

GLOBAL DYNAMICS OF A REACTION-DIFFUSION SYSTEM WITH INTRAGUILD PREDATION AND INTERNAL STORAGE

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ABSTRACT. This paper presents a reaction-diffusion system modeling interactions of the intraguild predator and prey in an unstirred chemostat, in which the predator can also compete with its prey for one single nutrient resource that can be stored within individuals. Under suitable conditions, we first show that there are at least three steady-state solutions for the full system, a trivial steady-state solution with neither species present, and two semitrivial steady-state solutions with just one of the species. Then we establish that coexistence of the intraguild predator and prey can occur if both of the semitrivial steady-state solutions are invulnerable by the missing species. Comparing with the system without predation, our numerical simulations show that the introduction of predation in an ecosystem can enhance the coexistence of species. Our mathematical arguments also work for the linear food chain model (top-down predation), in which the top-down predator only feeds on the prey but does not compete for nutrient resource with the prey. In our numerical studies, we also do a comparison of intraguild predation and top-down predation.

1. Introduction. Competition between species for resources is an important issue in ecology and has been extensively studied during recent decades. The simplest versions of resource competition theory assumed a direct relationship between the external concentration of nutrients and the population growth of species, leading to the assumption of a constant quota of nutrient per individual, or equivalently, a constant yield of individuals from consumption of a unit of nutrient [11]. In fact, it was observed that quotas may vary. To include this fact, the dynamics of

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quota for a species is further assumed to be governed by an ordinary differential equation, leading to another alternative system, variable-internal-stores models [7, 32]. The early theory of competition between competitors for one resource, with or without internal storage, in a well-mixed habitat usually draws a conclusion that the principle of competitive exclusion holds: only one competitor can survive [11, 15, 32]. Without introduction of other mechanisms into the aforementioned simple models in [15, 32], outcomes such as coexistence of competing populations, or bistability (outcomes that depend on initial conditions) can not occur.

The authors in [10] extended the previous model in [32] to combine competition for a single growth-limiting nutrient that is stored internally and competition through the production of allelopathic toxins. The numerical studies in [10] did not reveal any instances of coexistence. Instead, the outcomes of competitive exclusion independent of initial conditions, and bistability (competitive exclusion dependent on initial conditions) were observed in the model proposed by [10].

It was known that predation can be another important mechanism that potentially influences the outcomes of competition (see, e.g., [1, 2, 3, 4, 5, 14, 27, 28, 31]). Among those previous works, there is a specific phenomenon that predators consume prey species but also compete against these prey species by consumption the same resources. This phenomenon is sometimes referred to as “intraguild predation”. The authors in [36] found that *Ochromonas*, a mixotrophic organism, can act as an intraguild predator that consumes *Microcystis*, an autotrophic prey, and competes with them for ammonium (a nitrogen resource). Introducing the fact of intraguild predation into the chemostat model (see [32]), the dynamics of the chemostat experiments in [36] can be described by the following form:

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

Here $R^{(0)}$ and D stand for the nutrient supply concentration and dilution rate of the chemostat, respectively. $R(t)$ 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. 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. As in [36], we also assume that both mortality rates of $N_1(t)$ and $N_2(t)$ were equal to the dilution rate (D) of the chemostat.

Following [36], we assume that the predation rate, $g(N_1)$, of the mixotroph feeding on the autotroph follows a Holling type III functional response, that is, $g(N_1)$

takes the form

$$g(N_1) = \frac{g_{\max} N_1^b}{K_0^b + N_1^b}, \quad b > 1, \quad (2)$$

where g_{\max} is the maximum ingestion rate, K_0 is the half saturation constant, and b is a parameter defining the curvature of the type III functional response. According to [36], the specific growth rates of the autotroph and mixotroph take the forms (see also [6])

$$\mu_i(Q_i) = \mu_{\max,i} \left(1 - \frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}}\right), \quad i = 1, 2, \quad (3)$$

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 [22]):

$$f_i(R, Q_i) = \frac{a_{\max,i} R}{K_i + R} \frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}}, \quad i = 1, 2, \quad (4)$$

where $Q_{\min,i} \leq Q_i \leq Q_{\max,i}$, $a_{\max,i}$ is the maximum nutrient uptake rate of species i and K_i is its half-saturation constant for nutrient uptake.

Motivated by the examples in (3) and (4), we always assume that the functions $\mu_i(Q_i)$ and $f_i(R, Q_i)$, $i = 1, 2$, satisfy the following assumptions (see [17]):

- (H1): there exists $Q_{\min,i} > 0$ such that $\mu_i(Q_i)$ is Lipschitz continuous for $Q_i \geq Q_{\min,i}$, and $\mu_i(Q_{\min,i}) = 0$. Moreover, $\mu'_i(Q_i) > 0$ for a.e. $Q_i \geq Q_{\min,i}$.
- (H2): (i) $f_i(R, Q_i)$ and $\frac{\partial f_i(R, Q_i)}{\partial R}$ are Lipschitz continuous for $R \geq 0$ and $Q_i \geq Q_{\min,i}$;
- (ii) $\frac{\partial f_i(R, Q_i)}{\partial R} \geq 0$, $\frac{\partial f_i(R, Q_i)}{\partial Q_i} \leq 0$ and $f_i(R, Q_i) \geq 0$ for a.e. $R \geq 0$ and $Q_i \geq Q_{\min,i}$;
- (iii) there exists $Q_{Bi} \in (Q_{\min,i}, +\infty]$ such that

$$f_i(R, Q_i) > 0, \quad \frac{\partial f_i(R, Q_i)}{\partial R} > 0 \text{ in } (R, Q_i) \in \mathbb{R}_+ \times [Q_{\min,i}, Q_{Bi}),$$

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

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

The authors in [35] mathematically analyzed system (1). If *Microcystis* (the prey) is a better competitor for ammonium (the limiting resource), then the mathematical results in [35] reveal that coexistence of *Ochromonas* (the intraguild predator) and *Microcystis* (the prey) is possible. This is consistent with the experimental results in [36] as well as some existing intraguild predation theory. The purpose of this paper is to extend system (1) to incorporate the factor that the habitat may be poorly mixed, in which both the distributions of quotas in populations and the distributions of populations and the nutrient over space should be considered. The unstirred chemostat (see, e.g., [19, 25, 33, 37, 38]), the chemostat without mixing the vessel, is a common laboratory apparatus which is usually regarded as a spatially variable habitat in which nutrients and organisms are transported by diffusion. There have been some works investigating the ecological models with variable quotas in spatially variable habitats (see, e.g., [8, 9, 16, 17, 18]). It is worth pointing out that the author in [8] (see also [17]) summarizes three possible approaches of modeling in this direction. Here we will adopt the approach of extending system (1) into a reaction-diffusion system (see, e.g. [8, 16]), which is more tractable mathematically

among three existing approaches. Substituting $U_1 = Q_1 N_1$ and $U_2 = Q_2 N_2$ into system (1), we arrive at the following model:

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

Then we propose the following system of reaction-diffusion equations with internal storage and predation in an unstirred chemostat:

$$\begin{cases} \frac{\partial R}{\partial t} = d \frac{\partial^2 R}{\partial x^2} - f_1(R, \frac{U_1}{N_1})N_1 - f_2(R, \frac{U_2}{N_2})N_2, \\ \frac{\partial N_1}{\partial t} = d \frac{\partial^2 N_1}{\partial x^2} + \mu_1(\frac{U_1}{N_1})N_1 - g(N_1)N_2, \\ \frac{\partial U_1}{\partial t} = d \frac{\partial^2 U_1}{\partial x^2} + f_1(R, \frac{U_1}{N_1})N_1 - g(N_1)\frac{U_1}{N_1}N_2, \\ \frac{\partial N_2}{\partial t} = d \frac{\partial^2 N_2}{\partial x^2} + \mu_2(\frac{U_2}{N_2})N_2, \\ \frac{\partial U_2}{\partial t} = d \frac{\partial^2 U_2}{\partial x^2} + f_2(R, \frac{U_2}{N_2})N_2 + g(N_1)\frac{U_1}{N_1}N_2, \end{cases} \quad (5)$$

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

$$\begin{cases} \frac{\partial R}{\partial x}(0, t) = -R^{(0)}, \quad \frac{\partial R}{\partial x}(1, t) + \gamma R(1, t) = 0, \quad t > 0, \\ \frac{\partial N_i}{\partial x}(0, t) = 0, \quad \frac{\partial N_i}{\partial x}(1, t) + \gamma N_i(1, t) = 0, \quad t > 0, \quad i = 1, 2, \\ \frac{\partial U_i}{\partial x}(0, t) = 0, \quad \frac{\partial U_i}{\partial x}(1, t) + \gamma U_i(1, t) = 0, \quad t > 0, \quad i = 1, 2, \end{cases} \quad (6)$$

and initial conditions

$$\begin{cases} R(x, 0) = R^0(x) \geq 0, \quad N_i(x, 0) = N_i^0(x) \geq 0, \\ U_i(x, 0) = U_i^0(x) \geq 0, \quad 0 < x < 1, \quad i = 1, 2. \end{cases} \quad (7)$$

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

The rest of this paper is organized as follows. In Section 2, the threshold dynamics of the associated single population model is established in terms of the sign of the principal eigenvalue of a nonlinear eigenvalue problem similar to the one in [17]. Furthermore, the uniqueness and global stability of the positive steady state can be also investigated if it exists. Section 3 is devoted to the establishment of coexistence of the intraguild predator (*Ochromonas*) and the prey (*Microcystis*). The simulation results and biological interpretations are presented in Sections 4 and 5, respectively.

2. Single population model. In this section, we first consider the single population model. Mathematically, it simply means that we set $(N_1, U_1) = (0, 0)$ or $(N_2, U_2) = (0, 0)$ in equations (5)-(7). In order to simplify notations, all subscripts

are dropped in the remaining equations and we consider

$$\begin{cases} \frac{\partial R}{\partial t} = d \frac{\partial^2 R}{\partial x^2} - f(R, \frac{U}{N})N, & x \in (0, 1), t > 0, \\ \frac{\partial N}{\partial t} = d \frac{\partial^2 N}{\partial x^2} + \mu(\frac{U}{N})N, & x \in (0, 1), t > 0, \\ \frac{\partial U}{\partial t} = d \frac{\partial^2 U}{\partial x^2} + f(R, \frac{U}{N})N, & x \in (0, 1), t > 0, \\ \frac{\partial R}{\partial x}(0, t) = -R^{(0)}, \quad \frac{\partial R}{\partial x}(1, t) + \gamma R(1, t) = 0, & t > 0, \\ \frac{\partial w}{\partial x}(0, t) = \frac{\partial w}{\partial x}(1, t) + \gamma w(1, t) = 0, & t > 0, w = N, U, \\ w(x, 0) = w^0(x) \geq 0, \quad 0 < x < 1, & w = R, N, U. \end{cases} \quad (8)$$

By [21, Theorem 1 and Remark 1.1], we can show that system (8) admits a unique noncontinuable solution, and the solutions to (8) remain non-negative on their interval of existence if they are non-negative initially. The biologically relevant domain for system (8) is given by

$$\mathbf{X} = \{(\mathcal{R}, \mathcal{N}, \mathcal{U}) \in C([0, 1]; \mathbb{R}_+^3) : \text{there exists } \tilde{Q} > 0 \\ \text{such that } Q_{\min} \mathcal{N}(\cdot) \leq \mathcal{U}(\cdot) \leq \tilde{Q} \mathcal{N}(\cdot) \text{ in } [0, 1]\}$$

with the usual maximum norm in $C([0, 1]; \mathbb{R}^3)$, denoted by $\|\cdot\|$. Substituting the new variable $\Theta(x, t) = R(x, t) + U(x, t)$ into (8), it follows that

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

By [19], we conclude that $\Theta(x, t)$ satisfies

$$\lim_{t \rightarrow \infty} \Theta(x, t) = z(x) := R^{(0)} \left(\frac{1 + \gamma}{\gamma} - x \right) \text{ uniformly on } [0, 1]. \quad (9)$$

Inspired by [17], we define Q^* to be the unique positive number so that

$$Q^* = \inf\{Q > 0 : f(z(x), Q) - \mu(Q)Q \leq 0 \text{ in } [0, 1]\}.$$

By the similar arguments in [17, Lemma 4.2], we can show the following results.

