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Spatiotemporal Patterns of a Reaction–Diffusion Substrate–Inhibition Seelig Model

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Abstract In this paper, the spatiotemporal patterns of a reaction–diffusion substrate–inhibition chemical Seelig model are considered. We first prove that this parabolic Seelig model has an invariant rectangle in the phase plane which attracts all the solutions of the model regardless of the initial values. Then, we consider the long time behaviors of the solutions in the invariant rectangle. In particular, we prove that, under suitable "lumped parameter assumption" conditions, these solutions either converge exponentially to the unique positive constant steady states or to the spatially homogeneous periodic solutions. Finally, we study the existence and non-existence of Turing patterns. To find parameter ranges where system does not exhibit Turing patterns, we use the properties of non-constant steady states, including obtaining several useful estimates. To seek the parameter ranges where system possesses Turing patterns, we use the techniques of global bifurcation theory. These two different parameter ranges are distinguished in a delicate bifurcation diagram. Moreover, numerical experiments are also presented to support and strengthen our analytical analysis.

Keywords Seelig reaction–diffusion chemical model · Invariant rectangle · Lumped parameter assumption · Global bifurcation analysis · Turing patterns

1 Introduction

A fundamental problem in theoretical biology is to understand how patterns and shapes are formed. In his seminal paper, Turing [20] proposed a striking idea of "diffusion-driven instability," which states that diffusion could destabilize an otherwise stable steady state of a reaction–diffusion system and generate new stable time-independent nonuniform spatial

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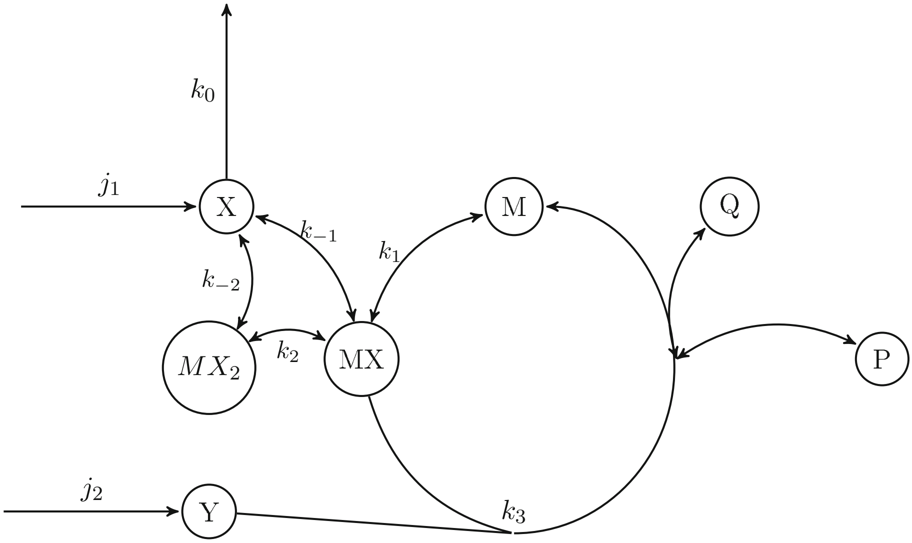

Fig. 1 Schematic chemical reaction of Seelig model (1.1)

patterns. Over the years, Turing's idea has attracted the attention of many researchers and has been successfully developed on the theoretical backgrounds. Not only has it been studied in biological and chemical fields, but also some investigations range as far as economics, semiconductor physics, and star formation [5].

The existence of Turing patterns in biology is still controversial, but it had been observed in chemistry. The first experimental evidence of Turing patterns was reported in 1990 by D. Kepper and her associates on the chlorite-iodide-malonic acid and starch reaction (CIMA reaction) in an open unstirred gel reactor [2,4], nearly forty years after the publication of [20]. This CIMA reaction can be modeled by the famous Lengyel–Epstein system [12,13] which has been extensively studied experimentally, numerically and theoretically (see [1,7–11,15,22–24] and the references therein).

In this paper, we consider a reaction–diffusion model which has a very similar mathematical form to the Lengyel–Epstein CIMA reaction system, even though they describe different chemical reactions. Our model was first proposed by Seelig in [18] to explain the observed oscillatory behavior in substrate–inhibition chemical reaction: $X + Y \rightarrow P + Q$ effected by a catalyst M such as an enzyme. The chemical reaction scheme is (see also Fig. 1): The substrates X and Y are supplied at constant rates j_1 and j_2 respectively. The substrate X flows out at rate k_0. The substrate X reacts with catalyst M to form the inert complex MX at rate k_1. This reaction is reversible in the sense that MX can form X and M at rate k_{-1}. Whenever there is MX, then X will react with MX, and form MX_2 at a rate k_2. This reaction is also reversible, MX_2 can form X and MX at rate k_{-2}. The substrate Y reacts with MX, forming P, Q and M at rate k_3. This reaction is irreversiable. In the whole substrate–inhibition chemical reactions, all the reversible reactions are taken to be fast and all the irreversible ones are slow.

Let $[\cdot]$ denote the concentrations of the chemical substances at time τ, then by the law of mass action, we obtain the following kinetic equations for the reaction mechanism:

$$\begin{aligned}
\frac{d[X]}{d\tau} &= j_1 - k_0[X] - k_1[X][M] + k_{-1}[MX] - k_2[X][MX] + k_{-2}[MX_2],\\
\frac{d[Y]}{d\tau} &= j_2 - k_3[Y][MX],\\
\frac{d[M]}{d\tau} &= -k_1[X][M] + k_{-1}[MX] + k_3[Y][MX],\\
\frac{d[MX_2]}{d\tau} &= k_2[X][MX] - k_{-2}[MX_2],\\
\frac{d[MX]}{d\tau} &= k_1[X][M] - k_{-1}[MX] - k_2[X][MX] - k_3[Y][MX] + k_{-2}[MX_2].
\end{aligned} \tag{1.1}$$

It is assumed that the sum of the various forms of the catalyst M, MX, MX_2 is constant and is represented by the adjustable parameter $[M]_{\text{total}} := [M]+[MX]+[MX_2]$. We also assume a quasi steady state for the concentrations of M, MX, and MX_2, since their concentrations are normally small compared to $[X]$ and $[Y]$ so that they can follow virtually inertness the movements of $[X]$ and $[Y]$. Namely., letting $d[M]/d\tau$, $d[MX]/d\tau$ and $d[MX_2]/d\tau$ equal to zero. Thus,

$$\begin{aligned}
\frac{d[X]}{d\tau} &= j_1 - k_0[X] - k_3[Y][MX],\\
\frac{d[Y]}{d\tau} &= j_2 - k_3[Y][MX],\\
0 &= -k_1[X][M] + k_{-1}[MX] + k_3[Y][MX],\\
0 &= k_2[X][MX] - k_{-2}[MX_2],\\
0 &= k_1[X][M] - k_{-1}[MX] - k_2[X][MX] - k_3[Y][MX] + k_{-2}[MX_2].
\end{aligned} \tag{1.2}$$

From the last three equations of (1.2), we obtain

$$k_3[Y][MX] = k_{-1}[M]_{\text{total}} \cdot \frac{\dfrac{k_1[X]}{k_{-1}} \cdot \dfrac{k_3[Y]}{k_{-1}}}{1 + \dfrac{k_1[X]}{k_{-1}} + \dfrac{k_1k_2[X]^2}{k_{-1}k_{-2}} + \dfrac{k_3[Y]}{k_{-1}}}. \tag{1.3}$$

Introducing the following dimensionless quantities,

$$\begin{gathered}
u = \frac{k_1[X]}{k_{-1}},\ v = \frac{k_3[Y]}{k_{-1}},\ t = k_0\tau,\ K = \frac{k_2k_{-1}}{k_{-2}k_1},\ \beta_1 = \frac{k_1 j_1}{k_0k_{-1}}, \beta_2 = \frac{k_3 j_2}{k_0k_{-1}},\\
\gamma_1 = \frac{[M]_{\text{total}}k_1}{k_0},\ \gamma_2 = \frac{[M]_{\text{total}}k_3}{k_0},
\end{gathered} \tag{1.4}$$

one can reduce the first two equations of (1.2) to the following system of ordinary differential equations (ODEs):

$$\frac{du}{dt} = \beta_1 - u - \frac{\gamma_1 uv}{1+u+v+Ku^2},\ \frac{dv}{dt} = \beta_2 - \frac{\gamma_2 uv}{1+u+v+Ku^2}. \tag{1.5}$$

Since the chemical reaction obeys the diffusion process, it is natural to add diffusion to the model (1.5), which leads to the following reaction–diffusion system

$$\begin{cases} \frac{\partial u}{\partial t} - d_1 \Delta u = \beta_1 - u - \frac{\gamma_1 uv}{1+u+v+Ku^2}, & x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} - d_2 \Delta v = \beta_2 - \frac{\gamma_2 uv}{1+u+v+Ku^2}, & x \in \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega,\ t \geq 0, \\ u(x,0) = u_0(x) > 0, v(x,0) = v_0(x) > 0, & x \in \Omega, \end{cases} \tag{1.6}$$

where $u = u(x,t)$ and $v = v(x,t)$ stand for the rescaled concentrations of the chemical substances at time t and position $x \in \Omega$. Here Ω is an open bounded domain in $\mathbf{R}^N$, $N \geq 1$, with smooth boundary $\partial\Omega$; d_1 and d_2 are diffusion coefficients of u and v respectively. $u_0, v_0 \in C^2(\Omega) \cap C^0(\overline{\Omega})$ and the Neumann boundary conditions indicate that there are no flux of the chemical substances of u and v on the boundary.

The Seelig model (1.6) has been studied extensively by several authors, but most of the research focuses either on the corresponding ODE system (1.5) or on the R–D system (1.6) in the one-dimensional spatial domain. Seelig [18] considered the boundedness of the solutions of ODE system (1.5) by proving the existence of invariant rectangles. He also proved the existence of stable time-periodic limit cycle by applying Poincare–Bendixson theorem. However, the authors did not prove whether the PDE system (1.6) has the invariant rectangles or not. Mimura and Murray [14] studied the steady state patterns of system (1.6) subject to homogeneous Neumann boundary conditions. However, the spatial dimension is only restricted to one dimension. Nishiura [16] considered the global structure of the bifurcating steady state solutions of some reaction–diffusion equations whose reaction terms share with common properties. Seelig model is one of these reaction–diffusion models. In his work, to gain detailed information of global bifurcation branches, it is crucial to assume the uniform boundedness of the solutions (especially bounded regardless of the diffusion coefficients). To the best of our knowledge, for the Seelig model, the uniform boundedness of the solutions are still completely open so far.

In this paper, we first answer the open questions in [16] and [18]. We show that the R–D system (1.6) have an invariant rectangle which attracts all its solutions regardless of the initial values u_0 and v_0.

