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Steady-state solutions of a reaction–diffusion system arising from intraguild predation and internal storage

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Abstract

Intraguild predation is added to a mathematical model of competition between two species for a single nutrient with internal storage in the unstirred chemostat. At first, we established the sharp a priori estimates for nonnegative solutions of the system, which assure that all of nonnegative solutions belong to a special cone. The selection of this special cone enables us to apply the topological fixed point theorems in cones to establish the existence of positive solutions. Secondly, existence for positive steady state solutions of intraguild prey and intraguild predator is established in terms of the principal eigenvalues of associated nonlinear eigenvalue problems by means of the degree theory in the special cone. It turns out that positive steady state solutions exist when the associated principal eigenvalues are both negative or both positive.

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Keywords: Intraguild predation; Internal storage; Unstirred chemostat; Positive steady-state solutions; Degree theory in cones

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1. Introduction

Intraguild predation is a common phenomenon in ecosystems, in which the predators not only feed on the prey but also consume the same prey resources. Ecological theory predicts that coexistence of intraguild predators and intraguild prey can occur in intraguild predation ecosystems (see, e.g., [2,3,6,14–16]). Recently, Wilken et al. [20] proposed a mathematical model describing the population dynamics of a intraguild predation system, and their experimental results support the theoretical predictions. In the experiments of [20], *Ochromonas* (a mixotrophic organism) and *Microcystis* (an autotrophic prey) share *ammonium* (a nitrogen resource), and *Ochromonas* also feeds on *Microcystis* for growth.

The dynamics of the chemostat experiments in [20] is governed by the following ordinary differential equations:

$$\begin{cases} \frac{dR}{dt} = (R^{(0)} - R)D - f_1(R, Q_1)N_1 - f_2(R, Q_2)N_2, \\ \frac{dN_1}{dt} = [\mu_1(Q_1) - D]\, N_1 - g(N_1)N_2, \\ \frac{dQ_1}{dt} = f_1(R, Q_1) - \mu_1(Q_1)Q_1, \\ \frac{dN_2}{dt} = [\mu_2(Q_2) - D]\, N_2, \\ \frac{dQ_2}{dt} = f_2(R, Q_2) - \mu_2(Q_2)Q_2 + g(N_1)Q_1, \\ R(0) \geq 0,\ N_i(0) \geq 0,\ Q_i(0) \geq Q_{\min,i},\ i = 1, 2, \end{cases} \tag{1.1}$$

where $R(t)$ represents the concentration of nutrient (ammonium) at time t; $N_1(t)$ and $N_2(t)$ denote the population densities of autotrophic prey organism (*Microcystis*) and mixotrophic chrysophyte (*Ochromonas*), respectively. For i=1,2, $Q_i(t)$ represents the average amount of stored nutrient per cell of i-th population at time t. $\mu_i(Q_i)$ is the growth rate of species i as a function of cell quota Q_i, $f_i(R, Q_i)$ is the per capita nutrient uptake rate, per cell of species i as a function of nutrient concentration R and cell quota Q_i; $Q_{\min,i}$ denotes the threshold cell quota below which no growth of species i occurs; $R^{(0)}$ and D stand for the nutrient supply concentration and dilution rate of the chemostat, respectively. Both mortality rates of $N_1(t)$ and $N_2(t)$ are assumed to be equal to the dilution rate (D) of the chemostat (see [20]). The function $g(N_1)$ is the functional response of the mixotroph feeding on the autotroph; the term $g(N_1)Q_1$ describes the assimilation of nutrients from ingested prey. The predation rate of the mixotroph feeding on the autotroph, $g(N_1)$, follows a Holling type III functional response:

$$g(N_1) = \frac{g_{\max} N_1^b}{K_{\max}^b + N_1^b},\ b > 1. \tag{1.2}$$

The specific growth rates of the autotroph and mixotroph take the form (see also [4])

$$\mu_i(Q_i) = \mu_{\max,i}(1 - \frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}}),\ i = 1, 2,$$

where $Q_{\min,i} \leq Q_i \leq Q_{\max,i}$, $\mu_{\max,i}$ is the maximum specific growth rate of species i, and $Q_{\max,i}$ and $Q_{\min,i}$ are its maximum and minimum cell quotas, respectively. The nutrient uptake rates of the species take the form (see also [13]):

$$f_i(R, Q_i) = \frac{a_{\max,i} R}{K_i + R} \frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}}, \ i = 1, 2,$$

where $Q_{\min,i} \le Q_i \le Q_{\max,i}$, $a_{\max,i}$ is the maximum nutrient uptake rate of species i and K_i is its half-saturation constant for nutrient uptake. For the rest of this paper, we assume that the functions $\mu_i(Q_i)$ and $f_i(R, Q_i)$ satisfy the following assumptions with $i = 1, 2$

(H1) $\mu_i(Q_i)$ is Lipschitz continuous for $Q_i \ge Q_{\min,i}$, and satisfies $\mu_i(Q_i) \ge 0$, $\mu_i'(Q_i) > 0$ for a.e. $Q_i \ge Q_{\min,i}$, $\mu_i(Q_{\min,i}) = 0$, where K is a positive constant;

(H2) $f_i(R, Q_i)$ and $\frac{\partial f_i(R,Q_i)}{\partial R}$ are Lipschitz continuous for $R \ge 0$ and $Q_i \ge Q_{\min,i}$; $\frac{\partial f_i(R,Q_i)}{\partial R} \ge 0$, $\frac{\partial f_i(R,Q_i)}{\partial Q_i} \le 0$ and $f_i(R, Q_i) \ge 0$ for a.e. $R \ge 0$ and $Q_i \ge Q_{\min,i}$; there exists $Q_{Bi} \in (Q_{\min,i}, +\infty]$ such that

$$f_i(R, Q_i) > 0, \ \frac{\partial f_i(R, Q_i)}{\partial R} > 0 \text{ in } (R, Q_i) \in \mathbb{R}_+ \times [Q_{\min,i}, Q_{Bi}),$$
$$f_i(R, Q_i) = 0 \ \text{ in } \{(R, Q_i) \in \mathbb{R}_+ \times [Q_{\min,i}, +\infty) : R = 0 \text{ or } Q_i \ge Q_{Bi}\}.$$

(When $Q_{Bi} = +\infty$, it is understood that $f_i(R, Q_i) = 0$ if and only if $R = 0$.)

System (1.1) was mathematically analyzed by the authors in [22]. Theoretical predictions in [22] and the experimental results in [20] have the same conclusions that coexistence of *Ochromonas* (the intraguild predator) and *Microcystis* (the prey) can happen if *Microcystis* is a better competitor for ammonium. In a real ecosystem, the habitat is poorly mixed, and it is more realistic to extend system (1.1) to include spatial variations. For this purpose, the authors in [11] assumed that $U_1 = Q_1 N_1$ and $U_2 = Q_2 N_2$ are the total amounts of stored nutrients at time t for the intraguild prey and predator, respectively. Then system (1.1) is equivalent to the following system

$$\begin{cases} \frac{dR}{dt} = (R^{(0)} - R)D - f_1(R, \frac{U_1}{N_1})N_1 - f_2(R, \frac{U_2}{N_2})N_2, \\ \frac{dN_1}{dt} = \left[\mu_1(\frac{U_1}{N_1}) - D\right] N_1 - g(N_1)N_2, \\ \frac{dU_1}{dt} = f_1(R, \frac{U_1}{N_1})N_1 - DU_1 - h(N_1)U_1N_2, \\ \frac{dN_2}{dt} = \left[\mu_2(\frac{U_2}{N_2}) - D\right] N_2, \\ \frac{dU_2}{dt} = f_2(R, \frac{U_2}{N_2})N_2 - DU_2 + h(N_1)U_1N_2, \\ R(0) \ge 0, \ N_i(0) \ge 0, \ U_i(0) \ge 0, \ i = 1, 2, \end{cases} \tag{1.3}$$

where

$$h(N_1) := \frac{g(N_1)}{N_1}. \tag{1.4}$$

By virtue of (1.2) and $b > 1$, one can conclude that $h(N_1)$ is continuously differentiable on $[0, +\infty)$ with $h(0) = 0$. The unstirred chemostat (see, e.g., [10,12,18,21,23]) is a common laboratory apparatus which is usually regarded as a spatially variable habitat in which nutrients and organisms are transported by diffusion. Inspired by the previous models with variable quotas in spatially variable habitats (see, e.g., [5,7–9]), the authors in [11] extended system (1.3) to the following unstirred chemostat model with internal storage:

$$\begin{cases} \frac{\partial R}{\partial t} = d\frac{\partial^2 R}{\partial x^2} - f_1(R, \frac{U_1}{N_1})N_1 - f_2(R, \frac{U_2}{N_2})N_2, & x \in (0,1),\ t > 0, \\ \frac{\partial N_1}{\partial t} = d\frac{\partial^2 N_1}{\partial x^2} + \mu_1(\frac{U_1}{N_1})N_1 - g(N_1)N_2, & x \in (0,1),\ t > 0, \\ \frac{\partial U_1}{\partial t} = d\frac{\partial^2 U_1}{\partial x^2} + f_1(R, \frac{U_1}{N_1})N_1 - h(N_1)U_1N_2, & x \in (0,1),\ t > 0, \\ \frac{\partial N_2}{\partial t} = d\frac{\partial^2 N_2}{\partial x^2} + \mu_2(\frac{U_2}{N_2})N_2, & x \in (0,1),\ t > 0, \\ \frac{\partial U_2}{\partial t} = d\frac{\partial^2 U_2}{\partial x^2} + f_2(R, \frac{U_2}{N_2})N_2 + h(N_1)U_1N_2, & x \in (0,1),\ t > 0, \end{cases} \tag{1.5}$$

with boundary conditions

$$\begin{cases} \frac{\partial R}{\partial x}(0,t) = -R^{(0)},\ \frac{\partial R}{\partial x}(1,t) + \gamma R(1,t) = 0,\ t > 0, \\ \frac{\partial N_i}{\partial x}(0,t) = 0,\ \frac{\partial N_i}{\partial x}(1,t) + \gamma N_i(1,t) = 0,\ t > 0,\ i = 1,2, \\ \frac{\partial U_i}{\partial x}(0,t) = 0,\ \frac{\partial U_i}{\partial x}(1,t) + \gamma U_i(1,t) = 0,\ t > 0,\ i = 1,2, \end{cases} \tag{1.6}$$

and initial conditions

$$\begin{cases} R(x,0) = R^0(x) \ge 0,\ N_i(x,0) = N_i^0(x) \ge 0, \\ U_i(x,0) = U_i^0(x) \ge 0,\ x \in [0,1],\ i = 1,2, \end{cases} \tag{1.7}$$

where d and γ represent the diffusion coefficient and the washout constant, respectively.

For system (1.5)–(1.7), the authors in [11] first determined conditions such that there is a trivial steady-state solution with neither species present, and two semitrivial steady-state solutions with just one of the species. Then coexistence of the intraguild predator and prey for system (1.5)–(1.7) is possible if both of the semitrivial steady-state solutions are "uniform weak repellers". The authors in [11] also discussed another interesting case that coexistence for system (1.5)–(1.7) is possible if the semitrivial steady-state solution with the presence of prey and the absence of predator is a "uniform weak repeller", but the semitrivial steady-state solution with the presence of predator and the absence of prey does not exist. Basically, arguments used in [11] rely on the theory of uniform persistence.

There is another common competitive outcome for an ecosystem, namely, bistability, that is, competitive exclusion depends on initial conditions. This phenomenon usually arises when both of the semitrivial steady-state solutions are locally asymptotically stable, and we point out that the arguments in [11] can not be applied to this case. Instead, we will use the degree theory in cones (see [1, Lemma 12.1]) to investigate the existence of positive steady-state solutions for system (1.5)–(1.7). Substituting the new variable (see, e.g., [10])

$$\Phi(x,t) = R(x,t) + U_1(x,t) + U_2(x,t)$$

into (1.5)–(1.7), it follows that

$$\begin{cases} \frac{\partial \Phi}{\partial t} = d\frac{\partial^2 \Phi}{\partial x^2},\ x \in (0,1),\ t > 0, \\ \frac{\partial \Phi}{\partial x}(0,t) = -R^{(0)},\ \frac{\partial \Phi}{\partial x}(1,t) + \gamma\Phi(1,t) = 0,\ t > 0. \end{cases}$$

It is easy to see that $\Phi(x,t)$ satisfies $\lim_{t\to\infty} \Phi(x,t) = z(x)$ uniformly in $x \in [0,1]$, where $z(x) = R^{(0)}(\frac{1+\gamma}{\gamma} - x)$. Thus we obtain the limiting system of (1.5)–(1.7) as follows

$$\begin{cases} \frac{\partial N_1}{\partial t} = d\frac{\partial^2 N_1}{\partial x^2} + \mu_1(\frac{U_1}{N_1})N_1 - g(N_1)N_2, \\ \frac{\partial U_1}{\partial t} = d\frac{\partial^2 U_1}{\partial x^2} + f_1(z(x) - U_1 - U_2, \frac{U_1}{N_1})N_1 - h(N_1)U_1N_2, \\ \frac{\partial N_2}{\partial t} = d\frac{\partial^2 N_2}{\partial x^2} + \mu_2(\frac{U_2}{N_2})N_2, \\ \frac{\partial U_2}{\partial t} = d\frac{\partial^2 U_2}{\partial x^2} + f_2(z(x) - U_1 - U_2, \frac{U_2}{N_2})N_2 + h(N_1)U_1N_2, \end{cases} \tag{1.8}$$

for $(x,t) \in (0,1) \times (0,\infty)$ with boundary conditions

$$\begin{cases} \frac{\partial N_i}{\partial x}(0,t) = 0, \ \frac{\partial N_i}{\partial x}(1,t) + \gamma N_i(1,t) = 0, \ t > 0, \ i = 1,2, \\ \frac{\partial U_i}{\partial x}(0,t) = 0, \ \frac{\partial U_i}{\partial x}(1,t) + \gamma U_i(1,t) = 0, \ t > 0, \ i = 1,2, \end{cases} \tag{1.9}$$

and initial conditions

$$N_i(x,0) = N_i^0(x) \geq 0, \ \ U_i(x,0) = U_i^0(x) \geq 0, \ 0 < x < 1, \ i = 1,2. \tag{1.10}$$

Thus, we will only focus on the study of the positive steady-state solutions of system (1.8)–(1.10). It is worth mentioning that (if necessary) we can extend the functions $f_i(R, Q_i)$ and $\mu_i(Q_i)$ with $i = 1,2$ as follows

$$\hat{f}_i(R, Q_i) = \begin{cases} f_i(R, Q_i) & \text{for } R \geq 0, \ Q_i \geq Q_{\min,i}, \\ f_i(R, Q_{\min,i}) & \text{for } R > 0, \ Q_i < Q_{\min,i}, \\ 0 & \text{for } R < 0, \end{cases} \tag{1.11}$$

$$\hat{\mu}_i(Q_i) = \begin{cases} \mu_i(Q_i) & \text{for } Q_i \geq Q_{\min,i}, \\ \mu_i'(Q_{\min,i})(Q_i - Q_{\min,i}) & \text{for } Q_i < Q_{\min,i}. \end{cases} \tag{1.12}$$

Then it is easy to check that $\hat{\mu}_i'(Q_i) > 0$ for all $Q_i \in \mathbb{R}$ and $\hat{f}_i(R, Q_i)$ satisfies (H2) for a.e. $(R, Q_i) \in \mathbb{R} \times \mathbb{R}$ with $i = 1,2$. We will denote $\hat{f}_i(R, Q_i)$, $\hat{\mu}_i(Q_i)$ by $f_i(R, Q_i)$, $\mu_i(Q_i)$ respectively for the sake of simplicity.

The organization of this paper is as follows. In Section 2, we first collect some existing results on nonlinear eigenvalue problems and the threshold dynamics of the single species associated with system (1.5)–(1.7) or (1.8)–(1.10). Section 3 is the main part of this paper. Existence of positive steady state solutions will be established by calculation of fixed point indices. A brief discussion will be presented in Section 4. In the Appendix section, we provide rigorous arguments for the local stability of two semi-trivial solutions.

