

## STABILITY OF POSITIVE STATIONARY SOLUTIONS TO A SPATIALLY HETEROGENEOUS COOPERATIVE SYSTEM WITH CROSS-DIFFUSION

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ABSTRACT. In the previous article [Y.-X. Wang and W.-T. Li, *J. Differential Equations*, 251 (2011) 1670-1695], the authors have shown that the set of positive stationary solutions of a cross-diffusive Lotka-Volterra cooperative system can form an unbounded fish-hook shaped branch  $\Gamma_p$ . In the present paper, we will show some criteria for the stability of positive stationary solutions on  $\Gamma_p$ . Our results assert that if  $d_1/d_2$  is small enough, then unstable positive stationary solutions bifurcate from semitrivial solutions, the stability changes only at every turning point of  $\Gamma_p$  and no Hopf bifurcation occurs. While as  $d_1/d_2$  becomes large, the stability has a drastic change when  $\mu < 0$  in the supercritical case. Original stable positive stationary solutions at certain point may lose their stability, and Hopf bifurcation can occur. These results are very different from those of the spatially homogeneous case.

### 1. INTRODUCTION

It is known that the spatial heterogeneity has an important impact on the population dynamics besides the interactions between species [1, 2, 3, 5, 7, 13, 12, 14, 15, 23]. Cross-diffusion has also been shown to produce richer stationary patterns by many researchers, see [9, 8, 21, 19, 20, 22, 25, 28, 27, 33, 36, 34, 38, 37, 35, 41, 42, 39, 40, 6, 43] and references therein. In this paper, we study the following Lotka-Volterra cooperative system with cross-diffusion in a spatially heterogeneous environment:

$$\begin{aligned} u_t &= d_1 \Delta u + u(a_1 - b_1 u + c_1(x)v), & x \in \Omega, t > 0, \\ v_t &= \Delta[(d_2 + \rho(x)u)v] + v(a_2 - b_2 v + c_2(x)u), & x \in \Omega, t > 0, \\ \partial_\nu u &= \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) &= u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \bar{\Omega}. \end{aligned} \tag{1.1}$$

Here  $\Omega$  is a bounded domain in  $\mathbb{R}^N$  ( $N \geq 1$ ) with smooth boundary  $\partial\Omega$ ;  $\nu$  is the outward unit normal vector on  $\partial\Omega$  and  $\partial_\nu = \partial/\partial\nu$ ;  $u(x, t)$  and  $v(x, t)$  represent the population densities of the two species interacting and migrating in the same habitat  $\Omega$ ;  $a_1$  and  $a_2$ , which are real constants and may be negative, denote the birth

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or death rates of the respective species; positive constants  $b_1$  and  $b_2$  represent the intra-specific pressures of  $u$  and  $v$ ; the inter-specific pressures  $c_1(x)$  and  $c_2(x)$  with  $c_1(x), c_2(x) \geq \neq 0$  are assumed to be spatially heterogeneous and continuous in  $\bar{\Omega}$ ; positive constants  $d_1$  and  $d_2$  represent the natural dispersive forces of movements of the species, respectively;  $\rho(x)$  is a smooth positive function in  $\bar{\Omega}$  with  $\partial_\nu \rho(x)|_{\partial\Omega} = 0$ . Furthermore, the system is self-contained, and there is no flux on  $\partial\Omega$ .

The nonlinear diffusion term

$$\Delta(\rho(x)uv) = \nabla \cdot [\rho(x)u\nabla v + v\nabla(\rho(x)u)]$$

is usually referred as the cross-diffusion term. This is first proposed by Shigesada et al. [32] to model the segregation phenomenon of two species. The diffusion term here means that the diffusive direction of  $v$  is affected not only by the population pressure of  $u$  but also the heterogeneity of the environment, which implies that  $v$  diffuses to the low density region of  $\rho(x)u$ . See [30] for more ecological backgrounds.

By a simple scaling

$$(\lambda, \mu, k, b(x), d(x), \tilde{u}, \tilde{v}) = \left( \frac{a_1}{d_1}, \frac{a_2}{d_2}, \frac{d_1}{d_2 b_1}, \frac{d_2}{d_1 b_2} c_1(x), \frac{d_1}{d_2 b_1} c_2(x), \frac{b_1}{d_1} u, \frac{b_2}{d_2} v \right),$$

system (1.1) is reduced to the coupled system

$$\begin{aligned} d_1^{-1} u_t &= \Delta u + u(\lambda - u + b(x)v), & x \in \Omega, t > 0, \\ d_2^{-1} v_t &= \Delta[(1 + k\rho(x)u)v] + v(\mu - v + d(x)u), & x \in \Omega, t > 0, \\ \partial_\nu u &= \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) &= \bar{u}_0(x) \geq 0, & v(x, 0) = \bar{v}_0(x) \geq 0, & x \in \bar{\Omega}. \end{aligned} \quad (1.2)$$

For simplicity, we have dropped the “ $\sim$ ” sign in (1.2). Local solvability of (1.2) has been established by Amann [2], whereas the global solvability is very difficult and needs a careful and further study. In the paper, we are mainly interested in the dynamical behavior of nonnegative solutions to (1.2). Clearly, the corresponding stationary problem of (1.2) is

$$\begin{aligned} \Delta u + u(\lambda - u + b(x)v) &= 0, & x \in \Omega, \\ \Delta[(1 + k\rho(x)u)v] + v(\mu - v + d(x)u) &= 0, & x \in \Omega, \\ \partial_\nu u = \partial_\nu v &= 0, & x \in \partial\Omega. \end{aligned} \quad (1.3)$$

In a previous article [36], the authors have obtained the global bifurcation branch of positive solutions of (1.3) under weak cooperation ( $\|b\|_\infty \|d\|_\infty < \frac{\min_{\bar{\Omega}} \rho}{\rho/\| \rho \|_\infty}$ ) and large cross-diffusion effect, where  $(u, v)$  is said to be a positive solution of (1.3) if  $u > 0$  and  $v > 0$  in  $\bar{\Omega}$ . So a positive solution  $(u, v)$  means a coexistence state of the two interacting species. We expect that the bifurcation curve  $\Gamma_p$  can not only yield multiple positive stationary solutions but also show us much more complicated spatio-temporal patterns of (1.2). Since it is very difficult to obtain the complete structure of the solution set of (1.3) and many problems still remain open now, our main attention is focused on the stability analysis of the positive stationary solutions and large time behaviors of (1.2) under weak cooperation.

For the stability of positive stationary solutions to cross-diffusion systems, Kanon [16] has given some criteria on the stability of nonconstant stationary solutions to a singular perturbed type competition model proposed by Mimura et al. [29]. In 2004, Kuto [20] considered a cross-diffusion system arising in a prey-predator population model. By the method of linearization principle for quasilinear parabolic

equations developed by Potier-Ferry [31], he investigated the asymptotic stability of positive stationary solutions obtained by him and Yamada [21]. Furthermore, he showed that Hopf bifurcation phenomenon could occur on the positive stationary solution branch under some conditions. However, the coefficients in the prey-predator population model are all spatially homogeneous. Recently, he [19] further considered the predator-prey population model in a spatially heterogeneous environment and established the stability and Hopf bifurcation of positive stationary solutions obtained in [18] by similar methods. Motivated by [20, 19], the aim of this paper is to establish some criteria for the stability of positive stationary solutions of the Lotka-Volterra cooperative model (1.2) by our existence results [36].

Our first result is concerned with the case that the diffusive ratio  $d_1/d_2$  is small enough, in which case the stability of all positive stationary solutions on the bifurcation continuum can be determined clearly. To be precise, unstable positive stationary solutions bifurcate from semitrivial solutions, and the stability changes only at every critical point of the bifurcation curve with respect to the bifurcation parameter  $\lambda$ , and no Hopf bifurcation occurs. Moreover, different from [20] and [19], we can further determine that the number of the critical points is odd. From the above stability result, we see that although the spatial heterogeneity has an ability to produce multiple positive stationary solutions, while it does not have a strongly beneficial effect on the species in low densities. Furthermore, if the bifurcation at the semitrivial solution is supercritical (the bifurcation curve is no longer  $\subset$ -shaped), then stable positive stationary solutions bifurcate from semitrivial solutions, and the number of critical points is even. On the contrary, if the diffusive ratio  $d_1/d_2$  is sufficiently large, the stability result totally changes, which is our second result. At this time, we only show that the spatial segregation of  $\rho(x)$  and  $b(x)$  and small  $\|b\|_\infty$  can produce Hopf bifurcation at certain point on  $\Gamma_p$  if  $\mu < 0$ . More precisely, if the bifurcation direction is supercritical, in which case both  $(0, 0)$  and  $(\lambda, 0)$  are unstable near the bifurcation point, as  $d_1/d_2$  varies from a small number to a large one, stable positive stationary solutions bifurcate from the semitrivial solution for small  $d_1/d_2$ , and some stable positive stationary solutions will lose their stability and Hopf bifurcation occurs near the bifurcation point for large  $d_1/d_2$ . Therefore, time periodic solutions are obtained for problem (1.2) near the Hopf bifurcation point. Whereas, two Hopf bifurcation points can be found for the predator-prey system [19].