The second question arises naturally. Once the solutions of system (1.6) are attracted by the attraction region (rectangle), where do they go eventually? And what are the global attractors? We prove that, under suitable conditions, these solutions either converge exponentially to the unique positive constant equilibrium or to the spatially homogeneous periodic solutions. Our results thus verify the striking idea of "lumped parameter assumption", stating that, under suitable conditions, the dynamics of the PDEs (1.6) can be completely determined by the dynamics of the ODEs (1.5) (see [3] for lumped parameter assumption).

Finally, we prove the existence and nonexistence of Turing patterns of system (1.6). Mathematically, Ni and Tang [15], and Peng et al. [17] have already reported the critical role of the system parameters in leading to Turing patterns of the Lengyel–Epstein system and Degn–Harrison system respectively. We show that, although these three chemical reaction models have similar mathematical forms, system parameters leading to Turing patterns are quite different.

This paper is organized as follows. In Sect. 2, we study the boundedness and uniqueness of global-in-time solutions of the system (1.6). In particular, we show that an invariant rectangle exists which attracts all the solutions of system (1.6) regardless of the initial values. Then, we consider the long time behaviors of the solutions of system (1.6), and derive precise conditions so that the solutions of R–D (1.6) converge exponentially either to its unique constant steady state solution, or to its spatially homogeneous orbitally periodic solutions. In Sect. 3, we derive conditions so that system (1.6) does not have non-constant positive steady states, including Turing patterns. In Sect. 4, we use global bifurcation theory to prove the existence of Turing patterns. In Sect. 5, we included the numerical simulations to support our analytical analysis. In appendix, we include the results on dynamics of ODEs system. Throughout this paper, we use $\mathbb{N}_0$ to stand for the set of nonnegative integers, and use $|\Omega|$ to represent the Lebesgue measure of Ω.

2 Attraction Region and Large Time Behaviors of the Solutions

For convenience of our discussions, we copy (1.6) here:

$$\begin{cases} \frac{\partial u}{\partial t} - d_1 \Delta u = \beta_1 - u - \frac{\gamma_1 uv}{1+u+v+Ku^2}, & x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} - d_2 \Delta v = \beta_2 - \frac{\gamma_2 uv}{1+u+v+Ku^2}, & x \in \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega,\ t \geq 0, \\ u(x,0) = u_0(x) > 0, v(x,0) = v_0(x) > 0, & x \in \Omega. \end{cases} \tag{2.1}$$

System (2.1) has (u_*, v_*) as the unique constant equilibrium solution, with

$$u_* := \beta_1 - \frac{\gamma_1}{\gamma_2}\beta_2,\ v_* := \frac{\beta_2(1+u_*+Ku_*^2)}{\gamma_2 u_* - \beta_2}, \tag{2.2}$$

which are positive if and only if $\frac{\beta_1}{1+\gamma_1} > \frac{\beta_2}{\gamma_2}$ holds.

We first show that (2.1) has a unique solution $(u(x,t), v(x,t))$ defined for all $t > 0$ and is bounded by some positive constants depending on β_1, β_2, γ_1, γ_2, K, and the maximum and minimum of the initial conditions, $u_0(x)$ and $v_0(x)$.

Proposition 1 *Suppose that $\beta_1, \beta_2, \gamma_1, \gamma_2, K > 0$, with $\frac{\beta_1}{1+\gamma_1} > \frac{\beta_2}{\gamma_2}$. Then, for any $d_1, d_2 > 0$, the initial boundary value problem (2.1) admits a unique solution $(u(x,t), v(x,t))$, defined for all $x \in \Omega$ and $t > 0$. Moreover, there exist two positive constants $\mathcal{M}_1$ and $\mathcal{M}_2$, depending on β_1, β_2, γ_1, γ_2, K, $u_0(x)$ and $v_0(x)$, such that*

$$\mathcal{M}_1 < u(x,t), v(x,t) < \mathcal{M}_2,\ x \in \overline{\Omega},\ t > 0. \tag{2.3}$$

Proof The existence and uniqueness of local-in-time solutions to the initial-boundary value problem (2.1) is classical [6].

For the global existence and the boundedness of the solutions, we partially use the techniques of invariant region [15,21]. Recall from [15,21] that a region (rectangle) $\mathcal{R} := [U_1, U_2] \times [V_1, V_2]$ in the (u, v) phase plane is called a positively invariant region of system (2.1) if the vector field

$$\left(\beta_1 - u - \frac{\gamma_1 uv}{1+u+v+Ku^2},\ \beta_2 - \frac{\gamma_2 uv}{1+u+v+Ku^2}\right) \tag{2.4}$$

points inward on the boundary of $\mathcal{R}$ for all $t \geq 0$. Thus, if one can find such a positively invariant rectangle $\mathcal{R}$, then the solution $(u(x,t), v(x,t))$ of (2.1) exists for all $x \in \Omega$ and $t \geq 0$, and stays in $\mathcal{R}$.

We consider two cases:

Case 1 Suppose that $\min_{x\in\overline{\Omega}}\{u_0(x)\} > \beta_2/\gamma_2$ holds. We construct the invariant rectangle $\mathcal{R} := [U_1, U_2] \times [V_1, V_2]$ in the following way:

$$\begin{aligned} U_1 &:= \min\left\{\frac{\beta_1}{1+\gamma_1}, \min_{x\in\overline{\Omega}}\{u_0(x)\}\right\},\ U_2 := \max\left\{\beta_1, \max_{x\in\overline{\Omega}}\{u_0(x)\}\right\}, \\ V_1 &:= \min\left\{\frac{\beta_2}{\gamma_2}, \min_{x\in\overline{\Omega}}\{v_0(x)\}\right\},\ V_2 := \max\left\{\frac{\beta_2(1+U_2+KU_2^2)}{\gamma_2 U_1-\beta_2}, \max_{x\in\overline{\Omega}}\{v_0(x)\}\right\}. \end{aligned} \tag{2.5}$$

Clearly, $u_0(x)$ and $v_0(x)$ are closed by the rectangle $\mathcal{R}$. We now prove that the vector field (2.4) points inward on the boundary of $\mathcal{R}$. In fact,

On the left side $u = U_1$, $V_1 \le v \le V_2$, by the definition of U_1, we have,

$$\beta_1-u-\frac{\gamma_1 uv}{1+u+v+Ku^2} = \beta_1-U_1-\frac{\gamma_1 U_1 v}{1+U_1+v+KU_1^2} > \beta_1-U_1-\gamma_1 U_1 \ge 0. \tag{2.6}$$

On the right side $u = U_2$, $V_1 \le v \le V_2$, by the definition of U_2, we have

$$\beta_1 - u - \frac{\gamma_1 uv}{1+u+v+Ku^2} = \beta_1 - U_2 - \frac{\gamma_1 U_2 v}{1+U_2+v+KU_2^2} < \beta_1 - U_2 \le 0. \tag{2.7}$$

On the bottom side $v = V_1$, $U_1 \le u \le U_2$, by the definition of V_1, we have

$$\beta_2 - \frac{\gamma_2 uv}{1+u+v+Ku^2} = \beta_2 - \frac{\gamma_2 u V_1}{1+u+V_1+Ku^2} > \beta_2 - \gamma_2 V_1 \ge 0. \tag{2.8}$$

On the top side $v = V_2$, $U_1 \le u \le U_2$, by the definition of V_2, we have

$$\beta_2 - \frac{\gamma_2 uv}{1+u+v+Ku^2} = \beta_2 - \frac{\gamma_2 u V_2}{1+u+V_2+Ku^2} < \beta_2 - \frac{\gamma_2 U_1 V_2}{1+U_2+V_2+KU_2^2} \le 0. \tag{2.9}$$

So far, we have proved that $\mathcal{R} := [U_1, U_2] \times [V_1, V_2]$ is the invariant rectangle for the vector field (2.4). Thus, we can choose $\mathcal{M}_1 = \min\{U_1, V_1\}$ and $\mathcal{M}_2 = \max\{U_2, V_2\}$.

Case 2 Suppose that $0 < \min_{x\in\overline{\Omega}}\{u_0(x)\} \le \beta_2/\gamma_2$ holds. In this case, the aforementioned $\mathcal{R}$ is not the invariant rectangle anymore, since the last inequality in (2.9) fails. (In fact, we have $U_1 \le \beta_2/\gamma_2$. Thus, the term $\gamma_2 U_1 - \beta_2$ in the definition of V_2 is negative or zero.) But, the inequalities in (2.6), (2.7) and (2.8) still hold.

We divide $[U_1, U_2]$ into two parts: $[U_1, \beta_2/\gamma_2]$ and $[\beta_2/\gamma_2, U_2]$.

We now show that if $(u_0(x), v_0(x)) \in [U_1, \beta_2/\gamma_2]\times[V_1, \infty)$ holds, then solutions initiating from $(u_0(x), v_0(x))$ will be bounded in $[U_1, \beta_2/\gamma_2]\times[V_1, \infty)$. Moreover, these solutions will go through the "line" $u \equiv \beta_2/\gamma_2$ and enter into $[\beta_2/\gamma_2, U_2] \times [V_1, \infty)$. Suppose not. Then, by (2.6) and (2.8), for any fixed $x^* \in \Omega$, there exist positive constants $\widehat{U}(\le \beta_2/\gamma_2)$, $T_\infty(0 < T_\infty \le +\infty)$, and a subsequence of solutions $(u(x^*, t_k), v(x^*, t_k))$ of system (2.1), such that as $t_k \to T_\infty$, we have

$$u(x^*, t_k) \to \widehat{U},\ v(x^*, t_k) \to +\infty. \tag{2.10}$$

Substituting $u(x^*, t_k)$ and $v(x^*, t_k)$ into (2.1), we have

$$\frac{\partial u(x^*, t_k)}{\partial t} - d_1\Delta u(x^*, t_k) = \beta_1 - u(x^*, t_k) - \frac{\gamma_1 u(x^*, t_k)v(x^*, t_k)}{1+u(x^*, t_k)+v(x^*, t_k)+Ku(x^*, t_k)^2}. \tag{2.11}$$

Setting $k \to \infty$ (or equiv. $t_k \to T_\infty$) in (2.11), one has $0 = \beta_1 - \widehat{U} - \gamma_1\widehat{U}$. Thus, $\widehat{U} = \beta_1/(1+\gamma_1)$. However, this is impossible, since $\widehat{U} \le \beta_2/\gamma_2 < \beta_1/(1+\gamma_1)$. We then reach a contradiction.