Lemma 2.1. *Let $(R(x, t), N(x, t), U(x, t))$ be a solution of (8) for $t \in [0, \tau)$, with initial data $(R^0, N^0, U^0) \in \mathbf{X}$. Then*

(i) *it holds that*

$$\inf_{x \in [0, 1]} \frac{U(x, t)}{N(x, t)} \geq Q_{\min} \quad \text{for all } t \in [0, \tau).$$

(ii) *there exists $\bar{Q} \in [Q^*, +\infty)$ depending on $\|R^0\|$ and $\|U^0/N^0\|$ such that*

$$\sup_{x \in [0, 1]} \frac{U(x, t)}{N(x, t)} \leq \bar{Q} \quad \text{for all } t \in [0, \tau).$$

Moreover, if $\tau = +\infty$, then for each $Q > Q^*$, we have

$$\limsup_{t \rightarrow \infty} \left[\sup_{x \in [0, 1]} (U(x, t) - QN(x, t)) \right] \leq 0. \quad (10)$$

Furthermore, if $\|N(\cdot, t)\|$ is bounded uniformly in $t > 0$, then (10) holds for $Q = Q^*$.

Corollary 1. *System (8) generates a semiflow in \mathbf{X} in the sense that for each initial data in \mathbf{X} , system (8) admits a unique classical solution $(R(\cdot, t), N(\cdot, t), U(\cdot, t))$ that exists for all $t > 0$. Moreover, the solution satisfies $(R(\cdot, t), N(\cdot, t), U(\cdot, t)) \in \mathbf{X}$ for all $t > 0$.*

In order to investigate the dynamics of system (8), we first consider the following reduced system:

$$\begin{cases} \frac{\partial N}{\partial t} = d \frac{\partial^2 N}{\partial x^2} + \mu \left(\frac{U}{N} \right) N, & x \in (0, 1), t > 0, \\ \frac{\partial U}{\partial t} = d \frac{\partial^2 U}{\partial x^2} + f(z(x) - U, \frac{U}{N}) N, & x \in (0, 1), t > 0, \\ \frac{\partial w}{\partial x}(0, t) = \frac{\partial w}{\partial x}(1, t) + \gamma w(1, t) = 0, & t > 0, w = N, U, \\ w(x, 0) = w^0(x) \geq 0, & 0 < x < 1, w = N, U. \end{cases} \quad (11)$$

The following nonlinear system will play an important role in the dynamics of (11):

$$\begin{cases} \frac{\partial N}{\partial t} = d \frac{\partial^2 N}{\partial x^2} + \mu \left(\frac{U}{N} \right) N, & x \in (0, 1), t > 0, \\ \frac{\partial U}{\partial t} = d \frac{\partial^2 U}{\partial x^2} + f(z(x), \frac{U}{N}) N, & x \in (0, 1), t > 0, \\ \frac{\partial w}{\partial x}(0, t) = \frac{\partial w}{\partial x}(1, t) + \gamma w(1, t) = 0, & t > 0, w = N, U. \end{cases} \quad (12)$$

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

$$\mathcal{C} = \{(N, U) \in \mathcal{D} : Q_{\min} N(x) \leq U(x) \leq Q^* N(x) \text{ for } x \in [0, 1]\}.$$

It is clear that \mathcal{D} and \mathcal{C} 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 $(\phi_1, \varphi_1) \gg_{\mathcal{D}} (\phi_2, \varphi_2)$ if and only if $(\phi_1, \varphi_1) - (\phi_2, \varphi_2) \in \text{Int} \mathcal{D}$. Using the maximum principle, one can show that system (12) generates a semiflow on \mathcal{C} . Substituting $N(x, t) = e^{\lambda t} \phi(x)$, and $U(x, t) = e^{\lambda t} \varphi(x)$ into (12), we obtain the associated nonlinear eigenvalue problem

$$\begin{cases} \lambda \phi(x) = d \phi''(x) + \mu \left(\frac{\varphi(x)}{\phi(x)} \right) \phi(x), & x \in (0, 1), \\ \lambda \varphi(x) = d \varphi''(x) + f(z(x), \frac{\varphi(x)}{\phi(x)}) \phi(x), & x \in (0, 1), \\ w'(0) = w'(1) + \gamma w(1) = 0, & w = \phi, \varphi. \end{cases} \quad (13)$$

By the similar arguments as in Lemmas 5.1 and 7.1 in [17], we have the following result.

Lemma 2.2. *The eigenvalue problem (13) admits a principal eigenvalue $\lambda^0(d)$ corresponding to which there is a strongly positive eigenfunction $(\phi^0(x), \varphi^0(x)) \gg_{\mathcal{D}} (0, 0)$ in \mathcal{C} . Moreover, there is a $d_0 > 0$ such that*

$$\lambda^0(d) > 0 \text{ if } 0 < d < d_0, \quad \lambda^0(d) = 0 \text{ if } d = d_0, \quad \lambda^0(d) < 0 \text{ if } d > d_0.$$

The biologically relevant domain for system (11) takes the form:

$$\begin{aligned} \Omega = \{(\mathcal{N}, \mathcal{U}) \in C([0, 1]; \mathbb{R}_+^2) : \mathcal{U}(\cdot) \leq z(\cdot) \text{ and there exists } \tilde{Q} > 0 \\ \text{such that } Q_{\min} \mathcal{N}(\cdot) \leq \mathcal{U}(\cdot) \leq \tilde{Q} \mathcal{N}(\cdot) \text{ in } [0, 1]\}. \end{aligned}$$

It is not hard to see that system (11) is strongly monotone (see [30]) in the interior of Ω , and it is strictly subhomogeneous ([39]). Then one can modify the arguments in [16, 17] together with the eigenvalue problem (13) to show that following result holds.

Lemma 2.3. *Let $(N(\cdot, t), U(\cdot, t))$ be the solution of system (11) with initial condition $(N^0, U^0) \in \Omega$.*

- (i) *If $0 < d < d_0$, then system (11) admits a unique positive steady-state solution $(N^*(\cdot), U^*(\cdot))$. Moreover, if the initial condition satisfies $N^0 \not\equiv 0$, then*

$$\lim_{t \rightarrow \infty} (N(x, t), U(x, t)) = (N^*(x), U^*(x)) \text{ uniformly on } [0, 1].$$

(i) If $d \geq d_0$, then

$$\lim_{t \rightarrow \infty} (N(x, t), U(x, t)) = (0, 0) \text{ uniformly on } [0, 1].$$

The following result is concerned with the dynamics of system (8):

Theorem 2.4. *Let $(R(\cdot, t), N(\cdot, t), U(\cdot, t))$ be the solution of system (8) with initial condition $(R^0, N^0, U^0) \in \mathbf{X}$.*

(i) *If $0 < d < d_0$, then system (8) admits a unique positive steady-state solution $(R^*(x), N^*(x), U^*(x))$ with $R^*(x) + U^*(x) = z(x)$ on $[0, 1]$. Moreover, if $N^0 \neq 0$, then*

$$\lim_{t \rightarrow \infty} (R(x, t), N(x, t), U(x, t)) = (R^*(x), N^*(x), U^*(x)) \text{ uniformly for } x \in [0, 1];$$

(ii) *If $d \geq d_0$, then*

$$\lim_{t \rightarrow \infty} (R(x, t), N(x, t), U(x, t)) = (z(x), 0, 0) \text{ uniformly for } x \in [0, 1].$$

Proof. By Lemma 2.3 and the theory of chain transitive sets (see, e.g., [13] or [39]), together with the similar arguments in [17, Theorem 7.1], one can prove Part (i). Part (ii) can be proved by the same arguments as in [17, Theorem 2.2(i)]. \square

3. Two-species model. This section is devoted to the investigation of the existence of coexistence solution for (5)-(7). By [21, Theorem 1 and Remark 1.1], we can show that system (5)-(7) admits a unique noncontinuable solution, and the solutions to (5)-(7) remain non-negative on their interval of existence if they are non-negative initially. The biologically relevant domain for system (5)-(7) is given by

$$\mathbf{Y} = \{(\mathcal{R}, \mathcal{N}_1, \mathcal{U}_1, \mathcal{N}_2, \mathcal{U}_2) \in C([0, 1]; \mathbb{R}_+^5) : \text{for } i = 1, 2, \text{ there exist } \tilde{Q}_i > 0 \text{ such that } Q_{\min, i} \mathcal{N}_i(\cdot) \leq \mathcal{U}_i(\cdot) \leq \tilde{Q}_i \mathcal{N}_i(\cdot) \text{ in } [0, 1]\}.$$

3.1. Well-posedness. In this subsection, we further show the boundedness of trajectories of system (5)-(7). Introducing the new variable

$$W(x, t) = R(x, t) + U_1(x, t) + U_2(x, t) \quad (14)$$

into (5)-(7), it follows from similar arguments as in (9) that $W(x, t)$ satisfies

$$\lim_{t \rightarrow \infty} W(x, t) = z(x) \text{ uniformly in } x \in [0, 1], \quad (15)$$

where $z(x) = R^{(0)}(\frac{1+\gamma}{\gamma} - x)$ on $[0, 1]$ as mentioned before.

Inspired by [17], we define Q_i^* to be the unique positive number so that

$$Q_i^* = \inf\{Q_i > 0 : f_i(z(x), Q_i) - \mu_i(Q_i)Q_i \leq 0 \text{ in } [0, 1]\}, \text{ for } i = 1, 2, \quad (16)$$

and we also define Q_2^{**} to be the unique positive number so that

$$Q_2^{**} = \inf\{Q > 0 : f_2(z(x), Q) - \mu_2(Q)Q + g\left(\frac{z(x)}{Q_{\min, 1}}\right)Q_1^* \leq 0 \text{ in } [0, 1]\}. \quad (17)$$

Then, we have the following results concerning with the boundedness of trajectories of system (5)-(7).

Lemma 3.1. *Let $(R(x, t), N_1(x, t), U_1(x, t), N_2(x, t), U_2(x, t))$ be a solution of (5)-(7) for $t \in [0, \tau)$, with initial data $(R^0, N_1^0, U_1^0, N_2^0, U_2^0) \in \mathbf{Y}$. Then*

(i) it holds that

$$\inf_{x \in [0,1]} \frac{U_i(x,t)}{N_i(x,t)} \geq Q_{\min,i} \quad \text{for all } t \in [0, \tau), \quad i = 1, 2. \quad (18)$$

(ii) there exists $\bar{Q}_i \in [Q_{\min,i}, +\infty)$ depending on $\|R^0\|$, $\|U_1^0/N_1^0\|$, and $\|U_2^0/N_2^0\|$ such that

$$\sup_{x \in [0,1]} \frac{U_i(x,t)}{N_i(x,t)} \leq \bar{Q}_i \quad \text{for all } t \in [0, \tau), \quad i = 1, 2. \quad (19)$$

Moreover, if $\tau = +\infty$, then for each $Q_1 > Q_1^*$ (resp. $Q_2 > Q_2^{**}$), we have

$$\limsup_{t \rightarrow \infty} \left[\sup_{x \in [0,1]} (U_i(x,t) - Q_i N_i(x,t)) \right] \leq 0, \quad i = 1 \text{ (resp. } i = 2). \quad (20)$$

Furthermore, if $\|N_1(\cdot, t)\|$ (resp. $\|N_2(\cdot, t)\|$) is bounded uniformly in $t > 0$, then (20) holds for $i = 1$ and $Q_1 = Q_1^*$ (resp. $i = 2$ and $Q_2 = Q_2^{**}$).

Proof. The following arguments are inspired by [17, 23]. For $i = 1, 2$, one can rewrite

$$\mu_i \left(\frac{U_i(x,t)}{N_i(x,t)} \right) = \mu_i(Q_{\min,i}) + \xi_i(x,t; Q_{\min,i}) \left(\frac{U_i(x,t)}{N_i(x,t)} - Q_{\min,i} \right)$$

where

$$\xi_i(x,t; Q_i) = \int_0^1 \mu_i' \left(s \frac{U_i(x,t)}{N_i(x,t)} + (1-s)Q_i \right) ds > 0, \quad Q_i \geq Q_{\min,i}. \quad (21)$$

Let $H_i(x,t) = U_i(x,t) - Q_{\min,i} N_i(x,t)$. Then $\mu_i \left(\frac{U_i}{N_i} \right) = \mu_i(Q_{\min,i}) + \xi_i(x,t; Q_{\min,i}) \frac{H_i}{N_i}$.