If the coefficients are spatially homogeneous, then the situation is rather different. As pointed out in [36], we know that under weak cooperation and constant coefficients, the corresponding cooperative system with large cross-diffusion coefficient  $k$  has a unique positive stationary solution if  $\lambda \in (\lambda^*, \infty)$  and no positive stationary solutions if  $\lambda \leq \lambda^*$  in case  $\mu > 0$ . If  $\mu < 0$ ,  $\lambda^*$  should be replaced by  $\lambda_*$ . Furthermore, our results imply that the unique positive stationary solution is asymptotic stable, nondegenerate, and Hopf bifurcation can never appear regardless of the values of the natural diffusive rates  $d_1$  and  $d_2$ . Thus, if the environment is spatially heterogeneous, there exist much more complicated dynamical behaviors for the weakly cooperative system, including the change of the stability of some positive stationary solutions and the appearing of Hopf bifurcation.

Finally, we point out that there is a common point for the predator-prey and cooperative system under either Neumann or Dirichlet boundary condition. That is, if one species has a large cross-diffusion rate, and the interacting species has a rather

small natural diffusion rate comparing to the species, then the stability changes at every turning point of the bifurcation curve; while if the interacting species has a relatively large natural diffusion rate, then Hopf bifurcation can occur. Thus, one sees that the diffusion has a stronger effect on the stability of positive stationary solutions than the boundary condition, while the boundary condition can have an important effect on the existence of positive stationary solutions as pointed out in [36].

The organization of this paper is as follows: In Section 2, we show the global positive stationary bifurcation branch  $\Gamma_p$  of (1.2) obtained in [36]. The main results including the asymptotic stability and Hopf bifurcation are stated in Section 3. Finally, the proofs of asymptotic stability and Hopf bifurcation are given in Sections 4 and 5, respectively.

In this article, the usual norm of  $C(\bar{\Omega})$  is defined by  $\|u\|_\infty = \max_{\bar{\Omega}} |u(x)|$ . Moreover, we denote the average of  $f(x)$  over  $\Omega$  by  $f_\Omega = \frac{1}{|\Omega|} \int_\Omega f dx$  and let  $\lambda_1(q)$  represent the principal eigenvalue of the problem

$$-\Delta u + q(x)u = \lambda u \quad \text{in } \Omega, \quad \partial_\nu u = 0 \quad \text{on } \partial\Omega,$$

for a continuous function  $q(x)$ .

## 2. PRELIMINARY RESULTS

In this section, we give the bifurcation structure of positive stationary solutions of (1.2). One can refer to [36] for details.

In this paper, we work in the following Sobolev spaces

$$X = W_\nu^{2,p}(\Omega) \times W_\nu^{2,p}(\Omega), \quad Y = L^p(\Omega) \times L^p(\Omega), p > N,$$

where  $W_\nu^{2,p}(\Omega) = \{u \in W^{2,p}(\Omega) : \partial_\nu u = 0 \text{ on } \partial\Omega\}$ .

Set

$$u = \varepsilon w, \quad (1 + k\rho(x)u)v = \varepsilon z, \quad \lambda = \varepsilon\alpha, \quad \mu = \varepsilon\beta, \quad k = \frac{1}{\varepsilon}, \quad (2.1)$$

where  $\varepsilon > 0$  is a small constant,  $\alpha$  and  $\beta$  are real numbers. Then (1.2) is equivalent to the following system

$$\begin{aligned} d_1^{-1}w_t &= \Delta w + \varepsilon F(w, z, \alpha), \quad x \in \Omega, t > 0, \\ d_2^{-1} \left[ -\frac{\rho(x)z}{(1 + \rho(x)w)^2} w_t + \frac{z_t}{1 + \rho(x)w} \right] &= \Delta z + \varepsilon G(w, z), \quad x \in \Omega, t > 0, \\ \partial_\nu w &= \partial_\nu z = 0, \quad x \in \partial\Omega, t > 0, \\ w(x, 0) &= u_0/\varepsilon, \quad z(x, 0) = (1 + \rho(x)w_0)v_0/\varepsilon, \quad x \in \bar{\Omega}, \end{aligned} \quad (2.2)$$

where

$$\begin{aligned} F(w, z, \alpha) &= w \left( \alpha - w + \frac{b(x)z}{1 + \rho(x)w} \right), \\ G(w, z) &= \frac{z}{1 + \rho(x)w} \left( \beta - \frac{z}{1 + \rho(x)w} + d(x)w \right). \end{aligned}$$

By defining  $H : X \rightarrow Y$  and  $B : X \times \mathbb{R} \rightarrow Y$  as

$$H(w, z) = (\Delta w, \Delta z), \quad B(w, z, \alpha) = (F(w, z, \alpha), G(w, z)),$$

the positive stationary solution problem associated with (2.2) becomes

$$H(w, z) + \varepsilon B(w, z, \alpha) = \mathbf{0}. \quad (2.3)$$

Let  $P : X \rightarrow X_1$  and  $Q : Y \rightarrow Y_1$  be the orthogonal projections, where  $X_1$  and  $Y_1$  represent the  $L^2$ -orthogonal complements of  $\mathbb{R}^2$  in  $X$  and  $Y$ , respectively. Then the Lyapunov-Schmidt reduction asserts the following lemma.

**Lemma 2.1.** *For any  $C > 0$ , there exist a small positive number  $\varepsilon_0$  and a neighborhood  $N_0$  of  $\{(w, z, \alpha, \varepsilon) = (r, s, \alpha, 0) \in X \times \mathbb{R}^2 : |r|, |s|, |\alpha| \leq C\}$  such that the function  $(w, z, \alpha, \varepsilon)$  is a positive solution of (2.3) contained in  $N_0$  if and only if*

$$(w, z, \alpha, \varepsilon) = ((r, s) + \varepsilon \mathbf{U}(r, s, \alpha, \varepsilon), \alpha, \varepsilon)$$

and

$$\Phi^\varepsilon(r, s, \alpha) = (I - Q)B((r, s) + \varepsilon \mathbf{U}(r, s, \alpha, \varepsilon), \alpha) = \mathbf{0}.$$

In the extreme case  $\varepsilon = 0$ , we know that

$$\Phi^0(r, s, \alpha) = \left( \begin{array}{c} r \left( \alpha - r + s \int_{\Omega} \frac{b(x)}{1+r\rho(x)} \right) \\ s \left( \int_{\Omega} \frac{1}{1+r\rho(x)} \left( \beta - \frac{s}{1+r\rho(x)} + rd(x) \right) \right) \end{array} \right).$$

Then  $\mathcal{L}_p = \{(r, f(r), g(r)) : r \in \mathbb{R}\} \subseteq \mathcal{N}(\Phi^0)$ , where

$$f(r) = \int_{\Omega} \frac{\beta + rd(x)}{1+r\rho(x)} \Big/ \int_{\Omega} \frac{1}{(1+r\rho(x))^2}, \quad g(r) = r - f(r) \int_{\Omega} \frac{b(x)}{1+r\rho(x)}. \quad (2.4)$$

In fact,  $\mathcal{L}_p$  yields a limiting set of positive solutions of (2.3). More precisely, we have the following two propositions.

**Proposition 2.2.** *Assume  $\beta > 0$ ,  $\|b\|_{\infty}\|d\|_{\infty} < \frac{\min_{\Omega} \rho}{\|\rho\|_{\infty}}$ . Then for a sufficiently large  $A > 0$ , there exist a small constant  $\varepsilon_1 > 0$  and a family of bounded smooth curves*

$$\{S(\xi, \varepsilon) = (r(\xi, \varepsilon), s(\xi, \varepsilon), \alpha(\xi, \varepsilon)) \in \mathbb{R}^3 : (\xi, \varepsilon) \in [0, C_{\varepsilon}] \times [0, \varepsilon_1]\} \quad (2.5)$$

such that for any  $\varepsilon \in (0, \varepsilon_1]$ , all positive solutions of (2.3) with  $\alpha \in [-c\beta\|b\|_{\infty}, A]$  can be expressed by

$$\Gamma^\varepsilon = \left\{ (w(\xi, \varepsilon), z(\xi, \varepsilon), \alpha(\xi, \varepsilon)) = ((r, s) + \varepsilon \mathbf{U}(r, s, \alpha, \varepsilon), \alpha) : (r, s, \alpha) = (r(\xi, \varepsilon), s(\xi, \varepsilon), \alpha(\xi, \varepsilon)), \xi \in (0, C_{\varepsilon}) \right\}, \quad (2.6)$$

where  $\mathbf{U}(r, s, \alpha, \varepsilon)$  is defined in Lemma 2.1,  $S(\xi, 0) = (\xi, f(\xi), g(\xi))$  and  $S(0, \varepsilon) = (0, \beta, \alpha^*(\varepsilon))$ . Here  $\alpha^*(\varepsilon) = \frac{\lambda^*(\varepsilon\beta)}{\varepsilon}$ ,  $C_{\varepsilon}$  is a certain smooth positive function in  $\varepsilon \in [0, \varepsilon_1]$  with  $C_0 = C$  and  $\alpha(C_{\varepsilon}, \varepsilon) = A, w(C_{\varepsilon}, \varepsilon), z(C_{\varepsilon}, \varepsilon) > 0$  in  $\Omega$ .