Since the solutions will eventually enter into $[\beta_2/\gamma_2, U_2] \times (V_1, \infty)$, one can construct a new invariant rectangle as we did in Case 1. This leads to another suitable positive constants $\mathcal{M}_1$ and $\mathcal{M}_2$. Thus, we have prove the global existence and boundedness of the solutions. □

Our next result shows that system (2.1) has an attraction region defined by

$$\mathcal{A} := \left(\frac{\beta_1}{1+\gamma_1}, \beta_1\right) \times \left(\frac{\beta_2}{\gamma_2}, \frac{\beta_2(1+\beta_1+K\beta_1^2)(\gamma_1+1)}{\beta_1\gamma_2 - \beta_2(1+\gamma_1)}\right) \tag{2.12}$$

in the phase plane which actually attracts all solutions of this system, regardless of the initial values u_0 and v_0.

Theorem 2 *Suppose that* $\frac{\beta_1}{1+\gamma_1} > \frac{\beta_2}{\gamma_2}$ *holds and let* $(u(x,t), v(x,t))$ *be the unique solution of system* (2.1)*. Then, for any* $x \in \overline{\Omega}$*, we have,*

1. $\frac{\beta_1}{1+\gamma_1} < \lim\inf_{t\to\infty} u \le \lim\sup_{t\to\infty} u < \beta_1$;
2. $\frac{\beta_2}{\gamma_2} < \lim\inf_{t\to\infty} v \le \lim\sup_{t\to\infty} v < \frac{\beta_2(1+\beta_1+K\beta_1^2)(\gamma_1+1)}{\beta_1\gamma_2 - \beta_2(\gamma_1+1)}$.

Proof 1) We first prove that $\lim\inf_{t\to\infty} u > \frac{\beta_1}{1+\gamma_1}$. By Proposition 1, there exists a sufficiently small $\rho > 0$ such that for all $x \in \overline{\Omega}$ and $t > 0$, $\frac{\gamma_1 uv}{1+u+v+Ku^2} + \rho < \frac{\gamma_1 uv}{v} = \gamma_1 u$ holds. Let u_ρ be the unique solution of the following ODE:

$$\frac{du_\rho(t)}{dt} = \beta_1 + \rho - (1+\gamma_1)u_\rho(t), \;\; u_\rho(0) = (1-\rho)\min_{x\in\overline{\Omega}} u_0(x). \tag{2.13}$$

Setting $w_1(x,t) = u(x,t) - u_\rho(t)$, and by (2.1) and (2.13), we have

$$\begin{aligned} -\frac{\partial w_1(x,t)}{\partial t} + d_1\Delta w_1(x,t) &= w_1(x,t) - \gamma_1 u_\rho(t) + \frac{\gamma_1 uv}{1+u+v+Ku^2} + \rho \\ &< w_1(x,t) - \gamma_1 u_\rho(t) + \gamma_1 u = (1+\gamma_1)w_1(x,t), \\ w_1(x,0) > 0. \end{aligned} \tag{2.14}$$

Thus,

$$-\frac{\partial w_1(x,t)}{\partial t} + d_1\Delta w_1(x,t) - (1+\gamma_1)w_1(x,t) < 0, \;\; w_1(x,0) > 0. \tag{2.15}$$

Then by the maximum principle for parabolic equations, we have $w_1(x,t) > 0$, which implies that $u(x,t) > u_\rho(t)$ for all $x \in \overline{\Omega}$ and $t \ge 0$. From (2.13), it follows that $\lim_{t\to\infty} u_\rho(t) = (\beta_1+\rho)/(1+\gamma_1)$. Thus, we have $\lim\inf_{t\to\infty} u > \beta_1/(1+\gamma_1)$.

2) We then prove that $\lim\sup_{t\to\infty} u < \beta_1$. By Proposition 1, there exists a sufficiently small $0 < \delta < \beta_1$ such that for all $x \in \overline{\Omega}$ and $t > 0$, $\delta < \gamma_1 uv/(1+u+v+Ku^2)$ holds. Let $u_\delta = u_\delta(t)$ be the unique solution of the following ODE:

$$\frac{du_\delta(t)}{dt} = \beta_1 - \delta - u_\delta(t), \;\; u_\delta(0) = (1+\delta)\max_{x\in\overline{\Omega}} u_0(x). \tag{2.16}$$

Setting $w_2(x,t) = u(x,t) - u_\delta(t)$, and by (2.1) and (2.16), we have

$$-\frac{\partial w_2(x,t)}{\partial t} + d_1\Delta w_2(x,t) - w_2(x,t) = \frac{\gamma_1 uv}{1+u+v+Ku^2} - \delta > 0, \;\; w_2(x,0) < 0. \tag{2.17}$$

Then by the maximum principle for parabolic equations, we have $w_2(x,t) < 0$, which implies that $u(x,t) < u_\delta(t)$ for all $x \in \overline{\Omega}$ and $t \geq 0$. From (2.16), it follows that $\lim_{t\to\infty} u_\delta(t) = \beta_1 - \delta$. Thus, we have $\lim\sup_{t\to\infty} u < \beta_1$.

3) We now prove that $\lim\inf_{t\to\infty} v > \dfrac{\beta_2}{\gamma_2}$. By Proposition 1, there exists a sufficiently small $\tau > 0$ such that for all $x \in \overline{\Omega}$ and $t > 0$, $\dfrac{\gamma_2 uv}{1+u+v+Ku^2} + \tau < \dfrac{\gamma_2 uv}{u} = \gamma_2 v$ holds. Let v_τ be the unique solution of the following ODE:

$$\frac{dv_\tau(t)}{dt} = \beta_2 + \tau - \gamma_2 v_\tau(t), \;\; v_\tau(0) = (1-\tau)\min_{x\in\overline{\Omega}} v_0(x). \tag{2.18}$$

Setting $p_1(x,t) = v(x,t) - v_\tau(t)$, and by (2.1) and (2.18), we have

$$\begin{aligned} -\frac{\partial p_1(x,t)}{\partial t} + d_2\Delta p_1(x,t) - \gamma_2 p_1(x,t) &= \frac{\gamma_2 uv}{1+u+v+Ku^2} + \tau - \gamma_2 v < 0, \\ p_1(x,0) &> 0. \end{aligned} \tag{2.19}$$

Then by the maximum principle for parabolic equations, we have $p_1(x,t) > 0$, which implies that $v(x,t) > v_\tau(t)$ for all $x \in \overline{\Omega}$. From (2.18), it follows that $\lim_{t\to\infty} v_\tau(t) = (\beta_2 + \tau)/\gamma_2$. Thus, we have $\lim\inf_{t\to\infty} v > \beta_2/\gamma_2$.

4) Finally, we prove that $\lim\sup_{t\to\infty} v < \dfrac{\beta_2(1+\beta_1+K\beta_1^2)(\gamma_1+1)}{\beta_1\gamma_2 - \beta_2(\gamma_1+1)}$. By

$$\lim\inf_{t\to\infty} u > \frac{\beta_1}{1+\gamma_1}, \;\; \lim\sup_{t\to\infty} u < \beta_1, \tag{2.20}$$

there exists a finite number t_0, depending on u_0 and v_0, such that for any $t \geq t_0$ and all $x \in \overline{\Omega}$,

$$\frac{\beta_1}{1+\gamma_1} < u(x,t) < \beta_1, \;\; t \geq t_0. \tag{2.21}$$

By Proposition 1 and (2.21), there exists a sufficiently small $\chi > 0$, such that for all $x \in \overline{\Omega}$ and $t \geq t_0$, one has

$$0 < \frac{\gamma_2\beta_1}{(1+\beta_1+v+K\beta_1^2-\chi)(\gamma_1+1)} < \frac{\gamma_2 u}{1+u+v+Ku^2}. \tag{2.22}$$

This can be done by choosing $\chi > 0$ sufficiently small, since when $\chi = 0$, (2.22) holds automatically.

Let v_χ be the unique solution of the following ODE:

$$\begin{aligned} &\frac{dv_\chi(t)}{dt} = \beta_2 - \frac{\gamma_2\beta_1 v_\chi}{(1+\beta_1+v_\chi+K\beta_1^2-\chi)(\gamma_1+1)}, \;\; t > t_0, \\ &v_\chi(t_0) = (1+\chi)\max_{x\in\overline{\Omega}} v(x,t_0). \end{aligned} \tag{2.23}$$

Setting $p_2(x,t) = v(x,t) - v_\chi(t)$, and by (2.1) and (2.23), we have

$$\begin{aligned} -\frac{\partial p_2(x,t)}{\partial t} + d_2\Delta p_2(x,t) &= \frac{\gamma_2 uv}{1+u+v+Ku^2} - \frac{\gamma_2\beta_1 v_\chi}{(1+\beta_1+v_\chi+K\beta_1^2-\chi)(\gamma_1+1)}, \\ &t > t_0, \; p_2(x,t_0) < 0. \end{aligned} \tag{2.24}$$

The maximum principle for parabolic equations cannot be directly applicable to this case. Motivated by [15], we now use an elementary argument of Hopf's boundary lemma for elliptic equations to prove that for all $x \in \overline{\Omega}$ and $t > t_0$, $p_2(x,t) < 0$, and thus $v(x,t) < v_\chi(t)$.

Suppose not. Then, there exists a $T^* > t_0$, such that $p_2(x,t) < 0$ for all $(x,t) \in \overline{\Omega} \times (t_0, T^*)$, and $p_2(x, T^*) = 0$ for some $x \in \overline{\Omega}$. Thus, $\max_{x \in \overline{\Omega}} p_2(x, T^*) = 0$.

If for some $x_* \in \Omega$, such that $p_2(x_*, T^*) = 0$. Then, we have $\partial p_2(x_*, T^*)/\partial t \geq 0$ and $\Delta p_2(x_*, T^*) \leq 0$. Thus,

$$-\frac{\partial p_2(x_*, T^*)}{\partial t} + \Delta p_2(x_*, T^*) \leq 0. \tag{2.25}$$

At $(x,t) = (x_*, T^*)$, we have $v = v_\chi$. And $u < \beta_1$. Then, we have,

$$\begin{aligned} \frac{\gamma_2 \beta_1 v_\chi}{(1+\beta_1+v_\chi+K\beta_1^2-\chi)(\gamma_1+1)} &= \frac{\gamma_2 \beta_1 v}{(1+\beta_1+v+K\beta_1^2-\chi)(\gamma_1+1)} \\ &< \frac{\gamma_2 u v}{1+u+v+Ku^2}. \end{aligned} \tag{2.26}$$

Then, (2.26) and (2.24) reveals that $-\partial p_2(x_*, T^*)/\partial t + d_2 \Delta p_2(x_*, T^*) > 0$, which contradicts with (2.25). Thus, one can not find such point $x_* \in \Omega$, such that $p_2(x_*, T^*) = 0$.

