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Strategy and stationary pattern in a three-species predator–prey model

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Abstract

In this paper, we study a strongly coupled system of partial differential equations which models the dynamics of a two-predator-one-prey ecosystem in which the prey exercises a defense switching mechanism and the predators collaboratively take advantage of the prey's strategy. We demonstrate the emergence of stationary patterns for this system, and show that it is due to the cross diffusion that arises naturally in the model. As far as the authors are aware, this is the first example of stationary patterns in a predator–prey system arising solely from the effect of cross diffusion.

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1. Introduction

In this paper, we study an ecosystem consisting of two predators and one prey. In such a system, we might expect the prey to develop two separate sets of defensive capabilities, one effective against each of the predators, and would switch from one

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set to the other depending on the relative abundance of the two predator species. Such defense switching behavior has been described, for example, for a fish species in Lake Tanganyika against two phenotypes of the scale-eating cichlid *P. microlepis* [33]. On the other hand, we might also expect the predators to develop migratory strategies to take advantage of the prey's defense switching behavior. Such migratory behavior, which depends on the concentration of both predators, constitutes a cross diffusion which is in addition to each species' natural tendency to diffuse to areas of smaller population concentration. As the predators cross diffuse, and the prey switches its defense, we might expect such an ecosystem to exhibit a rich dynamical interplay among the three species. In this paper, we will show that this is indeed the case. In particular, we will demonstrate the emergence of so-called stationary patterns.

The role of diffusion in the modelling of many physical, chemical and biological processes has been extensively studied. Starting with Turing's seminal 1952 paper [34], diffusion and cross diffusion have been observed as causes of the spontaneous emergence of ordered structures, called patterns, in a variety of nonequilibrium situations. These include the Gierer–Meinhardt model [14,18,39–41], the Sel'kov model [11,36], the Noyes–Field model for Belousov–Zhabotinskii reaction [31], the chemotactic diffusion model [21,38], the competition model [6,10,22–24], the predator–prey model [7,8,12,13,17,19,20,29,30,37], as well as models of semiconductors, plasmas, chemical waves, combustion systems, embryogenesis, etc., see e.g. [3,5,9] and references therein. Diffusion-driven instability, also called Turing instability, has also been verified empirically [4,28].

In mathematical ecology, the classical predator–prey model, due independently to Lotka and Volterra in the 1920s, reflects only population changes due to predation in a situation where predator and prey densities are not spatially dependent. It does not take into account either the fact that population is usually not homogeneously distributed, nor the fact that predators and preys naturally develop strategies for survival. Both of these considerations involve diffusion processes which can be quite intricate as different concentration levels of preys and predators cause different population movements. Such movements can be determined by the concentration of the same species (diffusion) or that of other species (cross diffusion).

What is of interest in a predator–prey system is whether the various species can co-exist. Sometimes, the species co-exist in a steady state. In the case where the species are homogeneously distributed, this would be indicated by a constant positive solution to the mathematical model. In the spatially inhomogeneous case, the existence of a non-constant time-independent positive solution, also called stationary pattern, is an indication of the dynamical richness of the system. Many authors have established the existence of stationary patterns in various population dynamics models in the presence of diffusion; some of these have been cited above. However, as far as the authors are aware, in all the predator–prey models with cross diffusion studied so far (such as [7,8]), stationary patterns arise already with the introduction of the diffusion term for each species. The model being studied in this paper seems to be the first where stationary patterns do not emerge from the diffusion of individual species, but only appear with the introduction of cross diffusion. We also remark

that a number of authors have studied strategic behaviors in preys as well as predators that dampen oscillatory dynamics inherent in predator–prey models. By introducing a mutualism between the predators through a cross-diffusive strategy, our result shows that stationary pattern emerges in a striking way.

While the present paper is written specifically for a predator–prey model, it can be seen that the results are of wider interest and would apply also to other three-component systems with similar dynamical relations among the components.

2. Mathematical model

A simple Lotka–Volterra model of a two-predator-one-prey system may be written as the ODE system

$$\begin{cases} \frac{dP_1}{dt} = P_1(-\alpha_1 + \sigma_1 f_1 R), \\ \frac{dP_2}{dt} = P_2(-\alpha_2 + \sigma_2 f_2 R), \\ \frac{dR}{dt} = R\left(\alpha_3\left(1 - \frac{R}{K}\right) - f_1 P_1 - f_2 P_2\right), \end{cases} \quad (2.1)$$

where P_1, P_2 and R are the population densities of two predator species and a prey species respectively, α_1 and α_2 are the respective mortality rates of the first and second predators, α_3 is the intrinsic growth rate of the prey, K is the carrying capacity of the prey, f_1 and f_2 are the respective predation rates of the first and second predators, and σ_1 and σ_2 are the conversion rates of the first and second predators.

Defense switching behavior exercised by the prey may be modelled by taking predation rates f_1 and f_2 as functions of P_1 and P_2 , such as

$$f_1(P_1, P_2) = \frac{\beta_1}{1 + P_1/P_2}, \quad f_2(P_1, P_2) = \beta_2\left(1 - \frac{f_1}{\beta_1}\right), \quad (2.2)$$

where β_1 and β_2 are the predation coefficients of the first and second predators respectively [32]. In these functions, we see that, as a result of the defense switching behavior of the prey, the predation rate decreases as the concentration of that predator increases.

Substituting (2.2) into (2.1), we have

$$\begin{cases} \frac{dP_1}{dt} = P_1\left(-\alpha_1 + \frac{\sigma_1 \beta_1 P_2 R}{P_1 + P_2}\right), \\ \frac{dP_2}{dt} = P_2\left(-\alpha_2 + \frac{\sigma_2 \beta_2 P_1 R}{P_1 + P_2}\right), \\ \frac{dR}{dt} = R\left(\alpha_3\left(1 - \frac{R}{K}\right) - \frac{(\beta_1 + \beta_2)P_1 P_2}{P_1 + P_2}\right). \end{cases} \quad (2.3)$$

Using the scaling

$$\sigma_1 P_2 = \tilde{P}_2, \quad \sigma_2 P_1 = \tilde{P}_1, \quad \sigma_1 \sigma_2 R = \tilde{R}, \quad \sigma_1 \sigma_2 K = \tilde{K}, \quad \frac{\beta_1}{\sigma_1 \sigma_2} = \tilde{\beta}_1, \quad \frac{\beta_2}{\sigma_1 \sigma_2} = \tilde{\beta}_2,$$

and omitting the symbol “ \sim ”, then (2.3) becomes

$$\begin{cases} \frac{dP_1}{dt} = P_1 \left(-\alpha_1 + \frac{\beta_1 P_2 R}{(P_1/\sigma_2) + (P_2/\sigma_1)} \right), \\ \frac{dP_2}{dt} = P_2 \left(-\alpha_2 + \frac{\beta_2 P_1 R}{(P_1/\sigma_2) + (P_2/\sigma_1)} \right), \\ \frac{dR}{dt} = R \left(\alpha_3 \left(1 - \frac{R}{K} \right) - \frac{(\beta_1 + \beta_2) P_1 P_2}{(P_1/\sigma_2) + (P_2/\sigma_1)} \right). \end{cases} \quad (2.4)$$

For simplicity of calculation, we shall consider only the case $\sigma_1 = \sigma_2 = 1$. The conclusions of this paper continue to hold for general σ_1 and σ_2 . In fact, in our discussions we use only the special structure of the three non-linear terms of (2.4):

$$\frac{\beta_1 P_1 P_2 R}{(P_1/\sigma_2) + (P_2/\sigma_1)}, \quad \frac{\beta_2 P_1 P_2 R}{(P_1/\sigma_2) + (P_2/\sigma_1)}, \quad \frac{(\beta_1 + \beta_2) P_1 P_2 R}{(P_1/\sigma_2) + (P_2/\sigma_1)},$$

that is, they have the same denominators and the first plus the second equals the third.

Using the non-dimensional variables and parameters

$$\begin{aligned} u_1 &= \frac{\beta_1}{\alpha_1} P_1, & u_2 &= \frac{\beta_1}{\alpha_1} P_2, & u_3 &= \frac{\beta_1}{\alpha_1} R, & \tau &= \alpha_1 t, \\ \alpha &= \frac{\alpha_2}{\alpha_1}, & \beta &= \frac{\beta_2}{\beta_1}, & r &= \frac{\alpha_3}{\alpha_1}, & \theta &= \frac{\alpha_3}{\beta_1 K} \end{aligned}$$

and re-denoting τ by t , the non-dimensionalized form of (2.3) becomes

$$\begin{cases} \frac{du_1}{dt} = u_1 \left(-1 + \frac{u_2 u_3}{u_1 + u_2} \right), \\ \frac{du_2}{dt} = u_2 \left(-\alpha + \frac{\beta u_1 u_3}{u_1 + u_2} \right), \\ \frac{du_3}{dt} = u_3 \left(r - \theta u_3 - \frac{(1 + \beta) u_1 u_2}{u_1 + u_2} \right), \end{cases} \quad (2.5)$$

where α, β, r and θ are positive parameters (defined above). To avoid excessive technicalities, we shall take $\theta = 1$ throughout this paper.

Denote $\mathbf{u} = (u_1, u_2, u_3)^T$ and

$$\mathbf{G}(\mathbf{u}) = \begin{pmatrix} G_1(\mathbf{u}) \\ G_2(\mathbf{u}) \\ G_3(\mathbf{u}) \end{pmatrix} = \begin{pmatrix} u_1 g_1(\mathbf{u}) \triangleq u_1 \left(-1 + \frac{u_2 u_3}{u_1 + u_2} \right) \\ u_2 g_2(\mathbf{u}) \triangleq u_2 \left(-\alpha + \frac{\beta u_1 u_3}{u_1 + u_2} \right) \\ u_3 g_3(\mathbf{u}) \triangleq u_3 \left(r - u_3 - \frac{(1 + \beta) u_1 u_2}{u_1 + u_2} \right) \end{pmatrix}.$$

It is easy to see that (2.5) has a positive steady state if and only if

$$r\beta > \alpha + \beta. \quad (2.6)$$

In this case, the positive steady state is uniquely given by

$$\tilde{u}_1 = (\alpha + \beta) \frac{r\beta - (\alpha + \beta)}{\beta^2(1 + \beta)}, \quad \tilde{u}_2 = (\alpha + \beta) \frac{r\beta - (\alpha + \beta)}{\alpha\beta(1 + \beta)}, \quad \tilde{u}_3 = \frac{\alpha + \beta}{\beta}. \quad (2.7)$$

Throughout this paper, we will always assume that (2.6) holds, and denote $\tilde{\mathbf{u}} = (\tilde{u}_1, \tilde{u}_2, \tilde{u}_3)^T$.

To take into account the inhomogeneous distribution of the predators and prey in different spatial locations within a fixed bounded domain $\Omega \subset \mathbb{R}^N$ at any given time, and the natural tendency of each species to diffuse to areas of smaller population concentration, we are led to the following PDE system of reaction–diffusion type:

$$\begin{cases} u_{1t} - d_1 \Delta u_1 = G_1(\mathbf{u}), & x \in \Omega, \quad t > 0, \\ u_{2t} - d_2 \Delta u_2 = G_2(\mathbf{u}), & x \in \Omega, \quad t > 0, \\ u_{3t} - d_3 \Delta u_3 = G_3(\mathbf{u}), & x \in \Omega, \quad t > 0, \\ \partial_n u_1 = \partial_n u_2 = \partial_n u_3 = 0, & x \in \partial\Omega, \quad t > 0, \\ u_i(x, 0) = u_{i0}(x) \geq 0, \quad i = 1, 2, 3, & x \in \Omega. \end{cases} \quad (2.8)$$

In the above, n is the outward unit normal vector of the boundary $\partial\Omega$ which we will assume is smooth. The homogeneous Neumann boundary condition indicates that the predator–prey system is self-contained with zero population flux across the boundary. The constants d_1, d_2 and d_3 , called *diffusion coefficients*, are positive, and the initial data u_{i0} , $i = 1, 2, 3$, are continuous functions. It is obvious that $\tilde{\mathbf{u}}$ is the only positive constant steady state of (2.8).