It follows from the second and third equations in (5) that

$$\begin{cases} \frac{\partial H_1}{\partial t} - d \frac{\partial^2 H_1}{\partial x^2} + [\xi_1(x,t; Q_{\min,1}) Q_{\min,1} + \frac{g(N_1)}{N_1} N_2] H_1 \\ \quad = f_1 \left(R, \frac{U_1}{N_1} \right) N_1 \geq 0, \quad \text{for } x \in [0, 1], t \in [0, \tau), \\ \frac{\partial H_1}{\partial x}(0,t) = \frac{\partial H_1}{\partial x}(1,t) + \gamma H_1(1,t) = 0, \quad \text{for } t \in [0, \tau), \end{cases}$$

where we used (6), $f_1 \geq 0$, and $\mu_i(Q_{\min,i}) = 0$. Using $H_1(x,0) = U_1^0(x) - Q_{\min,1} N_1^0(x) \geq 0$ and maximum principle for linear parabolic equations, we conclude that $H_1(\cdot, t) \geq 0$ in $[0, 1]$ for all $t \in [0, \tau)$. This proves (18) when $i = 1$. Similarly, we see that H_2 satisfies

$$\begin{cases} \frac{\partial H_2}{\partial t} - d \frac{\partial^2 H_2}{\partial x^2} + \xi_2(x,t; Q_{\min,2}) Q_{\min,2} H_2 \\ \quad = f_2 \left(R, \frac{U_2}{N_2} \right) N_2 + g(N_1) \frac{U_1}{N_1} N_2 \geq 0, \quad \text{for } x \in [0, 1], t \in [0, \tau), \\ \frac{\partial H_2}{\partial x}(0,t) = \frac{\partial H_2}{\partial x}(1,t) + \gamma H_2(1,t) = 0, \quad \text{for } t \in [0, \tau), \end{cases}$$

and hence, we can also prove (18) when $i = 2$.

Next, we show (19). Fix a solution (R, N_1, U_1, N_2, U_2) of (5)-(7) that exists up to time $\tau \in (0, \infty]$. By (14) and (15), there exists a number $\bar{Q}_1 \geq \sup_{[0,1]} \frac{U_1^0(x)}{N_1^0(x)}$ depending possibly on the initial data, such that

$$f_1(R(x,t), \bar{Q}_1) - \mu_1(\bar{Q}_1) \bar{Q}_1 \leq 0 \quad \text{for } x \in [0, 1], t \in [0, \tau). \quad (22)$$

Similarly, there exists a number $\bar{Q}_2 \geq \sup_{[0,1]} \frac{U_2^0(x)}{N_2^0(x)}$ depending possibly on the initial data, such that

$$f_2(R(x, t), \bar{Q}_2) + g(N_1) \frac{U_1}{N_1} - \mu_2(\bar{Q}_2) \bar{Q}_2 \leq 0 \quad \text{for } x \in [0, 1], t \in [0, \tau]. \quad (23)$$

Then we rewrite

$$f_i \left(R(x, t), \frac{U_i(x, t)}{N_i(x, t)} \right) = f_i(R(x, t), \bar{Q}_i) + \vartheta_i(x, t; \bar{Q}_i) \left(\frac{U_i(x, t)}{N_i(x, t)} - \bar{Q}_i \right),$$

where

$$\vartheta_i(x, t; Q_i) = \int_0^1 \frac{\partial f_i}{\partial Q_i} \left(R(x, t), s \frac{U_i(x, t)}{N_i(x, t)} + (1-s)Q_i \right) ds \leq 0, \quad i = 1, 2. \quad (24)$$

Also, we have

$$\mu_i \left(\frac{U_i(x, t)}{N_i(x, t)} \right) = \mu_i(\bar{Q}_i) + \xi_i(x, t; \bar{Q}_i) \left(\frac{U_i(x, t)}{N_i(x, t)} - \bar{Q}_i \right),$$

where $\xi_i(x, t; Q_i)$ is given in (21). Let $\bar{H}_i := U_i - \bar{Q}_i N_i$, $i = 1, 2$. Then \bar{H}_1 satisfies

$$\frac{\partial \bar{H}_1}{\partial x}(0, t) = \frac{\partial \bar{H}_1}{\partial x}(1, t) + \gamma \bar{H}_1(1, t) = 0, \quad \text{for } t \in [0, \tau], \quad (25)$$

and \bar{H}_1 satisfies the differential inequality

$$\begin{aligned} & \frac{\partial \bar{H}_1}{\partial t} - d \frac{\partial^2 \bar{H}_1}{\partial x^2} \\ &= f_1 \left(R, \frac{U_1}{N_1} \right) N_1 - \mu_1 \left(\frac{U_1}{N_1} \right) \bar{Q}_1 N_1 - g(N_1) \frac{U_1}{N_1} N_2 + g(N_1) N_2 \bar{Q}_1 \\ &= [\vartheta_1(x, t; \bar{Q}_1) - \xi_1(x, t; \bar{Q}_1) \bar{Q}_1 - \frac{g(N_1)}{N_1} N_2] \left(\frac{U_1(x, t)}{N_1(x, t)} - \bar{Q}_1 \right) N_1 \\ & \quad + [f_1(R, \bar{Q}_1) - \mu_1(\bar{Q}_1) \bar{Q}_1] N_1 \\ &\leq \bar{E}_1(x, t) \bar{H}_1, \quad \text{for } x \in [0, 1], t \in [0, \tau], \end{aligned}$$

where

$$\bar{E}_1(x, t) = \vartheta_1(x, t; \bar{Q}_1) - \xi_1(x, t; \bar{Q}_1) \bar{Q}_1 - \frac{g(N_1)}{N_1} N_2 < 0, \quad \text{for } x \in [0, 1], t \in [0, \tau],$$

and we have used (22). By the choice of \bar{Q}_1 , we have $\bar{H}_1(x, 0) \leq 0$. Then the comparison principle implies that $U_1(x, t) - \bar{Q}_1 N_1(x, t) = \bar{H}_1(x, t) \leq 0$ for all $x \in [0, 1]$ and $t \in [0, \tau]$. This proves (19) with $i = 1$. Using (23), we see that \bar{H}_2 satisfies

$$\frac{\partial \bar{H}_2}{\partial t} - d \frac{\partial^2 \bar{H}_2}{\partial x^2} \leq \bar{E}_2(x, t) \bar{H}_2, \quad \text{for } x \in [0, 1], t \in [0, \tau],$$

where

$$\bar{E}_2(x, t) = \vartheta_2(x, t; \bar{Q}_2) - \xi_2(x, t; \bar{Q}_2) \bar{Q}_2 < 0, \quad \text{for } x \in [0, 1], t \in [0, \tau].$$

Since \bar{H}_2 also satisfies $\bar{H}_2(x, 0) \leq 0$ and the same boundary condition (25), we can conclude that (19) holds when $i = 2$.

Finally, we prove (20). It follows from (16) and (17) that for each $\eta > 0$, there exists an $\epsilon > 0$ such that for $x \in [0, 1]$,

$$f_1(z(x) + \epsilon, Q_1^* + \eta) - \mu_1(Q_1^* + \eta)(Q_1^* + \eta) \leq 0, \quad (26)$$

$$f_2(z(x) + \epsilon, Q_2^{**} + \eta) - \mu_2(Q_2^{**} + \eta)(Q_2^{**} + \eta) + g \left(\frac{z(x)}{Q_{\min, 1}} + \epsilon \right) (Q_1^* + \epsilon) \leq 0. \quad (27)$$

By (14) and (15), we may assume without loss of generality (by translation in t) that

$$R(x, t) \leq z(x) + \epsilon \text{ for all } x \in [0, 1], t \geq 0. \quad (28)$$

Let $H_1^\eta(x, t) = U_1(x, t) - (Q_1^* + \eta)N_1(x, t)$. Observing that

$$\begin{aligned} \mu_1 \left(\frac{U_1(x, t)}{N_1(x, t)} \right) &= \mu_1(Q_1^* + \eta) + \xi_1(x, t; Q_1^* + \eta) \left(\frac{U_1(x, t)}{N_1(x, t)} - (Q_1^* + \eta) \right), \\ f_1 \left(R(x, t), \frac{U_1(x, t)}{N_1(x, t)} \right) &= f_1(R(x, t), Q_1^* + \eta) + \vartheta_1(x, t; Q_1^* + \eta) \left(\frac{U_1(x, t)}{N_1(x, t)} - (Q_1^* + \eta) \right), \end{aligned}$$

where $\xi_1(x, t; Q_1^* + \eta)$ and $\vartheta_1(x, t; Q_1^* + \eta)$ are defined in (21) and (24), respectively. Then $H_1^\eta(x, t)$ satisfies the boundary condition (25) and the following differential inequality

$$\begin{aligned} &\frac{\partial H_1^\eta}{\partial t} - d \frac{\partial^2 H_1^\eta}{\partial x^2} \\ &= [\vartheta_1(x, t; Q_1^* + \eta) - \xi_1(x, t; Q_1^* + \eta)(Q_1^* + \eta) - \frac{g(N_1)}{N_1} N_2] \left(\frac{U_1}{N_1} - (Q_1^* + \eta) \right) N_1 \\ &\quad + [f_1(R, Q_1^* + \eta) - \mu_1(Q_1^* + \eta)(Q_1^* + \eta)] N_1 \\ &\leq E_1^\eta(x, t) H_1^\eta, \quad \text{for } x \in [0, 1], t \geq 0, \end{aligned}$$

where

$$E_1^\eta(x, t) = \vartheta_1(x, t; Q_1^* + \eta) - \xi_1(x, t; Q_1^* + \eta)(Q_1^* + \eta) - \frac{g(N_1)}{N_1} N_2 < 0, \text{ for } x \in [0, 1], t \geq 0,$$

and we have used (26) and (28). Assume σ_1 satisfies

$$0 < \sigma_1 < -E_1^\eta(x, t), \quad \forall x \in [0, 1], t \in [0, \infty).$$

Let $\tilde{H}_1(x, t) = B_1 e^{-\sigma_1 t}$, where $B_1 > 0$ and $B_1 \geq H_1^\eta(x, 0)$. Then

$$\begin{aligned} &\frac{\partial \tilde{H}_1}{\partial t} - d \frac{\partial^2 \tilde{H}_1}{\partial x^2} - E_1^\eta(x, t) \tilde{H}_1 > -\sigma_1 \tilde{H}_1 + \sigma_1 \tilde{H}_1 = 0, \text{ for } x \in [0, 1], t \geq 0, \\ &\frac{\partial \tilde{H}_1}{\partial x}(0, t) = 0, \quad \frac{\partial \tilde{H}_1}{\partial x}(1, t) + \gamma \tilde{H}_1(1, t) > 0, t \geq 0. \end{aligned}$$

By comparison principle,

$$H_1^\eta(x, t) \leq \tilde{H}_1(x, t), \text{ for } x \in [0, 1], t \geq 0.$$

Using the fact that $\tilde{H}_1(x, t) \rightarrow 0$ uniformly in $x \in [0, 1]$ as $t \rightarrow \infty$, we obtain

$$\limsup_{t \rightarrow \infty} \left\{ \sup_{x \in [0, 1]} [U_1(x, t) - (Q_1^* + \eta)N_1(x, t)] \right\} \leq 0, \text{ for all } \eta > 0. \quad (29)$$

This proves that (20) holds for $i = 1$.

