness lemma, and a key observation used in our proof is that the function $v(x, t) := \int_0^x u(y, t)dy$ satisfies an equation which has the order preserving property (see (3.4)). In section 4, we consider the two species model, and prove the existence of positive steady states by making use of the fixed point index theory and global bifurcation arguments. In section 5, we prove the uniform persistence and some extinction results for the two species dynamical system under certain suitable conditions. The analysis in sections 4 and 5 relies heavily on our results for the single species case in sections 2 and 3.

We end the introduction by mentioning some closely related mathematical research. In [19], a reaction-diffusion model for a single phytoplankton species was studied, and global dynamical behavior of the equation was determined, where the water column was assumed to have infinite depth, and the sinking effect of the phytoplankton species is included. In [24], the two species model of a similar nature to [19] was considered, but only for the special case that the functions $g_i(I)$ ($i = 1, 2$) are linear. However, the proof of the main result in [24] seems to contain serious gaps (the proof of Lemma 7 in [24] does not seem complete; for example, under the assumption that two positive solutions exist, there are more possibilities than (i) and (ii) listed there). The single species model in [19] but with finite water depth was considered in two recent papers [9] and [21]. In [9], for the special case that $g(I) = I^\alpha$, $\alpha \in (0, 1]$, the authors showed that there is a critical water depth for the existence and uniqueness of positive steady-state solutions. This work covered the case of bouyant phytoplankton (apart from the sinking type as in [19]), and it also characterized the phytoplankton bloom (for both sinking and bouiyant type) by some critical values of the verticle turbulent diffusion coefficient. Moreover, it investigated the phase transition curve by reducing the equation to a Bessel equation (by taking advantage of the special nonlinearity $g(I) = I^\alpha$). However, the stability of the steady-state solution or the dynamical behavior of the parabolic equation was not considered. In [21], under suitable conditions, the existence and uniqueness of a positive steady-state was proved, and it was also shown that the

steady-state is locally asymptotically stable. Our Theorem 3.3 below shows that the unique positive steady-state is not only locally asymptotically stable, but it is also globally attractive. On the other hand, our Theorem 2.1 implies that the conditions imposed in [21] for the existence of positive steady-state are not sharp. (To be accurate, our results here only cover the special case that the sinking velocity v is 0 in [21], but a simple modification of our techniques shows that both our Theorems 2.1 and 3.1 are valid for nonzero v.) In [7, 8], a reaction-diffusion model proposed by Klausmeier and Litchman [20] was examined, where both nutrient and light limitations for the growth of a single phytoplankton species were included, and the focus was on the location of biomass concentration under the assumption that, apart from passive diffusion caused by currents movement, the species actively move to the optimal spatial location for its growth (determined by the light and nutrient distributions).

2. The steady states of a single population species

In this section we study the steady states of a single population growth, i.e. (1.1)-(1.5) with $n = 1$, namely

$$(2.1) \qquad u_t = Du_{xx} + (g(I(x,t)) - d)u, \ 0 < x < L, \ t > 0,$$

$$(2.2) \qquad u_x(0,t) = 0, \ u_x(L,t) = 0, \ t > 0,$$

$$(2.3) \qquad u(x,0) = u_0(x) \gneqq 0, \ 0 \le x \le L,$$

where $g \in C^1([0,\infty))$ satisfies

$$(2.4) \qquad g(0) = 0 \text{ and } g \text{ is strictly increasing},$$

$$(2.5) \qquad I(x,t) = I_0 e^{-k_0 x} \exp\Big(-k \int_0^x u(s,t)ds\Big), \ I_0, k_0, k > 0.$$

With suitable scaling, we may assume that $L = 1$, and by replacing $g(\cdot)$ by $g(I_0 \cdot)$ we may assume $I_0 = 1$. With these conventions the steady state problem becomes

$$(2.6) \qquad -Du'' = \big[g\big(e^{-k_0 x} e^{-k\int_0^x u(s)ds}\big) - d\big]u \text{ in } (0,1), \ u'(0) = u'(1) = 0,$$

where D, k_0, k and d are positive constants, $g : [0,\infty) \to [0,\infty)$ is a C^1 increasing function, with $g(0) = 0$.

The following eigenvalue problem will play an important role in our analysis to follow:

$$(2.7) \qquad \begin{cases} -D\phi'' + \Psi(x)\phi = \lambda\phi \text{ in } (0,1), \\ \phi'(0) = 0, \ \phi'(1) = 0, \end{cases}$$

where $\Psi(x)$ is a continuous function in $[0,1]$. It is well-known that (2.7) has a smallest eigenvalue $\lambda_1 = \lambda_1(\Psi)$, which corresponds to a positive eigenfunction ϕ_1, and λ_1 is the only eigenvalue whose

corresponding eigenfunction does not change sign. Moreover, $\Psi_1 \geq \Psi_2$ implies $\lambda_1(\Psi_1) \geq \lambda_1(\Psi_2)$, and equality holds only if $\Psi_1 \equiv \Psi_2$; $\Psi_n \to \Psi$ in $C([0,1])$ implies $\lambda_1(\Psi_n) \to \lambda_1(\Psi)$.

Define

(2.8) $$\Psi_0(x) := -g(e^{-k_0 x}), \ d_* := -\lambda_1(\Psi_0).$$

We are now ready to state and prove our main result of this section.

Theorem 2.1. *Problem* (2.6) *has a unique positive solution for $d \in (0, d_*)$, and it has no positive solution if $d \notin (0, d_*)$. Moreover, if we denote the unique positive solution by u_d, then*

(i) $d \to u_d$ *is continuous from* $(0, d_*)$ *to* $C^2([0,1])$,

(ii) $0 < d_1 < d_2 < d_*$ *implies* $u_{d_1}(0) > u_{d_2}(0)$,

(iii) $u_d \to \infty$ *uniformly on* $[0,1]$ *as* $d \to 0$,

(iv) $0 < d_1 < d_2 < d_*$ *implies* $\int_0^x u_{d_1}(s)ds > \int_0^x u_{d_2}(s)ds$ *for all* $x \in (0,1]$.

Proof. It follows from a standard bifurcation argument of Crandall and Rabinowitz [3] and Rabinowitz [22] that (2.6) has an unbounded branch of positive solutions, which we denote as $\Gamma = \{(d, u)\} \subset R^1 \times C^1([0,1])$, that bifurcates from the trivial solution branch $\{(d, 0)\}$ at $(d_*, 0)$. If (d, u) is a positive solution of (2.6), then from the equation we deduce

$$-d = \lambda_1\big[-g\big(e^{-k_0 x}e^{-k\int_0^x u(s)ds}\big)\big] \in \Big(\lambda_1\big[-g\big(e^{-k_0 x}\big)\big], \lambda_1(0)\Big) = (-d_*, 0).$$

That is,

$$0 < d < d_*.$$

Therefore (2.6) has no positive solution when $d \notin (0, d_*)$.

We show next that the branch Γ can only become unbounded through $(d, u) \in \Gamma$ satisfying $d \to 0$ and $\|u\|_\infty \to \infty$. We argue indirectly and assume that there exists $(d_n, u_n) \in \Gamma$ satisfying $d_n \to d_0 \in (0, d_*]$ and $\|u_n\|_\infty \to \infty$. Denote $\hat{u}_n = u_n/\|u_n\|_\infty$. Then

$$-D\hat{u}_n'' = \big[g\big(e^{-k_0 x}e^{-k\int_0^x u_n(s)ds}\big) - d_n\big]\hat{u}_n \text{ in } (0,1), \ \hat{u}_n'(0) = \hat{u}_n'(1) = 0.$$

Therefore $\{\hat{u}_n\}$ and $\{\hat{u}_n''\}$ are both bounded sequences in $L^\infty([0,1])$. By standard L^p theory of elliptic equations, $\{\hat{u}_n\}$ is bounded in $W^{2,p}([0,1])$ for any $p > 1$, and hence, by the Sobolev embedding theorem, it is precompact in $C^1([0,1])$. By passing to a subsequence, we may assume that $\hat{u}_n \to \hat{u}$ in $C^1([0,1])$. Since $f_n(x) := g\big(e^{-k_0 x}e^{-k\int_0^x u_n(s)ds}\big)$ is a bounded sequence in $L^\infty([0,1])$, by passing to a subsequence, we may assume that $f_n \to f$ weakly in $L^2([0,1])$. We note that $0 \leq f \leq g(1)$ in $[0,1]$ since each f_n has this property. It is now easily seen that $\hat{u}$ is a weak solution of

$$-D\hat{u}'' = (f - d_0)\hat{u} \text{ in } (0,1), \ \hat{u}'(0) = \hat{u}'(1) = 0,$$

and $\hat{u} \geq 0$, $\|\hat{u}\|_\infty = 1$. Since $(f - d_0) \in L^\infty([0,1])$, we can apply the strong maximum principle to conclude that $\hat{u} > 0$ on $[0,1]$ and $-d_0 = \lambda_1(-f)$.

On the other hand, from $\hat{u}_n \to \hat{u} > 0$ uniformly in $[0,1]$ and $\|u_n\|_\infty \to \infty$, we deduce that $u_n \to \infty$ uniformly on $[0,1]$. It follows that

$$e^{-k\int_0^x u_n(s)ds} \to 0$$

uniformly on any compact subset of $(0, 1]$. This implies that $f \equiv 0$ and hence

$$-d_0 = \lambda_1(-f) = \lambda_1(0) = 0,$$

a contradiction to our assumption that $d_0 \in (0, d_*]$. Therefore Γ can only become unbounded through the existence of a sequence $(d_n, u_n) \in \Gamma$ such that $d_n \to 0$ and $\|u_n\|_\infty \to \infty$; moreover, the above proof shows that in such a case, $u_n \to \infty$ uniformly on $[0, 1]$. (In fact, $u_n/\|u_n\|_\infty \to 1$ in $C^1([0, 1])$.)

As a consequence of the connectedness of Γ, we conclude that (2.6) has at least one positive solution for each $d \in (0, d_*)$.

We next prove the uniqueness conclusion. Suppose by way of contradiction that for some $d \in (0, d_*)$, (2.6) has two positive solutions u_1 and u_2. We first observe that $u_1 - u_2$ must change sign in $(0, 1)$. Otherwise we may assume that $u_1 \leq u_2$ and $u_1 \not\equiv u_2$ in $[0, 1]$. From this and the equations for u_1 and u_2 we deduce

$$-d = \lambda_1\big[-g\big(e^{-k_0 x} e^{-k \int_0^x u_1(s)ds}\big)\big] < \lambda_1\big[-g\big(e^{-k_0 x} e^{-k \int_0^x u_2(s)ds}\big)\big] = -d,$$

a contradiction. Therefore $u_1 - u_2$ changes sign in $(0, 1)$.

We claim that $u_1(0) \neq u_2(0)$. Otherwise, for $i = 1, 2$, we denote $v_i(x) = \int_0^x u_i(s)ds$, $w_i(x) = u_i'(x)$, and find that (u_i, v_i, w_i) are solutions of the initial value system

$$(u', v', w') = \big(w, u, -D^{-1}\big[g\big(e^{-k_0 x} e^{-kv}\big) - d\big]u\big), \quad \big(u(0), v(0), w(0)\big) = \big(u_1(0), 0, 0\big).$$

By the well-known existence and uniqueness theorem of ODE, we conclude that $(u_1, v_1, w_1) \equiv (u_2, v_2, w_2)$ in a small neighborhood $[0, \delta]$. We may then repeat this argument to conclude that $u_1 \equiv u_2$ as long as they are defined, which is a contradiction to our assumption that they are different solutions of (2.6). Therefore $u_1(0) \neq u_2(0)$.

For definiteness we assume that $u_1(0) < u_2(0)$. Since $u_1 - u_2$ changes sign in $(0, 1)$, there exists $x_0 \in (0, 1)$ such that $u_2(x) > u_1(x)$ in $[0, x_0)$ and $u_1(x_0) = u_2(x_0)$. We have

$$\int_0^{x_0} [-u_1'' u_2]dx = D^{-1} \int_0^{x_0} \big[g\big(e^{-k_0 x} e^{-k \int_0^x u_1(s)ds}\big) - d\big]u_1 u_2 dx.$$

Using integration by parts, we deduce

$$-u_1' u_2\big|_0^{x_0} + \int_0^{x_0} u_1' u_2' dx = D^{-1} \int_0^{x_0} g\big(e^{-k_0 x} e^{-k \int_0^x u_1(s)ds}\big)u_1 u_2 dx - D^{-1}d \int_0^{x_0} u_1 u_2 dx.$$

Similarly,

$$\int_0^{x_0} [-u_2'' u_1]dx = D^{-1} \int_0^{x_0} \big[g\big(e^{-k_0 x} e^{-k \int_0^x u_2(s)ds}\big) - d\big]u_1 u_2 dx,$$

and

$$-u_2' u_1\big|_0^{x_0} + \int_0^{x_0} u_1' u_2' dx = D^{-1} \int_0^{x_0} g\big(e^{-k_0 x} e^{-k \int_0^x u_2(s)ds}\big)u_1 u_2 dx - D^{-1}d \int_0^{x_0} u_1 u_2 dx.$$

Therefore

$$(2.9) \quad [u_1 u_2' - u_1' u_2]\big|_0^{x_0} = D^{-1} \int_0^{x_0} \big[g\big(e^{-k_0 x} e^{-k \int_0^x u_1(s)ds}\big) - \big[g\big(e^{-k_0 x} e^{-k \int_0^x u_2(s)ds}\big)\big]u_1 u_2 dx.$$

Since $u_1'(0) = u_2'(0) = 0$ by the boundary condition, and $u_1(x_0) = u_2(x_0)$, $u_1'(x_0) \geq u_2'(x_0)$, we have

$$[u_1u_2' - u_1'u_2]\Big|_0^{x_0} = u_1(x_0)[u_2'(x_0) - u_1'(x_0)] \leq 0.$$

Therefore (2.9) implies that

$$\int_0^{x_0} \left[g\left(e^{-k_0x}e^{-k\int_0^x u_1(s)ds}\right) - g\left(e^{-k_0x}e^{-k\int_0^x u_2(s)ds}\right)\right]u_1u_2dx \leq 0.$$

But on the other hand, from $u_1(x) < u_2(x)$ in $(0, x_0)$ we deduce

$$\int_0^{x_0} \left[g\left(e^{-k_0x}e^{-k\int_0^x u_1(s)ds}\right) - g\left(e^{-k_0x}e^{-k\int_0^x u_2(s)ds}\right)\right]u_1u_2dx > 0.$$

This contradiction proves our uniqueness conclusion, and we can now denote the unique positive solution of (2.6) by u_d.