2. Preliminaries

In this section, we collect some existing results which will be used in the subsequent investigation. We review the results of the global dynamics on the single population model associated with system (1.8)–(1.10):

$$\begin{cases} \frac{\partial N_i}{\partial t} = d\frac{\partial^2 N_i}{\partial x^2} + \mu_i(\frac{U_i}{N_i})N_i, & x \in (0,1),\ t>0, \\ \frac{\partial U_i}{\partial t} = d\frac{\partial^2 U_i}{\partial x^2} + f_i(z(x)-U_i, \frac{U_i}{N_i})N_i, & x \in (0,1),\ t>0, \\ \frac{\partial N_i}{\partial x}(0,t)=0,\ \frac{\partial N_i}{\partial x}(1,t)+\gamma N_i(1,t)=0, & t>0, \\ \frac{\partial U_i}{\partial x}(0,t)=0,\ \frac{\partial U_i}{\partial x}(1,t)+\gamma U_i(1,t)=0, & t>0, \\ N_i(x,0)=N_i^0(x)\ge 0,\ \ U_i(x,0)=U_i^0(x)\ge 0, & x\in[0,1], \end{cases} \tag{2.1}$$

with $i=1$ or 2. The global dynamics of system (2.1) can be determined by the following nonlinear eigenvalue problem

$$\begin{cases} \lambda\phi(x) = d\phi''(x) + \mu_i(\frac{\varphi(x)}{\phi(x)})\phi(x),\ x\in(0,1), \\ \lambda\varphi(x) = d\varphi''(x) + f_i(z(x),\frac{\varphi(x)}{\phi(x)})\phi(x),\ x\in(0,1), \\ \phi'(0)=\phi'(1)+\gamma\phi(1)=0,\ \varphi'(0)=\varphi'(1)+\gamma\varphi(1)=0 \end{cases} \tag{2.2}$$

with $i=1$ or 2. As in [8], we first define Q_i^* to be the unique positive number so that

$$Q_i^* := \inf\{Q_i>0 : f_i(z(x),Q_i) - \mu_i(Q_i)Q_i \le 0 \ \text{ in } [0,1]\}, \ \text{ for } \ i=1,2. \tag{2.3}$$

Let $\mathcal{D} = C^0([0,1],\mathbb{R}^2_+)$ and

$$\mathcal{C}_i = \{(N,U)\in\mathcal{D} : Q_{\min,i}N(x) \le U(x) \le Q_i^* N(x) \text{ for } x\in[0,1]\},\ i=1 \text{ or } 2.$$

It is clear that $\mathcal{D}$ and $\mathcal{C}_1, \mathcal{C}_2$ are complete cones in the normed linear space $C^0([0,1],\mathbb{R}^2)$ and that $\mathcal{D}$ is both normal and solid. We say that $(u_1,v_1)\ge_{\mathcal{D}}(u_2,v_2)$ if and only if $(u_1,v_1)-(u_2,v_2)\in\mathcal{D}$, and $(u_1,v_1)\gg_{\mathcal{D}}(u_2,v_2)$ if and only if $(u_1,v_1)-(u_2,v_2)\in \mathrm{Int}\mathcal{D}$. By the similar arguments as in Lemmas 5.1 and 7.1 in [8], the eigenvalue problem (2.2) admits a principal eigenvalue $\lambda_i^0(d)$ corresponding to a strongly positive eigenfunction $(\phi_i(x),\varphi_i(x))\gg_{\mathcal{D}}(0,0)$ in $\mathcal{C}_i$ with $i=1,2$. Moreover, there is a $d_{0,i}>0$ ($i=1,2$) such that

$$\lambda_i^0(d)>0 \text{ if } 0<d<d_{0,i},\ \lambda_i^0(d)=0 \text{ if } d=d_{0,i},\ \lambda_i^0(d)<0 \text{ if } d>d_{0,i}. \tag{2.4}$$

By similar arguments as in [8, Theorem 2.3] (see also [11]), we have the following results, which indicate that there exists a threshold diffusion coefficient for species survival. Here the existence of the threshold diffusion coefficient is determined by (2.4). Indeed, these results have already been proven in [9, Theorem 2.2]. They established the existence of the threshold diffusion coefficient by analyzing the monotonicity of the positive steady states of the single population model (2.1) on the diffusion coefficient. For $i=1,2$, let

$$\Delta_i = \{(N_i^0,U_i^0)\in C([0,1];\mathbb{R}^2_+) : U_i^0(\cdot)\le z(\cdot) \text{ and there exists } \tilde{Q}_i>0 \\ \text{such that } Q_{\min,i}N_i^0(\cdot)\le U_i^0(\cdot)\le \tilde{Q}_i N_i^0(\cdot) \text{ in } [0,1]\}.$$

Lemma 2.1. *([9, Theorem 2.2]) Suppose* $d>0$, f_i,μ_i *satisfy* (H1) *and* (H2). *Then there exists* $d_{0,i}>0$ *such that*

(i) *if* $d \geq d_{0,i}$, (2.1) *has no positive steady state solution in* Δ_i, *and every solution of* (2.1) *with initial conditions in* Δ_i *satisfies* $(N_i(\cdot,t), U_i(\cdot,t)) \to (0,0)$ *as* $t \to \infty$.
(ii) *if* $0 < d < d_{0,i}$, *there is a unique positive steady state solution* $(N_i^*(d,\cdot), U_i^*(d,\cdot))$ *which is globally asymptotically stable in* Δ_i. *Moreover,* $(N_i^*(d,\cdot), U_i^*(d,\cdot))$ *is strictly decreasing in* d *such that*

$$\lim_{d \to d_{0,i}-} (N_i^*(d,\cdot), U_i^*(d,\cdot)) = (0,0) \textit{ uniformly on } [0,1],$$

$$\lim_{d \to 0+} (N_i^*(d,\cdot), U_i^*(d,\cdot)) = (z(x)/Q_{\min,i}, z(x)) \textit{ uniformly on } [0,1].$$

We finish this section by stating the following lemma, which is essential to the calculation of the indices of fixed points related to compact maps. To this end, we denote by $(\mathcal{E}, P)$ an arbitrary ordered Banach space with open unit ball B. For every $\rho > 0$, we define $P_\rho := \rho B \cap P$. Then the boundary S_ρ^+ of P_ρ in P equals $\rho S \cap P$, where S denotes the unit sphere in $\mathcal{E}$. It follows from the fixed point index theory in [1] that for every open subset O of P and every compact map $f : \overline{O} \to P$, the fixed point index $\mathrm{index}(f, O, P)$ is well-defined, provided f has no fixed points on ∂O. Moreover, for an arbitrary positive number ρ, we have the following results.

Lemma 2.2. *([1, Lemma 12.1]) Let* $f : \overline{P}_\rho \to P$ *be a compact map.*

(i) *If* $f(x) \neq \lambda x$ *for every* $x \in S_\rho^+$ *and every* $\lambda \geq 1$, *then* $\mathrm{index}(f, P_\rho, P) = 1$.
(ii) *If there exists an element* $p > 0$ *such that* $x - f(x) \neq \lambda p$ *for every* $x \in S_\rho^+$ *and every* $\lambda \geq 0$, *then* $\mathrm{index}(f, P_\rho, P) = 0$.

3. Steady state solutions

This section is devoted to the investigation of the existence of positive steady-state solutions of system (1.8)–(1.10), that is, we shall consider the following elliptic system:

$$\begin{cases} dN_1'' + \mu_1(\frac{U_1}{N_1})N_1 - g(N_1)N_2 = 0, \ x \in (0,1), \\ dU_1'' + f_1(z(x) - U_1 - U_2, \frac{U_1}{N_1})N_1 - h(N_1)U_1N_2 = 0, \ x \in (0,1), \\ dN_2'' + \mu_2(\frac{U_2}{N_2})N_2 = 0, \ x \in (0,1), \\ dU_2'' + f_2(z(x) - U_1 - U_2, \frac{U_2}{N_2})N_2 + h(N_1)U_1N_2 = 0, \ x \in (0,1) \end{cases} \tag{3.1}$$

with boundary conditions

$$\begin{cases} N_i'(0) = 0, \ N_i'(1) + \gamma N_i(1) = 0, \ i = 1,2, \\ U_i'(0) = 0, \ U_i'(1) + \gamma U_i(1) = 0, \ i = 1,2. \end{cases} \tag{3.2}$$

Here we call $(N_1, U_1, N_2, U_2) \in C^2([0,1])$ a steady-state solution if the ratio $\frac{U_i}{N_i}$ are finite a.e., and the equations (3.1) and (3.2) are satisfied a.e. in $(0,1)$.

For $i = 1,2$, the functions $\mu_i(U_i/N_i)N_i$ and $f_i(z(x) - U_1 - U_2, U_i/N_i)N_i$ can be respectively extended to those similar to Eq. (4.9) and Eq. (4.10) in [8], if necessary. Then it follows from Lemma 2.1 that there are three types of nonnegative steady-state solutions of (3.1)–(3.2):

(i) Trivial solution $E_0(x) = (0, 0, 0, 0)$ always exists;
(ii) Semi-trivial solution $E_1(x) = (N_1^*(d, x), U_1^*(d, x), 0, 0)$ exists provided that $0 < d < d_{0,1}$, and semi-trivial solution $E_2(x) = (0, 0, N_2^*(d, x), U_2^*(d, x))$ exists provided that $0 < d < d_{0,2}$;
(iii) Positive solutions with $(N_1(x), U_1(x), N_2(x), U_2(x)) > 0$ may exist.

The main task below is to study the positive solutions of (3.1)–(3.2). To this end, we first establish a priori estimates for nonnegative solutions of the system (3.1)–(3.2).

Lemma 3.1. *Suppose (N_1, U_1, N_2, U_2) is a nonnegative solution of the system (3.1)–(3.2) with $N_i \not\equiv 0, U_i \not\equiv 0$. Then*

(i) $N_i(x) > 0, U_i(x) > 0$ *on* $[0, 1]$ *with* $i = 1, 2$;
(ii) $U_1(x) + U_2(x) < z(x)$ *on* $[0, 1]$;
(iii) $N_1(x)Q_{\min,1} < U_1(x) < N_1(x)Q_1^*$ *and* $N_2(x)Q_{\min,2} < U_2(x) < N_2(x)Q_2^{**}$ *on* $[0, 1]$*, where* Q_1^* *is defined by* (2.3)*, and*

$$Q_2^{**} := \inf\{Q > 0 : f_2(z(x), Q) - \mu_2(Q)Q + g\left(\frac{z(x)}{Q_{\min,1}}\right) Q_1^* \leq 0 \text{ in } [0, 1]\}.$$

Proof. We first prove $N_i(x) > 0$ with $i = 1, 2$. For any nonnegative solution $(N_1(x), U_1(x), N_2(x), U_2(x))$ of (3.1)–(3.2) with $N_i \not\equiv 0, U_i \not\equiv 0$, one concludes that $C_i(x) := \mu_i(\frac{U_i}{N_i})$ is well defined for all $x \in (0, 1)$ with $i = 1, 2$. Rewrite $C_i(x) = C_i^+(x) - C_i^-(x)$, where $C_i^+(x), C_i^-(x)$ are the positive part and negative part of $C_i(x)$, respectively, $i = 1, 2$. In view of $g(N_1) = h(N_1)N_1$, the first equation of (3.1) becomes

$$dN_1'' - [C_1^-(x) + h(N_1)N_2]N_1 = -C_1^+(x)N_1 \leq 0$$

for $x \in (0, 1)$. Clearly, $C_1^-(x) = \mu_1(\frac{U_1}{N_1})^- \in L^\infty(0, 1)$ based on the extension (1.12), and $C_1^-(x) + h(N_1)N_2 \geq 0$ on $[0, 1]$. It follows from the strong maximum principle that $N_1(x) > 0$ in $(0, 1)$. If $N_1(0) = 0$, it follows from the Hopf boundary lemma that $N_1'(0) > 0$, contradicting the boundary condition $N_1'(0) = 0$. Hence, $N_1(0) > 0$. Similarly, $N_1(1) > 0$. Thus $N_1(x) > 0$ on $[0, 1]$.

The equation for N_2 can be rewritten as

$$dN_2'' - C_2^-(x)N_2 = -C_2^+(x)N_2 \leq 0 \text{ in } (0, 1).$$

In view of $C_2^-(x) = \mu_2(\frac{U_2}{N_2})^- \in L^\infty(0, 1)$, similar arguments as above imply that $N_2(x) > 0$ on $[0, 1]$. Thus, we have $\frac{U_i}{N_i} \in C([0, 1])$, and hence, the solution satisfying (3.1) is in the classical sense everywhere.

Next, we claim $U_1 + U_2 < z(x)$ on $[0, 1]$. Let $\Psi = z - U_1 - U_2$. Then Ψ satisfies

$$\begin{cases} -d\Psi'' + [N_1 \int_0^1 \frac{\partial f_1}{\partial R}(\tau\Psi, \frac{U_1}{N_1})\mathrm{d}\tau + N_2 \int_0^1 \frac{\partial f_2}{\partial R}(\tau\Psi, \frac{U_2}{N_2})\mathrm{d}\tau]\Psi = 0, \ x \in (0, 1), \\ \Psi'(0) = -R^{(0)}, \quad \Psi'(1) + \gamma\Psi(1) = 0. \end{cases}$$

By the strong maximum principle, we have $\Psi > 0$ on [0, 1]. That is, $U_1 + U_2 < z(x)$ on [0, 1]. Noting that $U_i \not\equiv 0$ (i=1, 2), and U_1, U_2 satisfy

$$\begin{cases} -dU_1'' + h(N_1)N_2U_1 = f_1(z(x) - U_1 - U_2, \frac{U_1}{N_1})N_1 \geq 0, \ x \in (0,1), \\ U_1'(0) = U_1'(1) + \gamma U_1(1) = 0, \end{cases}$$

and

$$\begin{cases} -dU_2'' = f_2(z(x) - U_1 - U_2, \frac{U_2}{N_2})N_2 + h(N_1)U_1N_2 \geq 0, \ x \in (0,1), \\ U_2'(0) = U_2'(1) + \gamma U_2(1) = 0. \end{cases}$$

Then we have $U_1 > 0, U_2 > 0$ on [0, 1] by the strong maximum principle.

In order to show $U_i > N_i Q_{\min,i}$ on [0, 1] with $i = 1, 2$, we set $\omega_i = U_i - N_i Q_{\min,i}$. Note that for $i = 1, 2$,

$$\mu_i(\frac{U_i}{N_i}) = \mu_i(Q_{\min,i}) + \zeta_i(x, Q_{\min,i})(\frac{U_i}{N_i} - Q_{\min,i}), \tag{3.3}$$

where

$$\zeta_i(x, Q_i) = \int_0^1 \mu_i'(\tau\frac{U_i}{N_i} + (1-\tau)Q_i)\mathrm{d}\tau > 0. \tag{3.4}$$

Then $\omega_1(x), \omega_2(x)$ satisfy

$$\begin{cases} d\omega_1'' - (h(N_1)N_2 + Q_{\min,1}\zeta_1(x, Q_{\min,1}))\omega_1 = -N_1 f_1(z - U_1 - U_2, \frac{U_1}{N_1}) \leq 0, \\ \omega_1'(0) = 0, \ \ \omega_1'(1) + \gamma\omega_1(1) = 0, \end{cases}$$

and

$$\begin{cases} d\omega_2'' - Q_{\min,2}\zeta_2(x, Q_{\min,2})\omega_2 = -N_2 f_2(z - U_1 - U_2, \frac{U_2}{N_2}) - g(N_1)\frac{U_1}{N_1}N_2 \leq 0, \\ \omega_2'(0) = 0, \ \ \omega_2'(1) + \gamma\omega_2(1) = 0. \end{cases}$$

By the strong maximum principle and the boundary conditions, we have $\omega_1(x) > 0$ on [0, 1] or $\omega_1(x) \equiv 0$ on [0, 1]. If $\omega_1(x) \equiv 0$ on [0, 1], then $U_1 \equiv N_1 Q_{\min,1}$, and

$$\begin{cases} -dN_1'' + h(N_1)N_2 \cdot N_1 = \mu_1(Q_{\min,1})N_1 = 0, \ x \in (0,1), \\ N_1'(0) = N_1'(1) + \gamma N_1(1) = 0, \end{cases}$$

which implies $N_1 \equiv 0$ on [0, 1], contradicting the fact $N_1 > 0$ on [0, 1]. Hence $\omega_1(x) > 0$ on [0, 1], that is $U_1 > N_1 Q_{\min,1}$ on [0, 1]. Similarly, we can show that $U_2 > N_2 Q_{\min,2}$ on [0, 1].

It remains to show that $U_1(x) < N_1(x)Q_1^*$ and $U_2(x) < N_2(x)Q_2^{**}$ on [0, 1]. By the definition of Q_1^*, (H2) and $0 < z - U_1 - U_2 < z$ on [0, 1], we can conclude that

$$f_1(z - U_1 - U_2, Q_1^*) - \mu_1(Q_1^*)Q_1^* < 0 \text{ for } x \in [0,1]. \tag{3.5}$$

Let $\chi_1 = U_1 - N_1 Q_1^*$. Note that

$$f_1(z - U_1 - U_2, \frac{U_1}{N_1}) = f_1(z - U_1 - U_2, Q_1^*) + \xi_1(x, Q_1^*)(\frac{U_1}{N_1} - Q_1^*), \tag{3.6}$$

$$\mu_1(\frac{U_1}{N_1}) = \mu_1(Q_1^*) + \zeta_1(x, Q_1^*)(\frac{U_1}{N_1} - Q_1^*), \tag{3.7}$$

where $\zeta_1(x, Q_1)$ is given by (3.4), and

$$\xi_1(x, Q_1) = \int_0^1 \frac{\partial f_1}{\partial Q_1}(z - U_1 - U_2, \tau\frac{U_1}{N_1} + (1-\tau)Q_1)\mathrm{d}\tau \le 0. \tag{3.8}$$

Then $\chi_1(x)$ satisfies

$$\begin{cases} -d\chi_1'' + \big(-\xi_1(x, Q_1^*) + \zeta_1(x, Q_1^*)Q_1^* + h(N_1)N_2\big)\,\chi_1 \\ \qquad = [f_1(z - U_1 - U_2, Q_1^*) - \mu_1(Q_1^*)Q_1^*]N_1 < 0, \ x \in (0,1), \\ \chi_1'(0) = 0, \ \ \chi_1'(1) + \gamma\chi_1(1) = 0. \end{cases}$$

In view of (1.2), (3.4) and (3.8), we conclude that $-\xi_1(x, Q_1^*) + \zeta_1(x, Q_1^*)Q_1^* + h(N_1)N_2 > 0$ in $(0, 1)$. It follows from the strong maximum principle that $\chi_1 < 0$ on $[0, 1]$, that is, $U_1(x) < N_1(x)Q_1^*$ on $[0, 1]$.