By (14), (15), (18) and (20) with $i = 1$, we may assume without loss of generality (by translation in t) that

$$N_1(x, t) \leq \frac{z(x)}{Q_{\min, 1}} + \epsilon \text{ and } \frac{U_1(x, t)}{N_1(x, t)} \leq Q_1^* + \epsilon \text{ for all } x \in [0, 1], t \geq 0. \quad (30)$$

Let $H_2^\eta(x, t) = U_2(x, t) - (Q_2^{**} + \eta)N_2(x, t)$. Observing that

$$\begin{aligned} \mu_2 \left(\frac{U_2(x, t)}{N_2(x, t)} \right) &= \mu_2(Q_2^{**} + \eta) + \xi_2(x, t; Q_2^{**} + \eta) \left(\frac{U_2(x, t)}{N_2(x, t)} - (Q_2^{**} + \eta) \right), \\ f_2 \left(R(x, t), \frac{U_2(x, t)}{N_2(x, t)} \right) &= f_2(R(x, t), Q_2^{**} + \eta) + \vartheta_2(x, t; Q_2^{**} + \eta) \left(\frac{U_2(x, t)}{N_2(x, t)} - (Q_2^{**} + \eta) \right), \end{aligned}$$

where $\xi_2(x, t; Q_2^{**} + \eta)$ and $\vartheta_2(x, t; Q_2^{**} + \eta)$ are defined in (21) and (24), respectively. Then $H_2^\eta(x, t)$ satisfies the boundary condition (25) and the following differential inequality

$$\begin{aligned} & \frac{\partial H_2^\eta}{\partial t} - d \frac{\partial^2 H_2^\eta}{\partial x^2} \\ &= [\vartheta_2(x, t; Q_2^{**} + \eta) - \xi_2(x, t; Q_2^{**} + \eta)(Q_2^{**} + \eta)] \left(\frac{U_2}{N_2} - (Q_2^{**} + \eta) \right) N_2 \\ & \quad + [f_2(R, Q_2^{**} + \eta) - \mu_2(Q_2^{**} + \eta)(Q_2^{**} + \eta) + g(N_1) \frac{U_1}{N_1}] N_2 \\ & \leq E_2^\eta(x, t) H_2^\eta, \quad \text{for } x \in [0, 1], t \geq 0, \end{aligned}$$

where

$$E_2^\eta(x, t) = \vartheta_2(x, t; Q_2^{**} + \eta) - \xi_1(x, t; Q_2^{**} + \eta)(Q_2^{**} + \eta) < 0, \quad \text{for } x \in [0, 1], t \geq 0,$$

and we have used (27), (28) and (30). Assume σ_2 satisfies

$$0 < \sigma_2 < -E_2^\eta(x, t), \quad \forall x \in [0, 1], t \in [0, \infty).$$

Let $\tilde{H}_2(x, t) = B_2 e^{-\sigma_2 t}$, where $B_2 > 0$ and $B_2 \geq H_2^\eta(x, 0)$. Then we may once again conclude by comparison with $\tilde{H}_2(x, t)$ that

$$\limsup_{t \rightarrow \infty} \left\{ \sup_{x \in [0, 1]} [U_2(x, t) - (Q_2^{**} + \eta) N_2(x, t)] \right\} \leq 0, \quad \text{for all } \eta > 0. \quad (31)$$

This proves that (20) holds for $i = 2$.

The last statement follows by letting $\eta \searrow 0$ in (29) and (31), which is possible if $\|N_i(\cdot, t)\|$ is bounded uniformly in t . \square

Corollary 2. *System (5)-(7) generates a semiflow in \mathbf{Y} in the sense that for each initial condition in \mathbf{Y} , system (5)-(7) admits a unique classical solution*

$$(R(\cdot, t), N_1(\cdot, t), U_1(\cdot, t), N_2(\cdot, t), U_2(\cdot, t))$$

that exists for all $t > 0$. Moreover, the solution satisfies

$$(R(\cdot, t), N_1(\cdot, t), U_1(\cdot, t), N_2(\cdot, t), U_2(\cdot, t)) \in \mathbf{Y}$$

for all $t > 0$.

Proof. We first do extensions on the functions $\mu_i(U_i/N_i)N_i$ and $f_i(R, U_i/N_i)N_i$ in the following way:

$$\tilde{\mu}_i(N_i, U_i) = \begin{cases} 0 & \text{if } N_i = 0, \\ \mu_i\left(\frac{U_i}{N_i}\right)N_i & \text{if } N_i > 0. \end{cases} \quad (32)$$

$$\tilde{f}_i(R, N_i, U_i) = \begin{cases} 0 & \text{if } N_i = 0, \\ f_i\left(R, \frac{U_i}{N_i}\right)N_i & \text{if } N_i > 0. \end{cases} \quad (33)$$

Then it is easy to check that $\tilde{\mu}_i(N_i, U_i)$ and $\tilde{f}_i(R, N_i, U_i)$ are Lipschitz continuous in \mathbf{Y} . Hence, we can proceed further as in the proof of Theorem 2.1(i) in [17] to show that the conclusions hold. \square

3.2. Coexistence. For $i = 1, 2$, we assume $\lambda_i^0(d)$ is the principal eigenvalue of (13) with functions $\mu = \mu_i$ and $f = f_i$. It follows from Lemma 2.2 that there is a unique $d_{0,i} > 0$ ($i = 1, 2$) such that

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

For $i = 1, 2$, we note that the functions $\mu_i(U_i/N_i)N_i$ and $f_i(R, U_i/N_i)N_i$ can be respectively extended to (32) and (33), if necessary. Hence, we conclude from Theorem 2.4 that system (5)-(7) may admit the following trivial and semi-trivial steady-state solutions:

- (i) Trivial solution $E_0(x) = (z(x), 0, 0, 0, 0)$ always exists;
- (ii) Semi-trivial solution $E_1(x) = (R_1^*(x), N_1^*(x), U_1^*(x), 0, 0)$ exists provided that $0 < d < d_{0,1}$;
- (iii) Semi-trivial solution $E_2(x) = (R_2^*(x), 0, 0, N_2^*(x), U_2^*(x))$ exists provided that $0 < d < d_{0,2}$.

Here, $(R_i^*(x), N_i^*(x), U_i^*(x))$, $i = 1, 2$, denotes the unique positive steady-state solution of the single population system (8) with functions $\mu = \mu_i$ and $f = f_i$. The two species can coexist if a stable positive steady-state solution of (5)-(7) exists.

By Lemma 3.1 and Corollary 2, we may assume that

$$\Psi_t : \mathbf{Y} \rightarrow \mathbf{Y}$$

is the solution map associated with system (5)-(7). Let

$$\mathbf{Y}_0 = \{(R^0(\cdot), N_1^0(\cdot), U_1^0(\cdot), N_2^0(\cdot), U_2^0(\cdot)) \in \mathbf{Y} : N_1^0(\cdot) \not\equiv 0 \text{ and } N_2^0(\cdot) \not\equiv 0\},$$

and

$$\partial\mathbf{Y}_0 = \mathbf{Y} \setminus \mathbf{Y}_0.$$

Due to the singularity in the ratio U_i/N_i at the case $U_i = N_i = 0$, we cannot linearize system (5)-(7) at trivial and semi-trivial steady-state solutions $E_i(x)$, $i = 0, 1, 2$. We next show that the instability of $E_i(x)$, $i = 0, 1, 2$, can be determined by the principal eigenvalue of the associated nonlinear eigenvalue problem.

The following result is concerned with the instability of $E_0(x)$.

Lemma 3.2. *Assume that $0 < d < d_{0,1}$ or $0 < d < d_{0,2}$. Then $E_0(\cdot)$ is a uniform weak repeller for \mathbf{Y}_0 in the sense that there exists a $\delta_0 > 0$ such that*

$$\limsup_{t \rightarrow \infty} \|\Psi_t(P^0) - E_0(\cdot)\| \geq \delta_0 \quad (34)$$

for all $P^0 := (R^0(\cdot), N_1^0(\cdot), U_1^0(\cdot), N_2^0(\cdot), U_2^0(\cdot)) \in \mathbf{Y}_0$.

Proof. We first consider the case where $0 < d < d_{0,2}$. Then it follows from Lemma 2.2 that $\lambda_2^0(d) > 0$. Hence, there exists a sufficiently small $\epsilon_0 > 0$ such that $\lambda_2^{\epsilon_0} > 0$, where $\lambda_2^{\epsilon_0}$ is the principal eigenvalue of

$$\begin{cases} \lambda\phi(x) = d\phi''(x) + \mu_2\left(\frac{\varphi(x)}{\phi(x)}\right)\phi(x), & x \in (0, 1), \\ \lambda\varphi(x) = d\varphi''(x) + [f_2(z(x), \frac{\varphi(x)}{\phi(x)}) - \epsilon_0]\varphi(x), & x \in (0, 1), \\ w'(0) = w'(1) + \gamma w(1) = 0, & w = \phi, \varphi. \end{cases}$$

By the continuity, there exists a $\delta_0 > 0$ such that

$$f_2(R(\cdot), \frac{U_2}{N_2}) > f_2(z(\cdot), \frac{U_2}{N_2}) - \epsilon_0, \quad \forall \|R(\cdot) - z(\cdot)\| < \delta_0. \quad (35)$$

Suppose by contradiction that (34) is not true. Then there exists $P^0 \in \mathbf{Y}_0$ such that

$$\limsup_{t \rightarrow \infty} \|\Psi_t(P^0) - E_0(\cdot)\| < \delta_0.$$

Thus, there exists a $t_0 > 0$ such that

$$\|R(\cdot, t) - z(\cdot)\| < \delta_0, \quad \forall t \geq t_0, \quad (36)$$

and

$$\|(N_2(\cdot, t), U_2(\cdot, t)) - (0, 0)\| < \delta_0, \quad \forall t \geq t_0. \quad (37)$$

From (35), (36), and the last two equations in (5), we have

$$\begin{cases} \frac{\partial N_2}{\partial t} \geq d \frac{\partial^2 N_2}{\partial x^2} + \mu_2 \left(\frac{U_2}{N_2}\right) N_2, & x \in (0, 1), t \geq t_0, \\ \frac{\partial U_2}{\partial t} \geq d \frac{\partial^2 U_2}{\partial x^2} + [f_2(z(x), \frac{U_2}{N_2}) - \epsilon_0] N_2, & x \in (0, 1), t \geq t_0, \\ \frac{\partial w}{\partial x}(0, t) = \frac{\partial w}{\partial x}(1, t) + \gamma w(1, t) = 0, & t \geq t_0, w = N_2, U_2. \end{cases} \quad (38)$$

Since $P^0 \in \mathbf{Y}_0$, it is not hard to show that $N_2(\cdot, t_0) > 0$ and $U_2(\cdot, t_0) > 0$, and hence, there exists an $a_0 > 0$ such that

$$(N_2(\cdot, t_0), U_2(\cdot, t_0)) \geq (a_0 \phi_0^{\epsilon_0}(\cdot), a_0 \varphi_0^{\epsilon_0}(\cdot)), \quad (39)$$

where $(\phi_0^{\epsilon_0}(x), \varphi_0^{\epsilon_0}(x))$ is the strongly positive eigenfunction associated with $\lambda_2^{\epsilon_0}$. Let

$$(\underline{N}_2(x, t), \underline{U}_2(x, t)) = (a_0 e^{\lambda_2^{\epsilon_0}(t-t_0)} \phi_0^{\epsilon_0}(x), a_0 e^{\lambda_2^{\epsilon_0}(t-t_0)} \varphi_0^{\epsilon_0}(x)).$$

Then $(\underline{N}_2(x, t), \underline{U}_2(x, t))$ satisfies the following system

$$\begin{cases} \frac{\partial \underline{N}_2}{\partial t} = d \frac{\partial^2 \underline{N}_2}{\partial x^2} + \mu_2 \left(\frac{\underline{U}_2}{\underline{N}_2}\right) \underline{N}_2, & x \in (0, 1), t \geq t_0, \\ \frac{\partial \underline{U}_2}{\partial t} = d \frac{\partial^2 \underline{U}_2}{\partial x^2} + [f_2(z(x), \frac{\underline{U}_2}{\underline{N}_2}) - \epsilon_0] \underline{N}_2, & x \in (0, 1), t \geq t_0, \\ \frac{\partial w}{\partial x}(0, t) = \frac{\partial w}{\partial x}(1, t) + \gamma w(1, t) = 0, & t \geq t_0, w = \underline{N}_2, \underline{U}_2, \\ (\underline{N}_2(\cdot, t_0), \underline{U}_2(\cdot, t_0)) = (a_0 \phi_0^{\epsilon_0}(\cdot), a_0 \varphi_0^{\epsilon_0}(\cdot)). \end{cases} \quad (40)$$

From (38), (39), (40), and the comparison principle, it follows that for $t \geq t_0$ and $x \in [0, 1]$, we have

$$(N_2(x, t), U_2(x, t)) \geq (\underline{N}_2(x, t), \underline{U}_2(x, t)) = (a_0 e^{\lambda_2^{\epsilon_0}(t-t_0)} \phi_0^{\epsilon_0}(x), a_0 e^{\lambda_2^{\epsilon_0}(t-t_0)} \varphi_0^{\epsilon_0}(x)).$$

Since $\lambda_2^{\epsilon_0} > 0$, it follows that $\lim_{t \rightarrow \infty} (N_2(\cdot, t), U_2(\cdot, t))$ is unbounded, contradicting (37). This contradiction proves the results for the case $0 < d < d_{0,2}$.

