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Lotka-Volterra system of predator-prey type with time-dependent diffusive

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Abstract

The dynamics of a Lotka-Volterra system of predator-prey type with time-dependent diffusive is studied. First, the existence and uniquely of positively global solution, uniform boundedness, and extinction are investigated. The analytical investigation uses a C_0-quasi semi-group approach. The stabilities of the positively homogeneous steady states of the system are analyzed. Further, a simple analysis of Turing instability and Hopf bifurcation due to diffusion is also discussed that is confirmed by the bifurcation diagram.

Key words and phrases. Predator-prey; time-dependent diffusive; C_0-quasi semigroup; stability of steady state; Turing-Hopf bifurcation.

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1. Introduction

The diffusive Lotka-Volterra system is a type of reaction-diffusion system that is still being developed today. At the beginning of its modeling, the Lotka-Volterra system did not involve the diffusion process. Some applications of such systems in economics and banking system can be found in [1–4]. There have been many researches investigating the dynamics of the constant-coefficient diffusive Lotka-Volterra system from various view-points and applications. Most of the investigations are concerned with the stability of the homogeneous steady states and bifurcations and also their

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interpretation according to the applications, see [5–10]. The most of bifurcations discussed are Hopf bifurcation and Turing instability (the diffusion-driven bifurcation), see [11–17]. A slightly different analysis, Kirane [18] analyzes explicitly the dynamics of solutions of the diffusive Lotka-Volterra predator-prey system using a C_0-semigroup approach.

A question rises, how is the dynamics of the Lotka-Volterra predator-prey system if the diffusion is dependent on time? In facts, there are many problems in the real problems that can be described by the model. For an example, Hess [19] has specifically initiated in establishing the sufficient conditions for the existence of a positive periodic solution and a little discussion of the steady states of the system. There are still many aspects that can be investigated in further of the system, including the properties of solution and the stability-bifurcation of the steady states. The time-dependent diffusive Lotka-Volterra predator-prey system in one dimension is modeled as a system of partial differential equations:

$$\begin{aligned} u_t &= k_1(t)u_{xx} + u(a_1 - b_1u - c_1v), \qquad (x, t) \in \Omega \times (0, \infty), \\ v_t &= k_2(t)v_{xx} + v(-a_2 + b_2u - c_2v), \qquad (x, t) \in \Omega \times (0, \infty), \end{aligned} \tag{1}$$

subject to the initial conditions

$$u(x, 0) = u_0(x), \qquad v(x, 0) = v_0(x), \qquad x \in \Omega, \tag{2}$$

where Ω is a domain in $\mathbb{R}$, u, v are two populations occupying the domain Ω, ∂_{xx} is the diffusion (one-dimensional Laplace operator), a_i, b_i, c_i, $i = 1, 2$, are positive constants, and k_i, $i = 1, 2$, are positive functions. The diffusion terms control the random movements of the individuals within one dimensional habitat. The well-posedness (existence, uniqueness, continuous dependence of solution) and the stability of system (1)–(2) are important characteristics that require further investigation.

Problem (1)–(2) can be considered as a non-autonomous abstract Cauchy problem:

$$\begin{aligned} \dot{x}(t) &= A(t)x(t), \qquad t \geq 0, \\ x(0) &= x_0, \end{aligned}$$

where each $A(t)$ is a densely closed operator in a domain of a Banach space. In this case, a strongly continuous quasi semigroup (C_0-quasi semigroup) is the powerful tool to handle the non-autonomous abstract Cauchy problems. In this case, the family $A(t)$ is conditioned to be the infinitesimal generator of a C_0-quasi semigroup in a Banach space, see [20, 21]. Further, the C_0-quasi semigroup can also be used to analyze the controllability, observability, stability and optimal control of a non-autonomous linear control system, see [22–25]. These facts confirm that the C_0-quasi semigroup is an appropriate analytical tool to deal with problem (1)–(2).