Similarly, by the definition of Q_2^{**}, the assumption (H2) and $0 < z - U_1 - U_2 < z$ on $[0, 1]$, we can conclude that

$$f_2(z - U_1 - U_2, Q_2^{**}) - \mu_2(Q_2^{**})Q_2^{**} + g\left(\frac{z(x)}{Q_{\min,1}}\right)Q_1^* < 0 \text{ for } x \in [0,1]. \tag{3.9}$$

Let $\chi_2 = U_2 - N_2 Q_2^{**}$. Note that

$$f_2(z - U_1 - U_2, \frac{U_2}{N_2}) = f_2(z - U_1 - U_2, Q_2^{**}) + \xi_2(x, Q_2^{**})(\frac{U_2}{N_2} - Q_2^{**}), \tag{3.10}$$

$$\mu_2(\frac{U_2}{N_2}) = \mu_2(Q_2^{**}) + \zeta_2(x, Q_2^{**})(\frac{U_2}{N_2} - Q_2^{**}), \tag{3.11}$$

where $\zeta_2(x, Q_2)$ is given by (3.4), and

$$\xi_2(x, Q_2) = \int_0^1 \frac{\partial f_2}{\partial Q_2}(z - U_1 - U_2, \tau\frac{U_2}{N_2} + (1-\tau)Q_2)\mathrm{d}\tau \le 0. \tag{3.12}$$

It follows from $N_1(x) < \frac{U_1(x)}{Q_{\min,1}} < \frac{z(x)}{Q_{\min,1}}$, $\frac{U_1(x)}{N_1(x)} < Q_1^*$ and (3.9) that $\chi_2(x)$ satisfies

$$\begin{cases} -d\chi_2'' + (-\xi_2(x, Q_2^{**}) + \zeta_2(x, Q_2^{**})Q_2^{**})\chi_2 \\ \qquad = [f_2(z - U_1 - U_2, Q_2^{**}) - \mu_2(Q_2^{**})Q_2^{**} + h(N_1)U_1]N_2 < 0, \ x \in (0,1), \\ \chi_2'(0) = 0, \ \ \chi_2'(1) + \gamma\chi_2(1) = 0 \end{cases}$$

It follows from (3.4) and (3.12) that $-\xi_2(x, Q_2^{**}) + \zeta_2(x, Q_2^{**})Q_2^{**} > 0$ in (0, 1). By the strong maximum principle, we deduce that $\chi_2 < 0$ on [0, 1], that is, $U_2(x) < N_2(x)Q_2^{**}$ on [0, 1]. □

Next, we show the existence of positive steady state solutions by degree theory. By virtue of Lemma 3.1, we introduce the spaces

$$
\begin{aligned}
& X = C([0,1];\mathbb{R}^4), \quad X_+ = C([0,1];\mathbb{R}_+^4), \quad \mathcal{D} = C^0([0,1],\mathbb{R}_+^2), \\
& W_1 = \mathcal{C}_1 = \{(N_1, U_1) \in \mathcal{D} : Q_{\min,1}N_1(x) \le U_1(x) \le Q_1^* N_1(x) \text{ on } x \in [0,1]\}, \\
& W_2 = \{(N_2, U_2) \in \mathcal{D} : Q_{\min,2}N_2(x) \le U_2(x) \le Q_2^{**} N_2(x) \text{ on } x \in [0,1]\}. \\
& W = W_1 \times W_2, \\
& \Omega = \{(N_1, U_1, N_2, U_2) \in W : \|N_1\| + \|U_1\| + \|N_2\| + \|U_2\| \le M_0\},
\end{aligned}
$$

where $\|\cdot\|$ is the usual norm in $C([0,1])$ and $M_0 = 4\max\{1, \frac{1}{Q_{\min,1}}, \frac{1}{Q_{\min,2}}\}\|z\|$. Clearly, $W \subset X_+$ is also a cone of X, where X_+ is the natural positive cone of X.

Observe that for any $(N_1, U_1, N_2, U_2) \in \Omega \subset W$, we have $U_i(x_0) = 0$ if $N_i(x_0) = 0$ at some point $x_0 \in [0,1]$ with $i = 1, 2$. Motivated by Eq. (4.9) and Eq. (4.10) in [8], for $i = 1, 2$ and any $(N_1, U_1, N_2, U_2) \in \Omega$, we define

$$
\tilde{\mu}_i(U_i(x), N_i(x)) = \begin{cases} 0 & \text{when } N_i(x) = 0, \text{ for some } x \in [0,1], \\ \mu_i(U_i(x)/N_i(x))N_i(x) & \text{when } N_i(x) > 0, \ \forall\, x \in [0,1], \end{cases} \tag{3.13}
$$

and $\tilde{f}_i(R(x), U_i(x), N_i(x))$

$$
= \begin{cases} 0 & \text{when } N_i(x) = 0, \text{ for some } x \in [0,1], \\ f_i(R(x), U_i(x)/N_i(x))N_i(x) & \text{when } N_i(x) > 0, \ \forall\, x \in [0,1], \end{cases} \tag{3.14}
$$

with $R(x) = z(x) - U_1(x) - U_2(x)$. Then for $i = 1, 2$, the functions $\tilde{\mu}_i(U_i(x), N_i(x))$ and $\tilde{f}_i(z(x) - U_1(x) - U_2(x), U_i(x), N_i(x))$ are continuous in Ω. In particular, these two functions are continuous at the steady-state solutions E_0, E_1 and E_2. For our convenience, we will still denote $\tilde{\mu}_i(U_i(x), N_i(x))$ (resp. $\tilde{f}_i(R(x), U_i(x), N_i(x))$) by $\mu_i(U_i/N_i)N_i$ (resp. $f_i(R(x), U_i/N_i)N_i$) in the subsequent discussions.

Define $F : \Omega \to X$ by

$$
F\begin{pmatrix} N_1 \\ U_1 \\ N_2 \\ U_2 \end{pmatrix} := (-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M)^{-1} \begin{pmatrix} \mu_1(\frac{U_1}{N_1})N_1 - g(N_1)N_2 + MN_1 \\ f_1(z(x) - U_1 - U_2, \frac{U_1}{N_1})N_1 - h(N_1)U_1N_2 + MU_1 \\ \mu_2(\frac{U_2}{N_2})N_2 + MN_2 \\ f_2(z(x) - U_1 - U_2, \frac{U_2}{N_2})N_2 + h(N_1)U_1N_2 + MU_2 \end{pmatrix},
$$

where $(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M)^{-1}$ is the inverse operator of $-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M$ subject to the boundary conditions $u_x(0) = u_x(1) + \gamma u(1) = 0$, and M is sufficiently large such that

$$\begin{cases} \mu_1(\frac{U_1}{N_1}) - h(N_1)N_2 + M > 0, \\ f_1(z(x) - U_1 - U_2, \frac{U_1}{N_1})\frac{N_1}{U_1} - h(N_1)N_2 + M > 0, \\ \mu_2(\frac{U_2}{N_2}) + M > 0, \\ f_2(z(x) - U_1 - U_2, \frac{U_2}{N_2})\frac{N_2}{U_2} + h(N_1)\frac{N_2}{U_2}U_1 + M > 0, \\ \xi_1(x, Q_{\min,1}) - Q_{\min,1}\zeta_1(x, Q_{\min,1}) - h(N_1)N_2 + M > 0, \\ \xi_1(x, Q_1^*) - Q_1^*\zeta_1(x, Q_1^*) - h(N_1)N_2 + M > 0, \\ \xi_2(x, Q_{\min,2}) - Q_{\min,2}\zeta_2(x, Q_{\min,2}) + M > 0, \\ \xi_2(x, Q_2^{**}) - Q_2^{**}\zeta_2(x, Q_2^{**}) + M > 0 \end{cases} \tag{3.15}$$

for all $(N_1, U_1, N_2, U_2) \in \Omega$. Here $\zeta_i(x, Q_i)$, $\xi_1(x, Q_1)$ and $\xi_2(x, Q_2)$ are defined by (3.4), (3.8) and (3.12) respectively. By the assumptions (H1)-(H2) and the extensions (1.11)–(1.12) and (3.13)–(3.14), one can conclude that F is compact.

Next, we show that $F(\Omega) \subset W$ by direct computations and the maximum principle. To this end, let $F(N_1, U_1, N_2, U_2) = (\overline{N_1}, \overline{U_1}, \overline{N_2}, \overline{U_2})$ for any $(N_1, U_1, N_2, U_2) \in \Omega$. Then $(\overline{N_1}, \overline{U_1}, \overline{N_2}, \overline{U_2})$ satisfies

$$\begin{cases} -d\overline{N_1}'' + M\overline{N_1} = \mu_1(\frac{U_1}{N_1})N_1 - g(N_1)N_2 + MN_1, \\ -d\overline{U_1}'' + M\overline{U_1} = f_1(z(x) - U_1 - U_2, \frac{U_1}{N_1})N_1 - h(N_1)U_1N_2 + MU_1, \\ -d\overline{N_2}'' + M\overline{N_2} = \mu_2(\frac{U_2}{N_2})N_2 + MN_2, \\ -d\overline{U_2}'' + M\overline{U_2} = f_2(z(x) - U_1 - U_2, \frac{U_2}{N_2})N_2 + h(N_1)U_1N_2 + MU_2, \end{cases} \tag{3.16}$$

for $x \in (0, 1)$ with boundary conditions

$$\begin{cases} \overline{N_i}'(0) = 0, \ \overline{N_i}'(1) + \gamma\overline{N_i}(1) = 0, \ i = 1, 2, \\ \overline{U_i}'(0) = 0, \ \overline{U_i}'(1) + \gamma\overline{U_i}(1) = 0, \ i = 1, 2. \end{cases} \tag{3.17}$$

In view of (3.15), it follows from the maximum principle that $\overline{N_1} \geq 0, \overline{U_1} \geq 0, \overline{N_2} \geq 0, \overline{U_2} \geq 0$ on [0, 1]. It remains to show that $Q_{\min,1}\overline{N_1} \leq \overline{U_1} \leq Q_1^*\overline{N_1}$ and $Q_{\min,2}\overline{N_2} \leq \overline{U_2} \leq Q_2^{**}\overline{N_1}$ on [0, 1]. With this in mind, let $\overline{\omega_i} = \overline{U_i} - \overline{N_i}Q_{\min,i}$ and $\omega_i = U_i - N_iQ_{\min,i}$ with $i = 1, 2$. Then $\omega_i \geq 0$ on [0, 1] based on $(N_1, U_1, N_2, U_2) \in \Omega \subset W$. Note that for $i = 1, 2$,

$$f_i(z - U_1 - U_2, \frac{U_i}{N_i}) = f_i(z - U_1 - U_2, Q_{\min,i}) + \xi_i(x, Q_{\min,i})(\frac{U_i}{N_i} - Q_{\min,i}),$$

where $\xi_1(x, Q_1), \xi_2(x, Q_2)$ are given by (3.8) and (3.12) respectively. It follows from (3.16)–(3.17) and (3.3) that $\overline{\omega_i}'(0) = 0$, $\overline{\omega_i}'(1) + \gamma\overline{\omega_i}(1) = 0$ and for $x \in (0, 1)$,

$$\begin{aligned} &-d\overline{\omega_1}'' + M\overline{\omega_1} \\ &= f_1(z(x) - U_1 - U_2, \frac{U_1}{N_1})N_1 - \mu_1(\frac{U_1}{N_1})N_1Q_{\min,i} - h(N_1)N_2\omega_1 + M\omega_1 \\ &= (\xi_1(x, Q_{\min,1}) - Q_{\min,1}\zeta_1(x, Q_{\min,1}) - h(N_1)N_2 + M)\omega_1 + f_1(z - U_1 - U_2, Q_{\min,1})N_1 \\ &\geq (\xi_1(x, Q_{\min,1}) - Q_{\min,1}\zeta_1(x, Q_{\min,1}) - h(N_1)N_2 + M)\omega_1, \end{aligned}$$

and

$$
\begin{aligned}
&-d\overline{\omega_2}'' + M\overline{\omega_2} \\
&= f_2(z(x) - U_1 - U_2, \frac{U_2}{N_2})N_2 - \mu_2(\frac{U_2}{N_2})N_2 Q_{\min,2} + h(N_1)U_1N_2 + M\omega_1 \\
&= (\xi_2(x, Q_{\min,2}) - Q_{\min,2}\zeta_2(x, Q_{\min,2}) + M)\omega_2 + h(N_1)U_1N_2 + f_2(z - U_1 - U_2, Q_{\min,2})N_2 \\
&\geq (\xi_2(x, Q_{\min,2}) - Q_{\min,2}\zeta_2(x, Q_{\min,2}) + M)\omega_2.
\end{aligned}
$$

By using (3.15) and the maximum principle, it is easy to see that $\overline{\omega_i} \geq 0$ on [0, 1]. Also, we have $Q_{\min,i}\overline{N_i} \leq \overline{U_i}$ on [0, 1].

Similarly, let $\overline{\chi_1} = \overline{U_1} - Q_1^*\overline{N_1}$, $\overline{\chi_2} = \overline{U_2} - Q_2^{**}\overline{N_2}$ and $\chi_1 = U_1 - Q_1^* N_1$, $\chi_2 = U_2 - Q_2^{**}N_2$. Then $\chi_i \leq 0$ on [0, 1] based on $(N_1, U_1, N_2, U_2) \in \Omega \subset W$. It follows from (3.5)–(3.7), (3.9)–(3.11), (3.15) and (3.16)–(3.17) that $\overline{\chi_i} \leq 0$ on [0, 1] by similar computations and the maximum principle. That is, $\overline{U_1} \leq Q_1^*\overline{N_1}$ and $\overline{U_2} \leq Q_2^{**}\overline{N_1}$ on [0, 1]. Hence, by the definition of M, we have $F(\Omega) \subset W$. By Lemma 3.1, we conclude that (3.1)–(3.2) have nonnegative solutions if and only if the operator F has a fixed point in Ω.

As mentioned before, due to a priori estimates for nonnegative solutions of the system (3.1)–(3.2), we can establish the existence of positive solutions to (3.1)–(3.2) by using the topological fixed point theorems in the cone W (see Lemma 2.2). The selection of this special cone W ensures the existence of M satisfying (3.15), and guarantees $F(\Omega) \subset W$, which enables us to apply Lemma 2.2.

Lemma 3.2. *For $\lambda \geq 1$, the equation $F(N_1, U_1, N_2, U_2) = \lambda(N_1, U_1, N_2, U_2)$ has no solution in W satisfying $\|N_1\| + \|U_1\| + \|N_2\| + \|U_2\| = M_0$.*

Proof. Suppose $(N_1, U_1, N_2, U_2) \in W$ satisfies $F(N_1, U_1, N_2, U_2) = \lambda(N_1, U_1, N_2, U_2)$. Then $0 \leq N_i \leq \frac{U_i}{Q_{\min,i}}$ on [0, 1] with $i = 1, 2$, and for $x \in (0, 1)$,

$$
\begin{cases}
\lambda dN_1'' + \mu_1(\frac{U_1}{N_1})N_1 - g(N_1)N_2 = (\lambda - 1)MN_1 \geq 0, \\
\lambda dU_1'' + f_1(z(x) - U_1 - U_2, \frac{U_1}{N_1})N_1 - h(N_1)U_1N_2 = (\lambda - 1)MU_1 \geq 0, \\
\lambda dN_2'' + \mu_2(\frac{U_2}{N_2})N_2 = (\lambda - 1)MN_2 \geq 0, \\
\lambda dU_2'' + f_2(z(x) - U_1 - U_2, \frac{U_2}{N_2})N_2 + h(N_1)U_1N_2 = (\lambda - 1)MU_2 \geq 0
\end{cases}
$$

with the boundary conditions (3.2). By similar arguments as in Lemma 3.1, we have $U_1 + U_2 < z(x)$ on [0, 1], which implies that $0 \leq N_i \leq \frac{U_i}{Q_{\min,i}} < \frac{z(x)}{Q_{\min,i}}$. Hence, there exists no solution of $F(N_1, U_1, N_2, U_2) = \lambda(N_1, U_1, N_2, U_2)$ in W satisfying $\|N_1\| + \|U_1\| + \|N_2\| + \|U_2\| = M_0$. $\square$

As a consequence of Lemma 3.2 and Lemma 2.2, we have the following outcome.

Lemma 3.3. index$(F, \dot{\Omega}, W) = 1$, *where $\dot{\Omega}$ denotes the interior of Ω in W.*

Lemma 3.4. *Suppose $0 < d < d_{0,2}$. Then for $\delta > 0$ small enough,*

$$\text{index}(F, O_\delta^+(E_0), W) = 0,$$

where $O_\delta^+(E_0)=\{(N_1,U_1,N_2,U_2)\in W: \|N_1\|+\|U_1\|+\|N_2\|+\|U_2\|<\frac{\delta}{\gamma}R^{(0)}\}$ *is a neighborhood of* E_0 *in* W.

Proof. By the definition of $N_2^*(x), U_2^*(x)$, there exists $\epsilon_0, \delta_0>0$ small, such that

$$\frac{\delta}{\gamma}R^{(0)}\le N_2^*(x)-\epsilon_0,\ \ \frac{\delta}{\gamma}R^{(0)}\le U_2^*(x)-\epsilon_0$$

hold for all $x\in[0,1]$ and all $\delta\in(0,\delta_0]$. Denote the boundary

$$\partial O_\delta^+(E_0)=\{(N_1,U_1,N_2,U_2)\in W: \|N_1\|+\|U_1\|+\|N_2\|+\|U_2\|=\frac{\delta}{\gamma}R^{(0)}\}.$$

Thus $\|N_i\|\le\delta z$, $\|U_i\|\le\delta z$ $(i=1,2)$ whenever $(N_1,U_1,N_2,U_2)\in\partial O_\delta^+(E_0)$.