The arguments for the case $0 < d < d_{0,1}$ will be similar to Lemma 3.6, and we omit the details. Thus, we completes the proof of this lemma. \square

In order to discuss the instability of $E_1(x)$, we consider the following nonlinear system

$$\begin{cases} \frac{\partial N_2}{\partial t} = d \frac{\partial^2 N_2}{\partial x^2} + \mu_2 \left(\frac{U_2}{N_2}\right) N_2, & x \in (0, 1), t > 0, \\ \frac{\partial U_2}{\partial t} = d \frac{\partial^2 U_2}{\partial x^2} + f_2(R_1^*(x), \frac{U_2}{N_2}) N_2 + g(N_1^*(x)) \frac{U_1^*(x)}{N_1^*(x)} N_2, & x \in (0, 1), t > 0, \\ \frac{\partial w}{\partial x}(0, t) = \frac{\partial w}{\partial x}(1, t) + \gamma w(1, t) = 0, & t > 0, w = N_2, U_2, \end{cases} \quad (41)$$

where $(R_1^*(x), N_1^*(x), U_1^*(x))$ is given in $E_1(x)$. Let $\mathcal{D} = C^0([0, 1], \mathbb{R}_+^2)$ again and

$$\mathcal{C}_2 = \{(N_2, U_2) \in \mathcal{D} : Q_{\min,2} N_2(x) \leq U_2(x) \leq Q_2^{**} N_2(x) \text{ for } x \in [0, 1]\},$$

where Q_2^{**} is given by (17). Using the facts that $R_1^*(x) \leq z(x)$, $N_1^*(x) \leq \frac{z(x)}{Q_{\min,1}}$ (see Lemma 2.2 in [16]), and $\frac{U_1^*(x)}{N_1^*(x)} \leq Q_1^*$ (see Lemma 2.1), together with the maximum principle, one can show that system (41) generates a semiflow on \mathcal{C}_2 . Substituting

$N_2(x, t) = e^{\Lambda_2 t} \phi_2(x)$, and $U_2(x, t) = e^{\Lambda_2 t} \varphi_2(x)$ into (41), we obtain the associated nonlinear eigenvalue problem

$$\begin{cases} \Lambda_2 \phi_2(x) = d\phi_2''(x) + \mu_2 \left(\frac{\varphi_2(x)}{\phi_2(x)} \right) \phi_2(x), & x \in (0, 1), \\ \Lambda_2 \varphi_2(x) = d\varphi_2''(x) + f_2(R_1^*(x), \frac{\varphi_2(x)}{\phi_2(x)}) \phi_2(x) \\ \quad + g(N_1^*(x)) \frac{U_1^*(x)}{N_1^*(x)} \phi_2(x), & x \in (0, 1), \\ w'(0) = w'(1) + \gamma w(1) = 0, & w = \phi_2, \varphi_2. \end{cases} \quad (42)$$

By the similar arguments as in [17, Lemma 5.1], we have the following result.

Lemma 3.3. *The eigenvalue problem (42) admits a principal eigenvalue Λ_2^0 corresponding to which there is a strongly positive eigenfunction $(\phi_2^0(x), \varphi_2^0(x)) \gg_{\mathcal{D}} (0, 0)$.*

The following result indicates that the instability of $E_1(x)$ can be determined by the sign of Λ_2^0 .

Lemma 3.4. *Assume $0 < d < d_{0,1}$ and $\Lambda_2^0 > 0$. Then $E_1(\cdot)$ is a uniform weak repeller for \mathbf{Y}_0 in the sense that there exists a $\delta > 0$ such that*

$$\limsup_{t \rightarrow \infty} \|\Psi_t(P^0) - E_1(\cdot)\| \geq \delta, \text{ for all } P^0 \in \mathbf{Y}_0. \quad (43)$$

Proof. Since $\Lambda_2^0 > 0$, it follows that there exists a sufficiently small $\epsilon > 0$ such that $\Lambda_2^\epsilon > 0$, where Λ_2^ϵ is the principal eigenvalue of

$$\begin{cases} \Lambda_2 \phi_2(x) = d\phi_2''(x) + \mu_2 \left(\frac{\varphi_2(x)}{\phi_2(x)} \right) \phi_2(x), & x \in (0, 1), \\ \Lambda_2 \varphi_2(x) = d\varphi_2''(x) + [f_2(R_1^*(x), \frac{\varphi_2(x)}{\phi_2(x)}) - \epsilon] \phi_2(x) \\ \quad + [g(N_1^*(x)) \frac{U_1^*(x)}{N_1^*(x)} - \epsilon] \phi_2(x), & x \in (0, 1), \\ w'(0) = w'(1) + \gamma w(1) = 0, & w = \phi_2, \varphi_2. \end{cases}$$

By the continuity, there exists a $\delta > 0$ such that

$$f_2(R(\cdot), \frac{U_2}{N_2}) > f_2(R_1^*(\cdot), \frac{U_2}{N_2}) - \epsilon, \quad \forall \|R(\cdot) - R_1^*(\cdot)\| < \delta, \quad (44)$$

and

$$g(N_1) \frac{U_1}{N_1} > g(N_1^*(x)) \frac{U_1^*(x)}{N_1^*(x)} - \epsilon, \quad \forall \|(N_1(\cdot), U_1(\cdot)) - (N_1^*(\cdot), U_1^*(\cdot))\| < \delta. \quad (45)$$

Suppose by contradiction that (43) is not true. Then there exists $P^0 \in \mathbf{Y}_0$ such that

$$\limsup_{t \rightarrow \infty} \|\Psi_t(P^0) - E_1(\cdot)\| < \delta.$$

Thus, there exists a $t_1 > 0$ such that

$$\|R(\cdot, t) - R_1^*(\cdot)\| < \delta \text{ and } \|(N_1(\cdot, t), U_1(\cdot, t)) - (N_1^*(\cdot), U_1^*(\cdot))\| < \delta, \quad \forall t \geq t_1, \quad (46)$$

and

$$\|(N_2(\cdot, t), U_2(\cdot, t)) - (0, 0)\| < \delta, \quad \forall t \geq t_1. \quad (47)$$

From the last two equations of (5) together with (44), (45) and (46), we have

$$\begin{cases} \frac{\partial N_2}{\partial t} \geq d \frac{\partial^2 N_2}{\partial x^2} + \mu_2 \left(\frac{U_2}{N_2} \right) N_2, & x \in (0, 1), t \geq t_1, \\ \frac{\partial U_2}{\partial t} \geq d \frac{\partial^2 U_2}{\partial x^2} + [f_2(R_1^*(x), \frac{U_2}{N_2}) - \epsilon] N_2 \\ \quad + [g(N_1^*(x)) \frac{U_1^*(x)}{N_1^*(x)} - \epsilon] N_2, & x \in (0, 1), t \geq t_1, \\ \frac{\partial w}{\partial x}(0, t) = \frac{\partial w}{\partial x}(1, t) + \gamma w(1, t) = 0, & t \geq t_1, w = N_2, U_2. \end{cases} \quad (48)$$

Since $P^0 \in \mathbf{Y}_0$, it is not hard to show that $N_2(\cdot, t_1) > 0$ and $U_2(\cdot, t_1) > 0$, and hence, there exists an $a_1 > 0$ such that

$$(N_2(\cdot, t_1), U_2(\cdot, t_1)) \geq (a_1 \phi_2^\epsilon(\cdot), a_1 \varphi_2^\epsilon(\cdot)), \quad (49)$$

where $(\phi_2^\epsilon(x), \varphi_2^\epsilon(x))$ is the strongly positive eigenfunction associated with Λ_2^ϵ . Let

$$(\tilde{N}_2(x, t), \tilde{U}_2(x, t)) = (a_1 e^{\Lambda_2^\epsilon(t-t_1)} \phi_2^\epsilon(x), a_1 e^{\Lambda_2^\epsilon(t-t_1)} \varphi_2^\epsilon(x)).$$

Then $(\tilde{N}_2(x, t), \tilde{U}_2(x, t))$ satisfies the following system

$$\begin{cases} \frac{\partial \tilde{N}_2}{\partial t} = d \frac{\partial^2 \tilde{N}_2}{\partial x^2} + \mu_2 \left(\frac{\tilde{U}_2}{\tilde{N}_2} \right) \tilde{N}_2, & x \in (0, 1), t \geq t_1, \\ \frac{\partial \tilde{U}_2}{\partial t} = d \frac{\partial^2 \tilde{U}_2}{\partial x^2} + [f_2(R_1^*(x), \frac{\tilde{U}_2}{\tilde{N}_2}) - \epsilon] \tilde{N}_2 \\ \quad + [g(N_1^*(x)) \frac{U_1^*(x)}{N_1^*(x)} - \epsilon] \tilde{N}_2, & x \in (0, 1), t \geq t_1, \\ \frac{\partial w}{\partial x}(0, t) = \frac{\partial w}{\partial x}(1, t) + \gamma w(1, t) = 0, & t \geq t_1, w = \tilde{N}_2, \tilde{U}_2, \\ (\tilde{N}_2(\cdot, t_1), \tilde{U}_2(\cdot, t_1)) = (a_1 \phi_2^\epsilon(\cdot), a_1 \varphi_2^\epsilon(\cdot)). \end{cases} \quad (50)$$

From (48), (49), (50), and the comparison principle, it follows that for $t \geq t_1$ and $x \in [0, 1]$, we have

$$(N_2(x, t), U_2(x, t)) \geq (\tilde{N}_2(x, t), \tilde{U}_2(x, t)) = (a_1 e^{\Lambda_2^\epsilon(t-t_1)} \phi_2^\epsilon(x), a_1 e^{\Lambda_2^\epsilon(t-t_1)} \varphi_2^\epsilon(x)).$$

Since $\Lambda_2^\epsilon > 0$, it follows that $\lim_{t \rightarrow \infty} (N_2(\cdot, t), U_2(\cdot, t))$ is unbounded, contradicting (47). This contradiction completes the proof of the lemma. \square

Next, we study the instability of $E_2(x)$. For this purpose, we consider the following system

$$\begin{cases} \frac{\partial N_1}{\partial t} = d \frac{\partial^2 N_1}{\partial x^2} + \mu_1 \left(\frac{U_1}{N_1} \right) N_1, & x \in (0, 1), t > 0, \\ \frac{\partial U_1}{\partial t} = d \frac{\partial^2 U_1}{\partial x^2} + f_1(R_2^*(x), \frac{U_1}{N_1}) N_1, & x \in (0, 1), t > 0, \\ \frac{\partial w}{\partial x}(0, t) = \frac{\partial w}{\partial x}(1, t) + \gamma w(1, t) = 0, & t > 0, w = N_1, U_1, \end{cases} \quad (51)$$

where $R_2^*(x)$ is given in $E_2(x)$. Let $\mathcal{D} = C^0([0, 1], \mathbb{R}_+^2)$ and

$$\mathcal{C}_1 = \{(N_1, U_1) \in \mathcal{D} : Q_{\min, 1} N_1(x) \leq U_1(x) \leq Q_1^* N_1(x) \text{ for } x \in [0, 1]\},$$

where Q_1^* is given by (16). Using the fact that $R_2^*(x) \leq z(x)$, together with the maximum principle, one can show that system (51) generates a semiflow on \mathcal{C}_1 . Substituting $N_1(x, t) = e^{\Lambda_1 t} \phi_1(x)$, and $U_1(x, t) = e^{\Lambda_1 t} \varphi_1(x)$ into (51), we obtain the associated nonlinear eigenvalue problem

$$\begin{cases} \Lambda_1 \phi_1(x) = d \phi_1''(x) + \mu_1 \left(\frac{\varphi_1(x)}{\phi_1(x)} \right) \phi_1(x), & x \in (0, 1), \\ \Lambda_1 \varphi_1(x) = d \varphi_1''(x) + f_1(R_2^*(x), \frac{\varphi_1(x)}{\phi_1(x)}) \phi_1(x), & x \in (0, 1), \\ w'(0) = w'(1) + \gamma w(1) = 0, & w = \phi_1, \varphi_1. \end{cases} \quad (52)$$

By the similar arguments as in [17, Lemma 5.1], we have the following result.