If for some $x^* \in \partial\Omega$, such that $p_2(x^*, T^*) = 0$. The right-hand side of (2.24) is positive at (x^*, T^*), and by continuity it remains positive in $\Omega_0 \times \{T^*\}$, where Ω_0 is a sub-domain of Ω and $x^* \in \partial\Omega_0$. Then, on $\Omega_0 \times \{T^*\}$, we have $-\partial p_2(x,t)/\partial t + d_2 \Delta p_2(x,t) \geq 0$. Treating (2.24) as an elliptic equation in $\Omega_0 \times \{T^*\}$ and by Hopf's boundary lemma, we have $\partial_\nu p_2(x^*, T^*) = \partial_\nu v(x^*, T^*) > 0$, which contradicts the Neumann boundary condition. Thus, for any $x \in \overline{\Omega}$ and $t > t_0$, we have $v(x,t) < v_\chi(t)$.

From (2.23), it follows that

$$\lim_{t\to\infty} v_\chi(t) = \frac{\beta_2(1+\beta_1+K\beta_1^2-\chi)(\gamma_1+1)}{\beta_1\gamma_2 - \beta_2(\gamma_1+1)} < \frac{\beta_2(1+\beta_1+K\beta_1^2)(\gamma_1+1)}{\beta_1\gamma_2 - \beta_2(\gamma_1+1)}. \tag{2.27}$$

Thus, we have proved that $\lim\sup_{t\to\infty} v < \frac{\beta_2(1+\beta_1+K\beta_1^2)(\gamma_1+1)}{\beta_1\gamma_2 - \beta_2(\gamma_1+1)}$. □

Our final result in this section is that under certain conditions ("lumped parameter assumption" [3]), the dynamics of system (2.1) can be determined by the dynamics of the corresponding ODEs (1.5).

Following [3], we define $\sigma := d\lambda_1 - \mathcal{Q}$, where λ_1 is the principal eigenvalue of $-\Delta$ on Ω subject to homogeneous Neumann boundary conditions, $d := \min\{d_1, d_2\}$, and

$$\mathcal{Q} := \sup_{(u,v)\in\mathcal{A}} \{||J(u,v)||\}, \tag{2.28}$$

where the Jacobin matrix $J(u,v)$ is given by

$$J(u,v) = \begin{pmatrix} -1-\gamma_1\rho_1(u,v), & -\gamma_1\rho_2(u,v) \\ -\gamma_2\rho_1(u,v), & -\gamma_2\rho_2(u,v) \end{pmatrix}, \tag{2.29}$$

where

$$\rho_1(u,v) := \frac{v(1+v-Ku^2)}{(1+u+v+Ku^2)^2}, \quad \rho_2(u,v) := \frac{u(1+u+Ku^2)}{(1+u+v+Ku^2)^2}. \tag{2.30}$$

Obviously, for $u, v > 0$, the following inequalities hold

$$|\rho_1(u,v)| < \frac{1+u+Ku^2}{1+u+v+Ku^2}, \quad |\rho_2(u,v)| < \frac{1+u+Ku^2}{1+u+v+Ku^2}. \tag{2.31}$$

For any $(u, v) \in \mathcal{A}$, defined precisely in (2.12), we have

$$\frac{1+u+Ku^2}{1+u+v+Ku^2} < \xi := \frac{\gamma_2(1+\gamma_1)^2(1+\beta_1+K\beta_1^2)}{\gamma_2(1+\gamma_1)^2+\beta_1\gamma_2(1+\gamma_1)+\beta_2(1+\gamma_1)^2+K\gamma_2\beta_1^2}. \tag{2.32}$$

Thus,

$$\begin{aligned}\mathcal{Q} &= \max\left\{\sup_{(u,v)\in\mathcal{A}}(\left|1+\gamma_1\rho_1(u,v)\right|+\gamma_1\rho_2(u,v)),\ \sup_{(u,v)\in\mathcal{A}}(\left|\gamma_2\rho_1(u,v)\right|+\gamma_2\rho_2(u,v))\right\}\\ &< \mathcal{D} := \max\{1+2\gamma_1\xi, 2\gamma_2\xi\}.\end{aligned} \tag{2.33}$$

We conclude that, when d_1 and d_2 fall into certain ranges, the solutions of system (1.6) either converge exponentially to the unique positive constant steady states or to the spatially homogeneous periodic solutions.

Theorem 3 *Suppose that $\beta_1/(1+\gamma_1) > \beta_2/\gamma_2$, and that $(d_1, d_2) \in [\mathcal{D}/\lambda_1, \infty)\times[\mathcal{D}/\lambda_1, \infty)$, where $\mathcal{D}$ is defined in (2.33). If (6.8) holds, then every solution $(u(x,t), v(x,t))$ of system (2.1) converges exponentially to (u_*, v_*); while if (6.7) holds, then every solution $(u(x,t), v(x,t))$ of system (2.1) converges exponentially to the spatially homogeneous periodic solutions.*

Proof By Theorem 2, there exists $T > 0$, such that for any $t > T$, the solution $(u(x,t), v(x,t)) \in \mathcal{A}$ for all $x \in \overline{\Omega}$. Without loss of generality, we can assume that $T = 0$.

Clearly, from (2.33), if $(d_1, d_2) \in [\mathcal{D}/\lambda_1, \infty) \times [\mathcal{D}/\lambda_1, \infty)$, then $\sigma > 0$. Define

$$f(u,v) := \beta_1 - u - \frac{\gamma_1 uv}{1+u+v+Ku^2}, \quad g(u,v) := \beta_2 - \frac{\gamma_2 uv}{1+u+v+Ku^2}. \tag{2.34}$$

Then by [3,24], there exist constants $\mathcal{N}_i > 0, i = 1, 2, 3$, such that, for any solution $(u(t,x), v(t,x))$ of system (2.1)

$$||\nabla_x(u(\cdot,t), v(\cdot,t))||_{L^2(\Omega)} \le \mathcal{N}_1 e^{-\sigma t},\ ||(u(\cdot,t), v(\cdot,t)) - (\overline{u}(t), \overline{v}(t))||_{L^2(\Omega)} \le \mathcal{N}_2 e^{-\sigma t}, \tag{2.35}$$

where $\overline{u}, \overline{v}$ are the average of u and v over Ω respectively satisfying

$$\begin{cases} \dfrac{d\overline{u}}{dt} = f(\overline{u}, \overline{v}) + o_1(t), & \overline{u}(0) = \dfrac{1}{|\Omega|}\displaystyle\int_\Omega u_0(x)dx, |o_1(t)| \le \mathcal{N}_3 e^{-\rho t},\\ \dfrac{d\overline{v}}{dt} = g(\overline{u}, \overline{v}) + o_2(t), & \overline{v}(0) = \dfrac{1}{|\Omega|}\displaystyle\int_\Omega v_0(x)dx, |o_2(t)| \le \mathcal{N}_3 e^{-\rho t}. \end{cases} \tag{2.36}$$

Moreover, the $\omega-$limit set of (2.36) is the subset of the $\omega-$limit set of the following ODEs

$$\begin{cases} \dfrac{du}{dt} = f(u,v), & u(0) = \dfrac{1}{|\Omega|}\displaystyle\int_\Omega u_0(x)dx,\\ \dfrac{dv}{dt} = g(u,v), & v(0) = \dfrac{1}{|\Omega|}\displaystyle\int_\Omega v_0(x)dx. \end{cases} \tag{2.37}$$

Finally, combining the results of Lemmas 9 and 10 in Appendix, we complete the proof of the Theorem 3. □

3 Non-existence of Turing Patterns: Some Estimates

In this section, we show the non-existence of the non-constant positive steady state solutions of the system:

$$\begin{cases} -d_1\Delta u = \beta_1 - u - \dfrac{\gamma_1 uv}{1+u+v+Ku^2}, & x\in\Omega, \\ -d_2\Delta v = \beta_2 - \dfrac{\gamma_2 uv}{1+u+v+Ku^2}, & x\in\Omega, \\ \partial_\nu u = \partial_\nu v = 0, & x\in\partial\Omega. \end{cases} \tag{3.1}$$

Lemma 4 (A priori estimates) *Suppose that* $\dfrac{\beta_1}{1+\gamma_1} > \dfrac{\beta_2}{\gamma_2}$ *holds, and let* $(u(x), v(x))$ *be any given positive steady state solution of system* (1.6)*. Then, for any* $x\in\overline{\Omega}$*, the following conclusions hold:*

$$\frac{\beta_1}{1+\gamma_1} < u(x) < \beta_1,\ \frac{\beta_2}{\gamma_2} < v(x) < \frac{\beta_2(1+\beta_1+K\beta_1^2)(\gamma_1+1)}{\beta_1\gamma_2-\beta_2(\gamma_1+1)}. \tag{3.2}$$

Remark 5 Lemma 4 is the direct consequence of Theorem 2.

For a steady state solution pair $(u(x), v(x))$ of system (3.1), we define

$$\overline{u} = \frac{1}{|\Omega|}\int_\Omega u(x)dx,\ \overline{v} = \frac{1}{|\Omega|}\int_\Omega v(x)dx. \tag{3.3}$$

Multiplying the first equation of (3.1) by γ_2, the second equation of (3.1) by $-\gamma_1$, and adding them, we can obtain that

$$\Delta(\gamma_2 d_1 u - \gamma_1 d_2 v) + \gamma_2\beta_1 - \gamma_1\beta_2 - \gamma_2 u = 0. \tag{3.4}$$

Integrating (3.4) over Ω, we obtain

$$\overline{u} = \frac{1}{|\Omega|}\int_\Omega u dx = \beta_1 - \frac{\gamma_1}{\gamma_2}\beta_2 = u_* > 0. \tag{3.5}$$

Define

$$\phi(x) := u(x) - \overline{u},\ \psi(x) := v(x) - \overline{v}. \tag{3.6}$$

We are now stating the following useful estimates on the steady state solutions:

Lemma 6 *Suppose that* $(u(x), v(x))$ *is the solution pair of* (3.1)*, and let* $\phi(x), \psi(x)$ *be defined in* (3.6)*. Then,*

$$\frac{\gamma_1^2 d_2^2\lambda_1^2}{\gamma_2^2(2d_1^2\lambda_1^2+2d_1\lambda_1+1)}\int_\Omega |\nabla\psi|^2 dx \le \int_\Omega |\nabla\phi|^2 dx \le \frac{\gamma_1^2 d_2^2}{\gamma_2^2 d_1^2}\int_\Omega |\nabla\psi|^2 dx, \tag{3.7}$$

where λ_1 *is the principle eigenvalue of* $-\Delta$ *on* Ω *subject to the homogeneous Neumann boundary conditions.*

Proof Rewrite (3.4) as

$$\Delta(\gamma_2 d_1 u - \gamma_1 d_2 v) = \gamma_2(u-\overline{u}) = \gamma_2\phi. \tag{3.8}$$

Multiplying (3.8) by $\gamma_2 d_1 u - \gamma_1 d_2 v$, integrating over Ω by parts, and noticing that $\int_\Omega \phi dx = \int_\Omega \psi dx = 0$, we can yield

$$-\int_\Omega \left|\nabla(d_1\gamma_2 u - d_2\gamma_1 v)\right|^2 dx = \gamma_2^2 d_1\int_\Omega \phi^2 dx - \gamma_1\gamma_2 d_2\int_\Omega \phi\psi dx. \tag{3.9}$$