**Proposition 2.3.** *Assume  $\beta < 0$ ,  $\|b\|_{\infty}\|d\|_{\infty} < \frac{\min_{\Omega} \rho}{\|\rho\|_{\infty}}$ . Then for a sufficiently large number  $A_1 > 0$ , there also exist a small  $\varepsilon_2 > 0$  and a family of bounded curves  $\{S(\xi, \varepsilon) = (\xi, \varepsilon) \in [0, C_{\varepsilon}] \times [0, \varepsilon_2]\}$  of the form (2.5) such that for any fixed  $\varepsilon \in (0, \varepsilon_2]$ , all positive solutions of (2.3) with  $\alpha \in [-\frac{\beta}{\|d\|_{\infty}}, A_1]$  can be expressed by  $\Gamma_{\varepsilon}$  of the form (2.6). Here  $S(\xi, \varepsilon)$  satisfies  $S(\xi, 0) = (r_0 + \xi, f(r_0 + \xi), g(r_0 + \xi))$  and  $S(0, \varepsilon) = (\alpha_*(\varepsilon), 0, \alpha_*(\varepsilon))$ . Moreover,  $\alpha_*(\varepsilon) = \frac{\lambda_*(\varepsilon\beta)}{\varepsilon} > 0$ ,  $C_{\varepsilon}$  is a smooth function in  $[0, \varepsilon_2]$  such that  $C_0 = C_1$  and  $\alpha(C_{\varepsilon}, \varepsilon) = A_1, w(C_{\varepsilon}, \varepsilon), z(C_{\varepsilon}, \varepsilon) > 0$  in  $\Omega$ .*

An analysis of the limiting set  $\{(r, f(r), g(r))\}$  deduces the bifurcation structure of (2.3).

**Theorem 2.4.** Assume  $\beta > 0$ ,  $\|b\|_\infty \|d\|_\infty < \frac{\min_{\bar{\Omega}} \rho}{\|\rho\|_\infty}$ ,  $f_\Omega b(x)\rho(x) < f_\Omega b(x) f_\Omega \rho(x)$ . Then for any small constant  $\eta > 0$ , there exists a small positive number  $\varepsilon_3$  such that if  $(\beta, \varepsilon) \in [\frac{1-f_\Omega d(x) f_\Omega b(x)}{f_\Omega b(x) f_\Omega \rho(x) - f_\Omega b(x)\rho(x)} + \eta, \eta^{-1}] \times [0, \varepsilon_3]$ , the bifurcation direction at  $(0, \beta, \alpha^*(\varepsilon))$  is subcritical, and an unbounded C-shaped curve  $\Gamma^\varepsilon$  bifurcates from  $(0, \beta, \alpha^*(\varepsilon))$ . While if  $(\beta, \varepsilon) \in [\eta, \frac{1-f_\Omega d(x) f_\Omega b(x)}{f_\Omega b(x) f_\Omega \rho(x) - f_\Omega b(x)\rho(x)} - \eta] \times [0, \varepsilon_3]$ , the bifurcation at  $(0, \beta, \alpha^*(\varepsilon))$  is supercritical.

**Theorem 2.5.** Assume  $\beta < 0$ ,  $\|b\|_\infty \|d\|_\infty < \frac{\min_{\bar{\Omega}} \rho}{\|\rho\|_\infty}$ . If  $\min_{\bar{\Omega}} b(x)$  is very large and  $\|d\|_\infty$  is very small such that  $g'(r_0) < 0$ , then for any small number  $\eta > 0$ , there exists  $\varepsilon_4 > 0$  such that if  $(\beta, \varepsilon) \in [-\eta^{-1}, -\eta] \times [0, \varepsilon_4]$ , the bifurcation at  $(\alpha_*(\varepsilon), 0, \alpha_*(\varepsilon))$  is subcritical, and an unbounded C-shaped curve  $\Gamma_\varepsilon$  bifurcates from  $(\alpha_*(\varepsilon), 0, \alpha_*(\varepsilon))$ ; if  $\|b\|_\infty$  is very small such that  $g'(r_0) > 0$ , then the bifurcation at  $(\alpha_*(\varepsilon), 0, \alpha_*(\varepsilon))$  is supercritical for  $(\beta, \varepsilon) \in [-\eta^{-1}, -\eta] \times [0, \varepsilon_4]$ .

The one-to-one correspondence (2.1) between  $(u, v)$  and  $(w, z)$  immediately yields the following result:

**Theorem 2.6.** If  $\mu > 0$  is sufficiently small,  $k$  is sufficiently large, and the assumptions in Theorem 2.4 hold, then the set of positive solutions of (1.3) forms an unbounded smooth curve

$$\Gamma_p = \{(u(x; s), v(x; s), \lambda(s)) : s > 0\}$$

with  $(u(x; 0), v(x; 0), \lambda(0)) = (0, \mu, \lambda^*)$  for a negative number  $\lambda^*$ . Furthermore, there exists a small positive number  $\mu^*$  such that the following hold:

- (i) if  $0 < \mu \leq \mu^*/3$ , then  $\lambda'(0) > 0$ ,  $\Gamma_p$  supercritically bifurcates from  $(0, \mu, \lambda^*)$ ;
- (ii) if  $2\mu^*/3 \leq \mu \leq \mu^*$ , then  $\lambda'(0) < 0$ ,  $\Gamma_p$  subcritically bifurcates from  $(0, \mu, \lambda^*)$ .

**Theorem 2.7.** If  $\mu < 0$  is sufficiently close to 0,  $k$  is sufficiently large, and  $\|b\|_\infty \|d\|_\infty < \frac{\min_{\bar{\Omega}} \rho}{\|\rho\|_\infty}$ , then the set of positive solutions of (1.3) also forms an unbounded smooth curve

$$\Gamma_p = \{(u(x; s), v(x; s), \lambda(s)) : s > 0\},$$

with  $(u(x; 0), v(x; 0), \lambda(0)) = (\lambda_*, 0, \lambda_*)$  for a positive number  $\lambda_*$ . Furthermore, if  $\min b(x)$  is very large and  $\|d(x)\|_\infty$  is very small, the bifurcation direction is subcritical for  $\mu_* \leq \mu < 0$  with some  $\mu_* < 0$ ; if  $\|b\|_\infty$  is very small, the bifurcation direction is supercritical for  $\mu_* \leq \mu < 0$ .

### 3. MAIN RESULTS

In this section, we give the stability and Hopf bifurcation results of positive stationary solutions of (1.2).

Firstly, we truncate  $\Gamma_p$  shown in Theorems 2.6 and 2.7 at every turning point with respect to the bifurcation parameter  $\lambda$ . Denote all the local maximum or minimum points of  $\lambda(\xi)$  in  $(0, C)$  by

$$0 < \xi_1 < \xi_2 < \cdots < \xi_{n-1} < C.$$

Then if  $\mu > 0$ ,  $(u(0), v(0)) = (0, \mu)$ , and  $u(C), v(C) > 0$ ; if  $\mu < 0$ ,  $(u(0), v(0)) = (\lambda_*, 0)$  with  $\lambda_*$  defined in Theorem 2.7, and  $u(C), v(C) > 0$ . It should be noted that  $\lambda(\xi)$  possesses at least one local minimum point if  $\Gamma_p$  is C-shaped. Moreover, we set

$$\Gamma_p(j) = \{(u(\xi), v(\xi), \lambda(\xi)) \in \Gamma_p : \xi \in (\xi_{j-1}, \xi_j)\}$$

for each  $1 \leq j \leq n$  with  $\xi_0 = 0$  and  $\xi_n = C$ . Therefore,

$$\cup_{j=1}^n \Gamma_p(j) = \Gamma_p \setminus \cup_{j=1}^{n-1} \{(u(\xi_j), v(\xi_j), \lambda(\xi_j))\}.$$

As will be shown in Section 4, one can see that, different from the predator-prey system, the number  $n - 1$  of the turning points of  $\lambda(\xi)$  can be determined. More precisely, if  $\Gamma_p$  is C-shaped, then  $n = 2\ell$  for a positive integer  $\ell$ ; if the bifurcation direction is supercritical, then  $n = 2\ell - 1$  for some positive integer  $\ell$ .

