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Non-existence of non-constant positive steady states of two Holling type-II predator–prey systems: Strong interaction case

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ABSTRACT

We prove the non-existence of non-constant positive steady state solutions of two reaction–diffusion predator–prey models with Holling type-II functional response when the interaction between the predator and the prey is strong. The result implies that the global bifurcating branches of steady state solutions are bounded loops.

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1. Introduction

For spatial biological systems, the positive feedback control between consumer (predator, plants) and limited resources (prey, water, nutrients) suggests a reaction–diffusion system with consumer–resource (predator–prey) type interaction:

$$u_t = D_u \Delta u + f(u) - b\phi(u)v, \quad v_t = D_v \Delta v + g(v) + c\phi(u)v, \tag{1.1}$$

where $u(x, t)$ and $v(x, t)$ are the densities of the prey and predator respectively, D_u and D_v are the diffusion coefficients, f and g represent the self-growth of the two species, and $\phi(u)$ is the predator functional response, see [2,26,27,29]. In consideration of the limited ability of a predator to consume its prey, general forms of functional response of the predator $\phi(u)$ were introduced by Holling [11], and $\phi(u)$ is a positive and nondecreasing function of prey density. Among many possible choices of $\phi(u)$, the Holling type-II functional response is most commonly used in the ecological literature, which is defined by

$$\phi(u) = \frac{u}{1 + Ku}, \tag{1.2}$$

where K is a positive constant measuring the ability of a generic predator to kill and consume a generic prey. Predator–prey system with Holling type-II functional response is also called Rosenzweig–MacArthur model, which is widely used in real-life ecological applications [35].

It has been shown that the diffusive predator–prey system is capable to generate complex spatiotemporal patterns. Levin and Segel [20] pointed out that diffusive instabilities might explain instances of spatial irregularity in natural communities in which the prey population survived in a clumped pattern forced upon it by the predator’s more rapid dispersion that caused the initial breakdown of the uniform state. An example is the observed patchy distribution of plankton in the ocean, and other different dispersal ability of this sort has been documented in arthropod predator–prey systems characterized by patchy distribution patterning both in laboratory (Huffaker [13]) and field experiments (Kareiva, Odell [16,17]). Medvinsky et al. [24] used (1.1) with Holling type-II functional response as a simplest possible mathematical model to investigate the pattern formation of a phytoplankton–zooplankton system, and their numerical studies show a rich spectrum of spatiotemporal patterns.

In a recent analytic approach by Yi, Wei and Shi [41], the system (1.1) with Holling type-II functional response is considered, that is,

$$\begin{cases} u_t - d_1 \Delta u = u \left(1 - \frac{u}{k} \right) - \frac{muv}{u + 1} & \text{in } \Omega, t > 0, \\ v_t - d_2 \Delta v = -\theta v + \frac{muv}{u + 1} & \text{in } \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0 & \text{on } \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0 & \text{in } \Omega. \end{cases} \tag{1.3}$$

Here Ω is a bounded domain in \mathbf{R}^N ($N \geq 1$) with a smooth boundary $\partial\Omega$. The two unknown functions $u(x, t)$ and $v(x, t)$ represent the spatial distribution density of the prey and predator, respectively. The constants d_1, d_2 are the diffusion coefficients of the corresponding species and are hence assumed to be positive, k accounts for the carrying capacity of the prey, θ is the death rate of the predator, and m can be regarded as the measure of the interaction strength between of the two species. Moreover, ν is the outward unit normal vector on $\partial\Omega$ and $\partial_\nu = \partial/\partial\nu$, and we impose a homogeneous Neumann type boundary condition, which implies that (1.3) is a closed system and there is no flux across the boundary $\partial\Omega$.

It was shown that system (1.3) possesses complex spatiotemporal dynamics via a sequence of bifurcation of spatial nonhomogeneous periodic orbits and spatial nonhomogeneous steady state solutions [41]. It is well known that when m is larger than a threshold value, the corresponding ODE

system has a periodic orbit [12], and the results in [41] suggests a much richer oscillatory and stationary dynamics. The periodic patterns found here are “self-organized” in the sense that the system parameters in (1.3) are all spatially and temporally constant. On the other hand, it is known that spatial heterogeneity may induce complex spatiotemporal patterns [6,7]. We refer to Du and Shi [6] for a comprehensive review on mathematical results for diffusive predator–prey systems.

In this article, we show that in contrast to the complex dynamics in the case of intermediate range of parameter m , the system (1.3) has only the constant steady state solution when m is sufficiently large. Biologically large m corresponds to strong interaction between the prey and predator species. To be more precise, we consider the steady state equation of (1.3), which is a coupled elliptic system:

$$\begin{cases} -d_1 \Delta u = u \left(1 - \frac{u}{k} \right) - \frac{mu v}{u + 1} & \text{in } \Omega, \\ -d_2 \Delta v = -\theta v + \frac{mu v}{u + 1} & \text{in } \Omega, \\ \partial_\nu u = \partial_\nu v = 0 & \text{on } \partial\Omega. \end{cases} \tag{1.4}$$

The system (1.4) has three non-negative constant solutions: $(0, 0)$, $(k, 0)$ and (λ, v_λ) , where

$$\lambda = \frac{\theta}{m - \theta} \quad \text{and} \quad v_\lambda = \frac{(k - \lambda)(1 + \lambda)}{km}.$$

The positive constant solution (λ, v_λ) exists if and only if

$$m > \frac{(1 + k)\theta}{k}. \tag{1.5}$$

It was proved in [18,41] that $(k, 0)$ is globally asymptotically stable when $\lambda \geq k$, and (λ, v_λ) is globally asymptotically stable when $\lambda \in [k - 1, k)$. Hence, (1.4) has no non-constant positive solution if $\lambda \geq k - 1$ is satisfied. Thus, from now on, we always assume $0 < \lambda < k - 1$ holds true. Our main result is

Theorem 1.1. *Suppose that $N \leq 3$. For any given constants $d_1, d_2, \theta > 0, k > 1$ and a fixed domain Ω , there exists a positive constant M_1 , which depends only on d_1, d_2, k, θ and Ω , such that (1.4) has no non-constant positive solution provided that $m \geq M_1$.*

It is known that when m is large, then (1.3) has an unstable constant coexistence steady state solution (λ, v_λ) , and a unique spatial homogeneous limit cycle. Hence Theorem 1.1, together with the instability of (λ, v_λ) , strongly suggests that temporal oscillatory patterns dominate the dynamics in the strong predator–prey interaction. An important corollary of Theorem 1.1 is that the global bifurcation branches of steady state solutions of (1.3) obtained in [41] are bounded in the space of (m, u, v) , hence they are “loops” instead of unbounded branches, see more details in Section 5. This provides another crucial step towards a complete understanding of the dynamics of (1.3).

Our analysis can also be carried over to a similar system in which the predator has alternate food source, and the corresponding steady state system is

$$\begin{cases} -d_1 \Delta u = u(a - u) - \frac{mu v}{u + 1} & \text{in } \Omega, \\ -d_2 \Delta v = v(d - v) + \frac{mu v}{u + 1} & \text{in } \Omega, \\ \partial_\nu u = \partial_\nu v = 0 & \text{on } \partial\Omega, \end{cases} \tag{1.6}$$

where the constant d may be non-positive.

Theorem 1.2. *Let $N \leq 3$. For any given d_1, d_2, a, d and Ω , there exists a positive constant M_2 , which depends only on d_1, d_2, a, d and Ω , such that if $m \geq M_2$, then (1.6) has no non-constant positive solution when $d \leq 0$ and has no positive solution when $d > 0$.*

We remark that, although it has been shown in this work that Theorems 1.1 and 1.2 hold only for $N \leq 3$ due to mathematical difficulties, we suspect these results continue to be true for arbitrary spatial dimensions. Of course, the above conclusions are sufficient as far as the possible application in biology is concerned. Also we comment that although our analysis requires $m \rightarrow \infty$, numerical investigation and calculation of bifurcation points in [41] suggest that the threshold value m_0 for the non-existence of non-constant steady state solutions is still in the biologically realistic range.

In the remaining part of this paper, we shall carry out the detailed proof of Theorems 1.1 and 1.2. Some preliminaries are prepared in Section 2; the cases of (1.4) and (1.6) are discussed in Section 3 and Section 4, respectively; and finally in Section 5, we give some remarks on the implications of our results to the global bifurcations of steady state solutions to the related reaction–diffusion systems.