The fact that $d \to u_d$ is continuous as a map from $(0, d_*)$ to $C^1([0,1])$ follows from a standard compactness and uniqueness consideration: If $d_n \to d_0 \in (0, d_*)$, then a subsequence of u_{d_n} converges in $C^1([0,1])$ to a positive solution of (2.6) with $d = d_0$. By uniqueness, this positive solution must be u_{d_0}. Therefore the entire sequence converges to u_{d_0}. Moreover, from the equation of u_{d_n} we easily see that $u_{d_n} \to u_{d_0}$ in $C^1([0,1])$ implies that the convergence also holds in $C^2([0,1])$. Conclusion (i) is now proved.

We now show that $0 < d_1 < d_2 < d_*$ implies $u_{d_1}(0) > u_{d_2}(0)$. To simplify notations, we will write $u_1 = u_{d_1}$, $u_2 = u_{d_2}$ in the following discussion.

We argue indirectly and assume that for some $0 < d_1 < d_2 < d_*$ the inequality $u_1(0) \leq u_2(0)$ holds. Consider firstly the case $u_1(0) < u_2(0)$. Then we can show $u_1 - u_2$ changes sign and define $[0, x_0]$ as in the above uniqueness proof. We similarly have

$$[u_1u_2' - u_1'u_2]\Big|_0^{x_0} \leq 0.$$

On the other hand,

$$\begin{aligned}
[u_1u_2' - u_1'u_2]\Big|_0^{x_0} &= \int_0^{x_0}[-u_1''u_2 + u_2''u_1]dx \\
&= D^{-1}\int_0^{x_0}\left[g\left(e^{-k_0x}e^{-k\int_0^x u_1(s)ds}\right) - g\left(e^{-k_0x}e^{-k\int_0^x u_2(s)ds}\right)\right]u_1u_2dx \\
&\quad + D^{-1}(d_2 - d_1)\int_0^{x_0} u_1u_2dx \\
&> 0,
\end{aligned}$$

a contradiction.

Consider now the case $u_1(0) = u_2(0)$. Then from (2.6) and $d_2 > d_1$ we find that $u_2''(0) > u_1''(0)$. Since $u_1'(0) = u_2'(0) = 0$, it follows that $u_2(x) > u_1(x)$ for $x > 0$ small. Thus we can still find an interval $(0, x_0)$ as above and derive a contradiction. Therefore $u_1(0) > u_2(0)$. Conclusion (ii) is now proved.

Conclusion (iii) follows from our argument earlier, where we proved that Γ can only become unbounded through a sequence $(d_n, u_n) \in \Gamma$ with $d_n \to 0$ and $\|u_n\|_\infty \to \infty$.

We now consider (iv). We observe that if u is a positive solution of (2.6) then, by integrating (2.6) from 0 to x, $v(x) := \int_0^x u(s)ds$ satisfies

$$
\begin{aligned}
-Dv'' &= -dv + \int_0^x g(e^{-k_0 s - kv(s)})u(s)ds \\
&= -dv + k^{-1}\int_0^x g(e^{-k_0 s - kv(s)})d(k_0 s + kv(s)) - k_0 k^{-1}\int_0^x g(e^{-k_0 s - kv(s)})ds \\
&= -dv + k^{-1}\int_0^{k_0 x + kv(x)} g(e^{-\xi})d\xi - k_0 k^{-1}\int_0^x g(e^{-k_0 s - kv(s)})ds \\
&= -dv + G(k_0 x + kv(x)) - k_0 k^{-1}\int_0^x g(e^{-k_0 s - kv(s)})ds,
\end{aligned}
$$

where

$$
G(\eta) := k^{-1}\int_0^\eta g(e^{-\xi})d\xi.
$$

(The use of the function G in the above equation for v was motivated by [19].)

For $d \in (0, d_*)$ we set $v_d(x) = \int_0^x u_d(s)ds$. Fix any $d_2 \in (0, d_*)$, we want to show that $v_{d_1}(x) > v_{d_2}(x)$ for all $x \in (0, 1]$ if $0 < d_1 < d_2$. To simplify notations, whenever no confusion is caused, we write $u_i = u_{d_i}$ and $v_i = v_{d_i}$. By (iii), if $d_1 > 0$ is small enough, we have $u_1 > u_2$ on $[0, 1]$ and hence $v_1 > v_2$ for $x \in (0, 1]$. If the desired conclusion does not hold, then we can find a maximal $d_1 < d_2$ such that $v_d(x) > v_{d_2}(x)$ in $(0, 1]$ for $d \in (0, d_1)$. Then clearly $v_{d_1} \geq v_{d_2}$. We claim that $v_{d_1}(x) = v_{d_2}(x)$ holds for some $x \in (0, 1]$. Otherwise $v_1(x) > v_2(x)$ for all $x \in (0, 1]$. Fix $d_0 \in (d_1, d_2)$. By (ii), for any $d \in [d_1, d_0]$, $u_d(0) \geq u_{d_0}(0) > u_{d_2}(0)$. By (i), there exists $C > 0$ such that $\|u_d\|_{C^2([0,1])} < C$ for all $d \in [d_1, d_0]$. Therefore we can find $\delta > 0$ small enough such that $v_d(x) > v_{d_2}(x)$ for $d \in [d_1, d_0]$ and $x \in (0, \delta)$. Since $v_1(x) > v_2(x)$ in $[\delta, 1]$, by (i) we can find $\tilde{d}_1 \in (d_1, d_0]$ such that $v_d(x) > v_{d_2}(x)$ for $d \in [d_1, \tilde{d}_1]$ and $x \in [\delta, 1]$. Thus $v_d(x) > v_{d_2}(x)$ for $d \in (0, \tilde{d}_1]$ and $x \in (0, 1]$, contradicting the maximality of d_1. This proves our claim that $v_{d_1}(x) = v_{d_2}(x)$ holds for some $x \in (0, 1]$. We show that this leads to a contradiction.

Consider firstly the possibility that $x = 1$, i.e., $v_1(1) = v_2(1)$. Since $v_1''(1) = v_2''(1) = 0$, we deduce from the above equation for v that, for $i = 1, 2$,

$$
d_i v_i(1) = G(k_0 + kv_i(1)) - k_0 k^{-1}\int_0^1 g(e^{-k_0 s - kv_i(s)})ds.
$$

Denote $\sigma := v_1(1) = v_2(1)$. We obtain from the above identity

$$
(d_2 - d_1)\sigma = k_0 k^{-1}\int_0^1 \left[g(e^{-k_0 s - kv_1(s)}) - g(e^{-k_0 s - kv_2(s)})\right]ds.
$$

Since $v_1 \geq v_2$, the right side of the above identity is less than or equal to 0, but the left side is positive, and we arrive at a contradiction. Hence we necessarily have $v_1(1) > v_2(1)$.

Consider next the remaining possibility, namely $x \in (0, 1)$. Denote $w := v_1 - v_2$ we obtain

$$
\begin{aligned}
-Dw'' &= d_2 v_2 - d_1 v_1 + C(x)w - k_0 k^{-1}\int_0^x \left[g(e^{-k_0 s - kv_1(s)}) - g(e^{-k_0 s - kv_2(s)})\right]ds \\
&\geq [C(x) - d_1]w, \\
w(0) &= 0, \ w(1) > 0,
\end{aligned}
$$

where $C(x) = G'(k_0 x + k\theta(x))$ for some $\theta(x) \in [v_2(x), v_1(x)]$. By the strong maximum principle we deduce $w > 0$ in $(0, 1]$, again reaching a contradiction.

The proof is now complete. $\qquad\square$

3. The dynamics of a single population species

In this section we study the asymptotic behavior of the solution of the partial differential equation (2.1)-(2.3) satisfying (2.4) and (2.5). As before without loss of generality we assume $I_0 = 1$, $L = 1$ in (2.1)-(2.5). The initial boundary value problem now has the form

$$(3.1) \qquad u_t = Du_{xx} + \left[g(e^{-k_0 x - k \int_0^x u(s,t)ds}) - d \right] u, \ 0 < x < 1, \ t > 0,$$

$$(3.2) \qquad u_x(0, t) = 0, \ u_x(1, t) = 0, \ t > 0,$$

$$(3.3) \qquad u(x, 0) = u_0(x) \gneqq 0, \ 0 \le x \le 1.$$

We assume that $u_0 \in C([0, 1])$.

By standard argument, it is not difficult to prove the uniqueness and global existence of the solution $u(x, t)$ of (3.1)-(3.3). By the maximum principle, $u(x, t) > 0$ for $t > 0$ and $x \in [0, 1]$. Our aim here is to understand the long-time behavior of $u(x, t)$.

Recall that $d_* = -\lambda_1(\Psi_0)$ is defined in (2.8). If $d > d_*$ then using

$$u_t \le Du_{xx} - du + g(e^{-k_0 x})u,$$

and the comparison principle we deduce $u(x, t) \le Ce^{-(d-d_*)t}\phi_1(x) \to 0$ as $t \to \infty$ uniformly in $x \in [0, 1]$, where ϕ_1 is a positive eigenfunction corresponding to $\lambda_1(\Psi_0)$ and C is a positive constant such that $u_0(x) \le C\phi_1(x)$ in $[0, 1]$. Therefore

$$\lim_{t \to \infty} u(x, t) = 0 \ \text{ uniformly for } x \in [0, 1] \text{ if } d > d_*.$$

We consider next the case $d \in (0, d_*)$; the case $d = d_*$ will be discussed last. So we suppose now $0 < d < d_*$. By Theorem 2.1, (3.1)-(3.2) has a unique positive steady state $u_d(x)$. We will show that $u(x, t) \to u_d(x)$ as $t \to \infty$ uniformly for x in $[0, 1]$. To prove this conclusion, we need two key results, namely a comparison lemma and a boundedness lemma.

Set

$$v(x, t) = \int_0^x u(s, t)ds.$$

Then $v(x, t)$ satisfies $v(0, t) \equiv 0$ and

$$(3.4) \qquad \begin{aligned} v_t &= Dv_{xx} - dv + \int_0^x g(e^{-k_0 s - kv(s,t)})u(s, t)ds \\ &= Dv_{xx} - dv + G(k_0 x + kv(x, t)) - k_0 k^{-1} \int_0^x g(e^{-k_0 s - kv(s,t)})ds, \end{aligned}$$

where $G(\eta) = k^{-1} \int_0^\eta g(e^{-\xi})d\xi$.

In the following two lemmas, we do not require $d \in (0, d_*)$.

Lemma 3.1. (Comparison Lemma) *Suppose $d \in (-\infty, \infty)$ and $u, \tilde{u} \in C^{2,1}([0,1] \times (0,\infty))$ satisfy*

$$u_t \leq Du_{xx} + \left[g\left(e^{-k_0 x - k\int_0^x u(s,t)ds}\right) - d\right]u, \ 0 \leq x \leq 1, \ t > 0,$$

$$u_x(0,t) = 0, \ u_x(1,t) = 0, \ t > 0,$$

and

$$\tilde{u}_t \geq D\tilde{u}_{xx} + \left[g\left(e^{-k_0 x - k\int_0^x \tilde{u}(s,t)ds}\right) - d\right]\tilde{u}, \ 0 \leq x \leq 1, \ t > 0,$$

$$\tilde{u}_x(0,t) = 0, \ \tilde{u}_x(1,t) = 0, \ t > 0.$$

If $u(x,t) < \tilde{u}(x,t)$ for $x \in [0,1]$ and all small $t \geq 0$ (say $t \in [0,\epsilon]$), then $v(x,t) < \tilde{v}(x,t)$ for all $t > 0$ and $x \in (0,1]$, where

$$v(x,t) = \int_0^x u(s,t)ds, \ \ \tilde{v}(x,t) = \int_0^x \tilde{u}(s,t)ds.$$

Proof. Since $u(x,t) < \tilde{u}(x,t)$ for $t \geq 0$ small and $x \in [0,1]$ we have

(3.5) $v(x,t) < \tilde{v}(x,t)$ for $t \geq 0$ small and $x \in (0,1]$.

