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ORIGINAL ARTICLE

Bifurcation and Pattern Formation in an Activator–Inhibitor Model with Non-local Dispersal

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Abstract
In this paper, by approximating the non-local spatial dispersal equation by an associated reaction–diffusion system, an activator–inhibitor model with non-local dispersal is transformed into a reaction–diffusion system coupled with one ordinary differential equation. We prove that, to some extent, the non-locality-induced instability of the non-local system can be regarded as diffusion-driven instability of the reaction–diffusion system for sufficiently small perturbation. We study the structure of the spectrum of the corresponding linearized operator, and we use linear stability analysis and steady-state bifurcations to show the existence of non-constant steady states which generates non-homogeneous spatial patterns. As an example of our results, we study the bifurcation and pattern formation of a modified Klausmeier–Gray–Scott model of water–plant interaction.

Keywords Non-local dispersal · Water–plant model · Reaction–diffusion-ODE system · Pattern formation · Spectrum · Bifurcation

Mathematics Subject Classification 92C15 · 35K57 · 35B36 · 35B35 · 35B32

In Memory of Professor Masayasu Mimura

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1 Introduction

Reaction–diffusion models have been proposed to describe the reaction, growth and spatial movement of organic or inorganic substance in the space over time (Meinhardt 1992; Turing 1952). A particular important feature of the reaction–diffusion models is that spatial–temporal patterns can be generated in certain parameter regimes, which has been extensively used in many fields of physical and biological sciences. The theoretical predication from the model and laboratory or field observation of spatial patterns often match well (Kondo and Miura 2010; Rietkerk et al. 2004).

The foremost important mechanism of spatial pattern generation is Turing's diffusion-induced instability: slow activator diffusion and fast inhibitor diffusion can destabilize a spatially homogeneous steady state, and spatially non-homogeneous steady states may emerge as the result of symmetry-breaking bifurcation (Sheth et al. 2012; Sick et al. 2006; Turing 1952; Yi et al. 2009). Other movement mechanisms of spatiotemporal pattern formation have been also proposed: (i) directed advective movement such as chemotaxis (Bellomo et al. 2015; Horstmann 2003; Keller and Segel 1971); (ii) density-dependent diffusion such as cross diffusion (Lou and Ni 1996; Mimura and Kawasaki 1980; Mimura et al. 1984; Ni 1998); and (iii) memory-based delayed movement (Shi et al. 2019, 2021, 2020, 2021). Non-local effect on the reaction or growth of the biological population has also been recognized as a possible mechanism of rich spatiotemporal pattern formation (Chen and Shi 2012; Chen and Yu 2018; Ei and Ishii 2021; Fu et al. 2020; Fuentes et al. 2003; Furter and Grinfeld 1989; Gourley et al. 2001; Shi et al. 2022; Tian et al. 2019; Zaytseva et al. 2020).

In this paper, we consider the instability caused by a non-local dispersal and associated spatial pattern formation. The model is presented by the following modified Klausmeier–Gray–Scott model with periodic boundary condition in $[-l, l]$:

$$\begin{cases} u_t = d_u u_{xx} + A - u - v^2 u, & x \in (-l, l),\ t > 0, \\ v_t = d_v (J * v - v) + v^2 u - Bv, & x \in (-l, l),\ t > 0, \\ u(-l, t) = u(l, t), u_x(-l, t) = u_x(l, t), & t > 0. \end{cases} \tag{1.1}$$

Here, $u(x, t)$ is water density, $v(x, t)$ is plant density, t is time, and x is a one-dimensional space variable; A can be interpreted as rainfall, which controls water input; B measures plant losses; the movement of water is modeled by diffusion with a diffusion coefficient d_u; and the dispersal of plant is modeled by a the convolution integral $J * v$ defined by $(J * v)(x) = \int_{-l}^{l} J(x - y)v(y)dy$, which can be used to describe the free movement of individuals in a long range area. The function $J(x)$ satisfies $J(x) \in C^1(\mathbb{R})$, $J(x) > 0$ in $(-l, l)$, $J(x) = 0$ in $\mathbb{R} \setminus (-l, l)$, $J(-x) = J(x)$, and $\int_{-l}^{l} J(x)dx = 1$. Biologically, the kernel function $J(x - y)$ means the probability per unit length of seeds originating at the point y being dispersed to point x (Eigentler and Sherratt 2018; Pueyo et al. 2008). In this paper, we consider the kernel function $J(x)$ with the following form

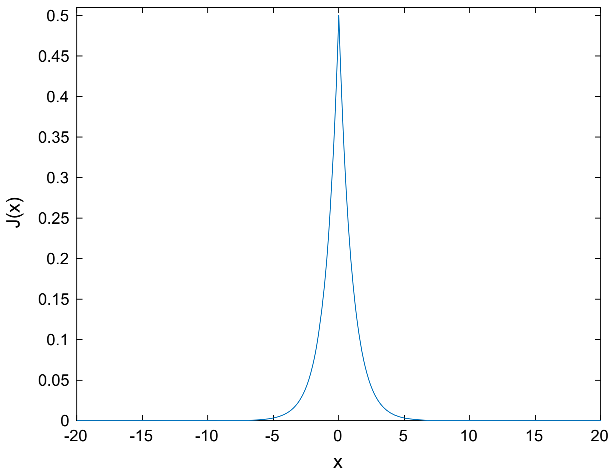


Fig. 1 The kernel (1.2) with $d_w = 1, l = 20$ (Color figure online)

$$J(x) = \begin{cases} \dfrac{1}{2\sqrt{d_w}\sinh(l/\sqrt{d_w})}\cosh\left(\dfrac{l-|x|}{\sqrt{d_w}}\right), & -l < x < l, \\ 0, & \text{otherwise}, \end{cases} \tag{1.2}$$

where l, d_w are positive constants, and d_v is the dispersal rate of the plant. A typical example of the kernel (1.2) is shown in Fig. 1.

Recall that for a general activator–inhibitor reaction–diffusion model

$$\begin{cases} u_t = d_u u_{xx} + f(u, v), & x \in (-l, l),\ t > 0, \\ v_t = d_v v_{xx} + g(u, v), & x \in (-l, l),\ t > 0, \\ u(-l, t) = u(l, t), u_x(-l, t) = u_x(l, t), & t > 0, \\ v(-l, t) = v(l, t), v_x(-l, t) = v_x(l, t), & t > 0, \end{cases} \tag{1.3}$$

where $f(u, v), g(u, v)$ are nonlinear functions modeling reactions between species u and v, if the model (1.3) admits a constant positive steady state (u^*, v^*) and is stable for the corresponding kinetic system, then the Jacobian matrix

$$J = \begin{pmatrix} f_u^* & f_v^* \\ g_u^* & g_v^* \end{pmatrix}$$

satisfies

(C_1) $f_u^* + g_v^* < 0, \quad f_u^* g_v^* - f_v^* g_u^* > 0.$

Throughout this paper, we use f_u^*, f_v^*, g_u^* and g_v^* represent the first order partial derivatives of f and g with respect to the first variable u and the second one v at (u^*, v^*), respectively. Furthermore, we assume u is an inhibitor and v is an activator, that is, the Jacobian matrix has the sign pattern

(C_2) $\begin{pmatrix} - & - \\ + & + \end{pmatrix}$, or $\begin{pmatrix} - & + \\ - & + \end{pmatrix}$.

Then, under the assumptions (C_1) and (C_2), diffusion-induced Turing instability could occur in system (1.3).

A general non-local dispersal activator–inhibitor model with $J(x)$ defined as in (1.1) is

$$\begin{cases} u_t = d_u u_{xx} + f(u, v), & x \in (-l, l), \ t > 0, \\ v_t = d_v (J * v - v) + g(u, v), & x \in (-l, l), \ t > 0, \\ u(-l, t) = u(l, t), u_x(-l, t) = u_x(l, t), & t > 0. \end{cases} \tag{1.4}$$

Through this paper, we always assume the assumptions (C_1) and (C_2) are satisfied and attempt to study the non-local interaction-induced instability of system (1.4) with periodic boundary condition in $[-l, l]$.

Pattern formation for non-local dispersal for a constant kernel was studied in Chen et al. (2021), and the dynamics of spatial population models with non-local dispersal was also studied in Bai and Li (2018); Hutson et al. (2003); Li et al. (2014); Kot et al. (1996); Wang and Zhang (2021); Yang et al. (2019). The relationship between the instability induced by non-local interaction and diffusion-driven instability and the realization of non-local interactions by reaction–diffusion systems were also considered in Ninomiya et al. (2017). The water–plant interaction model with non-local dispersal was considered in Alfaro et al. (2018); Eigentler and Sherratt (2018), and the corresponding reaction–diffusion model was studied in Wang et al. (2021).

The paper is organized as follows. In Sect. 2, we give the spectral analysis of two linear operators and establish the equivalence of two related stability notions. In Sect. 3, we give the linear stability analysis of the constant steady state of the corresponding reaction–diffusion system, and we prove the existence of non-constant steady states through bifurcation analysis. In Sect. 4, we analyze the existence, local stability of constant steady states, bifurcation and pattern formation of the non-local modified Klausmeier–Gray–Scott model. We end with some more discussions in Sect. 5.

Throughout this paper, we use the following notations.

$\mathbb{N}_0 = \mathbb{N} \cup \{0\}$.

$\mathbb{C}^+ = \{a + bi : a, b \in \mathbb{R}, a > 0\}$.

$R(\mathcal{L})$: *The range of the linear operator* $\mathcal{L}$.

$\mathcal{N}(\mathcal{L})$: *The kernel of the linear operator* $\mathcal{L}$.

$\sigma(\mathcal{L})$: *The spectrum of the linear operator* $\mathcal{L}$.

$\sigma_p(\mathcal{L})$: *The point spectrum of the linear operator* $\mathcal{L}$.

$\sigma_c(\mathcal{L})$: *The continuous spectrum of the linear operator* $\mathcal{L}$.

$C^0([-l, l])$: *The Banach space of all continuous on the interval* $[-l, l]$.