This paper concerns on the global existence of solutions and the stability of steady states of system (1)–(2). The rest of this paper is organized as follows. Section 2 is devoted to the global existence, positive, uniform bundedness and extinction of solution using the C_0-quasi semigroup. The asymptotical stability of steady states and its relationship to the solution are analyzed in Section 3. In Section 4, the sufficiency for Turing instability, the critical condition of Hopf bifurcation, and the bifurcation diagram of the system under the certain parameters are investigated.

2. Positive solution, uniform boundedness and extiction

In what follows, let X be the space of boundedly uniformly continuous real functions on $\Omega \subset \mathbb{R}$ endowed by the supremum norm $\|f\| = \sup_{x\in\Omega} |f(x)|$. It is well-known that the linear operator $k_i(t)\dfrac{\partial^2}{\partial x^2}$ generates the quasi semigroup of contraction $R_i(t, s)$ on the Banach space X given by

$$R_i(t, s)w = T\,(g_i(t + s) - g_i(t))w, \qquad w \in X, \tag{3}$$

where

$$g_i(t) = \int_0^t k_i(\tau)d\tau, \quad [T(t)w](x) = \frac{1}{\sqrt{4\pi t}}\int_{-\infty}^{\infty} e^{-\frac{(x-\tau)^2}{4t}} w(\tau)d\tau, \qquad (4)$$
$$T(0) = I, \quad t > 0,$$

I is the identity operator on X and $i = 1, 2$. We see that $u(t) = R_1(0, t)u_0$ and $v(t) = R_2(0, t)v_0$ are the unique solutions of

$$u_t = k_1(t)u_{xx}, \qquad t \geq 0,$$
$$v_t = k_2(t)v_{xx}, \qquad t \geq 0, \qquad (5)$$

subject to the initial conditions (2), respectively (Corollary 4 of [22]).

We also assume that the initial conditions u_0 and v_0 in (2) are the non-negative elements of X. We use the quasi semigroup approach as a generalization of the approach used in [18] to analyze the coexisting solution (u, v) of problem (1)–(2).

Theorem 2.1. *Lotka-Volterra predator-prey system with time-dependent diffusive* (1)–(2) *has a uniquely nonnegatively globally classical solution.*

Proof. By the uniqueness coexisting solution (u, v) of Cauchy problems (5) and Definition 5 of [22], there exists a $\tau_0 > 0$ such that problem (1)–(2) has a unique coexisting local mild solution $(u, v) \in C([0, \tau_0], X) \times C([0, \tau_0], X)$, i.e.,

$$u(t) = R_1(0,t)u_0 + \int_0^t R_1(s, t-s)f(s)ds, \quad t \in [0, \tau_0]$$
$$v(t) = R_2(0,t)v_0 + \int_0^t R_2(s, t-s)g(s)ds, \quad t \in [0, \tau_0],$$

where $f(t) = u(t)[a_1\ b_1u(t)\ c_1v(t)]$ and $g(t) = v(t)[\ a_2 + b_2u(t)\ c_2v(t)]$ for all $t \in [0, \tau_0]$. We verify that $f, g \in C^1([0, \tau_0], X)$. Theorem 4 of [24] implies that the local mild solutions u, v are the classical solutions.

Next, we prove the nonnegativity of the solutions. Let $\mu_1 = \inf\{\|u(t)\|; 0 \leq t \leq \tau_0\}$, $\mu_2 = \inf\{\|v(t)\|; 0 \leq t \leq \tau_0\}$, $\mu_3 = \sup\{\|u(t)\|; 0 \leq t \leq \tau_0\}$, and $\mu_0 = \max\{a_1 + b_1\mu_1 + c_1\mu_2,\ a_2 + b_2\mu_3 + c_2\mu_2\}$. Substituting $v = e^{\mu_0 t}\varphi$ and $u = e^{\mu_0 t}\phi$ into system (1)–(2) yields

$$\phi_t - k_1(t)\phi_{xx} + (\mu_0 - a_1 + b_1u + c_1v)\ \phi \equiv 0, \qquad x \in \Omega, \qquad 0 < t \leq \tau_0,$$

$$\varphi_t - k_2(t)\varphi_{xx} + (\mu_0 + a_2 - b_2u + c_2v)\varphi \equiv 0, \qquad x \in \Omega, \qquad 0 < t \leq \tau_0$$

with

$$\phi(x, 0) = u_0(x) \geq 0 \qquad \text{and} \qquad \varphi(x, 0) = v_0(x) \geq 0, \qquad x \in \Omega.$$