Let $\chi=2+\gamma-\gamma x^2$. Then $\chi>0$ on $[0,1]$ and satisfies

$$\chi_{xx}<0 \text{ in } (0,1),\ \ \chi_x(0)=0,\ \chi_x(1)+\gamma\chi(1)=0.$$

Moreover, $(\chi, Q_{\min,1}\chi,\chi,Q_{\min,2}\chi)\in W$. Next, we show that for $\lambda\ge0$,

$$(N_1,U_1,N_2,U_2)-F(N_1,U_1,N_2,U_2)=\lambda(\chi,Q_{\min,1}\chi,\chi,Q_{\min,2}\chi)$$

has no solution on S_δ for small δ. Assume on the contrary that it has a solution (N_1,U_1,N_2,U_2) on S_δ. Then (N_2,U_2) satisfies

$$\begin{aligned}&dN_2''+\mu_2(\tfrac{U_2}{N_2})N_2=\lambda(d\chi''-M\chi),\ \ x\in(0,1),\\&dU_2''+f_2(z(x)-U_1-U_2,\tfrac{U_2}{N_2})N_2+h(N_1)U_1N_2=\lambda Q_{\min,2}(d\chi''-M\chi),\ x\in(0,1).\end{aligned}$$

By the definition of χ, we have

$$\begin{aligned}&dN_2''+\mu_2(\tfrac{U_2}{N_2})N_2\le0,\ \ x\in(0,1),\\&dU_2''+f_2((1-\delta)z(x)-U_2,\tfrac{U_2}{N_2})N_2\le0,\ x\in(0,1).\end{aligned}$$

Let $\Delta_2^\delta=\{(N^0,U^0)\in C([0,1];\mathbb{R}^2): N^0>0,\ 0<U^0\le(1-\delta)z(x),\ \frac{U^0(x)}{N^0(x)}\ge Q_{\min,2} \text{ on } [0,1]\}$. We consider the following auxiliary problem

$$\begin{cases}dN_2''+\mu_2(\frac{U_2}{N_2})N_2=0,\ \ x\in(0,1),\\ dU_2''+f_2((1-\delta)z(x)-U_2,\frac{U_2}{N_2})N_2=0,\ \ x\in(0,1),\\ N_2'(0)=0,\ N_2'(1)+\gamma N_2(1)=0,\ \ U_2'(0)=0,\ U_2'(1)+\gamma U_2(1)=0.\end{cases}\tag{3.18}$$

Let $\lambda_2^\delta(d)$ be the principal eigenvalue of the following nonlinear eigenvalue problem

$$\begin{cases}\lambda\phi(x)=d\phi''(x)+\mu_2(\frac{\varphi(x)}{\phi(x)})\phi(x),\ x\in(0,1),\\ \lambda\varphi(x)=d\varphi''(x)+f_2((1-\delta)z(x),\frac{\varphi(x)}{\phi(x)})\phi(x),\ x\in(0,1),\\ \phi'(0)=\phi'(1)+\gamma\phi(1)=0,\ \varphi'(0)=\varphi'(1)+\gamma\varphi(1)=0.\end{cases}$$

By similar arguments as in [8, Lemma 7.1], there is a $d_{0,2}^{\delta} > 0$ such that

$$\lambda_2^{\delta}(d) > 0 \text{ if } 0 < d < d_{0,2}^{\delta}, \ \ \lambda_2^{\delta}(d) = 0 \text{ if } d = d_{0,2}^{\delta}, \ \ \lambda_2^{\delta}(d) < 0 \text{ if } d > d_{0,2}^{\delta}.$$

By standard regularity theory, it is easy to deduce that $d_{0,2}^{\delta} \to d_{0,2}$ as $\delta \to 0$. In view of $0 < d < d_{0,2}$, there exists $\delta_1 > 0$ small such that for any $0 < \delta \leq \delta_1$, we have $0 < d < d_{0,2}^{\delta}$. It follows from Lemma 2.1 that (3.18) has a unique positive solution $(N_2^{\delta}(x), U_2^{\delta}(x))$ which is globally asymptotically stable in Δ_2^{δ}. Since (3.18) is cooperative, it follows from the monotone method and uniqueness of $(N_2^{\delta}(x), U_2^{\delta}(x))$ that $N_2(x) \geq N_2^{\delta}(x)$, $U_2(x) \geq U_2^{\delta}(x)$. Meanwhile, by L^p estimates and the Sobolev embedding theorem, we proceed as in the proof of Theorem 2.5 in [23] to obtain

$$\lim_{\delta \to 0} N_2^{\delta}(x) = N_2^*(x), \ \ \lim_{\delta \to 0} U_2^{\delta}(x) = U_2^*(x).$$

Hence, there exists $\delta_2 > 0$ such that for $0 < \delta \leq \delta_2$, $N_2^{\delta}(x) > N_2^*(x) - \epsilon_0$, $U_2^{\delta}(x) > U_2^*(x) - \epsilon_0$. Set $\bar{\delta} = \min\{\delta_0, \delta_1, \delta_2\}$. Then for any $0 < \delta \leq \bar{\delta}$, we can find that $N_2(x) > N_2^*(x) - \epsilon_0 \geq \frac{\delta}{\gamma} R^{(0)}$, $U_2(x) > U_2^*(x) - \epsilon_0 \geq \frac{\delta}{\gamma} R^{(0)}$, which contradicts $(N_1, U_1, N_2, U_2) \in \partial O_{\delta}^{+}(E_0)$. Therefore, index$(F, O_{\delta}^{+}(E_0), W) = 0$ by Lemma 2.2. □

Consider the following two nonlinear eigenvalue problems

$$\begin{cases} \Lambda_1 \Phi_1 = d\Phi_1'' + \mu_1(\frac{\Psi_1}{\Phi_1})\Phi_1, \ x \in (0,1), \\ \Lambda_1 \Psi_1 = d\Psi_1'' + f_1(z - U_2^*, \frac{\Psi_1}{\Phi_1})\Phi_1, \ x \in (0,1), \\ \Phi_1'(0) = \Phi_1'(1) + \gamma\Phi_1(1) = 0, \ \Psi_1'(0) = \Psi_1'(1) + \gamma\Psi_1(1) = 0, \end{cases} \tag{3.19}$$

and

$$\begin{cases} \Lambda_2 \Phi_2 = d\Phi_2'' + \mu_2(\frac{\Psi_2}{\Phi_2})\Phi_2, \ x \in (0,1), \\ \Lambda_2 \Psi_2 = d\Psi_2'' + f_2(z - U_1^*, \frac{\Psi_2}{\Phi_2})\Phi_2 + h(N_1^*)U_1^*\Phi_2, \ x \in (0,1), \\ \Phi_2'(0) = \Phi_2'(1) + \gamma\Phi_2(1) = 0, \ \Psi_2'(0) = \Psi_2'(1) + \gamma\Psi_2(1) = 0. \end{cases} \tag{3.20}$$

By similar arguments as in [8, Lemma 5.1] (see also [11]), the eigenvalue problem (3.19) (resp. (3.20)) admits its principal eigenvalue, denoted by Λ_1^0 (resp. Λ_2^0) with the corresponding strongly positive eigenfunctions $(\Phi_1, \Psi_1) \gg_{\mathcal{D}} (0,0)$ in W_1 (resp. $(\Phi_2, \Psi_2) \gg_{\mathcal{D}} (0,0)$ in W_2).

Now we turn to calculate the indices of the compact operator F at the neighborhood of the semi-trivial positive solutions $E_1(x) = (N_1^*(d,x), U_1^*(d,x), 0, 0)$ and $E_2(x) = (0, 0, N_2^*(d,x), U_2^*(d,x))$ in W.

Lemma 3.5. *Suppose $0 < d < d_{0,1}$ and F has no fixed point in $\dot{\Omega}$. Then for $\delta > 0$ small enough*

$$\text{index}(F, O_{\delta}^{+}(E_1), W) = \begin{cases} 1 \ \text{if} \ \Lambda_2^0 < 0, \\ 0 \ \text{if} \ \Lambda_2^0 > 0, \end{cases}$$

where $O_{\delta}^{+}(E_1) = \{(N_1, U_1, N_2, U_2) \in W : \|N_1 - N_1^*\| + \|U_1 - U_1^*\| + \|N_2\| + \|U_2\| < \delta\}$ is a neighborhood of $E_1(x)$ in W.

Proof. For $\tau \in [0, 1]$, define

$$F(\tau)\begin{pmatrix} N_1 \\ U_1 \\ N_2 \\ U_2 \end{pmatrix} = (-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}+M)^{-1}\begin{pmatrix} \mu_1(\frac{U_1}{N_1})N_1 - \tau g(N_1)N_2 + MN_1 \\ f_1(z(x)-U_1-\tau U_2, \frac{U_1}{N_1})N_1 - \tau h(N_1)U_1N_2 + MU_1 \\ \mu_2(\frac{U_2}{N_2})N_2 + MN_2 \\ f_2(z(x)-U_1-\tau U_2, \frac{U_2}{N_2})N_2 + h(N_1)U_1N_2 + MU_2 \end{pmatrix},$$

where M is large enough such that (3.15) holds for all $(N_1, U_1, N_2, U_2) \in \Omega$. Then $F(\tau)(N_1, U_1, N_2, U_2) = (N_1, U_1, N_2, U_2)$ leads to

$$\begin{cases} dN_1'' + \mu_1(\frac{U_1}{N_1})N_1 - \tau g(N_1)N_2 = 0, \ x \in (0, 1), \\ dU_1'' + f_1(z(x)-U_1-\tau U_2, \frac{U_1}{N_1})N_1 - \tau h(N_1)U_1N_2 = 0, \ x \in (0, 1), \\ dN_2'' + \mu_2(\frac{U_2}{N_2})N_2 = 0, \ x \in (0, 1), \\ dU_2'' + f_2(z(x)-U_1-\tau U_2, \frac{U_2}{N_2})N_2 + h(N_1)U_1N_2 = 0, \ x \in (0, 1) \end{cases} \tag{3.21}$$

with the boundary conditions (3.2). If (N_1, U_1, N_2, U_2) is a fixed point of $F(\tau)$ on the boundary $\partial O_\delta^+(E_1) = \{(N_1, U_1, N_2, U_2) \in W : \|N_1 - N_1^*\| + \|U_1 - U_1^*\| + \|N_2\| + \|U_2\| = \delta\}$ of $O_\delta^+(E_1)$ in W, we can deduce that

$$N_1(x) > 0, U_1(x) > 0, N_2(x) \geq 0, U_2(x) \geq 0$$

and

$$N_1(x)Q_{\min,1} \leq U_1(x) \leq N_1(x)Q_1^*, \ N_2(x)Q_{\min,2} \leq U_2(x) \leq N_2(x)Q_2^{**}$$

on $[0, 1]$. Furthermore, we can show that $N_2(x) > 0, U_2(x) > 0$, otherwise we have $(N_1, U_1, N_2, U_2) = E_1$. This is a contradiction to $(N_1, U_1, N_2, U_2) \in \partial O_\delta^+(E_1)$.

Next, we show that for $\tau \in [0, 1]$, $F(\tau)$ has no fixed point on $\partial O_\delta^+(E_1)$. Assume on the contrary that $(N_1, U_1, N_2, U_2) \in \partial O_\delta^+(E_1)$ is a fixed point of $F(\tau)$. Then $N_i(x) > 0, U_i(x) > 0$ and $N_1(x)Q_{\min,1} \leq U_1(x) \leq N_1(x)Q_1^*, N_2(x)Q_{\min,2} \leq U_2(x) \leq N_2(x)Q_2^{**}$ on $[0, 1]$ by the above arguments. But for $\tau = 0$, we can find that $(N_1, U_1) = (N_1^*, U_1^*)$ based on $0 < d < d_{0,1}$, and $(N_2, U_2) \in W_2$ satisfies

$$\begin{cases} dN_2'' + \mu_2(\frac{U_2}{N_2})N_2 = 0, \\ dU_2'' + f_2(z(x)-U_1^*, \frac{U_2}{N_2})N_2 + h(N_1^*)U_1^*N_2 = 0 \end{cases} \tag{3.22}$$

with the usual boundary conditions, which implies $\Lambda_2^0 = 0$, a contradiction to $\Lambda_2^0 \neq 0$. For $\tau > 0$, it follows from the equation (3.21) that $(N_1, U_1, \tau N_2, \tau U_2) \in W$ is a fixed point of F in $\dot{\Omega}$, which is a contradiction to the hypothesis of this lemma. Thus by the homotopy invariance of topological degree that

$$\mathrm{index}(F, O_\delta^+(E_1), W) = \mathrm{index}(F(1), O_\delta^+(E_1), W) = \mathrm{index}(F(0), O_\delta^+(E_1), W),$$

where

$$F(0)\begin{pmatrix} N_1\\ U_1\\ N_2\\ U_2\end{pmatrix}=(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}+M)^{-1}\begin{pmatrix} \mu_1(\frac{U_1}{N_1})N_1+MN_1\\ f_1(z(x)-U_1,\frac{U_1}{N_1})N_1+MU_1\\ \mu_2(\frac{U_2}{N_2})N_2+MN_2\\ f_2(z(x)-U_1,\frac{U_2}{N_2})N_2+h(N_1)U_1N_2+MU_2\end{pmatrix}.$$

The remain task is to calculate index$(F(0), O_\delta^+(E_1), W)$. For this purpose, we first investigate the fixed points of $F(0)$. Suppose (N_1, U_1, N_2, U_2) is a fixed point of $F(0)$ in $O_\delta^+(E_1)$. Then $N_1>0, U_1>0, N_2\geq 0, U_2\geq 0$ and

$$\begin{cases} dN_1''+\mu_1(\frac{U_1}{N_1})N_1=0,\ x\in(0,1),\\ dU_1''+f_1(z(x)-U_1,\frac{U_1}{N_1})N_1=0,\ x\in(0,1),\\ dN_2''+\mu_2(\frac{U_2}{N_2})N_2=0,\ x\in(0,1),\\ dU_2''+f_2(z(x)-U_1,\frac{U_2}{N_2})N_2+h(N_1)U_1N_2=0,\ x\in(0,1)\end{cases}$$

with the boundary conditions (3.2). It is easy to conclude that $(N_1, U_1)=(N_1^*, U_1^*)$ based on $0<d<d_{0,1}$, and (N_2, U_2) satisfies (3.22). Similar arguments as before indicate that $(N_2, U_2)\equiv(0,0)$ when $\Lambda_2^0\neq 0$. Hence, E_1 is the unique fixed point of $F(0)$ in $O_\delta^+(E_1)$, and

$$\text{index}(F(0), O_\delta^+(E_1), W)=\text{index}(F(0), E_1, W).$$

For $\sigma\in[0,1]$, let $T(\sigma)$ be defined by

$$T(\sigma)\begin{pmatrix} N_1\\ U_1\\ N_2\\ U_2\end{pmatrix}=(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}+M)^{-1}\begin{pmatrix} \mu_1(\frac{U_1}{N_1})N_1+MN_1\\ f_1(z-U_1,\frac{U_1}{N_1})N_1+MU_1\\ \mu_2(\frac{U_2}{N_2})N_2+MN_2\\ T_4(N_1,U_1,N_2,U_2)+MU_2\end{pmatrix},$$

where $T_4(N_1, U_1, N_2, U_2)=f_2(z-[(1-\sigma)U_1+\sigma U_1^*], \frac{U_2}{N_2})N_2+h((1-\sigma)N_1+\sigma N_1^*)[(1-\sigma)U_1+\sigma U_1^*]N_2$. Then $T(\sigma)(N_1, U_1, N_2, U_2)=(N_1, U_1, N_2, U_2)$ satisfies

$$\begin{cases} dN_1''+\mu_1(\frac{U_1}{N_1})N_1=0,\ x\in(0,1),\\ dU_1''+f_1(z(x)-U_1,\frac{U_1}{N_1})N_1=0,\ x\in(0,1),\\ dN_2''+\mu_2(\frac{U_2}{N_2})N_2=0,\ x\in(0,1),\\ dU_2''+f_2(z-[(1-\sigma)U_1+\sigma U_1^*],\frac{U_2}{N_2})N_2\\ \qquad +h((1-\sigma)N_1+\sigma N_1^*)[(1-\sigma)U_1+\sigma U_1^*]N_2=0,\ x\in(0,1)\end{cases}\tag{3.23}$$

with the boundary conditions (3.2). Next, we show that $T(\sigma)$ has no fixed point on $\partial O_\delta^+(E_1)\cap W$. Otherwise, it follows from the first and second equations of (3.23) that $(N_1, U_1)=(N_1^*, U_1^*)$, and hence (N_2, U_2) satisfies (3.22). Similar arguments as before indicate that $(N_2, U_2)\equiv(0,0)$ when $\Lambda_2^0\neq 0$. Hence the only fixed point of $T(\sigma)$ on $\partial O_\delta^+(E_1)$ is E_1, a contradiction. On the other hand, it is easy to see that

$$F(0)=T(0),\quad T(1)=T_1\times T_2,$$

where

$$T_1(N_1, U_1) = (-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M)^{-1} \begin{pmatrix} \mu_1(\frac{U_1}{N_1})N_1 + MN_1 \\ f_1(z - U_1, \frac{U_1}{N_1})N_1 + MU_1 \end{pmatrix},$$

$$T_2(N_2, U_2) = (-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M)^{-1} \begin{pmatrix} \mu_2(\frac{U_2}{N_2})N_2 + MN_2 \\ f_2(z - U_1^*, \frac{U_2}{N_2})N_2 + h(N_1^*)U_1^* N_2 + MU_2 \end{pmatrix},$$

and $(T_1 \times T_2)(N_1, U_1, N_2, U_2) = (T_1(N_1, U_1), T_2(N_2, U_2))$. Hence, by the homotopy invariance of topological degree and the product theorem for fixed points that

$$\begin{aligned} \mathrm{index}(F(0), E_1, W) &= \mathrm{index}(T(0), E_1, W) = \mathrm{index}(T(1), E_1, W) \\ &= \mathrm{index}(T_1, (N_1^*, U_1^*), W_1) \cdot \mathrm{index}(T_2, (0, 0), W_2). \end{aligned}$$

Next, we show that $\mathrm{index}(T_1, (N_1^*, U_1^*), W_1) = 1$. Let $\Lambda = 2\max\{1, \frac{1}{Q_{\min,1}}\}\|z\|$, $P_\Lambda = \{(N_1, U_1) \in W_1 : \|N_1\| + \|U_1\| \le \Lambda\}$, $\partial P_\Lambda = \{(N_1, U_1) \in W_1 : \|N_1\| + \|U_1\| = \Lambda\}$. For $\lambda \ge 1$, $T_1(N_1, U_1) = \lambda(N_1, U_1)$ leads to

$$\begin{cases} dN_1'' + \frac{1}{\lambda}\mu_1(\frac{U_1}{N_1})N_1 = (1 - \frac{1}{\lambda})MN_1 \ge 0, \ x \in (0, 1), \\ dU_1'' + \frac{1}{\lambda} f_1(z(x) - U_1, \frac{U_1}{N_1})N_1 = (1 - \frac{1}{\lambda})MU_1 \ge 0, \ x \in (0, 1), \end{cases}$$

with the usual boundary conditions. By the similar arguments as in the proof of Lemma 3.1, we can show that $\|N_1\| < \frac{\Lambda}{2}$, $\|U_1\| < \frac{\Lambda}{2}$. Hence for $\lambda \ge 1$, $T_1(N_1, U_1) = \lambda(N_1, U_1)$ has no solution on ∂P_Λ. It follows from Lemma 2.2 that

$$\mathrm{index}(T_1, P_\Lambda, W_1) = 1.$$

Let $0 < \delta_0 \le \frac{1}{2}\min_{[0,1]}\{N_1^*, U_1^*\}$. Observe that $\chi = 2 + \gamma - \gamma x^2 > 0$ on $[0, 1]$. Hence, $(\chi, Q_{\min,1}\chi) \in W_1$. Suppose that for $\lambda \ge 0$, the equation $(N_1, U_1) - T_1(N_1, U_1) = \lambda(\chi, Q_{\min,1}\chi)$ has a solution (N_1, U_1) on ∂P_{δ_0}. Then we have

$$\begin{cases} dN_1'' + \mu_1(\frac{U_1}{N_1})N_1 = \lambda(d\chi'' - M\chi) \le 0, \ x \in (0, 1), \\ dU_1'' + f_1(z(x) - U_1, \frac{U_1}{N_1})N_1 = \lambda Q_{\min,1}(d\chi'' - M\chi) \le 0, \ x \in (0, 1), \end{cases}$$

with the usual boundary conditions, which implies that (N_1, U_1) is a super-solution of

$$\begin{cases} d\hat{N}_1'' + \mu_1(\frac{\hat{U}_1}{\hat{N}_1})\hat{N}_1 = 0, \ x \in (0, 1), \\ d\hat{U}_1'' + f_1(z(x) - \hat{U}_1, \frac{\hat{U}_1}{\hat{N}_1})\hat{N}_1 = 0, \ x \in (0, 1), \\ \hat{N}_1'(0) = 0, \ \hat{N}_1'(1) + \gamma\hat{N}_1(1) = 0, \ x \in (0, 1), \\ \hat{U}_1'(0) = 0, \ \hat{U}_1'(1) + \gamma\hat{U}_1(1) = 0, \ x \in (0, 1). \end{cases}$$