Suppose the conclusion of Lemma 3.1 is not true. Then there exists a finite maximal time denoted by t^* such that (3.5) holds for every $t \in [0, t^*)$. Clearly $v(x,t^*) \leq \tilde{v}(x,t^*)$ for all $x \in [0,1]$. We claim that

(3.6) $v(x,t^*) = \tilde{v}(x,t^*)$ for some $x \in (0,1]$.

Otherwise we have $v(x,t^*) < \tilde{v}(x,t^*)$ for all $x \in (0,1]$. Denote

$$w(x,t) = \tilde{v}(x,t) - v(x,t).$$

Then $w(x,t) \geq 0$ for $0 \leq t \leq t^*$, $0 \leq x \leq 1$, and

$$w_t \geq Dw_{xx} - dw + C(x,t)w + k_0 k^{-1} \int_0^x \left[g\left(e^{-k_0 s - kv(s,t)}\right) - g\left(e^{-k_0 s - k\tilde{v}(s,t)}\right)\right]ds$$

(3.7) $\geq Dw_{xx} + \left[C(x,t) - d\right]w$ for $0 \leq x \leq 1, \ t \in (0, t^*]$,

$$w(0,t) = 0, \ w(1,t) > 0 \ \text{ for } 0 < t \leq t^*,$$

$$w(x,0) > 0 \ \text{ for } 0 < x \leq 1,$$

where

$$C(x,t) = G'(k_0 x + k\theta(x,t)), \ \theta(x,t) \in \left[v(x,t), \tilde{v}(x,t)\right].$$

Thus we may use the strong maximum principle and the Hopf boundary lemma to conclude that $w(x,t) > 0$ for $t \in (0, t^*]$ and $x \in (0,1]$, and $w_x(0,t^*) > 0$. Then by the smoothness of $w(x,t)$, we obtain $w_x(x,t) > 0$ for all t close to t^* and x close to 0. Thus from $w(0,t) \equiv 0$ we deduce $w(x,t) > 0$ for $0 < x \leq \delta$, $t^* \leq t \leq t^* + \delta$, $\delta > 0$ small. From $w(x,t^*) > 0$ for $x \in [\delta,1]$, we can find $\delta_0 \in (0,\delta)$ such that $w(x,t) > 0$ for $x \in [\delta,1]$ and $t \in [t^*, t^* + \delta_0]$. Thus $w(x,t) > 0$ for $x \in (0,1]$ and $t \in (0, t^* + \delta_0]$, contradicting the maximality of t^*. This proves (3.6).

Thus there exists $x_0 \in (0,1]$ such that $w(x_0, t^*) = 0$. If $x_0 = 1$, i.e., $w(1,t^*) = 0$, then $w_t(1,t^*) \leq 0$. By the boundary condition $v_{xx}(1,t^*) = u_x(1,t^*) = 0$, $\tilde{v}_{xx}(1,t^*) = \tilde{u}_x(1,t^*) = 0$, and hence $w_{xx}(1,t^*) = 0$. Therefore we can use (3.7) to obtain

$$0 \geq w_t(1,t^*) \geq k_0 k^{-1} \int_0^1 \left[g(e^{-k_0 s - kv(s,t^*)}) - g(e^{-k_0 s - k\tilde{v}(s,t^*)}) \right] ds.$$

Since $v(x,t^*) \leq \tilde{v}(x,t^*)$ in $[0,1]$, the above inequality holds only if $v(x,t^*) \equiv \tilde{v}(x,t^*)$, which implies $u(x,t^*) \equiv \tilde{u}(x,t^*)$.

From the inequality in (3.7), $w(x,t)$ is an upper solution of the problem

$$\begin{cases} \tilde{w}_t & = D\tilde{w}_{xx} - d\tilde{w}, \quad 0 < x < 1,\ 0 < t \leq t^*, \\ \tilde{w}(0,t) & = \tilde{w}(1,t) = 0, \quad 0 < t \leq t^*, \\ \tilde{w}(x,0) & = w(x,0) > 0, \quad 0 < x < 1. \end{cases}$$

By the strong maximum principle, $\tilde{w}(x,t) > 0$ for $x \in (0,1)$ and $0 < t \leq t^*$. On the other hand, by the comparison principle, we have $w(x,t) \geq \tilde{w}(x,t)$ for $x \in (0,1)$ and $0 < t \leq t^*$. Hence $w(x,t^*) > 0$ for $x \in (0,1)$. This contradicts our earlier conclusion that $w(x,t^*) \equiv 0$. Therefore we must have $w(1,t^*) > 0$. We may now apply the strong maximum principle to (3.7) to conclude that $w(x,t^*) > 0$ for $x \in (0,1]$, which is a contradiction to (3.6). The proof is now complete. $\qquad \square$

Lemma 3.2. (Boundedness Lemma) *Suppose $d > 0$, and let $u(x,t)$ be the unique solution of (3.1)-(3.3). Then there exists $C > 0$ such that*

$$(3.8) \qquad \qquad u(x,t) \leq C \text{ for all } x \in [0,1],\ t > 0.$$

Proof. Our assumption on g implies that

$$g(I) \leq \sigma I \text{ for some } \sigma > 0 \text{ and all } I \in [0,1].$$

Therefore with

$$I(x,t) = \exp\left(-k_0 x - k \int_0^x u(y,t) dy \right),$$

we have

$$g(I(x,t)) \leq \sigma I(x,t) \leq \sigma e^{-k \int_0^x u dy},$$

and from the equation for u we deduce that

$$u_t \leq Du_{xx} + \left[\sigma e^{-k \int_0^x u dy} - d \right] u.$$

Integrating for x from 0 to 1 we obtain

$$\left[\int_0^1 u dx \right]_t \leq \sigma \int_0^1 e^{-k \int_0^x u dy} u dx - d \int_0^1 u dx.$$

Denote

$$w(t) = \int_0^1 u(x,t) dx, \quad v(x,t) = \int_0^x u(y,t) dy.$$

Then

$$\int_0^1 e^{-k \int_0^x u \, dy} u \, dx = \int_0^1 e^{-kv} v_x \, dx$$

$$= k^{-1} \left[e^{-kv(0,t)} - e^{-kv(1,t)} \right]$$

$$= k^{-1} \left[1 - e^{-kw(t)} \right].$$

Therefore,

$$w_t \le \sigma k^{-1} \left[1 - e^{-kw} \right] - dw,$$

and

$$w_t + dw \le C_0 := \sigma k^{-1}.$$

It follows that

$$\left(e^{dt} w \right)_t \le C_0 e^{dt},$$

from which we deduce

(3.9) $$\qquad w(t) \le w(0) e^{-dt} + C_0 e^{-dt} \int_0^t e^{ds} \, ds \le C := w(0) + C_0/d.$$

To show the boundedness of $u(x,t)$ we set

$$W(t) := \max_{x \in [0,1], s \in [0,t]} u(x,s).$$

Clearly $W(t)$ is non-decreasing. Suppose for contradiction that $W(t) \to \infty$ as $t \to \infty$.

Since $W(t) \to \infty$, we can find $t_n \to \infty$ such that $W(t_n) = \max_{x \in [0,1]} u(x,t_n)$. We may assume that $t_n > 1$ for all $n \ge 1$. We then define

$$v_n(x,t) = \frac{u(x, t + t_n - 1)}{W(t_n)}.$$

Clearly v_n satisfies

$$\begin{cases} (v_n)_t &= D(v_n)_{xx} + c_n v_n, \\ (v_n)_x &= 0 \quad \text{for } x \in \{0,1\} \text{ and } t > 0, \\ v_n(x,0) &\in [0,1], \end{cases}$$

where $c_n(x,t) = g(I(x, t + t_n - 1)) - d$, and $|c_n| \le M_0 := \max_{I \in [0,1]} |g(I) - d|$. A simple comparison consideration gives

$$0 \le v_n(x,t) \le e^{M_0 t} \text{ for } x \in [0,1] \text{ and } t \ge 0.$$

Hence we may apply standard parabolic regularity to conclude that $\{v_n\}$ is bounded in $C^{1+\alpha, \alpha}([0,1] \times [\frac{1}{2}, 2])$, for any $\alpha \in (0,1)$. Therefore by passing to a subsequence if necessary we have $v_n \to v^*$ in $C^{1,0}([0,1] \times [\frac{1}{2}, 2])$. Since $|c_n| \le M_0$, by passing to a further subsequence, we may assume that $c_n \to c$ weakly in $L^2([0,1] \times [\frac{1}{2}, 2])$. Clearly we have $|c| \le M_0$. It follows that v^* is a weak solution to

$$\begin{cases} v_t^* &= D v_{xx}^* + c v^* &\text{for } x \in [0,1], \ t \in [1/2, 2], \\ v_x^* &= 0 &\text{for } x \in \{0,1\} \text{ and } t \in [1/2, 2], \\ v^* &\in [0, e^{2M_0}] &\text{for } x \in [0,1], \ t \in [1/2, 2]. \end{cases}$$

Since $\max_{x \in [0,1]} v_n(x, 1) = 1$, we have $\max_{x \in [0,1]} v^*(x, 1) = 1$ and hence v^* is not identically zero. By the strong maximum principle we deduce $v^*(x, 1) \geq \delta_0 > 0$ in $[0, 1]$. It follows that $v_n(x, 1) \geq \delta_0/2$ for all large n and $x \in [0, 1]$. Therefore

$$u(x, t_n) \geq (\delta_0/2) W(t_n) \text{ for all large } n \text{ and } x \in [0, 1].$$

But then we deduce

$$w(t_n) \geq (\delta_0/2) W(t_n) \to \infty$$

as $n \to \infty$, which contradicts (3.9). Therefore there exists $C > 0$ such that

$$u(x, t) \leq C \text{ for all } x \in [0, 1] \text{ and } t > 0.$$

The proof is complete. $\square$

We are now ready to prove the main result of this section.

Theorem 3.3. *Let $0 < d < d^*$. Then the solution $u(x, t)$ of (3.1)-(3.3) converges to the unique steady state $u_d(x)$ as $t \to \infty$ uniformly in $x \in [0, 1]$.*

Proof. We may assume that the initial data u_0 satisfies $u_0 > 0$ in $[0, 1]$ for otherwise we can replace $u(x, t)$ by $u(x, 1 + t)$ and $u_0(x)$ by $u(x, 1)$.

Since $d < d^* = -\lambda_1(\Psi_0)$ and

$$\Psi_\delta(x) := -g\left(e^{-(k_0 + k\delta)x}\right) \to \Psi_0(x)$$

uniformly in $[0, 1]$ as $\delta \to 0$, we can find $\delta > 0$ sufficiently small such that $d < -\lambda_1(\Psi_\delta)$. Fix such a δ and let ϕ be a positive eigenfunction corresponding to $\lambda_1(\Psi_\delta)$. Then we choose $\epsilon > 0$ small so that $\epsilon\phi < u_0$, $\epsilon\phi < \delta$ in $[0, 1]$. Let $\underline{u}(x, t)$ be the unique solution of (3.1)-(3.2) with initial condition $\underline{u}(x, 0) = \epsilon\phi(x)$. Then we can find $\sigma > 0$ small such that

$$0 < \underline{u}(x, t) < \delta \text{ for } t \in (0, \sigma] \text{ and } x \in [0, 1].$$

Hence for $t \in (0, \sigma]$,

$$
\begin{aligned}
\underline{u}_t &= D\underline{u}_{xx} + \left[g\left(e^{-k_0 x - k \int_0^x \underline{u}(y,t) dy}\right) - d\right]\underline{u} \\
&\geq D\underline{u}_{xx} + \left[-\Psi_\delta(x) - d\right]\underline{u} \\
&> D\underline{u}_{xx} + \left[-\Psi_\delta(x) + \lambda_1(\Psi_\delta)\right]\underline{u}.
\end{aligned}
$$

It follows that

$$
\begin{cases}
(\underline{u} - \epsilon\phi)_t > D(\underline{u} - \epsilon\phi)_{xx} + \left[-\Psi_\delta(x) + \lambda_1(\Psi_\delta)\right](\underline{u} - \epsilon\phi), & x \in [0, 1], t \in (0, \sigma], \\
(\underline{u} - \epsilon\phi)_x = 0, & x = 0, 1, \ t \in (0, \sigma], \\
\underline{u} - \epsilon\phi = 0, & x \in [0, 1], t = 0.
\end{cases}
$$

By the strong maximum principle we deduce $\underline{u}(x, t) - \epsilon\phi(x) > 0$ for $t \in (0, \sigma]$ and $x \in [0, 1]$. Fix $s \in (0, \sigma]$, we thus have

$$\underline{u}(x, s) > \underline{u}(x, 0) \text{ in } [0, 1].$$

By continuity,

$$\underline{u}(x, s + t) > \underline{u}(x, t) \text{ in } [0, 1] \text{ for all small } t \geq 0.$$

Thus we can use Lemma 3.1 to conclude that $\underline{v}(x,t) < \underline{v}(x, s+t)$ for $x \in [0,1]$ and $t > 0$, where $\underline{v}(x,t) = \int_0^x \underline{u}(s,t)ds$. It follows that $\underline{v}(x,t)$ is monotone increasing in t.