Now we show the main results obtained in the paper.

**Theorem 3.1.** *Let  $\mu = \varepsilon\beta > 0$ ,  $k = 1/\varepsilon$ . If the assumptions in Theorem 2.4 hold, then for almost every  $\mu > 0$ , there exist three positive small numbers  $\delta, \mu^*$  and  $\varepsilon_0$  such that when*

$$2\mu^*/3 \leq \mu \leq \mu^*, \quad d_1/d_2 \leq \delta, \quad \varepsilon \leq \varepsilon_0,$$

*then  $n = 2\ell$ , and all positive solutions on  $\Gamma_p(2j)(j = 1, 2, \dots, \ell)$  are asymptotically stable in the topology of  $X$ , while all positive solutions on  $\Gamma_p(2j-1)(j = 1, 2, \dots, \ell)$  are unstable; when*

$$0 < \mu \leq \mu^*/3, \quad d_1/d_2 \leq \delta, \quad \varepsilon \leq \varepsilon_0,$$

*then  $n = 2\ell - 1$ , and all positive solutions on  $\Gamma_p(2j-1)(j = 1, 2, \dots, \ell)$  are asymptotically stable in the topology of  $X$ , while all positive solutions on  $\Gamma_p(2j)(j = 1, 2, \dots, \ell - 1)$  are unstable.*

**Theorem 3.2.** *Let  $\mu = \varepsilon\beta < 0$ ,  $k = 1/\varepsilon$ , and  $\|b\|_\infty \|d\|_\infty < \min_{\bar{\Omega}} \rho / \|\rho\|_\infty$ . Then if  $\min_{\bar{\Omega}} b(x)$  is very large and  $\|d\|_\infty$  is very small, for almost every  $\mu < 0$ , there exist three positive small numbers  $\delta, -\mu_*$  and  $\varepsilon_0$  such that when*

$$\mu_* \leq \mu < 0, \quad d_1/d_2 \leq \delta, \quad \varepsilon \leq \varepsilon_0,$$

*the first stability conclusion in Theorem 3.1 holds; if  $\|b\|_\infty$  is very small, then under the same conditions, the second stability conclusion in Theorem 3.1 holds.*

From Theorems 3.1 and 3.2, we see that when the spatial heterogeneity produces multiple positive stationary solutions in the subcritical case, if  $u$  moves much slower than  $v$ , then at least one of the multiple positive stationary solutions is unstable and the other one is stable. In particular, unstable positive stationary solutions bifurcate from semitrivial solutions, which implies that the spatial heterogeneity cannot have a strongly beneficial effect on the species in low densities.

Next we assume that the segregation condition of  $b(x)$  and  $\rho(x)$

$$\int_{\Omega} \frac{b(x)}{1+r\rho(x)} \int_{\Omega} \frac{\rho(x)}{(1+r\rho(x))^2} > \int_{\Omega} \frac{b(x)\rho(x)}{(1+r\rho(x))^2} \int_{\Omega} \frac{1}{1+r\rho(x)} \tag{3.1}$$

holds for  $r \in [r_0, C_0 + r_0]$  in case  $\beta < 0$ . In fact, we can show that (3.1) does hold under a spatial segregation of  $b(x)$  and  $\rho(x)$ . Precisely, for any small  $\varepsilon$  satisfying  $\varepsilon < \frac{\int_{\Omega} b(x)}{1+(C_0+r_0)\|\rho\|_\infty}$ , if  $\text{supp } \rho \cap \text{supp}(b - \varepsilon)_+ = \emptyset$ , then

$$\begin{aligned} \int_{\Omega} \frac{1}{1+r\rho(x)} \int_{\Omega} \frac{b(x)\rho(x)}{(1+r\rho(x))^2} &\leq \varepsilon \int_{\Omega} \frac{1}{1+r\rho(x)} \int_{\Omega} \frac{\rho(x)}{(1+r\rho(x))^2} \\ &\leq \varepsilon \int_{\Omega} \frac{\rho(x)}{(1+r\rho(x))^2} \\ &< \int_{\Omega} \frac{b(x)}{1+(C_0+r_0)\|\rho\|_\infty} \int_{\Omega} \frac{\rho(x)}{(1+r\rho(x))^2} \end{aligned}$$

$$\leq \int_{\Omega} \frac{b(x)}{1+r\rho(x)} \int_{\Omega} \frac{\rho(x)}{(1+r\rho(x))^2}.$$

**Remark 3.3.** We point out that the segregation condition (3.1) is equivalent to

$$\int_{\Omega} \int_{\Omega} \frac{(b(x) - b(y))(\rho(x) - \rho(y))}{(1+r\rho(x))^2(1+r\rho(y))^2} < 0. \quad (3.2)$$

From the equivalent inequality (3.2), we see that if  $\rho(x) = f(b(x))$  for some strictly decreasing function  $f$  and  $b(x) \not\equiv \text{constant}$ , then (3.2) holds, i.e., (3.1) holds. In particular, when the spatial dimension is 1 and  $\Omega$  is an interval, if  $b(x)$  is strictly increasing and  $\rho(x)$  is strictly decreasing, then (3.1) and (3.2) also hold.

Therefore, the segregation between  $b(x)$  and  $\rho(x)$  does hold under certain circumstances.

One will see that if  $d_1/d_2$  becomes sufficiently large, the segregation of  $\rho(x)$  and  $b(x)$  can cause Hopf bifurcation on the positive stationary solutions of  $\Gamma_p$  in case  $\mu < 0$ .

**Theorem 3.4.** *Let  $\mu = \varepsilon\beta < 0$ ,  $k = 1/\varepsilon$ , and  $\|b\|_{\infty}\|d\|_{\infty} < \min_{\bar{\Omega}} \rho/\|\rho\|_{\infty}$ . Suppose  $b(x)$  and  $\rho(x)$  satisfy the segregation condition (3.1). Then if  $-\beta$  is sufficiently large, and  $\|b\|_{\infty}$  is small, there exist a large number  $D > 0$  and a small number  $\varepsilon_0 > 0$  such that if  $\frac{d_1}{d_2} \geq D$  and  $\varepsilon \leq \varepsilon_0$ , Hopf bifurcation appears at a certain point on  $\Gamma_p$ .*

Note that in Theorem 3.4, small  $\|b\|_{\infty}$  deduces  $g'(r_0) > 0$ . Thus, the bifurcation curve is not fish-hook shaped.

By the stability result in Section 4 and the Hopf bifurcation result in Section 5, we can see much clearer that: when  $d_1/d_2$  is small enough, the stability is rather clear, and no Hopf bifurcation occurs due to (4.7); while as  $d_1/d_2$  becomes large, some stable positive stationary solutions bifurcating from  $(\lambda_*, 0)$  for  $\mu < 0$  will lose their stability, and Hopf bifurcation occurs.

#### 4. STABILITY ANALYSIS

In the section, we will deduce the stability result of positive stationary solutions of (2.2). Since the change of variables in (2.1) is regular, the stability of positive stationary solutions  $(w, z) = (u/\varepsilon, (1+k\rho(x)u)v/\varepsilon)$  of (2.2) immediately yields that of the positive stationary solutions  $(u, v)$  of (1.2). Therefore, we only need to study the stability of positive stationary solutions on  $\Gamma^{\varepsilon}$  and  $\Gamma_{\varepsilon}$  given in Propositions 2.2 and 2.3.