$C^2_P([-l, l])$: *The Banach space of all twice continuously differential functions on the interval* $[-l, l]$ *satisfying periodic boundary conditions.*

2 Equivalence of Stability

The solution of the linear elliptic equation

$$\begin{cases} d_w w''(x) - w(x) + v(x) = 0, & x \in (-l, l), \\ w(-l) = w(l), \ \ w'(-l) = w'(l), \end{cases} \tag{2.1}$$

is given by $w(x) = (J * v)(x)$ where J is defined in (1.2). Then, the system (1.4) is equivalent to the following parabolic–elliptic-ordinary partial differential equation system:

$$\begin{cases} u_t = d_u u_{xx} + f(u, v), & x \in (-l, l), \ \ t > 0, \\ \ 0 = d_w w_{xx} - w + v, & x \in (-l, l), \ \ t > 0, \\ v_t = d_v(w - v) + g(u, v), & x \in (-l, l), \ \ t > 0, \\ u(-l, t) = u(l, t), u_x(-l, t) = u_x(l, t), & \ t > 0, \\ w(-l, t) = w(l, t), w_x(-l, t) = w_x(l, t), & \ t > 0. \end{cases} \tag{2.2}$$

We embed the system (2.2) into a parabolic-ordinary differential system

$$\begin{cases} u_t = d_u u_{xx} + f(u, v), & x \in (-l, l), \ \ t > 0, \\ \varepsilon w_t = d_w w_{xx} - w + v, & x \in (-l, l), \ \ t > 0, \\ v_t = d_v(w - v) + g(u, v), & x \in (-l, l), \ \ t > 0, \\ u(-l, t) = u(l, t), u_x(-l, t) = u_x(l, t), & \ t > 0, \\ w(-l, t) = w(l, t), w_x(-l, t) = w_x(l, t), & \ t > 0, \end{cases} \tag{2.3}$$

with $0 \le \varepsilon \ll 1$. A steady-state solution $(u(x), v(x))$ of (1.4) is equivalent to $(u(x), w(x), v(x))$ for (2.2) or (2.3). In this section, we compare the stability of a steady state with respect to (1.4) with non-local dispersal and the stability of the same steady state with respect to (2.2) or (2.3) which has diffusive dispersal, and the relation between the two stabilities reveals the relation between the non-local dispersal-induced instability of (1.4) and the diffusion-driven instability of (2.3).

The eigenvalue problem

$$-\varphi'' = \mu\varphi, \quad x \in (-l, l), \quad \varphi(-l) = \varphi(l), \ \ \varphi'(-l) = \varphi'(l)$$

has eigenvalues $\mu_k = (k\pi/l)^2$, $(k = 0, 1, 2, \cdots)$ with corresponding eigenfunctions for $k \ge 1$ $\varphi_k(x) = c_{1k} \cos(\pi k x/l) + c_{2k} \sin(\pi k x/l)$, where c_{1k}, c_{2k} are constants which are not equal to zero simultaneously, and $\varphi_0(x) = 1$.

For system (1.4), define a mapping G_1 by

$$G_1 \begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} d_u u_{xx} + f(u, v) \\ d_v(J * v - v) + g(u, v) \end{pmatrix}, \tag{2.4}$$

where $(u, v) \in C_P^2([-l, l]) \times C^0([-l, l]) \equiv X_1$. Then, $G_1 : X_1 \to Y_1$, where $Y_1 \equiv C^0([-l, l]) \times C^0([-l, l])$, is Fréchet differentiable, and at a constant steady state (u^*, v^*), the linearized operator of G_1 is defined as

$$\mathcal{L}_1 \begin{pmatrix} \phi \\ \psi \end{pmatrix} \equiv \partial_{(u,v)} G_1(u^*, v^*) \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \begin{pmatrix} d_u \phi'' + f_u^* \phi + f_v^* \psi \\ d_v(-\psi + J * \psi) + g_u^* \phi + g_v^* \psi \end{pmatrix}. \tag{2.5}$$

Lemma 2.1 *Define* $\tilde{\lambda}_{\pm,k} = \dfrac{-a_0 \pm \sqrt{a_0^2 - 4a_1}}{2}$ *where*

$$\begin{aligned} a_0 &= d_u \mu_k + d_v - f_u^* - g_v^* - \frac{d_v}{d_w \mu_k + 1}, \\ a_1 &= (f_u^* - d_u \mu_k)(g_v^* - d_v) - f_v^* g_u^* + \frac{d_v (f_u^* - d_u \mu_k)}{d_w \mu_k + 1}. \end{aligned} \tag{2.6}$$

Then, $\sigma(\mathcal{L}_1) = \sigma_p(\mathcal{L}_1) = \{\tilde{\lambda}_{\pm,k} : k \in \mathbb{N}_0\}$.

Proof For $\lambda \in \mathbb{C}$, the associated eigenvalue problem of $\mathcal{L}_1$ is

$$\partial_{(u,v)} G_1(u^*, v^*) \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \lambda \begin{pmatrix} \phi \\ \psi \end{pmatrix},$$

which is equivalent to

$$\begin{cases} \lambda \phi = d_u \phi'' + f_u^* \phi + f_v^* \psi, \\ \lambda \psi = d_v(-\psi + J * \psi) + g_u^* \phi + g_v^* \psi. \end{cases} \tag{2.7}$$

With the kth term of the Fourier series expansion of ϕ and ψ

$$\begin{aligned} \phi_k &:= c_k \exp\Big(\frac{k\pi i}{l} x\Big), \quad c_k := \frac{1}{2l} \int_{-l}^{l} \phi(x) \exp\Big(-\frac{k\pi i}{l} x\Big) dx, \\ \psi_k &:= e_k \exp\Big(\frac{k\pi i}{l} x\Big), \quad e_k := \frac{1}{2l} \int_{-l}^{l} \psi(x) \exp\Big(-\frac{k\pi i}{l} x\Big) dx, \end{aligned}$$

we obtain

$$\begin{cases} \lambda \phi_k = -d_u \mu_k \phi_k + f_u^* \phi_k + f_v^* \psi_k, \\ \lambda \psi_k = d_v(-\psi_k + J * \psi_k) + g_u^* \phi_k + g_v^* \psi_k. \end{cases}$$

By the method of Ninomiya et al. (2017), changing the variable, we can have

$$\begin{cases} \lambda \phi_k = -d_u \mu_k \phi_k + f_u^* \phi_k + f_v^* \psi_k, \\ \lambda \psi_k = d_v(-\psi_k + (\hat{J})_k \psi_k) + g_u^* \phi_k + g_v^* \psi_k, \end{cases}$$

with

$$(\hat{J})_k = \int_{-l}^{l} J(y)\exp\Big(-\frac{k\pi i}{l}y\Big)dy = \frac{1}{d_w\mu_k + 1}. \tag{2.8}$$

Then, the eigenvalues $\tilde{\lambda}_{\pm,k}$ satisfy the following equation

$$\lambda^2 + a_0\lambda + a_1 = 0, \tag{2.9}$$

where a_0, a_1 are defined as in (2.6). This completes the proof. $\square$

For the system (2.3), define a mapping G_2 by

$$G_2\begin{pmatrix} u \\ w \\ v \end{pmatrix} = \begin{pmatrix} d_u u_{xx} + f(u, v) \\ \frac{d_w}{\varepsilon} w_{xx} - \frac{1}{\varepsilon} w + \frac{1}{\varepsilon} v \\ d_v(w - v) + g(u, v) \end{pmatrix}, \tag{2.10}$$

where $(u, w, v) \in C_P^2([-l, l]) \times C_P^2([-l, l]) \times C^0([-l, l]) \equiv X_2$. Then, $G_2 : X_2 \to Y_2$, where $Y_2 \equiv C^0([-l, l]) \times C^0([-l, l]) \times C^0([-l, l])$, is Fréchet differentiable, and at a constant steady state (u^*, v^*, v^*), the linearized operator is defined by

$$\mathcal{L}_{2,\varepsilon}\begin{pmatrix} \phi \\ \psi \\ \vartheta \end{pmatrix} \equiv \partial_{(u,w,v)} G_2(u^*, v^*, v^*)\begin{pmatrix} \phi \\ \psi \\ \vartheta \end{pmatrix} = \begin{pmatrix} d_u\phi'' + f_u^*\phi + f_v^*\vartheta \\ \frac{d_w\psi''}{\varepsilon} - \frac{\psi}{\varepsilon} + \frac{\vartheta}{\varepsilon} \\ g_u^*\phi + d_v\psi + (g_v^* - d_v)\vartheta \end{pmatrix}.$$

The spectral set of $\mathcal{L}_{2,\varepsilon}$ is described in the following proposition.

Proposition 2.2 *Suppose that the parameters $d_u, d_v, d_w, \varepsilon$ are all positive and (u^*, v^*, v^*) is a constant steady state of system (2.3). Then, the spectral set*

$$\sigma(\mathcal{L}_{2,\varepsilon}) = \{\lambda_{1,k}(\varepsilon), \lambda_{2,k}(\varepsilon), \lambda_{3,k}(\varepsilon) : k \in \mathbb{N}_0\} \cup \{g_v^* - d_v\},$$

where $\lambda_{1,k}(\varepsilon), \lambda_{2,k}(\varepsilon), \lambda_{3,k}(\varepsilon)$ are the roots of

$$\begin{aligned}\Psi_k(\varepsilon,\lambda) := \lambda^3 &+ \Big(d_u\mu_k - f_u^* + d_v - g_v^* + \frac{d_w\mu_k + 1}{\varepsilon}\Big)\lambda^2 \\ &+ \Big((d_u\mu_k - f_u^*)(\frac{d_w\mu_k + 1}{\varepsilon} + d_v - g_v^*) - f_v^* g_u^* \\ &+ \frac{(d_w\mu_k + 1)(d_v - g_v^*) - d_v}{\varepsilon}\Big)\lambda \\ &+ \Big((d_u\mu_k - f_u^*)\frac{(d_w\mu_k + 1)(d_v - g_v^*) - d_v}{\varepsilon} \\ &- \frac{f_v^* g_u^*(d_w\mu_k + 1)}{\varepsilon}\Big) = 0.\end{aligned} \tag{2.11}$$

Moreover $\{\lambda_{1,k}(\varepsilon), \lambda_{2,k}(\varepsilon), \lambda_{3,k}(\varepsilon) : k \in \mathbb{N}_0\} \subseteq \sigma_p(\mathcal{L}_{2,\varepsilon})$; and $g_v^* - d_v \in \sigma_c(\mathcal{L}_{2,\varepsilon})$ if one of the following conditions is satisfied

1. $d_w g_u^* f_v^* + d_u d_v \neq 0$ *and* $\dfrac{d_v(f_u^* + d_v - g_v^*) - g_u^* f_v^*(1 + (g_v^* - d_v)\varepsilon)}{d_w g_u^* f_v^* + d_u d_v} \notin \{\mu_k\}_{k=0}^{\infty}$;
2. $d_w g_u^* f_v^* + d_u d_v = 0$ *and* $d_v(f_u^* + d_v - g_v^*) - g_u^* f_v^*(1 + (g_v^* - d_v)\varepsilon) \neq 0$;

and if neither condition 1 nor 2 is satisfied, $g_v^* - d_v \in \sigma_p(\mathcal{L}_{2,\varepsilon})$.