By Lemma 3.2, $\underline{v}(x,t) \leq C$ for all $x \in [0,1]$ and $t > 0$ for some $C > 0$. Hence $\lim_{t\to\infty} \underline{v}(x,t) = v_*(x)$ exists. On the other hand, due to the boundedness of $\|\underline{u}(\cdot,t)\|_\infty$ (which follows from Lemma 3.2), we can apply the standard parabolic regularity theory to (3.1)-(3.2) to conclude that, for any sequence $t_n \to \infty$, $\{\underline{u}(\cdot, t_n)\}$ has a subsequence which converges in $C^1([0,1])$, say $\underline{u}(\cdot, t_{n_k}) \to u_*$. Since $\underline{v}(\cdot, t_n) \to v_*$, we necessarily have $v_*(x) = \int_0^x u_*(y)dy$. Hence $u_* = v_*'$. This implies that $\lim_{t\to\infty} \underline{u}(x,t)$ exists and equals $v_*'(x)$. It follows that v_*' must be a nonnegative steady state of (3.1), (3.2). Since $v_*(0) = 0$ and v_* is the limit of an increasing sequence, we have $v_*(x) > 0$ for $x \in (0,1]$ and $v_*' \not\equiv 0$. Therefore v_*' is a nontrivial nonnegative steady state of (3.1), (3.2). By the strong maximum principle v_*' is positive and hence we can use Theorem 2.1 to conclude that $v_*' \equiv u_d$.

Next we consider $d_M = -\lambda_1(\Psi_M))$ with $M > 0$ large. Recall that $\Psi_M(x) = -g(e^{-(k_0+kM)x})$. Let $\phi_M(x)$ be the positive eigenfunction corresponding to $\lambda_1(\Psi_M)$ with $\|\phi_M\|_\infty = 1$. It is easy to see by a regularity and compactness argument that as $M \to \infty$, $\lambda_1(\Psi_M) \to 0$ and $\phi_M \to 1$ in $C^1([0,1])$. Therefore we can find $M_0 > 0$ large so that

$$d > -\lambda_1(\Psi_M), \ \frac{1}{2} < \phi_M(x) \leq 1 \text{ for } M \geq M_0.$$

We now fix $M > M_0$ such that $2M > u_0(x)$ in $[0,1]$. Then

$$u_0(x) < 2M\phi_M(x) \text{ and } M < 2M\phi_M(x) \ \text{ for } x \in [0,1].$$

Let $\bar{u}(x,t)$ be the solution of (3.1)-(3.2) with initial condition $\bar{u}(x,0) = 2M\phi_M(x)$. Then we can find $\delta_0 > 0$ small so that $u_0(x) < \bar{u}(x,t)$, $M < \bar{u}(x,t)$ for $t \in (0, \delta_0]$ and $x \in [0,1]$. Hence for $t \in (0, \delta_0]$, we have

$$\begin{aligned}
\bar{u}_t &= D\bar{u}_{xx} + \left[g\left(e^{-k_0 x - k\int_0^x \bar{u}(y,t)dy}\right) - d\right]\bar{u} \\
&\leq D\bar{u}_{xx} + \left[-\Psi_M(x) - d\right]\bar{u} \\
&< D\bar{u}_{xx} + \left[-\Psi_M(x) + \lambda_1(\Psi_M)\right]\bar{u}.
\end{aligned}$$

Thus for $w(x,t) := \bar{u}(x,t) - 2M\phi_M(x)$, we have

$$\begin{cases}
w_t < Dw_{xx} + \left[-\Psi_M(x) + \lambda_1(\Psi_M)\right]w, & x \in [0,1], \ t \in (0, \delta_0], \\
w_x = 0, & x = 0, 1, \ t \in (0, \delta_0], \\
w = 0, & x \in [0,1], \ t = 0.
\end{cases}$$

By the strong maximum principle we deduce $w = \bar{u} - 2M\phi_M < 0$ for $t \in (0, \delta_0]$ and $x \in [0,1]$. It follows that $\bar{u}(x,s) < \bar{u}(x,0)$ for $0 < s \leq \delta_0$. Using the same argument as before, we deduce that

$$\bar{v}(x,t) := \int_0^x \bar{u}(s,t)ds$$

is monotone decreasing in t. Moreover, from Lemma 3.1 it follows that $\bar{v}(x,t) > v(x,t) := \int_0^x u(s,t)ds > \underline{v}(x,t)$ for all $t > 0$ and $x \in (0,1]$. Hence $\lim_{t\to\infty} \bar{v}(x,t) = v^*(x) \geq \int_0^x u_d(s)ds$. We may then use parabolic regularity theory much as before to deduce that $\bar{u}(x,t) \to (v^*)'(x)$

in $C^1([0,1])$, and $(v^*)'(x)$ is a positive steady state of (3.1)-(3.2). Thus we must have $(v^*)'(x) \equiv u_d(x)$.

Since $\underline{v} \le v \le \bar{v}$, and $\lim_{t\to\infty} \underline{v}(x,t) = \lim_{t\to\infty} \bar{v}(x,t) = \int_0^x u_d(s)ds$, we necessarily have

$$\lim_{t\to\infty} v(x,t) = \int_0^x u_d(s)ds.$$

Thus we can repeat the above argument to conclude that $u(x,t) \to u_d(x)$ as $t \to \infty$ uniformly for $x \in [0,1]$. This completes the proof. $\qquad\square$

Finally we consider the case $d = d_*$.

Theorem 3.4. *Suppose $d = d_*$. Then the solution $u(x,t)$ to (3.1)-(3.3) converges to 0 as $t \to \infty$ uniformly in $x \in [0,1]$.*

Proof. This follows from a simple modification of the second part of the proof of Theorem 3.3. Indeed, let $\bar{u}(x,t)$ be defined exactly as in the proof of Theorem 3.3. Then we know that $\bar{v}(x,t) := \int_0^x \bar{u}(s,t)ds > 0$ is strictly decreasing in t. Hence $\lim_{t\to\infty} \bar{v}(x,t) = v^*(x) \ge 0$ exists. By the same consideration as in the proof of Theorem 3.3 we can show that $\bar{u}(x,t) \to (v^*)'(x)$ as $t \to \infty$ in the norm of $C^1([0,1])$, and hence $(v^*)'(x)$ is a nonnegative steady-state of (3.1)-(3.2). However, since $d = d_*$, by Theorem 2.1, the only nonnegative steady state of (3.1)-(3.2) is the trivial solution 0. Hence $\bar{u}(x,t) \to 0$ as $t \to \infty$ uniformly for $x \in [0,1]$, and thus $\bar{v}(x,t) \to 0$ as $t \to \infty$.

Using Lemma 3.1 we deduce $0 < v(x,t) < \bar{v}(x,t)$, which implies that $v(x,t) \to 0$ as $t \to \infty$. Using this fact and the parabolic regularity, as before, we deduce $\lim_{t\to\infty} u(\cdot,t)$ exists in the $C^1([0,1])$ norm, and the limit is a nonnegative steady state of (3.1)-(3.2). Since $d = d_*$, this limit must be 0. This completes the proof. $\qquad\square$

4. STEADY-STATES OF THE TWO SPECIES MODEL

In this section we study the steady-states of the system (1.1)-(1.3) with $n = 2$. As before we assume, without loss of generality, $L = 1$ and $I_0 = 1$. Thus we are interested in the nonnegative solutions of the elliptic system

(4.1)
$$\begin{cases} D_1(u_1)_{xx} + \big[g_1(I(x)) - d_1\big]u_1 = 0, & 0 < x < 1, \\ D_2(u_2)_{xx} + \big[g_2(I(x)) - d_2\big]u_2 = 0, & 0 < x < 1, \\ (u_i)_x(0) = (u_i)_x(1) = 0, & i = 1,2, \end{cases}$$

where $g_1(I), g_2(I)$ satisfy (2.4), and

$$I(x) = e^{-k_0 x} \exp\Big(- \int_0^x \big[k_1 u_1(y) + k_2 u_2(y)\big]dy \Big),$$

with $k_0, k_1, k_2 > 0$.

In the following we will regard k_0, k_1, k_2 as fixed constants and treat d_1 and d_2 as varying parameters. We need to introduce some notations first. We will use $\lambda_1(\Psi)$ to denote the first

eigenvalue of (2.7) with $D = D_1$ and use $\mu_1(\Psi)$ to denote the first eigenvalue of (2.7) with $D = D_2$. We also denote

$$d_1^* = -\lambda_1(-g_1(e^{-k_0 x})), \ d_2^* = -\mu_1(-g_2(e^{-k_0 x})).$$

Nonnegative solutions of (4.1) can be classified into three classes: The unique trivial solution $(u_1, u_2) \equiv (0, 0)$, which exists for all d_1 and d_2. Two semitrivial solutions $(u_1, u_2) = (0, u_{d_2}^*)$ and $(u_1, u_2) = (u_{d_1}^*, 0)$, the former exists for $d_2 \in (0, d_2^*)$ and the latter exists for $d_1 \in (0, d_1^*)$, where $u_{d_1}^*, u_{d_2}^*$ denote the unique steady state for the u_1 and u_2 equations, respectively, guaranteed by Theorem 2.1. The third class are positive solutions (u_1, u_2) with $u_1(x) > 0$ and $u_2(x) > 0$ in $[0, 1]$, which are the most difficult to understand and are the main interest here.

Some necessary conditions for the existence of a positive solution to (4.1) can be easily observed. Suppose that (u_1, u_2) is a positive solution of (4.1). Then from the equation for u_1 we obtain

$$-d_1 = \lambda_1(-g_1(e^{-k_0 x - \int_0^x (k_1 u_1 + k_2 u_2) dy})) \in (\lambda_1(-g_1(e^{-k_0 x})), \lambda_1(0)) = (-d_1^*, 0).$$

That is $d_1 \in (0, d_1^*)$. Similarly from the equation for u_2 we deduce $d_2 \in (0, d_2^*)$. Thus for (4.1) to possess a positive solution we necessarily have

(4.2)
$$0 < d_1 < d_1^*, \ 0 < d_2 < d_2^*.$$

Next we assume (4.2) and use a global bifurcation argument to find sufficient conditions for the existence of positive solutions to (4.1). We will rewrite (4.1) as an abstract equation involving a completely continuous operator. Let $E = C([0, 1])$ and let P be the usual positive cone in E: $P = \{u \in E : u(x) \geq 0 \text{ in } [0, 1]\}$. We define $A : E \times E \to E \times E$ by

$$A(u_1, u_2) = (A_1(u_1, u_2), A_2(u_1, u_2)),$$

where

$$A_1(u_1, u_2) = L_1 \circ G_1(d_1, u_1, u_2), \ A_2(u_1, u_2) = L_2 \circ G_2(d_2, u_1, u_2),$$
$$G_1(d_1, u_1, u_2)(x) = \left[d_1^* - d_1 + g_1(e^{-k_0 x - \int_0^x (k_1 u_1 + k_2 u_2) dy})\right] u_1(x),$$
$$G_2(d_2, u_1, u_2)(x) = \left[d_2^* - d_2 + g_2(e^{-k_0 x - \int_0^x (k_1 u_1 + k_2 u_2) dy})\right] u_2(x),$$

and for $i = 1, 2$, L_i is the solution operator for the problem

$$-D_i u_{xx} + d_i^* u = f_i(x), \ u_x(0) = u_x(1) = 0,$$

namely $u = L_i(f_i)$. It is easily seen that (u_1, u_2) solves (4.1) if and only if $(u_1, u_2) = A(u_1, u_2)$.