Finally, to take into account the strategy adopted by the predators to take advantage of the defense switching behavior of the prey, we will introduce a cross diffusion between the predators. Noting that the relationship between the two predators in (2.8) is co-operative, we shall include the cross diffusion term in the

first equation only as follows:

$$\begin{cases} u_{1t} - \Delta \left(d_1 u_1 + \frac{k u_1}{\varepsilon + u_2^2} \right) = G_1(\mathbf{u}), & x \in \Omega, \quad t > 0, \\ u_{2t} - d_2 \Delta u_2 = G_2(\mathbf{u}), & x \in \Omega, \quad t > 0, \\ u_{3t} - d_3 \Delta u_3 = G_3(\mathbf{u}), & x \in \Omega, \quad t > 0, \\ \partial_n u_1 = \partial_n u_2 = \partial_n u_3 = 0, & x \in \partial\Omega, \quad t > 0, \\ u_i(x, 0) = u_{i0}(x) \geq 0, \quad i = 1, 2, 3, & x \in \Omega. \end{cases} \quad (2.9)$$

In the above, k and ε are positive constants, and k is called the *cross-diffusion coefficient*. In this model, the first predator u_1 diffuses with flux

$$J = -\nabla \left(d_1 u_1 + \frac{k u_1}{\varepsilon + u_2^2} \right) = - \left(d_1 + \frac{k}{\varepsilon + u_2^2} \right) \nabla u_1 + \frac{2 k u_1 u_2}{(\varepsilon + u_2^2)^2} \nabla u_2.$$

We observe that, as $2 k u_1 u_2 (\varepsilon + u_2^2)^{-2} \geq 0$, the part $\{2 k u_1 u_2 (\varepsilon + u_2^2)^{-2}\} \nabla u_2$ of the flux is directed toward the increasing population density of u_2 . In this way, the first predator moves in anticipation of the defense switching behavior of the prey. For further details we refer the readers to [25,27, Chapter 10]. Referring to [1], we note that (2.9) has a unique non-negative local solution (u_1, u_2, u_3) .

Remark 1. We remark that the general form of the cross-diffusion system appears as [25,27, Chapter 10]

$$\begin{cases} u_{1t} - \operatorname{div}\{K_{11}(\mathbf{u})\nabla u_1 + K_{12}(\mathbf{u})\nabla u_2 + K_{13}(\mathbf{u})\nabla u_3\} = G_1(\mathbf{u}), & x \in \Omega, \quad t > 0, \\ u_{2t} - \operatorname{div}\{K_{22}(\mathbf{u})\nabla u_2 + K_{21}(\mathbf{u})\nabla u_1 + K_{23}(\mathbf{u})\nabla u_3\} = G_2(\mathbf{u}), & x \in \Omega, \quad t > 0, \\ u_{3t} - \operatorname{div}\{K_{33}(\mathbf{u})\nabla u_3 + K_{31}(\mathbf{u})\nabla u_1 + K_{32}(\mathbf{u})\nabla u_2\} = G_3(\mathbf{u}), & x \in \Omega, \quad t > 0, \\ \partial_n u_1 = \partial_n u_2 = \partial_n u_3 = 0, & x \in \partial\Omega, \quad t > 0, \\ u_i(x, 0) = u_{i0}(x) \geq 0, \quad i = 1, 2, 3, & x \in \Omega, \end{cases}$$

where the coefficients $K_{ij}(\mathbf{u})$ satisfy

$$K_{11}, K_{22}, K_{33} > 0, \quad K_{12}, K_{13}, K_{21}, K_{23} \leq 0, \quad K_{31}, K_{32} \geq 0.$$

To make the problem more tractable mathematically, we consider only the case where one or two of the coefficients K_{ij} , $i \neq j$, to be non-zero (identically). We note that if $K_{12} = K_{21} \equiv 0$, then no stationary pattern is created.

It seems to us that the term $k u_1 / (\varepsilon + u_2^2)$ is the simplest reasonable function to realize stationary patterns. We observe that the term $k u_1 / (\varepsilon + u_2)$ does not give stationary patterns; however, any $k u_1 / (\varepsilon + u_2^{1+\delta})$ with $\delta > 0$ gives the same results of this paper.

Finally, we remark that, due to the symmetry of the two equations, adding the cross-diffusion term to either the first equation or the second equation gives us the same result. It seems to be a more difficult mathematical problem to incorporate

cross-diffusion terms to both equations. However, as we show in this paper, by adding the cross-diffusion term only to the first equation as in (2.8), the effect is sufficient to create stationary patterns.

The main result of this paper is to show that stationary patterns emerge only with the introduction of the cross-diffusion term. First, we will show that the constant positive steady state $\tilde{\mathbf{u}}$ of (2.8) is global asymptotically stable; as a consequence (2.8) has no non-constant positive steady states (Theorem 2). Then we will show that under appropriate conditions, (2.9) possesses non-constant positive steady states, i.e., stationary patterns (Theorems 5 and 6).

The organization of this paper is follows: In Section 3, we will show that the equilibrium solution $\tilde{\mathbf{u}}$ of (2.5) is globally asymptotically stable. In Section 4, we prove that the solution $(u_1(x, t), u_2(x, t), u_3(x, t))$ of (2.8) tends to the constant positive steady state $\tilde{\mathbf{u}}$ uniformly on $\bar{\Omega}$ as $t \rightarrow \infty$. This implies that (2.8) has no non-constant positive steady states. The methods of Sections 3 and 4 are the local stability analysis via linearization and the Liapunov method. In the remaining sections, we study the problem (2.9). First, in Section 5, we establish a priori positive upper and lower bounds for its positive steady states. In Section 6, we analyze the linearized steady state problem of (2.9) at $\tilde{\mathbf{u}}$. In Section 7, we study the global existence of non-constant positive steady states for suitable values of the cross-diffusion coefficient k and the diffusion coefficient d_3 , respectively. This is done using the Leray–Schauder degree theory. In the last section, we discuss the non-existence and bifurcation of non-constant positive steady states of (2.9).

3. Equilibrium solution of the ODE system

In this section we look at the ODE system (2.5). Let $\mathbf{u} = (u_1, u_2, u_3)$ be a positive solution of (2.5), i.e., $u_i > 0$, $i = 1, 2, 3$. It is easy to see that $u_1(t)$, $u_2(t)$ and $u_3(t)$ are bounded.

The objective of this section is to prove the following result.

Theorem 1. *The equilibrium solution $\tilde{\mathbf{u}}$ of (2.5) is globally asymptotically stable.*

Proof. Define

$$E(t) = E(\mathbf{u})(t) = p \left\{ u_1 - \tilde{u}_1 - \tilde{u}_1 \ln \left(\frac{u_1}{\tilde{u}_1} \right) \right\} + u_2 - \tilde{u}_2 - \tilde{u}_2 \ln \left(\frac{u_2}{\tilde{u}_2} \right) \\ + q \left\{ u_3 - \tilde{u}_3 - \tilde{u}_3 \ln \left(\frac{u_3}{\tilde{u}_3} \right) \right\}$$

with

$$p = \frac{\beta^2}{\alpha}, \quad q = \frac{\beta(\alpha + \beta)}{\alpha(1 + \beta)}. \quad (3.1)$$

Then $E(\tilde{\mathbf{u}}) = 0$, $E(\mathbf{u}) > 0$ if $\mathbf{u} \neq \tilde{\mathbf{u}}$. Referring to (2.5), we compute

$$\begin{aligned} \frac{dE}{dt} &= p(1 - \tilde{u}_1/u_1)u'_1 + (1 - \tilde{u}_2/u_2)u'_2 + q(1 - \tilde{u}_3/u_3)u'_3 \\ &= p(u_1 - \tilde{u}_1)g_1(\mathbf{u}) + (u_2 - \tilde{u}_2)g_2(\mathbf{u}) + q(u_3 - \tilde{u}_3)g_3(\mathbf{u}) \\ &= p\tilde{u}_1 + \alpha\tilde{u}_2 - rq\tilde{u}_3 - \{pu_1 + \alpha u_2 - rq u_3 + qu_3(u_3 - \tilde{u}_3)\} \\ &\quad + \{p + \beta - q(1 + \beta)\} \frac{u_1 u_2 u_3}{u_1 + u_2} + \frac{q(1 + \beta)\tilde{u}_3 u_1 u_2 - \beta\tilde{u}_2 u_1 u_3 - p\tilde{u}_1 u_2 u_3}{u_1 + u_2}. \end{aligned} \quad (3.2)$$

We note, in view of (2.7) and (3.1), that

$$\begin{cases} p + \beta - q(1 + \beta) = 0, & p\tilde{u}_1 + \alpha\tilde{u}_2 - rq\tilde{u}_3 = -\frac{(\alpha + \beta)^3}{\alpha\beta(1 + \beta)}, \\ p\tilde{u}_1 = \beta\tilde{u}_2, & q(1 + \beta)\tilde{u}_3 = \frac{(\alpha + \beta)^2}{\alpha}, & rq + q\tilde{u}_3 - \beta\tilde{u}_2 = \frac{2(\alpha + \beta)^2}{\alpha(1 + \beta)}, \end{cases} \quad (3.3)$$

and hence

$$\begin{aligned} & -\{pu_1 + \alpha u_2 - rq u_3 + qu_3(u_3 - \tilde{u}_3)\} + \frac{q(1 + \beta)\tilde{u}_3 u_1 u_2 - \beta\tilde{u}_2 u_1 u_3 - p\tilde{u}_1 u_2 u_3}{u_1 + u_2} \\ &= -pu_1 - \alpha u_2 + rq u_3 - qu_3^2 + q\tilde{u}_3 u_3 + \frac{(\alpha + \beta)^2 u_1 u_2}{\alpha(u_1 + u_2)} - \beta\tilde{u}_2 u_3 \\ &= -pu_1 - \alpha u_2 + (rq + q\tilde{u}_3 - \beta\tilde{u}_2)u_3 - qu_3^2 + \frac{(\alpha + \beta)^2 u_1 u_2}{\alpha(u_1 + u_2)} \\ &= -qu_3^2 + \frac{2(\alpha + \beta)^2}{\alpha(1 + \beta)} u_3 - \frac{(\beta u_1 - \alpha u_2)^2}{\alpha(u_1 + u_2)}. \end{aligned} \quad (3.4)$$

Using (3.2)–(3.4), we get

$$\begin{aligned} \frac{dE}{dt} &= -\frac{(\beta u_1 - \alpha u_2)^2}{\alpha(u_1 + u_2)} - \left(qu_3^2 - \frac{2(\alpha + \beta)^2}{\alpha(1 + \beta)} u_3 + \frac{(\alpha + \beta)^3}{\alpha\beta(1 + \beta)} \right) \\ &= -\frac{(\beta u_1 - \alpha u_2)^2}{\alpha(u_1 + u_2)} - \frac{\alpha + \beta}{\alpha\beta(1 + \beta)} (\alpha + \beta - \beta u_3)^2 \leq 0, \end{aligned}$$

$$\frac{dE}{dt} < 0 \quad \text{if} \quad \mathbf{u} \neq \tilde{\mathbf{u}}.$$

By the Lyapunov–LaSalle invariance principle [15], $\tilde{\mathbf{u}}$ is global asymptotically stable. \square

4. Steady state solution of the PDE system without cross diffusion

Let $0 = \mu_1 < \mu_2 < \mu_3 < \dots$ be the eigenvalues of the operator $-\Delta$ on Ω with the homogeneous Neumann boundary condition, and $E(\mu_i)$ be the eigenspace corresponding to μ_i in $C^1(\bar{\Omega})$. Let $\mathbf{X} = \{\mathbf{u} \in [C^1(\bar{\Omega})]^3 \mid \partial_n \mathbf{u} = 0 \text{ on } \partial\Omega\}$, $\{\phi_{ij}; j = 1, \dots, \dim E(\mu_i)\}$ be an orthonormal basis of $E(\mu_i)$, and $\mathbf{X}_{ij} = \{\mathbf{c}\phi_{ij} \mid \mathbf{c} \in \mathbb{R}^3\}$. Then,

$$\mathbf{X} = \bigoplus_{i=1}^{\infty} \mathbf{X}_i \quad \text{and} \quad \mathbf{X}_i = \bigoplus_{j=1}^{\dim E(\mu_i)} \mathbf{X}_{ij}. \quad (4.1)$$

We note that (2.8) has a unique non-negative global solution $\mathbf{u} = (u_1, u_2, u_3)$. By the maximum principle we know that if $u_{i0} \neq 0$, $i = 1, 2, 3$, then $u_i(x, t) > 0$ on $\bar{\Omega}$ for all $t > 0$, $i = 1, 2, 3$. The maximum principle gives

$$\sup_{\bar{\Omega} \times [0, \infty)} u_3(x, t) \leq \max\{r, \max_{\bar{\Omega}} u_{30}(x)\}. \quad (4.2)$$

Integrating the equations of (2.8) over Ω and adding the results, we have that, by (4.2),

$$\begin{aligned} \frac{d}{dt} \int_{\Omega} (u_1 + u_2 + u_3) dx &= - \int_{\Omega} (u_1 + u_2) dx + \int_{\Omega} u_3(r - u_3) dx \\ &\leq - \int_{\Omega} (u_1 + u_2 + u_3) dx + C \end{aligned}$$

for some positive constant C depending only on r and $\max_{\bar{\Omega}} u_{30}(x)$. Therefore, $\|u_i(t)\|_{L^1(\Omega)}$ are bounded in $[0, \infty)$. Using [16, Exercise 5 of Section 3.5] we obtain that $\|u_i(t)\|_{L^\infty(\Omega)}$ are also bounded in $[0, \infty)$.