2. Some preliminaries

In this section, let us first recall some general results for elliptic equations; these results will be frequently used later in obtaining *a priori* upper and lower bounds for non-negative solutions to (1.4) and (1.6). Some of these results can be found in [30] or [32].

To begin with, we recall a local result for weak super-solution of linear elliptic equations from [21] (also see, for example, [8, Theorem 8.18]).

Lemma 2.1. *Let Ω be a bounded Lipschitz domain in \mathbf{R}^N , and let Λ be a non-negative constant. Suppose that $z \in W^{1,2}(\Omega)$ is a non-negative weak solution of the inequalities*

$$0 \leq -\Delta z + \Lambda z \quad \text{in } \Omega, \quad \partial_\nu z \leq 0 \quad \text{on } \partial\Omega.$$

Then, for any $q \in [1, N/(N - 2))$, there exists a positive constant C_0 , depending only on q, Λ and Ω , such that

$$\|z\|_q \leq C_0 \inf_{\Omega} z.$$

Next is a Harnack inequality for weak solutions, whose strong form was obtained in [22].

Lemma 2.2. *Let Ω be a bounded Lipschitz domain in \mathbf{R}^N , and let $c(x) \in L^q(\Omega)$ for some $q > N/2$. If $z \in W^{1,2}(\Omega)$ is a non-negative weak solution of the boundary value problem*

$$\Delta z + c(x)z = 0 \quad \text{in } \Omega, \quad \partial_\nu z = 0 \quad \text{on } \partial\Omega,$$

then there is a positive constant C_1 , determined only by $\|c\|_q, q$ and Ω such that

$$\sup_{\Omega} z \leq C_1 \inf_{\Omega} z.$$

Finally, we cite a strong maximum principle (see, e.g., Proposition 2.2 in [23]), and the weak form of the analogue can be found in [21,32].

Lemma 2.3. *Suppose that Ω is smooth and $g \in C(\overline{\Omega} \times \mathbf{R}^1)$. Assume that $z \in C^2(\Omega) \cap C^1(\overline{\Omega})$ and satisfies*

$$\Delta z(x) + g(x, z(x)) \geq 0 \quad \text{in } \Omega, \quad \partial_\nu z \leq 0 \quad \text{on } \partial\Omega.$$

If $z(x_0) = \max_{\overline{\Omega}} z(x)$, then $g(x_0, z(x_0)) \geq 0$.

We also prove a non-existence result on a Lotka–Volterra type predator–prey model:

Lemma 2.4. Assume that $d_1, d_2, \theta > 0$ and Ω are fixed. Then the system

$$\begin{cases} -d_1 \Delta w = w - wz & \text{in } \Omega, \\ -d_2 \Delta z = -\theta z + wz & \text{in } \Omega, \\ \partial_\nu w = \partial_\nu z = 0 & \text{on } \partial\Omega, \end{cases} \tag{2.1}$$

has a unique positive solution $(w, z) = (\theta, 1)$.

Proof. We adopt a technique of Lyapunov function to derive the desired result. To this end, we consider the corresponding reaction–diffusion system of (2.1):

$$\begin{cases} w_t - d_1 \Delta w = w - wz & \text{in } \Omega \times (0, \infty), \\ z_t - d_2 \Delta z = -\theta z + wz & \text{in } \Omega \times (0, \infty), \\ \partial_\nu w = \partial_\nu z = 0 & \text{on } \partial\Omega \times (0, \infty), \\ w(x, 0) = w_0(x) \geq 0, \neq 0 & \text{in } \Omega, \\ z(x, 0) = z_0(x) \geq 0, \neq 0 & \text{in } \Omega. \end{cases} \tag{2.2}$$

Here, the admissible initial data $w_0(x), z_0(x)$ are continuous functions on $\overline{\Omega}$. The standard theory for parabolic equations shows that the unique solution $(w(x, t), z(x, t))$ of (2.2) exists and is positive on $\overline{\Omega} \times [0, \infty)$.

Notice that $(\theta, 1)$ is the unique constant positive steady state solution to (2.2), and we denote this trivial solution by (w^*, z^*) . We construct a well-known Lyapunov function as follows: for $(w, z) \in [W^{1,2}(\Omega)]^2$,

$$V(w, z) = \int_{\Omega} E(w(x), z(x)) \, dx,$$

with

$$E(w, z) = \int \frac{w - w^*}{w} \, dw + \int \frac{z - z^*}{z} \, dz.$$

Using some straightforward calculation, for a solution $(w(x, t), z(x, t))$ of (2.2) we have

$$\begin{aligned} \frac{dV}{dt} &= \int_{\Omega} \left\{ \frac{w - w^*}{w} w_t + \frac{z - z^*}{z} z_t \right\} \, dx \\ &= \int_{\Omega} \left\{ \frac{w - w^*}{w} (d_1 \Delta w + w - wz) + \frac{z - z^*}{z} (d_2 \Delta z - \theta z + wz) \right\} \, dx \\ &= \int_{\Omega} \left\{ -d_1 \frac{w^* |\nabla w|^2}{w^2} - d_2 \frac{z^* |\nabla z|^2}{z^2} + (w - w^*)(1 - z) - (z - z^*)(\theta - w) \right\} \, dx \\ &= \int_{\Omega} \left\{ -d_1 \frac{w^* |\nabla w|^2}{w^2} - d_2 \frac{z^* |\nabla z|^2}{z^2} \right\} \, dx. \end{aligned}$$

Therefore, V is a Lyapunov functional for the system (2.2), namely, for any $t > 0$, $V'(t) \leq 0$ along trajectories. Let $C = \{(w, z) \in [W^{1,2}(\Omega)]^2 : V'(t) = 0\}$. Then from proofs in [3,19,36], the orbit $\{(w(\cdot, t), z(\cdot, t)) : t \geq 0\}$ is compact, and consequently $(w(\cdot, t), z(\cdot, t)) \rightarrow C$ as $t \rightarrow \infty$ from LaSalle’s invariance principle (see Theorem 4.3.4 in [10]).

Now, assume that $(w(x), z(x))$ is a positive solution of (2.1), then $(w(x), z(x)) \in C$. But $C = \{(w, z) \in [W^{1,2}(\Omega)]^2: w(x) \equiv w_0, z(x) \equiv z_0\}$ (the subspace of constant functions), and the only equilibrium solution of (2.2) in C is $(w(x), z(x)) = (w^*, z^*) = (\theta, 1)$. The proof is thus complete. \square

Remark 2.1. The dynamics of the system (2.2) is of independent interest. The constant equilibrium (w^*, z^*) is not globally asymptotically stable for the system (2.2). The set C is a 2-dimensional invariant subspace for (2.2), and there are infinitely many spatially homogeneous periodic orbits on C with common center (w^*, z^*) . Each spatially homogeneous periodic orbit can be the ω -limit set of a solution to (2.2). In fact, for each spatially homogeneous periodic orbit, there exists a codimension-2 invariant manifold in $[W^{1,2}(\Omega)]^2$ which converges to the periodic orbit with exponential attracting rate. The convergence to periodic solution of (2.2) has been shown in Rothe [36], and the constant equilibrium is globally asymptotically stable if there is a damping term (crowding effect) in the system, see Hastings [9] and Leung [19].

3. Proof of Theorem 1.1

First we recall the following *a priori* estimates from [41]:

Lemma 3.1. *Suppose that $d_1, d_2, \theta > 0, k > 1, \Omega$ is any bounded smooth domain, and $(u(x), v(x))$ is a non-negative $W^{1,2}(\Omega)$ solution to (1.4). Then either $(u, v) = (0, 0)$, or $(u, v) = (k, 0)$ or for all $x \in \bar{\Omega}$,*

$$0 < u(x) < k \quad \text{and} \quad 0 < v(x) < \frac{k(d_2 + \theta d_1)}{\theta d_2}.$$

It is easily noted that, by virtue of Lemma 3.1, we can apply the standard regularity theory of elliptic equations and the embedding theorems (see, e.g., [8]) to claim that any non-negative $W^{1,2}(\Omega)$ solution to (1.4) must be a classical one, that is, $u, v \in C^2(\Omega) \cap C^1(\bar{\Omega})$ and (u, v) satisfies (1.4). Furthermore, if $u \geq 0, \neq 0$ and $v \geq 0, \neq 0$ in Ω , then the well-known maximum principle and Hopf boundary lemma guarantee that $u, v > 0$ on $\bar{\Omega}$.