Proof For $\lambda \in \mathbb{C}$ and $(\sigma, \tau, \gamma) \in Y_2$, we consider the following non-homogeneous problem:

$$\begin{cases} d_u \phi'' + f_u^* \phi + f_v^* \vartheta = \lambda \phi + \sigma, & (2.12a) \\ \dfrac{d_w}{\varepsilon} \psi'' - \dfrac{1}{\varepsilon} \psi + \dfrac{1}{\varepsilon} \vartheta = \lambda \psi + \tau, & (2.12b) \\ g_u^* \phi + d_v \psi + (g_v^* - d_v) \vartheta = \lambda \vartheta + \gamma, & (2.12c) \\ \phi(-l) = \phi(l), \ \phi'(-l) = \phi'(l), & (2.12d) \\ \psi(-l) = \psi(l), \ \psi'(-l) = \psi'(l). & (2.12e) \end{cases}$$

If $\lambda \neq g_v^* - d_v$, from (2.12c) we have

$$\vartheta = \frac{\gamma - g_u^* \phi - d_v \psi}{(g_v^* - d_v) - \lambda}. \tag{2.13}$$

Then, problem (2.12) becomes

$$\begin{cases} d_u \phi'' + \Big(f_u^* - \lambda - \dfrac{f_v^* g_u^*}{(g_v^* - d_v) - \lambda}\Big)\phi - \dfrac{f_v^* d_v}{(g_v^* - d_v) - \lambda}\psi = \sigma - \dfrac{f_v^* \gamma}{(g_v^* - d_v) - \lambda}, \\ \dfrac{d_w}{\varepsilon}\psi'' - \Big(\dfrac{1}{\varepsilon} + \lambda + \dfrac{d_v}{\varepsilon[(g_v^* - d_v) - \lambda]}\Big)\psi - \dfrac{g_u^*}{\varepsilon[(g_v^* - d_v) - \lambda]}\phi = \tau - \dfrac{\gamma}{\varepsilon[(g_v^* - d_v) - \lambda]}. \end{cases} \tag{2.14}$$

The non-homogeneous problem (2.14) has a unique solution if and only if

$$\frac{e_1 \pm \sqrt{e_1^2 - 4e_0 e_2}}{2e_0} \notin \{\mu_k\}_{k=0}^{\infty}, \tag{2.15}$$

where

$$\begin{aligned} e_0 &= d_w d_u (\lambda + d_v - g_v^*), \\ e_1 &= -(d_w + d_u \varepsilon)\lambda^2 + (d_w f_u^* + d g_v^* + d_u g_v^* \varepsilon - d_w d_v - d_u - d_u d_v \varepsilon)\lambda \\ &\quad + d_w d_v f_u^* + d_u g_v^* - d_w f_u^* g_v^* + d_w f_v^* g_u^*, \\ e_2 &= \varepsilon \lambda^3 + (d_v \varepsilon - f_u^* \varepsilon - g_v^* \varepsilon + 1)\lambda^2 + (f_u^* g_v^* \varepsilon - d_v f_u^* \varepsilon - f_v^* g_u^* \varepsilon - f_u^* - g_v^*)\lambda \\ &\quad + f_u^* g_v^* - f_v^* g_u^*. \end{aligned} \tag{2.16}$$

Furthermore, if (2.15) holds, then the unique solution (ϕ, ψ) of (2.14) satisfies

$$||\phi||_\infty + ||\psi||_\infty \leq C_0(||\sigma||_\infty + ||\tau||_\infty + ||\gamma||_\infty),$$

for some constant $C_0 > 0$. Thus, ϑ can be obtained by (2.13) and satisfies

$$||\vartheta||_\infty \leq C_1(||\sigma||_\infty + ||\tau||_\infty + ||\gamma||_\infty),$$

for some constant $C_1 > 0$. Thus, $(\mathcal{L}_{2,\varepsilon} - \lambda I)^{-1}$ exists and is bounded if $\lambda \neq g_v^* - d_v$ and (2.15) is satisfied. So such $\lambda \notin \sigma(\mathcal{L}_{2,\varepsilon})$.

On the other hand, if there exists some $k \in \mathbb{N}_0$ such that $\frac{e_1 \pm \sqrt{e_1^2 - 4e_0e_2}}{2e_0} = \mu_k$, *i.e.*, λ satisfies (2.11) which is the characteristic equation of $\mathcal{L}_{2,\varepsilon}$, then Eq. (2.11) has three roots denoted by $\lambda_{1,k}(\varepsilon)$, $\lambda_{2,k}(\varepsilon)$, $\lambda_{3,k}(\varepsilon)$.

Now we prove $\lambda = g_v^* - d_v$ is in the spectrum of $\mathcal{L}_{2,\varepsilon}$. If $\lambda = g_v^* - d_v$, problem (2.12) becomes

$$\begin{cases} d_u\phi'' + f_u^*\phi + f_v^*\vartheta = (g_v^* - d_v)\phi + \sigma, & (2.17a) \\ \dfrac{d_w}{\varepsilon}\psi'' - \dfrac{1}{\varepsilon}\psi + \dfrac{1}{\varepsilon}\vartheta = (g_v^* - d_v)\psi + \tau, & (2.17b) \\ g_u^*\phi + d_v\psi = \gamma. & (2.17c) \end{cases}$$

First we prove that, under suitable conditions, $\lambda = g_v^* - d_v$ is in the continuous spectrum of $\mathcal{L}_{2,\varepsilon}$, which means that $\mathcal{L}_{2,\varepsilon} - (g_v^* - d_v)I$ is injective and the range $R(\mathcal{L}_{2,\varepsilon} - (g_v^* - d_v)I)$ is dense in Y_2. Indeed we prove that

$$R(\mathcal{L}_{2,\varepsilon} - (g_v^* - d_v)I) = C^0([-l,l]) \times C^0([-l,l]) \times C_P^2([-l,l]).$$

From (2.17a) and (2.17b), we have $\sigma, \tau \in C^0([-l,l])$. From (2.17c) and $\phi, \psi \in C_P^2([-l,l])$, it is necessary $\gamma \in C_P^2([-l,l])$. Then, $R(\mathcal{L}_{2,\varepsilon} - (g_v^* - d_v)I) \subseteq C^0([-l,l]) \times C^0([-l,l]) \times C_P^2([-l,l])$. Conversely, if $(\sigma, \tau, \gamma) \in C^0([-l,l]) \times C^0([-l,l]) \times C_P^2([-l,l])$, we can eliminate ϑ from (2.17a) and (2.17b) and obtain

$$d_u\phi'' - d_w f_v^*\psi'' + f_u^*\phi + f_v^*\psi = (g_v^* - d_v)\phi - f_v^*(g_v^* - d_v)\varepsilon\psi + \sigma - \tau\varepsilon. \tag{2.18}$$

From (2.12d) and (2.17c),

$$\phi(-l) = \phi(l),\ \phi'(-l) = \phi'(l),\ \phi = \frac{\gamma - d_v\psi}{g_u^*} \tag{2.19}$$

for $g_u^* \neq 0$. Substituting (2.19) into (2.18), we get the following non-homogeneous problem about ψ

$$\begin{aligned} &\Big(d_w f_v^* + \frac{d_u d_v}{g_u^*}\Big)\psi'' + \Big(\frac{d_v(f_u^* + d_v - g_v^*)}{g_u^*} - f_v^*(1 + (g_v^* - d_v)\varepsilon)\Big)\psi \\ &\quad = \frac{d_u\gamma'' + (f_u^* + d_v - g_v^*)\gamma}{g_u^*} + \tau\varepsilon - \sigma. \end{aligned} \tag{2.20}$$

If $d_w g_u^* f_v^* + d_u d_v \neq 0$, problem (2.20) has a unique solution ψ if and only if

$$\frac{d_v(f_u^* + d_v - g_v^*) - g_u^* f_v^*(1 + (g_v^* - d_v)\varepsilon)}{d_w g_u^* f_v^* + d_u d_v} \notin \{\mu_k\}_{k=0}^{\infty}. \tag{2.21}$$

If $d_w g_u^* f_v^* + d_u d_v = 0$ and $d_v(f_u^* + d_v - g_v^*) - g_u^* f_v^*(1 + (g_v^* - d_v)\varepsilon) \neq 0$, problem (2.20) has a unique solution ψ given by

$$\psi = \frac{d_u \gamma'' + (f_u^* + d_v - g_v^*)\gamma + g_u^*(\tau\varepsilon - \sigma)}{d_v(f_u^* + d_v - g_v^*) - g_u^* f_v^*(1 + (g_v^* - d_v)\varepsilon)}. \tag{2.22}$$

If ψ is solved uniquely, then ϕ and ϑ can be determined by (2.19) and (2.17b), respectively. Then, $C^0([-l,l]) \times C^0([-l,l]) \times C_P^2([-l,l]) \subseteq R(\mathcal{L}_{2,\varepsilon} - (g_v^* - d_v)I)$. Thus, $R(\mathcal{L}_{2,\varepsilon} - (g_v^* - d_v)I) = C^0([-l,l]) \times C^0([-l,l]) \times C_P^2([-l,l])$. Therefore, $R(\mathcal{L}_{2,\varepsilon} - (g_v^* - d_v)I)$ is dense in $C^0([-l,l]) \times C^0([-l,l]) \times C^0([-l,l])$ as $C_P^2([-l,l])$ is dense in $C^0([-l,l])$. Furthermore, $R(\mathcal{L}_{2,\varepsilon} - (g_v^* - d_v)I)$ is injective. Therefore, $\lambda = g_v^* - d_v$ is the continuous spectrum if the condition 1 or 2 is satisfied.