The aim of this section is to prove Theorem 2 which shows that the problem (2.8) has no non-constant positive steady state no matter what the diffusion coefficients d_1, d_2 and d_3 are; in other words, diffusion alone (without cross diffusion) cannot drive instability and cannot generate patterns for this predator–prey model. First, we recall the following result which can be found in [35]:

Lemma 1. *Let a and b be positive constants. Assume that $\varphi, \psi \in C^1([a, \infty))$, $\psi(t) \geq 0$ and φ is bounded from below. If $\varphi'(t) \leq -b\psi(t)$ and $\psi'(t) \leq K$ in $[a, \infty)$ for some constant K , then $\lim_{t \rightarrow \infty} \psi(t) = 0$.*

Theorem 2. *The constant positive steady state $\tilde{\mathbf{u}}$ of (2.8) is global asymptotically stable. As a consequence, problem (2.8) has no non-constant positive steady states.*

Proof. We present the proof in two steps:

Step 1: Local stability. Let $\mathcal{D} = \text{diag}(d_1, d_2, d_3)$ and $\mathcal{L} = \mathcal{D}\Delta + \mathbf{G}_{\mathbf{u}}(\tilde{\mathbf{u}})$. The linearization of (2.8) at $\tilde{\mathbf{u}}$ is

$$\mathbf{u}_t = \mathcal{L}\mathbf{u}.$$

For each $i \geq 1$, \mathbf{X}_i is invariant under the operator \mathcal{L} , and λ is an eigenvalue of \mathcal{L} on \mathbf{X}_i if and only if it is an eigenvalue of the matrix $-\mu_i \mathcal{D} + \mathbf{G}_u(\tilde{\mathbf{u}})$.

The characteristic polynomial of $-\mu_i \mathcal{D} + \mathbf{G}_u(\tilde{\mathbf{u}})$ is given by

$$\psi_i(\lambda) = \lambda^3 + B_1 \lambda^2 + B_2 \lambda + B_3,$$

where

$$\begin{aligned} B_1 &= \mu_i(d_1 + d_2 + d_3) + \tilde{u}_3 + \frac{(1 + \beta)\tilde{u}_1}{\tilde{u}_1 + \tilde{u}_2} > 0, \\ B_2 &= \mu_i^2(d_1 d_2 + d_1 d_3 + d_2 d_3) + \mu_i \left\{ (d_1 + d_2)\tilde{u}_3 + (d_1 + d_3)\frac{\beta\tilde{u}_1}{\tilde{u}_1 + \tilde{u}_2} + (d_2 + d_3)\frac{\tilde{u}_1}{\tilde{u}_1 + \tilde{u}_2} \right\} \\ &\quad + (1 + \beta) \left\{ \frac{\tilde{u}_1 \tilde{u}_3}{\tilde{u}_1 + \tilde{u}_2} + \frac{\tilde{u}_1 \tilde{u}_2 (\tilde{u}_2 + \alpha \tilde{u}_1)}{(\tilde{u}_1 + \tilde{u}_2)^2} \right\} > 0, \\ B_3 &= \mu_i^3 d_1 d_2 d_3 + \mu_i^2 \left\{ d_1 d_2 \tilde{u}_3 + d_1 d_3 \frac{\beta \tilde{u}_1}{\tilde{u}_1 + \tilde{u}_2} + d_2 d_3 \frac{\tilde{u}_1}{\tilde{u}_1 + \tilde{u}_2} \right\} \\ &\quad + \mu_i \left\{ \frac{d_1 \tilde{u}_1}{\tilde{u}_1 + \tilde{u}_2} \left(\beta \tilde{u}_3 + \frac{\alpha(1 + \beta)\tilde{u}_1 \tilde{u}_2}{\tilde{u}_1 + \tilde{u}_2} \right) + d_2 \frac{\tilde{u}_1}{\tilde{u}_1 + \tilde{u}_2} \left(\tilde{u}_3 + \frac{(1 + \beta)\tilde{u}_2^2}{\tilde{u}_1 + \tilde{u}_2} \right) \right\} \\ &\quad + (1 + \beta)(\alpha + \beta)^2 \frac{\tilde{u}_1^2 \tilde{u}_2^2}{\beta(\tilde{u}_1 + \tilde{u}_2)^3} > 0. \end{aligned}$$

A direct calculation yields

$$B_1 B_2 - B_3 = c_3 \mu_i^3 + c_2 \mu_i^2 + \mu_i \{c_{11} d_1 + c_{12} d_2 + c_{13} d_3\} + A_1 A_2 - A_3,$$

where A_1, A_2 and A_3 are given by

$$\begin{aligned} A_1 &= \tilde{u}_3 + \frac{(1 + \beta)\tilde{u}_1}{\tilde{u}_1 + \tilde{u}_2} > 0, \\ A_2 &= (1 + \beta) \left\{ \frac{\tilde{u}_1 \tilde{u}_3}{\tilde{u}_1 + \tilde{u}_2} + \tilde{u}_1 \tilde{u}_2 \frac{\tilde{u}_2 + \alpha \tilde{u}_1}{(\tilde{u}_1 + \tilde{u}_2)^2} \right\} > 0, \\ A_3 &= -\det\{\mathbf{G}_u(\tilde{\mathbf{u}})\} = (1 + \beta)(\alpha + \beta)^2 \frac{\tilde{u}_1^2 \tilde{u}_2^2}{\beta(\tilde{u}_1 + \tilde{u}_2)^3} > 0. \end{aligned}$$

One can verify that $c_3, c_2, c_{11}, c_{12}, c_{13} > 0$, and

$$\begin{aligned} A_1 A_2 - A_3 &> \frac{(1 + \beta)\tilde{u}_1}{\tilde{u}_1 + \tilde{u}_2} (1 + \beta) \tilde{u}_1 \tilde{u}_2 \frac{\tilde{u}_2 + \alpha \tilde{u}_1}{(\tilde{u}_1 + \tilde{u}_2)^2} - (1 + \beta)(\alpha + \beta)^2 \frac{\tilde{u}_1^2 \tilde{u}_2^2}{\beta(\tilde{u}_1 + \tilde{u}_2)^3} \\ &= \frac{(1 + \beta)\tilde{u}_1^2 \tilde{u}_2}{\beta(\tilde{u}_1 + \tilde{u}_2)^3} [\beta(1 + \beta)(\alpha \tilde{u}_1 + \tilde{u}_2) - (\alpha + \beta)^2 \tilde{u}_2] \\ &= (1 + \beta)(1 - \alpha)^2 \frac{\tilde{u}_1^2 \tilde{u}_2^2}{(\tilde{u}_1 + \tilde{u}_2)^3} \\ &> 0. \end{aligned}$$

Hence, $B_1 B_2 - B_3 > 0$. It thus follows from the Routh–Hurwitz criterion that, for each $i \geq 1$, the three roots $\lambda_{i,1}, \lambda_{i,2}, \lambda_{i,3}$ of $\psi_i(\lambda) = 0$ all have negative real parts.

In the following, we shall prove that there exists a positive constant δ such that

$$\operatorname{Re}\{\lambda_{i,1}\}, \operatorname{Re}\{\lambda_{i,2}\}, \operatorname{Re}\{\lambda_{i,3}\} \leq -\delta, \quad \forall i \geq 1. \quad (4.3)$$

Consequently, the spectrum of \mathcal{L} , which consists of eigenvalues, lies in $\{\operatorname{Re} \lambda \leq -\delta\}$, and local stability of $\bar{\mathbf{u}}$ follows [16, Theorem 5.1.1].

Now we prove (4.3). Let $\lambda = \mu_i \xi$, then

$$\psi_i(\lambda) = \mu_i^3 \xi^3 + B_1 \mu_i^2 \xi^2 + B_2 \mu_i \xi + B_3 \triangleq \tilde{\psi}_i(\xi).$$

Since $\mu_i \rightarrow \infty$ as $i \rightarrow \infty$, it follows that

$$\begin{aligned} \lim_{i \rightarrow \infty} \{\tilde{\psi}_i(\xi)/\mu_i^3\} &= \xi^3 + (d_1 + d_2 + d_3)\xi^2 + (d_1 d_2 + d_1 d_3 + d_2 d_3)\xi + d_1 d_2 d_3 \\ &\triangleq \tilde{\psi}(\xi). \end{aligned}$$

Applying the Routh–Hurwitz criterion it follows that the three roots ξ_1, ξ_2, ξ_3 of $\tilde{\psi}(\xi) = 0$ all have negative real parts. Thus, there exists a positive constant $\bar{\delta}$ such that $\operatorname{Re}\{\xi_1\}, \operatorname{Re}\{\xi_2\}, \operatorname{Re}\{\xi_3\} \leq -\bar{\delta}$. By continuity, we see that there exists i_0 such that the three roots $\xi_{i,1}, \xi_{i,2}, \xi_{i,3}$ of $\tilde{\psi}_i(\xi) = 0$ satisfy $\operatorname{Re}\{\xi_{i,1}\}, \operatorname{Re}\{\xi_{i,2}\}, \operatorname{Re}\{\xi_{i,3}\} \leq -\bar{\delta}/2, \forall i \geq i_0$. In turn, $\operatorname{Re}\{\lambda_{i,1}\}, \operatorname{Re}\{\lambda_{i,2}\}, \operatorname{Re}\{\lambda_{i,3}\} \leq -\mu_i \bar{\delta}/2 \leq -\bar{\delta}/2, \forall i \geq i_0$. Let

$$-\tilde{\delta} = \max_{1 \leq i \leq i_0} \{\operatorname{Re}\{\lambda_{i,1}\}, \operatorname{Re}\{\lambda_{i,2}\}, \operatorname{Re}\{\lambda_{i,3}\}\}.$$

Then $\tilde{\delta} > 0$, and (4.3) holds for $\delta = \min\{\tilde{\delta}, \bar{\delta}/2\}$.