By the monotone method and the uniqueness of (N_1^*, U_1^*), one can conclude that $(N_1, U_1) \ge (N_1^*, U_1^*)$. This is a contradiction to $\|N_1\| + \|U_1\| = \delta_0$. Hence,

$$\text{index}(T_1, P_{\delta_0}, W_1) = 0.$$

Since (N_1^*, U_1^*) is the unique fixed point of T_1 in $P_\Lambda \setminus P_{\delta_0}$, we have

$$\begin{aligned}\text{index}(T_1, (N_1^*, U_1^*), W_1) &= \text{index}(T_1, P_\Lambda \setminus P_{\delta_0}, W_1)\\ &= \text{index}(T_1, P_\Lambda, W_1) - \text{index}(T_1, P_{\delta_0}, W_1) = 1.\end{aligned}$$

Next, we claim that

$$\text{index}(T_2, (0,0), W_2) = \begin{cases} 1 & \text{provided } \Lambda_2^0 < 0, \\ 0 & \text{provided } \Lambda_2^0 > 0. \end{cases}$$

We first consider the case of $\Lambda_2^0 < 0$. Suppose that for $\lambda \geq 1$, $T_2(N_2, U_2) = \lambda(N_2, U_2)$ has a solution (N_2, U_2) on $\partial O_2^+(0,0)$, where $O_2^+(0,0)$ is a small neighborhood of $(0,0)$ in W_2. Then we have

$$\begin{cases} dN_2'' + \mu_2(\frac{U_2}{N_2})N_2 = (1 - \frac{1}{\lambda})(M + \mu_2(\frac{U_2}{N_2})N_2, \ x \in (0,1), \\ dU_2'' + f_2(z(x) - U_1^*, \frac{U_2}{N_2})N_2 + h(N_1^*)U_1^* N_2 \\ \quad = (1 - \frac{1}{\lambda})(MU_2 + f_2(z(x) - U_1^*, \frac{U_2}{N_2})N_2 + h(N_1^*)U_1^* N_2), \ x \in (0,1) \end{cases}$$

with the usual boundary conditions, which implies that

$$\begin{cases} dN_2'' + \mu_2(\frac{U_2}{N_2})N_2 \geq 0, \ x \in (0,1), \\ dU_2'' + f_2(z(x) - U_1^*, \frac{U_2}{N_2})N_2 + h(N_1^*)U_1^* N_2 \geq 0, \ x \in (0,1). \end{cases}$$

Therefore, (N_2, U_2) is a lower solution to the following cooperative parabolic system

$$\begin{cases} \frac{\partial \widetilde{N}_2}{\partial t} = d\frac{\partial^2 \widetilde{N}_2}{\partial x^2} + \mu_2(\frac{\widetilde{U}_2}{\widetilde{N}_2})\widetilde{N}_2, \ x \in (0,1), t > 0 \\ \frac{\partial \widetilde{U}_2}{\partial t} = d\frac{\partial^2 \widetilde{U}_2}{\partial x^2} + f_2(z(x) - U_1^*, \frac{\widetilde{U}_2}{\widetilde{N}_2})\widetilde{N}_2 + h(N_1^*)U_1^* \widetilde{N}_2, \ x \in (0,1), t > 0, \\ \frac{\partial \widetilde{N}_2}{\partial x}(0,t) = 0, \ \frac{\partial \widetilde{N}_2}{\partial x}(1,t) + \gamma \widetilde{N}_2(1,t) = 0, \ t > 0, \\ \frac{\partial \widetilde{U}_2}{\partial x}(0,t) = 0, \ \frac{\partial \widetilde{U}_2}{\partial x}(1,t) + \gamma \widetilde{U}_2(1,t) = 0, \ t > 0, \\ \widetilde{N}_2(x,0) = N_2(x), \ \ \widetilde{U}_2(x,0) = U_2(x), \ x \in [0,1]. \end{cases} \tag{3.24}$$

Meanwhile, observing that $(N_2, U_2) \in \partial O_2^+(0,0)$, there exists an $\alpha_2 > 0$ such that $(N_2, U_2) \leq (\alpha_2 \Phi_2, \alpha_2 \Psi_2)$, where (Φ_2, Ψ_2) is the strongly positive eigenfunction associated with Λ_2^0. Let $(\hat{N}_2(x,t), \hat{U}_2(x,t)) = (\alpha_2 e^{\Lambda_2^0 t}\Phi_2, \alpha_2 e^{\Lambda_2^0 t}\Psi_2)$. Then it is easy to see that $(\hat{N}_2(x,t), \hat{U}_2(x,t))$ is an upper solution to (3.24) based on $\Lambda_2^0 < 0$. It follows from the comparison principle for cooperative parabolic system that

$$(N_2, U_2) \leq (\hat{N}_2(x,t), \hat{U}_2(x,t)) = (\alpha_2 e^{\Lambda_2^0 t}\Phi_2, \alpha_2 e^{\Lambda_2^0 t}\Psi_2)$$

for all $x \in [0,1]$ and $t > 0$. Letting $t \to \infty$ in the above inequality, and using $\Lambda_2^0 < 0$, we deduce that $(N_2, U_2) = (0,0)$ on $[0, 1]$, contradicting the fact $(N_2, U_2) \in \partial O_2^+(0,0)$.

Hence, $T_2(N_2, U_2) = \lambda(N_2, U_2)$ has no solution on $\partial O_2^+(0,0)$, and index$(T_2, (0,0), W_2) = 1$ by Lemma 2.2(i).

In the case of $\Lambda_2^0 > 0$, let $\chi = 2 + \gamma - \gamma x^2$ on [0, 1]. Then $(\chi, Q_{\min,2}\chi) \in W_2$. Suppose for $\lambda \geq 0$, $(N_2, U_2) - T_2(N_2, U_2) = \lambda(\chi, Q_{\min,2}\chi)$ has a solution (N_2, U_2) on $\partial O_2^+(0,0)$. Then we have

$$\begin{cases} dN_2'' + \mu_2(\frac{U_2}{N_2})N_2 = \lambda(d\chi'' - M\chi) \leq 0, \ x \in (0,1), \\ dU_2'' + f_2(z(x) - U_1^*, \frac{U_2}{N_2})N_2 + h(N_1^*)U_1^*N_2 = \lambda Q_{\min,2}(d\chi'' - M\chi) \leq 0, \ x \in (0,1) \end{cases}$$

with the usual boundary conditions, which implies (N_2, U_2) is a upper solution of (3.24). Meanwhile, observing that $(N_2, U_2) \in \partial O_2^+(0,0)$, there exists an $\epsilon > 0$ such that $(N_2, U_2) \geq \epsilon(\Phi_2, \Psi_2)$. In view of $\Lambda_2^0 > 0$, it is easy to check that $(\epsilon e^{\Lambda_2^0 t}\Phi_2, \epsilon e^{\Lambda_2^0 t}\Psi_2)$ is a lower solution of (3.24). It follows from the comparison principle for cooperative parabolic system that

$$(N_2, U_2) \geq (\epsilon e^{\Lambda_2^0 t}\Phi_2, \epsilon e^{\Lambda_2^0 t}\Psi_2)$$

for all $x \in [0,1]$ and $t > 0$. Letting $t \to \infty$ in the above inequality, and using $\Lambda_2^0 > 0$, we deduce that (N_2, U_2) is unbounded. This contradicts the fact $(N_2, U_2) \in \partial O_2^+(0,0)$. Hence, for $\lambda \geq 0$, $(N_2, U_2) - T_2(N_2, U_2) = \lambda(\chi, Q_{\min,2}\chi)$ has no solution on $\partial O_2^+(0,0)$ when $\Lambda_2^0 > 0$. It follows from Lemma 2.2(ii) that index$(T_2, (0,0), W_2) = 0$ when $\Lambda_2^0 > 0$.

Combining the above results, we obtain

$$\begin{aligned} \text{index}(F, O_\delta^+(E_1), W) &= \text{index}(F(0), O_\delta^+(E_1), W) = \text{index}(F(0), E_1, W) \\ &= \text{index}(T(1), E_1, W) \\ &= \text{index}(T_1, (N_1^*, U_1^*), W_1) \cdot \text{index}(T_2, (0,0), W_2) \\ &= \begin{cases} 1 & \text{provided } \Lambda_2^0 < 0, \\ 0 & \text{provided } \Lambda_2^0 > 0. \end{cases} \qquad \square \end{aligned}$$

Lemma 3.6. *Suppose* $0 < d < d_{0,2}$. *Then for* $\delta > 0$ *small enough*

$$\text{index}(F, O_\delta^+(E_2), W) = \begin{cases} 1 \ \textit{if} \ \Lambda_1^0 < 0, \\ 0 \ \textit{if} \ \Lambda_1^0 > 0, \end{cases}$$

where $O_\delta^+(E_2) = \{(N_1, U_1, N_2, U_2) \in W : \|N_1\| + \|U_1\| + \|N_2 - N_2^*\| + \|U_2 - U_2^*\| < \delta\}$.

Proof. For $\tau \in [0,1]$, define

$$\widetilde{F}(\tau)\begin{pmatrix} N_1 \\ U_1 \\ N_2 \\ U_2 \end{pmatrix} = (-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M)^{-1}\begin{pmatrix} \mu_1(\frac{U_1}{N_1})N_1 - \tau g(N_1)N_2 + MN_1 \\ f_1(z(x) - \tau U_1 - U_2, \frac{U_1}{N_1})N_1 - \tau h(N_1)U_1N_2 + MN_2 \\ \mu_2(\frac{U_2}{N_2})N_2 + MU_1 \\ f_2(z(x) - \tau U_1 - U_2, \frac{U_2}{N_2})N_2 + \tau h(N_1)U_1N_2 + MU_2 \end{pmatrix},$$

where M is large enough such that (3.15) holds for all $(N_1, U_1, N_2, U_2) \in \Omega$. At first, we claim that $\widetilde{F}(\tau)$ has no fixed point on $\partial O_\delta^+(E_2)$ if $\Lambda_1^0 \neq 0$. Here $\partial O_\delta^+(E_2) = \{(N_1, U_1, N_2, U_2) \in$

$W : \|N_1\| + \|U_1\| + \|N_2 - N_2^*\| + \|U_2 - U_2^*\| = \delta\}$. Otherwise, there exists $(N_1, U_1, N_2, U_2) \in \partial O_\delta^+(E_2)$ such that $\widetilde{F}(\tau)(N_1, U_1, N_2, U_2) = (N_1, U_1, N_2, U_2)$, which leads to

$$\begin{cases} dN_1'' + \mu_1(\frac{U_1}{N_1})N_1 - \tau g(N_1)N_2 = 0, \ x \in (0,1), \\ dU_1'' + f_1(z(x) - \tau U_1 - U_2, \frac{U_1}{N_1})N_1 - \tau h(N_1)U_1N_2 = 0, \ x \in (0,1), \\ dN_2'' + \mu_2(\frac{U_2}{N_2})N_2 = 0, \ x \in (0,1), \\ dU_2'' + f_2(z(x) - \tau U_1 - U_2, \frac{U_2}{N_2})N_2 + \tau h(N_1)U_1N_2 = 0, \ x \in (0,1) \end{cases} \tag{3.25}$$

with the boundary conditions (3.2).

For $\tau = 0$, we can find that $(N_2, U_2) = (N_2^*, U_2^*)$ based on $0 < d < d_{0,2}$, and $(N_1, U_1) \in W_1$ satisfies

$$\begin{cases} dN_1'' + \mu_1(\frac{U_1}{N_1})N_1 = 0, \ x \in (0,1), \\ dU_1'' + f_1(z(x) - U_2^*, \frac{U_1}{N_1})N_1 = 0, \ x \in (0,1) \end{cases}$$

with the usual boundary conditions, which implies $\Lambda_1^0 = 0$, a contradiction to $\Lambda_1^0 \neq 0$.

For $\tau > 0$, in view of $(N_1, U_1, N_2, U_2) \in \partial O_\delta^+(E_2)$, we get

$$0 \le N_1 \le \delta, \ 0 \le U_1 \le \delta, \ N_2^* - \delta \le N_2 \le N_2^* + \delta, \ U_2^* - \delta \le U_2 \le U_2^* + \delta. \tag{3.26}$$

Thus it follows from (3.25) that

$$\begin{aligned} &dN_1'' + \mu_1(\tfrac{U_1}{N_1})N_1 \ge 0, \ x \in (0,1), \\ &dU_1'' + f_1(z(x) + \delta - U_2^*, \tfrac{U_1}{N_1})N_1 \ge 0, \ x \in (0,1) \end{aligned}$$

with the usual boundary conditions. Hence, (N_1, U_1) is a lower solution to the following cooperative parabolic system

$$\begin{cases} \frac{\partial \hat{N}_1}{\partial t} = d\frac{\partial^2 \hat{N}_1}{\partial x^2} + \mu_1(\frac{\hat{U}_1}{\hat{N}_1})\hat{N}_1, \ x \in (0,1), t > 0, \\ \frac{\partial \hat{U}_1}{\partial t} = d\frac{\partial^2 \hat{U}_1}{\partial x^2} + f_1(z(x) + \delta - U_2^*, \frac{\hat{U}_1}{\hat{N}_1})\hat{N}_1, \ x \in (0,1), t > 0, \\ \frac{\partial \hat{N}_1}{\partial x}(0,t) = 0, \ \frac{\partial \hat{N}_1}{\partial x}(1,t) + \gamma \hat{N}_1(1,t) = 0, \ t > 0, \\ \frac{\partial \hat{U}_1}{\partial x}(0,t) = 0, \ \frac{\partial \hat{U}_1}{\partial x}(1,t) + \gamma \hat{U}_1(1,t) = 0, \ t > 0, \\ \hat{N}_1(x,0) = N_1(x), \quad \hat{U}_1(x,0) = U_1(x), \ x \in [0,1]. \end{cases} \tag{3.27}$$

If $\Lambda_1^0 < 0$, by choosing δ small enough, we have $\Lambda_1^\delta < 0$, where Λ_1^δ is the principal eigenvalue of the following eigenvalue problem with the corresponding strongly positive eigenfunction $(\Phi_1^\delta, \Psi_1^\delta)$

$$\begin{cases} \Lambda_1^\delta \Phi_1^\delta = d\Phi_{1xx}^\delta + \mu_1(\frac{\Psi_1^\delta}{\Phi_1^\delta})\Phi_1^\delta, \ x \in (0,1), \\ \Lambda_1^\delta \Psi_1^\delta = d\Psi_{1xx}^\delta + f_1(z + \delta - U_2^*, \frac{\Psi_1^\delta}{\Phi_1^\delta})\Phi_1^\delta, \ x \in (0,1), \\ \Phi_{1x}^\delta(0) = \Phi_{1x}^\delta(1) + \gamma\Phi_1^\delta(1) = 0, \ \Psi_{1x}^\delta(0) = \Psi_{1x}^\delta(1) + \gamma\Psi_1^\delta(1) = 0. \end{cases}$$

In view of (3.26), there exists an $\alpha_1 > 0$ such that $(N_1, U_1) \leq (\alpha_1 \Phi_1^\delta, \alpha_1 \Psi_1^\delta)$. Let $(\hat{N}_1(x,t), \hat{U}_1(x,t)) = (\alpha_1 e^{\Lambda_1^\delta t}\Phi_1^\delta, \alpha_1 e^{\Lambda_1^\delta t}\Psi_1^\delta)$. Then it is easy to see that $(\hat{N}_1(x,t), \hat{U}_1(x,t))$ is an upper solution to (3.27). It follows from the comparison principle for cooperative parabolic system that

$$(N_1, U_1) \leq (\hat{N}_1(x,t), \hat{U}_1(x,t)) = (\alpha_1 e^{\Lambda_1^\delta t}\Phi_1^\delta, \alpha_1 e^{\Lambda_1^\delta t}\Psi_1^\delta)$$

for all $x \in [0, 1]$ and $t > 0$. Since $\Lambda_1^0 < 0$, we immediately deduce that $(N_1, U_1) = (0, 0)$ on $[0, 1]$ after we let $t \to \infty$ in the above inequality. It follows from (3.25) that $(N_2, U_2) = (N_2^*, U_2^*)$ based on $0 < d < d_{0,2}$. That is, $(N_1, U_1, N_2, U_2) = E_2$, a contradiction to $(N_1, U_1, N_2, U_2) \in \partial O_\delta^+(E_2)$.