On the other hand, one should observe that $(\lambda, v_\lambda) \rightarrow (0, 0)$ as $m \rightarrow \infty$. As a consequence, to derive a positive lower bound for any positive solution of (1.4), the restriction for the upper bound of m is necessary. With this simple observation, for bounded m , the authors in [41] also obtained the following lower estimates, which are similar to Theorem 3.4 in [18].

Lemma 3.2. *Suppose that $d_1, d_2, \theta > 0, k > 1$ and Ω is fixed, and $\theta k / (k - 1) < m \leq M$ for some $M > 0$. Then, there exists a positive constant \underline{C} depending possibly on d_1, d_2, θ, k, M and Ω , such that any positive solution $(u(x), v(x))$ of (1.4) satisfies*

$$u(x), v(x) \geq \underline{C}, \quad \text{for } x \in \bar{\Omega}.$$

In order to establish more precise estimates of lower bounds for positive solutions (u, v) to (1.4), we make use of the scaling

$$w = mu \quad \text{and} \quad z = mv, \tag{3.1}$$

and thus the original system (1.4) becomes

$$\begin{cases} -d_1 \Delta w = w \left(1 - \frac{u}{k} \right) - \frac{wz}{u+1} & \text{in } \Omega, \\ -d_2 \Delta z = -\theta z + \frac{wz}{u+1} & \text{in } \Omega, \\ \partial_\nu w = \partial_\nu z = 0 & \text{on } \partial\Omega. \end{cases} \tag{3.2}$$

Based on the above preparation, we are ready to derive the *a priori* lower bounds for any positive solutions to (1.4). More precisely, we have

Theorem 3.1. *Suppose that $N \leq 3$, and let $d_1, d_2, \theta > 0, k > 1$ and Ω be fixed. Denote (u_m, v_m) to be a positive solution of (1.4), then there exist two positive constants \underline{C} and \bar{C} , which depend only on d_1, d_2, k, θ and Ω , such that*

$$\underline{C} \leq mu_m(x), mv_m(x) \leq \bar{C}, \quad \text{for } x \in \bar{\Omega}.$$

Moreover, as $m \rightarrow \infty$, we have

$$(mu_m, mv_m) \rightarrow (\theta, 1) \quad \text{in } C^2(\bar{\Omega}).$$

Proof. From Lemmas 3.1 and 3.2, it remains to verify our conclusion in the case of $m \rightarrow \infty$. Furthermore, owing to the scaling (3.1), it is sufficient to consider the system (3.2). Firstly, from the second equation of (3.2), it follows that

$$-d_2 \Delta z_m + \theta z_m > 0 \quad \text{in } \Omega, \quad \partial_\nu z_m = 0 \quad \text{on } \partial\Omega.$$

Hence we can use Lemma 2.1 to get that

$$\|z_m\|_q \leq C_0 \inf_{\Omega} z_m, \tag{3.3}$$

where $q \geq 1$ can be arbitrarily large if $N = 1$ or $2, q \in (N/2, N/(N - 2))$ if $N = 3$, and C_0 depends only on q, d_2, θ and Ω .

We now claim that $\|z_m\|_q$ must be bounded as $m \rightarrow \infty$. We prove it by contradiction. Suppose that it is not true, then there exists a sequence $\{m_n\}_{n=1}^\infty$ with $m_n \rightarrow \infty$ as $n \rightarrow \infty$, and the corresponding sequence of positive solutions (u_{m_n}, v_{m_n}) of (1.4) for $m = m_n$, which is denoted by (u_n, v_n) for convenience, such that $(w_n, z_n) = (m_n u_n, m_n v_n)$ satisfies

$$\begin{cases} -d_1 \Delta w_n = w_n \left(1 - \frac{u_n}{k} \right) - \frac{w_n z_n}{u_n + 1} & \text{in } \Omega, \\ -d_2 \Delta z_n = -\theta z_n + \frac{w_n z_n}{u_n + 1} & \text{in } \Omega, \\ \partial_\nu w_n = \partial_\nu z_n = 0 & \text{on } \partial\Omega \end{cases} \tag{3.4}$$

and

$$\|z_n\|_q \rightarrow \infty, \quad \text{as } n \rightarrow \infty.$$

It follows from (3.3) that

$$z_n \rightarrow \infty \quad \text{uniformly on } \bar{\Omega}, \quad \text{as } n \rightarrow \infty.$$

On the other hand, integrating the equation of w_m in (3.4) over Ω and using the no-flux boundary condition, we obtain that

$$\int_{\Omega} w_n \left(1 - \frac{u_n}{k} - \frac{z_n}{u_n + 1} \right) dx = 0, \tag{3.5}$$

which leads to a contradiction since $u_n \leq k$. Consequently, for a given large M , we can find a positive constant C_2 , determined only by q, d_2, θ, M and Ω , such that for $m \geq M$,

$$\|z_m\|_q \leq C_2. \tag{3.6}$$

Now, for the chosen q as above, combining with Lemma 3.1 we find that

$$\left\| 1 - \frac{u_m}{k} - \frac{z_m}{u_m + 1} \right\|_q \leq C_3, \tag{3.7}$$

for $m \geq M$ and some positive constant C_3 , which depends only on q, d_2, θ, M and Ω . Therefore, if $m \geq M$, by virtue of (3.7), we apply Lemma 2.2 to the equation of w_m in (3.4) to see that

$$\sup_{\Omega} w_m \leq C_4 \inf_{\Omega} w_m. \tag{3.8}$$

Here, C_4 depends only on $d_1, d_2, k, \theta, q, M$ and Ω . Using (3.8), we claim that there is a positive constant C_5 such that when $m \geq M$, the following holds:

$$\sup_{\Omega} w_m \leq C_5. \tag{3.9}$$

In fact, suppose that (3.9) does not hold, as before, we can find a sequence of $\{m_n\}_{n=1}^{\infty}$ with $m_n \rightarrow \infty$ as $n \rightarrow \infty$, and an associated sequence of positive solutions (w_n, z_n) of (3.4), such that $\sup_{\Omega} w_n \rightarrow \infty$ as $n \rightarrow \infty$. Hence, (3.8) implies that $w_n \rightarrow \infty$ uniformly on $\overline{\Omega}$ as $n \rightarrow \infty$. We then integrate the second equation in (3.4) to obtain

$$\int_{\Omega} z_n \left(\theta - \frac{w_n}{u_n + 1} \right) dx = 0, \tag{3.10}$$

which again is a contradiction. This verifies (3.9).

Next, due to the Harnack inequality again (namely, Lemma 2.2), by the equation of z_m , one immediately sees that

$$\sup_{\Omega} z_m \leq C_6 \inf_{\Omega} z_m \tag{3.11}$$

if $m \geq M$. Here, C_6 depends on $d_1, d_2, k, \theta, q, M$ and Ω . In a similar manner, together with (3.5), we can derive the upper bound of z_m : there is a positive constant C_7 depending on $d_1, d_2, k, \theta, q, M$ and Ω such that

$$\sup_{\Omega} z_m \leq C_7, \quad \text{for } m \geq M. \tag{3.12}$$

In what follows, we are going to establish the positive lower bounds for (w_m, z_m) . That is, there is a positive constant C_8 , which depends only on $d_1, d_2, k, \theta, q, M$ and Ω , such that

$$\inf_{\Omega} w_m \geq C_8 \quad \text{and} \quad \inf_{\Omega} z_m \geq C_8, \quad \text{for } m \geq M. \tag{3.13}$$

Suppose that (3.13) is false, it is necessary that there is a sequence $m_n \rightarrow \infty$ as $n \rightarrow \infty$ such that

$$\inf_{\Omega} w_n \rightarrow 0 \quad \text{or} \quad \inf_{\Omega} z_n \rightarrow 0, \quad \text{as } n \rightarrow \infty.$$

Then, (3.8) and (3.11) imply that

$$w_n \rightarrow 0 \quad \text{or} \quad z_n \rightarrow 0 \quad \text{uniformly on } \overline{\Omega}, \text{ as } n \rightarrow \infty.$$

In any case, we always have $u_n = w_n/m_n \rightarrow 0$ uniformly on $\overline{\Omega}$. If $w_n \rightarrow 0$ uniformly on $\overline{\Omega}$, then (3.10) causes a contradiction. If the latter case happens, a contradiction is arrived by using Eq. (3.5). Hence (3.13) holds. Now we have deduced the positive upper and lower bounds of any positive solution (w_m, z_m) to (3.2), which finishes the proof of the first part of our conclusion in Theorem 3.1.