Lemma 3.5. *The eigenvalue problem (52) admits a principal eigenvalue Λ_1^0 corresponding to which there is a strongly positive eigenfunction $(\phi_1^0(x), \varphi_1^0(x)) \gg_{\mathcal{D}} (0, 0)$.*

The following result indicates that the instability of $E_2(x)$ can be determined by the sign of Λ_1^0 .

Lemma 3.6. *Assume $0 < d < d_{0,2}$ and $\Lambda_1^0 > 0$. Then $E_2(\cdot)$ is a uniform weak repeller for \mathbf{Y}_0 in the sense that there exists a $\sigma > 0$ such that*

$$\limsup_{t \rightarrow \infty} \|\Psi_t(P^0) - E_2(\cdot)\| \geq \sigma, \text{ for all } P^0 \in \mathbf{Y}_0. \quad (53)$$

Proof. Since $\Lambda_1^0 > 0$, there exists a sufficiently small $\rho > 0$ such that $\Lambda_1^\rho > 0$, where Λ_1^ρ is the principal eigenvalue of

$$\begin{cases} \Lambda_1 \phi_1(x) = d\phi_1''(x) + \mu_1\left(\frac{\varphi_1(x)}{\phi_1(x)}\right)\phi_1(x) - \rho\phi_1(x), & x \in (0, 1), \\ \Lambda_1 \varphi_1(x) = d\varphi_1''(x) + [f_1(R_2^*(x), \frac{\varphi_1(x)}{\phi_1(x)}) - \rho]\phi_1(x) - \rho\varphi_1(x), & x \in (0, 1), \\ w'(0) = w'(1) + \gamma w(1) = 0, & w = \phi_1, \varphi_1. \end{cases}$$

Using (2), it follows that

$$g(N_1)N_2 = C(N_1, N_2)N_1, \text{ and } g(N_1)\frac{U_1}{N_1}N_2 = C(N_1, N_2)U_1, \quad (54)$$

where $C(N_1, N_2) = \frac{g_{\max}N_1^{b-1}}{K_0^b + N_1^b}N_2$, and $b > 1$. Note that

$$\lim_{(N_1(\cdot), N_2(\cdot)) \rightarrow (0, N_2^*(\cdot))} C(N_1, N_2) = C(0, N_2^*(\cdot)) = 0.$$

By the continuity, there exists a $\sigma > 0$ such that

$$f_1(R(\cdot), \frac{U_1}{N_1}) > f_1(R_2^*(\cdot), \frac{U_1}{N_1}) - \rho, \quad \forall \|R(\cdot) - R_2^*(\cdot)\| < \sigma, \quad (55)$$

and

$$0 \leq C(N_1(\cdot), N_2(\cdot)) < \rho, \quad \forall \|(N_1(\cdot), N_2(\cdot)) - (0, N_2^*(\cdot))\| < \sigma. \quad (56)$$

From (54) and (56), it follows that

$$g(N_1)N_2 \leq \rho N_1 \text{ and } g(N_1)\frac{U_1}{N_1}N_2 \leq \rho U_1, \quad \forall \|(N_1(\cdot), N_2(\cdot)) - (0, N_2^*(\cdot))\| < \sigma. \quad (57)$$

Suppose by contradiction that (53) is not true. Then there exists $P^0 \in \mathbf{Y}_0$ such that

$$\limsup_{t \rightarrow \infty} \|\Psi_t(P^0) - E_2(\cdot)\| < \sigma.$$

Thus, there exists a $t_2 > 0$ such that

$$\|R(\cdot, t) - R_2^*(\cdot)\| < \sigma \text{ and } \|(N_1(\cdot, t), N_2(\cdot, t)) - (0, N_2^*(\cdot))\| < \sigma, \quad \forall t \geq t_2, \quad (58)$$

and

$$\|(N_1(\cdot, t), U_1(\cdot, t)) - (0, 0)\| < \sigma, \quad \forall t \geq t_2. \quad (59)$$

In view of the second and third equations of system (5), together with (55), (57), and (58), we have

$$\begin{cases} \frac{\partial N_1}{\partial t} \geq d\frac{\partial^2 N_1}{\partial x^2} + \mu_1\left(\frac{U_1}{N_1}\right)N_1 - \rho N_1, & x \in (0, 1), t \geq t_2, \\ \frac{\partial U_1}{\partial t} \geq d\frac{\partial^2 U_1}{\partial x^2} + [f_1(R_2^*(x), \frac{U_1}{N_1}) - \rho]N_1 - \rho U_1, & x \in (0, 1), t \geq t_2, \\ \frac{\partial w}{\partial x}(0, t) = \frac{\partial w}{\partial x}(1, t) + \gamma w(1, t) = 0, & t \geq t_2, w = N_1, U_1. \end{cases} \quad (60)$$

Since $P^0 \in \mathbf{Y}_0$, it is not hard to show that $N_1(\cdot, t_2) > 0$ and $U_1(\cdot, t_2) > 0$, and hence, there exists an $a_2 > 0$ such that

$$(N_1(\cdot, t_2), U_1(\cdot, t_2)) \geq (a_2\phi_1^\rho(\cdot), a_2\varphi_1^\rho(\cdot)), \quad (61)$$

where $(\phi_1^\rho(x), \varphi_1^\rho(x))$ is the strongly positive eigenfunction associated with Λ_1^ρ . Let

$$(\hat{N}_1(x, t), \hat{U}_1(x, t)) = (a_2e^{\Lambda_1^\rho(t-t_2)}\phi_1^\rho(x), a_2e^{\Lambda_1^\rho(t-t_2)}\varphi_1^\rho(x)).$$

Then $(\hat{N}_1(x, t), \hat{U}_1(x, t))$ satisfies the following system

$$\begin{cases} \frac{\partial \hat{N}_1}{\partial t} = d \frac{\partial^2 \hat{N}_1}{\partial x^2} + \mu_1 \left(\frac{\hat{U}_1}{\hat{N}_1} \right) \hat{N}_1 - \rho \hat{N}_1, & x \in (0, 1), t \geq t_2, \\ \frac{\partial \hat{U}_1}{\partial t} = d \frac{\partial^2 \hat{U}_1}{\partial x^2} + [f_1(R_2^*(x), \frac{\hat{U}_1}{\hat{N}_1}) - \rho] \hat{N}_1 - \rho \hat{U}_1, & x \in (0, 1), t \geq t_2, \\ \frac{\partial w}{\partial x}(0, t) = \frac{\partial w}{\partial x}(1, t) + \gamma w(1, t) = 0, & t \geq t_2, w = \hat{N}_1, \hat{U}_1, \\ (\hat{N}_1(\cdot, t_2), \hat{U}_1(\cdot, t_2)) = (a_2 \phi_1^\rho(\cdot), a_2 \varphi_1^\rho(\cdot)). \end{cases} \quad (62)$$

From (60)-(62), and the comparison principle, it follows that for $t \geq t_2$ and $x \in [0, 1]$, we have

$$(N_1(x, t), U_1(x, t)) \geq (\hat{N}_1(x, t), \hat{U}_1(x, t)) = (a_2 e^{\Lambda_1^\rho(t-t_2)} \phi_1^\rho(x), a_2 e^{\Lambda_1^\rho(t-t_2)} \varphi_1^\rho(x)).$$

Since $\Lambda_1^\rho > 0$, it follows that $\lim_{t \rightarrow \infty} (N_1(\cdot, t), U_1(\cdot, t))$ is unbounded, contradicting (59). This contradiction completes the proof of the lemma. \square

Now we are in a position to show that if both of the semitrivial steady states exist and both of them are uniform weak repellers, then both of the intraguild prey and predator can coexist.

Theorem 3.7. *Assume $0 < d < \min\{d_{0,1}, d_{0,2}\}$ and $\Lambda_i^0 > 0$ for $i = 1, 2$. Then system (5)-(7) is uniformly persistent with respect to $(\mathbf{Y}_0, \partial \mathbf{Y}_0)$ in the sense that there is a constant $\eta > 0$ such that every solution*

$$(R(\cdot, t), N_1(\cdot, t), U_1(\cdot, t), N_2(\cdot, t), U_2(\cdot, t))$$

of (5)-(7) with $(R(\cdot, 0), N_1(\cdot, 0), U_1(\cdot, 0), N_2(\cdot, 0), U_2(\cdot, 0)) \in \mathbf{Y}_0$ satisfying

$$\liminf_{t \rightarrow \infty} N_i(\cdot, t) \geq \eta, \quad \forall i = 1, 2. \quad (63)$$

Furthermore, system (5)-(7) admits at least one (componentwise) positive steady-state solution $(\bar{R}(\cdot), \bar{N}_1(\cdot), \bar{U}_1(\cdot), \bar{N}_2(\cdot), \bar{U}_2(\cdot))$.

Proof. Recall that $\Psi_t : \mathbf{Y} \rightarrow \mathbf{Y}$ is the solution maps associated with system (5)-(7). By the strong maximum principle and the Hopf boundary lemma (see [29]), it follows that for any $P^0(\cdot) := (R^0(\cdot), N_1^0(\cdot), U_1^0(\cdot), N_2^0(\cdot), U_2^0(\cdot)) \in \mathbf{Y}_0$, we have

$$N_i(x, t, P^0(\cdot)) > 0, \quad \forall x \in [0, 1], t > 0, i = 1, 2,$$

that is, $\Psi_t \mathbf{Y}_0 \subseteq \mathbf{Y}_0$ for all $t \geq 0$.

Let $M_\partial := \{P^0 \in \partial \mathbf{Y}_0 : \Psi_t P^0 \in \partial \mathbf{Y}_0, \forall t \geq 0\}$, and $\omega(P^0)$ be the omega limit set of the orbit $O^+(P^0) := \{\Psi_t P^0 : t \geq 0\}$. We claim that

$$\omega(\psi) = \{E_0(\cdot)\} \cup \{E_1(\cdot)\} \cup \{E_2(\cdot)\}, \quad \forall \psi \in M_\partial.$$

Indeed, for any given $\psi \in M_\partial$, we have $\Psi(t)\psi \in \partial \mathbf{Y}_0$, $\forall t \geq 0$, that is, $N_1(\cdot, t, \psi) \equiv 0$ or $N_2(\cdot, t, \psi) \equiv 0$, for all $t \geq 0$. In the case where $N_1(\cdot, t, \psi) \equiv 0$ for all $t \geq 0$, it follows from Lemma 3.1 and Corollary 2 that $U_1(\cdot, t, \psi) \equiv 0$ for all $t \geq 0$. Thus, $(R(\cdot, t, \psi), N_2(\cdot, t, \psi), U_2(\cdot, t, \psi))$ satisfies system (8) with functions $\mu = \mu_2$ and $f = f_2$. By Theorem 2.4, we can conclude that either $\lim_{t \rightarrow \infty} (R(\cdot, t), N_2(\cdot, t), U_2(\cdot, t)) = (R_2^*(\cdot), N_2^*(\cdot), U_2^*(\cdot))$ or $\lim_{t \rightarrow \infty} (R(\cdot, t), N_2(\cdot, t), U_2(\cdot, t)) = (z(\cdot), 0, 0)$. In the case where $N_1(\cdot, \tau_0, \psi) \neq 0$ for some $\tau_0 > 0$, it follows from the maximum principle that $N_1(\cdot, t, \psi) > 0$ for all $t > \tau_0$. This implies that $N_2(\cdot, t, \psi) \equiv 0$, for all $t > \tau_0$, and hence, $U_2(\cdot, t, \psi) \equiv 0$. Thus, we see that $(R(\cdot, t, \psi), N_1(\cdot, t, \psi), U_1(\cdot, t, \psi))$ satisfies system (8) with functions $\mu = \mu_1$ and $f = f_1$ for all $t > \tau_0$. Using Theorem 2.4 again, it follows that either $\lim_{t \rightarrow \infty} (R(\cdot, t), N_1(\cdot, t), U_1(\cdot, t)) = (R_1^*(\cdot), N_1^*(\cdot), U_1^*(\cdot))$ or

$\lim_{t \rightarrow \infty} (R(\cdot, t), N_1(\cdot, t), U_1(\cdot, t)) = (z(\cdot), 0, 0)$. These discussions complete the proof of the above claim.