If $\Lambda_1^0 > 0$, then there exists $\rho_1 > 0$ small such that $\widetilde{\Lambda}_1^\rho > 0$ for all $\rho \in [0, \rho_1)$, where $\widetilde{\Lambda}_1^\rho$ is the principal eigenvalue of the following eigenvalue problem with the corresponding strongly positive eigenfunction $(\widetilde{\Phi}_1^\rho, \widetilde{\Psi}_1^\rho)$:

$$\begin{cases} \widetilde{\Lambda}_1^\rho \widetilde{\Phi}_1^\rho = d\widetilde{\Phi}_{1xx}^\delta + \mu_1(\frac{\widetilde{\Psi}_1^\rho}{\widetilde{\Phi}_1^\rho})\widetilde{\Phi}_1^\rho - \rho\widetilde{\Phi}_1^\rho, \ x \in (0,1), \\ \widetilde{\Lambda}_1^\rho \widetilde{\Psi}_1^\rho = d\widetilde{\Psi}_{1xx}^\delta + (f_1(z - U_2^*, \frac{\widetilde{\Psi}_1^\rho}{\widetilde{\Phi}_1^\rho}) - \rho)\widetilde{\Phi}_1^\rho - \rho\widetilde{\Psi}_1^\rho, \ x \in (0,1), \\ \widetilde{\Phi}_{1x}^\rho(0) = \widetilde{\Phi}_{1x}^\rho(1) + \gamma\widetilde{\Phi}_1^\rho(1) = 0, \ \widetilde{\Psi}_{1x}^\rho(0) = \widetilde{\Psi}_{1x}^\rho(1) + \gamma\widetilde{\Psi}_1^\rho(1) = 0. \end{cases}$$

Consider the following cooperative system

$$\begin{cases} d\widetilde{N}_1'' + (\mu_1(\frac{\widetilde{U}_1}{\widetilde{N}_1}) - \rho)\widetilde{N}_1 = 0, \ x \in (0,1), \\ d\widetilde{U}_1'' + (f_1(z(x) - U_2^* - \widetilde{U}_1, \frac{\widetilde{U}_1}{\widetilde{N}_1}) - \rho)\widetilde{N}_1 - \rho\widetilde{U}_1 = 0, \ x \in (0,1) \end{cases} \tag{3.28}$$

with the usual boundary conditions. Noting that $\widetilde{\Lambda}_1^\rho > 0$, for $\epsilon_1 > 0$ small, it is easy to check that $(\epsilon_1\widetilde{\Phi}_1^\rho, \epsilon_1\widetilde{\Psi}_1^\rho)$ is a lower solution of (3.28). Furthermore, by similar arguments as in Lemma 2.1, one can conclude that (3.28) has a unique positive solution $(\widetilde{N}_{1,\rho}, \widetilde{U}_{1,\rho})$. Moreover, $(\widetilde{N}_{1,\rho}, \widetilde{U}_{1,\rho}) \to (N_1^*, U_1^*)$ as $\rho \to 0$ by standard elliptic regularity theory. Hence, by further choosing $\rho > 0$ small, we have $(\widetilde{N}_{1,\rho}, \widetilde{U}_{1,\rho}) > \frac{1}{2}(N_1^*, U_1^*)$ on $[0, 1]$.

In view of (3.26), we conclude that for $\rho > 0$ given above, there exists $\delta_0 > 0$ small such that

$$\begin{aligned} &g(N_1)N_2 = h(N_1)N_2 \cdot N_1 \leq \rho N_1, \\ &h(N_1)U_1N_2 = h(N_1)N_2 \cdot U_1 \leq \rho U_1, \\ &f_1(z - \tau U_1 - U_2, \tfrac{U_1}{N_1}) > f_1(z - U_2^* - \tau U_1, \tfrac{U_1}{N_1}) - \rho \end{aligned}$$

and

$$(N_1, U_1) < \frac{1}{2}(N_1^*, U_1^*) \tag{3.29}$$

hold for all $(N_1, U_1, N_2, U_2) \in \partial O_\delta^+(E_2)$ and $\delta \in (0, \delta_0]$. It follows from (3.25) that

$$\begin{aligned} &dN_1'' + (\mu_1(\tfrac{U_1}{N_1}) - \rho)N_1 \leq 0, \ x \in (0,1), \\ &dU_1'' + (f_1(z(x) - U_2^* - \tau U_1, \tfrac{U_1}{N_1}) - \rho)N_1 - \rho U_1 \leq 0, \ x \in (0,1) \end{aligned}$$

with the usual boundary conditions. Hence, $(\tau N_1, \tau U_1)$ is an upper solution to (3.28). Recall that $(\epsilon_1\widetilde{\Phi}_1^{\rho}, \epsilon_1\widetilde{\Psi}_1^{\rho})$ is a lower solution of (3.28). It follows from the monotone method and the uniqueness of positive solutions to (3.28) that $(\tau N_1, \tau U_1) \geq (\widetilde{N}_{1,\rho}, \widetilde{U}_{1,\rho})$. Hence, $(\tau N_1, \tau U_1) > \frac{1}{2}(N_1^*, U_1^*)$, which contradicts (3.29). Therefore, $\widetilde{F}(\tau)$ has no fixed point on $\partial O_\delta^+(E_2)$ if $\Lambda_1^0 \neq 0$.

By the homotopy invariance of topological degree that

$$\mathrm{index}(F, O_\delta^+(E_2), W) = \mathrm{index}(\widetilde{F}(1), O_\delta^+(E_2), W) = \mathrm{index}(\widetilde{F}(0), O_\delta^+(E_2), W),$$

where

$$\widetilde{F}(0)\begin{pmatrix} N_1 \\ U_1 \\ N_2 \\ U_2 \end{pmatrix} = (-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M)^{-1}\begin{pmatrix} \mu_1(\frac{U_1}{N_1})N_1 + MN_1 \\ f_1(z(x) - U_2, \frac{U_1}{N_1})N_1 + MU_1 \\ \mu_2(\frac{U_2}{N_2})N_2 + MN_2 \\ f_2(z(x) - U_2, \frac{U_2}{N_2})N_2 + MU_2 \end{pmatrix}.$$

It remains to calculate $\mathrm{index}(\widetilde{F}(0), O_\delta^+(E_2), W)$. To this end, we first work out the fixed points (N_1, U_1, N_2, U_2) of $\widetilde{F}(0)$. Suppose (N_1, U_1, N_2, U_2) is a fixed point of $\widetilde{F}(0)$ in $O_\delta^+(E_2)$. Then $N_1 \geq 0, U_1 \geq 0, N_2 > 0, U_2 > 0$, $Q_{\min,1} \leq \frac{U_1}{N_1} \leq Q_1^*$, $Q_{\min,2} \leq \frac{U_2}{N_2} \leq Q_2^{**}$ and

$$\begin{cases} dN_1'' + \mu_1(\frac{U_1}{N_1})N_1 = 0, \ x \in (0,1), \\ dU_1'' + f_1(z(x) - U_2, \frac{U_1}{N_1})N_1 = 0, \ x \in (0,1), \\ dN_2'' + \mu_2(\frac{U_2}{N_2})N_2 = 0, \ x \in (0,1), \\ dU_2'' + f_2(z(x) - U_2, \frac{U_2}{N_2})N_2 = 0, \ x \in (0,1) \end{cases}$$

with the boundary conditions (3.2). It is easy to see that $(N_2, U_2) = (N_2^*, U_2^*)$ based on $0 < d < d_{0,2}$, and $(N_1, U_1) \in W_1$ satisfies

$$\begin{cases} dN_1'' + \mu_1(\frac{U_1}{N_1})N_1 = 0, \ x \in (0,1), \\ dU_1'' + f_1(z(x) - U_2^*, \frac{U_1}{N_1})N_1 = 0, \ x \in (0,1) \end{cases} \tag{3.30}$$

with the usual boundary conditions. Similar arguments as before implies that $(N_1, U_1) = (0, 0)$ when $\Lambda_1^0 \neq 0$. That is, E_2 is the unique fixed point of $\widetilde{F}(0)$ in $O_\delta^+(E_2)$, and

$$\mathrm{index}(\widetilde{F}(0), O_\delta^+(E_2), W) = \mathrm{index}(\widetilde{F}(0), E_2, W).$$

For $\sigma \in [0, 1]$, let $\widetilde{T}(\sigma)$ be defined by

$$\widetilde{T}(\sigma)\begin{pmatrix} N_1 \\ U_1 \\ N_2 \\ U_2 \end{pmatrix} = (-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M)^{-1}\begin{pmatrix} \mu_1(\frac{U_1}{N_1})N_1 + MN_1 \\ f_1(z - [(1-\sigma)U_2 + \sigma U_2^*], \frac{U_1}{N_1})N_1 + MU_1 \\ \mu_2(\frac{U_2}{N_2})N_2 + MN_2 \\ f_2(z - U_2, \frac{U_2}{N_2})N_2 + MU_2 \end{pmatrix}.$$

Then $\widetilde{T}(\sigma)(N_1, U_1, N_2, U_2) = (N_1, U_1, N_2, U_2)$ satisfies

$$\begin{cases} dN_1'' + \mu_1(\frac{U_1}{N_1})N_1 = 0, \ x \in (0,1), \\ dU_1'' + f_1(z(x) - [(1-\sigma)U_2 + \sigma U_2^*], \frac{U_1}{N_1})N_1 = 0, \ x \in (0,1), \\ dN_2'' + \mu_2(\frac{U_2}{N_2})N_2 = 0, \ x \in (0,1), \\ dU_2'' + f_2(z - U_2, \frac{U_2}{N_2})N_2 = 0, \ x \in (0,1) \end{cases} \tag{3.31}$$

with the boundary conditions (3.2). First, we show that $\widetilde{T}(\sigma)$ has no fixed point on $\partial O_\delta^+(E_2)$. Otherwise, it follows from the last two equations of (3.31) that $(N_2, U_2) = (N_2^*, U_2^*)$, and hence (N_1, U_1) satisfies (3.30). Similar arguments as before indicate that $(N_1, U_1) \equiv (0,0)$ when $\Lambda_1^0 \neq 0$. Hence the only fixed point of $\widetilde{T}(\sigma)$ on $\partial O_\delta^+(E_2)$ is E_2, a contradiction. On the other hand, it is easy to see that

$$\widetilde{F}(0) = \widetilde{T}(0), \quad \widetilde{T}(1) = \widetilde{T}_1 \times \widetilde{T}_2,$$

where

$$\widetilde{T}_1(N_1, U_1) = (-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M)^{-1} \begin{pmatrix} \mu_1(\frac{U_1}{N_1})N_1 + MN_1 \\ f_1(z - U_2^*, \frac{U_1}{N_1})N_1 + MU_1 \end{pmatrix},$$

$$\widetilde{T}_2(N_2, U_2) = (-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M)^{-1} \begin{pmatrix} \mu_2(\frac{U_2}{N_2})N_2 + MN_2 \\ f_2(z - U_2, \frac{U_2}{N_2})N_2 + MU_2 \end{pmatrix},$$

and $(\widetilde{T}_1 \times \widetilde{T}_2)(N_1, U_1, N_2, U_2) = (\widetilde{T}_1(N_1, U_1), \widetilde{T}_2(N_2, U_2))$. Hence, by the homotopy invariance of topological degree and the product theorem for fixed points that

$$\begin{aligned} \mathrm{index}(\widetilde{F}(0), E_2, W) &= \mathrm{index}(\widetilde{T}(0), E_2, W) = \mathrm{index}(\widetilde{T}(1), E_2, W) \\ &= \mathrm{index}(\widetilde{T}_1, (0,0), W_1) \cdot \mathrm{index}(\widetilde{T}_2, (N_2^*, U_2^*), W_2). \end{aligned}$$

By similar arguments as in Lemma 3.5, we can show $\mathrm{index}(\widetilde{T}_2, (N_2^*, U_2^*), W_2) = 1$, and

$$\mathrm{index}(\widetilde{T}_1, (0,0), W_1) = \begin{cases} 1 & \text{provided } \Lambda_1^0 < 0, \\ 0 & \text{provided } \Lambda_1^0 > 0. \end{cases}$$

In summary, we obtain

$$\begin{aligned} \mathrm{index}(F, O_\delta^+(E_2), W) &= \mathrm{index}(\widetilde{F}(0), O_\delta^+(E_2), W) = \mathrm{index}(\widetilde{T}(1), O_\delta^+(E_2), W) \\ &= \mathrm{index}(\widetilde{T}_1, (0,0), W_1) \cdot \mathrm{index}(\widetilde{T}_2, (N_2^*, U_2^*), W_2) \\ &= \begin{cases} 1 & \text{provided } \Lambda_1^0 < 0, \\ 0 & \text{provided } \Lambda_1^0 > 0. \end{cases} \qquad \square \end{aligned}$$

Theorem 3.1. *Suppose* $0 < d < \min\{d_{0,1}, d_{0,2}\}$. *Then the steady state system* (3.1)–(3.2) *has positive solution if* $\Lambda_1^0 < 0, \Lambda_2^0 < 0$ *or* $\Lambda_1^0 > 0, \Lambda_2^0 > 0$.

Proof. It follows from Lemma 3.1 that (N_1, U_1, N_2, U_2) is a positive solution to system (3.1)–(3.2) if and only if it is a fixed point of the operator F in $\dot{\Omega}$. Assume that F has no fixed point in $\dot{\Omega}$. Then F has only a trivial solution E_0 and two semi-trivial solutions $E_1(x)$ and $E_2(x)$. It follows from the additivity of the fixed point index that

$$\mathrm{index}(F, \dot{\Omega}, W) = \mathrm{index}(F, W_\delta(E_0), W) \\ + \mathrm{index}(F, O_\delta^+(E_1), W) + \mathrm{index}(F, O_\delta^+(E_2), W).$$

If $\Lambda_1^0 < 0$, $\Lambda_2^0 < 0$, it follows from Lemmas 3.3, 3.4, 3.5 and 3.6 that

$$\mathrm{index}(F, W_\delta(E_0), W) + \mathrm{index}(F, O_\delta^+(E_1), W) + \mathrm{index}(F, O_\delta^+(E_2), W) = 2,$$

which contradicts $\mathrm{index}(F, \dot{\Omega}, W) = 1$.

If $\Lambda_1^0 > 0$, $\Lambda_2^0 > 0$, it follows from Lemmas 3.3, 3.4, 3.5 and 3.6 that

$$\mathrm{index}(F, W_\delta(E_0), W) + \mathrm{index}(F, O_\delta^+(E_1), W) + \mathrm{index}(F, O_\delta^+(E_2), W) = 0.$$

This also contradicts $\mathrm{index}(F, \dot{\Omega}, W) = 1$, which implies the conclusion holds. □

4. Discussion

In this paper, we focus on the investigation of the existence of positive steady-state solutions of system (1.5)–(1.7) (or (1.8)–(1.10)) describing the interactions of an intraguild predator (*Ochromonas*) and an intraguild prey (*Microcystis*) when grown in *ammonium*. System (1.5)–(1.7) was extended from the ordinary differential equation (1.1) in [20] by incorporating the spatial factors. As pointed out in the previous works [7–9], the main difficulties in mathematical analysis of system (1.5)–(1.7) are caused by the singularity in the ratios U_1/N_1 and U_2/N_2 at the trivial or semitrivial steady states with $(U_1, N_1) = (0, 0)$ or $(U_2, N_2) = (0, 0)$. Thus, standard technique such as linearization can not be applied here.

Instead of doing linearization around semitrivial steady states of system (1.5)–(1.7), the authors in [11] directly used the following cooperative systems

$$\begin{cases} \frac{\partial N_1}{\partial t} = d\frac{\partial^2 N_1}{\partial x^2} + \mu_1(\frac{U_1}{N_1})N_1, \ x \in (0,1), \ t > 0, \\ \frac{\partial U_1}{\partial t} = d\frac{\partial^2 U_1}{\partial x^2} + f_1(z(x) - U_2^*(x), \frac{U_1}{N_1})N_1, \ x \in (0,1), \ t > 0, \\ \frac{\partial w}{\partial x}(0,t) = \frac{\partial w}{\partial x}(1,t) + \gamma w(1,t) = 0, \ t > 0, \ w = N_1, \ U_1, \end{cases} \tag{4.1}$$

and

$$\begin{cases} \frac{\partial N_2}{\partial t} = d\frac{\partial^2 N_2}{\partial x^2} + \mu_2(\frac{U_2}{N_2})N_2, \ x \in (0,1), \ t > 0, \\ \frac{\partial U_2}{\partial t} = d\frac{\partial^2 U_2}{\partial x^2} + f_2(z(x) - U_1^*(x), \frac{U_2}{N_2})N_2 \\ \qquad + h(N_1^*(x))U_1^*(x)N_2, \ x \in (0,1), \ t > 0, \\ \frac{\partial w}{\partial x}(0,t) = \frac{\partial w}{\partial x}(1,t) + \gamma w(1,t) = 0, \ t > 0, \ w = N_2, \ U_2, \end{cases} \tag{4.2}$$

to determine the conditions such that two semitrivial steady states are "uniform weak repellers", respectively (see also [8]). Note that the nonlinear eigenvalue problem (3.19) (resp. (3.20)) comes from system (4.1) (resp. (4.2)) and admits the principal eigenvalue Λ_1^0 (resp. Λ_2^0). Such kinds of nonlinear eigenvalue problems were also studied in [8]. Under the condition $0 < d < \min\{d_{0,1}, d_{0,2}\}$, we see that both of the semitrivial steady-state solutions exist, that is, each species can survive alone in the absence of its competitor. Then the authors in [11] established the existence of a (robust) coexistence steady state of system (1.5)–(1.7) by applying the theory of uniform persistence, provided that $\Lambda_1^0 > 0$ and $\Lambda_2^0 > 0$, which corresponds to the case where both of the semitrivial steady-state solutions are uniform weak repellers. Under the condition $0 < d_{0,2} < d < d_{0,1}$, we see that the semi-trivial solution $E_1(x)$ exists but $E_2(x)$ does not exist. This means the intraguild prey can survive in the absence of predator, but the intraguild predator can not survive in the absence of prey. Then another interesting case of coexistence for system (1.5)–(1.7) can also occur when $E_1(x)$ is a uniform weak repeller (i.e. $\Lambda_2^0 > 0$). We note that this case is also included in [11], and it can be established by the theory of uniform persistence.

Ecologically, we also expect another case that if both of the semitrivial steady-state solutions exist (i.e. $0 < d < \min\{d_{0,1}, d_{0,2}\}$) and neither of the semitrivial steady states can be invaded, then positive steady-state solutions of system (1.5)–(1.7) can also exist. By using the theory of the fixed point index in cones, we proved our main results in Theorem 3.1 of this paper, where we showed that a positive steady state solution (should be unstable) of system (1.5)–(1.7) exists if $\Lambda_1^0 < 0$ and $\Lambda_2^0 < 0$, which usually corresponds to the case where both of the semitrivial steady-state solutions are locally asymptotically stable. In the Appendix section, we will rigorously show that the semi-trivial solution $E_2(x)$ (resp. $E_1(x)$) is locally asymptotically stable for system (1.8)–(1.10) if $\Lambda_1^0 < 0$ (resp. $\Lambda_2^0 < 0$). Thus, this study may answer the possibility of bistability for system (1.5)–(1.7).