Step 2: Global stability. In the following, C denotes a generic positive constant which does not depend on $x \in \bar{\Omega}$ and $t \geq 0$. As the solution $\mathbf{u}(\cdot, t)$ of (2.8) is bounded uniformly on $\bar{\Omega}$, that is, $\|u_i(\cdot, t)\|_\infty \leq C$ for all $t \geq 0$, by [2, Theorem A₂],

$$\|u_i(\cdot, t)\|_{C^{2,\alpha}(\bar{\Omega})} \leq C, \quad \forall t \geq 1. \quad (4.4)$$

Define

$$\begin{aligned} E(t) &= \int_{\Omega} \left(p \left\{ u_1 - \tilde{u}_1 - \tilde{u}_1 \ln \left(\frac{u_1}{\tilde{u}_1} \right) \right\} + u_2 - \tilde{u}_2 - \tilde{u}_2 \ln \left(\frac{u_2}{\tilde{u}_2} \right) \right. \\ &\quad \left. + q \left\{ u_3 - \tilde{u}_3 - \tilde{u}_3 \ln \left(\frac{u_3}{\tilde{u}_3} \right) \right\} \right) dx, \end{aligned}$$

where p and q are given by (3.1). Then $E(t) \geq 0$ for all $t \geq 0$. Using (2.8) and integrating by parts, we have

$$\begin{aligned} E'(t) = & - \int_{\Omega} \left\{ \frac{pd_1\tilde{u}_1}{u_1^2} |\nabla u_1|^2 + \frac{d_2\tilde{u}_2}{u_2^2} |\nabla u_2|^2 + \frac{qd_3\tilde{u}_3}{u_3^2} |\nabla u_3|^2 \right\} dx \\ & + \int_{\Omega} \{p(u_1 - \tilde{u}_1)g_1(\mathbf{u}) + (u_2 - \tilde{u}_2)g_2(\mathbf{u}) + q(u_3 - \tilde{u}_3)g_3(\mathbf{u})\} dx. \end{aligned}$$

As in Section 3, we note that

$$\begin{aligned} & p(u_1 - \tilde{u}_1)g_1(\mathbf{u}) + (u_2 - \tilde{u}_2)g_2(\mathbf{u}) + q(u_3 - \tilde{u}_3)g_3(\mathbf{u}) \\ &= - \frac{(\beta u_1 - \alpha u_2)^2}{\alpha(u_1 + u_2)} - \frac{\alpha + \beta}{\alpha\beta(1 + \beta)}(\alpha + \beta - \beta u_3)^2. \end{aligned}$$

Therefore,

$$\begin{aligned} E'(t) = & - \int_{\Omega} \left\{ \frac{pd_1\tilde{u}_1}{u_1^2} |\nabla u_1|^2 + \frac{d_2\tilde{u}_2}{u_2^2} |\nabla u_2|^2 + \frac{qd_3\tilde{u}_3}{u_3^2} |\nabla u_3|^2 \right\} dx \\ & - \int_{\Omega} \left\{ \frac{(\beta u_1 - \alpha u_2)^2}{\alpha(u_1 + u_2)} + \frac{\alpha + \beta}{\alpha\beta(1 + \beta)}(\alpha + \beta - \beta u_3)^2 \right\} dx. \end{aligned}$$

As $u_i^2 \leq C$, it follows that

$$\begin{aligned} E'(t) \leq & - \frac{1}{C} \int_{\Omega} (|\nabla u_1|^2 + |\nabla u_2|^2 + |\nabla u_3|^2) dx \\ & - \int_{\Omega} \left\{ \frac{(\beta u_1 - \alpha u_2)^2}{\alpha(u_1 + u_2)} + \frac{\alpha + \beta}{\alpha\beta(1 + \beta)}(\alpha + \beta - \beta u_3)^2 \right\} dx \\ \triangleq & -\psi_1(t) - \psi_2(t). \end{aligned} \tag{4.5}$$

By (4.4) and (2.8), we know that $\psi'_1(t)$ and $\psi'_2(t)$ are bounded in $[1, \infty)$. Applying Lemma 1 to (4.5), we conclude that $\psi_1(t), \psi_2(t) \rightarrow 0$ as $t \rightarrow \infty$. Therefore,

$$\lim_{t \rightarrow \infty} \int_{\Omega} (|\nabla u_1|^2 + |\nabla u_2|^2 + |\nabla u_3|^2) dx = 0, \tag{4.6}$$

$$\lim_{t \rightarrow \infty} \int_{\Omega} \frac{(\beta u_1 - \alpha u_2)^2}{(u_1 + u_2)} dx = 0, \quad \lim_{t \rightarrow \infty} \int_{\Omega} (\alpha + \beta - \beta u_3)^2 dx = 0. \tag{4.7}$$

From (4.6) and the Poincaré inequality, we deduce that

$$\lim_{t \rightarrow \infty} \int_{\Omega} \{(u_1 - \bar{u}_1)^2 + (u_2 - \bar{u}_2)^2 + (u_3 - \bar{u}_3)^2\} dx = 0, \tag{4.8}$$

where $\bar{f} = \frac{1}{|\Omega|} \int_{\Omega} f \, dx$ for a function $f \in L^1(\Omega)$. Thus, it follows from (4.7) and (4.8) that

$$\lim_{t \rightarrow \infty} \int_{\Omega} (u_3 - \tilde{u}_3)^2 \, dx = \lim_{t \rightarrow \infty} \int_{\Omega} |\alpha u_2 - \beta u_1| \, dx = 0. \quad (4.9)$$

Now, using the first differential equation of (2.8), it follows from (4.9) that

$$|\Omega| \bar{u}'_1(t) = \frac{d}{dt} \int_{\Omega} u_1(t) \, dx = \int_{\Omega} \frac{u_1(\alpha u_2 - \beta u_1)}{\beta(u_1 + u_2)} \, dx + \int_{\Omega} \frac{u_1 u_2}{u_1 + u_2} (u_3 - \tilde{u}_3) \, dx \rightarrow 0$$

as $t \rightarrow \infty$. Similarly, $\bar{u}'_2(t) \rightarrow 0$ as $t \rightarrow \infty$. Since $\bar{u}_3(t) \rightarrow \tilde{u}_3$, and $\bar{u}_1(t)$ and $\bar{u}_2(t)$ are bounded, we infer that there exist a sequence $\{t_m\}$ with $t_m \rightarrow \infty$, and a non-negative constant \hat{u}_1 , such that

$$\bar{u}'_3(t_m) \rightarrow 0, \quad \bar{u}_1(t_m) \rightarrow \hat{u}_1, \quad \bar{u}_2(t_m) \rightarrow \hat{u}_1 \beta / \alpha. \quad (4.10)$$

At $t = t_m$, we write

$$\begin{aligned} \bar{u}'_3 &= \int_{\Omega} (u_3 - \tilde{u}_3) \left(r - u_3 - \tilde{u}_3 - (1 + \beta) \frac{u_1 u_2}{u_1 + u_2} \right) dx \\ &\quad + \tilde{u}_3 \int_{\Omega} \left(r - \tilde{u}_3 - \frac{\beta(1 + \beta)}{\alpha + \beta} u_1 \right) dx + \frac{1 + \beta}{\beta} \int_{\Omega} \frac{u_1(\beta u_1 - \alpha u_2)}{u_1 + u_2} \, dx. \end{aligned} \quad (4.11)$$

Applying (4.9) and (4.10), it follows from (4.11) that $\hat{u}_1 \neq 0$ and $r - \tilde{u}_3 - \hat{u}_1 \beta(1 + \beta)/(\alpha + \beta) = 0$, and hence $\hat{u}_1 = \tilde{u}_1$. Consequently,

$$\lim_{t \rightarrow \infty} \bar{u}_i(t_m) = \tilde{u}_i, \quad i = 1, 2, 3. \quad (4.12)$$

Since $\|u_i(\cdot, t_m)\|_{C^{2,\alpha}(\bar{\Omega})} \leq C$, there exist a subsequence of $\{t_m\}$, still denoted by the same notation, and non-negative functions $w_i \in C^2(\bar{\Omega})$, such that

$$\lim_{t \rightarrow \infty} \|u_i(\cdot, t_m) - w_i(\cdot)\|_{C^2(\bar{\Omega})} = 0, \quad i = 1, 2, 3.$$

In view of (4.12), we know that $w_i \equiv \tilde{u}_i$. Therefore,

$$\lim_{t \rightarrow \infty} \|u_i(\cdot, t_m) - \tilde{u}_i\|_{C^2(\bar{\Omega})} = 0, \quad i = 1, 2, 3. \quad (4.13)$$

The global asymptotic stability of $\tilde{\mathbf{u}}$ follows from (4.13) and the local stability of $\tilde{\mathbf{u}}$. Theorem 2 is thus proved. \square

5. Bounds for positive steady states of PDE system with cross diffusion

The corresponding steady state problem of (2.9) is

$$\begin{cases} -\Delta\left(d_1u_1 + \frac{ku_1}{\varepsilon + u_2^2}\right) = G_1(\mathbf{u}) & \text{in } \Omega, \\ -d_2\Delta u_2 = G_2(\mathbf{u}) & \text{in } \Omega, \\ -d_3\Delta u_3 = G_3(\mathbf{u}) & \text{in } \Omega, \\ \partial_n u_1 = \partial_n u_2 = \partial_n u_3 = 0 & \text{on } \partial\Omega. \end{cases} \quad (5.1)$$

In the following, the generic constants $C_1, C_2, C_*, \underline{C}, \bar{C}$, etc., will depend on the domain Ω . However, as Ω is fixed, we will not mention this dependence explicitly. Also, for convenience, we denote the constants (α, β, r) collectively by Λ .

The main purpose of this section is to give a priori positive upper and lower bounds for the positive solutions to (5.1). For this, we shall make use of the following two results.

Proposition 1 (Harnack inequality (Lin et al. [21])). *Let $w \in C^2(\Omega) \cap C^1(\bar{\Omega})$ be a positive solution to $\Delta w(x) + c(x)w(x) = 0$, where $c \in C(\bar{\Omega})$, satisfying the homogeneous Neumann boundary condition. Then there exists a positive constant C_* which depends only on $\|c\|_\infty$ such that*

$$\max_{\bar{\Omega}} w \leq C_* \min_{\bar{\Omega}} w.$$

Proposition 2 (maximum principle (Lou and Ni [23])). *Let $g \in C(\Omega \times \mathbb{R}^1)$ and $b_j \in C(\bar{\Omega})$, $j = 1, 2, \dots, N$.*

(i) *If $w \in C^2(\Omega) \cap C^1(\bar{\Omega})$ satisfies*

$$\begin{cases} \Delta w(x) + \sum_{j=1}^N b_j(x)w_{x_j} + g(x, w(x)) \geq 0 & \text{in } \Omega, \\ \partial_n w \leq 0 & \text{on } \partial\Omega, \end{cases}$$

and $w(x_0) = \max_{\bar{\Omega}} w$, then $g(x_0, w(x_0)) \geq 0$.

(ii) *If $w \in C^2(\Omega) \cap C^1(\bar{\Omega})$ satisfies*

$$\begin{cases} \Delta w(x) + \sum_{j=1}^N b_j(x)w_{x_j} + g(x, w(x)) \leq 0 & \text{in } \Omega, \\ \partial_n w \geq 0 & \text{on } \partial\Omega, \end{cases}$$

and $w(x_0) = \min_{\bar{\Omega}} w$, then $g(x_0, w(x_0)) \leq 0$.

Theorem 3 (upper bound). *Let d be a fixed positive number. There exist positive constants $C(\Lambda, d)$ and $\bar{C}(\Lambda, d)$ such that, when $d_i \geq d$, $i = 1, 2, 3$, the positive solution (u_1, u_2, u_3) of (5.1) satisfies*

$$\max_{\bar{\Omega}} u_i \leq C(\Lambda, d) \min_{\bar{\Omega}} u_i \quad \text{and} \quad \max_{\bar{\Omega}} u_i \leq \bar{C}(\Lambda, d), \quad i = 1, 2, 3. \quad (5.2)$$

Proof. First, a direct application of the maximum principle to the third equation of (5.1) gives $u_3 \leq r$ on $\bar{\Omega}$. Define

$$z(x) = d_1 u_1 + \frac{k u_1}{\varepsilon + u_2^2} + d_2 u_2 + d_3 u_3.$$

Then we have

$$\begin{cases} -\Delta z = -u_1 - \alpha u_2 + u_3(r - u_3) & \text{in } \Omega, \\ \partial_n z = 0 & \text{on } \partial\Omega. \end{cases}$$

Let $z(x_0) = \max_{\bar{\Omega}} z$. Proposition 2 implies that

$$u_1(x_0) + \alpha u_2(x_0) \leq u_3(x_0)(r - u_3(x_0)) \leq r^2. \quad (5.3)$$

Note that $0 < u_1 u_3 / (u_1 + u_2) \leq u_3 \leq r$. Applying Proposition 1 to the second equation of (5.1), we have $\max_{\bar{\Omega}} u_2 \leq C_1 \min_{\bar{\Omega}} u_2$ for some positive constant $C_1 = C_1(\Lambda, d)$. This combined with (5.3) yields $u_2 \leq C_2$ on $\bar{\Omega}$ for some positive constant $C_2 = C_2(\Lambda, d)$. Write $\varphi(x) = d_1 u_1 + k u_1 / (\varepsilon + u_2^2)$. Then

$$\begin{cases} -\Delta \varphi = \varphi \left\{ -1 + \frac{u_2 u_3}{u_1 + u_2} \right\} \left\{ d_1 + \frac{k}{\varepsilon + u_2^2} \right\}^{-1} \triangleq c(x) \varphi & \text{in } \Omega, \\ \partial_n \varphi = 0 & \text{on } \partial\Omega. \end{cases}$$