**4.1. Linearized Stability.** We firstly deduce the linearized stability. Note that the positive stationary solutions of (2.2) with  $\alpha \in [-c\beta\|b\|_{\infty}, A]$  in case  $\beta > 0$  and  $\alpha \in [-\beta/\|d\|_{\infty}, A_1]$  in case  $\beta < 0$  can be parameterized as

$$\Gamma^{\varepsilon}(\Gamma_{\varepsilon}) = \{(w(\xi, \varepsilon), z(\xi, \varepsilon), \alpha(\xi, \varepsilon)) : \xi \in (0, C_{\varepsilon})\}$$

for small  $\varepsilon > 0$ . Then for any  $(w(\xi, \varepsilon), z(\xi, \varepsilon), \alpha(\xi, \varepsilon)) \in \Gamma^{\varepsilon}(\Gamma_{\varepsilon})$ , we define the linearized operator  $L(\xi, \varepsilon) : X \rightarrow Y$  by

$$L(\xi, \varepsilon) \begin{pmatrix} h \\ k \end{pmatrix} = H \begin{pmatrix} h \\ k \end{pmatrix} + \varepsilon B_{(w,z)}(w(\xi, \varepsilon), z(\xi, \varepsilon), \alpha(\xi, \varepsilon)) \begin{pmatrix} h \\ k \end{pmatrix},$$



where  $B_{(w,z)}$  denotes the Fréchet derivative of  $B$  with respect to  $(w, z)$ . By virtue of the left-hand side of (2.2), we further set

$$J(\xi, \varepsilon) = \begin{pmatrix} \frac{1}{d_1} & 0 \\ -\frac{\rho(x)z(\xi, \varepsilon)}{d_2(1+\rho(x)w(\xi, \varepsilon))^2} & \frac{1}{d_2(1+\rho(x)w(\xi, \varepsilon))} \end{pmatrix}.$$

Substituting

$$(w, z) = (w(\xi, \varepsilon) + he^{-\lambda t}, z(\xi, \varepsilon) + ke^{-\lambda t})$$

into (2.2) and neglecting the higher order terms, one sees that the linearized eigenvalue problem associated with  $(w(\xi, \varepsilon), z(\xi, \varepsilon))$  is given by

$$L(\xi, \varepsilon) \begin{pmatrix} h \\ k \end{pmatrix} = -\lambda J(\xi, \varepsilon) \begin{pmatrix} h \\ k \end{pmatrix}. \tag{4.1}$$

In the following, we use the spectral theory to show the linearized stability of positive stationary solutions on  $\Gamma^\varepsilon(\Gamma_\varepsilon)$ .

**Lemma 4.1.** *Let  $\{\lambda_j(\xi, \varepsilon)\}$  ( $\text{Re } \lambda_j(\xi, \varepsilon) \leq \text{Re } \lambda_{j+1}(\xi, \varepsilon)$ ) be the eigenvalues (counting multiplicity) of (4.1). If  $\varepsilon > 0$  is sufficiently small, then the following holds:*

$$\lim_{\varepsilon \rightarrow 0} \lambda_1(\xi, \varepsilon) = \lim_{\varepsilon \rightarrow 0} \lambda_2(\xi, \varepsilon) = 0$$

and  $\text{Re } \lambda_j(\xi, \varepsilon) > \kappa$  for  $j \geq 3$  and  $\xi \in (0, C_\varepsilon)$  with some positive constant  $\kappa$  independent of  $(\xi, \varepsilon)$ .

*Proof.* We give only the proof of the case  $\beta > 0$ , since the proof of the case  $\beta < 0$  is similar. Proposition 2.2 asserts that

$$(w(\xi, \varepsilon), z(\xi, \varepsilon), \alpha(\xi, \varepsilon)) \rightarrow (\xi, f(\xi), g(\xi)) \quad \text{in } C^1(\bar{\Omega}) \times C^1(\bar{\Omega}) \times \mathbb{R}$$

as  $\varepsilon \rightarrow 0$  for any  $\xi \in (0, C_\varepsilon)$ . Then as  $\varepsilon \rightarrow 0$ , (4.1) reduces to

$$\begin{aligned} -d_1 \Delta h &= \lambda h, & x \in \Omega, \\ -d_2 \Delta k &= \lambda \left( \frac{1}{1 + \xi \rho(x)} k - \frac{\rho(x) f(\xi)}{(1 + \xi \rho(x))^2} h \right), & x \in \Omega, \\ \partial_\nu h &= \partial_\nu k = 0, & x \in \partial\Omega. \end{aligned} \tag{4.2}$$

The eigenvalues of (4.2) comprise only  $\{\bar{\lambda}_j\} \cup \{\tilde{\lambda}_j\}$ , where  $\bar{\lambda}_j$  and  $\tilde{\lambda}_j$  are eigenvalues of

$$\begin{aligned} -d_1 \Delta h &= \lambda h, & x \in \Omega, \\ \partial_\nu h &= 0, & x \in \partial\Omega, \end{aligned} \tag{4.3}$$

and

$$\begin{aligned} -d_2 \Delta k &= \lambda \frac{1}{1 + \xi \rho(x)} k, & x \in \Omega, \\ \partial_\nu k &= 0, & x \in \partial\Omega, \end{aligned} \tag{4.4}$$

respectively. Since both of the principal eigenvalues of (4.3) and (4.4) are zero, and all the other eigenvalues possess positive real parts and are bounded away from zero. Thus the limiting problem (4.2) has a double eigenvalue  $\lambda = 0$ , and the other eigenvalues have positive real parts. Then the perturbation theory by Kato [17, Chapter 8] yields the lemma.  $\square$

As  $\{\lambda_j(\xi, \varepsilon)\}$  is a symmetric set with respect to the real axis in  $\mathbb{C}$ , the eigenvalues  $\lambda_1(\xi, \varepsilon)$  and  $\lambda_2(\xi, \varepsilon)$  (shown in Lemma 4.1) must satisfy either (i) or (ii):

- (i) both of  $\lambda_1(\xi, \varepsilon)$  and  $\lambda_2(\xi, \varepsilon)$  are real numbers;
- (ii)  $\lambda_1(\xi, \varepsilon)$  is a complex conjugate of  $\lambda_2(\xi, \varepsilon)$ .

In the sequel, we always assume that  $\operatorname{Re} \lambda_1(\xi, \varepsilon) \leq \operatorname{Re} \lambda_2(\xi, \varepsilon)$  and  $\operatorname{Im} \lambda_1(\xi, \varepsilon) \geq \operatorname{Im} \lambda_2(\xi, \varepsilon)$ .

The definition of the linearized stability of positive stationary solutions on  $\Gamma^\varepsilon(\Gamma_\varepsilon)$  can be given as follows.

**Definition 4.2.** If  $\operatorname{Re} \lambda_1(\xi, \varepsilon) > 0$ , then  $(w(\xi, \varepsilon), z(\xi, \varepsilon))$  of (2.2) is called linearly stable; if  $\operatorname{Re} \lambda_1(\xi, \varepsilon) < 0$ , it is called linearly unstable.

From the definition, we see that the linearized stability of any positive stationary solution  $(w(\xi, \varepsilon), z(\xi, \varepsilon))$  on  $\Gamma^\varepsilon(\Gamma_\varepsilon)$  is determined by the sign of  $\operatorname{Re} \lambda_1(\xi, \varepsilon)$ . A similar argument to that of Lemma 5.3 in [19] or Lemma 4.3 in [20] can further deduce the following lemma associated with  $\lambda_1(\xi, \varepsilon)$  and  $\lambda_2(\xi, \varepsilon)$ .

**Lemma 4.3.** Let  $\lambda_1(\xi, \varepsilon)$  and  $\lambda_2(\xi, \varepsilon)$  be eigenvalues of (4.1) shown in Lemma 4.1. Then for any fixed  $r \in (0, C_0)$ , we have

$$\lim_{(\xi, \varepsilon) \rightarrow (r, 0)} \frac{\lambda_j(\xi, \varepsilon)}{\varepsilon} = \mu_j(r) \quad (j = 1, 2)$$

in the case  $\beta > 0$ ; and

$$\lim_{(\xi, \varepsilon) \rightarrow (r, 0)} \frac{\lambda_j(\xi, \varepsilon)}{\varepsilon} = \mu_j(r + r_0) \quad (j = 1, 2)$$

in the case  $\beta < 0$ , where  $\mu_j(r)$  satisfying  $\operatorname{Re} \mu_1(r) \leq \operatorname{Re} \mu_2(r)$  and  $\operatorname{Im} \mu_1(r) \geq \operatorname{Im} \mu_2(r)$  are eigenvalues of

$$M(r) = -J(r)^{-1} \Phi_{(r,s)}^0(r, f(r), g(r)), \quad (4.5)$$

where  $\Phi_{(r,s)}^0(r, f(r), g(r))$  denotes the Jacobian matrix of  $\Phi^0$ , and

$$J(r) = \begin{pmatrix} \frac{1}{d_1} & 0 \\ -\frac{f(r)}{d_2} f_\Omega \frac{\rho(x)}{(1+r\rho(x))^2} & f_\Omega \frac{1}{d_2(1+r\rho(x))} \end{pmatrix}.$$

By some calculations, we can show that

$$\begin{aligned} & \Phi_{(r,s)}^0(r, f(r), g(r)) \\ &= \begin{pmatrix} -r[1 + f(r) f_\Omega \frac{b(x)\rho(x)}{(1+r\rho(x))^2}] & r f_\Omega \frac{b(x)}{1+r\rho(x)} \\ f(r) [f_\Omega \frac{d(x)-\beta\rho(x)}{(1+r\rho(x))^2} + 2f(r) f_\Omega \frac{\rho(x)}{(1+r\rho(x))^3}] & -f(r) f_\Omega \frac{1}{(1+r\rho(x))^2} \end{pmatrix}. \end{aligned}$$

It can also be verified that

$$\Phi_{(r,s)}^0(r, f(r), g(r)) = \begin{pmatrix} -r[g'(r) + f'(r) f_\Omega \frac{b(x)}{1+r\rho(x)}] & r f_\Omega \frac{b(x)}{1+r\rho(x)} \\ f(r) f'(r) f_\Omega \frac{1}{(1+r\rho(x))^2} & -f(r) f_\Omega \frac{1}{(1+r\rho(x))^2} \end{pmatrix},$$

from which we know that

$$\det \Phi_{(r,s)}^0(r, f(r), g(r)) = r f(r) g'(r) \int_\Omega \frac{1}{(1+r\rho(x))^2}. \quad (4.6)$$

By the perturbation theory of the Fredholm operator developed by Du and Lou [11], we can further deduce the following lemma characterizing the degenerate solution ( $\lambda_1(\xi, \varepsilon) = 0$  or  $\lambda_2(\xi, \varepsilon) = 0$  for some  $\xi \in (0, C_\varepsilon)$ ).