By standard elliptic regularity theory we know that $A : E \times E \to E \times E$ is completely continuous. Moreover, by the strong maximum principle and the fact that (due to (4.2))

$$d_i^* - d_i + g_i(e^{-k_0 x - \int_0^x (k_1 u_1 + k_2 u_2) dy}) > 0 \text{ in } [0, 1],$$

we find that if $u_i \in P$ then $A_i(u_1, u_2) \in P$, and if $u_i \in \dot{P} := P \setminus \{0\}$ then $A_i(u_1, u_2) \in P^\circ := \{u \in P : u(x) > 0 \text{ in } [0, 1]\}$. Thus we have

$$A(P \times P) \subset P \times P, \ A(\dot{P} \times \dot{P}) \subset P^\circ \times P^\circ,$$
$$A(\dot{P} \times P) \subset P^\circ \times P, \ A(P \times \dot{P}) \subset P \times P^\circ.$$

To apply the bifurcation argument, we will fix $d_1 \in (0, d_1^*)$ and use d_2 as the bifurcation parameter. To stress the dependence of $A(u_1, u_2)$ on d_2, we rewrite it as $A(d_2, u_1, u_2)$. We will examine how a positive solution branch $\Gamma = \{(d_2, u_1, u_2)\} \subset R^1 \times P \times P$ bifurcates from the semitrivial solution branches $\Gamma_1 = \{(d_2, u_{d_1}^*, 0) : d_2 \in R^1\}$ and $\Gamma_2 = \{(d_2, 0, u_{d_2}^*) : d_2 \in (0, d_2^*)\}$. To this end, the Fréchet derivative of $A(d_2, u_1, u_2)$ with respect to (u_1, u_2) at $(u_{d_1}^*, 0)$ and at $(0, u_{d_2}^*)$, and the associated eigenvalue problems play a crucial role. We will denote these derivatives by $A'_{(u_1, u_2)}(d_2, u_{d_1}^*, 0)$ and $A'_{(u_1, u_2)}(d_2, 0, u_{d_2}^*)$, respectively, and the associated eigenvalue problems are

$$(4.3) \qquad A'_{(u_1, u_2)}(d_2, u_{d_1}^*, 0)(h_1, h_2)^T = \xi(h_1, h_2)^T,$$

and

$$(4.4) \qquad A'_{(u_1, u_2)}(d_2, 0, u_{d_2}^*)(h_1, h_2)^T = \eta(h_1, h_2)^T.$$

Here we use $(h_1, h_2)^T$ to denote the transpose of the row matrix (h_1, h_2). A direct calculation shows that $\eta = 1$ is an eigenvalue of (4.4) if and only if the following problem has a solution $(h_1, h_2) \neq (0, 0)$:

$$(4.5) \qquad \begin{cases} -D_1 h_1'' = [g_1(\sigma_2(x)) - d_1]h_1, & x \in (0, 1), \\ -D_2 h_2'' = [g_2(\sigma_2(x)) - d_2]h_2 \\ \qquad\quad - g_2'(\sigma_2(x))u_{d_2}^*(x)\sigma_2(x) \int_0^x [k_1 h_1(y) + k_2 h_2(y)]dy, & x \in (0, 1), \\ h_1' = h_2' = 0, & x = 0, 1, \end{cases}$$

where

$$\sigma_2(x) = e^{-k_0 x - \int_0^x k_2 u_{d_2}^*(y)dy}.$$

Similarly, if we define

$$\sigma_1(x) = e^{-k_0 x - \int_0^x k_1 u_{d_1}^*(y)dy},$$

then $\xi = 1$ is an eigenvalue of (4.3) if and only if the following problem has a solution $(h_1, h_2) \neq (0, 0)$:

$$(4.6) \qquad \begin{cases} -D_1 h_1'' = [g_1(\sigma_1(x)) - d_1]h_1 \\ \qquad\quad - g_1'(\sigma_1(x))u_{d_1}^*(x)\sigma_1(x) \int_0^x [k_1 h_1(y) + k_2 h_2(y)]dy, & x \in (0, 1), \\ -D_2 h_2'' = [g_2(\sigma_1(x)) - d_2]h_2, & x \in (0, 1), \\ h_1' = h_2' = 0, & x = 0, 1. \end{cases}$$

The following lemma holds the key for solving (4.5) and (4.6).

Lemma 4.1. *Let $i \in \{1, 2\}$. If $\psi \in C^2([0, 1])$ satisfies*

$$(4.7) \qquad \begin{cases} -D_i \psi'' = [g_i(\sigma_i(x)) - d_i]\psi - g_i'(\sigma_i(x))u_{d_i}^*(x)\sigma_i(x) \int_0^x k_i \psi(y)dy, & x \in (0, 1), \\ \psi'(0) = \psi'(1) = 0, \end{cases}$$

then $\psi \equiv 0$.

Proof. We argue indirectly. Suppose $\psi \not\equiv 0$ solves (4.7). We first claim that $\psi(0) \neq 0$. Otherwise, define

$$\xi(x) = \int_0^x \psi(y)dy, \ \eta(x) = \psi'(x).$$

Then $(\xi(x), \psi(x), \eta(x))$ is a solution of the ODE system

$$\begin{cases} \xi' = & \psi, \\ \psi' = & \eta, \\ \eta' = & -D_i^{-1}[g_i(\sigma_i(x)) - d_i]\psi + D_i^{-1}g_i'(\sigma_i(x))u_{d_i}^*(x)\sigma_i(x)k_i\xi, \end{cases}$$

with initial condition $(\xi(0), \psi(0), \eta(0)) = (0, 0, 0)$. Clearly $(\xi, \psi, \eta) \equiv (0, 0, 0)$ is the unique solution of this initial value ODE problem. Hence $\psi \equiv 0$, contradicting our assumption that $\psi \not\equiv 0$. This proves our claim that $\psi(0) \neq 0$.

Without loss of generality we may assume that $\psi(0) > 0$. Next we claim that $\psi(x)$ changes sign in $(0, 1)$. Otherwise $\psi(x) \geq, \not\equiv 0$ in $[0, 1]$. Multiply the first equation in (4.7) by $u_{d_i}^*$ and integrate it over $[0, 1]$; we easily deduce

$$\int_0^1 \left(g_i'(\sigma_i(x))[u_{d_i}^*(x)]^2\sigma_i(x) \int_0^x k_i\psi(y)dy \right)dx = 0.$$

But the integrand function of x is clearly nonnegative and not identically zero in $[0, 1]$. Hence the integral should be positive. This contradiction shows that $\psi(x)$ changes sign in $(0, 1)$.

Let $x_0 \in (0, 1)$ be the first zero of $\psi(x)$, namely $\psi(x) > 0$ in $[0, x_0)$ and $\psi(x_0) = 0$. We now consider the eigenvalue problem

(4.8) $-D_i\phi'' = [g_i(\sigma_i(x)) - d_i]\phi + \lambda\phi$ in $(0, x_0)$, $\phi'(0) = \phi(x_0) = 0$.

We claim that the first eigenvalue λ_1 of this problem is positive. Indeed, let ϕ_1 be a positive eigenfunction corresponding to λ_1. By the Hopf boundary lemma, $\phi_1'(x_0) < 0$. Multiplying the first equation in (4.8) (with $\lambda = \lambda_1$, $\phi = \phi_1$) by $u_{d_i}^*$ and integrating over $[0, x_0]$ we obtain

$$\begin{aligned} \int_0^{x_0}[g_i(\sigma_i) - d_i]\phi_1 u_{d_i}^* + \lambda_1 \int_0^{x_0}\phi_1 u_{d_i}^* = & \ -D_i \int_0^{x_0}\phi_1'' u_{d_i}^* \\ = & \ -D_i\phi_1'(x_0)u_{d_i}^*(x_0) - D_i \int_0^{x_0}(u_{d_i}^*)''\phi_1 \\ > & \ \int_0^{x_0}[g_i(\sigma_i) - d_i]\phi_1 u_{d_i}^*. \end{aligned}$$

Hence $\lambda_1 \int_0^{x_0}\phi_1 u_{d_i}^* > 0$, which gives $\lambda_1 > 0$, as claimed.

To obtain the desired contradiction, we now multiply the first equation in (4.8) (with $\lambda = \lambda_1$, $\phi = \phi_1$) by ψ and then integrate it over $[0, x_0]$. It results

$$\begin{aligned} & \int_0^{x_0}[g_i(\sigma_i) - d_i]\phi_1\psi + \lambda_1 \int_0^{x_0}\phi_1\psi \\ & = -D_i \int_0^{x_0}\phi_1''\psi = -D_i \int_0^{x_0}\psi''\phi_1 \\ & = \int_0^{x_0}[g_i(\sigma_i) - d_i]\phi_1\psi - \int_0^{x_0}\left[g_i'(\sigma_i)\sigma_i u_{d_i}^* \int_0^x k_i\psi dy\right]\phi_1 dx. \end{aligned}$$

It follows that

$$(4.9) \qquad \lambda_1 \int_0^{x_0} \phi_1 \psi = -\int_0^{x_0} \left[g_i'(\sigma_i) \sigma_i u_{d_i}^* \int_0^x k_i \psi dy \right] \phi_1 dx.$$

Since $\lambda_1 > 0$ and $\psi(x) > 0$ in $[0, x_0)$, the left side of the above identity is positive. However, the bracketed integrand function in the right side of (4.9) is nonnegative and hence the right side of (4.9) is not positive. This contradiction completes the proof. $\qquad \square$

Using Lemma 4.1, we can easily prove the following result.

Lemma 4.2. *Problem* (4.5) *has a solution* $(h_1, h_2) \neq (0, 0)$ *if and only if* $h_1 \neq 0$ *and*

$$-D_1 h_1'' = [g_1(\sigma_2(x)) - d_1] h_1, \ h_1'(0) = h_1'(1) = 0.$$

Moreover, with h_1 *given,* h_2 *can be uniquely solved from the second equation in* (4.5) *together with the Neumann boundary conditions.*

Similarly, (4.6) *has a solution* $(h_1, h_2) \neq (0, 0)$ *if and only if* $h_2 \neq 0$ *and*

$$-D_2 h_2'' = [g_2(\sigma_1(x)) - d_2] h_2, \ h_2'(0) = h_2'(1) = 0.$$

Moreover, with h_2 *given,* h_1 *can be uniquely solved from the first equation in* (4.6) *together with the Neumann boundary conditions.*

Proof. We only consider the statement for (4.5); the proof of that for (4.6) is analogous. Let (h_1, h_2) solve (4.5). If $h_1 = 0$, then by Lemma 4.1 we deduce $h_2 = 0$. Suppose now $h_1 \neq 0$. Then we can apply the Fredholm alternative for compact operators and Lemma 4.1 to conclude that the second equation in (4.5) together with the Neumann boundary conditions is uniquely solvable for any given h_1. $\qquad \square$

Recall that

$$\sigma_2(x) = \sigma_2(d_2, x) = e^{-k_0 x - \int_0^x k_2 u_{d_2}^*(y) dy},$$

and

$$\sigma_1(x) = \sigma_1(d_1, x) = e^{-k_0 x - \int_0^x k_1 u_{d_1}^*(y) dy}.$$

By Theorem 2.1 (iv), we know that $d_2 \to \sigma_2(d_2, x)$ is strictly increasing for $x \in (0, 1]$. This implies that

$$\lambda(d_2) := -\lambda_1 \big(- g_1(\sigma_2(d_2, \cdot)) \big)$$

is strictly increasing for $d_2 \in (0, d_2^*)$. By Theorem 2.1 (i), we know that $\lambda(d_2)$ is continuous. Since $u_{d_2}^*(x) \to 0$ uniformly in $[0, 1]$ as $d_2 \to d_2^*$ and $u_{d_2}^*(x) \to \infty$ uniformly in $[0, 1]$ as $d_2 \to 0$, we easily see that

$$\lim_{d_2 \to 0} \lambda(d_2) = 0, \quad \lim_{d_2 \to d_2^*} \lambda(d_2) = d_1^*.$$

Therefore for any given $d_1 \in (0, d_1^*)$, there exists a unique $\hat{d}_2 = \hat{d}_2(d_1) \in (0, d_1^*)$ such that

$$(4.10) \qquad \lambda(\hat{d}_2) = d_1.$$

Let us also introduce

$$(4.11) \qquad \tilde{d}_2 = \tilde{d}_2(d_1) := -\mu_1 \big(- g_2(\sigma_1(d_1, \cdot)) \big).$$

It is easily seen that $\tilde{d}_2 \in (0, d_2^*)$.

We are now ready to state and prove our main result of this section.

Theorem 4.3. *For fixed $d_1 \in (0, d_1^*)$ let $\hat{d}_2$ and $\tilde{d}_2$ be defined as above. Then (4.1) has a positive solution (u_1, u_2) if d_2 lies between $\hat{d}_2$ and $\tilde{d}_2$. Moreover, there exists a branch of positive solutions $\Gamma = \{(d_2, u_1, u_2)\} \subset R^1 \times E \times E$ that meets the semitrivial solution branch $\Gamma_1 = \{(d_2, u_{d_1}^*, 0) : d_2 \in R^1\}$ precisely at $(\tilde{d}_2, u_{d_1}^*, 0)$, and meets the semitrivial solution branch $\Gamma_2 = \{(d_2, 0, u_{d_2}^*) : d_2 \in (0, d_2^*)\}$ precisely at $(\hat{d}_2, 0, u_{\hat{d}_2}^*)$. More accurately, Γ is a connected set in $R^1 \times E \times E$ such that $\Gamma \cap \Gamma_1 = \{(\tilde{d}_2, u_{d_1}^*, 0)\}$, $\Gamma \cap \Gamma_2 = \{(\hat{d}_2, 0, u_{\hat{d}_2}^*)\}$, and $\Gamma \setminus \{(\tilde{d}_2, u_{d_1}^*, 0), (\hat{d}_2, 0, u_{\hat{d}_2}^*)\}$ consists of positive solutions of (4.1).*

Proof. For clarity we divide the proof into four steps.