Finally, we determine the asymptotic behavior of any positive solution (w_m, z_m) to (3.2) as $m \rightarrow \infty$. Since $u_m \rightarrow 0$ uniformly on $\overline{\Omega}$ and both w_m and z_m have positive upper and lower bounds for any large m , by the standard regularity theory for elliptic equations and the embedding theorems, it is clear to see that $(w_m, z_m) \rightarrow (w_0, z_0)$ in $C^2(\overline{\Omega})$ as $m \rightarrow \infty$, where (w_0, z_0) is a positive solution of (2.1). By Lemma 2.4, we know $(w_0, z_0) = (\theta, 1)$. This ends our proof of Theorem 3.1. \square

We now present the proof of Theorem 1.1.

Proof of Theorem 1.1. We shall use the implicit function theorem to derive the result. For this purpose, we set $\rho = 1/m$, and we rewrite (3.2) as

$$\begin{cases} -d_1 \Delta w = w \left(1 - \frac{\rho w}{k} \right) - \frac{wz}{\rho w + 1} & \text{in } \Omega, \\ -d_2 \Delta z = -\theta z + \frac{wz}{\rho w + 1} & \text{in } \Omega, \\ \partial_\nu w = \partial_\nu z = 0 & \text{on } \partial\Omega. \end{cases} \tag{3.14}$$

Theorem 3.1 shows that the system (3.14) is a regular perturbation of (2.1) with $\rho \rightarrow 0$. Furthermore, by the routine computation for the linearized problem at point $(w^*, z^*) = (\theta, 1)$ for the reaction–diffusion system (2.2) as in Lemma 3.1 of [32], it is noted that (w^*, z^*) is non-degenerate in the sense that zero is not the eigenvalue of such linearized problem (but not locally linearly stable since $\pm i\sqrt{\theta}$ is a pair of conjugate imaginary eigenvalues of this linearized problem). Then, by the implicit function theorem and Theorem 3.1 again, we see that the constant positive solution is the unique positive solution of (3.14) when ρ is small enough. Equivalently, the original system (1.4) admits no non-constant positive solution if m is sufficiently large. This finishes the proof of Theorem 1.1. \square

4. Proof of Theorem 1.2

This section is devoted to the study of (1.6). First of all, we collect some existing results concerning (1.6) obtained in [5] (see also [6]).

Firstly, we analyze the distribution of constant positive solutions of (1.6). As pointed out in [5], the function

$$H(u) = \frac{(a - u)(1 + u)}{m} - \frac{mu}{1 + u}$$

turns out to be very useful. Actually, it is easy to observe that (u, v) is a constant positive solution of (1.6) if and only if u is a solution of $H(u) = d$ in the interval $(0, a)$. In what follows, we define d^* by

$$d^* = \max_{u \in [0, a]} H(u).$$

Note also that

$$\min_{u \in [0, a]} H(u) = H(a) = -\frac{am}{1 + a}.$$

By an elementary analysis of the curve $d = H(u)$, which is essentially cubic, the following result was given by Theorem 2.1 in [5].

Theorem 4.1. Let $m_2 = a^{-1}(1 + m^2)$ and

$$m_1 = \begin{cases} m_2 & \text{if } m^2 \leq 1, \\ a^{-1}[3m^{2/3} - 1] < m_2 & \text{if } m^2 > 1. \end{cases}$$

Then the following statements hold:

- (i) The system (1.6) has no constant positive solution for $d \notin (-am/(1 + a), d^*]$, and at least one constant positive solution for $d \in (-am/(1 + a), d^*)$.
- (ii) If $1 < m_1$, then $H(u)$ is strictly decreasing in $(0, a)$, $d^* = a/m$ and (1.6) has a unique constant positive solution if $d \in (-am/(1 + a), d^*)$.
- (iii) If $m_2 < 1$, then $H'(u)$ changes sign exactly once, from positive to negative, in $(0, a)$, $d^* > a/m$ and (1.6) has no constant positive solution for $d \notin (-am/(1 + a), d^*]$, a unique constant positive solution for $d \in (-am/(1 + a), a/m] \cup \{d^*\}$, and exactly two constant positive solutions for $d \in (a/m, d^*)$.
- (iv) If $m_1 < 1 < m_2$, $H'(u)$ changes sign exactly twice in $(0, a)$, and there are ranges of d such that (1.6) has three constant positive solutions.

It should be noted from (i) and (ii) of Theorem 4.1 that (1.6) has a unique constant positive solution if and only $d \in (-am/(1 + a), a/m)$ if m is properly large.

When $a \leq 1$, Theorem 1 in [3] (see also Theorem 2.3 of [5]) gives a complete understanding of the solution of the associated dynamics of (1.6):

$$\begin{cases} u_t - d_1 \Delta u = u(a - u) - \frac{mu v}{u + 1} & \text{in } \Omega \times (0, \infty), \\ v_t - d_2 \Delta v = v(d - v) + \frac{mu v}{u + 1} & \text{in } \Omega \times (0, \infty), \\ \partial_\nu u = \partial_\nu v = 0 & \text{on } \partial\Omega \times (0, \infty), \\ u(x, 0) = u_0(x) \geq 0, \neq 0 & \text{in } \Omega, \\ v(x, 0) = v_0(x) \geq 0, \neq 0 & \text{in } \Omega \end{cases} \tag{4.1}$$

as follows.

Theorem 4.2. Assume that $a \leq 1$. Then we have the following:

- (i) If $d \in (-am/(1 + a), a/m)$, the unique positive constant solution is globally attractive, i.e., any solution of (4.1) converges to the constant positive solution as $t \rightarrow \infty$.
- (ii) If $d \geq a/m$, then $(0, d)$ is globally attractive.
- (iii) If $d \leq -am/(1 + a)$, then $(a, 0)$ is globally attractive.

In fact the global stability result above can be extended to $a > 1$ as long as $d > 0$ is large or $m > 0$ is large by using the same technique of invariant rectangle as in [3]:

Theorem 4.3. Assume that $a > 1$ and $d > (a + 1)^2/(4m)$. Then $(0, d)$ is globally attractive.

The proof of Theorem 4.3 is essentially the same as that of Theorem 1 in [3], thus we will not provide details. We only point out that the condition $a > 1$ implies that the u -isocline $mv = (a - u)(1 + u)$ is not monotone as in [3]. However the condition $d > (a + 1)^2/(4m)$ makes the lowest point of the v -isocline $v = d + mu/(1 + u)$ is still higher than the highest point of the u -isocline $mv = (a - u)(1 + u)$. Hence comparison arguments and invariant rectangle technique can still be used under these conditions.

Since we are mainly interested in the case of large m in this paper, then for fixed $d > 0$, from Theorems 4.2(ii) and 4.3, regardless of the value of $a > 0$, then $(0, d)$ is globally asymptotically stable provided that

$$m > \max \left\{ \frac{(a + 1)^2}{4d}, \frac{a}{d} \right\}. \tag{4.2}$$

In particular, when (4.2) is satisfied, (1.6) has no positive solutions, which proves the case of $d > 0$ in Theorem 1.2. Hence in the remaining part of this section, we only consider the case of $d \leq 0$.

By the weak maximum principle (see, e.g., [30,32]), the simple analysis similar to that in Lemma 3.5 of [41] shows any non-negative $W^{1,2}(\Omega)$ solution (u, v) of (1.6) satisfies $u \leq a$ and $v \leq d + ma/(1 + a)$. Note that the argument there works for any number of dimension. Moreover, the standard theory concludes that such non-negative solution $(u, v) \in [C^2(\overline{\Omega})]^2$. Thus, by the well-known strong maximum principle and the Hopf boundary lemma, one easily sees that any non-negative solution (u, v) of (1.6) with $u \not\equiv 0, v \not\equiv 0$ satisfies

$$0 < u(x) < a \quad \text{and} \quad 0 < v(x) < d + \frac{ma}{1 + a}. \tag{4.3}$$

Therefore, we also know that (1.6) has no positive solution if $d \leq -am/(1 + a)$ (see also Proposition 2.4 in [5]). From now on, unless otherwise specified, it is always assumed that

$$d > -\frac{ma}{1 + a}. \tag{4.4}$$

When m is bounded, by using the similar proof as that of Lemma 3.6 in [41], we have the following estimates of lower bounds for positive solutions of (1.6).