Now, we consider $d_w g_u^* f_v^* + d_u d_v \neq 0$ and

$$\frac{d_v(f_u^* + d_v - g_v^*) - g_u^* f_v^*(1 + (g_v^* - d_v)\varepsilon)}{d_w g_u^* f_v^* + d_u d_v} \in \{\mu_k\}_{k=0}^{\infty}. \tag{2.23}$$

Letting $\sigma = \tau = \gamma = 0$ in (2.17). Then, from (2.20), we have

$$\left(d_w f_v^* + \frac{d_u d_v}{g_u^*}\right)\psi'' + \left(\frac{d_v(f_u^* + d_v - g_v^*)}{g_u^*} - f_v^*(1 + (g_v^* - d_v)\varepsilon)\right)\psi = 0. \tag{2.24}$$

If the condition (2.23) is satisfied, then $\varphi_k(x)$ solves (2.24). Then, $\mathcal{N}(\mathcal{L}_{2,\varepsilon} - (g_v^* - d_v)I) = span\{(-d_v\varphi_k/g_u^*, \varphi_k, (d_w\mu_k + 1 + (g_v^* - d_v)\varepsilon)\varphi_k\}$. This implies that $\lambda = g_v^* - d_v \in \sigma_p(\mathcal{L}_{2,\varepsilon})$. If $d_w g_u^* f_v^* + d_u d_v = 0$ and $d_v(f_u^* + d_v - g_v^*) - g_u^* f_v^*(1 + (g_v^* - d_v)\varepsilon) = 0$, then $\mathcal{N}(\mathcal{L}_{2,\varepsilon} - (g_v^* - d_v)I) \supset \{(-d_v\varphi/g_u^*, \varphi, (d_w\mu_k + 1 + (g_v^* - d_v)\varepsilon)\varphi : \varphi \in C_P^2([-l,l])\}$. This completes the proof. □

Set $\tilde{\Psi}_k(\varepsilon, \sigma) = \dfrac{\varepsilon}{d_w\mu_k + 1}\Psi_k(\varepsilon, \sigma)$. Then, the characteristic Eq. (2.11) of $\mathcal{L}_{2,\varepsilon}$ can be rewritten as the following equation:

$$\tilde{\Psi}_k(\varepsilon, \lambda) = b_0\varepsilon\lambda^3 + (1 + b_0\tilde{a}_0\varepsilon)\lambda^2 + (a_0 + b_0\tilde{a}_1\varepsilon)\lambda + a_1 = 0, \tag{2.25}$$

with a_0, a_1 defined in (2.6) and

$$b_0 = \frac{1}{d_w\mu_k + 1}, \quad \tilde{a}_0 = d_u\mu_k - f_u^* + d_v - g_v^*, \quad \tilde{a}_1 = (f_u^* - d_u\mu_k)(g_v^* - d_v) - f_v^* g_u^*. \tag{2.26}$$

The three roots of (2.25), which are the same as the roots of (2.11), are $\lambda_{j,k}(\varepsilon)$ ($j = 1, 2, 3$). When $\varepsilon \to 0$, uniformly for bounded λ, we have

$$\tilde{\Psi}_k(\varepsilon, \lambda) \to \lambda^2 + a_0\lambda + a_1, \tag{2.27}$$

which is (2.9). Then, for sufficiently small $\varepsilon > 0$, (2.25) can be considered as a perturbed equation of (2.9). So without loss of generality, we assume that there are two eigenvalues, saying $\lambda_{1,k}(\varepsilon)$ and $\lambda_{2,k}(\varepsilon)$, satisfying $\lim\limits_{\varepsilon\to 0^+} \lambda_{1,k}(\varepsilon) = \tilde{\lambda}_{+,k}$ and $\lim\limits_{\varepsilon\to 0^+} \lambda_{2,k}(\varepsilon) = \tilde{\lambda}_{-,k}$.

Differentiating (2.25) with respect to ε, we have

$$\partial_\varepsilon \tilde{\Psi}_k(\varepsilon, \lambda) = b_0(\lambda^3 + \tilde{a}_0\lambda^2 + \tilde{a}_1\lambda). \tag{2.28}$$

Assume

(H_1) $a_0^2 - 4a_1 = \left[d_u\mu_k - d_v - f_u^* + g_v^* + \dfrac{d_v}{d_w\mu_k + 1}\right]^2 + 4f_v^*g_u^* \neq 0;$

and

(H_2) $\tilde{\lambda}_{\pm,k} \neq 0$ and $\tilde{\lambda}_{\pm,k} \neq f_u^* - d_u\mu_k$.

With the assumption (H_1), we have $\tilde{\lambda}_{+,k} \neq \tilde{\lambda}_{-,k}$. From (2.28) and (H_2), we have

$$\begin{aligned} &\partial_\varepsilon \tilde{\Psi}_k(0, \tilde{\lambda}_{\pm,k}) = b_0\tilde{\lambda}_{\pm,k}(\tilde{\lambda}_{\pm,k}^2 + \tilde{a}_0\tilde{\lambda}_{\pm,k} + \tilde{a}_1) \\ =&b_0\tilde{\lambda}_{\pm,k}[(\tilde{a}_0 - a_0)\tilde{\lambda}_{\pm,k} + \tilde{a}_1 - a_1] = d_v\tilde{\lambda}_{\pm,k}(\tilde{\lambda}_{\pm,k} - f_u^* + d_u\mu_k) \neq 0. \end{aligned} \tag{2.29}$$

Then, the implicit function theorem can be applied to ensure the existence of $\lambda_{j,k}(\varepsilon)$ ($j = 1, 2$) for sufficiently small ε with $\lambda_{1,k}(0) = \tilde{\lambda}_{+,k} \neq 0$ and $\lambda_{2,k}(0) = \tilde{\lambda}_{-,k} \neq 0$. In particular, for sufficiently small ε, $Sign(\lambda_{1,k}(\varepsilon) = Sign(\tilde{\lambda}_{+,k})$ and $Sign(\lambda_{2,k}(\varepsilon) = Sign(\tilde{\lambda}_{-,k})$. Finally from (2.9) and (2.25), we have $a_1 = \tilde{\lambda}_{+,k}\tilde{\lambda}_{-,k}$ and $\dfrac{a_1}{b_0\varepsilon} = -\lambda_{1,k}(\varepsilon)\lambda_{2,k}(\varepsilon)\lambda_{3,k}(\varepsilon)$. Thus, we have $\lambda_{3,k}(\varepsilon) < 0$ and $\lambda_{3,k}(\varepsilon) \approx -\dfrac{1}{b_0\varepsilon}$.

According to the discussion above, we have the following result.

Proposition 2.3 *Assume* (u^*, v^*) *is the constant steady state of system (1.4),* (u^*, v^*, v^*) *is the constant steady state of system (2.2) and (2.3) and the assumptions* (H_1) *and* (H_2) *are satisfied. If* $g_v^* - d_v < 0$*, then for sufficiently small* $\varepsilon > 0$*, the constant steady state* (u^*, v^*) *of (1.4 has the same linear stability as the one for the constant steady state* (u^*, v^*, v^*) *of (2.2 and (2.3.*

From Proposition 2.3, to some extent, the study of non-local interaction-induced instability of (1.4) can be achieved through studying the diffusion-driven instability of (2.3). The system (2.3) is a reaction–diffusion system coupled with one ordinary differential equation, called as a RDO system for simplicity. This stability of constant steady state of this type of system has been studied in Li et al. (2017); Marciniak-Czochra et al. (2018, 2017). In Li et al. (2017); Marciniak-Czochra et al. (2017), some rigorous results on the nonlinear instability have been given for a two-dimensional

RDO system, which involves the analysis of a continuous spectrum of a linear operator. In the following, we will study the spectrum of the corresponding linearized system of the three-dimensional RDO system and the existence of eigenvalues with positive real parts. We will also study the bifurcation of the steady states and explore the pattern formation of the RDO system. The aim of our paper is to approximate the dynamics of the water-biomass model with non-local diffusion term by a reaction–diffusion system with a sufficiently small diffusion term.

3 Linear Stability and Bifurcation

In this section, we consider the linear stability of the constant steady state (u^*, v^*, v^*) of (2.3). To be more precise, we consider the conditions under which $\mathcal{L}_{2,\varepsilon}$ possesses eigenvalues with positive real parts. Recall that the constant steady state (u^*, v^*, v^*) of (2.3) is linearly stable if $g_v^* - d_v < 0$ and all eigenvalues of $\mathcal{L}_{2,\varepsilon}$ have negative real parts, and otherwise it is unstable. Note that the characteristic Eq. (2.11) can be rewritten as

$$\varepsilon\lambda^3 + d_1(d_u)\lambda^2 + d_2(d_u)\lambda + d_3(d_u) = 0, \tag{3.1}$$

where

$$\begin{aligned} d_1(d_u) =\ & \mu_k\varepsilon d_u + d_v\varepsilon - f_u^*\varepsilon - g_v^*\varepsilon + d_w\mu_k + 1, \\ d_2(d_u) =\ & [d_w\mu_k^2 + (d_v\varepsilon + 1 - g_v^*\varepsilon)\mu_k]d_u + d_w(d_v - f_u^* - g_v^*)\mu_k \\ & + \varepsilon(f_u^* g_v^* - g_u^* f_v^* - f_u^* d_v) - (f_u^* + g_v^*), \\ d_3(d_u) =\ & [d_w(d_v - g_v^*)\mu_k^2 - g_v^*\mu_k]d_u + d_w(f_u^* g_v^* - g_u^* f_v^* - f_u^* d_v)\mu_k \\ & + f_u^* g_v^* - g_u^* f_v^*. \end{aligned} \tag{3.2}$$

For fixed mode-k, from the well-known Routh–Hurwitz stability criterion, all roots of (3.1) have negative real parts if

$$d_1(d_u) > 0, \quad d_1(d_u)d_2(d_u) - \varepsilon d_3(d_u) > 0, \quad \text{and} \quad d_3(d_u) > 0. \tag{3.3}$$

Under the assumption (C_1), it is clear that for any $k \in \mathbb{N}_0$ and $\varepsilon > 0$, $d_1(d_u) > 0$ as $f_u^* + g_v^* < 0$. For $\varepsilon > 0$ sufficiently small, again assuming (C_1), we have

$$\begin{aligned} & d_1(d_u)d_2(d_u) - \varepsilon d_3(d_u) \\ \to & (d_w\mu_k + 1)[d_u(d_w\mu_k^2 + \mu_k) + d_w(d_v - f_u^* - g_v^*)\mu_k - (f_u^* + g_v^*)] > 0. \end{aligned}$$

Hence, we can choose $\varepsilon > 0$ sufficiently small so that $d_1(d_u)d_2(d_u) - \varepsilon d_3(d_u) > 0$.