**Lemma 4.4.** *Assume that  $\varepsilon > 0$  is small enough. Then  $(w(\xi^*, \varepsilon), z(\xi^*, \varepsilon), \alpha(\xi^*, \varepsilon))$  for some  $\xi^* \in (0, C_\varepsilon)$  is a degenerate solution if and only if*

$$\partial_\xi \alpha(\xi^*, \varepsilon) = 0.$$

Next we show that  $\lim_{r \rightarrow +\infty} g'(r) > 0$ . Due to (2.4), some calculations yield that

$$g'(r) = 1 - f'(r) \int_\Omega \frac{b(x)}{1 + r\rho(x)} + f(r) \int_\Omega \frac{b(x)\rho(x)}{(1 + r\rho(x))^2}$$

and

$$\lim_{r \rightarrow +\infty} g'(r) = 1 - \int_\Omega \frac{b(x)}{\rho(x)} \int_\Omega \frac{d(x)}{\rho(x)} \left( \int_\Omega \frac{1}{\rho^2(x)} \right)^{-1}.$$

Thus under the weak cooperation condition,  $\lim_{r \rightarrow +\infty} g'(r) > 0$  holds true. Then for large number  $C_0$  shown in Propositions 2.2 and 2.3, we have that

$$g'(C_0) > 0 \quad \text{and} \quad g'(C_0 + r_0) > 0.$$

Since  $g$  is analytic, and  $g'(r) > 0$  for all large  $r$ ,  $g'(r) = 0$  must possess at most finitely many solutions  $r_i$ . Then the finiteness deduces that any zero of  $g'$  must be a strictly critical point of  $g$  for almost every  $\beta$ . For such  $\beta$ , we denote all the zeros of  $\partial_\xi \alpha(\xi, \varepsilon)$  by

$$0 < \xi_1(\varepsilon) < \xi_2(\varepsilon) < \dots < \xi_{n-1}(\varepsilon) < C_\varepsilon$$

when  $\varepsilon > 0$  is sufficiently small. So,

$$(w_i, z_i, \alpha^i) = (w(\xi_i(\varepsilon), \varepsilon), z(\xi_i(\varepsilon), \varepsilon), \alpha(\xi_i(\varepsilon), \varepsilon)) \quad \text{for } 1 \leq i \leq n - 1$$

are all turning points on  $\Gamma^\varepsilon(\Gamma_\varepsilon)$  with respect to the bifurcation parameter  $\alpha$  in either case  $\beta > 0$  or case  $\beta < 0$ . Then we truncate  $\Gamma^\varepsilon(\Gamma_\varepsilon)$  at every turning point as

$$\Gamma^\varepsilon(i)(\Gamma_\varepsilon(i)) = \{(w(\xi, \varepsilon), z(\xi, \varepsilon), \alpha(\xi, \varepsilon)) : \xi \in (\xi_{i-1}(\varepsilon), \xi_i(\varepsilon))\}$$

for  $1 \leq i \leq n$ , with  $\xi_0(\varepsilon) = 0$  and  $\xi_n(\varepsilon) = C_\varepsilon$ . Therefore,

$$\cup_{i=1}^n \Gamma^\varepsilon(i)(\Gamma_\varepsilon(i)) = \Gamma^\varepsilon(\Gamma_\varepsilon) \setminus \cup_{i=1}^{n-1} \{(w_i, z_i, \alpha^i)\}.$$

**Lemma 4.5.** *For almost every  $\beta > 0$ , under the assumptions of Theorem 2.4, there exist two small positive constants  $\delta$  and  $\varepsilon_0$  such that if  $d_1/d_2 \leq \delta$ ,  $\varepsilon \leq \varepsilon_0$  and the bifurcation at  $(0, \beta, \alpha^*)$  is subcritical, then  $n = 2\ell$  for some positive integer  $\ell$ , and all positive stationary solutions are linearly unstable on  $\Gamma^\varepsilon(2j - 1)(j = 1, 2, \dots, \ell)$ , and linearly stable on  $\Gamma^\varepsilon(2j)(j = 1, 2, \dots, \ell)$ ; if the bifurcation direction is supercritical, then  $n = 2\ell - 1$ , and all positive stationary solutions are linearly stable on  $\Gamma^\varepsilon(2j - 1)(j = 1, 2, \dots, \ell)$ , and linearly unstable on  $\Gamma^\varepsilon(2j)(j = 1, 2, \dots, \ell - 1)$ .*

*Proof.* From the expression of  $M(r)$ , we can obtain that

$$\begin{aligned} & (\mu_1(r) + \mu_2(r)) \int_\Omega \frac{1}{1 + r\rho(x)} \\ &= d_2 \left\{ f(r) \int_\Omega \frac{1}{(1 + r\rho(x))^2} + \frac{rd_1}{d_2} \left[ \int_\Omega \frac{1}{1 + r\rho(x)} - f(r)K(r) \right] \right\}, \end{aligned}$$

where

$$K(r) = \int_\Omega \frac{b(x)}{1 + r\rho(x)} \int_\Omega \frac{\rho(x)}{(1 + r\rho(x))^2} - \int_\Omega \frac{b(x)\rho(x)}{(1 + r\rho(x))^2} \int_\Omega \frac{1}{1 + r\rho(x)}.$$

Then if  $\frac{d_1}{d_2}$  is sufficiently small, we have

$$\mu_1(r) + \mu_2(r) > 0 \quad \text{for } r \in [0, C_0].$$

So Lemma 4.3 yields that if  $\varepsilon > 0$  is sufficiently small,

$$\lambda_1(\xi, \varepsilon) + \lambda_2(\xi, \varepsilon) > 0 \quad \text{for } \xi \in [0, C_\varepsilon]. \quad (4.7)$$

Furthermore, we can show that

$$\mu_1(r)\mu_2(r) = d_1 d_2 r f(r) g'(r) \int_{\Omega} \frac{1}{(1+r\rho(x))^2} \left( \int_{\Omega} \frac{1}{1+r\rho(x)} \right)^{-1},$$

which means that

$$\text{sign } \mu_1(r)\mu_2(r) = \text{sign } g'(r) \quad \text{for } r \in (0, C_0). \quad (4.8)$$

Therefore, for any fixed  $r \in (0, C_0)$ , if  $g'(r) > 0$  and  $(\xi, \varepsilon)$  is near  $(r, 0)$ , then  $\lambda_1(\xi, \varepsilon)\lambda_2(\xi, \varepsilon) > 0$ . Together with (4.7), we deduce that  $\text{Re } \lambda_1(\xi, \varepsilon) > 0$ ; while if  $g'(r) < 0$  and  $(\xi, \varepsilon)$  is near  $(r, 0)$ , then  $\lambda_1(\xi, \varepsilon)\lambda_2(\xi, \varepsilon) < 0$ , and  $\text{Re } \lambda_1(\xi, \varepsilon) < 0$ . Moreover, if  $\varepsilon > 0$  is sufficiently small,  $\text{Re } \lambda_2(\xi, \varepsilon) > 0$  holds for all  $\xi \in [0, C_\varepsilon]$  by (4.7), then  $\lambda_1(\xi, \varepsilon) = 0$  if and only if  $\xi = \xi_i(\varepsilon)$  for some  $1 \leq i \leq n-1$ .