Note that $\|c\|_\infty \leq (1 + r)/d_1$, and the Harnack inequality holds for φ , i.e., $\max_{\bar{\Omega}} \varphi \leq C_3 \min_{\bar{\Omega}} \varphi$ for some positive constant $C_3 = C_3(\Lambda, d)$. Since $u_1 = \varphi \{d_1 + k/(\varepsilon + u_2^2)\}^{-1}$, and

$$\max_{\bar{\Omega}} u_1 \leq \frac{\max_{\bar{\Omega}} \varphi}{d_1 + k/[\varepsilon + (\max_{\bar{\Omega}} u_2)^2]}, \quad \min_{\bar{\Omega}} u_1 \geq \frac{\min_{\bar{\Omega}} \varphi}{d_1 + k/[\varepsilon + (\min_{\bar{\Omega}} u_2)^2]}$$

and $\max_{\bar{\Omega}} u_2 \leq C_1 \min_{\bar{\Omega}} u_2$, we have

$$\begin{aligned} \frac{\max_{\bar{\Omega}} u_1}{\min_{\bar{\Omega}} u_1} &\leq \frac{\max_{\bar{\Omega}} \varphi \frac{d_1 + k/[\varepsilon + (\min_{\bar{\Omega}} u_2)^2]}{\min_{\bar{\Omega}} \varphi \frac{d_1 + k/[\varepsilon + (\max_{\bar{\Omega}} u_2)^2]}} \\ &\leq C_3 \frac{d_1 + k/[\varepsilon + (\min_{\bar{\Omega}} u_2)^2]}{d_1 + k/[\varepsilon + (\max_{\bar{\Omega}} u_2)^2]} \\ &\leq C_3 \frac{\varepsilon + (\max_{\bar{\Omega}} u_2)^2}{\varepsilon + (\min_{\bar{\Omega}} u_2)^2} \\ &\leq C_3 \frac{(\max_{\bar{\Omega}} u_2)^2}{(\min_{\bar{\Omega}} u_2)^2} \\ &\leq C(A, d). \end{aligned}$$

This combined with (5.3) yields $u_1 \leq C_4$ on $\bar{\Omega}$ for some positive constant $C_4 = C_4(A, d)$. Applying Proposition 1 to the third equation of (5.1), we see that the Harnack inequality holds for u_3 . This completes the proof. \square

Turning now to the lower bound, we first give the following preliminary result.

Lemma 2. *Let k_m, ε_m and $d_{i,m}, i = 1, 2, 3$, be positive constants, $m = 1, 2, \dots$, and $\mathbf{u}_m = (u_{1,m}, u_{2,m}, u_{3,m})^T$ be the corresponding positive solution of (5.1) with $d_i = d_{i,m}$, $k = k_m$ and $\varepsilon = \varepsilon_m$. If $\mathbf{u}_m \rightarrow \bar{\mathbf{u}}$ as $m \rightarrow \infty$ and $\bar{\mathbf{u}}$ is a constant vector, then $\bar{\mathbf{u}} = \hat{\mathbf{u}}$. Recall that $\hat{\mathbf{u}}$, given by (2.7), is the unique positive solution of $\mathbf{G}(\mathbf{u}) = 0$.*

Proof. It is easy to see that for all m , $\int_{\Omega} u_{1,m} g_1(\mathbf{u}_m) dx = 0$. If $g_1(\bar{\mathbf{u}}) > 0$, then $g_1(\mathbf{u}_m) > 0$ when m is large since $\mathbf{u}_m \rightarrow \bar{\mathbf{u}}$. But since $u_{1,m}$ is positive, this is impossible. Similarly, $g_1(\bar{\mathbf{u}}) < 0$ is impossible. Therefore, $g_1(\bar{\mathbf{u}}) = 0$. The same argument shows that $g_2(\bar{\mathbf{u}}) = g_3(\bar{\mathbf{u}}) = 0$. Consequently, $\bar{\mathbf{u}} = \hat{\mathbf{u}}$. \square

Theorem 4 (lower bound). *Let d be a fixed positive number. There exists a positive constant $\underline{C}(A, d)$ such that, when $\varepsilon \leq 1/d$ and $d_i \geq d$, $i = 1, 2, 3$, the positive solution (u_1, u_2, u_3) of (5.1) satisfies*

$$\min_{\bar{\Omega}} u_i \geq \underline{C}(A, d), \quad i = 1, 2, 3.$$

Proof. Assume on the contrary that there exists a sequence $\{(d_{1,m}, d_{2,m}, d_{3,m}, k_m, \varepsilon_m)\}$, $m = 1, 2, \dots$, satisfying $\varepsilon_m \leq 1/d$ and $d_{1,m}, d_{2,m}, d_{3,m} \geq d$, such that the corresponding positive solution $\mathbf{u}_m = (u_{1,m}, u_{2,m}, u_{3,m})$ to (5.1) with $(d_1, d_2, d_3, k, \varepsilon) = (d_{1,m}, d_{2,m}, d_{3,m}, k_m, \varepsilon_m)$ satisfies

$$\lim_{m \rightarrow \infty} \min_{\bar{\Omega}} u_{1,m} = 0, \quad \text{or} \quad \lim_{m \rightarrow \infty} \min_{\bar{\Omega}} u_{2,m} = 0, \quad \text{or} \quad \lim_{m \rightarrow \infty} \min_{\bar{\Omega}} u_{3,m} = 0.$$

By (5.2), this implies that

$$\lim_{m \rightarrow \infty} \max_{\bar{\Omega}} u_{1,m} = 0, \quad \text{or} \quad \lim_{m \rightarrow \infty} \max_{\bar{\Omega}} u_{2,m} = 0, \quad \text{or} \quad \lim_{m \rightarrow \infty} \max_{\bar{\Omega}} u_{3,m} = 0. \quad (5.4)$$

We may assume, by passing to a subsequence if necessary, that as $m \rightarrow \infty$,

$$\begin{aligned} (d_{1,m}, d_{2,m}, d_{3,m}, k_m, \varepsilon_m) &\rightarrow (d_1, d_2, d_3, k, \varepsilon) \in [d, \infty]^3 \times [0, \infty] \times [0, 1/d], \\ (u_{1,m}, u_{2,m}, u_{3,m}) &\rightarrow (u_1, u_2, u_3), \end{aligned} \quad (5.5)$$

where u_i , $i = 1, 2, 3$, are non-negative functions.

In this proof, we only discuss the case that $d_i < \infty$, $i = 1, 2, 3$. When some of d_1, d_2 and d_3 are infinity, the discussions are similar to the case that $k = \infty$ of the following.

We will show:

- (i) If $k < \infty$ then (u_1, u_2, u_3) satisfies (5.1); and
- (ii) If $k = \infty$ then $u_1 = \tau(\varepsilon + u_2^2)$ for some constant $\tau \geq 0$ and (u_2, u_3, τ) satisfies

$$\begin{cases} -d_2 \Delta u_2 = u_2 \left(-\alpha + \frac{\beta \tau (\varepsilon + u_2^2) u_3}{\tau (\varepsilon + u_2^2) + u_2} \right) & \text{in } \Omega, \\ -d_3 \Delta u_3 = u_3 \left(r - u_3 - \frac{(1 + \beta) \tau (\varepsilon + u_2^2) u_2}{\tau (\varepsilon + u_2^2) + u_2} \right) & \text{in } \Omega, \\ \partial_n u_2 = \partial_n u_3 = 0 & \text{on } \partial \Omega. \end{cases} \quad (5.6)$$

We note that (5.6) implies that $\tau > 0$, for otherwise, $u_2 \equiv 0$, and either $u_3 \equiv 0$ or $u_3 \equiv r$, which contradicts Lemma 2.

To see (i), write

$$\varphi_m = u_{1,m} + \frac{k_m u_{1,m}}{d_{1,m}(\varepsilon_m + u_{2,m}^2)}. \quad (5.7)$$

Then

$$\begin{cases} -d_{1,m} \Delta \varphi_m = \mathbf{G}_1(\mathbf{u}_m) & \text{in } \Omega, \\ -d_{2,m} \Delta u_{2,m} = \mathbf{G}_2(\mathbf{u}_m) & \text{in } \Omega, \\ -d_{3,m} \Delta u_{3,m} = \mathbf{G}_3(\mathbf{u}_m) & \text{in } \Omega, \\ \partial_n \varphi_m = \partial_n u_{2,m} = \partial_n u_{3,m} = 0 & \text{on } \partial \Omega. \end{cases}$$

By (5.2) and the regularity theory for elliptic equations, we see that the $C^{1,\alpha}(\bar{\Omega})$ norms of $\varphi_m, u_{2,m}$ and $u_{3,m}$ are uniformly bounded with respect to m . From (5.7) we see that the $C^{1,\alpha}(\bar{\Omega})$ norms of $u_{1,m}$ are uniformly bounded with respect to m . Similarly, the $C^{2,\alpha}(\bar{\Omega})$ norms of $\varphi_m, u_{1,m}, u_{2,m}$ and $u_{3,m}$ are uniformly bounded with respect to m . It follows that there exist non-negative functions φ and u_1, u_2, u_3

such that

$$(\varphi_m, u_{1,m}, u_{2,m}, u_{3,m}) \rightarrow (\varphi, u_1, u_2, u_3) \quad \text{as } m \rightarrow \infty,$$

and (u_1, u_2, u_3) satisfies (5.1).

For the case $k = \infty$, we have $k_m \rightarrow \infty$ as $m \rightarrow \infty$. As $d_{1,m} \leq 1/d$ and the upper bounds of $(u_{1,m}, u_{2,m}, u_{3,m})$ do not depend on k_m , we see that

$$\lim_{m \rightarrow \infty} \frac{d_{1,m} u_{1,m}}{k_m} = \lim_{m \rightarrow \infty} \frac{G_1(\mathbf{u}_m)}{k_m} = 0. \quad (5.8)$$

Write $\psi_m(x) = [d_{1,m}/k_m + 1/(\varepsilon_m + u_{2,m}^2)]u_{1,m}$. Then

$$\begin{cases} -\Delta \psi_m = \frac{G_1(\mathbf{u}_m)}{k_m} & \text{in } \Omega, \\ \partial_n \psi_m = 0 & \text{on } \partial\Omega. \end{cases}$$

Thanks to (5.8), we have $\psi_m \rightarrow \tau$ for some non-negative constant τ , from which we deduce that $u_{1,m} \rightarrow \tau(\varepsilon + u_2^2)$. As in the case $k < \infty$, $(u_{2,m}, u_{3,m}) \rightarrow (u_2, u_3)$ for some non-negative functions u_2 and u_3 . It is easy to see that (u_2, u_3, τ) satisfies (5.6). Our claim is proved.

To complete the proof, we shall derive a contradiction from (5.4). We first discuss the case of $k < \infty$. Let (u_1, u_2, u_3) satisfy (5.1). By (5.2), for each $i \in \{1, 2, 3\}$, either $u_i > 0$ on $\bar{\Omega}$, or $u_i \equiv 0$ on $\bar{\Omega}$.

(1) If $u_1 \equiv 0$ and $u_2 > 0$ on $\bar{\Omega}$, then we have

$$\begin{cases} -d_2 \Delta u_2 = -\alpha u_2 & \text{in } \Omega, \\ \partial_n u_2 = 0 & \text{on } \partial\Omega, \end{cases}$$

which is a contradiction. Thus, $u_2 \equiv 0$. Therefore, u_3 satisfies

$$\begin{cases} -d_3 \Delta u_3 = u_3(r - u_3) & \text{in } \Omega, \\ \partial_n u_3 = 0 & \text{on } \partial\Omega. \end{cases}$$

This implies that either $u_3 \equiv 0$ or $u_3 \equiv r$, which contradicts Lemma 2. Similarly, if $u_2 \equiv 0$ then $u_1 \equiv 0$, again a contradiction.

(2) If $u_1, u_2 > 0$ on $\bar{\Omega}$ and $u_3 \equiv 0$, then u_2 satisfies

$$\begin{cases} -d_2 \Delta u_2 = -\alpha u_2 & \text{in } \Omega, \\ \partial_n u_2 = 0 & \text{on } \partial\Omega, \end{cases}$$

which is a contradiction.