Thus, we have

$$\gamma_1\gamma_2 d_2 \int_\Omega \phi\psi dx = \gamma_2^2 d_1 \int_\Omega \phi^2 dx + \int_\Omega \left|\nabla(d_1\gamma_2 u - d_2\gamma_1 v)\right|^2 dx \geq 0. \tag{3.10}$$

If we multiplify (3.8) by ϕ and integrate over Ω by parts, we have

$$\gamma_2 \int_\Omega \phi^2 dx = -d_1\gamma_2 \int_\Omega |\nabla\phi|^2 dx + d_2\gamma_1 \int_\Omega \nabla\phi\nabla\psi dx, \tag{3.11}$$

which implies that

$$d_2\gamma_1 \int_\Omega \nabla\phi\nabla\psi dx = \gamma_2 \int_\Omega \phi^2 dx + d_1\gamma_2 \int_\Omega |\nabla\phi|^2 dx. \tag{3.12}$$

On the other hand, the left side of (3.9) also equals

$$\begin{aligned} -\int_\Omega \left|\nabla(d_1\gamma_2 u - d_2\gamma_1 v)\right|^2 dx &= -\int_\Omega \left(d_1^2\gamma_2^2|\nabla u|^2 - 2d_1d_2\gamma_1\gamma_2\nabla u\nabla v + d_2^2\gamma_1^2|\nabla v|^2\right) dx \\ &= -\int_\Omega \left(d_1^2\gamma_2^2|\nabla \phi|^2 - 2d_1d_2\gamma_1\gamma_2\nabla \phi\nabla \psi + d_2^2\gamma_1^2|\nabla \psi|^2\right) dx. \end{aligned} \tag{3.13}$$

Then, from (3.9), (3.12) and (3.13), we have

$$d_2^2\gamma_1^2 \int_\Omega |\nabla\psi|^2 dx = d_1^2\gamma_2^2 \int_\Omega |\nabla\phi|^2 dx + d_1\gamma_2^2 \int_\Omega \phi^2 dx + \gamma_1\gamma_2 d_2 \int_\Omega \phi\psi dx, \tag{3.14}$$

which together with (3.10) implies that

$$d_1^2\gamma_2^2 \int_\Omega |\nabla\phi|^2 dx \leq d_2^2\gamma_1^2 \int_\Omega |\nabla\psi|^2 dx. \tag{3.15}$$

Thus,

$$\int_\Omega |\nabla\phi|^2 dx \leq \frac{d_2^2\gamma_1^2}{d_1^2\gamma_2^2} \int_\Omega |\nabla\psi|^2 dx. \tag{3.16}$$

On the other hand, by the Poincare inequality, it follows that

$$\int_\Omega \phi^2 dx \leq \frac{1}{\lambda_1} \int_\Omega |\nabla\phi|^2 dx. \tag{3.17}$$

The Cauchy inequality says that, for any given real number x and y, and $\epsilon > 0$, the inequality $xy \leq \frac{1}{4\epsilon}x^2 + \epsilon y^2$ always holds. It then follows that

$$\int_\Omega \phi\psi dx \leq \frac{\gamma_2}{2\lambda_1\gamma_1 d_2} \int_\Omega \phi^2 dx + \frac{\lambda_1\gamma_1 d_2}{2\gamma_2} \int_\Omega \psi^2 dx. \tag{3.18}$$

Then,

$$\begin{aligned} \gamma_1\gamma_2 d_2 \int_\Omega \phi\psi dx &\leq \frac{\gamma_2^2}{2\lambda_1} \int_\Omega \phi^2 dx + \frac{1}{2}\lambda_1\gamma_1^2 d_2^2 \int_\Omega \psi^2 dx \\ &\leq \frac{\gamma_2^2}{2\lambda_1^2} \int_\Omega |\nabla\phi|^2 dx + \frac{1}{2}\gamma_1^2 d_2^2 \int_\Omega |\nabla\psi|^2 dx. \end{aligned} \tag{3.19}$$

Thus, from (3.14), (3.17) and (3.19), we have

$$\frac{1}{2}\gamma_1^2 d_2^2 \int_\Omega |\nabla\psi|^2 dx \leq \gamma_2^2 \left(d_1^2 + \frac{d_1}{\lambda_1} + \frac{1}{2\lambda_1^2}\right) \int_\Omega |\nabla\phi|^2 dx, \tag{3.20}$$

which implies

$$\frac{\gamma_1^2 d_2^2 \lambda_1^2}{\gamma_2^2(2d_1^2\lambda_1^2 + 2d_1\lambda_1 + 1)} \int_\Omega |\nabla\psi|^2 dx \le \int_\Omega |\nabla\phi|^2 dx. \tag{3.21}$$

This completes the proof. □

For the convenience of our later discussions, we define

$$\begin{cases} h_1(u,v) := (1+u+v+Ku^2)^{-1}(K\overline{u}u - (1+\overline{v}))\dfrac{\overline{v}}{1+\overline{u}+\overline{v}+K\overline{u}^2}, \\ h_2(u,v) := (1+u+v+Ku^2)^{-1}\left(\dfrac{\overline{u}\,\overline{v}}{1+\overline{u}+\overline{v}+K\overline{u}^2} - u\right), \\ h_3(u,v) := (1+u+v+Ku^2)^{-1}\dfrac{1+\overline{u}+\overline{u}\,\overline{v}}{1+\overline{u}+\overline{v}+K\overline{u}^2}, \\ h_4(u,v) := \dfrac{\overline{u}\,\overline{v}}{1+\overline{u}+\overline{v}+K\overline{u}^2} - \overline{u}, \end{cases} \tag{3.22}$$

where $\overline{u}$ and $\overline{v}$ are defined precisely in (3.3).

From Lemma 4, it follows that, any positive solutions (u, v) of system (3.1) satisfies $(u, v) \in \mathcal{A}$, where $\mathcal{A}$ is defined in (2.12). Define

$$\mathcal{H}_i := \sup_{(u,v)\in\mathcal{A}} |h_i(u,v)|, \ i = 1, 2, 3, 4, \tag{3.23}$$

and

$$\chi_1(x) := \frac{\mathcal{H}_2\gamma_2 x}{\lambda_1 x - \mathcal{H}_1\gamma_1}, \ \chi_2(x) := \frac{\mathcal{H}_4\gamma_2\sqrt{2\lambda_1^2x^2 + 2\lambda_1 x + 1}}{\lambda_1(\lambda_1 x - \mathcal{H}_3\gamma_1)}. \tag{3.24}$$

Clearly, the functions $\chi_1(x)$ and $\chi_2(x)$ are decreasing functions defined on $(\mathcal{H}_2\gamma_1/\lambda_1, \infty)$ and $(\mathcal{H}_3\gamma_1/\lambda_1, \infty)$ respectively, satisfying

$$\begin{aligned} &\lim_{x\to\ (\mathcal{H}_1\gamma_1/\lambda_1)^+} \chi_1(x) = +\infty, &&\lim_{x\to+\infty} \chi_1(x) = \frac{\mathcal{H}_2\gamma_2}{\lambda_1}, \\ &\lim_{x\to\ (\mathcal{H}_3\gamma_1/\lambda_1)^+} \chi_2(x) = +\infty, &&\lim_{x\to+\infty} \chi_2(x) = \frac{\sqrt{2}\mathcal{H}_4\gamma_2}{\lambda_1}. \end{aligned} \tag{3.25}$$

We are now in the position to state the following theorem regarding the non-existence of non-constant positive solutions of the system (3.1):

Theorem 7 *Let $h_i(u,v)$, $\mathcal{H}_i$, $i = 1, 2, 3, 4$, and $\chi_j(x)$, $j = 1, 2$, be defined in (3.22), (3.23) and (3.25) respectively. Then, for any $(d_1, d_2) \in \Sigma$, system (3.1) does not have non-constant positive solutions, where*

$$\begin{aligned} \Sigma \ := &\left\{(d_1,d_2) \in \mathbf{R}^2 : d_1 > \frac{\mathcal{H}_1\gamma_1}{\lambda_1},\ d_2 > \chi_1(d_1)\right\} \cup \Big\{(d_1,d_2) \in \mathbf{R}^2 : d_1 \\ &> \frac{\mathcal{H}_3\gamma_1}{\lambda_1}, d_2 > \chi_2(d_1)\Big\}. \end{aligned} \tag{3.26}$$

Proof We first prove that if $(d_1, d_2) \in \{(d_1, d_2) \in \mathbf{R}^2 : d_1 > \frac{\mathcal{H}_1\gamma_1}{\lambda_1},\ d_2 > \chi_1(d_1)\}$, then system (3.1) does not have non-constant positive solutions.

Multiplying the second equation of (3.1) by ψ and integrating over Ω, we have

$$\begin{aligned} -\int_\Omega d_2\psi\Delta\psi dx &= \beta_2\int_\Omega \psi dx - \gamma_2\int_\Omega \frac{uv\psi}{1+u+v+Ku^2}dx \\ &= -\gamma_2\int_\Omega \frac{uv\psi}{1+u+v+Ku^2}dx. \end{aligned} \tag{3.27}$$

Thus,

$$d_2\int_\Omega |\nabla\psi|^2 dx = -\gamma_2\int_\Omega \frac{uv\psi}{1+u+v+Ku^2}dx. \tag{3.28}$$

Direct calculations show that the right hand side of (3.28) is

$$\begin{aligned} &-\gamma_2\int_\Omega\left(\frac{u(v-\overline{v})}{1+u+v+Ku^2}+\frac{u\overline{v}}{1+u+v+Ku^2}-\frac{\overline{u}\,\overline{v}}{1+\overline{u}+\overline{v}+K\overline{u}^2}\right)\psi dx \\ &=-\gamma_2\int_\Omega \frac{u\psi^2}{1+u+v+Ku^2}dx-\gamma_2\int_\Omega \frac{\overline{v}\psi(\phi+\overline{v}u-\overline{u}v-K\overline{u}u\phi)}{(1+u+v+Ku^2)(1+\overline{u}+\overline{v}+K\overline{u}^2)}dx \\ &=-\gamma_2\int_\Omega \frac{u\psi^2}{1+u+v+Ku^2}dx-\frac{\gamma_2\overline{v}}{1+\overline{u}+\overline{v}+K\overline{u}^2}\int_\Omega \frac{(\phi+\overline{v}u-\overline{u}v-K\overline{u}u\phi)\psi}{1+u+v+Ku^2}dx \\ &=-\gamma_2\int_\Omega \frac{u}{1+u+v+Ku^2}\psi^2 dx-\frac{\gamma_2\overline{v}(1+\overline{v})}{1+\overline{u}+\overline{v}+K\overline{u}^2}\int_\Omega \frac{1}{1+u+v+Ku^2}\phi\psi dx \\ &\quad+\frac{\gamma_2\overline{u}\,\overline{v}}{1+\overline{u}+\overline{v}+K\overline{u}^2}\left(\int_\Omega \frac{Ku}{1+u+v+Ku^2}\phi\psi dx+\int_\Omega \frac{1}{1+u+v+Ku^2}\psi^2 dx\right) \\ &=\gamma_2\int_\Omega h_1(u,v)\phi\psi dx+\gamma_2\int_\Omega h_2(u,v)\psi^2 dx, \\ &\le\gamma_2\int_\Omega \mathcal{H}_1|\phi\psi|dx+\gamma_2\int_\Omega \mathcal{H}_2\psi^2 dx. \end{aligned} \tag{3.29}$$