For the sign of $d_3(d_u)$, we notice that $d_2(d_u)$ is a quadratic function of $\mu_k > 0$. Define

$$d_3(\mu) = d_w d_u(d_v - g_v^*)\mu^2 + [d_w(f_u^* g_v^* - g_u^* f_v^* - f_u^* d_v) - g_v^* d_u]\mu$$

$$+f_u^* g_v^* - g_u^* f_v^*, \tag{3.4}$$

and

$$\Delta_1 = [d_w(f_u^* g_v^* - g_u^* f_v^* - f_u^* d_v) - g_v^* d_u]^2 - 4d_w d_u (d_v - g_v^*)(f_u^* g_v^* - g_u^* f_v^*). \tag{3.5}$$

When $\Delta_1 < 0$, $d_3(\mu) > 0$ for all $\mu > 0$. We observe that there exists a critical value $d_u^*(d_v)$ such that $\Delta_1 < 0$ when $d_u < d_u^*(d_v)$; $\Delta_1 = 0$ when $d_u = d_u^*(d_v)$; and $\Delta_1 > 0$ when $d_u > d_u^*(d_v)$, where

$$d_u^*(d_v) = \frac{2d_w g_v^*(f_u^* g_v^* - g_u^* f_v^* - f_u^* d_v) + 4d_w(d_v - g_v^*)(f_u^* g_v^* - g_u^* g_v^*) + \sqrt{\Delta_2}}{2g_v^{*2}}, \tag{3.6}$$

with

$$\begin{aligned}\Delta_2 = &\ [2d_w g_v^*(f_u^* g_v^* - g_u^* f_v^* - f_u^* d_v) + 4d_w(d_v - g_v^*)(f_u^* g_v^* - g_u^* g_v^*)]^2 \\ &- 4d_w^2 g_v^{*2}(f_u^* g_v^* - g_u^* f_v^* - f_u^* d_v)^2.\end{aligned}$$

In particular, when $d_u < d_u^*(d_v)$, we always have $d_3(\mu) > 0$ for all $\mu > 0$ so in that case, (3.3) is satisfied and (u^*, v^*, v^*) is stable with respect to (2.3).

When $d_u > d_u^*(d_v)$, it is possible that $d_3(d_u) < 0$. For $k = 0$, we also have $d_3(d_u) = f_u^* g_v^* - g_u^* f_v^* > 0$ from (C_1). For all $k \in \mathbb{N}$, $d_3(0) = d_w(f_u^* g_v^* - g_u^* f_v^* - f_u^* d_v)\mu_k + f_u^* g_v^* - g_u^* f_v^* > 0$ from (C_1). Define $I = \{k \in \mathbb{N} : d_w(d_v - g_v^*)\mu_k - g_v^* < 0\}$. For $k \in I$, there exists a unique $d_u = d_u^k > 0$ defined by

$$d_u^k = \frac{d_w(f_u^* g_v^* - g_u^* f_v^* - f_u^* d_v)\mu_k + f_u^* g_v^* - g_u^* f_v^*}{d_w(g_v^* - d_v)\mu_k^2 + g_v^* \mu_k}, \tag{3.7}$$

such that $d_3(d_u^k) = 0$, $d_3(d_u) > 0$ for $0 < d_u < d_u^k$, and $d_3(d_u) < 0$ for $d_u > d_u^k$. When $d_3(d_u) < 0$ for $k \in I$, (3.1) has at least one eigenvalue with positive real part corresponding to an eigenfunction with eigenmode $c_{1k}\cos(k\pi x/l) + c_{2k}\sin(k\pi x/l)$.

When $d_v - g_v^* < 0$, and $g_v^* > 0$ from (C_2), $I = \mathbb{N}$ so d_u^k exists for any $k \in \mathbb{N}$. Moreover $d_u^k \to 0$ when $k \to \infty$. Hence, when $d_v - g_v^* < 0$ and $d_u > 0$, there exist infinitely many $k \in \mathbb{N}$ such that $d_3(d_u) < 0$. When $d_v - g_v^* > 0$, and since $g_v^* > 0$ from (C_2), I is a finite set (could be even empty). In that case we set $d_u^M = \min\{d_u^k : k \in I\} > 0$. Summarizing the above discussion, we have

Theorem 3.1 *Assume that the parameters d_u, d_v, d_w are all positive, and $\varepsilon > 0$ is sufficiently small. Let (u^*, v^*, v^*) be a positive constant steady state of system (2.3), and (C_1)-(C_2) be satisfied. Define d_u^k as in (3.7).*

1. *For any $d_u > 0$, if $0 < d_v < g_v^*$, $\sigma_p(\mathcal{L}_{2,\varepsilon}) \cap \mathbb{C}^+$ has infinitely many elements and (u^*, v^*, v^*) is unstable.*

2. *For any* $d_v > g_v^*$, *if* $d_u > d_u^M$, *then* $\sigma_p(\mathcal{L}_{2,\varepsilon}) \cap \mathbb{C}^+ \neq \emptyset$ *and* $\sigma_p(\mathcal{L}_{2,\varepsilon}) \cap \mathbb{C}^+$ *has finitely many elements, and* (u^*, v^*, v^*) *is unstable; and if* $d_u < d_u^M$, *then* $\sigma_p(\mathcal{L}_{2,\varepsilon}) \cap \mathbb{C}^+ = \emptyset$ *and* (u^*, v^*, v^*) *is linearly stable. In particular, if* $d_u < d_u^*(d_v)$ *(defined as in (3.6)*, (u^*, v^*, v^*) *is linearly stable.*

Next, we consider the bifurcation of non-constant steady states of (2.3). The corresponding stationary problem for system (2.3) is equivalent to the following problem:

$$\begin{cases} d_u u_{xx} + f(u, v) = 0, & x \in (-l, l), \\ d_w w_{xx} - w + v = 0, & x \in (-l, l), \\ d_v(w - v) + g(u, v) = 0, & x \in (-l, l), \\ u(-l) = u(l), u_x(-l) = u_x(l), \\ w(-l) = w(l), w_x(-l) = w_x(l). \end{cases} \tag{3.8}$$

We restrict the solutions of (3.8) to be the even functions. Define $X_3 = \{(u, w, v) \in X_2 : z(-x) = z(x), x \in (-l, l), z = (u, w, v)\}$, $Y_3 = \{(u, w, v) \in Y_2 : z(-x) = z(x), x \in (-l, l), z = (u, w, v)\}$, and a mapping $G_3 : X_3 \times \mathbb{R}^+ \to Y_3$ by

$$G_3((u, w, v), d_u) = \begin{pmatrix} d_u u_{xx} + f(u, v) \\ d_w w_{xx} - w + v \\ d_v(w - v) + g(u, v) \end{pmatrix}. \tag{3.9}$$

Then, $G_3 : X_3 \times \mathbb{R}^+ \to Y_3$ is Fréchet differentiable, and at a constant steady state (u^*, v^*, v^*),

$$\mathcal{L}_3 \begin{pmatrix} \phi \\ \psi \\ \vartheta \end{pmatrix} \equiv \partial_{(u,w,v)} G_3(u^*, v^*, v^*) \begin{pmatrix} \phi \\ \psi \\ \vartheta \end{pmatrix} = \begin{pmatrix} d_u \phi'' + f_u^* \phi + f_v^* \vartheta \\ d_w \psi'' - \psi + \vartheta \\ g_u^* \phi + d_v \psi + (g_v^* - d_v)\vartheta \end{pmatrix}.$$

We prove the existence of non-constant solutions of (3.8) by using the classical Crandall–Rabinowitz bifurcation theorem (Crandall and Rabinowitz 1971).

Lemma 3.2 *Let* X *and* Y *be real Banach spaces and* W *be an open set in* $\mathbb{R} \times X$*; suppose* $(\lambda_0, 0) \in W$*, and* $\mathcal{F}$ *is a continuously differentiable mapping from* W *into* Y*. Assume that*

1. $\mathcal{F}(\lambda, 0) = 0$ *for all* $(\lambda, 0) \in W$*;*
2. *The partial derivative* $D_{\lambda y}\mathcal{F}(\lambda, 0)$ *exists and is continuous in* λ *near* λ_0*;*
3. $R(D_y\mathcal{F}(\lambda_0, 0))$ *is closed,* $\dim \mathcal{N}(D_y\mathcal{F}(\lambda_0, 0)) = 1$*, and* $\operatorname{codim} R(D_y\mathcal{F}(\lambda_0, 0)) = 1$*;*
4. $D_{\lambda y}\mathcal{F}(\lambda_0, 0)y_0 \notin R(D_y\mathcal{F}(\lambda_0, 0))$*, where* y_0 *spans* $\mathcal{N}(D_y\mathcal{F}(\lambda_0, 0))$*. Let* $Z \subset Y$ *be any closed complement of the one-dimensional space spanned by* y_0*. Then, there exist an open interval* I_0 *containing* 0 *and continuously differentiable function* $\lambda : I_0 \to \mathbb{R}$ *and* $\psi : I_0 \to Z$ *with* $\lambda(0) = \lambda_0$, $\psi(0) = 0$*, such that*

$$\mathcal{F}(\lambda(s), sy_0 + s\psi(s)) = 0 \quad for \quad s \in I_0.$$

In addition the entire solution set for $\mathcal{F}(\lambda, y) = 0$ *in any sufficiently small neighborhood of* $(\lambda, 0)$ *in* W *consists of the line* $\{(\lambda, 0)\}$ *and the curve* $\{(\lambda(s), sy_0 + s\psi(s)) : s \in I_0\}$.