The sharp a priori estimates for nonnegative solutions of the system (3.1)–(3.2) assure that any nonnegative solution of (3.1)–(3.2) belongs to the special cone W. Thus we only need to search positive solutions of (3.1)–(3.2) in this special cone W. The selection of this special cone ensures the existence of M satisfying (3.15), and guarantees $F(\Omega) \subset W$, which enables us to apply the topological fixed point theorems in the cone W (see Lemma 2.2) to establish the existence of positive solutions to (3.1)–(3.2).

5. Appendix

In this section, we shall prove that the semi-trivial solution $E_2(x)$ (resp. $E_1(x)$) is locally asymptotically stable for system (1.8)–(1.10) if $\Lambda_1^0 < 0$ (resp. $\Lambda_2^0 < 0$).

Proposition 5.1. *Suppose $0 < d < d_{0,2}$. Then the semi-trivial solution $E_2(x) = (0, 0, N_2^*(x), U_2^*(x))$ is locally asymptotically stable if $\Lambda_1^0 < 0$.*

Proof. Recall that $\mathcal{D} := C^0([0,1], \mathbb{R}_+^2)$ and $\geq_{\mathcal{D}}$ is the partial order in $C^0([0,1], \mathbb{R}^2)$. Let the cone $\mathbf{K} := \mathcal{D} \times (-\mathcal{D})$. Then $\mathbf{K}$ generates a partial order on $C^0([0,1], \mathbb{R}^4)$ as follows

$$(N_1, U_1, N_2, U_2) \leq_{\mathbf{K}} (\tilde{N}_1, \tilde{U}_1, \tilde{N}_2, \tilde{U}_2) \Leftrightarrow (N_1, U_1) \leq_{\mathcal{D}} (\tilde{N}_1, \tilde{U}_1) \text{ and } (N_2, U_2) \geq_{\mathcal{D}} (\tilde{N}_2, \tilde{U}_2).$$

For $\delta > 0$, we assume that $(N_1(x,t), U_1(x,t), N_2(x,t), U_2(x,t))$ is a solution of (1.8)–(1.9) with initial condition

$$(N_1(x,0), U_1(x,0), N_2(x,0), U_2(x,0)) = (N_1^0(x), U_1^0(x), N_2^0(x), U_2^0(x)) \in O_\delta^+(E_2).$$

Then $(N_1(x,t), U_1(x,t), N_2(x,t), U_2(x,t)) \geq 0$ for all $t > 0$ and $x \in [0,1]$. Moreover, it is easy to see that

$$\begin{cases} \frac{\partial N_1}{\partial t} \le d\frac{\partial^2 N_1}{\partial x^2} + \mu_1(\frac{U_1}{N_1})N_1, & t>0, x\in(0,1), \\ \frac{\partial U_1}{\partial t} \le d\frac{\partial^2 U_1}{\partial x^2} + f_1(z(x)-U_1-U_2, \frac{U_1}{N_1})N_1, & t>0, x\in(0,1), \\ \frac{\partial N_2}{\partial t} \ge d\frac{\partial^2 N_2}{\partial x^2} + \mu_2(\frac{U_2}{N_2})N_2, & t>0, x\in(0,1), \\ \frac{\partial U_2}{\partial t} \ge d\frac{\partial^2 U_2}{\partial x^2} + f_2(z(x)-U_1-U_2, \frac{U_2}{N_2})N_2, & t>0, x\in(0,1). \end{cases} \tag{5.1}$$

Hence, for all $t>0$, it follows that

$$(N_1(x,t), U_1(x,t), N_2(x,t), U_2(x,t)) \le_{\mathbf{K}} (\check{N}_1(x,t), \check{U}_1(x,t), \check{N}_2(x,t), \check{U}_2(x,t)) \text{ on } [0,1], \tag{5.2}$$

where $(\check{N}_1(x,t), \check{U}_1(x,t), \check{N}_2(x,t), \check{U}_2(x,t))$ is a solution of the following system

$$\begin{cases} \frac{\partial \check{N}_1}{\partial t} = d\frac{\partial^2 \check{N}_1}{\partial x^2} + \mu_1(\frac{\check{U}_1}{\check{N}_1})\check{N}_1, & t>0, x\in(0,1), \\ \frac{\partial \check{U}_1}{\partial t} = d\frac{\partial^2 \check{U}_1}{\partial x^2} + f_1(z(x)-\check{U}_1-\check{U}_2, \frac{\check{U}_1}{\check{N}_1})\check{N}_1, & t>0, x\in(0,1), \\ \frac{\partial \check{N}_2}{\partial t} = d\frac{\partial^2 \check{N}_2}{\partial x^2} + \mu_2(\frac{\check{U}_2}{\check{N}_2})\check{N}_2, & t>0, x\in(0,1), \\ \frac{\partial \check{U}_2}{\partial t} = d\frac{\partial^2 \check{U}_2}{\partial x^2} + f_2(z(x)-\check{U}_1-\check{U}_2, \frac{\check{U}_2}{\check{N}_2})\check{N}_2, & t>0, x\in(0,1), \end{cases} \tag{5.3}$$

with the boundary conditions (1.9) and the initial condition $(\check{N}_1, \check{U}_1, \check{N}_2, \check{U}_2)(x,0) = (N_1^0(x), U_1^0(x), N_2^0(x), U_2^0(x))$ on $[0,1]$. We note that system (5.3) is monotone under the partial order $\le_{\mathbf{K}}$ (see, e.g., [7,17]), and hence, the inequality in (5.2) holds (see, e.g., [17, Theorem 7.3.4]).

For small $\epsilon>0$, we define $(\overline{N}_1, \overline{U}_1, \underline{N}_2, \underline{U}_2) = (\epsilon\eta\Phi_1, \epsilon\eta\Psi_1, (1-\epsilon)N_2^*(x), (1-\epsilon)U_2^*(x))$, where $\eta>0$ is small such that $U_2^*(x)-\eta\Psi_1>0$ on $[0,1]$. If $\Lambda_1^0<0$ and $\epsilon>0$ is small enough, we can show that $(\overline{N}_1, \overline{U}_1, \underline{N}_2, \underline{U}_2)$ is an upper solution of (5.3) with the boundary conditions (1.9) under the partial order $\le_{\mathbf{K}}$ in the following sense,

$$\begin{cases} d(\overline{N}_1)_{xx} + \mu_1(\frac{\overline{U}_1}{\overline{N}_1})\overline{N}_1 = \epsilon\eta\left[d(\Phi_1)_{xx} + \mu_1(\frac{\Psi_1}{\Phi_1})\Phi_1\right] = \epsilon\eta\Lambda_1^0\Phi_1 < 0, \\ d(\overline{U}_1)_{xx} + f_1(z(x)-\overline{U}_1-\underline{U}_2, \frac{\overline{U}_1}{\overline{N}_1})\overline{N}_1 \\ \qquad = \epsilon\eta\left[\Lambda_1^0\Psi_1 + (f_1(z(x)-U_2^*+\epsilon(U_2^*-\eta\Psi_1), \frac{\Psi_1}{\Phi_1}) - f_1(z(x)-U_2^*, \frac{\Psi_1}{\Phi_1}))\Phi_1\right] < 0, \\ d(\underline{N}_2)_{xx} + \mu_2(\frac{\underline{U}_2}{\underline{N}_2})\underline{N}_2 = (1-\epsilon)\left[d(N_2^*)_{xx} + \mu_2(\frac{U_2^*}{N_2^*})N_2^*\right] = 0, \\ d(\underline{U}_2)_{xx} + f_2(z(x)-\overline{U}_1-\underline{U}_2, \frac{\underline{U}_2}{\underline{N}_2})\underline{N}_2 \\ \qquad = (1-\epsilon)\left[d(U_2^*)_{xx} + f_2(z-U_2^*+\epsilon(U_2^*-\eta\Psi_1), \frac{U_2^*}{N_2^*})N_2^*\right] > 0. \end{cases} \tag{5.4}$$

Since $(N_1^0(x), U_1^0(x), N_2^0(x), U_2^0(x)) \in O_\delta^+(E_2)$, we can choose a smaller $\delta>0$ such that

$$(N_1^0(x), U_1^0(x), N_2^0(x), U_2^0(x)) \le_{\mathbf{K}} (\overline{N}_1, \overline{U}_1, \underline{N}_2, \underline{U}_2) \text{ on } [0,1],$$

where $(\overline{N}_1, \overline{U}_1, \underline{N}_2, \underline{U}_2)$ satisfies (5.4). Thus, for all $t>0$ and $x\in[0,1]$, we have

$$(N_1, U_1, N_2, U_2)(x,t) \le_{\mathbf{K}} (\check{N}_1, \check{U}_1, \check{N}_2, \check{U}_2)(x,t) \le_{\mathbf{K}} (\overline{N}_1, \overline{U}_1, \underline{N}_2, \underline{U}_2)(x).$$

That is,

$$0 \leq_{\mathcal{D}} (N_1, U_1)(x,t) \leq_{\mathcal{D}} \epsilon(\eta\Phi_1, \eta\Psi_1) \text{ and } (N_2, U_2)(x,t) \geq_{\mathcal{D}} (1-\epsilon)(N_2^*, U_2^*) \tag{5.5}$$

for all $t > 0$ and $x \in [0, 1]$. Hence, there exists a positive constant $\mathcal{H}$ such that $h(N_1)U_1 \leq \mathcal{H}\epsilon$ for all $t > 0$ and $x \in [0, 1]$, which implies that

$$\begin{cases} \frac{\partial N_2}{\partial t} \leq d\frac{\partial^2 N_2}{\partial x^2} + \mu_2(\frac{U_2}{N_2})N_2, & t > 0, x \in (0,1), \\ \frac{\partial U_2}{\partial t} \leq d\frac{\partial^2 U_2}{\partial x^2} + (f_2(z(x) - U_2, \frac{U_2}{N_2}) + \mathcal{H}\epsilon)N_2, & t > 0, x \in (0,1). \end{cases}$$

It follows that $(N_2(x,t), U_2(x,t)) \leq_{\mathcal{D}} (\widetilde{N}_{2,\epsilon}(x,t), \widetilde{U}_{2,\epsilon}(x,t))$ for all $t > 0$ and $x \in [0, 1]$, where $(\widetilde{N}_{2,\epsilon}(x,t), \widetilde{U}_{2,\epsilon}(x,t))$ satisfies

$$\begin{cases} \frac{\partial \widetilde{N}_{2,\epsilon}}{\partial t} = d\frac{\partial^2 \widetilde{N}_{2,\epsilon}}{\partial x^2} + \mu_2(\frac{\widetilde{U}_{2,\epsilon}}{\widetilde{N}_{2,\epsilon}})\widetilde{N}_{2,\epsilon}, & t > 0, x \in (0,1), \\ \frac{\partial \widetilde{U}_{2,\epsilon}}{\partial t} = d\frac{\partial^2 \widetilde{U}_{2,\epsilon}}{\partial x^2} + (f_2(z(x) - \widetilde{U}_{2,\epsilon}, \frac{\widetilde{U}_{2,\epsilon}}{\widetilde{N}_{2,\epsilon}}) + \mathcal{H}\epsilon)\widetilde{N}_{2,\epsilon}, & t > 0, x \in (0,1), \\ \frac{\partial \widetilde{N}_{2,\epsilon}}{\partial x}(0,t) = 0, \ \frac{\partial \widetilde{N}_{2,\epsilon}}{\partial x}(1,t) + \gamma \widetilde{N}_{2,\epsilon}(1,t) = 0, & t > 0, \\ \frac{\partial \widetilde{U}_{2,\epsilon}}{\partial x}(0,t) = 0, \ \frac{\partial \widetilde{U}_{2,\epsilon}}{\partial x}(1,t) + \gamma \widetilde{U}_{2,\epsilon}(1,t) = 0, & t > 0, \\ \widetilde{N}_{2,\epsilon}(x,0) = N_2^0(x), \ \ \widetilde{U}_{2,\epsilon}(x,0) = U_2^0(x), & x \in [0,1]. \end{cases} \tag{5.6}$$

Since $0 < d < d_{0,2}$, we may use the similar arguments as in Lemma 2.1 (see also [9, Theorem 2.2]) together with perturbation theory to deduce that

$$(\widetilde{N}_{2,\epsilon}(x,t), \widetilde{U}_{2,\epsilon}(x,t)) \to (\widetilde{N}^*_{2,\epsilon}(x), \widetilde{U}^*_{2,\epsilon}(x)) \text{ on } [0,1] \text{ as } t \to \infty,$$

where $(\widetilde{N}^*_{2,\epsilon}(x), \widetilde{U}^*_{2,\epsilon}(x))$ is the unique positive steady state solution of (5.6). By standard regularity theory, it is easy to deduce that $(\widetilde{N}^*_{2,\epsilon}(x), \widetilde{U}^*_{2,\epsilon}(x)) \to (N_2^*(x), U_2^*(x))$ on $[0, 1]$ as $\epsilon \to 0$. Hence, there exists $T_0 > 0$ such that $(\widetilde{N}_{2,\epsilon}(x,t), \widetilde{U}_{2,\epsilon}(x,t)) \leq_{\mathcal{D}} (1+\epsilon)(N_2^*(x), U_2^*(x))$ for all $t \geq T_0$ and $x \in [0, 1]$, which implies that

$$(N_2(x,t), U_2(x,t)) \leq_{\mathcal{D}} (1+\epsilon)(N_2^*(x), U_2^*(x)), \ \forall\, t \geq T_0, \ x \in [0,1]. \tag{5.7}$$

In view of (5.5) and (5.7), we can conclude that the semi-trivial solution $E_2(x) = (0, 0, N_2^*(x), U_2^*(x))$ is locally stable when $\Lambda_1^0 < 0$.

We next show that the solutions of $(N_1(x,t), U_1(x,t))$ in system (1.8)–(1.10) exponentially decay to zero as $t \to \infty$, by constructing exponentially decaying in time solution associated with suitable eigenfunctions. In view of the first two equations of system (1.8)–(1.10) and (5.5), we have

$$\begin{cases} \frac{\partial N_1}{\partial t} \leq d\frac{\partial^2 N_1}{\partial x^2} + \mu_1(\frac{U_1}{N_1})N_1, & t > 0, x \in (0,1), \\ \frac{\partial U_1}{\partial t} \leq d\frac{\partial^2 U_1}{\partial x^2} + f_1(z(x) - (1-\epsilon)U_2^* - U_1, \frac{U_1}{N_1})N_1, & t > 0, x \in (0,1), \\ \frac{\partial N_1}{\partial x}(0,t) = 0, \ \frac{\partial N_1}{\partial x}(1,t) + \gamma N_1(1,t) = 0, & t > 0, \\ \frac{\partial U_1}{\partial x}(0,t) = 0, \ \frac{\partial U_1}{\partial x}(1,t) + \gamma U_1(1,t) = 0, & t > 0. \end{cases} \tag{5.8}$$

Since $\Lambda_1^0 < 0$, we may assume that $\epsilon > 0$ in the previous discussions is small enough such that $\Lambda_1^\epsilon < 0$, where Λ_1^ϵ is the principal eigenvalue of the following eigenvalue problem

$$\begin{cases} \Lambda_1^\epsilon \Phi_1^\epsilon = d\Phi_{1xx}^\epsilon + \mu_1(\frac{\Psi_1^\epsilon}{\Phi_1^\epsilon})\Phi_1^\epsilon, \ x \in (0,1), \\ \Lambda_1^\epsilon \Psi_1^\epsilon = d\Psi_{1xx}^\epsilon + f_1(z-(1-\epsilon)U_2^*, \frac{\Psi_1^\epsilon}{\Phi_1^\epsilon})\Phi_1^\epsilon, \ x \in (0,1), \\ \Phi_{1x}^\epsilon(0) = \Phi_{1x}^\epsilon(1) + \gamma\Phi_1^\epsilon(1) = 0, \ \Psi_{1x}^\epsilon(0) = \Psi_{1x}^\epsilon(1) + \gamma\Psi_1^\epsilon(1) = 0. \end{cases}$$

Let $(\Phi_1^\epsilon, \Psi_1^\epsilon)$ be a strongly positive eigenfunction associated with $\Lambda_1^\epsilon < 0$. Clearly, there exists a $\beta_1 > 0$ such that

$$(N_1^0(x), U_1^0(x)) \leq_{\mathcal{D}} \beta_1(\Phi_1^\epsilon, \Psi_1^\epsilon) \text{ on } [0,1]. \tag{5.9}$$

Let $(\widetilde{N}_1(x,t), \widetilde{U}_1(x,t)) = (\beta_1 e^{\Lambda_1^\epsilon t}\Phi_1^\epsilon, \beta_1 e^{\Lambda_1^\epsilon t}\Psi_1^\epsilon)$. Then $(\widetilde{N}_1(x,t), \widetilde{U}_1(x,t))$ satisfies the following system

$$\begin{cases} \frac{\partial \widetilde{N}_1}{\partial t} = d\frac{\partial^2 \widetilde{N}_1}{\partial x^2} + \mu_1(\frac{\widetilde{U}_1}{\widetilde{N}_1})\widetilde{N}_1, & x \in (0,1), t > 0, \\ \frac{\partial \widetilde{U}_1}{\partial t} = d\frac{\partial^2 \widetilde{U}_1}{\partial x^2} + f_1(z-(1-\epsilon)U_2^*, \frac{\widetilde{U}_1}{\widetilde{N}_1})\widetilde{N}_1, & x \in (0,1), t > 0, \\ \frac{\partial \widetilde{N}_1}{\partial x}(0,t) = 0, \ \frac{\partial \widetilde{N}_1}{\partial x}(1,t) + \gamma\widetilde{N}_1(1,t) = 0, & t > 0, \\ \frac{\partial \widetilde{U}_1}{\partial x}(0,t) = 0, \ \frac{\partial \widetilde{U}_1}{\partial x}(1,t) + \gamma\widetilde{U}_1(1,t) = 0, & t > 0, \\ \widetilde{N}_1(x,0) = \beta_1\Phi_1^\epsilon, \ \ \widetilde{U}_1(x,0) = \beta_1\Psi_1^\epsilon, & x \in [0,1]. \end{cases} \tag{5.10}$$