Then,

$$\frac{d_2}{\gamma_2}\int_\Omega |\nabla\psi|^2 dx \le \mathcal{H}_1\int_\Omega |\phi\psi|dx+\mathcal{H}_2\int \psi^2 dx \le \mathcal{H}_1\int_\Omega |\phi\psi|dx+\frac{\mathcal{H}_2}{\lambda_1}\int |\nabla\psi|^2 dx. \tag{3.30}$$

On the other hand, we have

$$\begin{aligned} \int_\Omega |\phi\psi|dx &\le \left(\int_\Omega |\phi|^2 dx\right)^{\frac{1}{2}}\left(\int_\Omega |\psi|^2 dx\right)^{\frac{1}{2}} \le \left(\frac{1}{\lambda_1}\int_\Omega |\nabla\phi|^2 dx\right)^{\frac{1}{2}}\left(\frac{1}{\lambda_1}\int_\Omega |\nabla\psi|^2 dx\right)^{\frac{1}{2}} \\ &= \frac{1}{\lambda_1}\left(\int_\Omega |\nabla\phi|^2 dx\right)^{\frac{1}{2}}\left(\int_\Omega |\nabla\psi|^2 dx\right)^{\frac{1}{2}}. \end{aligned} \tag{3.31}$$

Then, combining (3.7) and (3.31), we have

$$\int_\Omega |\phi\psi|dx \le \frac{d_2\gamma_1}{\lambda_1 d_1\gamma_2}\int_\Omega |\nabla\psi|^2 dx. \tag{3.32}$$

So far, (3.30) is reduced to

$$\frac{d_2}{\gamma_2}\int_\Omega |\nabla\psi|^2 dx \le \left(\frac{\mathcal{H}_2}{\lambda_1}+\frac{\mathcal{H}_1 d_2\gamma_1}{\lambda_1 d_1\gamma_2}\right)\int_\Omega |\nabla\psi|^2 dx. \tag{3.33}$$

For any $(d_1, d_2) \in \{(d_1, d_2) \in \mathbf{R}^2 : d_1 > \frac{\mathcal{H}_1\gamma_1}{\lambda_1},\ d_2 > \chi_1(d_1)\}$, we have

$$\frac{d_2}{\gamma_2} > \frac{\mathcal{H}_2}{\lambda_1} + \frac{\mathcal{H}_1 d_2 \gamma_1}{\lambda_1 d_1 \gamma_2}. \tag{3.34}$$

Thus, we have $\nabla\psi \equiv 0$. This together with (3.7), reveals that $\nabla\phi \equiv 0$. Then system (3.1) does not have non-constant positive solutions.

We then prove that if $(d_1, d_2) \in \{(d_1, d_2) \in \mathbf{R}^2 : d_1 > \frac{\mathcal{H}_3\gamma_1}{\lambda_1}, d_2 > \chi_2(d_1)\}$, then system (3.1) does not have non-constant positive solutions.

Multiplying the first equation of system by ϕ and integrating over Ω, we have

$$d_1 \int_\Omega |\nabla\phi|^2 dx = \int_\Omega \phi(\beta_1 - u)dx - \int_\Omega \frac{\gamma_1 uv}{1+u+v+Ku^2}\phi dx. \tag{3.35}$$

A direct calculation shows that

$$\begin{aligned}
d_1 \int_\Omega |\nabla\phi|^2 dx =& \gamma_1 \int_\Omega \left(\frac{\overline{u}\,\overline{v}}{1+\overline{u}+\overline{v}+K\overline{u}^2} - \overline{u}\right)\phi\psi dx \\
&- \int_\Omega \left(1 + \frac{\gamma_1 v}{1+u+v+Ku^2}\right)\psi^2 dx \\
&+ \gamma_1 \int_\Omega (1+u+v+Ku^2)^{-1} \frac{1+\overline{u}+\overline{u}\,\overline{v}}{1+\overline{u}+\overline{v}+K\overline{u}^2}\phi^2 dx \\
\le& \gamma_1 \int_\Omega \left(\frac{\overline{u}\,\overline{v}}{1+\overline{u}+\overline{v}+K\overline{u}^2} - \overline{u}\right)\phi\psi dx \\
&+ \gamma_1 \int_\Omega (1+u+v+Ku^2)^{-1} \frac{1+\overline{u}+\overline{u}\,\overline{v}}{1+\overline{u}+\overline{v}+K\overline{u}^2}\phi^2 dx \\
=& \gamma_1 \int_\Omega h_3(u,v)\phi^2 dx + \gamma_1 \int_\Omega h_4(u,v)\phi\psi dx, \\
\le& \gamma_1 \int_\Omega \mathcal{H}_3\phi^2 dx + \gamma_1 \int_\Omega \mathcal{H}_4 |\phi\psi| dx.
\end{aligned} \tag{3.36}$$

By (3.21) and (3.31), we have

$$\int_\Omega |\phi\psi| dx \le \frac{\gamma_2(2d_1^2\lambda_1^2 + 2d_1\lambda_1 + 1)^{\frac{1}{2}}}{\gamma_1 d_2 \lambda_1^2} \int_\Omega |\nabla\phi|^2 dx. \tag{3.37}$$

Thus,

$$d_1 \int_\Omega |\nabla\phi|^2 dx \le \left(\frac{\mathcal{H}_3\gamma_1}{\lambda_1} + \frac{\mathcal{H}_4\gamma_2(2d_1^2\lambda_1^2 + 2d_1\lambda_1 + 1)^{\frac{1}{2}}}{d_2\lambda_1^2}\right) \int_\Omega |\nabla\phi|^2 dx. \tag{3.38}$$

For any $(d_1, d_2) \in \{(d_1, d_2) \in \mathbf{R}^2 : d_1 > \frac{\mathcal{H}_3\gamma_1}{\lambda_1}, d_2 > \chi_2(d_1)\}$, we have

$$d_1 > \frac{\mathcal{H}_3\gamma_1}{\lambda_1} + \frac{\mathcal{H}_4\gamma_2(2d_1^2\lambda_1^2 + 2d_1\lambda_1 + 1)^{\frac{1}{2}}}{d_2\lambda_1^2}. \tag{3.39}$$

This together with (3.16), reveals that $\nabla\phi \equiv 0$. Then system (3.1) does not have non-constant positive solutions. □

4 Existence of Turing Patterns: Global Steady State Bifurcations

In this section, we use the global bifurcation theory to prove the existence of positive non-constant of steady state system (3.1). In particular, we are concerned with the existence of Turing patterns.

Let j_0 and k_0 be defined precisely in (6.4) in Appendix. Then, if $j_0 < -\frac{1}{\gamma_1}$ holds, system (2.1) is a substrate–inhibition system, that is the Jacobian matrix of the corresponding ODEs evaluated at (u_*, v_*) takes in the form of

$$\begin{pmatrix} +, & - \\ +, & - \end{pmatrix}. \tag{4.1}$$

And if

$$\frac{\beta_1}{1+\gamma_1} > \frac{\beta_2}{\gamma_2}, \; -\frac{1}{\gamma_1} - \frac{\gamma_2 k_0}{\gamma_1} < j_0, \tag{4.2}$$

holds, then (u_*, v_*) is positive and stable in the ODEs (1.5).

Thus, in the rest of the paper, we always assume that the conditions

$$\frac{\beta_1}{1+\gamma_1} > \frac{\beta_2}{\gamma_2}, \; -\frac{1}{\gamma_1} - \frac{\gamma_2 k_0}{\gamma_1} < j_0 < -\frac{1}{\gamma_1} \tag{4.3}$$

are satisfied.

The linearized operator of system (3.1) evaluated at (u_*, v_*) is given by (choosing d_1 as the bifurcation parameter)

$$L(d_1) = \begin{pmatrix} d_1\Delta - 1 - \gamma_1 j_0, & -\gamma_1 k_0 \\ -\gamma_2 j_0 & d_2\Delta - \gamma_2 k_0 \end{pmatrix}. \tag{4.4}$$

Let λ_i and $\xi_i(x)$, $i \in \mathbb{N}_0$, be the eigenvalues and the corresponding eigenfunctions of $-\Delta$ in Ω subject to Neumann boundary conditions. Then, by [15,25], the eigenvalues of $L(d_1)$ are given by those of the following operator $L_i(d_1)$:

$$L_i(d_1) = \begin{pmatrix} -d_1\lambda_i - 1 - \gamma_1 j_0, & -\gamma_1 k_0 \\ -\gamma_2 j_0 & -d_2\lambda_i - \gamma_2 k_0 \end{pmatrix}, \tag{4.5}$$

whose characteristic equation is

$$\mu^2 - \mu T_i(d_1) + D_i(d_1) = 0, \quad i \in \mathbb{N}_0,$$

where

$$\begin{cases} T_i(d_1) := -(d_1 + d_2)\lambda_i - (1 + \gamma_1 j_0 + \gamma_2 k_0), \\ D_i(d_1) := d_1 d_2 \lambda_i^2 + (\gamma_2 k_0 d_1 + (1 + \gamma_1 j_0) d_2)\lambda_i + \gamma_2 k_0. \end{cases} \tag{4.6}$$

According to [19,25], if there exist $i \in \mathbb{N}_0$ and $d_1^* > 0$, such that

$$D_i(d_1^*) = 0, \quad T_i(d_1^*) \neq 0, \quad T_j(d_1^*) \neq 0, \quad D_j(d_1^*) \neq 0 \;\text{ for all } j \neq i, \tag{4.7}$$

and the derivative $\frac{d}{dd_1} D_i(d_1^*) \neq 0$, then a global steady state bifurcation occurs at the critical point d_1^*.