Additionally, under the assumptions of Theorem 2.4, we know that if the bifurcation direction is subcritical, then  $g'(0) < 0$  and  $g'(C_0) > 0$ . Then the number  $n-1$  of turning points of  $\alpha(\xi)$  must be odd. If the bifurcation direction is supercritical, then  $g'(0) > 0$ ,  $g'(C_0) > 0$ , and  $n-1$  is even. Thus the conclusions in the lemma are proved.  $\square$

In the case  $\beta < 0$ , since

$$\mu_1(r_0) + \mu_2(r_0) = r_0 d_1 > 0,$$

we see that  $\mu_1(r) + \mu_2(r) > 0$  for  $r \in [r_0, r_0 + \delta]$  with a small positive number  $\delta$ . By virtue of  $f(r) > 0$  for  $r \in [r_0 + \delta, C_0 + r_0]$ , we can further choose  $d_1/d_2$  sufficiently small such that

$$\mu_1(r) + \mu_2(r) > 0 \quad \text{for } r \in [r_0 + \delta, C_0 + r_0].$$

Combining the above, we know

$$\mu_1(r) + \mu_2(r) > 0 \quad \text{for } r \in [r_0, C_0 + r_0].$$

A similar argument to the proof of Lemma 4.5 deduces the following lemma.

**Lemma 4.6.** *For almost every  $\beta < 0$ , under the assumptions of Theorem 2.5, there exist two small positive constants  $\delta$  and  $\varepsilon_0$  such that if  $d_1/d_2 \leq \delta$ ,  $\varepsilon \leq \varepsilon_0$  and the bifurcation at  $(\alpha_*, 0, \alpha_*)$  is subcritical, then the same conclusions as those of the subcritical case shown in Lemma 4.5 hold; if the bifurcation direction is supercritical, then the same conclusions as those of the supercritical case shown in Lemma 4.5 hold*

From Lemmas 4.5 and 4.6, together with [20, Lemma 4.5] and [19, Lemma 5.5], we can see that under large cross-diffusion effect for one species and comparatively small natural diffusion effect for the other species, the stability of positive stationary solutions changes at every turning point of the bifurcation curve with respect to the bifurcation parameter in either Neumann or Dirichlet boundary condition.

**Remark 4.7.** As pointed out in the previous paper, if all coefficients are spatially homogeneous; i.e.,  $\rho(x) \equiv \text{const.}$ ,  $b(x) \equiv \text{const.}$  and  $d(x) \equiv \text{const.}$ , then

$$f(r) = (\beta + rd)(1 + r\rho), \quad g(r) = r - b(\beta + rd).$$

Under the weak cooperation condition  $bd < 1$ , we have  $g'(r) = 1 - bd > 0$ . Thus when  $\varepsilon > 0$  is small enough,

$$\alpha_\xi(\xi, \varepsilon) > 0.$$

Then (2.3) has a unique positive solution if  $\alpha \in (\alpha^*(\varepsilon), \infty)$  and no positive solutions if  $\alpha \leq \alpha^*(\varepsilon)$  in case  $\beta > 0$ . If  $\beta < 0$ ,  $\alpha^*(\varepsilon)$  should be replaced by  $\alpha_*(\varepsilon)$ .

Next, we look at the linearized stability of the unique positive solution on the bifurcation curve. At this time,

$$\mu_1(r) + \mu_2(r) = d_2 \left( \beta + rd + r \frac{d_1}{d_2} \right).$$

Then if  $\beta > 0$ ,  $\mu_1(r) + \mu_2(r) > 0$  always holds for  $r \in [0, C_0]$  regardless of the values of  $d_1, d_2, r$  and  $d$ ; if  $\beta < 0$ , since  $r \geq r_0$ ,  $\mu_1(r) + \mu_2(r) > 0$  also holds for  $r \in [r_0, C_0 + r_0]$ . Furthermore,

$$\text{sign } \mu_1(r)\mu_2(r) = \text{sign } g'(r) > 0.$$

So we see that if the environment is homogeneous, all the unique positive stationary solutions are linearly stable, non-degenerate and Hopf bifurcation can never occur on  $\Gamma^\varepsilon(\Gamma_\varepsilon)$ .

Whereas, when the environment is heterogeneous and the heterogeneity causes multiple positive stationary solutions, if the natural diffusion rate  $d_1$  of the first cooperator is very small comparatively to that of the second cooperator, then at least one of the multiple coexistence states is unstable. Furthermore, Hopf bifurcation can be shown to occur under suitable conditions in Section 5, which is quite different from that of the homogeneous environment.

**4.2. Asymptotic stability.** By the linearization principle for quasilinear parabolic equations developed by Potier-Ferry [31], and the interpolation spaces  $[X, Y]_{\theta, p}$  ( $0 \leq \theta \leq 1$ ) in the sense of Lions-Peetre [24], we can show that the linearized stability implies the asymptotic stability. One can refer to [20] and [19] for the details. More precisely, we have the following lemma:

**Lemma 4.8.** *Under the assumptions of Lemmas 4.5 and 4.6, all linearly stable positive stationary solutions on  $\Gamma^\varepsilon$  or  $\Gamma_\varepsilon$  are asymptotically stable in the topology of  $X$ , and all linearly unstable positive stationary solutions on  $\Gamma^\varepsilon$  or  $\Gamma_\varepsilon$  are unstable.*

The regularity of the scaling (2.1) immediately yields Theorems 3.1 and 3.2.

## 5. HOPF BIFURCATION

In this section, we will give the Hopf bifurcation of positive stationary solutions of (2.2). To do so, set

$$\beta = m\tilde{\beta}, \quad d(x) = m\tilde{d}(x)$$

for  $\tilde{\beta} \in \mathbb{R}$  and nonnegative function  $\tilde{d}(x)$ . Then  $f(r)$  can be expressed as

$$f(r) = m \int_{\Omega} \frac{\tilde{\beta} + r\tilde{d}(x)}{1 + r\rho(x)} \left( \int_{\Omega} \frac{1}{(1 + r\rho(x))^2} \right)^{-1}.$$

In the case  $\beta > 0$ , we failed to obtain Hopf bifurcation on the bifurcation continuum. To the best of our knowledge, we can only give Hopf bifurcation when  $\beta < 0$  and the bifurcation direction at  $(\alpha_*, 0)$  is supercritical.

**Proposition 5.1.** *Assume  $\beta < 0$ ,  $\|b\|_\infty \|d\|_\infty < \frac{\min_{\bar{\Omega}} \rho}{\|\rho\|_\infty}$ ,  $\|b\|_\infty$  is very small such that the bifurcation at  $(\alpha_*, 0)$  is supercritical, then if  $\rho(x)$  and  $b(x)$  satisfy the segregation condition (3.1), and  $m > 0$  is sufficiently large, there exist a large number  $D > 0$  and a small number  $\varepsilon_0 > 0$  such that if  $d_1/d_2 \geq D$  and  $\varepsilon \leq \varepsilon_0$ , Hopf bifurcation occurs at a certain point on  $\Gamma^\varepsilon$ .*

*Proof.* To prove the proposition, we take two steps: at the first step, we show that under the conditions of the proposition, for the eigenvalues  $\mu_1(r)$  and  $\mu_2(r)$  of  $M(r)$  defined by (4.5), there exists  $\bar{r} > r_0$  such that  $\mu_1(\bar{r}) + \mu_2(\bar{r}) = 0$ ,  $\mu_1(\bar{r})\mu_2(\bar{r}) > 0$  and  $\mu'_1(\bar{r}) + \mu'_2(\bar{r}) < 0$ .

Note that

$$K(r) = \int_{\Omega} \frac{b(x)}{1+r\rho(x)} \int_{\Omega} \frac{\rho(x)}{(1+r\rho(x))^2} - \int_{\Omega} \frac{b(x)\rho(x)}{(1+r\rho(x))^2} \int_{\Omega} \frac{1}{1+r\rho(x)} > 0$$

for  $r \in [r_0, C_0 + r_0]$  is assumed. Due to the expression of  $f(r)$ ,

$$\begin{aligned} f(r)K(r) - \int_{\Omega} \frac{1}{1+r\rho(x)} \\ = m \int_{\Omega} \frac{\tilde{\beta} + r\tilde{d}(x)}{1+r\rho(x)} \left( \int_{\Omega} \frac{1}{(1+r\rho(x))^2} \right)^{-1} K(r) - \int_{\Omega} \frac{1}{1+r\rho(x)}. \end{aligned}$$

There exists a large number  $M_1 > 0$  such that if  $m \geq M_1$ ,

$$f(r)K(r) - \int_{\Omega} \frac{1}{1+r\rho(x)} > 0 \quad \text{for } r \in [r_0, C_0 + r_0].$$