Lemma 4.1. *Suppose that $d_1, d_2, a > 0, d \leq 0$ and Ω are fixed, and $0 < m \leq M$ for some $M > 0$. Then, there exists a positive constant \underline{C} depending possibly on d_1, d_2, a, d, M and Ω , such that any positive solution $(u(x), v(x))$ of (1.6) satisfies*

$$u(x), v(x) \geq \underline{C}, \quad \text{for } x \in \overline{\Omega}.$$

In the following, we establish the estimates of any positive solution $(u(x), v(x))$ of (1.6) as $m \rightarrow \infty$. To achieve this goal, we use the same scaling (3.1) to (1.6) and then (1.6) becomes

$$\begin{cases} -d_1 \Delta w = w(a - u) - \frac{wz}{u + 1} & \text{in } \Omega, \\ -d_2 \Delta z = z(d - v) + \frac{wz}{u + 1} & \text{in } \Omega, \\ \partial_\nu w = \partial_\nu z = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.5}$$

By using the system (4.5), we derive the following result:

Theorem 4.4. *Suppose that $N \leq 3$, and $d_1, d_2, a > 0, d \leq 0$ and Ω are fixed. Let (u_m, v_m) be a positive solution of (1.6), then there exist two positive constants \underline{C} and \overline{C} , which depend only on d_1, d_2, a, d and Ω , such that*

$$mu_m(x) \leq \overline{C}, \quad \text{and} \quad \underline{C} \leq mv_m(x) \leq \overline{C}, \quad \text{for } x \in \overline{\Omega}. \tag{4.6}$$

If in addition $d < 0$, then we have

$$\underline{C} \leq mu_m(x), mv_m(x) \leq \overline{C}, \quad \text{for } x \in \overline{\Omega}, \tag{4.7}$$

and

$$(mu_m, mv_m) \rightarrow (-d, a) \text{ in } C^2(\overline{\Omega}), \text{ as } m \rightarrow \infty.$$

Proof. In accordance with (4.3) and Lemma 4.1, it remains to prove the upper and lower bounds and the asymptotic behavior of (mu_m, mv_m) for $m \rightarrow \infty$. In fact, the key point is to establish the upper bound of v_m . From now on, we denote $(w_m, z_m) = (mu_m, mv_m)$.

We first claim that $\max_{\overline{\Omega}} v_m$ has upper bounds independent of m . Our strategy is that we first derive the estimates for the norms of $W^{1,2}$ and $W^{2,2}$ of v_m , then we use the Sobolev embedding theorem to obtain the desired result.

To this end, we begin with establishing the bound of $\|v_m\|_{L^2(\Omega)}$. Integrating the equations of u_m and v_m over Ω , respectively, we obtain

$$\int_{\Omega} u_m(a - u_m) \, dx = \int_{\Omega} v_m(v_m - d) \, dx.$$

From (4.3) and the Hölder inequality, we see

$$\int_{\Omega} v_m^2 \, dx \leq a^2|\Omega| + |d| \int_{\Omega} v_m \, dx \leq a^2|\Omega| + |d||\Omega|^{1/2} \left(\int_{\Omega} v_m^2 \, dx \right)^{1/2},$$

which implies that there exists a positive constant C^* , such that

$$\int_{\Omega} v_m \, dx \leq C^* \quad \text{and} \quad \int_{\Omega} v_m^2 \, dx \leq C^*. \tag{4.8}$$

Here and in what follows, C^* is determined only by d_1, d_2, a, d and Ω , and it can vary from line to line.

Next we estimate the L^2 -norm of the gradient ∇v_m . We assume that $m \geq 2d_1/d_2$ in the following discussion. Multiplying z_m and w_m to the equations of w_m and z_m respectively, and then integrating, we find

$$\begin{aligned} & \frac{1}{d_1} \int_{\Omega} w_m z_m (a - u_m) \, dx - \frac{d}{d_2} \int_{\Omega} w_m z_m \, dx + \frac{1}{d_2} \int_{\Omega} w_m z_m v_m \, dx \\ &= \frac{1}{d_1} \int_{\Omega} \frac{w_m z_m^2}{u_m + 1} \, dx + \frac{1}{d_2} \int_{\Omega} \frac{w_m^2 z_m}{u_m + 1} \, dx. \end{aligned}$$

Hence, it follows from (4.3) that

$$\frac{1}{d_1} \int_{\Omega} w_m z_m^2 \, dx + \frac{1}{d_2} \int_{\Omega} w_m^2 z_m \, dx \leq \left(\frac{a}{d_1} - \frac{d}{d_2} \right) (a + 1) \int_{\Omega} w_m z_m \, dx + \frac{a + 1}{d_2} \int_{\Omega} w_m z_m v_m \, dx. \tag{4.9}$$

On the other hand, from the Cauchy–Schwarz inequality, we have

$$\int_{\Omega} w_m z_m \, dx = \int_{\Omega} (w_m)^{1/2} z_m \cdot (w_m)^{1/2} \, dx \leq \left(\int_{\Omega} w_m z_m^2 \, dx \right)^{1/2} \left(\int_{\Omega} w_m \, dx \right)^{1/2}. \tag{4.10}$$

Note that

$$-d_2 \Delta v_m = v_m(d - v_m) + \frac{w_m v_m}{u_m + 1} \quad \text{in } \Omega, \quad \partial_\nu v_m = 0 \quad \text{on } \partial\Omega. \tag{4.11}$$

Dividing (4.11) by v_m and integrating over Ω , we have

$$-d_2 \int_{\Omega} \frac{|\nabla v_m|^2}{v_m^2} dx = \int_{\Omega} (d - v_m) dx + \int_{\Omega} \frac{w_m}{u_m + 1} dx,$$

from which, together with (4.8), it follows that

$$\int_{\Omega} w_m dx \leq C^*.$$

As a consequence, (4.10) implies that

$$\int_{\Omega} w_m z_m dx \leq C^* \left(\int_{\Omega} w_m z_m^2 dx \right)^{1/2}. \tag{4.12}$$

Combining (4.12) and (4.9), we get

$$\int_{\Omega} w_m z_m^2 dx \leq C^* \left(\int_{\Omega} w_m z_m^2 dx \right)^{1/2} + \frac{1}{2} \int_{\Omega} w_m z_m^2 dx. \tag{4.13}$$

Here, we used the restriction $m \geq 2d_1/d_2$ and the fact that

$$\int_{\Omega} w_m z_m v_m dx = \frac{1}{m} \int_{\Omega} w_m z_m^2 dx \leq \frac{d_2}{2d_1} \int_{\Omega} w_m z_m^2 dx. \tag{4.14}$$

Therefore, we conclude from (4.9), (4.13) and (4.14) that

$$\int_{\Omega} w_m z_m^2 dx \leq C^* \quad \text{and} \quad \int_{\Omega} w_m^2 z_m dx \leq C^*. \tag{4.15}$$

Next we derive an estimate for $\int_{\Omega} w_m^2 v_m^2 dx$. Observe that

$$\int_{\Omega} w_m^2 v_m^2 dx = \int_{\Omega} w_m^2 z_m \cdot \frac{v_m}{m} dx. \tag{4.16}$$

(4.3) indicates that for any $x \in \bar{\Omega}$, if we assume $m \geq 2d_1/d_2$, then

$$\frac{v_m(x)}{m} \leq \frac{d}{m} + \frac{a}{a+1} \leq C^*.$$

Hence, combining the above inequality, (4.15) and (4.16), we can assert that

$$\int_{\Omega} w_m^2 v_m^2 dx \leq C^*. \tag{4.17}$$

Based on the above results, we are able to establish the estimates of the $W^{1,2}$ -norm of v_m . Indeed we multiply Eq. (4.11) by v_m and then integrate to derive

$$d_2 \int_{\Omega} |\nabla v_m|^2 dx = \int_{\Omega} \left[v_m(d - v_m) + \frac{w_m z_m^2}{m^2(u_m + 1)} \right] dx.$$