Step 1: We show that for any small $\delta > 0$ and fixed $d_1 \in (0, d_1^*)$, there exists C such that any positive solution (u_1, u_2) of (4.1) with $d_2 \in [\delta, d_2^* - \delta]$ satisfies

$$(4.12) \qquad \|u_1\|_\infty + \|u_2\|_\infty < C.$$

Otherwise we can find a small $\delta > 0$ and a sequence $d_2^n \in [\delta, d_2^* - \delta]$ such that (4.1) with $d_2 = d_2^n$ has a positive solution (u_1^n, u_2^n) satisfying

$$\lim_{n \to \infty} (\|u_1^n\|_\infty + \|u_2^n\|_\infty) = \infty.$$

By passing to a subsequence, we have either $\|u_2^n\|_\infty \to \infty$ or $\|u_1^n\|_\infty \to \infty$. In the first case, we define $\hat{u}_n = u_2^n / \|u_2^n\|_\infty$. Then from the equation for u_2^n we deduce

$$(4.13) \qquad -D_2 \hat{u}_n'' = [g_2(f_n(x)) - d_2^n]\hat{u}_n, \ \hat{u}_n'(0) = \hat{u}_n'(1) = 0,$$

where

$$f_n(x) = e^{-k_0 x - \int_0^x (k_1 u_1^n + k_2 u_2^n) dy}.$$

Since $\|\hat{u}_n\|_\infty = 1$ and the right side of the first equation in (4.13) has a bound in $L^\infty([0,1])$ that is independent of n, by standard elliptic regularity we know that $\{\hat{u}_n\}$ is precompact in $C^1([0,1])$. Hence by passing to a subsequence we may assume that $\hat{u}_n \to \hat{u}$ in $C^1([0,1])$. Since $0 < f_n(x) \le 1$ and $\delta \le d_2^n \le d_2^* - \delta$, by passing to a subsequence we may assume that $f_n \to f$ weakly in $L^2([0,1])$ and $d_2^n \to d_2^\infty$, with $0 \le f \le 1$ and $d_2^\infty \in [\delta, d_2^* - \delta]$. Since g_2 is C^1, we easily see that $g_2(f_n) \to g_2(f)$ weakly in $L^2([0,1])$. Thus $\hat{u}$ is a weak solution to

$$-D_2 \hat{u}'' = [g_2(f(x)) - d_2^\infty]\hat{u}, \ \hat{u}'(0) = \hat{u}'(1) = 0.$$

Clearly $\hat{u} \ge 0$ and $\|\hat{u}\|_\infty = 1$. Thus we can apply the strong maximum principle to conclude that $\hat{u}(x) > 0$ in $[0,1]$. This implies that $u_2^n(x) \to \infty$ uniformly in $[0,1]$ and hence $f \equiv 0$, $g_2(f) \equiv 0$. Thus $\hat{u}$ is a positive solution of

$$-D_2 \hat{u}'' = -d_2^\infty \hat{u}, \ \hat{u}'(0) = \hat{u}'(1) = 0.$$

This implies that $-d_2^\infty = \mu_1(0) = 0$, a contradiction to $d_2^\infty \in [\delta, d_2^* - \delta]$.

If $\|u_1^n\|_\infty \to \infty$, then we can use the equation for u_1^n and a similar argument to reach a contradiction. This completes the proof of Step 1.

Step 2: We show that if $\delta > 0$ is small enough, then (4.1) has no positive solution if $d_2 \notin (\delta, d_2^* - \delta)$.

Otherwise, due to (4.2), we can find $d_2^n \downarrow 0$ or $d_2^n \uparrow d_2^*$ and a positive solution (u_1^n, u_2^n) of (4.1) with $d_2 = d_2^n$. In the first case we define $\hat{u}_n$ and f_n as in Step 1 above, and find by the same reasoning that by passing to a subsequence $\hat{u}_n \to \hat{u}$ in $C^1([0,1])$, $f_n \to f$ and $g_2(f_n) \to g_2(f)$ weakly in $L^2([0,1])$, and $\hat{u}$ is a positive solution to

$$-D_2\hat{u}'' = g_2(f)\hat{u}, \ \hat{u}'(0) = \hat{u}'(1) = 0.$$

Integrating the first equation for x over $[0,1]$, we deduce $\int_0^1 g_2(f)\hat{u}\,dx = 0$. Since $\hat{u} > 0$ in $[0,1]$ and $g_2(f(x)) \geq 0$ in $[0,1]$, the above identity implies that $g_2(f(x)) = 0$ a.e. in $[0,1]$. It follows that $f(x) = 0$ a.e. in $[0,1]$.

Now define $\hat{v}_n = u_1^n/\|u_1^n\|_\infty$ and we obtain from the equation for u_1^n that

$$-D_1\hat{v}_n = [g_1(f_n(x)) - d_1]\hat{v}_n, \ \hat{v}_n'(0) = \hat{v}_n'(1) = 0.$$

As before by elliptic regularity, subject to passing to a subsequence, $\hat{v}_n \to \hat{v}$ in $C^1([0,1])$ and $g_2(f_n) \to g_1(f) = 0$ weakly in $L^2([0,1])$, and $\hat{v}$ is a positive solution to

$$-D_1\hat{v}'' = -d_1\hat{v}, \ \hat{v}'(0) = \hat{v}'(1) = 0.$$

This implies $d_1 = 0$, a contradiction to our assumption $d_1 \in (0, d_1^*)$.

Next we consider the case $d_2^n \to d_2^*$. We define $\hat{u}_n$, $\hat{v}_n$ and f_n as above. By the same argument we know that by passing to a subsequence, $\hat{u}_n \to \hat{u}$ and $\hat{v}_n \to \hat{v}$ in $C^1([0,1])$, $f_n \to f$ and $g_i(f_n) \to g_i(f)$ weakly in $L^2([0,1])$, and $\hat{u}$, $\hat{v}$ are positive solutions to

$$(4.14) \qquad -D_2\hat{u}'' = [g_2(f) - d_2^*]\hat{u}, \ \hat{u}'(0) = \hat{u}'(1) = 0,$$

and

$$(4.15) \qquad -D_1\hat{v}'' = [g_1(f) - d_1]\hat{v}, \ \hat{v}'(0) = \hat{v}'(1) = 0,$$

respectively.

Let us now look at the sequence $\{\|u_1^n\|_\infty\}$. If this sequence is not bounded, then by passing to a subsequence we have $\|u_1^n\|_\infty \to \infty$ and hence $u_1^n = \|u_1^n\|_\infty \hat{v}_n \to \infty$ uniformly in $[0,1]$. This implies that $f \equiv 0$ and hence (4.15) becomes

$$-D_1\hat{v}'' = -d_1\hat{v}, \ \hat{v}'(0) = \hat{v}'(1) = 0,$$

which implies $d_1 = 0$, a contradiction. Thus $\{\|u_1^n\|_\infty\}$ is bounded. For the same reason, $\{\|u_2^n\|_\infty\}$ is bounded. So we may assume that

$$\|u_1^n\|_\infty \to \alpha_1 \geq 0, \ \|u_2^n\|_\infty \to \alpha_2 \geq 0.$$

It then follows that

$$f_n(x) \to e^{-k_0 x - \int_0^x (k_1\alpha_1\hat{v} + k_2\alpha_2\hat{u})dy} \text{ uniformly in } [0,1].$$

Thus

$$f(x) = e^{-k_0 x - \int_0^x (k_1\alpha_1\hat{v} + k_2\alpha_2\hat{u})dy} \leq e^{-k_0 x}$$

with equality holding for all $x \in [0, 1]$ if and only if $\alpha_1 = \alpha_2 = 0$. It follows that $g_2(f(x)) \leq g_2(e^{-k_0 x})$ with equality holding for all $x \in [0, 1]$ if and only if $\alpha_1 = \alpha_2 = 0$. From this and (4.14) we deduce

$$d_2^* = -\mu_1(-g_2(f)) \leq -\mu_1(-g_2(e^{-k_0 x})),$$

with equality holding if and only if $\alpha_1 = \alpha_2 = 0$. Thus in view of the definition of d_2^*, we necessarily have $\alpha_1 = \alpha_2 = 0$ and thus $f(x) = e^{-k_0 x}$. We now use (4.15) and find

$$d_1 = -\lambda_1(-g_1(f)) = -\lambda_1(-g_1(e^{-k_0 x})).$$

That is, $d_1 = d_1^*$, a contradiction to our assumption on d_1. This completes our proof of Step 2.
Step 3: Global bifurcation analysis.

Let us now fix $\delta > 0$ small enough such that (4.1) has no positive solution for $d_2 \notin \Lambda := (\delta, d_2^* - \delta)$, and $\tilde{d}_2, \hat{d}_2 \in \Lambda$. Then define $\Omega = \Lambda \times U \times V$ with

$$U = \{u_1 \in P : \|u_1\|_\infty < C\}, \ V = \{u_2 \in P : \|u_2\|_\infty < C\},$$

where $C > 0$ is large enough such that (4.12) holds and $\|u_{d_1}^*\|_\infty < C$.

We are going to apply the global bifurcation result of [5], namely Theorem 2.3 in [5], to the operator

$$(d_2, u_1, u_2) \in \Omega \to A(d_2, u_1, u_2) \in P \times P.$$

It is easily seen that the conditions (I'), (II') and (III') in that theorem are satisfied, with $T = \{(u_{d_1}^*, 0)\}$. By that theorem, if for some small $\epsilon > 0$, $A(d_2, u_1, u_2) = (u_1, u_2)$ has no bifurcation value in $(\tilde{d}_2 - \epsilon, \tilde{d}_2) \cup (\tilde{d}_2, \tilde{d}_2 + \epsilon)$, and

(4.16) $$\text{index}_{P \times P}(A(\lambda, \cdot), (u_{d_1}^*, 0)) \neq \text{index}_{P \times P}(A(\mu, \cdot), (u_{d_1}^*, 0))$$

for $\lambda \in (\tilde{d}_2 - \epsilon, \tilde{d}_2)$, $\mu \in (\tilde{d}_2, \tilde{d}_2 + \epsilon)$, then

(i) $d_2 = \tilde{d}_2$ is a bifurcation value,
(ii) there is a connected set $\Sigma \subset \overline{\Sigma}_*$, where $\Sigma_* = \{(d_2, u_1, u_2) \in \Omega : A(d_2, u_1, u_2) = (u_1, u_2), u_2 \neq 0\}$, such that Σ contains the point $(\tilde{d}_2, u_{d_1}^*, 0)$ and
    (a) a point $(\lambda_0, u_{d_1}^*, 0)$ with $\lambda_0 \neq \tilde{d}_2$, or
    (b) a point in $\partial\Omega$, or
    (c) a point in $\Lambda \times (0, 0)$.
    where

$$\partial\Omega := \{(d_2, u_1, u_2) \in \overline{\Omega} : d_2 = \delta, \text{ or } d_2 = d_2^* - \delta, \text{ or } \|u_1\|_\infty = C, \text{ or } \|u_2\|_\infty = C\}.$$

By Lemma 4.2 we find that for $\epsilon > 0$ small and $d_2 \in [\tilde{d}_2 - \epsilon, \tilde{d}_2 + \epsilon] \setminus \{\tilde{d}_2\}$, $(u_{d_1}^*, 0)$ is a nondegenerate solution of (4.1). Thus there is no bifurcation value in $[\tilde{d}_1 - \epsilon, \tilde{d}_2 + \epsilon] \setminus \{\tilde{d}_2\}$. It follows that the fixed point indices (with respect to the cone $P \times P$) in (4.16) are well-defined and are independent of λ and μ in their respective given ranges.

Suppose for the moment that (4.16) holds; we now analyze the connected set Σ. We first observe that $\Sigma \cap \Gamma_1 = \{(\tilde{d}_2, u_{d_1}^*, 0)\}$. Indeed, suppose $(\lambda, u_{d_1}^*, 0) \in \Sigma \cap \Gamma_1$. Then we can find

a sequence of points $(d_2^n, u_1^n, u_2^n) \in \Sigma_*$ that converges to $(\lambda, u_{d_1}^*, 0)$ in $R^1 \times E \times E$. Using the equation for u_2^n we obtain

$$-d_2^n = \mu_1(-g_2(e^{-k_0 x - \int_0^x (k_1 u_1^n + k_2 u_2^n) dy})) \to \mu_1(-g_2(e^{-k_0 x - \int_0^x k_1 u_{d_1}^* dy})) = -\tilde{d}_2.$$

Hence $\lambda = \tilde{d}_2$. This proves $\Sigma \cap \Gamma_1 = \{(\tilde{d}_2, u_{d_1}^*, 0)\}$, which implies that alternative (a) cannot occur.

We now show that alternative (c) does not happen either. Otherwise, we can find a sequence of points $(d_2^n, u_1^n, u_2^n) \in \Sigma_*$ that converges to $(\lambda, 0, 0) \in \Lambda \times (0, 0)$. Again we use the equation for u_2^n and obtain

$$-d_2^n = \mu_1(-g_2(e^{-k_0 x - \int_0^x (k_1 u_1^n + k_2 u_2^n) dy})) \to \mu_1(-g_2(e^{-k_0 x})) = -d_2^*.$$

Thus $d_2^* = \lambda \in \Lambda = (\delta, d_2^* - \delta)$, which is a contradiction. Hence (c) cannot occur.

So alternative (b) necessarily happens. But by our choice of δ and C used in the definition of Ω, no positive solution (d_2, u_1, u_2) belongs to $\partial\Omega$. Thus necessarily $\Sigma \cap \partial\Omega$ consists of semitrivial solutions. Since $\Sigma \cap \Gamma_1 = \{(\tilde{d}_2, u_{d_1}^*, 0)\}$ and $\tilde{d}_2 \in \Lambda$, $\|u_{d_1}^*\|_\infty < C$, the semitrivial solutions in $\Sigma \cap \partial\Omega$ must belong to Γ_2. This shows that Σ intersects Γ_2.