We apply Lemma 3.2 to the map G_3 defined in (3.9). We consider the bifurcation from the constant steady state (u^*, v^*, v^*) when $d_u = d_u^k$, which is defined as in (3.7). The condition 1 and 2 are obviously satisfied. The linearized operator $\mathcal{L}_3$ has an eigenvalue $\lambda_{j,k} = 0$ when $d_u = d_u^k$. Without loss of generality, we assume $\lambda_{1,k} = 0$. The following problem has a nontrivial solution:

$$\begin{cases} d_u^k \phi'' + f_u^* \phi + f_v^* \vartheta = 0, & x \in (-l, l), \\ d_w \psi'' - \psi + \vartheta = 0, & x \in (-l, l), \\ g_u^* \phi + d_v \psi + (g_v^* - d_v)\vartheta = 0, & x \in (-l, l), \\ \phi(-l) = \phi(l), \phi'(-l) = \phi'(l), \\ \psi(-l) = \psi(l), \psi'(-l) = \psi'(l). \end{cases} \tag{3.10}$$

Note that $\varphi_k(x) = \cos(k\pi x/l)$ satisfying $\varphi_k(-x) = \varphi_k(x)$ is the eigenfunction of $-d/dx^2$ corresponding the eigenvalue $\mu_k = (k\pi/l)^2$ with periodic boundary condition in $[-l, l]$. Then, direct calculation shows that

$$y_0 := (\phi_0, \psi_0, \vartheta_0) = \Big(-\frac{1}{(d_w \mu_k + 1) f_u^*}, \frac{1}{d_w \mu_k + 1}, 1 \Big) \cos\Big(\frac{k\pi}{l} x\Big) \tag{3.11}$$

is the corresponding eigenvector which belongs to $\lambda_{1,k} = 0$. Note that $\phi_0 < 0$ and $\vartheta_0 > 0$ which is consistent with u being the inhibitor and v being the activator. That means $\dim \mathcal{N}(\mathcal{L}_3) = 1$ when $d_u = d_u^k$.

With $\lambda_{1,k} = 0$, we consider the following non-homogeneous problem:

$$\begin{cases} d_u^k \phi'' + f_u^* \phi + f_v^* \vartheta = \sigma, & (3.12a) \\ d_w \psi'' - \psi + \vartheta = \tau, & (3.12b) \\ g_u^* \phi + d_v \psi + (g_v^* - d_v)\vartheta = \gamma. & (3.12c) \end{cases}$$

From (3.12c), if $d_v \neq g_v^*$ we have

$$\vartheta = \frac{\gamma - g_u^* \phi - d_v \psi}{g_v^* - d_v}. \tag{3.13}$$

Then, problem (3.12) reduces to

$$\begin{cases} (g_v^* - d_v) d_u^k \phi'' + (f_u^* g_v^* - f_v^* g_u^* - f_u^* d_v)\phi - f_v^* d_v \psi = (g_v^* - d_v)\sigma - f_v^* \gamma, \\ (g_v^* - d_v) d_w \psi'' - g_v^* \psi - g_u^* \phi = (g_v^* - d_v)\tau - \gamma. \end{cases} \tag{3.14}$$

Note that $d_w\mu_k(g_v^* - d_v) + g_v^* \neq 0$. Then,

$$\begin{cases}(g_v^* - d_v)d_u^k\phi'' + (f_u^* g_v^* - f_v^* g_u^* - f_u^* d_v)\phi - g_u^*\psi = 0,\\ (g_v^* - d_v)d_w\psi'' - g_v^*\psi - f_v^* d_v\phi = 0,\end{cases} \tag{3.15}$$

has a nontrivial solution $\Phi^* := (\phi^*, \psi^*) = (-d_w\mu_k(g_v^* - d_v) - g_v^*, f_v^* d_v)\cos(k\pi x/l)$. Define $F^* := ((g_v^* - d_v)\sigma - f_v^*\gamma, (g_v^* - d_v)\tau - \gamma)$. Then, according to the Fredholm alternative, problem (3.14) has a solution (ϕ, ψ) if and only if

$$\langle \Phi^*, F^* \rangle = 0. \tag{3.16}$$

Here, $\langle \cdot, \cdot \rangle$ is the complex-valued L^2 inner product on Hilbert space, which is defined as

$$\langle \Phi_1, \Phi_2 \rangle = \int_{-l}^{l} (\bar{\phi_1}\phi_2 + \bar{\psi_1}\psi_2)dx,$$

with $\Phi_j = (\phi_j, \psi_j) \in X_{\mathbb{C}}$ $(j = 1, 2)$. If (3.14) has a solution (ϕ^*, ψ^*), then we can solve ϑ^* uniquely by using (3.13). Then, (3.12) has a solution $(\phi^*, \psi^*, \vartheta^*)$ when $\lambda_{1,k} = 0$. Thus, $(\sigma, \tau, \gamma) \in R(\mathcal{L}_3)$ if and only if (3.16) is satisfied.

On the other hand, from (3.16) we have

$$\begin{aligned}&(g_v^* - d_v)[d_w\mu_k(g_v^* - d_v) + g_v^*]\int_{-l}^{l}\cos\big(\frac{k\pi}{l}x\big)\sigma dx - f_v^* d_v(g_v^* - d_v)\\ &\times\int_{-l}^{l}\cos\big(\frac{k\pi}{l}x\big)\tau dx - f_v^*(d_w\mu_k + 1)(g_v^* - d_v)\int_{-l}^{l}\cos\big(\frac{k\pi}{l}x\big)\gamma dx = 0.\end{aligned} \tag{3.17}$$

Then, if $d_v \neq g_v^*$, we have

$$\begin{aligned}&[d_w\mu_k(g_v^* - d_v) + g_v^*]\int_{-l}^{l}\cos\big(\frac{k\pi}{l}x\big)\sigma dx - f_v^* d_v\int_{-l}^{l}\cos\big(\frac{k\pi}{l}x\big)\tau dx\\ &- f_v^*(d_w\mu_k + 1)\int_{-l}^{l}\cos\big(\frac{k\pi}{l}x\big)\gamma dx = 0.\end{aligned} \tag{3.18}$$

Thus,

$$\begin{aligned}R(\mathcal{L}_3) = &\Big\{(\sigma, \tau, \gamma) \in Y_3 : [d_w\mu_k(g_v^* - d_v) + g_v^*]\int_{-l}^{l}\cos\big(\frac{k\pi}{l}x\big)\sigma dx\\ &- f_v^* d_v\int_{-l}^{l}\cos\big(\frac{k\pi}{l}x\big)\tau dx - f_v^*\mu_k(d_w\mu_k + 1)\int_{-l}^{l}\cos\big(\frac{k\pi}{l}x\big)\gamma dx = 0\Big\}.\end{aligned}$$

Therefore, $\operatorname{codim} R(\mathcal{L}_3) = 1$ if $d_v \neq g_v^*$. Then, the condition 3 in Lemma 3.2 is satisfied.

Calculating $\partial_{d_u}\partial_{(u,w,v)}G_3((u^*, v^*, v^*), d_u^k)$, we have

$$\partial_{d_u}\partial_{(u,w,v)}G_3((u^*, v^*, v^*), d_u^k) = \begin{pmatrix} \frac{d^2}{dx^2} & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$

Then, $\partial_{d_u}\partial_{(u,w,v)}G_3((u^*, v^*, v^*), d_u^k)y_0 = (\phi_0'', 0, 0)$, where ϕ_0 is defined as in (3.11). Choose $F^* = ((g_v^* - d_v)\phi_0'', 0)$. Note that

$$\phi_0'' = \frac{\mu_k}{(d_w\mu_k + 1)g_u^*}\cos\left(\frac{k\pi}{l}x\right),$$

and $d_w\mu_k(g_v^* - d_v) + g_v^* \neq 0$. Then, if $d_v \neq g_v^*$, we obtain

$$\langle\Phi^*, F^*\rangle = -\frac{\mu_k(g_v^* - d_v)[d_w\mu_k(g_v^* - d_v) + g_v^*]}{(d_w\mu_k + 1)g_u^*}\int_{-l}^{l}\cos^2\left(\frac{k\pi}{l}x\right)dx \neq 0. \quad (3.19)$$

Thus, the condition 4 in Lemma 3.2 is satisfied. Then, we can apply Lemma 3.2 to have the following result about the existence of a one-parameter family of non-constant solutions bifurcating from $((u^*, v^*, v^*), d_u^k)$.

Theorem 3.3 *Assume that the parameters d_u, d_v, d_w are all positive and conditions (C_1) and (C_2) are satisfied. Let d_u^k be defined as (3.7). If $d_v \neq g_v^*$ and $d_u^k \neq d_u^m$ for any $m \in I$ and $m \neq k$, then there is a smooth curve Γ of the steady-state solutions of (3.8) bifurcating from $((u^*, v^*, v^*), d_u^k)$. In a neighborhood of the bifurcation point, the bifurcating branch Γ can be parameterized as $\Gamma = \{((u^*(s), w^*(s), v^*(s)), d_u^k + d_u(s)) : s \in (-\epsilon, \epsilon)\}$, where*

$$u^*(s) = u^* - \frac{s}{(d_w\mu_k + 1)f_u^*}\cos\left(\frac{k\pi}{l}x\right) + s\phi(s),$$
$$w^*(s) = v^* + \frac{s}{d_w\mu_k + 1}\cos\left(\frac{k\pi}{l}x\right) + s\psi(s),$$
$$v^*(s) = v^* + s\cos\left(\frac{k\pi}{l}x\right) + s\vartheta(s),$$

and $d_u(s) : (-\epsilon, \epsilon) \to \mathbb{R}$, $\phi(s), \psi(s), \vartheta(s) : (-\epsilon, \epsilon) \to Z$ are C^1 functions, such that $d_u(0) = 0, \phi(0) = \psi(0) = \vartheta(0) = 0$. Here, Z is any closed complement of one-dimensional space spanned by $\left(-\frac{1}{(d_w\mu_k + 1)f_u^*}, \frac{1}{d_w\mu_k + 1}, 1\right)\cos\left(\frac{k\pi}{l}x\right)$.

4 Non-local Klausmeier–Gray–Scott Model

In this section, we apply the theoretical results in Sects. 2 and 3 to an example: the Klausmeier–Gray–Scott model of water–plant interaction with non-local plant dispersal.