Since $u, v \in C([0, \tau], X)$, $\mu_0\ a_1 + b_1u + c_1v \geq b_1\mu_1 + c_1\mu_2 \geq 0$ and $\mu_0 + a_2\ b_2u + c_2v \geq 2a_2 > 0$ for all $t \in [0, \tau_0]$, the maximum principle (Lemma 4.1, p. 19 of [26]) implies that ϕ and φ are nonnegative. This gives the nonnegativity of u and v.

The solutions of problem (1)-(2) can also be represented by

$$u(t) = e^{a_1 t}R_1(0,t)u_0 - \int_0^t e^{a_1(t-s)}R_1(s, t-s)[b_1u^2(s) + c_1u(s)v(s)]ds, \qquad (6)$$

$$v(t) = e^{-a_2 t}R_2(0,t)v_0 + \int_0^t e^{-a_2(t-s)}R_2(s, t-s)[b_2u(s)v(s) - c_2v^2(s)]ds. \qquad (7)$$

The contraction of $R_1(t, s)$, the nonnegativity of u, v, and (6) give

$$\|u(t)\| \leq e^{a_1 t}\|u_0\| \qquad \text{for all} \qquad t \geq 0, \qquad (8)$$

The results from (7) and (8) give

$$\|v(t)\| \le \|v_0\| + b_2\|u_0\|\int_0^t e^{a_1 s}\|v(s)\|ds \quad \text{for all} \quad t \ge 0.$$

Gronwall's inequality implies that

$$\|v(t)\| \le \|v_0\| e^{b_2\|u_0\|h(t)} \qquad \text{for all} \qquad t \ge 0, \tag{9}$$

where

$$h(t) = \begin{cases} \frac{1}{a_1}(e^{a_1 t} - 1), & a_1 > 0, \\ t, & a_1 = 0. \end{cases}$$

These show that the solutions u, v are global, i.e., ($\tau_0 = +\infty$). The solutions also show the continuous dependence on the initial data.

The solution of problem (1)-(2) established in Theorem 2.1 is not always bounded as shown in the following lemma.

Lemma 2.2. *If* u_0, $v_0 \neq 0$ *and* a_1, b_2 *are large enough, then the coexisting solution* (u, v) *of problem* (1)-(2) *grows exponentially as* $t \to \infty$.

Proof. If u_0, $v_0 \neq 0$ and a_1, b_2 are positive, the results in (8) and (9) describe that the solution (u, v) is exponential.

Lemma 2.2 also confirms that the coexisting solution (u, v) is unbounded. However, we can make constraints for the parameters such that the solutions are bounded.

Theorem 2.3. *If* u_0, $v_0 \in X$, *then*

$$\|u(t)\| \le \|u_0\| e^{a_1 t} \qquad \text{for all} \qquad t \ge 0, \tag{10}$$

$$\|v(t)\| \le e^{(b_2 e^{a_1 \tau}\|u_0\| - a_2)t}\|v_0\| \qquad \text{for all} \qquad t \in [0, \tau]. \tag{11}$$

Further, if $a_1 = 0$ *and* $a_2 > b_2\|u_0\|$, *then*

$$\lim_{t\to\infty}\|v(t)\| = 0.$$

Proof. Substituting $u = \phi e^{a_1 t}$ and $v = \varphi e^{-a_2 t}$ into (1) gives

$$\phi_t = k_1(t)\phi_{xx} - (b_1 e^{a_1 t}\phi^2 + c_1 e^{-a_2 t}\phi\varphi), \tag{12}$$

$$\varphi_t = k_2(t)\varphi_{xx} + b_2 e^{a_1 t}\phi\varphi - c_2 e^{-a_2 t}\varphi^2 \tag{13}$$