Thus, from (4.8) and (4.15), we can see that

$$\int_{\Omega} (|\nabla v_m|^2 + v_m^2) dx \leq C^*.$$

For $N = 1$, the Sobolev embedding theorem shows that $W^{1,2}(\Omega) \hookrightarrow C^{1/2}(\overline{\Omega})$. This implies that $\max_{\overline{\Omega}} v_m \leq C^*$. If $N = 2$, according to the embedding theorem $W^{1,2}(\Omega) \hookrightarrow L^p(\Omega)$ for any $1 \leq p < \infty$, we have

$$\int_{\Omega} v_m^p dx \leq C^*, \quad \text{for any fixed } p \geq 1. \tag{4.18}$$

As for $N = 3$, it follows from $W^{1,2}(\Omega) \hookrightarrow L^6(\Omega)$ that

$$\int_{\Omega} v_m^6 dx \leq C^*. \tag{4.19}$$

For the case of $N = 2, 3$, applying (4.17), (4.18) and (4.19), we obtain that

$$\begin{aligned} \int_{\Omega} \left| v_m(d - v_m) + \frac{w_m v_m}{u_m + 1} \right|^2 dx &\leq 2 \int_{\Omega} |v_m(d - v_m)|^2 dx + 2 \int_{\Omega} \left| \frac{w_m v_m}{u_m + 1} \right|^2 dx \\ &\leq d^2 C^* \left(\int_{\Omega} v_m^6 dx \right)^{1/3} + C^* \left(\int_{\Omega} v_m^6 dx \right)^{2/3} + C^* \int_{\Omega} w_m^2 v_m^2 dx \\ &\leq C^*. \end{aligned} \tag{4.20}$$

The standard L^p theory for elliptic equations ensures that $\|v_m\|_{W^{2,2}(\Omega)} \leq C^*$. So by the embedding theorem: $W^{2,2}(\Omega) \hookrightarrow C^\alpha(\overline{\Omega})$ for some $\alpha \in (0, 1)$ if $N = 2, 3$, we finally deduce that $\max_{\overline{\Omega}} v_m \leq C^*$ for $N = 2, 3$. Up to this point, we have established the desired upper bound of v_m when $N \leq 3$.

The remaining argument to the assertions (4.6) and (4.7) in Theorem 4.4 is quite similar to that in the proof of Theorem 3.1. Actually, from the second equation of (4.5), we find that

$$-d_2 \Delta z_m + (|d| + C^*) z_m > 0 \quad \text{in } \Omega, \quad \partial_\nu z_m = 0 \quad \text{on } \partial\Omega.$$

Then similar analysis shows that there exist two positive constants \underline{C} and \overline{C} , which depend only on d_1, d_2, a, d and Ω , such that

$$mu_m(x) \leq \overline{C}, \quad \text{and} \quad \underline{C} \leq mv_m(x) \leq \overline{C}, \quad \text{for } x \in \overline{\Omega}.$$

Furthermore, in the case of $d < 0$, we can also obtain the positive lower bound for mu_m , that is, for the same chosen \underline{C} and \overline{C} as above, the following assertion holds:

$$\underline{C} \leq mu_m(x), mv_m(x) \leq \overline{C}, \quad \text{for } x \in \overline{\Omega}.$$

When $d < 0$ holds, by use of (4.7), it is easy to determine the asymptotic behavior of positive solution (w_m, z_m) to (4.5) as $m \rightarrow \infty$. In fact, since $u_m, v_m \rightarrow 0$ uniformly on $\bar{\Omega}$ as $m \rightarrow \infty$, and both w_m and z_m have positive upper and lower bounds for any large m , we can use the standard regularity theory for elliptic equations and the embedding theorems to see that $(w_m, z_m) \rightarrow (w_0, z_0)$ in $C^2(\bar{\Omega})$ as $m \rightarrow \infty$, where (w_0, z_0) is a positive solution of

$$\begin{cases} -d_1 \Delta w = aw - wz & \text{in } \Omega, \\ -d_2 \Delta z = dz + wz & \text{in } \Omega, \\ \partial_\nu w = \partial_\nu z = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.21}$$

If $d \geq 0$, it is obvious that (4.21) has no positive solution; while for $d < 0$, (4.21) has a unique positive solution $(w_0, z_0) = (-d, a)$ by Lemma 2.4. Thus, we finish the proof of Theorem 4.4. \square

Proof of Theorem 1.2 for $d < 0$. Now, with the help of Theorem 4.4, we can proceed the proof of Theorem 1.2 for the case $d < 0$ in the same way as that of Theorem 1.1. Indeed, we let $\rho = 1/m$, and thus (4.5) is changed into the equivalent system

$$\begin{cases} -d_1 \Delta w = w(a - \rho w) - \frac{wz}{\rho w + 1} & \text{in } \Omega, \\ -d_2 \Delta z = z(d - \rho z) + \frac{wz}{\rho w + 1} & \text{in } \Omega, \\ \partial_\nu w = \partial_\nu z = 0 & \text{on } \partial\Omega. \end{cases}$$

We omit the details of the proof. \square

It should be pointed out that when $d = 0$, the function $mu_m(x)$, which was defined in Theorem 4.4, has no positive lower bound as m goes to infinity. This fact can be directly observed by the use of the distribution of the (unique) positive constant solution of (1.6). Indeed, in this special case, let us denote by (u^*, v^*) the unique positive constant solution of (1.6). Then, it is obvious that

$$a = u^* + \frac{mv^*}{u^* + 1} \quad \text{and} \quad \frac{mu^*}{u^* + 1} = v^*,$$

from which we have

$$(a - u^*)(u^* + 1)^2 = m^2 u^*.$$

Hence $u^* \rightarrow 0$, and in turn, $m^2 u^* \rightarrow a$ as $m \rightarrow \infty$.

Motivated by the simple observation above, we may use a different scaling:

$$\tilde{w} = m^2 u \quad \text{and} \quad z = mv \tag{4.22}$$

to derive the possible positive lower bound for this \tilde{w} .

According to the scaling (4.22), the original system (1.6) can be rewritten as

$$\begin{cases} -d_1 \Delta \tilde{w} = \tilde{w}(a - u) - \frac{\tilde{w}z}{u + 1} & \text{in } \Omega, \\ -d_2 \Delta z = \frac{z}{m} \left(\frac{\tilde{w}}{u + 1} - z \right) & \text{in } \Omega, \\ \partial_\nu \tilde{w} = \partial_\nu z = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.23}$$

In the sequel, we are ready to establish the positive lower bound for \tilde{w} defined in (4.22), where (u, v) is a positive solution of (1.6). That is, we can claim that

Theorem 4.5. Suppose that $N \leq 3$ and $d = 0$, and let $d_1, d_2, a > 0$ and Ω be fixed. Let (u_m, v_m) be a positive solution of (1.6), then there exist two positive constants \underline{C} and \bar{C} , which depend only on d_1, d_2, a and Ω , such that

$$\underline{C} \leq m^2 u_m, m v_m \leq \bar{C}, \quad \text{for } x \in \bar{\Omega}. \tag{4.24}$$

Moreover,

$$(m^2 u_m, m v_m) \rightarrow (a, a) \quad \text{in } C^2(\bar{\Omega}), \quad \text{as } m \rightarrow \infty. \tag{4.25}$$

Proof. First we prove (4.24). From the statements of (4.3), Lemma 4.1 and Theorem 4.4, we only need to verify the positive lower and upper bounds for $m^2 u_m$ as $m \rightarrow \infty$.

Since it has been shown that $u_m < a$ and $\underline{C} \leq z_m \leq \bar{C}$, where \underline{C} and \bar{C} are the same as those in Theorem 4.4, one can use the first equation in (4.23) and Lemma 2.2 to assert that there is a positive constant C_0 , depending only on d_1, d_2, a and Ω , such that $\tilde{w}_m = m^2 u_m$ satisfies

$$\sup_{\Omega} \tilde{w}_m \leq C_0 \inf_{\Omega} \tilde{w}_m. \tag{4.26}$$

Suppose that \tilde{w} has no finite upper bound, then it follows from (4.26) that we can find a subsequence of positive solutions (u_m, v_m) of (1.6), denoted by itself, such that $\tilde{w}_m \rightarrow \infty$ uniformly over $\bar{\Omega}$ when $m \rightarrow \infty$. On the other hand, we integrate the equation of z_m to see that

$$\int_{\Omega} z_m \left(\frac{\tilde{w}_m}{u_m + 1} - z_m \right) dx = 0. \tag{4.27}$$

As $z_m \leq \bar{C}$, (4.27) reaches a contradiction. Then, our analysis shows the existence of the desired positive upper bound for \tilde{w}_m . In a similar manner, together with (4.26) and (4.27), it is easy to obtain the positive lower bound for \tilde{w}_m .