For the case $k = \infty$, we have known that τ is a positive constant and (u_2, u_3) satisfies (5.6). Applying (5.6) it is easy to see that $u_2 \equiv 0$ implies $u_3 \equiv 0$ or $u_3 \equiv r$, and $u_3 \equiv 0$ implies $u_2 \equiv 0$. This contradicts Lemma 2. The proof of Theorem 4 is thus complete. \square

6. Local analysis at the constant positive steady state

In this section, we study the linearization of (5.1) at $\tilde{\mathbf{u}}$. Let \mathbf{X} be as in Section 4, and define

$$\begin{aligned}\mathbf{X}^+ &= \{\mathbf{u} \in \mathbf{X} \mid u_i > 0 \text{ on } \bar{\Omega}, i = 1, 2, 3\}, \\ B(C) &= \{\mathbf{u} \in \mathbf{X} \mid C^{-1} < u_i < C \text{ on } \bar{\Omega}, i = 1, 2, 3\}, \quad C > 0.\end{aligned}$$

Let $\Phi(\mathbf{u}) = (d_1 u_1 + k u_1 / (\varepsilon + u_2^2), d_2 u_2, d_3 u_3)^T$. Then (5.1) can be written as

$$\begin{cases} -\Delta \Phi(\mathbf{u}) = \mathbf{G}(\mathbf{u}) & \text{in } \Omega, \\ \partial_n \mathbf{u} = 0 & \text{on } \partial\Omega. \end{cases} \quad (6.1)$$

Since the determinant of $\Phi_{\mathbf{u}}(\mathbf{u})$ is positive for all non-negative \mathbf{u} , $\Phi_{\mathbf{u}}^{-1}(\mathbf{u})$ exists and $\det \Phi_{\mathbf{u}}^{-1}(\mathbf{u})$ is positive. Hence, \mathbf{u} is a positive solution to (6.1) if and only if

$$\mathbf{F}(\mathbf{u}) \triangleq \mathbf{u} - (\mathbf{I} - \Delta)^{-1} \{ \Phi_{\mathbf{u}}^{-1}(\mathbf{u}) [\mathbf{G}(\mathbf{u}) + \nabla \mathbf{u} \Phi_{\mathbf{uu}}(\mathbf{u}) \nabla \mathbf{u}] + \mathbf{u} \} = 0 \text{ in } \mathbf{X}^+,$$

where $(\mathbf{I} - \Delta)^{-1}$ is the inverse of $\mathbf{I} - \Delta$ in \mathbf{X} . As $\mathbf{F}(\cdot)$ is a compact perturbation of the identity operator, for any $B = B(C)$, the Leray–Schauder degree $\deg(\mathbf{F}(\cdot), 0, B)$ is well-defined if $\mathbf{F}(\mathbf{u}) \neq 0$ on ∂B .

Further, we note that

$$D_{\mathbf{u}}\mathbf{F}(\tilde{\mathbf{u}}) = \mathbf{I} - (\mathbf{I} - \Delta)^{-1} \{ \Phi_{\tilde{\mathbf{u}}}^{-1}(\tilde{\mathbf{u}}) \mathbf{G}_{\tilde{\mathbf{u}}}(\tilde{\mathbf{u}}) + \mathbf{I} \},$$

and recall that if $D_{\mathbf{u}}\mathbf{F}(\tilde{\mathbf{u}})$ is invertible, the index of \mathbf{F} at $\tilde{\mathbf{u}}$ is defined as $\text{index}(\mathbf{F}(\cdot), \tilde{\mathbf{u}}) = (-1)^\gamma$, where γ is the number of negative eigenvalues of $D_{\mathbf{u}}\mathbf{F}(\tilde{\mathbf{u}})$ [26, Theorem 2.8.1].

We refer to the decomposition (4.1) in our discussion of the eigenvalues of $D_{\mathbf{u}}\mathbf{F}(\tilde{\mathbf{u}})$. First, we note that, for each integer $i \geq 1$ and each integer $1 \leq j \leq \dim E(\mu_i)$, \mathbf{X}_{ij} is invariant under $D_{\mathbf{u}}\mathbf{F}(\tilde{\mathbf{u}})$, and λ is an eigenvalue of $D_{\mathbf{u}}\mathbf{F}(\tilde{\mathbf{u}})$ on \mathbf{X}_{ij} if and only if it is an eigenvalue of the matrix

$$\mathbf{I} - \frac{1}{1 + \mu_i} [\Phi_{\tilde{\mathbf{u}}}^{-1}(\tilde{\mathbf{u}}) \mathbf{G}_{\tilde{\mathbf{u}}}(\tilde{\mathbf{u}}) + \mathbf{I}] = \frac{1}{1 + \mu_i} [\mu_i \mathbf{I} - \Phi_{\tilde{\mathbf{u}}}^{-1}(\tilde{\mathbf{u}}) \mathbf{G}_{\tilde{\mathbf{u}}}(\tilde{\mathbf{u}})].$$

Thus, $D_{\mathbf{u}}\mathbf{F}(\tilde{\mathbf{u}})$ is invertible if and only if, for all $i \geq 1$, the matrix $\mathbf{I} - \frac{1}{1 + \mu_i} [\Phi_{\tilde{\mathbf{u}}}^{-1}(\tilde{\mathbf{u}}) \mathbf{G}_{\tilde{\mathbf{u}}}(\tilde{\mathbf{u}}) + \mathbf{I}]$ is nonsingular. Writing

$$H(\mu) = H(\tilde{\mathbf{u}}; \mu) \triangleq \det \{ \mu \mathbf{I} - \Phi_{\tilde{\mathbf{u}}}^{-1}(\tilde{\mathbf{u}}) \mathbf{G}_{\tilde{\mathbf{u}}}(\tilde{\mathbf{u}}) \}, \quad (6.2)$$

we note, furthermore, that if $H(\mu_i) \neq 0$, then for each $1 \leq j \leq \dim E(\mu_i)$, the number of negative eigenvalues of $D_{\mathbf{u}}\mathbf{F}(\tilde{\mathbf{u}})$ on \mathbf{X}_{ij} is odd if and only if $H(\mu_i) < 0$. In conclusion, we have the following:

Proposition 3. Suppose that, for all $i \geq 1$, the matrix $\mu_i \mathbf{I} - \Phi_{\mathbf{u}}^{-1}(\tilde{\mathbf{u}}) \mathbf{G}_{\mathbf{u}}(\tilde{\mathbf{u}})$ is non-singular. Then

$$\text{index}(\mathbf{F}(\cdot), \tilde{\mathbf{u}}) = (-1)^\gamma \quad \text{where} \quad \gamma = \sum_{i \geq 1, H(\mu_i) < 0} \dim E(\mu_i).$$

To facilitate our computation of $\text{index}(\mathbf{F}(\cdot), \tilde{\mathbf{u}})$, we will consider carefully the sign of $H(\mu_i)$. In particular, as the aim of this paper is to study the existence of stationary patterns with respect to the cross-diffusion coefficient k and diffusion coefficient d_3 , we will concentrate on the dependence of $H(\mu_i)$ on k and d_3 . At this point, we note that

$$H(\mu) = \det\{\Phi_{\mathbf{u}}^{-1}(\tilde{\mathbf{u}})\} \det\{\mu \Phi_{\mathbf{u}}(\tilde{\mathbf{u}}) - \mathbf{G}_{\mathbf{u}}(\tilde{\mathbf{u}})\}.$$

Since we have already established that $\det \Phi_{\mathbf{u}}^{-1}(\tilde{\mathbf{u}})$ is positive, we will only need to consider $\det\{\mu \Phi_{\mathbf{u}}(\tilde{\mathbf{u}}) - \mathbf{G}_{\mathbf{u}}(\tilde{\mathbf{u}})\}$.

As

$$\Phi_{\mathbf{u}}(\tilde{\mathbf{u}}) = \begin{pmatrix} d_1 + \frac{k}{\varepsilon + \tilde{u}_2^2} & -\frac{2k\tilde{u}_1\tilde{u}_2}{(\varepsilon + \tilde{u}_2^2)^2} & 0 \\ 0 & d_2 & 0 \\ 0 & 0 & d_3 \end{pmatrix},$$

we have

$$\begin{aligned} & (\tilde{u}_1 + \tilde{u}_2)^3 \det\{\mu \Phi_{\mathbf{u}}(\tilde{\mathbf{u}}) - \mathbf{G}_{\mathbf{u}}(\tilde{\mathbf{u}})\} \\ &= A_3(\varepsilon, k, d_3)\mu^3 + A_2(\varepsilon, k, d_3)\mu^2 + A_1(\varepsilon, k, d_3)\mu - \det\{\mathbf{G}_{\mathbf{u}}(\tilde{\mathbf{u}})\}(\tilde{u}_1 + \tilde{u}_2)^3 \\ &\triangleq \mathcal{A}(\varepsilon, k, d_3; \mu), \end{aligned} \tag{6.3}$$

where

$$\begin{aligned} A_3(\varepsilon, k, d_3) &= d_2 d_3 \left(d_1 + \frac{k}{\varepsilon + \tilde{u}_2^2} \right) (\tilde{u}_1 + \tilde{u}_2)^3, \\ A_2(\varepsilon, k, d_3) &= d_2 d_3 \tilde{u}_1 (\tilde{u}_1 + \tilde{u}_2)^2 + d_2 \left(d_1 + \frac{k}{\varepsilon + \tilde{u}_2^2} \right) \tilde{u}_3 (\tilde{u}_1 + \tilde{u}_2)^3 \\ &\quad + \beta d_3 \left(d_1 + \frac{k}{\varepsilon + \tilde{u}_2^2} \right) \tilde{u}_1 (\tilde{u}_1 + \tilde{u}_2)^2 - 2k\beta d_3 \frac{\tilde{u}_1 \tilde{u}_2^2 (\tilde{u}_1 + \tilde{u}_2)^2}{(\varepsilon + \tilde{u}_2^2)^2}, \\ A_1(\varepsilon, k, d_3) &= \tilde{u}_1 (\tilde{u}_1 + \tilde{u}_2) \{ d_2 \tilde{u}_3 (\tilde{u}_1 + \tilde{u}_2) + (1 + \beta) d_2 \tilde{u}_2^2 \} \\ &\quad + \beta \left(d_1 + \frac{k}{\varepsilon + \tilde{u}_2^2} \right) \tilde{u}_1 \tilde{u}_3 (\tilde{u}_1 + \tilde{u}_2)^2 + 2k\beta (1 + \beta) \frac{\tilde{u}_1^2 \tilde{u}_2^3 (\tilde{u}_1 + \tilde{u}_2)}{(\varepsilon + \tilde{u}_2^2)^2} \\ &\quad + \alpha (1 + \beta) \tilde{u}_1^2 \tilde{u}_2 \left(d_1 + \frac{k}{\varepsilon + \tilde{u}_2^2} \right) (\tilde{u}_1 + \tilde{u}_2) - 2k\beta \frac{\tilde{u}_1 \tilde{u}_2^2 \tilde{u}_3 (\tilde{u}_1 + \tilde{u}_2)^2}{(\varepsilon + \tilde{u}_2^2)^2}. \end{aligned}$$

First we consider the dependence of \mathcal{A} on k .

Let $\tilde{\mu}_1(k), \tilde{\mu}_2(k)$ and $\tilde{\mu}_3(k)$ be the three roots of $\mathcal{A}(\varepsilon, k, d_3; \mu) = 0$ with $\operatorname{Re}\{\tilde{\mu}_1(k)\} \leq \operatorname{Re}\{\tilde{\mu}_2(k)\} \leq \operatorname{Re}\{\tilde{\mu}_3(k)\}$. Then $\tilde{\mu}_1(k)\tilde{\mu}_2(k)\tilde{\mu}_3(k) = \det\{\mathbf{G}_u(\tilde{\mathbf{u}})\}(\tilde{u}_1 + \tilde{u}_2)^3$. Note that $\det\{\mathbf{G}_u(\tilde{\mathbf{u}})\} < 0$ and $A_3(\varepsilon, k, d_3) > 0$. Thus, one of $\tilde{\mu}_1(k), \tilde{\mu}_2(k), \tilde{\mu}_3(k)$ is real and negative, and the product of the other two is positive.