We show next that Σ has a subset Γ which is connected and has the following properties:

$$\Gamma \cap \Gamma_2 = \{(\hat{d}_2, 0, u_{\hat{d}_2}^*)\}, \ \Gamma \cap \Gamma_1 = \{(\tilde{d}_2, u_{d_1}^*, 0)\},$$

$$\Gamma \setminus \{(\tilde{d}_2, u_{d_1}^*, 0), (\hat{d}_2, 0, u_{\hat{d}_2}^*)\} \text{ consists of positive solutions of (4.1)}.$$

To this end we consider $\Gamma_* := \Sigma \setminus \Gamma_2$. By what was proved above, we know that $(\tilde{d}_2, u_{d_1}^*, 0) \in \Gamma_*$. From the connectedness of Σ we easily deduce that $\overline{\Gamma}_* \cap \Gamma_2 \neq \emptyset$. Then much as before we can show that $\overline{\Gamma}_* \cap \Gamma_2 = \{(\hat{d}_2, 0, u_{\hat{d}_2}^*)\}$. We claim that $\overline{\Gamma}_*$ has a connected component Γ which contains both $(\hat{d}_2, 0, u_{\hat{d}_2}^*)$ and $(\tilde{d}_2, u_{d_1}^*, 0)$. Otherwise, let Γ_*^1 be the maximal connected subset of $\overline{\Gamma}_*$ containing $(\tilde{d}_2, u_{d_1}^*, 0)$; then Γ_*^1 and $\Sigma \setminus \Gamma_*^1$ have positive distance to each other, which implies that Σ is not connected. This proves that the above mentioned Γ does exist. Much as before we can easily show that $\Gamma \cap \Gamma_2 = \{(\hat{d}_2, 0, u_{\hat{d}_2}^*)\}$ and $\Gamma \cap \Gamma_1 = \{(\tilde{d}_2, u_{d_1}^*, 0)\}$. It follows that $\Gamma \setminus \{(\tilde{d}_2, u_{d_1}^*, 0), (\hat{d}_2, 0, u_{\hat{d}_2}^*)\}$ consists of positive solutions of (4.1).

To complete the proof of the theorem, it remains to prove (4.16).

Step 4: Fixed point index calculation.

We now calculate the fixed point indices appearing in (4.16) by making use of Theorem 2.1 in [4]. Let B_1 be a small ball in E containing $u_{d_1}^*$. Since $u_{d_1}^* \in P^\circ$, we may assume that $B_1 \subset P^\circ$. Then by Theorem 2.1 of [4], we have

$$\text{index}_{P \times P}(A(d_2, \cdot), (u_{d_1}^*, 0)) = \begin{cases} 0 & \text{if } r(L) > 1, \\ \deg_P(I - A_1(\cdot, 0), B_1) & \text{if } r(L) < 1, \end{cases}$$

where $L = (A_2)'_{u_2}(u_{d_1}^*, 0)$ and $r(L)$ denotes the spectral radius of the linear operator L.

It is easily checked that $r(L) > 1$ if $d_2 < -\mu_1(-g_2(\sigma_1)) = \tilde{d}_2$, and $r(L) < 1$ if $d_2 > -\mu_1(-g_2(\sigma_1)) = \tilde{d}_2$. Thus

$$\text{index}_{P \times P}(A(d_2, \cdot), (u_{d_1}^*, 0)) = \begin{cases} 0 & \text{if } d_2 < \tilde{d}_2, \\ \deg_P(I - A_1(\cdot, 0), B_1) & \text{if } d_2 > \tilde{d}_2. \end{cases}$$

We show next that

$$\deg_P(I - A_1(\cdot, 0), B_1) = 1.$$

Since $u_{d_1}^*$ is the only fixed point of $A_1(\cdot, 0)$ in B_1, we clearly have

$$\deg_P(I - A_1(\cdot, 0), B_1) = \text{index}_P(A_1(\cdot, 0), u_{d_1}^*).$$

We will use a homotopy argument to $A_1(\lambda, u_1, 0) = L_1 \circ G_1(\lambda, u_1, 0)$ with $\lambda \in [d_1, d_1^* + 1]$. By Theorem 2.1 we know that for $\lambda \in [d_1, d_1^*)$ the equation $A_1(\lambda, u, 0) = u$ has exactly two solutions in P: The trivial solution $u = 0$ and the unique positive solution $u = u_\lambda > 0$. For $\lambda \in [d_1^*, d_1^*+1]$, there is one solution in P: $u = 0$. Moreover, one easily sees that 0 is a linearized stable fixed point of $A_1(\lambda, \cdot, 0)$ when $\lambda > d_1^*$, and it is a linearized unstable fixed point when $\lambda < d_1^*$. It follows that

$$\text{index}_P(A_1(\lambda, \cdot, 0), 0) = 0 \text{ for } \lambda < d_1^* \text{ and this index is } 1 \text{ for } \lambda > d_1^*.$$

Choose $C_0 > 0$ large enough such that $\|u_\lambda\|_\infty < C_0$ for $\lambda \in [d_1, d_1^*)$, and denote $P_{C_0} := \{u \in P : \|u\|_\infty < C_0\}$. Then by the homotopy invariance property of the topological degree, we find that $\deg_P(I - A(\lambda, \cdot, 0), P_{C_0})$ is well-defined and its value does not depend on λ for $\lambda \in [d_1, d_1^* + 1]$. By the additivity of the topological degree we have

$$\begin{aligned} \deg_P(I - A_1(\lambda, \cdot, 0), P_{C_0}) &= \text{index}_P(A_1(\lambda, \cdot, 0), 0) + \text{index}_P(A_1(\lambda, \cdot, 0), u_\lambda) \\ &= \text{index}_P(A_1(\lambda, \cdot, 0), u_\lambda) \end{aligned}$$

for $\lambda \in [d_1, d_1^*)$, and

$$\deg_P(I - A(\lambda, \cdot, 0), P_{C_0}) = \text{index}_P(A_1(\lambda, \cdot, 0), 0) = 1$$

for $\lambda \in (d_1^*, d_1^* + 1]$. It follows that

$$\text{index}_P(A_1(\lambda, \cdot, 0), u_\lambda) = 1$$

for $\lambda \in [d_1, d_1^*)$. Taking $\lambda = d_1$ we obtain

$$\deg_P(I - A_1(\cdot, 0), B_1) = \text{index}_P(A_1(\cdot, 0), u_{d_1}^*) = 1.$$

Thus (4.16) holds, and the proof is complete. $\square$

Remark 4.4. The degree calculation methods developed in [4, 6] and the bifurcation method of [5] can also be used to study the existence of positive steady states of the phytoplankton model with three and more species.

We note that the global bifurcation arguments in [2] do not seem easily applicable to our problem here. Firstly in the abstract global bifurcation result in [2] the fixed point index in the entire space is required, which was calculated there based on a good understanding of the eigenvalues of (4.3) with $\xi \neq 1$. This seems difficult to obtain due to the nonlocal terms in our problem. Secondly the analysis in [2] also relies on the local bifurcation result of [3], which requires the bifurcation point to correspond to a simple eigenvalue. In contrast, the global bifurcation result of [5] used here involves the fixed point index in the positive cone, which depends on (4.3) with $\xi = 1$ and the second equation in (4.6), which are much easier to handle. Moreover, the result of [5] can be used to discuss systems with more than two equations. (The fixed point index calculation in [2] can also be done by using Theorem 3.1 in [5], which avoids the analysis of the eigenvalues of (4.3) with $\xi \neq 1$.)

We complete this section with some further analysis on $\hat{d}_2$ and $\tilde{d}_2$. We now regard $d_i \in (0, d_i^*)$ $(i = 1, 2)$ as fixed and examine the variation of $\hat{d}_2$ and $\tilde{d}_2$ as k_1 and k_2 vary. Let us note that by definition, d_1^* and d_2^* are independent of k_1 and k_2. We now denote the unique positive solution of the equation for u_1 in (4.1) by $u_{k_1}^\dagger$. It is easily checked that $u_{k_1}^\dagger = k_1 u_1^\dagger$. Thus

$$\sigma_1(x) = e^{-k_0 x - \int_0^x k_1^2 u_1^\dagger dy}.$$

It follows that

$$\tilde{d}_2 = -\mu_1(-g_2(\sigma_1))$$

is continuous and strictly decreasing in k_1 and

$$\lim_{k_1 \to 0} \tilde{d}_2 = d_2^*, \quad \lim_{k_1 \to \infty} \tilde{d}_2 = 0.$$

Thus there exists a unique $k_1^* > 0$ such that

$$\tilde{d}_2 = d_2 \text{ if } k_1 = k_1^*, \ \tilde{d}_2 < d_2 \text{ if } k_1 > k_1^*, \ \tilde{d}_2 > d_2 \text{ if } 0 < k_1 < k_1^*.$$

Similarly, if we define

$$\tilde{d}_1 = -\lambda_1(-g_1(\sigma_2)),$$

then there exists a unique $k_2^* > 0$ such that

$$\tilde{d}_1 = d_1 \text{ if } k_2 = k_2^*, \ \tilde{d}_1 < d_1 \text{ if } k_2 > k_2^*, \ \tilde{d}_1 > d_1 \text{ if } 0 < k_2 < k_2^*.$$

On the other hand, it is easily seen that

$$d_1 < \tilde{d}_1 \text{ and } d_2 < \tilde{d}_2 \text{ imply } \hat{d}_2 < d_2 < \tilde{d}_2$$

and

$$d_1 > \tilde{d}_1 \text{ and } d_2 > \tilde{d}_2 \text{ imply } \hat{d}_2 > d_2 > \tilde{d}_2.$$

Hence we can use Theorem 4.3 to obtain the following conclusion:

For fixed $d_i \in (0, d_i^*)$ $(i = 1, 2)$, if $(k_1 - k_1^*)(k_2 - k_2^*) > 0$, then (4.1) has at least one positive solution.

We conjecture that (4.1) has no positive solution when $(k_1 - k_1^*)(k_2 - k_2^*) < 0$, and it has a continuum of positive solutions when $k_1 = k_1^*$ and $k_2 = k_2^*$.

Remark 4.5. It can be shown that when $0 < d_i < \tilde{d}_i$ $(i = 1, 2)$, the set of positive solutions of (4.1) has topological degree 1, and if $d_i > \tilde{d}_i$ $(i = 1, 2)$, the set of positive solutions of (4.1) has topological degree -1. The first conclusion can be extended to the $n \geq 3$ species case (by arguments similar to those in [6]).

5. Uniform persistence and extinction for the two species model

In this section we consider the corresponding parabolic system of (4.1), namely

$$(5.1) \quad \begin{cases} (u_1)_t = D_1(u_1)_{xx} + \big[g_1(I(x,t)) - d_1\big]u_1, & 0 < x < 1, \ t > 0, \\ (u_2)_t = D_2(u_2)_{xx} + \big[g_2(I(x,t)) - d_2\big]u_2, & 0 < x < 1, \ t > 0, \\ (u_i)_x(0,t) = (u_i)_x(1,t) = 0, & t > 0, \ i = 1, 2, \\ u_i(x,0) = u_i^0(x), & 0 < x < 1, \ i = 1, 2, \end{cases}$$

where $u_1^0, u_2^0 \in P$, $g_1(I), g_2(I)$ satisfy (2.4), and

$$I(x,t) = e^{-k_0 x} \exp\Big(-\int_0^x \big[k_1 u_1(y,t) + k_2 u_2(y,t)\big] dy \Big),$$

with $k_0, k_1, k_2 > 0$.

If the initial data in (5.1) satisfy $u_1^0 \in \dot{P}$ and $u_2^0 \equiv 0$, then from the results in section 3 we have:

$$(5.2) \quad \begin{array}{ll} (i) & \text{If } 0 < d_1 < d_1^* \text{ then } u_1(x,t) \to u_1^*(x) > 0 \text{ as } t \to \infty, \ u_2(x,t) \equiv 0. \\ (ii) & \text{If } d_1 \geq d_1^* \text{ then } u_1(x,t) \to 0 \text{ as } t \to \infty, \ u_2(x,t) \equiv 0, \end{array}$$

where we use u_i^* to denote $u_{d_i}^*$ for convenience.

Similarly, if $u_2^0 \in \dot{P}$ and $u_1^0 \equiv 0$, then we have:

$$(5.3) \quad \begin{array}{ll} (i) & \text{If } 0 < d_2 < d_2^* \text{ then } u_2(x,t) \to u_2^*(x) > 0 \text{ as } t \to \infty, \ u_1(x,t) \equiv 0. \\ (ii) & \text{If } d_2 \geq d_2^* \text{ then } u_2(x,t) \to 0 \text{ as } t \to \infty, \ u_1(x,t) \equiv 0. \end{array}$$

Next we consider the case that $u_i^0 \in \dot{P}$ for $i = 1, 2$. By standard arguments one sees that (5.1) has a unique solution (u_1, u_2) and $u_i(x,t) > 0$ for $t > 0$ and $x \in [0,1]$. Since

$$(u_i)_t \leq D_i(u_i)_{xx} + [g_i(1) - d_i]u_i,$$

one can use the comparison principle to see that u_i does not blow up in finite time, and hence it is defined for all $t > 0$. We show next that it is uniformly bounded for all $t > 0$. Indeed, since $g_i(I) \leq \sigma I$ for some $\sigma > 0$ and $I \in [0,1]$, we have, for $i = 1, 2$,

$$(u_i)_t \leq D_i(u_i)_{xx} + [\sigma e^{-k_i \int_0^x u_i dy} - d_i]u_i.$$

Hence by the argument used in the proof of Lemma 3.2 we deduce that for some $C > 0$,

$$(5.4) \quad 0 \leq u_i(x,t) \leq C \text{ for all } x \in [0,1] \text{ and } t > 0.$$

Theorem 5.1. (Uniform Persistence) *If $0 < d_1 < \tilde{d}_1$ and $0 < d_2 < \tilde{d}_2$ then the system (5.1) with initial data $u_i^0 \in \dot{P}$ $(i = 1, 2)$ is uniformly persistent: There exists $\epsilon_0 > 0$ such that*

$$\liminf_{t \to \infty} \|u_1(\cdot, t)\|_\infty \geq \epsilon_0, \quad \liminf_{t \to \infty} \|u_2(\cdot, t)\|_\infty \geq \epsilon_0.$$

Proof. We apply a general result of Hale and Waltman, namely Theorem 4.1 in [11]. We note that (5.1) generates a semigroup (more often called a semiflow) $T(t)$ on $P \times P$, and $T(t)$ is compact for $t > 0$. By the results of section 3 (for semitrivial solutions) and (5.4) (for positive solutions), $T(t)$ is point dissipative in $P \times P$.