Define a continuous function $\mathbf{p} : \mathbf{Y} \rightarrow [0, \infty)$ by

$$\mathbf{p}(\phi) := \min\left\{\min_{x \in [0,1]} \phi_2(x), \min_{x \in [0,1]} \phi_4(x)\right\}, \quad \forall \phi := (\phi_1, \phi_2, \phi_3, \phi_4, \phi_5) \in \mathbf{Y}.$$

By the maximum principle and the Hopf boundary lemma (see [29]), we see that $\mathbf{p}^{-1}(0, \infty) \subseteq \mathbf{Y}_0$ and \mathbf{p} has the property that if $\mathbf{p}(\phi) > 0$ or $\phi \in \mathbf{Y}_0$ with $\mathbf{p}(\phi) = 0$, then $\mathbf{p}(\Psi(t)\phi) > 0$, $\forall t > 0$. That is, \mathbf{p} is a generalized distance function for the semiflow $\Psi(t) : \mathbf{Y} \rightarrow \mathbf{Y}$ (see, e.g., [34]).

By Lemma 3.1 and Corollary 2, the semiflow $\Psi_t : \mathbf{Y} \rightarrow \mathbf{Y}$ is point dissipative. Obviously, $\Psi_t : \mathbf{Y} \rightarrow \mathbf{Y}$ is compact, $\forall t > 0$. By [12, Theorem 3.4.8], it follows that $\Psi_t : \mathbf{Y} \rightarrow \mathbf{Y}$, $t \geq 0$, admits a global compact attractor. By Lemmas 3.2, 3.4 and 3.6, it follows that $\{E_i\}$ is isolated in \mathbf{Y} and $W^s(\{E_i\}) \cap \mathbf{p}^{-1}(0, \infty) = \emptyset$, where $W^s(\{E_i\})$ is the stable set of $\{E_i\}$, $\forall i = 0, 1, 2$ (see [34]). Further, it is easy to see that no subsets of $\{E_0(\cdot)\} \cup \{E_1(\cdot)\} \cup \{E_2(\cdot)\}$ forms a cycle in $\partial\mathbf{Y}_0$. By [34, Theorem 3], it follows that there exists an $\eta > 0$ such that

$$\min_{\psi \in \omega(\phi)} \mathbf{p}(\psi) > \eta, \quad \forall \phi \in \mathbf{Y}_0.$$

This implies that (63) holds.

By [20, Theorem 3.7 and Remark 3.10], it follows that $\Psi_t : \mathbf{Y}_0 \rightarrow \mathbf{Y}_0$ admits a global attractor A_0 . It then follows from [20, Theorem 4.7] that Ψ_t admits a steady-state solution $(\bar{R}(\cdot), \bar{N}_1(\cdot), \bar{U}_1(\cdot), \bar{N}_2(\cdot), \bar{U}_2(\cdot)) \in \mathbf{Y}_0$, and hence, $\bar{N}_i(\cdot) > 0$, $i = 1, 2$. Using Lemma 3.1, it is easy to conclude that $\bar{U}_i(\cdot) > 0$, $i = 1, 2$. By the maximum principle and the Hopf boundary lemma (see [29]), we can further show that $\bar{R}(\cdot) > 0$. Thus, $(\bar{R}(\cdot), \bar{N}_1(\cdot), \bar{U}_1(\cdot), \bar{N}_2(\cdot), \bar{U}_2(\cdot))$ is a positive steady state solution of (5)-(7). \square

Finally, we consider another interesting case where the semi-trivial solution $E_1(x)$ exists but $E_2(x)$ does not exist. That is, the intraguild prey can survive in the absence of predator, but the intraguild predator can not survive in the absence of prey. Then one can use similar arguments as in Theorem 3.7 to show that coexistence for system (5)-(7) is also possible provided that $E_1(x)$ is a uniform weak repeller.

Theorem 3.8. *Assume $0 < d_{0,2} < d < d_{0,1}$ and $\Lambda_2^0 > 0$. Then system (5)-(7) is uniformly persistent with respect to $(\mathbf{Y}_0, \partial\mathbf{Y}_0)$ in the sense that there is a constant $\varrho > 0$ such that every solution $(R(\cdot, t), N_1(\cdot, t), U_1(\cdot, t), N_2(\cdot, t), U_2(\cdot, t))$ of (5)-(7) with $(R(\cdot, 0), N_1(\cdot, 0), U_1(\cdot, 0), N_2(\cdot, 0), U_2(\cdot, 0)) \in \mathbf{Y}_0$ satisfying*

$$\liminf_{t \rightarrow \infty} N_i(\cdot, t) \geq \varrho, \quad \forall i = 1, 2.$$

Furthermore, system (5)-(7) admits at least one (componentwise) positive steady-state solution $(\check{R}(\cdot), \check{N}_1(\cdot), \check{U}_1(\cdot), \check{N}_2(\cdot), \check{U}_2(\cdot))$.

4. Numerical simulations. In this section, we present some results of our numerical simulations performed with Matlab. Numerical simulations of system (5)-(7) were implemented using Eq. (2) for the predation rate $g(N_1)$, Eq. (3) for the specific growth rate $\mu_i(Q_i)$, and Eq. (4) for uptake rate $f_i(R, Q_i)$.

The predator-prey interaction in system (5)-(7) is usually referred to ‘‘intraguild predation’’, in which *Ochromonas* (N_2) can act as an intraguild predator that consumes *Microcystis* (N_1) and competes with N_1 for ammonium (a nitrogen resource).

In contrast to intraguild predation, there is an alternative predator-prey interaction, “top-down predation”, when grown on nitrate (rather than ammonium). In the top-down predation, *Ochromonas* acts as a top-down predator in a linear food chain but does not compete for nitrate with *Microcystis*. In our numerical simulations of system (5)-(7), we always take the maximum nutrient uptake rate $a_{\max,2} = 24.0 \times 10^{-14} \text{ mol cell}^{-1} \text{ day}^{-1}$ to simulate that the intraguild prey suffered from both competition and predation by the intraguild predator (intraguild predation), and we take $a_{\max,2} = 0 \text{ mol cell}^{-1} \text{ day}^{-1}$ to simulate that the prey suffered from top-down predation only (top-down predation). Varying the values of $R^{(0)}$, d , and g_{\max} , respectively, we can discuss the effects of the nutrient supply concentration ($R^{(0)}$), the diffusion rate (d), and the maximum prey ingestion rate (g_{\max}) on the intraguild predation ($a_{\max,2} = 24.0 \times 10^{-14} \text{ mol cell}^{-1} \text{ day}^{-1}$) and top-down predation ($a_{\max,2} = 0 \text{ mol cell}^{-1} \text{ day}^{-1}$). The rest of the biological parameters are given in Table 4.1, which are similar to those used by the authors in [36]. Our numerical studies also confirm one of the predictions in [36] that prey abundances are suppressed much more strongly by intraguild predation than by the usual predator-prey interaction of a linear food chain.

TABLE 1. Common parameters used in intraguild predation and top-down predation.

Quantity	Value	Quantity	Value
γ	10 day^{-1}	$a_{\max,1}$	$12.0 \times 10^{-14} \text{ mol cell}^{-1} \text{ day}^{-1}$
K_1	$9.0 \times 10^{-7} \text{ mol l}^{-1}$	K_2	$6.5 \times 10^{-7} \text{ mol l}^{-1}$
$\mu_{\max,1}$	0.7 day^{-1}	$\mu_{\max,2}$	2.2 day^{-1}
$Q_{\min,1}$	$2.6 \times 10^{-14} \text{ mol cell}^{-1}$	$Q_{\min,2}$	$1.0 \times 10^{-13} \text{ mol cell}^{-1}$
$Q_{\max,1}$	$9.5 \times 10^{-14} \text{ mol cell}^{-1}$	$Q_{\max,2}$	$32.0 \times 10^{-13} \text{ mol cell}^{-1}$
b	2.37	K_0	$4.0 \times 10^8 \text{ cells l}^{-1}$

4.1. Effect of nutrient supply. At first, we focus on the effect of the nutrient supply ($R^{(0)}$) in intraguild predation versus top-down predation. We put $d = 0.12 \text{ day}^{-1}$, $g_{\max} = 53 \text{ cells cell}^{-1} \text{ day}^{-1}$, and the other parameters are given in Table 4.1. Varying the nutrient supply concentration $R^{(0)}$, we observe that enrichment of the shared nutrient reduces the abundance of the intraguild prey (see Fig. 4.2 (A)). More precisely, the abundance of the intraguild predator increases with the increasing of $R^{(0)}$, and the intraguild prey declined in density with increasing enrichment (see Fig. 4.1 (A, C) and Fig. 4.2 (A)). Moreover, the intraguild prey was suppressed to near extinction although the intraguild prey is the superior competitor for the shared resource (see Fig. 4.2 (A)).

For top-down predation, we observe the increase of the abundances of two species in the low level of enrichment. Enrichment of the shared nutrient eventually causes no obvious change in the abundances of two species in top-down predation (see Fig. 4.1 (B, D) and Fig. 4.2 (B)). Moreover, in contrast to the top-down predation, the numerical results indicate strong dominance by the intraguild predator and low intraguild prey abundance with the enrichment of the nutrient (see Fig. 4.2).

4.2. Effect of diffusion. To investigate the effect of the diffusion (d), we put $R^{(0)} = 2.0 \times 10^{-5} \text{ mol l}^{-1}$, $g_{\max} = 53 \text{ cells cell}^{-1} \text{ day}^{-1}$, and the other parameters

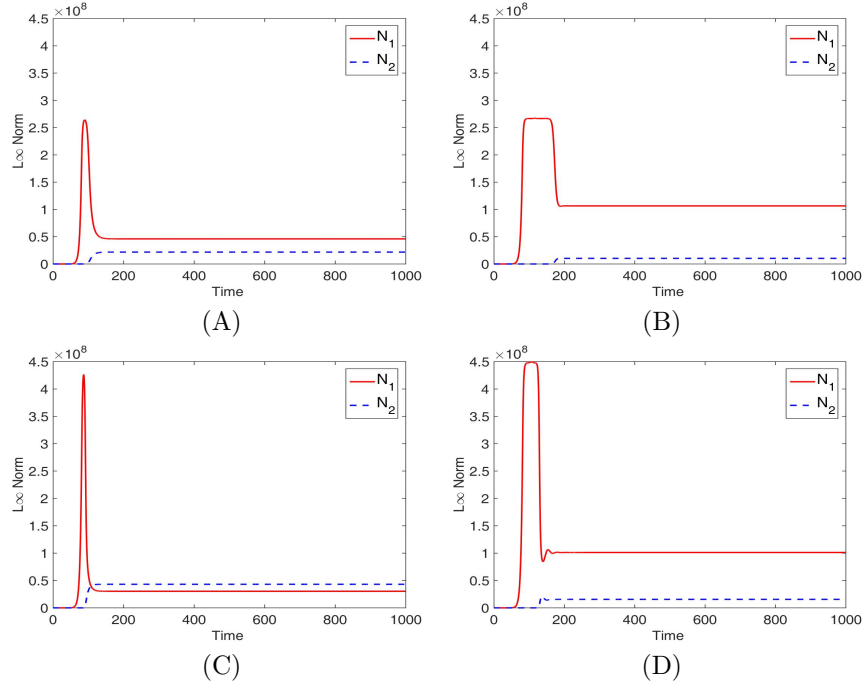


FIGURE 1. The effects of the nutrient supply concentration $R^{(0)}$: (A, C) Intraguild predation with $a_{\max,2} = 24.0 \times 10^{-14} \text{ mol cell}^{-1} \text{ day}^{-1}$, and (B, D) top-down predation with $a_{\max,2} = 0 \text{ mol cell}^{-1} \text{ day}^{-1}$. $R^{(0)} = 1.5 \times 10^{-5} \text{ mol l}^{-1}$ in (A, B), and $R^{(0)} = 2.5 \times 10^{-5} \text{ mol l}^{-1}$ in (C, D).