Consider the following limits:

$$\begin{aligned}\lim_{k \rightarrow \infty} \frac{A_3(\varepsilon, k, d_3)}{k} &= \frac{d_2 d_3}{\varepsilon + \tilde{u}_2^2} (\tilde{u}_1 + \tilde{u}_2)^3 \triangleq a_3(\varepsilon, d_3), \\ \lim_{k \rightarrow \infty} \frac{A_2(\varepsilon, k, d_3)}{k} &= \frac{(\tilde{u}_1 + \tilde{u}_2)^2}{\varepsilon + \tilde{u}_2^2} \left\{ d_2 \tilde{u}_3 (\tilde{u}_1 + \tilde{u}_2) + \beta d_3 \tilde{u}_1 - 2\beta d_3 \frac{\tilde{u}_1 \tilde{u}_2^2}{\varepsilon + \tilde{u}_2^2} \right\} \triangleq a_2(\varepsilon, d_3), \\ \lim_{k \rightarrow \infty} \frac{A_1(\varepsilon, k, d_3)}{k} &= \frac{\tilde{u}_1 (\tilde{u}_1 + \tilde{u}_2)}{\varepsilon + \tilde{u}_2^2} \left\{ \beta \tilde{u}_3 (\tilde{u}_1 + \tilde{u}_2) + 2\beta (1 + \beta) \frac{\tilde{u}_1 \tilde{u}_2^3}{\varepsilon + \tilde{u}_2^2} \right. \\ &\quad \left. + \alpha (1 + \beta) \tilde{u}_1 \tilde{u}_2 - 2\beta \frac{\tilde{u}_2^2 \tilde{u}_3 (\tilde{u}_1 + \tilde{u}_2)}{\varepsilon + \tilde{u}_2^2} \right\} \triangleq a_1(\varepsilon).\end{aligned}$$

If the parameters α, β and r satisfy

$$\frac{r\beta}{\alpha + \beta} < 1 + \frac{\beta}{\alpha + 2\beta}, \quad (6.4)$$

then

$$\begin{aligned}a_1(0) &= \frac{\tilde{u}_1 (\tilde{u}_1 + \tilde{u}_2)}{\tilde{u}_2^2} \{ \beta \tilde{u}_3 (\tilde{u}_1 + \tilde{u}_2) + 2\beta (1 + \beta) \tilde{u}_1 \tilde{u}_2 + \alpha (1 + \beta) \tilde{u}_1 \tilde{u}_2 - 2\beta \tilde{u}_3 (\tilde{u}_1 + \tilde{u}_2) \} \\ &= \tilde{u}_1 \left(1 + \frac{\tilde{u}_1}{\tilde{u}_2} \right)^2 \left\{ -\beta \tilde{u}_3 + (\alpha + 2\beta) (1 + \beta) \frac{\tilde{u}_1 \tilde{u}_2}{\tilde{u}_1 + \tilde{u}_2} \right\} \\ &= \tilde{u}_1 \left(1 + \frac{\tilde{u}_1}{\tilde{u}_2} \right)^2 \{ r(\alpha + 2\beta) - (\alpha + 3\beta) \tilde{u}_3 \} \\ &= \tilde{u}_1 \left(1 + \frac{\tilde{u}_1}{\tilde{u}_2} \right)^2 \left\{ r(\alpha + 2\beta) - \frac{1}{\beta} (\alpha + 3\beta)(\alpha + \beta) \right\} \\ &< 0.\end{aligned}$$

Thus, by continuity, there exists an $\varepsilon_0 > 0$ such that $a_1(\varepsilon) < 0$ for all $\varepsilon \leq \varepsilon_0$. In the following, we restrict our attention to $0 < \varepsilon \leq \varepsilon_0$. In this range, $a_1(\varepsilon) < 0$, and $A_1(\varepsilon, k, d_3) < 0$ for all sufficiently large k . Note that

$$\begin{aligned}\lim_{k \rightarrow \infty} \frac{\mathcal{A}(\varepsilon, k, d_3; \mu)}{k} &= a_3(\varepsilon, d_3) \mu^3 + a_2(\varepsilon, d_3) \mu^2 + a_1(\varepsilon) \mu \\ &= \mu [a_3(\varepsilon, d_3) \mu^2 + a_2(\varepsilon, d_3) \mu + a_1(\varepsilon)]\end{aligned}$$

and $a_1(\varepsilon) < 0 < a_3(\varepsilon, d_3)$. A continuity argument shows that, when k is large, $\tilde{\mu}_1(k)$ is real and negative. Furthermore, as $\tilde{\mu}_2(k)\tilde{\mu}_3(k) > 0$, $\tilde{\mu}_2(k)$ and $\tilde{\mu}_3(k)$ are real

and positive, and

$$\lim_{k \rightarrow \infty} \tilde{\mu}_1(k) = \frac{-a_2(\varepsilon, d_3) - \sqrt{a_2^2(\varepsilon, d_3) - 4a_1(\varepsilon)a_3(\varepsilon, d_3)}}{2a_3(\varepsilon, d_3)} < 0, \quad \lim_{k \rightarrow \infty} \tilde{\mu}_2(k) = 0, \quad (6.5)$$

$$\lim_{k \rightarrow \infty} \tilde{\mu}_3(k) = \frac{-a_2(\varepsilon, d_3) + \sqrt{a_2^2(\varepsilon, d_3) - 4a_1(\varepsilon)a_3(\varepsilon, d_3)}}{2a_3(\varepsilon, d_3)} \triangleq \tilde{\mu} > 0. \quad (6.6)$$

Thus we have:

Proposition 4. Assume that (6.4) holds and $0 < \varepsilon \leq \varepsilon_0$. Then there exists a positive number k^* such that, when $k \geq k^*$, the three roots $\tilde{\mu}_1(k), \tilde{\mu}_2(k), \tilde{\mu}_3(k)$ of $\mathcal{A}(\varepsilon, k, d_3; \mu) = 0$ are all real and satisfy (6.5) and (6.6). Moreover, for all $k \geq k^*$,

$$\begin{cases} -\infty < \tilde{\mu}_1(k) < 0 < \tilde{\mu}_2(k) < \tilde{\mu}_3(k), \\ \mathcal{A}(\varepsilon, k, d_3; \mu) < 0 \text{ when } \mu \in (-\infty, \tilde{\mu}_1(k)) \cup (\tilde{\mu}_2(k), \tilde{\mu}_3(k)), \\ \mathcal{A}(\varepsilon, k, d_3; \mu) > 0 \text{ when } \mu \in (\tilde{\mu}_1(k), \tilde{\mu}_2(k)) \cup (\tilde{\mu}_3(k), \infty). \end{cases} \quad (6.7)$$

Remark 2. It is obvious that, if

$$\frac{\alpha + \beta}{\beta} < r < \frac{(\alpha + \beta)(\alpha + 3\beta)}{\beta(\alpha + 2\beta)}, \quad (6.8)$$

then (2.5) and (6.4) hold. In terms of the original parameters α_i and β_i (6.8) takes the form

$$\frac{\alpha_2\beta_1 + \alpha_1\beta_2}{\beta_2} < \alpha_3 < \frac{(\alpha_2\beta_1 + \alpha_1\beta_2)(\alpha_2\beta_1 + 3\alpha_1\beta_2)}{\beta_2(\alpha_2\beta_1 + 2\alpha_1\beta_2)}. \quad (6.9)$$

This condition therefore gives a relationship between the intrinsic growth rate of the prey and the mortality rates and predation coefficients of the predators. For example, it is easy to see that if the prey grows too slowly, then it will die off and there will be no positive steady state solution.

Next we consider the dependence of \mathcal{A} on d_3 .

In this case, we consider the limits

$$\begin{aligned}\lim_{d_3 \rightarrow \infty} \frac{A_3(\varepsilon, k, d_3)}{d_3} &= d_2(\tilde{u}_1 + \tilde{u}_2)^3 \left(d_1 + \frac{k}{\varepsilon + \tilde{u}_2^2} \right) \triangleq b_3(\varepsilon, k), \\ \lim_{d_3 \rightarrow \infty} \frac{A_2(\varepsilon, k, d_3)}{d_3} &= \tilde{u}_1(\tilde{u}_1 + \tilde{u}_2)^2 \left(d_2 + \beta d_1 + \frac{k\beta(\varepsilon - \tilde{u}_2^2)}{(\varepsilon + \tilde{u}_2^2)^2} \right) \triangleq b_2(\varepsilon, k), \\ \lim_{d_3 \rightarrow \infty} \frac{A_1(\varepsilon, k, d_3)}{d_3} &= 0, \\ \lim_{d_3 \rightarrow \infty} \frac{\mathcal{A}(\varepsilon, k, d_3; \mu)}{d_3} &= \mu^2 [b_3(\varepsilon, k)\mu + b_2(\varepsilon, k)].\end{aligned}$$

When the parameters $d_1, d_2, \alpha, \beta, r, k$ and ε satisfy $b_2(\varepsilon, k) < 0$, i.e.,

$$(d_2 + \beta d_1)(\varepsilon + \tilde{u}_2^2)^2 < k\beta(\tilde{u}_2^2 - \varepsilon), \quad (6.10)$$

one can establish the following similarly as Proposition 4.

Proposition 5. Assume that (6.10) holds, i.e., the cross-diffusion coefficient k is large or the diffusion coefficients d_1 and d_2 are small. Then there exists a positive constant D such that when $d_3 \geq D$, the three roots $\bar{\mu}_1(d_3), \bar{\mu}_2(d_3), \bar{\mu}_3(d_3)$ of $\mathcal{A}(\varepsilon, k, d_3; \mu) = 0$ are all real and satisfy

$$\begin{aligned}\lim_{d_3 \rightarrow \infty} \bar{\mu}_1(d_3) &= \lim_{d_3 \rightarrow \infty} \bar{\mu}_2(d_3) = 0, \\ \lim_{d_3 \rightarrow \infty} \bar{\mu}_3(d_3) &= \frac{-b_2(\varepsilon, k)}{b_3(\varepsilon, k)} = \frac{\tilde{u}_1[k\beta(\tilde{u}_2^2 - \varepsilon) - (d_2 + \beta d_1)(\varepsilon + \tilde{u}_2^2)^2]}{d_2(\tilde{u}_1 + \tilde{u}_2)(\varepsilon + \tilde{u}_2^2)[k + d_1(\varepsilon + \tilde{u}_2^2)]} \triangleq \bar{\mu}.\end{aligned} \quad (6.11)$$

Moreover, when $d_3 \geq D$, (6.7) holds with $\tilde{\mu}_i(k)$ replaced by $\bar{\mu}_i(d_3)$.

7. Global existence of stationary patterns

In this section, we shall discuss the global existence of non-constant positive solutions to (5.1) with respect to the cross-diffusion coefficient k and the diffusion coefficient d_3 , respectively, as the other parameters $d_1, d_2, \varepsilon, \alpha, \beta$ and r are fixed. Our results are as follows.

Theorem 5. Let the parameters $\alpha, \beta, r, \varepsilon$ and $d_i, i = 1, 2, 3$, be fixed, and satisfy (6.4) and $0 < \varepsilon \leq \varepsilon_0$, where ε_0 is the constant in Proposition 4. Let $\bar{\mu}$ be given by the limit (6.6). If $\bar{\mu} \in (\mu_n, \mu_{n+1})$ for some $n \geq 2$, and the sum $\sigma_n = \sum_{i=2}^n \dim E(\mu_i)$ is odd, then there exists a positive constant K such that, if $k \geq K$, (5.1) has at least one non-constant positive solution.

Theorem 6. Let the parameters $\alpha, \beta, r, \varepsilon, d_1, d_2$ and k be fixed, and satisfy (6.10). Let $\bar{\mu}$ be given by the limit (6.11). If $\bar{\mu} \in (\mu_n, \mu_{n+1})$ for some $n \geq 2$, and the sum $\sigma_n = \sum_{i=2}^n \dim E(\mu_i)$ is odd, then there exists a positive constant D such that, if $d_3 \geq D$, (5.1) has at least one non-constant positive solution.

As the proofs of these results are similar, we will prove only Theorem 5.

Proof of Theorem 5. By (6.5), (6.6) and Proposition 4, there exists a positive constant K such that, when $k \geq K$, (6.7) holds and

$$0 = \mu_1 < \tilde{\mu}_2(k) < \mu_2, \quad \tilde{\mu}_3(k) \in (\mu_n, \mu_{n+1}). \quad (7.1)$$

We shall prove that for any $k \geq K$, (5.1) has at least one non-constant positive solution. The proof, which is by contradiction, is based on the homotopy invariance of the topological degree. Suppose on the contrary that the assertion is not true for some $k = \bar{k} \geq K$. In the sequel we fix $k = \bar{k}$.