To explain how nonlinear mechanisms is important in determining the regular stripes on hillsides and irregular mosaics on flat ground, Klausmeier proposed a simple nondimensionalized model of plant and water dynamics which reads as the following reaction–advection–diffusion form Klausmeier (1999):

$$\begin{cases} u_t = \nu u_x + A - u - v^2 u, \\ v_t = v_{xx} + v^2 u - Bv, \end{cases} \tag{4.1}$$

where ν is the slope gradient, which controls the rate at which water flows downhill. If horizontal water flow is considered, the dynamics between water and plant is governed by the following diffusive model, which is also proposed as a model of chemical reaction (Gray and Scott 1985; Pearson 1993):

$$\begin{cases} u_t = d_u u_{xx} + A - u - v^2 u, & x \in (-l, l),\ t > 0, \\ v_t = d_v v_{xx} + v^2 u - Bv, & x \in (-l, l),\ t > 0, \\ u(-l, t) = u(l, t), u_x(-l, t) = u_x(l, t), & t > 0, \\ v(-l, t) = v(l, t), v_x(-l, t) = v_x(l, t), & t > 0. \end{cases} \tag{4.2}$$

In this section, as an example of our theoretical study, we will consider the interaction of water and biomass with non-local spatial dispersal on flat ground and in a bounded domain. The model is presented by the following modified Klausmeier–Gray–Scott model with periodic boundary condition in $[-l, l]$:

$$\begin{cases} u_t = d_u u_{xx} + A - u - v^2 u, & x \in (-l, l),\ t > 0, \\ v_t = d_v (J * v - v) + v^2 u - Bv, & x \in (-l, l),\ t > 0, \\ u(-l, t) = u(l, t), u_x(-l, t) = u_x(l, t), & t > 0. \end{cases} \tag{4.3}$$

Here, $(J * v)(x) = \int_{-l}^{l} J(x - y)v(y)dy$, where $J(x)$ is given in (1.2). The corresponding RDO model is

$$\begin{cases} u_t = d_u u_{xx} + A - u - v^2 u, & x \in (-l, l),\ t > 0, \\ \varepsilon w_t = d_w w_{xx} - w + v, & x \in (-l, l),\ t > 0, \\ v_t = d_v (w - v) + v^2 u - Bv, & x \in (-l, l),\ t > 0, \\ u(-l, t) = u(l, t), u_x(-l, t) = u_x(l, t), & t > 0, \\ w(-l, t) = w(l, t), w_x(-l, t) = w_x(l, t). & t > 0. \end{cases} \tag{4.4}$$

The corresponding kinetic system of (4.4) is

$$\begin{cases} u_t = A - u - v^2 u, \\ w_t = -w + v, \\ v_t = d_v (w - v) + v^2 u - Bv, \end{cases} \tag{4.5}$$

which always has a trivial equilibrium $(u, w, v) = (A, 0, 0)$ for all parameters which means a bare-soil state. If $A > 2B$, the corresponding kinetic system (4.5) admits two positive constant steady states (u_1, v_1, v_1) and (u_2, v_2, v_2), where

$$u_1 = \frac{A + \sqrt{A^2 - 4B^2}}{2}, \quad v_1 = \frac{A - \sqrt{A^2 - 4B^2}}{2B}, \tag{4.6}$$

and

$$u_2 = \frac{A - \sqrt{A^2 - 4B^2}}{2}, \quad v_2 = \frac{A + \sqrt{A^2 - 4B^2}}{2B}. \tag{4.7}$$

The bare-soil state $(u, w, v) = (A, 0, 0)$ is always stable for all parameters. At a positive equilibrium (u_*, v_*, v_*),

$$f_u^* = -1 - v_*^2 < 0, \quad f_v^* = -2B < 0, \quad g_u^* = v_*^2 > 0, \quad g_v^* = B > 0.$$

Then, Jacobi matrix J at a positive equilibrium (u_*, v_*, v_*) of the kinetic system is given by

$$J = \begin{pmatrix} -1 - v_*^2 & 0 & -2B \\ 0 & -1 & 1 \\ v_*^2 & d_v & B - d_v \end{pmatrix},$$

and the corresponding characteristic equation is

$$\lambda^3 - \mathrm{Tr}J\lambda^2 + \lambda((B + d_v + 1)v_*^2 + d_v + 1 - 2B) - \mathrm{Det}J = 0,$$

where

$$\mathrm{Tr}J = -2 - d_v - v_*^2 + B, \quad \mathrm{Det}J = g_u^* f_v^* - f_u^* g_v^* = B(1 - v_*^2). \tag{4.8}$$

Note that $A \geq 2B$. Then, $v_1 < 1$ and $v_2 > 1$, which means that $\mathrm{Det}J_1 = \mathrm{Det}J(u_1, v_1, v_1) > 0$ and $\mathrm{Det}J_2 = \mathrm{Det}J(u_2, v_2, v_2) < 0$. Then, the positive equilibrium (u_1, v_1, v_1) is always unstable whenever it exists and the stability of (u_2, v_2, v_2) is determined by the sign of $\mathrm{Tr}J_2 = \mathrm{Tr}J(u_2, v_2, v_2)$ and $\Delta_0 = ((B + d_v + 1)v_2^2 + d_v + 1)\mathrm{Tr}J_2 - \mathrm{Det}J_2$. By the Hurwitz–Hurwitz criterion, we can easily obtain the stability of (u_2, v_2, v_2). Then, we have the following results about the stability of the constant steady states.

Proposition 4.1 *Assume that the parameters A, B, d_u, d_v, d_w are all positive. Then, the system has a constant trivial equilibrium $(u, w, v) = (A, 0, 0)$, which is always stable for all parameters. If $A \geq 2B$, then the system (4.4) admits two positive constant steady states (u_1, v_1, v_1) and (u_2, v_2, v_2), defined as in (4.6) and (4.7), respectively. Furthermore, for the corresponding kinetic system, (u_1, v_1, v_1) is unstable whenever it exists and (u_2, v_2, v_2) is stable if $\mathrm{Tr}J_2 < 0$ and $\Delta_0 < 0$ are both satisfied.*

As pointed out in Eigentler and Sherratt (2018), estimates of the parameters suggest that $B \leq 2$, which implies that the positive equilibrium (u_2, v_2, v_2) is stable. Then, in the following analysis, we always assume $B \leq 2$.

Now we apply Theorems 3.1 and 3.3 to obtain the following results regarding the stability of the positive equilibrium (u_2, v_2, v_2) with respect to (4.4) and associated bifurcations.

Theorem 4.2 *Assume that the parameters d_u, d_v, d_w are all positive, $\varepsilon > 0$ is sufficiently small, and $A > 0$, $0 < B \leq 2$. Let (u_2, v_2, v_2) be the positive constant steady state of system (4.4) defined as in (4.7).*

1. *If $0 < d_v < B$, for any $d_u > 0$, (u_2, v_2, v_2) is unstable with respect to (4.4) with infinitely many eigenvalues of positive real parts;*
2. *If $d_v > B$, define $I = \left\{ p \in \mathbb{N} : p < \left[\frac{Bl^2}{d_w(d_v - B)\pi^2} \right] \right\}$,*

$$d_u^k = \frac{(d_w\mu_k + 1)B(v_2^2 - 1) + d_w d_v (v_2^2 + 1)\mu_k}{d_w(B - d_v)\mu_k^2 + B\mu_k}, \quad k \in I, \tag{4.9}$$

and $d_u^M = \min_{k \in I} d_u^k$ ($d_u^M = \infty$ if $I = \emptyset$). Then, when $0 < d_u < d_u^M$, (u_2, v_2, v_2) is stable with respect to (4.4), and when $d_u > d_u^M$, (u_2, v_2, v_2) is unstable with respect to (4.4) with finitely many eigenvalues of positive real parts;
3. *If $d_v > B$, and for $k \in I$, $d_u^k \neq d_u^m$ for any $m \in I$ and $m \neq k$, then $d_u = d_u^k$ is a bifurcation point for (4.4); there is a smooth curve Γ of the steady-state solutions of (4.4) bifurcating from $((u_2, v_2, v_2), d_u^k)$, and Γ can be parameterized as $\Gamma = \{((u^*(s), w^*(s), v^*(s)), d_u^k + d_u(s)) : s \in (-\epsilon, \epsilon)\}$, where*

$$\begin{aligned}
u^*(s) &= u_2 + \frac{s}{(d_w\mu_k + 1)(1 + v_2^2)} \cos\left(\frac{k\pi}{l}x\right) + s\phi(s), \\
w^*(s) &= v_2 + \frac{s}{d_w\mu_k + 1} \cos\left(\frac{k\pi}{l}x\right) + s\psi(s), \\
v^*(s) &= v_2 + s\cos\left(\frac{k\pi}{l}x\right) + s\vartheta(s),
\end{aligned}$$

and $d_u(s) : (-\epsilon, \epsilon) \to \mathbb{R}$, $\phi(s), \psi(s), \vartheta(s) : (-\epsilon, \epsilon) \to Z$ are C^1 functions, such that $d_u(0) = 0$, $\phi(0) = \psi(0) = \vartheta(0) = 0$. Here, Z is any closed complement of one-dimensional space spanned by $\left(\frac{1}{(d_w\mu_k + 1)(1 + v_2^2)}, \frac{1}{d_w\mu_k + 1}, 1\right)$ $\cos\left(\frac{k\pi}{l}x\right)$.

We use some numerical simulations to verify and extend our theoretical results above. We choose $A = 1$, $B = 0.45$, $d_w = 1$, $l = 20$, and $d_v = 0.5$ which satisfies $d_v > g_v^* = B = 0.45$. Numerical calculation shows that $(u_2, v_2, v_2) = (0.282, 1.595, 1.595)$, $I = \{p \in \mathbb{N} : 1 \leq p \leq 19\}$, and $d_u^1 \approx 68.135 > d_u^2 \approx 21.395 > d_u^3 \approx 12.766 > d_u^4 \approx 9.834 > d_u^5 \approx 8.581 > d_u^6 \approx 8.018 > d_u^7 \approx 7.812$,

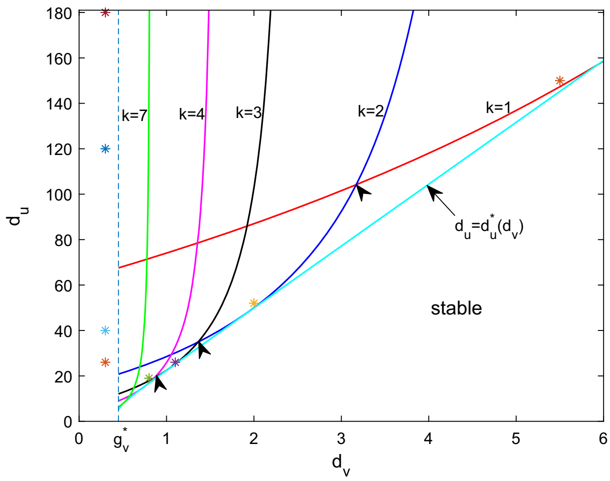


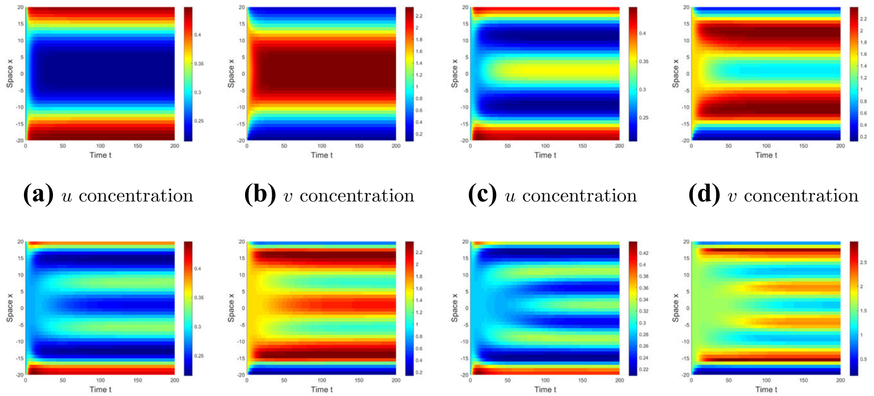
Fig. 2 The mode-j crossing curves on the $d_v - d_u$ plane. The dotted vertical line is $d_v = g_v^*$ and the cyan curve is $d_u = d_u^*(d_v)$. Parameters: $A = 1$, $B = 0.45$, $d_w = 1$, and $l = 20$ for $k = 1, 2, 3, 4$ and $k = 7$ (Color figure online)

and $d_u^7 \approx 7.812 < d_u^8 \approx 7.839 < d_u^9 \approx 8.043 < \cdots < d_u^{19} \approx 50.411$. So here $d_u^M = d_u^7$.