As

$$\begin{aligned} \mu_1(r) + \mu_2(r) = d_2 \left\{ f(r) \int_{\Omega} \frac{1}{(1+r\rho(x))^2} \left( \int_{\Omega} \frac{1}{1+r\rho(x)} \right)^{-1} \right. \\ \left. - \frac{rd_1}{d_2} [f(r)K(r) \left( \int_{\Omega} \frac{1}{1+r\rho(x)} \right)^{-1} - 1] \right\}, \end{aligned}$$

then

$$\mu_1(r_0) + \mu_2(r_0) = r_0 d_1 > 0.$$

Furthermore, (4.8) implies that  $\mu_1(r_0)\mu_2(r_0) > 0$ . Since

$$\begin{aligned} \mu'_1(r_0) + \mu'_2(r_0) = d_2 \left[ f'(r_0) \int_{\Omega} \frac{1}{(1+r_0\rho(x))^2} \left( \int_{\Omega} \frac{1}{1+r_0\rho(x)} \right)^{-1} \right. \\ \left. - \frac{d_1}{d_2} \left( r_0 f'(r_0) K(r_0) \left( \int_{\Omega} \frac{1}{1+r_0\rho(x)} \right)^{-1} - 1 \right) \right], \end{aligned}$$

$$f'(r_0) = m \int_{\Omega} \frac{\tilde{d}(x) - \tilde{\beta}\rho(x)}{(1+r_0\rho(x))^2} \left( \int_{\Omega} \frac{1}{(1+r_0\rho(x))^2} \right)^{-1} > 0,$$

there exists a large number  $M \geq M_1$  such that if  $m \geq M$ ,

$$r_0 f'(r_0) K(r_0) \left( \int_{\Omega} \frac{1}{1+r_0\rho(x)} \right)^{-1} > 1.$$

Then for fixed large  $m \geq M$ , we can choose  $d_1/d_2$  sufficiently large such that  $\mu'_1(r_0) + \mu'_2(r_0) < 0$ . By virtue of the expression of  $\mu_1(r) + \mu_2(r)$ , one sees that if  $d_1/d_2$  and  $m$  are large, there exists  $\bar{r} > r_0$  such that

$$\begin{aligned} \mu_1(r) + \mu_2(r) > 0 \quad \text{for } r \in (r_0, \bar{r}), \\ \mu_1(\bar{r}) + \mu_2(\bar{r}) = 0 \quad \text{and} \quad \mu'_1(\bar{r}) + \mu'_2(\bar{r}) < 0. \end{aligned} \tag{5.1}$$

In the following, if we find positive numbers  $\xi^*$  and  $\varepsilon$  such that  $\lambda_1(\xi^*, \varepsilon)$  and  $\lambda_2(\xi^*, \varepsilon)$  form a pure imaginary pair and satisfy  $\partial_\xi(\lambda_1(\xi^*, \varepsilon) + \lambda_2(\xi^*, \varepsilon)) < 0$ , then the abstract Hopf bifurcation theorem for strongly coupled parabolic equations from Amann [4] (see also [10]) can deduce the proposition. This is our step two.

To show this, by Lemma 4.3, we apply the implicit function theorem to construct the eigenvalue  $\lambda$  and its corresponding eigenfunction  $(\phi, \psi)$  of (4.1) as the forms

$$\lambda = \varepsilon\nu, \quad (\phi, \psi) = (1, \eta) + \varepsilon\mathbf{V}, \quad \mathbf{V} \in X_1.$$

Substituting  $\lambda$  and  $(\phi, \psi)$  of this form into (4.1), we obtain

$$H((1, \eta) + \varepsilon\mathbf{V}) + \varepsilon\hat{B}(\xi, \varepsilon)[(1, \eta) + \varepsilon\mathbf{V}] + \varepsilon\nu J(\xi, \varepsilon)[(1, \eta) + \varepsilon\mathbf{V}] = 0,$$

where  $\hat{B}(\xi, \varepsilon) = B_{(w,z)}(w(\xi, \varepsilon), z(\xi, \varepsilon), \alpha(\xi, \varepsilon))$ . Then after defining the mapping  $G : \mathbb{R}^2 \times \mathbb{C}^2 \times X_1 \rightarrow Y$  by

$$G(\xi, \varepsilon, \nu, \eta, \mathbf{V}) = H((1, \eta) + \varepsilon\mathbf{V}) + \varepsilon\hat{B}(\xi, \varepsilon)[(1, \eta) + \varepsilon\mathbf{V}] + \varepsilon\nu J(\xi, \varepsilon)[(1, \eta) + \varepsilon\mathbf{V}],$$

the eigenvalue problem (4.1) is equivalent to

$$G(\xi, \varepsilon, \nu, \eta, \mathbf{V}) = \mathbf{0}.$$

We further decompose this equation as

$$\begin{aligned} (I - Q)\hat{B}(\xi, \varepsilon)[(1, \eta) + \varepsilon\mathbf{V}] + \nu(I - Q)J(\xi, \varepsilon)[(1, \eta) + \varepsilon\mathbf{V}] &= 0, \\ QH(\mathbf{V}) + Q\hat{B}(\xi, \varepsilon)[(1, \eta) + \varepsilon\mathbf{V}] + \nu QJ(\xi, \varepsilon)[(1, \eta) + \varepsilon\mathbf{V}] &= 0, \end{aligned} \tag{5.2}$$

where  $Q : Y \rightarrow Y_1$  is the  $L^2$ -orthogonal projection. Then define the mapping

$$G^1 : \mathbb{R}^2 \times \mathbb{C}^2 \times X_1 \rightarrow \mathbb{R}^2$$

by the left-hand side of the first equation of (5.2) and

$$G^2 : \mathbb{R}^2 \times \mathbb{C}^2 \times X_1 \rightarrow Y_1$$

by the left-hand side of the second equation of (5.2).

Let  $\bar{r}$  be the positive number given above. Note that

$$\begin{aligned} (I - Q)\hat{B}(\bar{r}, 0) &= \Phi_{(r,s)}^0(\bar{r}, f(\bar{r}), g(\bar{r})), \\ (I - Q)J(\bar{r}, 0) &= J(\bar{r}), \end{aligned}$$

here  $\Phi_{(r,s)}^0$  and  $J(\bar{r})$  are given in Lemma 4.3. Let  $\nu_1$  and  $\nu_2$  be the eigenvalues of  $M(\bar{r})$  and denote  $(1, \eta_1)$  and  $(1, \eta_2)$  by the corresponding eigenfunctions. Note that we can choose  $d_1/d_2$  large enough such that all the entries of  $M(\bar{r})$  are nonzero, so the eigenfunctions can be of the form  $(1, \eta_i)$ . Therefore,

$$G(\bar{r}, 0, \nu_j, \eta_j, \mathbf{V}_j) = \mathbf{0},$$

with  $\mathbf{V}_j = -(QH)^{-1} \left( Q\hat{B}(\bar{r}, 0)(1, \eta_j) + \nu_j QJ(\bar{r}, 0)(1, \eta_j) \right)$  and  $j = 1, 2$ .

On the other hand,

$$\begin{aligned} &G_{(\nu, \eta, \mathbf{V})}^1(\bar{r}, 0, \nu_j, \eta_j, \mathbf{V}_j)[\bar{\nu}, \bar{\eta}, \bar{\mathbf{V}}] \\ &= \Phi_{(r,s)}^0(\bar{r}, f(\bar{r}), g(\bar{r}))(0, \bar{\eta}) + \bar{\nu}J(\bar{r})(1, \eta_j) + \nu_j J(\bar{r})(0, \bar{\eta}), \\ &G_{(\nu, \eta, \mathbf{V})}^2(\bar{r}, 0, \nu_j, \eta_j, \mathbf{V}_j)[\bar{\nu}, \bar{\eta}, \bar{\mathbf{V}}] \\ &= QH(\bar{\mathbf{V}}) + Q\hat{B}(\bar{r}, 0)(0, \bar{\eta}) + \bar{\nu}QJ(\bar{r}, 0)(1, \eta_j) + \nu_j QJ(\bar{r}, 0)(0, \bar{\eta}), \end{aligned}$$

then (4.6) and  $g'(\bar{r}) > 0$  deduce that  $\Phi_{(r,s)}^0(\bar{r}, f(\bar{r}), g(\bar{r}))$  is invertible. Then we can also deduce that  $G_{(\nu,\eta,\mathbf{v})}(\bar{r}, 0, \nu_j, \eta_j, \mathbf{V}_j)$  is invertible. Thus, by the implicit function theorem, the eigenvalue  $\lambda_j(\xi, \varepsilon)$  of (4.1) can be expressed by

$$\lambda_j(\xi, \varepsilon) = \varepsilon \nu_j(\xi, \varepsilon)$$

for a certain smooth function  $\nu_j(\xi, \varepsilon)$  in a neighborhood of  $(\bar{r}, 0)$  for  $j = 1, 2$ . Moreover,  $\nu_j(\bar{r}, 0) = \mu_j(\bar{r})$ . Then by the smoothness of the function  $\nu_j(\xi, \varepsilon)$  and (5.1), we can find the desired  $(\xi^*, \varepsilon)$ . The proposition is proved.  $\square$

Then, the regularity of the scaling (2.1) asserts Theorem 3.4 in Section 3.

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