By (4.3), we have $T_0(d_1) < 0$. Thus, for all $i \in \mathbb{N}_0$, we have $T_i(d_1) < 0$. Solving $D_i(d_1) = 0$, we have the set of critical values of (d_1, d_2), given by the hyperbolic curves C_i, with $i \in \mathbb{N} := \mathbb{N}_0 \backslash \{0\}$ (see also page 561 of [16]):

$$(C_i) : d_2^i = \frac{\gamma_1 \gamma_2 k_0 j_0 / \lambda_i^2}{d_1 + (1 + \gamma_1 j_0)/\lambda_i} - \frac{\gamma_2 k_0}{\lambda_i}, \ i \in \mathbb{N}. \tag{4.8}$$

Suppose that λ_i, $i \in \mathbb{N}$, is the simple eigenvalue of $-\Delta$. Following [16], we call $\mathcal{B} := \bigcup_{i=1}^{\infty} C_i$ the bifurcation set with respect to (u_*, v_*), and denote by $\mathcal{B}_0$ be the countable set of intersection points of two curves of $\{C_i\}_{i=1}^{\infty}$, and $\widehat{\mathcal{B}} = \mathcal{B} \backslash \mathcal{B}_0$.

Clearly, for any fixed $d_2 > 0$, there exists a unique d_1^i such that $(d_1^i, d_2) \in \widehat{\mathcal{B}} \cap C_i$, and at $d = d_1^i$, both (4.7) and $\frac{d}{dd_1} D_i(d_1^i) \neq 0$ are satisfied.

Then, from [16,25], we have the following results regarding the existence of Turing patterns:

Theorem 8 *Suppose that* (4.3) *holds and that* C_i *is defined in* (4.8)*, where* λ_i*,* $i \in \mathbb{N}$*, is the simple eigenvalue of* $-\Delta$*. Then for any* $(d_1^i, d_2) \in \widehat{\mathcal{B}} \cap C_i$ *with* d_2 *fixed, there is a smooth curve* Γ_i *of positive solutions of* (3.1) *bifurcating from* $(d_1, u, v) = (d_1^i, u_*, v_*)$*, with* Γ_i *contained in a global branch* $\mathcal{C}_i$ *of the positive solutions of* (3.1)*. Moreover*

1. *Near* $(d_1, u, v) = (d_1^i, u_*, v_*)$*,* $\Gamma_i = \{(d_1(s), u(s), v(s)) : s \in (-\epsilon, \epsilon)\}$*, where* $u(s) = u_* + s\boldsymbol{a}_i \xi_i(x) + s o_1(s)$*,* $v(s) = v_* + s\boldsymbol{b}_i \xi_i(x) + s o_2(s)$ *for* $s \in (-\epsilon, \epsilon)$ *for some* C^∞ *smooth functions* $d_1(s), o_1(s), o_2(s)$ *such that* $d_1(0) = d_1^i$ *and* $o_1(0) = o_2(0) = 0$*. Here* $\boldsymbol{a}_i$ *and* $\boldsymbol{b}_i$ *satisfy* $L_i(d_1)(\boldsymbol{a}_i, \boldsymbol{b}_i)^T = (0, 0)^T$*, and* $\xi_i(\cdot)$ *is the corresponding eigenfunction of the eigenvalue* λ_i *of* $-\Delta$*.*
2. *Moreover, the projection of* $\mathcal{C}_i$ *onto* d_1^i*-axis contains the interval* $(0, d_1^i)$*.*

Proof From discussions above, at $d_1 = d_1^i$, we can apply Theorem 3.2 in [25] to assert the existence of local and global steady state bifurcations. By Theorem 2.3 of [16], we can rule out the possibility that $\mathcal{C}_i$ contains another (d_1^j, u_*, v_*) with $i \neq j$. We thus complete the proof of this theorem (Fig. 2). □

5 Numerical Experiments

In this section we perform two numerical experiments to show that for some sets of parameters chosen accordingly the system (2.1) produces Turing patterns, that is., the solutions converge to spatially non-homogenous steady state. On the other hand, for some parameters the solutions of the system (2.1) either converge exponentially to uniform steady state or spatially homogenous periodic solution.

Experiment 1: Turing patterns

In this experiment, we show that the model (2.1) produces Turing patterns in a two-dimensional domain. The model (2.1) is defined in the square domain $\Omega = [0, \pi] \times [0, \pi]$ in $\mathbb{R}^2$ and the final time of interest is $T = 100$. Parameters are chosen according to the bifurcation analysis presented in Sect. 4 and by the eigenvalues of the Laplacian operator, $-\Delta$ in domain Ω which are $\lambda_{i,j} = i^2 + j^2$. The parameters for this experiment are $\beta_1 = 2.47, \beta_2 = 1, \gamma_1 = 150.8, \gamma_2 = 72.07, K = 25.5, d_1 = 0.09, d_2 = 2$. The parameters β_1, β_2, γ_1, γ_2, and K are fixed so that the inequality (4.3) holds. Thus in the absence of diffusion the uniform steady state $u_* = 0.38$ and $v_* = 0.19$ is locally asymptotically

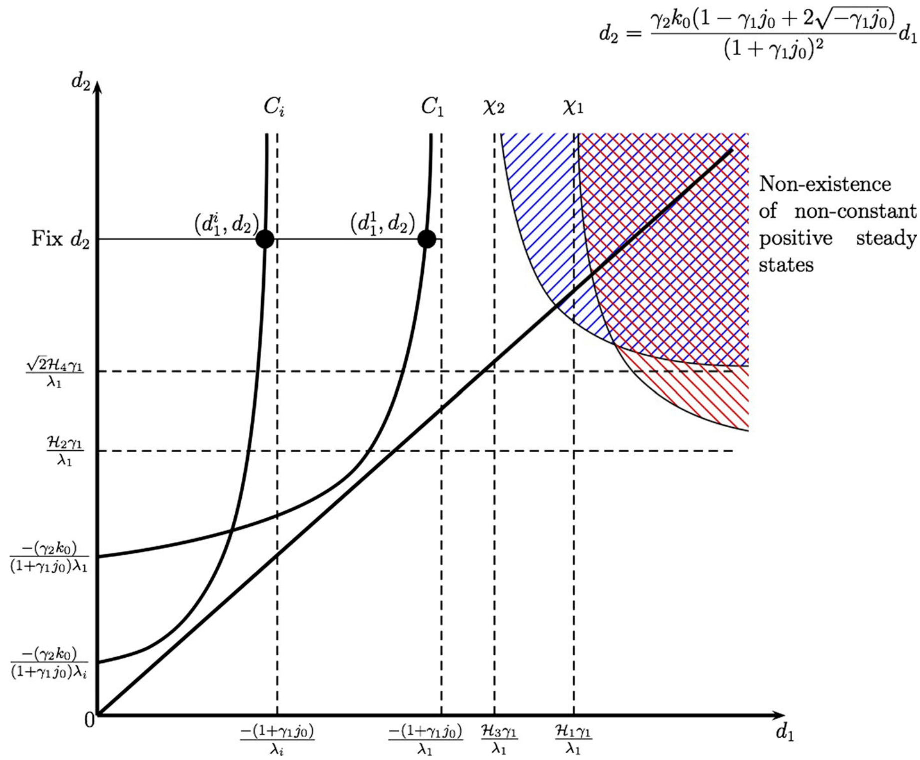

Fig. 2 Bifurcation diagram: For any $i \in \mathbb{N}$, C_i, defined precisely in (4.8), is the hyperbolic curve where the steady state bifurcation point (d_1^i, d_2) locates (for fixed $d_2 > 0$). The area on the *left side* of the vertical line $d_1 \equiv -(1+\gamma_1 j_0)/\lambda_1$, Turing patterns are possible; While in the *shaded area* on the *right side* of vertical line $d_1 \equiv \mathcal{H}_3\gamma_1/\lambda_1$, system (2.1) does not possess any non-constant positive steady states, including Turing patterns. Here $\mathcal{H}_i$, $i = 1, 2, 3, 4$, are defined in (3.23)

stable. For $d_2 = 2$, we find the diffusion constant d_1 such that the conditions in (4.7) satisfied. We take $\lambda = \lambda_{i,j} = 2^2 + 3^2 = 13$, in which the corresponding eigenfunctions are $\cos(2\pi x)\cos(3\pi y)$. Hence,

$$d_1 = \frac{-\gamma_2 k_0 - (1+\gamma_1 j_0) d_2 \lambda}{d_2 \lambda^2 + \gamma_2 k_0 \lambda} = 0.09 \text{ for } d_2 = 2 \text{ and } \lambda = 13.$$

We use finite element method for spatial discretization and implicit finite difference for the time derivative to approximate the solutions of the model (2.1). The mesh size $h = 0.0982$ which is achieved by 7938 elements (triangles), and the time step size is $\Delta t = 0.1$. Initial conditions are small random perturbations around the uniform steady state in the absence of diffusion. The chemical concentrations u and v at times $t = 0, 10, 50, 100$ are shown in the Fig. 5.

Experiment 2: Asymptotic behavior of the solutions
In this example we simulate the results of the Theorem 3. We show that for diffusion constants sufficiently large, namely for $(d_1, d_2) \in [\mathcal{D}/\lambda_1, \infty) \times [\mathcal{D}/\lambda_1, \infty)$, the solutions of the system (2.1) either converges to the constant steady state if (6.6) holds, or to the spatially homogenous periodic solutions if (6.7) holds. For the first case, we choose parameters as $\beta_1 = 5$, $\beta_2 =$

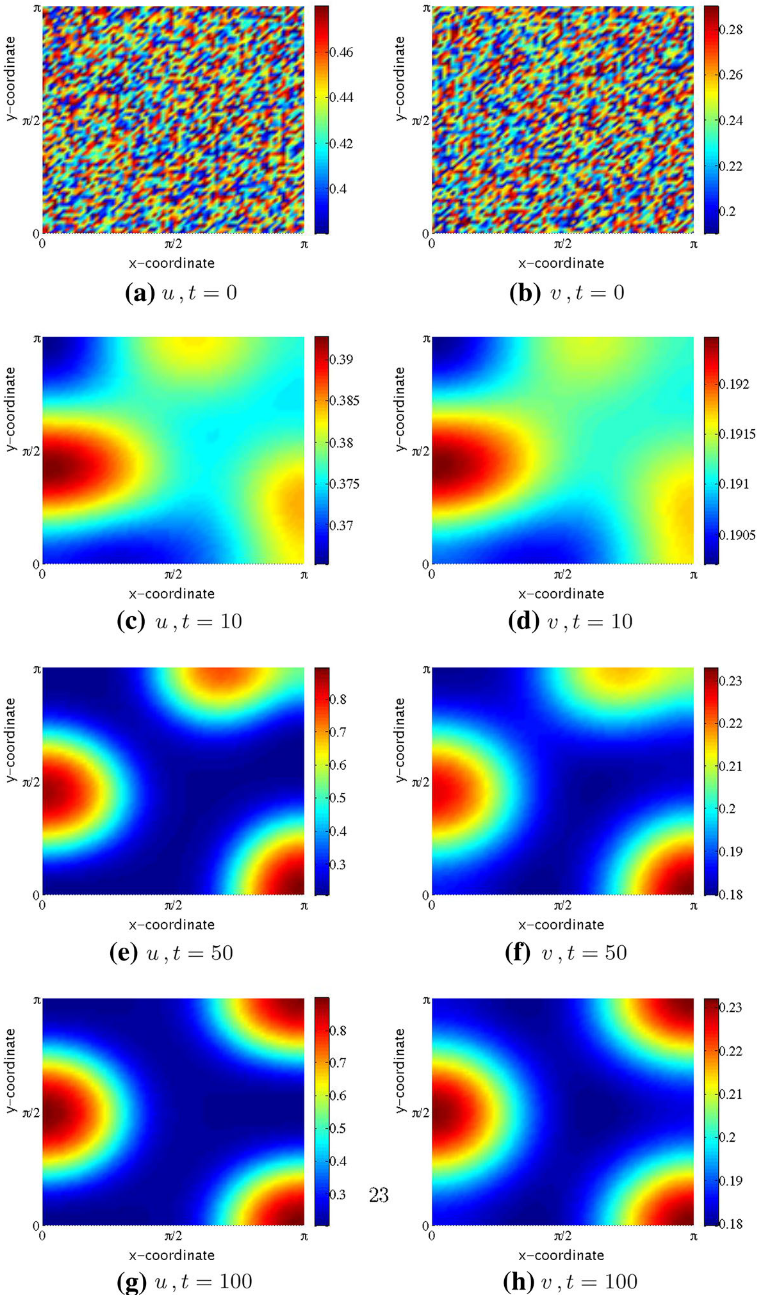

Fig. 3 Experiment 1: Turing patterns arising from the system (2.1) in a square domain Ω. The figures in the first column correspond to the chemical concentration u and the figures in the second column correspond to the chemical concentration v at specific time levels