with the initial data

$$\phi_0(x) = u_0(x), \qquad \varphi_0(x) = v_0(x). \tag{14}$$

By nonnegativity of ϕ and φ, (12) together with (14) give

$$\begin{aligned} \phi(t) &= R_1(0,t)u_0 - \int_0^t R_1(s, t-s)[b_1 e^{a_1 s}\phi^2(s) + c_1 e^{-a_2 s}\phi(s)\varphi(s)]ds \\ &\le R_1(0,t)u_0 \end{aligned} \tag{15}$$

for all $(x, t) \in \mathbb{R} \times [0, \infty)$. This implies that

$$\|u(t)\| = e^{a_1 t}\|\phi(t)\| \le \|u_0\| e^{a_1 t} \quad \text{for all} \qquad t \ge 0.$$

Next, by (15) and (13), we obtain

$$\varphi_t - k_2(t)\varphi_{xx} \le b_2 e^{a_1 t}\|u_0\|\varphi.$$

Transforming $\varphi = e^{b_2 e^{a_1\tau}\|u_0\| t} z$ on $\Omega \times [0, \tau]$ gives

$$z_t - k_2(t) z_{xx} \le 0, \quad z(0) = \varphi(0) = v_0.$$

This implies that

$$z(t) = R_2(0, t)v_0, \qquad t \ge 0.$$

Therefore, $\|\varphi(t)\| \le e^{b_2 e a_1\tau\|u_0\| t}\|v_0\|$ and

$$\|v(t)\| = \|\varphi(t)\| e^{-a_2 t} \le e^{(b_2 e^{a_1\tau}\|u_0\| - a_2)t}\|v_0\| \quad \textit{for all} \quad t \in [0, \tau]. \tag{16}$$

Further, for $a_1 = 0$ and $a_2 > b_2\|u_0\|$, (16) implies that

$$\lim_{t\to\infty}\|v(t)\| = 0.$$

Theorem 2.4. *If $a_1 = 0$ and k_1, k_2 are positive functions such that $g_1, g_2 \in X$ and $\sup_{t\ge 0} g_1(t) \ge \sup_{t\ge 0} g_2(t)$, then the solution (u, v) of system* (1)–(2) *is globally bounded. Moreover,*

$$\|u(t)\| \le \|u_0\| \quad \textit{for all} \quad t \ge 0, \tag{17}$$

$$\|v(t)\| \le \|v_0\| + \frac{b_2}{c_1}\sqrt{\frac{M_1}{M_2}}\|u_0\| \quad \text{for all} \quad t \ge 0, \tag{18}$$

where $M_i := \sup_{t\ge 0} g_i(t)$, $i = 1, 2$.

Proof. If $a_1 = 0$, (10) gives (17). On the other hand, the equations in (6) and (7) can be written by

$$u(t) = R_1(0,t)u_0 - b_1\int_0^t R_1(s,t-s)u^2(s)ds - c_1 U(t), \tag{19}$$

$$v(t) = e^{-a_2 t}R_2(0, t)v_0 + b_2 V(t), \tag{20}$$

respectively, where

$$\begin{aligned} U(t) &= \int_0^t R_1(s,t-s)u(s)v(s)ds, \\ V(t) &= \int_0^t e^{-a_2(t-s)}R_2(s,t-s)\left[u(s)v(s) - \frac{c_2}{b_2}v^2(s)\right]ds \\ &\le \int_0^t R_2(s,t-s)u(s)v(s)ds. \end{aligned} \tag{21}$$

Conditions $M_1 \ge M_2$ and (48) provide

$$R_2(t,s)w \le \sqrt{\frac{M_1}{M_2}}R_1(t,s)w \quad \text{for all} \quad w \in X, \quad t,s \ge 0. \tag{22}$$

By the nonnegativity of u, (19) implies that

$$U(t) \le \frac{1}{c_1}R_1(0,t)u_0 \quad \text{for all} \quad t \ge 0. \tag{23}$$

Equations (21), (22) and (23) give

$$V(t) \le \sqrt{\frac{M_1}{M_2}} U(t) \le \frac{1}{c_1}\sqrt{\frac{M_1}{M_2}} R_1(0,t)u_0 \quad \text{for all} \quad t \ge 0. \tag{24}$$

Therefore, (20) together with (31) imply (18).