Let

$$X^0 = \dot{P} \times \dot{P} \text{ and } X = \overline{X^0} = P \times P.$$

Then X^0 is invariant and relatively open in X, and $\partial X^0 = (P \times \{0\}) \cup (\{0\} \times P)$ is also invariant. From Theorem 3.3, the rest point $M_1 = (u_1^*, 0)$ attracts $(u_1^0, 0)$ with $u_1^0 \in \dot{P}$, and $M_2 = (0, u_2^*)$ attracts $(0, u_2^0)$ with $u_2^0 \in \dot{P}$. The omega limit sets of the semiflow on ∂X^0, denoted by $\tilde{A}_\partial$, are given by $\tilde{A}_\partial = \{M_0, M_1, M_2\}$, where $M_0 = (0, 0)$. Now $M = \{M_0, M_1, M_2\}$ is a covering of $\tilde{A}_\partial$. From (5.2) and (5.3), M_0 is a repeller, M contains no cycle, and this covering is isolated. To apply Theorem 4.1 in [11], it remains to check that the stable set of M_i, denoted by $W^s(M_i)$, does not intersect X^0, that is $W^s(M_i) \cap X^0 = \emptyset$.

Suppose that $(u_1^0, u_2^0) \in X^0$ lies in the stable set of $M_1 = (u_1^*, 0)$, so that the unique solution $(u_1(x, t), u_2(x, t))$ of (5.1) with these initial conditions satisfy $\lim_{t \to \infty} u_1(\cdot, t) = u_1^*(\cdot)$ and $\lim_{t \to \infty} u_2(\cdot, t) = 0$ uniformly in $[0, 1]$. Then for any given $\epsilon > 0$ there exists a $t_0 > 0$ such that for $t \geq t_0$,

$$g_2(I(x, t)) > g_2(e^{-k_0 x - k_1 \int_0^x u_1^*(s) ds}) - \epsilon, \ x \in [0, 1]$$

Hence for $t \geq t_0$, $u_2(x, t)$ satisfies

$$\begin{aligned} (u_2)_t &= D_2(u_2)_{xx} + \left[g_2(I(x, t)) - d_2\right] u_2 \\ &\geq D_2(u_2)_{xx} + \left[g_2(e^{-k_0 x - k_1 \int_0^x u_1^*(s) ds}) - \epsilon - d_2\right] u_2. \end{aligned}$$

Comparing $u_2(x, t)$ with the unique solution of

$$\begin{aligned} (U_2)_t &= D_2(U_2)_{xx} + \left[g_2(e^{-k_0 x - k_1 \int_0^x u_1^*(s) ds}) - \epsilon - d_2\right] U_2 \\ (U_2)_x&(0, t) = 0, \ (U_2)_x(1, t) = 0 \\ U_2&(x, t_0) = \frac{1}{2} u_2(x, t_0), \end{aligned}$$

we deduce

$$u_2(x, t) > U_2(x, t) \text{ for } t > t_0.$$

On the other hand, if $\varepsilon > 0$ has been chosen sufficiently small so that $d_2 + \varepsilon < \tilde{d}_2 = -\mu_1(-g_2(\sigma_1))$, then $U_2(x, t) \to \infty$ as $t \to \infty$ uniformly for $x \in [0, 1]$. Thus we obtain a contradiction.

Similarly using $0 < d_1 < \tilde{d}_1$ we can show that $W^s(M_2) \cap X^0 = \emptyset$.

Finally if $(u_1^0, u_2^0) \in X^0$ lies in the stable set of $M_0 = (0, 0)$, then we can similarly deduce that

$$u_2(x, t) > U_0(x, t) \text{ for all large } t,$$

where U_0 is the solution of the equation for U_2 except that u_1^* is replaced by 0. Since $U_0(x, t) \to \infty$ we obtain a contradiction.

Thus Theorem 4.1 of [11] can be applied, and the proof is complete. $\square$

Remark 5.2. From Theorem 1.3.7 in [27], uniform persistence implies the existence of a positive steady state of (5.1). Since the assumptions in Theorem 5.1 imply $\hat{d}_2 < d_2 < \tilde{d}_2$, this conclusion also follows from Theorem 4.3 of the previous section. On the other hand, when $d_1 > \tilde{d}_1$ and $d_2 > \tilde{d}_2$, we have $\hat{d}_2 > d_2 > \tilde{d}_2$ and hence (5.1) has a positive steady state by Theorem 4.3. However it is easily checked that in this case (5.1) is not uniformly persistent.

Theorem 5.3. (Extinction) *Let (u_1, u_2) be the unique solution of (5.1) with initial data $u_i^0 \in \dot{P}$ ($i = 1, 2$). Then the following conclusions hold:*

(1) *If $d_1 \geq d_1^*$ and $d_2 \geq d_2^*$ then $\lim_{t \to \infty} u_1(x, t) = 0$ and $\lim_{t \to \infty} u_2(x, t) = 0$ uniformly in $x \in [0, 1]$.*

(2) *If $0 < d_1 < d_1^*$ and $d_2 \geq d_2^*$ then $\lim_{t \to \infty} u_1(x, t) = u_1^*(x)$ and $\lim_{t \to \infty} u_2(x, t) = 0$ uniformly in $x \in [0, 1]$.*

(3) *If $d_1 \geq d_1^*$ and $0 < d_2 < d_2^*$ then $\lim_{t \to \infty} u_1(x, t) = 0$ and $\lim_{t \to \infty} u_2(x, t) = u_2^*(x)$ uniformly in $x \in [0, 1]$.*

Proof. Suppose that $d_1 \geq d_1^*$ and $d_2 \geq d_2^*$. For $i = 1, 2$, from the equation for u_i we obtain

$$(u_i)_t - D_i(u_i)_{xx} \leq \left[g_i(e^{-k_0 x - \int_0^x k_i u_i dy}) - d_i \right] u_i.$$

Applying the strong maximum principle to the equation satisfied by u_i we deduce $u_i(x, 1) > 0$ in $[0, 1]$. Let $u_i^0 = \frac{1}{2} u_i(x, 1)$ and let U_i be the unique solution to

$$\begin{cases} U_t = D_i U_{xx} + \left[g_i(e^{-k_0 x - \int_0^x k_i U dy}) - d_i \right] U, & 0 < x < 1, \ t > 0, \\ U_x(0, t) = U_x(1, t) = 0, & t > 0, \\ U(x, 0) = u_i^0(x), & 0 < x < 1. \end{cases}$$

By Lemma 3.1 we deduce $v_i(x, t+1) < V_i(x, t)$ for $t > 0$ and $x \in (0, 1]$, where $v_i(x, t) = \int_0^x u_i(y, t) dy$, $V_i(x, t) = \int_0^x U_i(y, t) dy$.

Since $d_i \geq d_i^*$, from our results in section 3 we know that $\lim_{t \to \infty} U_i(x, t) = 0$ uniformly in $x \in [0, 1]$. It follows that $\lim_{t \to \infty} V_i(x, t) = 0$ uniformly in $x \in [0, 1]$ and hence $\lim_{t \to \infty} v_i(x, t) = 0$ uniformly in $x \in [0, 1]$. We may now use (5.4) and parabolic regularity much as in the proof of Theorem 3.3 to conclude that $\lim_{t \to \infty} u_i(x, t) = 0$ uniformly in $x \in [0, 1]$. This proves conclusion (1).

We next prove conclusion (2). Since $d_2 \geq d_2^*$, the above argument can be repeated to show that $\lim_{t \to \infty} u_2(x, t) = 0$ uniformly in $x \in [0, 1]$. Therefore for any given small $\epsilon > 0$ we can find $t_0 > 0$ such that

$$g_1(I(x, t)) \in \left[g_1(e^{-k_0 x - \int_0^x k_1 u_1 dy}) - \epsilon, g_1(e^{-k_0 x - \int_0^x k_1 u_1 dy}) + \epsilon \right]$$

for all $t \geq t_0$ and $x \in [0, 1]$. It follows that for such x and t,

$$(u_1)_t - D_1(u_1)_{xx} \geq \left[g_1(e^{-k_0 x - \int_0^x k_1 u_1 dy}) - \epsilon - d_1 \right] u_1,$$

$$(u_1)_t - D_1(u_1)_{xx} \leq \left[g_1(e^{-k_0 x - \int_0^x k_1 u_1 dy}) + \epsilon - d_1 \right] u_1.$$

Let $u_\epsilon(x,t)$ be the unique solution to

$$
\begin{cases}
u_t = D_1 u_{xx} + \left[g_1(e^{-k_0 x - \int_0^x k_i u \, dy}) - \epsilon - d_1\right]u, & 0 < x < 1,\ t > t_0, \\
u_x(0,t) = u_x(1,t) = 0, & t > t_0, \\
u(x,t_0) = \frac{1}{2}u_1(x,t_0), & 0 < x < 1.
\end{cases}
$$

Then by Theorem 3.3 we have

$$
\lim_{t\to\infty} u_\epsilon(x,t) = u^*_{d_1+\epsilon}(x)
$$

uniformly in $x \in [0,1]$, where $u^*_{d_1+\epsilon}$ denotes the unique positive steady state of the above problem.

By Lemma 3.1 we deduce

$$
v_1(x,t) := \int_0^x u_1(y,t)dy > \int_0^x u_\epsilon(y,t)dy \text{ for } t > t_0,\ x > 0.
$$

It follows that

$$
\liminf_{t\to\infty} v_1(x,t) \geq \int_0^x u^*_{d_1+\epsilon}(y)dy.
$$

Letting $\epsilon \to 0$, we obtain

$$
\liminf_{t\to\infty} v_1(x,t) \geq \int_0^x u^*_{d_1}(y)dy.
$$

Similarly, if u^ϵ is the unique solution to

$$
\begin{cases}
u_t = D_1 u_{xx} + \left[g_1(e^{-k_0 x - \int_0^x k_i u \, dy}) + \epsilon - d_1\right]u, & 0 < x < 1,\ t > t_0, \\
u_x(0,t) = u_x(1,t) = 0, & t > t_0, \\
u(x,t_0) = \frac{3}{2}u_1(x,t_0), & 0 < x < 1,
\end{cases}
$$

then we can make use of Theorem 3.3 and Lemma 3.1 to deduce that

$$
\limsup_{t\to\infty} v_1(x,t) \leq \int_0^x u^*_{d_1-\epsilon}(y)dy.
$$

Letting $\epsilon \to 0$, we obtain

$$
\limsup_{t\to\infty} v_1(x,t) \leq \int_0^x u^*_{d_1}(y)dy.
$$

Thus we must have

$$
\lim_{t\to\infty} v_1(x,t) = \int_0^x u^*_{d_1}(y)dy.
$$

We may now use (5.4) and the parabolic regularity theory to conclude, as in the proof of Theorem 3.3, that $u_1(x,t) \to u^*_{d_1}(x)$ as $t \to \infty$ uniformly in $x \in [0,1]$. This proves conclusion (2).

The proof of conclusion (3) is parallel to the proof of (2) above. $\qquad\square$

Theorem 5.1 can be extended to the $n \geq 3$ species case. A complete understanding of the dynamical behavior for the model with three and more species seems out of reach at the moment. For the two species model, we conjecture the following:

(1) If $0 < d_2 < \tilde{d}_2$ and $\tilde{d}_1 < d_1 < d_1^*$ then $\lim_{t\to\infty} u_1(x,t) = 0$ and $\lim_{t\to\infty} u_2(x,t) = u_2^*(x)$ uniformly in $x \in [0,1]$.

(2) If $0 < d_1 < \tilde{d}_1$ and $\tilde{d}_2 < d_2 < d_2^*$ then $\lim_{t\to\infty} u_1(x,t) = u_1^*(x)$ and $\lim_{t\to\infty} u_2(x,t) = 0$ uniformly in $x \in [0,1]$.

(3) If $\tilde{d}_1 < d_1 < d_1^*$ and $\tilde{d}_2 < d_2 < d_2^*$ then the competition outcomes depend on the initial data.

(4) If $0 < d_1 < \tilde{d}_1$ and $0 < d_2 < \tilde{d}_2$ then there exists a unique positive steady state $(u_1^c(\cdot), u_2^c(\cdot))$ such that $\lim_{t\to\infty} u_1(x, t) = u_1^c(x)$, $\lim_{t\to\infty} u_2(x, t) = u_2^c(x)$ uniformly in $x \in [0, 1]$ for any initial data $u_i^0 \in \dot{P}$ $(i = 1, 2)$.

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