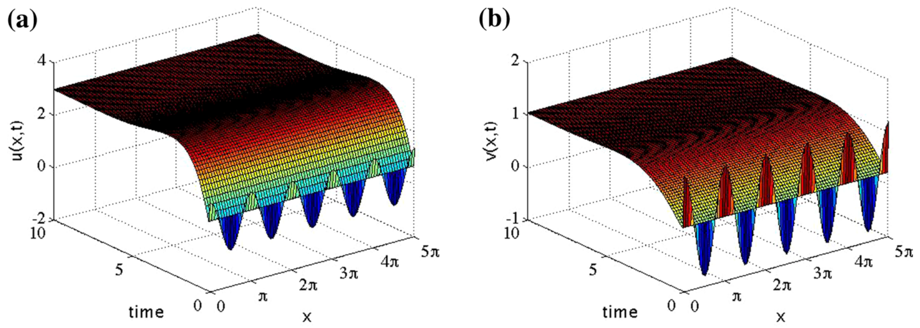

Fig. 4 Experiment 2: The solutions of the system (2.1) converging to constant steady state solutions $u_* = 2.95$ (**a**) and $v_* = 1.03$ (**b**)

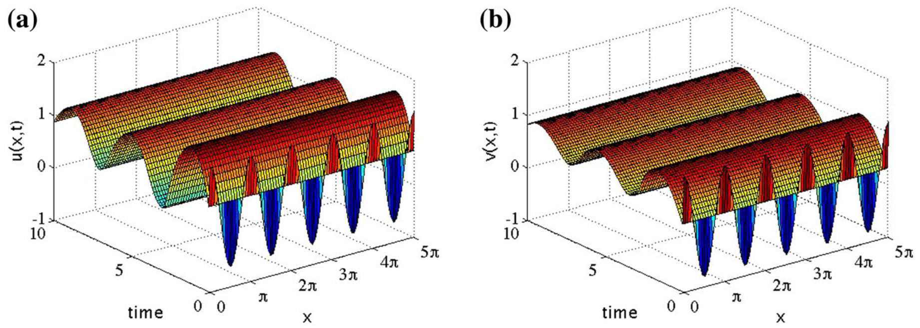

Fig. 5 Experiment 2: The solutions of the system (2.1) converging to the spatially homogenous temporally periodic steady state

1, $\gamma_1 = 150$, $\gamma_2 = 73$, and take the diffusion constants to be $d_1 = 2 \times 10^5$, $d_2 = 3 \times 10^5$. As shown in Fig. 5, the solutions converge to the constant steady states $u_* = 2.95$ and $v_* = 1.03$ (Figs. 3, 4).

For the latter case, we choose the parameters as $\beta_1 = 5$, $\beta_2 = 2$, $\gamma_1 = 146$, $\gamma_2 = 71$, and take the diffusion constants to be $d_1 = 2 \times 10^5$, $d_2 = 3 \times 10^5$. As shown in Fig. 5, the solutions converge to the spatially homogenous periodic solutions in time.

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Appendix: The Dynamics of ODEs

In this section, we consider the local/global asymptotic stability of (u_*, v_*), as well as the occurrence of stable periodic solutions of the following Ordinary Differential Equations (ODEs):

$$\frac{du}{dt} = \beta_1 - u - \frac{\gamma_1 uv}{1 + u + v + Ku^2} =: f(u, v), \quad \frac{dv}{dt} = \beta_2 - \frac{\gamma_2 uv}{1 + u + v + Ku^2} =: g(u, v). \tag{6.1}$$

System (6.1) has a positive equilibrium (u_*, v_*), with

$$u_* := \beta_1 - \frac{\gamma_1}{\gamma_2}\beta_2,\ \ v_* := \frac{\beta_2(1+u_*+Ku_*^2)}{\gamma_2 u_* - \beta_2}, \tag{6.2}$$

if and only if $\frac{\beta_1}{1+\gamma_1} > \frac{\beta_2}{\gamma_2}$ holds.

The linearized operator of system (6.1) evaluated at (u_*, v_*) is given by

$$J(u_*, v_*) := \begin{pmatrix} -1-\gamma_1 j_0 & -\gamma_1 k_0 \\ -\gamma_2 j_0, & -\gamma_2 k_0 \end{pmatrix}, \tag{6.3}$$

where

$$j_0 := \frac{v_*(1+v_*-Ku_*^2)}{(1+u_*+v_*+Ku_*^2)^2},\ \ k_0 := \frac{u_*(1+u_*+Ku_*^2)}{(1+u_*+v_*+Ku_*^2)^2}. \tag{6.4}$$

Then, the characteristic equation of (6.3) is given by

$$\mu^2 + (1+\gamma_1 j_0 + \gamma_2 k_0)\mu + \gamma_2 k_0 = 0. \tag{6.5}$$

Lemma 9 *Suppose that* $\frac{\beta_1}{1+\gamma_1} > \frac{\beta_2}{\gamma_2}$ *is satisfied so that* (u_*, v_*) *is the unique positive equilibrium of* (6.1). *If*

$$j_0 > -\frac{1+\gamma_2 k_0}{\gamma_1} \tag{6.6}$$

holds, then (u_*, v_*) *is locally asymptotically stable in system* (6.1). *However, if*

$$j_0 < -\frac{1+\gamma_2 k_0}{\gamma_1} \tag{6.7}$$

holds, then (u_*, v_*) *is unstable in system* (6.1)*, and the system* (6.1) *has a locally orbitally stable periodic orbit, denoted by* $(p(t), q(t))$.

Proof Suppose that (6.6) holds. Then, all the eigenvalues of (6.5) has strictly negative real parts, thus (u_*, v_*) is locally asymptotically stable; While if (6.7) holds, then (6.5) has one eigenvalue with positive real parts, thus (u_*, v_*) is unstable. According to Theorem 2, the solutions is bounded, then from Poincare–Bendixson theorem, we conclude the existence of a locally orbitally stable periodic orbit, denoted by $(p(t), q(t))$. □

The next result is on the global asymptotic stability of the positive equilibrium (u_*, v_*) in (6.1):

Lemma 10 *Suppose that* $\frac{\beta_1}{1+\gamma_1} > \frac{\beta_2}{\gamma_2}$ *is satisfied so that* (u_*, v_*) *is the unique positive equilibrium of* (6.1). *Assume also that* $0 < \beta_1 + \beta_2 \le 1$ *holds. Then,* (u_*, v_*) *is globally asymptotically stable in system* (6.1)*, if*

$$K \in \left(0, \frac{\gamma_2+2}{2\beta_1}\right] \cup \left[\frac{\gamma_2+2}{2\beta_1} + \frac{\epsilon_-}{2\beta_1^2}, \frac{\gamma_2+2}{2\beta_1} + \frac{\epsilon_+}{2\beta_1^2}\right], \tag{6.8}$$

where

$$\epsilon_\pm := \sqrt{9(1-\beta_1-\beta_2)^2 + 6\beta_1(\gamma_2+2)(1-\beta_1-\beta_2)} \pm 3(1-\beta_1-\beta_2) > 0. \tag{6.9}$$

Proof We first use the Dulac criteria to exclude the existence of periodic orbits in the first quadrant. Define $b(u, v) = 1 + u + v + Ku^2$, then, we have

$$\frac{\partial(fb)}{\partial u} + \frac{\partial(gb)}{\partial v} = \mathcal{W}(u) - (\gamma_1 + 1)v, \tag{6.10}$$

where $\mathcal{W}(u) := -3Ku^2 - (\gamma_2 + 2 - 2\beta_1 K)u + \beta_1 + \beta_2 - 1$.

Let $u_{\mathcal{W}}$ be the symmetry axis of the function $\mathcal{W}(u)$. Then, $u_{\mathcal{W}} = \frac{1}{3}\beta_1 K - \frac{1}{6}(2 + \gamma_2)$. If $K \in \big(0, \frac{\gamma_2 + 2}{2\beta_1}\big]$ holds, we have $u_{\mathcal{W}} \leq 0$. Thus, $\mathcal{W}(u) \leq 0$, which indicates that under $\partial(fb)/\partial u + \partial(gb)/\partial v < 0$ in the first quadrant.

On the other hand, let $\Delta_{\mathcal{W}}$ be the discriminant of the function $\mathcal{W}(u)$. Then,

$$\Delta_{\mathcal{W}} = (2\beta_1 K - 2 - \gamma_2)^2 + 12K(\beta_1 + \beta_2 - 1). \tag{6.11}$$

Suppose that $K \in \big[\frac{\gamma_2 + 2}{2\beta_1} + \frac{\epsilon_-}{2\beta_1^2}, \frac{\gamma_2 + 2}{2\beta_1} + \frac{\epsilon_+}{2\beta_1^2}\big]$ holds. Then $\Delta_{\mathcal{W}} \leq 0$. Again, we can conclude that $\mathcal{W}(u) \leq 0$, which indicates that under $\partial(fb)/\partial u + \partial(gb)/\partial v < 0$ in the first quadrant.

So far, under (6.8) and $0 < \beta_1 + \beta_2 \leq 1$, by Dulac criteria, system (6.1) does not have closed orbits in the first quadrant. By Theorem 2, it follows that the solution is bounded. Thus, by Poincare–Bendixson theorem, we know that (u_*, v_*) is globally asymptotically stable in ODEs. □

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