It follows from (5.8)–(5.10) and the comparison principle that for $t > 0$ and $x \in [0,1]$, we have

$$(0,0) \leq_{\mathcal{D}} (N_1(x,t), U_1(x,t)) \leq_{\mathcal{D}} (\widetilde{N}_1(x,t), \widetilde{U}_1(x,t)) = \beta_1 e^{\Lambda_1^\epsilon t}(\Phi_1^\epsilon, \Psi_1^\epsilon).$$

Since $\Lambda_1^\epsilon < 0$, it follows from the above inequality that $(N_1(x,t), U_1(x,t)) \to (0,0)$ uniformly on $[0,1]$ as $t \to \infty$. Thus, we have proved that the solutions of $(N_1(x,t), U_1(x,t))$ in system (1.8)–(1.10) exponentially decay to zero as $t \to \infty$. Then $(N_2(x,t), U_2(x,t))$ in system (1.8)–(1.10) is asymptotic to the system (2.1) with $i = 2$. Since $0 < d < d_{0,2}$, it follows from the theory for asymptotically autonomous semiflows (see, e.g., [19, Corollary 4.3]) and Lemma 2.1 (ii) that $(N_2(x,t), U_2(x,t)) \to (N_2^*(x), U_2^*(x))$ uniformly on $[0,1]$ as $t \to \infty$. Hence, the semi-trivial solution $E_2(x) = (0,0,N_2^*(x), U_2^*(x))$ is locally asymptotically stable if $\Lambda_1^0 < 0$. □

Next, we are in a position to investigate the local stability of $E_1(x)$. Since the function $h(N_1)$ is non-monotone with respect to N_1, we note that the arguments in Proposition 5.1 don't work for this case. We first consider the following auxiliary nonlinear system

$$\begin{cases} \frac{\partial \mathcal{N}_1}{\partial t} = d\frac{\partial^2 \mathcal{N}_1}{\partial x^2} + \left[\mu_1(\frac{U_1^*}{N_1^*}) - \frac{U_1^*}{N_1^*}\mu_1'(\frac{U_1^*}{N_1^*})\right]\mathcal{N}_1 + \mu_1'(\frac{U_1^*}{N_1^*})\mathcal{U}_1 - g(N_1^*)\mathcal{N}_2, \\ \frac{\partial \mathcal{U}_1}{\partial t} = d\frac{\partial^2 \mathcal{U}_1}{\partial x^2} + \left[f_1(z(x) - U_1^*, \frac{U_1^*}{N_1^*}) - \frac{\partial f_1}{\partial Q_1}(z(x) - U_1^*, \frac{U_1^*}{N_1^*})\frac{U_1^*}{N_1^*}\right]\mathcal{N}_1 \\ \quad + \left[-\frac{\partial f_1}{\partial R}(z(x) - U_1^*, \frac{U_1^*}{N_1^*})N_1^* + \frac{\partial f_1}{\partial Q_1}(z(x) - U_1^*, \frac{U_1^*}{N_1^*})\right]\mathcal{U}_1 \\ \quad - h(N_1^*)U_1^*\mathcal{N}_2 - \frac{\partial f_1}{\partial R}(z(x) - U_1^*, \frac{U_1^*}{N_1^*})N_1^*\mathcal{U}_2, \\ \frac{\partial \mathcal{N}_2}{\partial t} = d\frac{\partial^2 \mathcal{N}_2}{\partial x^2} + \mu_2(\frac{\mathcal{U}_2}{\mathcal{N}_2})\mathcal{N}_2, \\ \frac{\partial \mathcal{U}_2}{\partial t} = d\frac{\partial^2 \mathcal{U}_2}{\partial x^2} + f_2(z(x) - U_1^*, \frac{\mathcal{U}_2}{\mathcal{N}_2})\mathcal{N}_2 + h(N_1^*)U_1^*\mathcal{N}_2, \end{cases} \tag{5.11}$$

for $(x,t) \in (0,1) \times (0,\infty)$ with boundary conditions (1.9). Just as before, the functions $\mu_2(\mathcal{U}_2/\mathcal{N}_2)\mathcal{N}_2$ and $f_2(z(x) - U_1^*, \mathcal{U}_2/\mathcal{N}_2)\mathcal{N}_2$ can be respectively extended to those similar to Eq. (4.9) and Eq. (4.10) in [8], if necessary. Hence, we call $(\mathcal{N}_1, \mathcal{U}_1, \mathcal{N}_2, \mathcal{U}_2) \equiv (0,0,0,0)$ a steady state solution of (5.11) on [0, 1] with boundary conditions (1.9). Substituting

$$(\mathcal{N}_1(x,t), \mathcal{U}_1(x,t), \mathcal{N}_2(x,t), \mathcal{U}_2(x,t)) = e^{\Lambda t}(\theta_1(x), \vartheta_1(x), \theta_2(x), \vartheta_2(x))$$

into (5.11) with $(\theta_2(x), \vartheta_2(x)) \in W_2 \subset \mathcal{D} := C^0([0,1], \mathbb{R}_+^2)$, we obtain the associated nonlinear eigenvalue problem

$$\begin{aligned} &\Lambda\begin{pmatrix}\theta_1\\ \vartheta_1\end{pmatrix} = \mathcal{L}_1\begin{pmatrix}\theta_1\\ \vartheta_1\end{pmatrix} - \begin{pmatrix} g(N_1^*) & 0 \\ h(N_1^*)U_1^* & \frac{\partial f_1}{\partial R}(z(x) - U_1^*, \frac{U_1^*}{N_1^*})N_1^* \end{pmatrix}\begin{pmatrix}\theta_2\\ \vartheta_2\end{pmatrix}, \quad x \in (0,1), \\ &\Lambda\begin{pmatrix}\theta_2\\ \vartheta_2\end{pmatrix} = \mathcal{L}_2\begin{pmatrix}\theta_2\\ \vartheta_2\end{pmatrix}, \quad x \in (0,1), \\ &\frac{\partial w}{\partial x}(0) = \frac{\partial w}{\partial x}(1) + \gamma w(1) = 0, \ w = \theta_1, \ \vartheta_1, \ \theta_2, \ \vartheta_2, \end{aligned} \tag{5.12}$$

where

$$\mathcal{L}_1\begin{pmatrix}\theta_1\\ \vartheta_1\end{pmatrix} = \begin{pmatrix} d\theta_1'' + \left[\mu_1(\frac{U_1^*}{N_1^*}) - \frac{U_1^*}{N_1^*}\mu_1'(\frac{U_1^*}{N_1^*})\right]\theta_1 + \mu_1'(\frac{U_1^*}{N_1^*})\vartheta_1, \\ d\vartheta_1'' + \left[f_1(z(x) - U_1^*, \frac{U_1^*}{N_1^*}) - \frac{\partial f_1}{\partial Q_1}(z(x) - U_1^*, \frac{U_1^*}{N_1^*})\frac{U_1^*}{N_1^*}\right]\theta_1 \\ \quad + \left[-\frac{\partial f_1}{\partial R}(z(x) - U_1^*, \frac{U_1^*}{N_1^*})N_1^* + \frac{\partial f_1}{\partial Q_1}(z(x) - U_1^*, \frac{U_1^*}{N_1^*})\right]\vartheta_1 \end{pmatrix}$$

and

$$\mathcal{L}_2\begin{pmatrix}\theta_2\\ \vartheta_2\end{pmatrix} = \begin{pmatrix} d\theta_2'' + \mu_2(\frac{\vartheta_2}{\theta_2})\theta_2 \\ d\vartheta_2'' + f_2(z(x) - U_1^*, \frac{\vartheta_2}{\theta_2})\theta_2 + h(N_1^*)U_1^*\theta_2 \end{pmatrix}.$$

Clearly, the eigenvalues of (5.12) consist of the eigenvalues of $\mathcal{L}_1$ and $\mathcal{L}_2$. It follows from the proof of Lemma 2.1 in [9] that the principal eigenvalue $\Lambda_1(\mathcal{L}_1) < 0$ of the cooperative linear operator $\mathcal{L}_1$. Meanwhile, it is easy to see that the principal eigenvalue $\Lambda_1(\mathcal{L}_2) = \Lambda_2^0 < 0$. Hence, the steady state solution $(0,0,0,0)$ of (5.11) is exponentially stable. Finally, we will show that the exponential stability of the steady state solution $(0,0,0,0)$ to (5.11) implies the local asymptotic stability of the semi-trivial solution $E_1(x)$ to system (1.8)–(1.10). That is, we have the following result.

Proposition 5.2. *Suppose* $0 < d < d_{0,1}$. *Then the semi-trivial solution* $E_1(x) = (N_1^*(x), U_1^*(x), 0, 0)$ *is locally asymptotically stable if* $\Lambda_2^0 < 0$.

Proof. For $\delta > 0$, let $(N_1(x,t), U_1(x,t), N_2(x,t), U_2(x,t))$ be a solution of (1.8)–(1.9) with initial condition

$$(N_1(x,0), U_1(x,0), N_2(x,0), U_2(x,0)) = (N_1^0(x), U_1^0(x), N_2^0(x), U_2^0(x)) \in O_\delta^+(E_1).$$

Then $(N_1(x,t), U_1(x,t), N_2(x,t), U_2(x,t)) \geq 0$ for all $t > 0$ and $x \in [0,1]$. Let

$$\begin{aligned} V(x,t) &= (V_1(x,t), V_2(x,t), V_3(x,t), V_4(x,t)) \\ &= (N_1(x,t), U_1(x,t), N_2(x,t), U_2(x,t)) - (N_1^*(x), U_1^*(x), 0, 0). \end{aligned}$$

By using the Taylor expansion at $E_1(x) = (N_1^*(x), U_1^*(x), 0, 0)$, we have

$$\mu_1(\frac{U_1}{N_1})N_1 = \mu_1(\frac{U_1^*}{N_1^*})N_1^* + \left[\mu_1(\frac{U_1^*}{N_1^*}) - \frac{U_1^*}{N_1^*}\mu_1'(\frac{U_1^*}{N_1^*})\right]V_1 + \mu_1'(\frac{U_1^*}{N_1^*})V_2 + o(\|V_1\| + \|V_2\|),$$

$$\begin{aligned} & f_1(z(x) - U_1 - U_2, \tfrac{U_1}{N_1})N_1 \\ = \;& f_1(z(x) - U_1^*, \tfrac{U_1^*}{N_1^*})N_1^* + \left[f_1(z(x) - U_1^*, \tfrac{U_1^*}{N_1^*}) - \tfrac{\partial f_1}{\partial Q_1}(z(x) - U_1^*, \tfrac{U_1^*}{N_1^*})\tfrac{U_1^*}{N_1^*}\right]V_1 \\ = \;& \left[-\tfrac{\partial f_1}{\partial R}(z(x) - U_1^*, \tfrac{U_1^*}{N_1^*})N_1^* + \tfrac{\partial f_1}{\partial Q_1}(z(x) - U_1^*, \tfrac{U_1^*}{N_1^*})\right]V_2 - \tfrac{\partial f_1}{\partial R}(z(x) - U_1^*, \tfrac{U_1^*}{N_1^*})N_1^* V_4 \\ & + o(\|V_1\| + \|V_2\| + \|V_4\|), \end{aligned}$$

$$g(N_1) = g(N_1^*) + O(\|V_1\|), \quad h(N_1)U_1 = h(N_1^*)U_1^* + O(\|V_1\| + \|V_2\|),$$

$$f_2(z(x) - U_1 - U_2, \frac{U_2}{N_2})N_2 = f_2(z(x) - U_1^*, \frac{U_2}{N_2})N_2 + o(\|N_2\|).$$

Hence, $V(x,t)$ satisfies

$$\begin{cases} \dfrac{\partial}{\partial t}\begin{pmatrix} V_1 \\ V_2 \end{pmatrix} = \mathcal{L}_1 \begin{pmatrix} V_1 \\ V_2 \end{pmatrix} + \begin{pmatrix} \mathcal{F}_1(V) \\ \mathcal{F}_2(V) \end{pmatrix}, & t > 0, x \in (0,1), \\ \dfrac{\partial}{\partial t}\begin{pmatrix} V_3 \\ V_4 \end{pmatrix} = \mathcal{L}_2 \begin{pmatrix} V_3 \\ V_4 \end{pmatrix} + \begin{pmatrix} 0 \\ \mathcal{F}_4(V) \end{pmatrix}, & t > 0, x \in (0,1), \\ \dfrac{\partial V_i}{\partial x}(0,t) = \dfrac{\partial V_i}{\partial x}(1,t) + \gamma V_i(1,t) = 0, \; i = 1,2,3,4, & t > 0, \end{cases} \tag{5.13}$$

where

$$\begin{aligned} \mathcal{F}_1(V) &= -g(N_1^*)V_3 + o(\|V_1\| + \|V_2\|) + O(\|V_1\|)V_3, \\ \mathcal{F}_2(V) &= -h(N_1^*)U_1^* V_3 - \frac{\partial f_1}{\partial R}(z(x) - U_1^*, \frac{U_1^*}{N_1^*})N_1^* V_4 + o(\|V\|), \\ \mathcal{F}_4(V) &= o(\|N_2\|) + O(\|V_1\| + \|V_2\|)V_3, \end{aligned}$$

with initial condition $V(x,0) := V^0(x) = (N_1^0(x) - N_1^*, U_1^0(x) - U_1^*, N_2^0(x), U_2^0(x))$. Here we comment on the problem in linearizing system (1.8)–(1.9) around $E_1(x)$. Since both of $N_1^*(x)$

and $U_1^*(x)$ are strictly positive everywhere in x, we can linearize the first two equations of (1.8)–(1.9) around $E_1(x)$. This corresponds to the equations of V_1 and V_2 in (5.13). However, the linearization of the last two equations in (1.8)–(1.9) around $E_1(x)$ fails, due to the singularity in the ratio of U_2/N_2 at $(N_2, U_2) = (0, 0)$. Thus, one needs to introduce the 1-homogeneous operator $\mathcal{L}_2$ for the equations of V_3 and V_4 in (5.13). We rewrite system (5.13) as the abstract ordinary differential equation in $C([0, 1], \mathbb{R}^2) \times W_2$ and the so-called mild solutions can be obtained for any given initial data. More precisely,

$$\begin{pmatrix} V_1 \\ V_2 \end{pmatrix} = G_1(t) \begin{pmatrix} V_1^0 \\ V_2^0 \end{pmatrix} + \int_0^t G_1(t-s) \cdot \begin{pmatrix} \digamma_1(V(s)) \\ \digamma_2(V(s)) \end{pmatrix} \mathrm{d}s,$$

$$\begin{pmatrix} V_3 \\ V_4 \end{pmatrix} = G_2(t) \begin{pmatrix} N_2^0 \\ U_2^0 \end{pmatrix} + \int_0^t G_2(t-s) \cdot \begin{pmatrix} 0 \\ \digamma_4(V(s)) \end{pmatrix} \mathrm{d}s,$$

where $G_1(t)$ is the positive, non-expansive, analytic semigroup on $C([0, 1], \mathbb{R}^2)$ (see, e.g., Chapter 7 in [17]) such that $(\mathcal{V}_1, \mathcal{V}_2)^\mathsf{T} = G_1(t) \cdot (V_1^0, V_2^0)^\mathsf{T}$ satisfies the linear initial value problem

$$\begin{aligned}
&\frac{\partial}{\partial t} \begin{pmatrix} \mathcal{V}_1 \\ \mathcal{V}_2 \end{pmatrix} = \mathcal{L}_1 \begin{pmatrix} \mathcal{V}_1 \\ \mathcal{V}_2 \end{pmatrix}, \quad t > 0, x \in (0, 1), \\
&\frac{\partial \mathcal{V}_i}{\partial x}(0, t) = \frac{\partial \mathcal{V}_i}{\partial x}(1, t) + \gamma \mathcal{V}_i(1, t) = 0, \ i = 1, 2, \ t > 0, \\
&\mathcal{V}_1(x, 0) = V_1^0(x), \ \ \mathcal{V}_2(x, 0) = V_2^0(x), \ x \in [0, 1],
\end{aligned}$$

and $G_2(t)$ is the continuous, compact, homogeneous of degree one and $\mathcal{D}$-strongly-order-preserving semiflow on W_2 (see Lemma 5.1 in [8]) such that $(\mathcal{V}_3, \mathcal{V}_4)^\mathsf{T} = G_2(t) \cdot (V_3^0, V_4^0)^\mathsf{T}$ satisfies the initial value problem

$$\begin{aligned}
&\frac{\partial}{\partial t} \begin{pmatrix} \mathcal{V}_3 \\ \mathcal{V}_4 \end{pmatrix} = \mathcal{L}_2 \begin{pmatrix} \mathcal{V}_3 \\ \mathcal{V}_4 \end{pmatrix}, \quad t > 0, x \in (0, 1), \\
&\frac{\partial \mathcal{V}_i}{\partial x}(0, t) = \frac{\partial \mathcal{V}_i}{\partial x}(1, t) + \gamma \mathcal{V}_i(1, t) = 0, \ i = 3, 4, \ t > 0, \\
&\mathcal{V}_3(x, 0) = V_3^0(x), \ \ \mathcal{V}_4(x, 0) = V_4^0(x), \ x \in [0, 1].
\end{aligned}$$

Note that the positive steady state solution $(N_1^*(\cdot), U_1^*(\cdot))$ is globally asymptotically stable in Δ_1 for system (2.1) with $i = 1$ (see Lemma 2.1), and the principal eigenvalue of the cooperative linear operator $\mathcal{L}_1$ is negative, that is, $\Lambda_1(\mathcal{L}_1) < 0$. Clearly, the principal eigenvalue $\Lambda_1(\mathcal{L}_2) = \Lambda_2^0 < 0$. By arguments analogous to those in Theorem 9.6.3 of [24], one may deduce that the semi-trivial solution $E_1(x)$ is locally asymptotically stable. □

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