The mode-k ($k = 1, 2, 3, 4, 7$) bifurcation curves in $d_v - d_u$ plane are shown in Fig. 2. In this figure, the dotted vertical line is $d_v = g_v^*$; the cyan curve denotes the function $d_u = d_u^*(d_v)$. The mode-k curve intersects with the vertical line $d_v = g_v^*$ at $d_u = d_u^k$. Some points in Fig. 2 are marked and we will use these parameter points in the latter simulations. From Theorem 3.1, all mode-k bifurcation curves are above the curve $d_u = d_u^*(d_v)$. This implies that the constant steady state (u_2, v_2, v_2) is locally asymptotically stable when (d_v, d_u) lies in the region $\{(d_v, d_u) : d_v > g_v^*, d_u < d_u^*(d_v)\}$. On the other hand, above the curve $d_u = d_u^*(d_v)$, the constant steady state (u_2, v_2, v_2) may lose its stability and a spatially non-homogeneous steady-state solution can be observed.

In Fig. 3, we show the dynamic solutions of (4.4) when the diffusion coefficients d_u and d_v are varied. We choose (d_v, d_u) (marked in Fig. 2) $(5.5, 150)$, $(2, 52)$, $(1.1, 26)$ and $(0.8, 19)$, which are all on the right-hand side of the line $d_v = g_v^*$. For $k = 1, 2, 3, 4$, a mode-k spatially patterned steady states emerge near the mode-k bifurcation curve. The steady-state densities of water u and plant v of system (4.4) in these cases are shown in Fig. 4 Simulations show that the water amount in the patch with denser biomass decreases, which means that the biomass and the water distributions are anti-phase. The density of plant may have one, two, three or four spaced bumps. The two bumps have same maximum height in Fig. 4b. While as d_v and d_u are varied, a new bump emerges with a much less maximum height in Fig. 4c. In Fig. 4d, there are two bumps, but two spikes with a much larger maximum height emerge.

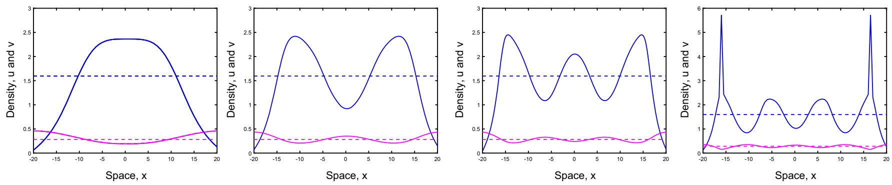
In Fig. 5, some solution profile of densities of water u and plant v for system (4.4) for (d_v, d_u) on the left-hand side of the line $d_v = g_v^*$ are shown, as marked in Fig. 2. Simulations show that water is almost exhausted and the plant density shows spiky



(a) u concentration **(b)** v concentration **(c)** u concentration **(d)** v concentration

(e) u concentration **(f)** v concentration **(g)** u concentration **(h)** v concentration

Fig. 3 Pattern formation of system (4.4) with $A = 1$, $B = 0.45$, $d_w = 1$, $l = 20$, $\varepsilon = 0.01$, and $(d_v, d_u) = (5.5, 150)$ in (**a, b**), $(d_v, d_u) = (2, 52)$ in (**c, d**), $(d_v, d_u) = (1.1, 26)$ in (**e, f**), $(d_v, d_u) = (0.8, 19)$ in (**g, h**) (Color figure online)

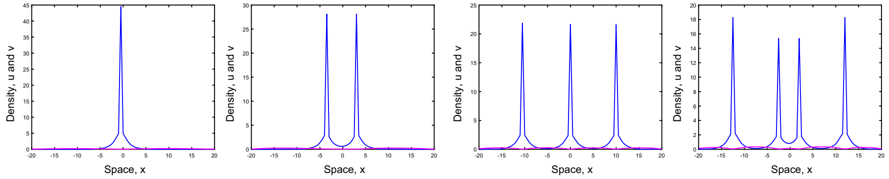


(a) $d_v = 5.5, d_u = 150.$ **(b)** $d_v = 2, d_u = 52.$ **(c)** $d_v = 1.1, d_u = 26.$ **(d)** $d_v = 0.8, d_u = 19.$

Fig. 4 Steady-state densities of water u and plant v of system (4.4) with $A = 1$, $B = 0.45$, $d_w = 1$, $l = 20$, $\varepsilon = 0.01$ and varied values of d_v, d_u. Here, the solid blue curve is the density of plant v, the solid purple curve denotes the density of water u, and the dotted blue (purple) line is the density of vegetated state v (u) (Color figure online)

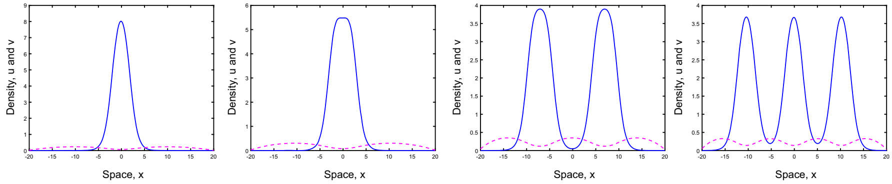
solutions which may have one, two, three or four spikes. Fixed d_v, as the decrease in d_u, more spikes emerge and the maximum height of all spiky solutions decreases from Fig. 5a–d. The two spikes or three spikes have same maximum height in Fig. 5b and c, respectively. While in Fig. 5d, there are two different maximum heights.

In order to compare the effect of the non-local dispersal term on the dynamics of the system to the diffusive effect, in Fig. 6, we show the densities of water u and plant v of the corresponding reaction–diffusion system (4.2) with the same parameter values and varied d_u as in Fig. 5. We find that the solutions for the reaction–diffusion system are smoothly bumped solutions instead of spiky solutions shown in Fig. 5. As the decrease in d_u, more bumps may emerge (see Fig. 6c–d) and the maximum height of all bumps decrease from Fig. 6a–d. Note that the solutions for the non-local dispersal system (4.4) are less smooth, as the solutions do not have high order of regularity as the ones of diffusive system.



(a) $d_v = 0.3, d_u = 180.$ **(b)** $d_v = 0.3, d_u = 120.$ **(c)** $d_v = 0.3, d_u = 40.$ **(d)** $d_v = 0.3, d_u = 26.$

Fig. 5 Interior spiky solutions of system (4.4) with $A = 1$, $B = 0.45$, $d_w = 1$, $l = 20$, $\varepsilon = 0.01$, $d_v = 0.3$ and varied values of d_u. Here, the solid blue curve is the density of plant v, the solid purple curve denotes the density of water u. **a** The one-spike solution; **b** the two-spike solution; **c** the three-spike solution; **d** the four-spike solution (Color figure online)



(a) $d_v = 0.3, d_u = 180.$ **(b)** $d_v = 0.3, d_u = 120.$ **(c)** $d_v = 0.3, d_u = 40.$ **(d)** $d_v = 0.3, d_u = 26.$

Fig. 6 Solutions of system (4.2) with $A = 1$, $B = 0.45$, $l = 20$, $d_v = 0.3$ and varied values of d_u. Here, the solid blue curve is the density of plant v, the solid purple curve denotes the density of water u (Color figure online)

5 Discussion

In this paper, we aim to study the stability of a constant steady state with respect to a general activator–inhibitor model with non-local dispersal term. By approximating the non-local spatial dispersal equation by an associated reaction–diffusion system, the non-local spatial dispersal model is transformed into a reaction–diffusion system coupled with one ordinary differential equation. For a very slow time scale, the dynamics of the non-local dispersal system can be approximated by the reaction–diffusion-ordinary differential system. To some extent, the non-local-induced instability of the non-local system can be regarded as diffusion-driven instability of the reaction–diffusion-ordinary differential system. The reaction–diffusion-ordinary differential system can be analyzed to gain insight to the dynamics of the non-local dispersal system. We show that Turing-type instability can occur for the reaction–diffusion-ordinary differential system, and non-constant steady states emerge as a result of symmetry-breaking bifurcations. This suggests that non-local dispersal can also play an active role in the generation of spatial patterns. Note that such analysis still depends on the choice of particular convolution kernel functions in the non-local dispersal. It is desirable to develop a more general theory of pattern formation for a more general kernel function.

As an example of our theoretical results, we study a modified Klausmeier–Gray–Scott model of water–plant with non-local diffusion term. By transforming it into a reaction–diffusion-ordinary differential system, we use theoretical approach and numerical simulations to show that the reaction–diffusion-ordinary differential system admits many different patterned steady-state solutions with different maximum height and width when the diffusion terms of water and plant are varied. Compared with the system in which local disperse strategy is considered, simulations show the existence of sharp spiky solutions instead of bump solutions found in the classical reaction–diffusion system through Turing bifurcation. There is much work to be done in these spiky solutions. Exploring these spiky solutions may be deferred to our future work. It would be of interest to study the stability of a constant steady state with respect to a general activator–inhibitor model with a general non-local dispersal term.

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