For $t \in [0, 1]$, define $\Phi(t; \mathbf{u}) = (d_1 u_1 + t k u_1 / (\varepsilon + u_2^2), d_2 u_2, d_3 u_3)^T$, and consider the problem

$$\begin{cases} -\Delta \Phi(t; \mathbf{u}) = \mathbf{G}(\mathbf{u}) & \text{in } \Omega, \\ \partial_n \mathbf{u} = 0 & \text{on } \partial\Omega. \end{cases} \quad (7.2)$$

Then \mathbf{u} is a positive non-constant solution of (5.1) if and only if it is such a solution of (7.2) for $t = 1$. It is obvious that $\tilde{\mathbf{u}}$ is the unique constant positive solution of (7.2) for any $0 \leq t \leq 1$. As we observed in Section 6, for any $0 \leq t \leq 1$, \mathbf{u} is a positive solution of (7.2) if and only if

$$\mathbf{F}(t; \mathbf{u}) \triangleq \mathbf{u} - (\mathbf{I} - \Delta)^{-1} \{ \Phi_{\mathbf{u}}^{-1}(t; \mathbf{u}) [\mathbf{G}(\mathbf{u}) + \nabla \mathbf{u} \Phi_{\mathbf{u}}(t; \mathbf{u}) \nabla \mathbf{u}] + \mathbf{u} \} = 0 \text{ in } \mathbf{X}^+.$$

It is obvious that $\mathbf{F}(1; \mathbf{u}) = \mathbf{F}(\mathbf{u})$. Theorem 2 shows that $\mathbf{F}(0; \mathbf{u}) = 0$ has only the positive solution $\tilde{\mathbf{u}}$ in \mathbf{X}^+ . By a direct computation,

$$D_{\mathbf{u}} \mathbf{F}(t; \tilde{\mathbf{u}}) = \mathbf{I} - (\mathbf{I} - \Delta)^{-1} \{ \Phi_{\tilde{\mathbf{u}}}^{-1}(t; \tilde{\mathbf{u}}) \mathbf{G}_{\tilde{\mathbf{u}}}(\tilde{\mathbf{u}}) + \mathbf{I} \}.$$

In particular,

$$\begin{aligned} D_{\mathbf{u}} \mathbf{F}(0; \tilde{\mathbf{u}}) &= \mathbf{I} - (\mathbf{I} - \Delta)^{-1} \{ \mathcal{D}^{-1} \mathbf{G}_{\tilde{\mathbf{u}}}(\tilde{\mathbf{u}}) + \mathbf{I} \}, \\ D_{\mathbf{u}} \mathbf{F}(1; \tilde{\mathbf{u}}) &= \mathbf{I} - (\mathbf{I} - \Delta)^{-1} \{ \Phi_{\tilde{\mathbf{u}}}^{-1}(\tilde{\mathbf{u}}) \mathbf{G}_{\tilde{\mathbf{u}}}(\tilde{\mathbf{u}}) + \mathbf{I} \} = D_{\mathbf{u}} \mathbf{F}(\tilde{\mathbf{u}}), \end{aligned}$$

where $\mathcal{D} = \text{diag}(d_1, d_2, d_3)$. From (6.2) and (6.3) we see that

$$H(\mu) = \det \{ \Phi_{\tilde{\mathbf{u}}}^{-1}(\tilde{\mathbf{u}}) \} (\tilde{u}_1 + \tilde{u}_2)^{-3} \mathcal{A}(\varepsilon, k, d_3; \mu). \quad (7.3)$$

In view of (6.7) and (7.1), it follows from (7.3) that

$$\begin{cases} H(\mu_1) = H(0) > 0, \\ H(\mu_i) < 0, & 2 \leq i \leq n, \\ H(\mu_i) > 0, & i \geq n+1. \end{cases}$$

Therefore, zero is not an eigenvalue of the matrix $\mu_i \mathbf{I} - \Phi_{\mathbf{u}}^{-1}(\tilde{\mathbf{u}}) \mathbf{G}_{\mathbf{u}}(\tilde{\mathbf{u}})$ for all $i \geq 1$, and

$$\sum_{i \geq 1, H(\mu_i) < 0} \dim E(\mu_i) = \sum_{i=2}^n \dim E(\mu_i) = \sigma_n \text{ which is odd.}$$

Thanks to Proposition 3, we have

$$\text{index}(\mathbf{F}(1; \cdot), \tilde{\mathbf{u}}) = (-1)^{\gamma} = (-1)^{\sigma_n} = -1. \quad (7.4)$$

Similarly, we can prove that

$$\text{index}(\mathbf{F}(0; \cdot), \tilde{\mathbf{u}}) = (-1)^0 = 1. \quad (7.5)$$

Now, by Theorems 3 and 4, there exists a positive constant C such that, for all $0 \leq t \leq 1$, the positive solutions of (7.2) satisfy $1/C < u_1, u_2, u_3 < C$. Therefore, $\mathbf{F}(t; \mathbf{u}) \neq 0$ on $\partial B(C)$ for all $0 \leq t \leq 1$. By the homotopy invariance of the topological degree,

$$\deg(\mathbf{F}(1; \cdot), 0, B(C)) = \deg(\mathbf{F}(0; \cdot), 0, B(C)). \quad (7.6)$$

On the other hand, by our supposition, both equations $\mathbf{F}(1; \mathbf{u}) = 0$ and $\mathbf{F}(0; \mathbf{u}) = 0$ have only the positive solution $\tilde{\mathbf{u}}$ in $B(C)$, and hence, by (7.4) and (7.5),

$$\deg(\mathbf{F}(0; \cdot), 0, B(C)) = \text{index}(\mathbf{F}(0; \cdot), \tilde{\mathbf{u}}) = 1,$$

$$\deg(\mathbf{F}(1; \cdot), 0, B(C)) = \text{index}(\mathbf{F}(1; \cdot), \tilde{\mathbf{u}}) = -1.$$

This contradicts (7.6) and the proof is complete. \square

8. Non-existence and bifurcation

In this section, we discuss the non-existence and bifurcation of non-constant positive solutions of (5.1).

Theorem 7. *If the parameters $\alpha, \beta, r, d_1, d_2, \varepsilon$ and k satisfy*

$$\beta k^2 \leq d_2(\varepsilon + \tilde{u}_2^2)[k + d_1(\varepsilon + \tilde{u}_2^2)], \quad (8.1)$$

then the problem (5.1) has no non-constant positive solutions. In particular, as long as one of d_1 and d_2 is sufficiently large, the problem (5.1) will have no non-constant positive solution.

Proof. Assume that \mathbf{u} is a positive solution of (5.1). Let p and q be given by (3.1). Multiplying the equations of (5.1) by $p(u_1 - \tilde{u}_1)/u_1$, $(u_2 - \tilde{u}_2)/u_2$ and $q(u_3 - \tilde{u}_3)/u_3$ respectively, and integrating by parts, as in Step 2 of the proof of Theorem 2, we obtain

$$0 = - \int_{\Omega} \left\{ p \left(d_1 + \frac{k}{\varepsilon + u_2^2} \right) \frac{\tilde{u}_1}{u_1^2} |\nabla u_1|^2 - 2pk \frac{\tilde{u}_1 u_2}{u_1 (\varepsilon + u_2^2)^2} \nabla u_1 \cdot \nabla u_2 + d_2 \frac{\tilde{u}_2}{u_2^2} |\nabla u_2|^2 \right\} dx \\ - \int_{\Omega} \frac{q d_3 \tilde{u}_3}{u_3^2} |\nabla u_3|^2 dx - \int_{\Omega} \left\{ \frac{(\beta u_1 - \alpha u_2)^2}{\alpha(u_1 + u_2)} + \frac{\alpha + \beta}{\alpha\beta(1 + \beta)} (\alpha + \beta - \beta u_3)^2 \right\} dx.$$

Applying (8.1) it is easy to prove that

$$p \left(d_1 + \frac{k}{\varepsilon + u_2^2} \right) \frac{\tilde{u}_1}{u_1^2} |\nabla u_1|^2 - 2pk \frac{\tilde{u}_1 u_2}{u_1 (\varepsilon + u_2^2)^2} \nabla u_1 \cdot \nabla u_2 + d_2 \frac{\tilde{u}_2}{u_2^2} |\nabla u_2|^2 \geq 0.$$

This implies that $\mathbf{u} \equiv \tilde{\mathbf{u}}$ on Ω and the proof is complete. \square

In the following we consider the bifurcation of non-constant positive solutions with respect to the cross-diffusion coefficient k and the diffusion coefficient d_3 .

In the consideration of bifurcation with respect to k , we recall that, for a constant solution \mathbf{u}^* , $(\tilde{k}; \mathbf{u}^*) \in (0, \infty) \times \mathbf{X}$ is a *bifurcation point* of (5.1) if, for any $\delta \in (0, \tilde{k})$, there exists $k \in [\tilde{k} - \delta, \tilde{k} + \delta]$ such that (5.1) has a non-constant positive solution. Otherwise, we say that $(\tilde{k}; \mathbf{u}^*)$ is a *regular point*. Bifurcation and regular points with respect to d_3 are defined analogously.

We shall consider the bifurcation of (5.1) at the equilibrium points $(\tilde{k}; \tilde{\mathbf{u}})$, $\tilde{k} > 0$, and $(\tilde{d}_3; \tilde{\mathbf{u}})$, $\tilde{d}_3 > 0$, respectively, while all other parameters are held fixed. Let $\mathcal{S}_p = \{\mu_1, \mu_2, \mu_3, \dots\}$, and $\Sigma = \{\mu > 0 \mid H(\mu) = 0\}$ where $H(\mu)$ is as defined in (6.2). To emphasize the dependence of $H(\mu)$ and Σ on k or d_3 , we write $H(k; \mu)$ or $H(d_3; \mu)$, and $\Sigma_k(k)$ or $\Sigma_{d_3}(d_3)$, respectively. We note that for each $k > 0$ and $d_3 > 0$, Σ may have 0 or 2 elements.

The results of this section are contained in the following two theorems. Their proofs are based on the topological degree arguments used earlier in this paper. We shall omit them but refer the reader to similar treatments in [30].

Theorem 8 (bifurcation with respect to k). (1) If $\mathcal{S}_p \cap \Sigma_k(\tilde{k}) = \emptyset$, then $(\tilde{k}; \tilde{\mathbf{u}})$ is a regular point of (5.1).

(2) Suppose $\mathcal{S}_p \cap \Sigma_k(\tilde{k}) \neq \emptyset$ and the positive roots of $H(\tilde{k}; \mu) = 0$ are all simple. If $\sum_{\mu_i \in \Sigma_k(\tilde{k})} \dim E(\mu_i)$ is odd, then $(\tilde{k}; \tilde{\mathbf{u}})$ is a bifurcation point of (5.1). In this

case, there exists an interval $(a, b) \subset \mathbb{R}^+$, where

- (i) $\tilde{k} = a < b < \infty$ and $\mathcal{S}_p \cap \Sigma_k(b) \neq \emptyset$, or
- (ii) $0 < a < b = \tilde{k}$ and $\mathcal{S}_p \cap \Sigma_k(a) \neq \emptyset$, or
- (iii) $(a, b) = (\tilde{k}, \infty)$,

such that for every $k \in (a, b)$, (5.1) admits a non-constant positive solution.

Theorem 9 (bifurcation with respect to d_3). (1) If $\mathcal{S}_p \cap \Sigma_{d_3}(\tilde{d}_3) = \emptyset$, then $(\tilde{d}_3; \tilde{\mathbf{u}})$ is a regular point of (5.1).

(2) Suppose $\mathcal{S}_p \cap \Sigma_{d_3}(\tilde{d}_3) \neq \emptyset$ and the positive roots of $H(\tilde{d}_3; \mu) = 0$ are all simple. If $\sum_{\mu_i \in \Sigma_{d_3}(\tilde{d}_3)} \dim E(\mu_i)$ is odd, then $(\tilde{d}_3; \tilde{\mathbf{u}})$ is a bifurcation point of (5.1). In this case, there exists an interval $(c, d) \subset \mathbb{R}^+$, where

- (i) $\tilde{d}_3 = c < d < \infty$ and $\mathcal{S}_p \cap \Sigma_{d_3}(d) \neq \emptyset$, or
- (ii) $0 < c < d = \tilde{d}_3$ and $\mathcal{S}_p \cap \Sigma_{d_3}(c) \neq \emptyset$, or
- (iii) $(c, d) = (\tilde{d}_3, \infty)$, or
- (iv) $(c, d) = (0, \tilde{d}_3)$,

such that for every $d_3 \in (c, d)$, (5.1) admits a non-constant positive solution.

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