In what follows, we determine the asymptotic behavior of (\tilde{w}_m, z_m) as $m \rightarrow \infty$. By the *a priori* estimates (4.24), from the standard regularity theory for elliptic equations and embedding theorems, passing up to a subsequence, we may assume that $(\tilde{w}_m, z_m) \rightarrow (\tilde{w}_0, z_0)$ in $C^2(\bar{\Omega})$ as $m \rightarrow \infty$. It is easily seen that z_0 must be a positive constant and $\tilde{w}_0 > 0$ on $\bar{\Omega}$. Moreover, as $u_m = m^{-2} \tilde{w}_m \rightarrow 0$ uniformly on $\bar{\Omega}$ when $m \rightarrow \infty$, from (4.23), it follows that (\tilde{w}_0, z_0) satisfies

$$-d_1 \Delta \tilde{w}_0 = (a - z_0) \tilde{w}_0 \quad \text{in } \Omega, \quad \partial_\nu \tilde{w}_0 = 0 \quad \text{on } \partial\Omega, \tag{4.28}$$

and

$$\int_{\Omega} (\tilde{w}_0 - z_0) dx = 0. \tag{4.29}$$

Eq. (4.28) indicates $z_0 \equiv a$ and \tilde{w}_0 is a positive constant. Thus, $\tilde{w}_0 \equiv z_0 = a$ by (4.29). The proof of Theorem 4.5 is now complete. \square

Finally, we finish the proof of Theorem 1.2 in the case of $d = 0$ by applying a different argument, which will also heavily rely on the implicit function theorem. Our main idea comes from [31,33].

Proof of Theorem 1.2 for $d = 0$. First we make a decomposition:

$$z = z_1 + z_2 \quad \text{with } \int_{\Omega} z_1 dx = 0 \quad \text{and } z_2 \in \mathbf{R}_+^1,$$

where \mathbf{R}_+^1 represents the set of all positive real numbers. As before, we denote $\rho = 1/m$. We also introduce the Banach spaces:

$$W_v^{2,2}(\Omega) = \{g \in W^{2,2}(\Omega) \mid \partial_\nu g = 0 \text{ on } \partial\Omega\}, \quad L_0^2(\Omega) = \left\{g \in L^2(\Omega) \mid \int_\Omega g \, dx = 0\right\}.$$

Then we observe that finding positive solutions of (1.6) is equivalent to solving the following problem

$$\begin{cases} d_1 \Delta \tilde{w} + \tilde{w}(a - \rho^2 \tilde{w}) - \frac{\tilde{w}(z_1 + z_2)}{\rho^2 \tilde{w} + 1} = 0 & \text{in } \Omega, \quad \partial_\nu \tilde{w} = 0 \text{ on } \partial\Omega, \\ d_2 \Delta z_1 + \rho(z_1 + z_2) \left[\frac{\tilde{w}}{\rho^2 \tilde{w} + 1} - (z_1 + z_2) \right] = 0 & \text{in } \Omega, \quad \partial_\nu z_1 = 0 \text{ on } \partial\Omega, \\ \int_\Omega (z_1 + z_2) \left[\frac{\tilde{w}}{\rho^2 \tilde{w} + 1} - (z_1 + z_2) \right] dx = 0, \\ z_2 > 0, \quad \tilde{w} > 0 & \text{in } \Omega. \end{cases} \tag{4.30}$$

It is also noted that $(\tilde{w}, z_1, z_2) = (\rho^{-2}u^*, 0, \rho^{-1}v^*)$ is a solution of (4.30) for all small $\rho > 0$. Here, (u^*, v^*) is the unique constant positive solution of (1.6) for large m . In addition, $(\rho^{-2}u^*, 0, \rho^{-1}v^*) \rightarrow (a, 0, a)$ as $\rho \rightarrow 0^+$.

To prove the claimed result, we also need to introduce some more notations as follows. For any $g \in L^2(\Omega)$, we also define

$$\mathbf{P}(g) = g - \frac{1}{|\Omega|} \int_\Omega g \, dx,$$

i.e., \mathbf{P} is the projective operator from $L^2(\Omega)$ to $L_0^2(\Omega)$. We define

$$F(\rho, \tilde{w}, z_1, z_2) = (f_1, f_2, f_3)(\rho, \tilde{w}, z_1, z_2),$$

with

$$\begin{aligned} f_1(\rho, \tilde{w}, z_1, z_2) &= d_1 \Delta \tilde{w} + \tilde{w}(a - \rho^2 \tilde{w}) - \frac{\tilde{w}(z_1 + z_2)}{\rho^2 \tilde{w} + 1}, \\ f_2(\rho, \tilde{w}, z_1, z_2) &= d_2 \Delta z_1 + \rho \mathbf{P} \left\{ (z_1 + z_2) \left[\frac{\tilde{w}}{\rho^2 \tilde{w} + 1} - (z_1 + z_2) \right] \right\}, \\ f_3(\rho, \tilde{w}, z_1, z_2) &= \int_\Omega (z_1 + z_2) \left[\frac{\tilde{w}}{\rho^2 \tilde{w} + 1} - (z_1 + z_2) \right] dx. \end{aligned}$$

Then

$$F : W_v^{2,2}(\Omega) \times (L_0^2(\Omega) \cap W_v^{2,2}(\Omega)) \times \mathbf{R}_+^1 \rightarrow L^2(\Omega) \times L_0^2(\Omega) \times \mathbf{R}^1$$

is a well-defined mapping. It is clear that (\tilde{w}, z_1, z_2) is a solution of (4.30) if and only if $F(\rho, \tilde{w}, z_1, z_2) = (0, 0, 0)$. Moreover, (4.30) has a unique solution $(\tilde{w}, z_1, z_2) = (a, 0, a)$ when $\rho = 0$ from the proof of Theorem 4.5. Clearly F is a continuously differentiable mapping, and its partial derivative at the point $(0, a, 0, a)$ with respect to the last three arguments is

$$\Psi \equiv D_{(\tilde{w}, z_1, z_2)} F(0, a, 0, a),$$

$$\Psi : W_v^{2,2}(\Omega) \times (L_0^2(\Omega) \cap W_v^{2,2}(\Omega)) \times \mathbf{R}^1 \rightarrow L^2(\Omega) \times L_0^2(\Omega) \times \mathbf{R}^1,$$

with

$$\Psi(h, k, \tau) = \begin{pmatrix} d_1 \Delta h - a(k + \tau) \\ d_2 \Delta k \\ a \int_{\Omega} (h - k - \tau) \, dx \end{pmatrix}.$$

We next claim that Ψ is an isomorphism. Assume that $\Psi(h, k, \tau) = (0, 0, 0)$, then it is clear that $k \equiv 0$ since the operator $-\Delta$ subject to homogeneous Neumann boundary condition over $\partial\Omega$ is invertible from $(L_0^2(\Omega) \cap W_v^{2,2}(\Omega))$ to $L_0^2(\Omega)$. Thus, as

$$-d_1 \Delta h = -a\tau \quad \text{in } \Omega, \quad \partial_\nu h = 0 \quad \text{on } \partial\Omega$$

and τ is a constant, one can integrate this equation over Ω to find $\tau = 0$, and so h must also be a constant. Hence we get $h \equiv 0$ by the integral equation that h satisfies. This verifies the injectivity of Ψ .

On the other hand, for a given $(g_1, g_2, g_3) \in L^2(\Omega) \times L_0^2(\Omega) \times \mathbf{R}^1$, one can also easily check that $\Psi(h, k, \tau) = (g_1, g_2, g_3)$ has a unique solution, which implies that Ψ is surjective. To see this, we need a well-known and simple fact: for a fixed $g \in L_0^2(\Omega)$ and a fixed constant c_0 , the following elliptic equation:

$$-d_1 \Delta h = g \quad \text{in } \Omega, \quad \partial_\nu h = 0 \quad \text{on } \partial\Omega, \quad \text{and} \quad \int_{\Omega} h \, dx = c_0$$

has a unique solution. Our analysis has confirmed that Ψ is an isomorphism.