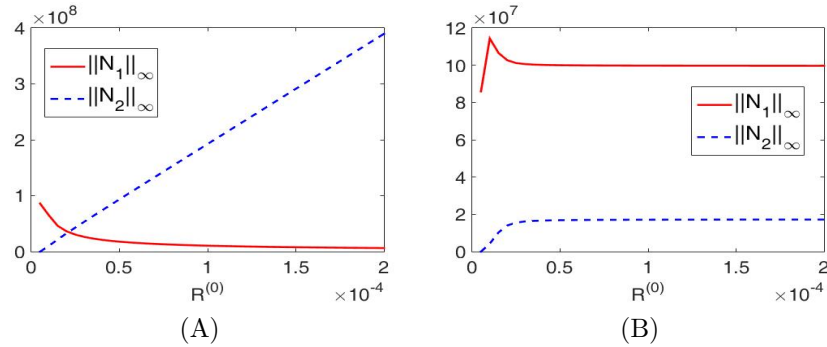


FIGURE 2. Bifurcation diagrams of positive steady state solutions to (5)-(7) with the bifurcation parameter $R^{(0)}$ ranging from 0.5×10^{-5} to $2.0 \times 10^{-4} \text{ mol l}^{-1}$. (A) Intraguild predation with $a_{\max,2} = 24.0 \times 10^{-14} \text{ mol cell}^{-1} \text{ day}^{-1}$, and (B) top-down predation with $a_{\max,2} = 0 \text{ mol cell}^{-1} \text{ day}^{-1}$.

are given in Table 4.1. Varying the diffusion rate d , we observe that the abundance of the intraguild predator increases with the decreasing of d , and the intraguild prey declines in density with the decreasing of d (see Fig. 4.3 (A, C, E)). Similar

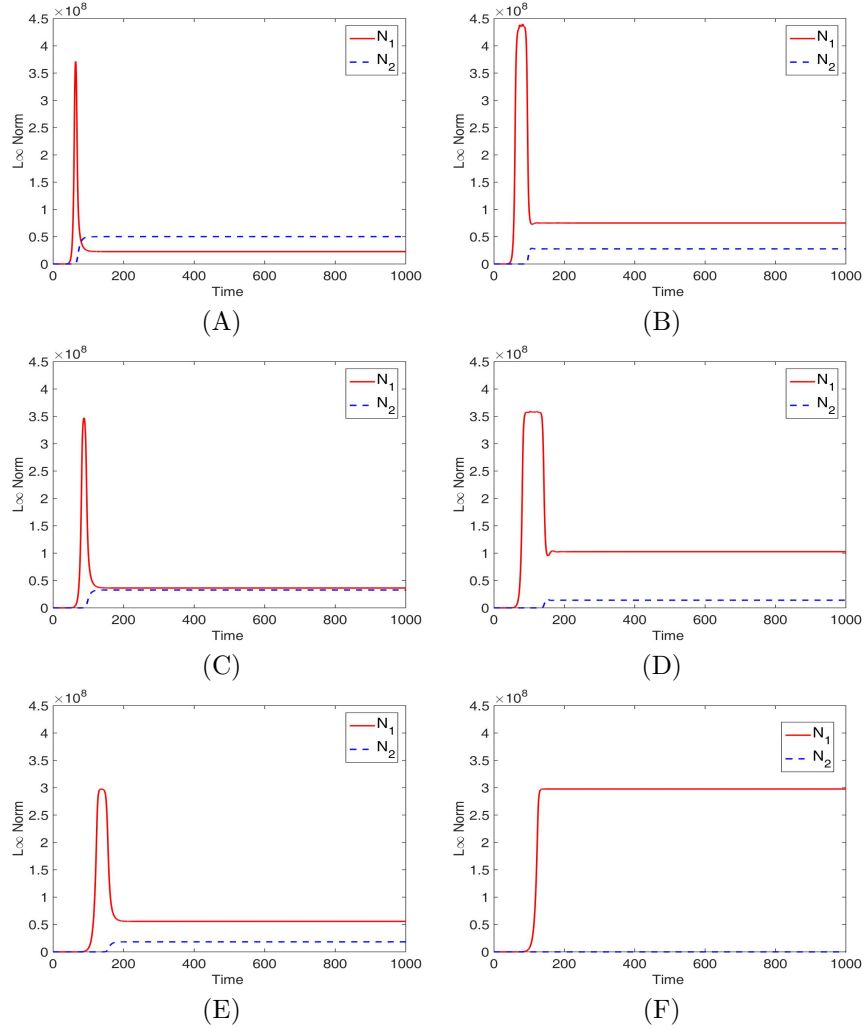


FIGURE 3. The effects of the diffusion rate d : (A, C, E) Intraguild predation with $a_{\max,2} = 24.0 \times 10^{-14} \text{ mol cell}^{-1} \text{ day}^{-1}$, and (B, D, F) top-down predation with $a_{\max,2} = 0 \text{ mol cell}^{-1} \text{ day}^{-1}$. $d = 0.08 \text{ day}^{-1}$ in (A, B), $d = 0.12 \text{ day}^{-1}$ in (C, D), and $d = 0.16 \text{ day}^{-1}$ in (E, F).

phenomena are observed in the population abundances of the two species for top-down predation (see Fig. 4.3 (B, D, F)).

In contrast to the top-down predation, the numerical results indicate that prey abundances are suppressed much more strongly by intraguild predation than by the classic predator-prey interaction of a linear food chain through grazing (see Fig. 4.3). Moreover, coexistence is more likely in systems with intraguild predation (see Fig. 4.3 (E, F)).

4.3. Effect of prey ingestion. To investigate the effect of the maximum ingestion rate (g_{\max}), we put $d = 0.12 \text{ day}^{-1}$, $R^{(0)} = 2.0 \times 10^{-5} \text{ mol}^{-1}$, and the other

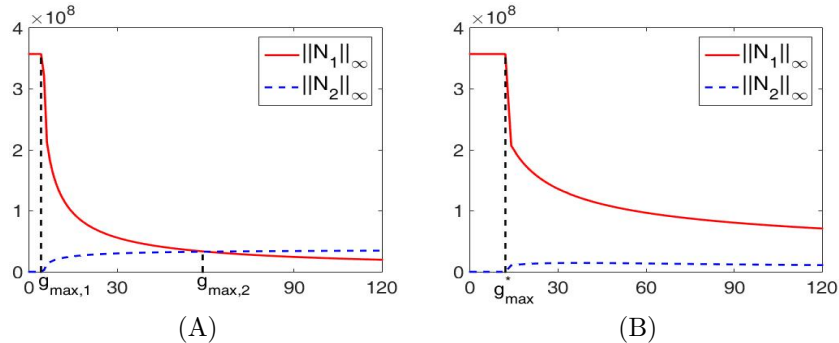


FIGURE 4. Bifurcation diagrams of positive steady state solutions to (5)-(7) with the bifurcation parameter g_{\max} ranging from 0 to 120 cells cell⁻¹ day⁻¹. (A) Intraguild predation with $a_{\max,2} = 24.0 \times 10^{-14}$ mol cell⁻¹ day⁻¹, and (B) top-down predation with $a_{\max,2} = 0$ mol cell⁻¹ day⁻¹.

parameters are given in Table 4.1. For top-down predation, numerical simulations indicate that there is a unique critical value of the maximum ingestion rate g_{\max}^* such that the top predator can coexist with the intermediate prey provided $g_{\max} > g_{\max}^*$ (see Fig. 4.4 (B)). Moreover, the intermediate prey is always dominated.

For intraguild predation, numerical simulations indicate that there exists two critical values $g_{\max,1} < g_{\max,2}$. If the maximum ingestion rate $g_{\max} > g_{\max,1}$, then the intraguild predator can invade successfully and coexist with the intraguild prey. Moreover, the gradual increase of the maximum ingestion rate may cause a gradual reduction in the abundance of intraguild prey. Increasing g_{\max} gradually, we observe that the dominance of the intraguild predator and the intraguild prey can be switched at some critical value $g_{\max,2}$ (see Fig. 4.4 (A)). We also observed that $g_{\max}^* > g_{\max,1}$, which means coexistence is more likely for the system with intraguild predation.

5. Discussion. This study proposed and analyzed a reaction-diffusion system (see (5)-(7)) modeling predator-prey interactions of mixotrophic plankton species and its autotrophic prey in an unstirred chemostat, in which the predator can also compete with its prey for one single nutrient resource that can be stored within individuals. Due to the singularity arising in the ratio of U_i/N_i with $(U_i, N_i) = (0, 0)$, $i = 1, 2$, it is worth noting that we cannot do linearization and bifurcation at the trivial or semitrivial steady states. This makes mathematical analysis more difficult and challenging.

Investigating the extinction/persistence of a single species is a preliminary step before we study the coexistence of two species. The dynamics of single species is governed by system (8), which is the same to the single population model proposed in [16]. The mathematical arguments in [16] only work when some specific parameters are relatively large or small, and results of extinction/persistence is left open for intermediate parameter values. In Theorem 2.4, we show that the threshold dynamics of system (8) is determined by the principal eigenvalue of the nonlinear eigenvalue problem (13), λ^0 , which is similar to the one studied in [17] (see also

[24]). We note that the eigenvalue λ^0 is affected by the physical transport characteristics of chemostat (i.e. the diffusivity d or the washout constant γ), the uptake rate, and the growth rate.

If both of the intraguild predator and intraguild prey can persist as a single species, then Theorem 2.4 guarantees that system (5)-(7) admits at least three steady states, that is a trivial steady state, and two semitrivial steady states. The trivial steady-state solution of (5)-(7), labeled $E_0(x)$, corresponds to the absence of both species. One of the semi-trivial steady-state solutions of (5)-(7), labeled $E_1(x)$, corresponds to the presence of the intraguild prey and the absence of the intraguild predator. The other semi-trivial steady-state solution of (5)-(7), labeled $E_2(x)$, corresponds to the presence of the intraguild predator and the absence of the intraguild prey. In Lemma 3.4, we show that the semitrivial steady state $E_1(x)$ is invisable by the missing intraguild predator if $\Lambda_2^0 > 0$, where Λ_2^0 is the principal eigenvalue of system (42). Thus, the invasibility of $E_1(x)$ depends on the physical transport characteristics of chemostat, the uptake rate of the intraguild predator, the growth rate of the intraguild predator, and the predation rate. In Lemma 3.6, we show that the semitrivial steady state $E_2(x)$ is invisable by the missing intraguild prey if $\Lambda_1^0 > 0$, where Λ_1^0 is the principal eigenvalue of system (52). Thus, the invasibility of $E_2(x)$ depends on the physical transport characteristics of chemostat, the uptake rate of the intraguild prey, and the growth rate of the intraguild prey. When both of the semitrivial steady states are invisable by the missing competitor, we theoretically prove that there is at least one positive steady states representing coexistence of the intraguild predator and the intraguild prey (Theorem 3.7). We also study another interesting case where the intraguild prey can persist as a single species, while the intraguild predator cannot survive as a single species. For this case, we can also show that coexistence of system (5)-(7) is possible when the semitrivial steady state $E_1(x)$ is invisable by the missing intraguild predator (see Theorem 3.8). We perform numerical studies which can confirm our analytical results. Finally, we point out that the local stability of the semi-trivial solutions $E_2(x)$ (resp. $E_1(x)$) have been rigorously discussed in the Appendix section of [26]. It was shown that $E_2(x)$ (resp. $E_1(x)$) is locally asymptotically stable if $\Lambda_1^0 < 0$ (resp. $\Lambda_2^0 < 0$), and the possibility of bistability for system (5)-(7) was studied by the authors in [26].

If we put $g(N_1) \equiv 0$ in system (5)-(7) (i.e., we put $g_{\max} = 0$ in (2)), then system (5)-(7) will become the system without predation investigated in [16]. The authors in [16] used another mathematical approach to show that coexistence is possible for the system without predation, however, our simulation indicates that coexistence only occurs for a narrow range of parameter values in their system. Further, our numerical simulations also confirm that intraguild predation can promote the diversity of species in a community (5)-(7). This observation is similar to the spatial homogeneous system (1). In Fig. 4.4 (A), we found that the prey (N_1) can persist, but the predator (N_2) will die out if the mechanism of predation is removed (i.e., $g_{\max} = 0$). Increasing the value of g_{\max} , we observed that the intraguild predator and the intraguild prey can coexist when g_{\max} belongs to a specific interval.

Besides intraguild predation, top-down predation is another significant predator-prey interaction. When the nitrogen resource (R) is nitrate rather than ammonium, *Ochromonas* acts as a top-down predator in a linear food chain but does not compete for nitrate with *Microcystis* (the prey) [36]. Mathematically, the governing system of top-down predation is the one with the substitution $f_2(R, \frac{U_2}{N_2}) \equiv 0$ into system

(5)-(7). We note that the analysis of the model with top-down predation is similar to those presented in this paper. In Section 4, we also numerically compare intraguild predation with top-down predation. Our simulation studies indicate that population densities of prey are suppressed much more strongly by intraguild predation than by top-down predation. Those results are parallel to the intraguild predation theory for the spatial homogeneous system (1), which is indeed one of the main predictions in [36].

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