Theorem 2.5. *If system* (1)-(2) *satisfies the hypothesis in Theorem 2.4, then the solution* (u, v) *is globally bounded. Moreover,*

$$\|u(t)\| \le \|u_0\| \quad \textit{for all} \quad t \ge 0, \tag{25}$$

$$\|v(t)\| \le \|v_0\| + \frac{b_2^2}{4b_1c_2}\sqrt{\frac{M_1}{M_2}}\|u_0\| \quad \textit{for all} \quad t \ge 0. \tag{26}$$

Proof. The equations in (19) and (20) can also be represented as

$$u(t) = R_1(0,t)u_0 - b_1U(t) - c_1\int_0^t R_1(s,t-s)u(s)v(s)ds, \tag{27}$$

$$v(t) = e^{-a_2t}R_2(0,t)v_0 + b_2V(t), \tag{28}$$

respectively, where

$$U(t) = \int_0^t R_1(s,t-s)u^2(s)ds,$$
$$V(t) = \int_0^t e^{-a_2(t-s)}R_2(s,t-s)\left[u(s)v(s) - \frac{c_2}{b_2}v^2(s)\right]ds$$
$$\le \frac{b_2}{4c_2}\int_0^t R_2(s,t-s)u^2(s)ds, \tag{29}$$

since the quadratic $p(v) = uv - \frac{c_2}{b_2}v^2$ attains the maximum while $v = \frac{b_2u}{2c_2}$.

From (27), we have

$$U(t) \le \frac{1}{b_1}R_1(0,t)u_0 \quad \text{for all} \quad t \ge 0. \tag{30}$$

Results in (29) and (30) give

$$V(t) \le \sqrt{\frac{M_1}{M_2}} U(t) \le \frac{1}{b_1}\sqrt{\frac{M_1}{M_2}} R_1(0,t)u_0 \quad \text{for all} \quad t \ge 0. \tag{31}$$

We have proved the assertion.

Theorem 2.6. *Let* $a_2 = 0$, $M_1 \ge M_2$ *and* $0 \le a_1 \le H(t)$ *for all* $t \ge \tau$, *where* H *is a positively continuous function such that* $\lim_{t\to\infty} tH(t) = 0$ *for some* $\tau > 0$. *The solution* (u, v) *of* (1)–(2) *is globally bounded. Moreover,*

$$\|u(t)\| \le c\|u_0\| \quad \textit{for all} \quad t \ge 0, \quad \textit{for some} \quad c > 0, \tag{32}$$

$$\|v(t)\| \le \|v_0\| + \frac{b_2}{c_1}\sqrt{\frac{M_1}{M_2}}\|u_0\| \quad \textit{for all} \quad t \ge 0. \tag{33}$$

Proof. If there exists $\tau > 0$ such that $a_1 \le H(t)$ for all $t \ge \tau$, where H is a positively continuous function such that $\lim_{t\to\infty} tH(t) = 0$, then (10) gives (32) where $c = e^{\tau H(\tau)}$.

Next, if $a_2 = 0$, (6) and (7) give

$$u(t) = e^{a_1 t}\left[R_1(0,t)u_0 - \int_0^t e^{-a_1 s} R_1(s,t-s)[b_1 u^2(s) + c_1 u(s)v(s)]ds\right], \tag{34}$$

$$v(t) = R_2(0,t)v_0 + \int_0^t R_2(s,t-s)[b_2 u(s)v(s) - c_2 v^2(s)]ds, \tag{35}$$

respectively. Since u is nonnegative, (34) implies that

$$\int_0^t e^{-a_1 s} R_1(s,t-s)[b_1 u^2(s) + c_1 u(s)v(s)]ds \le R_1(0,t)u_0. \tag{36}$$

Further, since b_1, $c_1 > 0$ and the function $f(s) = e^{-a_1 s}$ is decreasing on $[0, t]$, (36) gives

$$\int_0^t R_1(s,t-s)u(s)v(s)ds \le \frac{R_1(0,t)u_0}{c_1}.$$

Therefore, inserting (22) into (35) we obtain

$$v(t) \le R_2(0,t)v_0 + \frac{b_2}{c_1}\sqrt{\frac{M_1}{M_2}} R_1(0,t)u_0.$$

This proves (33).