Now, by the implicit function theorem, there exist positive constants ρ_0 and δ_0 such that, for each $\rho \in (0, \rho_0]$, $(\rho^{-2}u^*, 0, \rho^{-1}v^*)$ is the unique solution of $F(\rho, \tilde{w}, z_1, z_2) = 0$ in $B_{\delta_0}(a, 0, a)$, where $B_{\delta_0}(a, 0, a)$ is the ball in $W_v^{2,2}(\Omega) \times (L_0^2(\Omega) \cap W_v^{2,2}(\Omega)) \times \mathbf{R}^1$ centered at $(a, 0, a)$ with radius δ_0 . Taking smaller ρ_0 and δ_0 if necessary, by use of (4.25) of Theorem 4.5 we can conclude that (4.30) only has the solution $(\rho^{-2}u^*, 0, \rho^{-1}v^*)$ when ρ is small enough, which equivalently says that (u^*, v^*) is the unique positive solution of the original system (1.6) provided that m is sufficiently large. The proof for Theorem 1.2 is now complete. \square

5. Global bifurcations in diffusive predator–prey systems

The reaction–diffusion systems with predator–prey (or consumer–resource, activator–inhibitor) interactions possess rich spatiotemporal dynamics. The bifurcation of spatial nonhomogeneous steady state solutions from homogeneous ones is one of known mechanisms of pattern formation, hence it has been considered by many authors [1,4–7,14,15,25,28,37–41]. One famous example of bifurcations is the Turing bifurcation in which a diffusion coefficient is used as bifurcation parameter (see for example [14,28,37]), but recent studies show that other parameters can also generate bifurcations when there is no restriction on the diffusion coefficients (see [15,41]). The global properties of the bifurcating branches have also been considered (see [1,4,6,38]), following the celebrated global bifurcation theorem of Rabinowitz [34]. In particular, it was shown that in some cases, the branches of non-trivial steady state solutions are unbounded (see [14,15,28]).

It is well known that *a priori* estimates are important for the global bifurcations as well as topological degree calculations. Here we apply our main result in this paper to the global bifurcation of

solutions to (1.4), which recently has been considered in [41]. Following [41], we consider the one-dimensional problem:

$$\begin{cases} -d_1 u_{xx} = u \left(1 - \frac{u}{k} \right) - \frac{mu v}{1 + u}, & x \in (0, \ell\pi), \\ -d_2 v_{xx} = -\theta v + \frac{mu v}{1 + u}, & x \in (0, \ell\pi), \\ (u_x(x), v_x(x)) = 0, & x = 0, \ell\pi. \end{cases} \tag{5.1}$$

Here we assume that $d_1, d_2, \theta > 0$ and $k > 1$. We remark that our results can be extended to higher dimensional domain Ω as long as all eigenvalues of $-\Delta$ in $W^{1,2}(\Omega)$ are simple ones.

Recall that (5.1) has a constant positive steady state solution (λ, v_λ) which is defined by

$$\lambda = \frac{\theta}{m - \theta} \quad \text{and} \quad v_\lambda = \frac{(k - \lambda)(1 + \lambda)}{km}, \tag{5.2}$$

if $m \geq \theta(1 + k)/k$. We consider the bifurcation of non-constant solutions of (5.1) from the branch of the constant solutions $\{(m, u, v) = (m, \lambda, v_\lambda) : m > \theta k/(k - 1)\}$. It is known that no bifurcation occurs for $m \in (\theta(1 + k)/k, \theta k/(k - 1)]$ (see [41] Theorem 2.3). Notice that $m = \theta k/(k - 1)$ is equivalent to $\lambda = \lambda_0^H = (k - 1)/2$ which is the primary Hopf bifurcation point where a spatial homogeneous periodic orbit bifurcates from constant steady states. Define

$$A(\lambda) = \frac{\lambda(k - 1 - 2\lambda)}{k(1 + \lambda)}, \quad C(\lambda) = \frac{k - \lambda}{k(1 + \lambda)}, \quad h(\lambda) = \frac{\lambda^2(k - 1 - 2\lambda)^2}{k(1 + \lambda)(k - \lambda)}, \tag{5.3}$$

and

$$p = p_\pm(\lambda) := \frac{d_2 A(\lambda) \pm \sqrt{C(\lambda)(d_2^2 h(\lambda) - 4d_1 d_2 \theta)}}{2d_1 d_2}.$$

Then the following bifurcation result was proved in [41]:

Theorem 5.1. *Suppose that the constants $d_1, d_2, m, \theta > 0$ and $k > 1$ satisfy*

$$\frac{d_1}{d_2} < \frac{h(\lambda^\#)}{4\theta}, \tag{5.4}$$

where $h(\lambda)$ is defined in (5.3) and $\lambda^\#$ is the unique maximum point of $h(\lambda)$ for $\lambda \in (0, (k - 1)/2)$. Define

$$\tilde{\ell}_{n,+} = \frac{n}{\sqrt{\max p_+(\lambda)}}, \quad \tilde{\ell}_{n,-} = \frac{n}{\sqrt{\min p_-(\lambda)}}.$$

If for some $n \in \mathbb{N}$, $\ell \in (\tilde{\ell}_{n,+}, \tilde{\ell}_{n,-})$ but except a finitely many values of ℓ , there exist exactly two points $\lambda_{n,\pm}^S$ with $\lambda_{n,-}^S < \lambda_{n,+}^S$ such that $p_\pm(\lambda_{n,\pm}^S) = n^2/\ell^2$. Then there is a smooth curve $\Gamma_{n,\pm}$ of positive solutions of (5.1) bifurcating from $(\lambda, u, v) = (\lambda_{n,\pm}^S, \lambda_{n,\pm}^S, v_{\lambda_{n,\pm}^S})$, with $\Gamma_{n,\pm}$ contained in a global branch $\mathcal{C}_{n,\pm}$ of the non-constant positive solutions of (5.1). Moreover:

1. Near $(\lambda, u, v) = (\lambda_{n,\pm}^S, \lambda_{n,\pm}^S, v_{\lambda_{n,\pm}^S})$, $\Gamma_{n,\pm} = \{(\lambda(s), u(s), v(s)) : s \in (-\epsilon, \epsilon)\}$, where $u(s) = \lambda_{n,\pm}^S + sa_n \cos(n\pi/\ell) + s\psi_1(s)$, $v(s) = v_{\lambda_{n,\pm}^S} + sb_n \cos(n\pi/\ell) + s\psi_2(s)$ for $s \in (-\epsilon, \epsilon)$ for some C^∞ smooth functions λ, ψ_1, ψ_2 such that $\lambda(0) = \lambda_{n,\pm}^S$ and $\psi_1(0) = \psi_2(0) = 0$, and (a_n, b_n) is an associated eigenvector of the linearized equation.

2. Either $C_{n,\pm}$ contains another $(\lambda_{j,\pm}^S, \lambda_{j,\pm}^S, v_{\lambda_{j,\pm}^S})$, or the projection of $C_{n,\pm}$ onto λ -axis contains the interval $(0, \lambda_{j,\pm}^S)$.

An application of Theorem 1.1 eliminates one of the two alternatives in the last statement of Theorem 5.1:

Theorem 5.2. *Suppose that all conditions in Theorem 5.1 are satisfied, then the closure of each component $C_{n,\pm}$ of the set of non-constant solutions of (5.1) is bounded in the space $[0, (k-1)/2] \times [W^{1,2}((0, \ell\pi))]^2$, and it contains another $(\lambda_{j,\pm}^S, \lambda_{j,\pm}^S, v_{\lambda_{j,\pm}^S})$. Hence each $C_{n,\pm}$ is a bounded “loop” containing at least two bifurcation points.*

Notice that $\lambda = \theta/(m - \theta)$ hence $m \rightarrow \infty$ is equivalent to $\lambda \rightarrow 0^+$, then the proof is clear from the *a priori* estimates in Lemma 3.1 and the non-existence result in Theorem 1.1. Note that our result does not imply $C_{n,+} = C_{n,-}$.

For the dynamics of the reaction–diffusion system corresponding to (5.1) or (1.4), our main result in this paper shows that the constant one is the unique steady state which is unstable when m is large. It is known that the system possesses a spatial homogeneous periodic orbit for large m , and the periodic orbit also has some asymptotic profile (see [12]). In [41], it was shown that many Hopf bifurcations can generate spatial nonhomogeneous periodic orbits. We conjecture that when m is large, the spatial homogeneous one is the unique periodic orbit for the system.

We also remark that for the system (1.6), in the case of $d \leq 0$, a similar bifurcation analysis can be carried out, so our non-existence result again implies the boundedness of the global branches.

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