Remark 2.7. *Theorem 2.6 can be modified in the sense of Theorem 2.5. Moreover, we note that all the theorems above are still valid for* $a_1 = a_2 = 0$.

The following theorem gives the conditions of extinction. The result shows that the extinction of predators is strongly influenced by the initial condition. Naturally, the extinction of predators occurs due to the limited supply of prey.

Theorem 2.8. *If* $a_1 = c_2 = 0$ *and* $0 \le u_0(x) < a_2/b_2$ *for all* $x \in \Omega$, *then the solution* (u, v) *of* (1)–(2) *satisfies*

$$\|u(t)\| \le \|u_0\| \qquad \textit{for all} \qquad t \ge 0, \tag{37}$$

$$\|v(t)\| \le \|v_0\| \qquad \textit{for all} \qquad t \ge 0. \tag{38}$$

Moreover, if there exists $0 < \gamma < a_2/b_2$ *such that* $u_0(x) < \gamma$ *for all* $x \in \Omega$, *then*

$$\|v(t)\| \le e^{-(a_2-\gamma b_2)t}\|v_0\| \quad \textit{for all} \quad t \ge 0. \tag{39}$$

Proof. If $a_1 = 0$, (6) gives

$$u(t) = R_1(0,t)u_0 - \int_0^t R_1(s,t-s)[b_1 u^2(s) + c_1 u(s)v(s)]ds. \tag{40}$$

Since $u_0 < a_2/b_2$, (40) implies that

$$u(t) \le R_1(0,\, t)u_0 < R_1(0,\, t)(a_2/b_2) = a_2/b_2 \qquad \text{for all} \qquad t \ge 0$$

that also proves (37). We define a linear operator $B(t) := -a_2 + b_2 u(t)$ on X. Therefore, for $c_2 = 0$ the second equation of (1) can be written by

$$v_t(t) = [k_2(t)\Delta + B(t)]v(t). \tag{41}$$

The dissipativity of $B(t)$ for all $t \ge 0$ implies that there exists a contraction quasi semigroup $R(t, s)$ on X generated by $k_2(t)\Delta + B(t)$, Theorem 3 of [23].

Moreover, the problem (41)-(2) has a solution

$$v(t) = R(0, t)v_0 \qquad \text{for all} \qquad t \geq 0.$$

This proves (38).

If $u_0 \leq \gamma < a_2/b_2$, again from (40), we have $u(t) \leq \gamma$. Further, $-a_2 + b_2u(t) < -a_2 + \gamma b_2 < 0$ for all $t \geq 0$. Therefore, (41) can be rewritten by

$$v_t(t) = [k_2 t)\Delta + B(t) + \omega I]v(t) - \omega v(t), \tag{42}$$

where $\omega := a_2 - \gamma b_2 > 0$. Since $B(t) + \omega I$ is a dissipative operator on X, operator $k_2(t)\Delta + B(t) + \omega I$ generates a contraction quasi semigroup $G(t, s)$. Therefore, the quasi semigroup $R(t, s)$ generated by $k_2(t)\Delta + B(t)$ can be represented by

$$R(t, s) = e^{-\omega s}G(t, s) \qquad \textit{for all} \qquad t, s \geq 0.$$

Thus, the solution of (42)-(2) is given by

$$v(t) = R(0, t)v_0 = e^{-\omega t}G(0, t)v_0 \qquad \textit{for all} \qquad t \geq 0. \tag{43}$$

The result in (37) follows from (43).

Similar to Theorem 2.8, we have the following theorem.

Theorem 2.9. *If $a_2 = b_1 = 0$ and $v_0(x) > a_1/c_1$ for all $x \in \Omega$, then the solution (u, v) of (1)-(2) satisfies*

$$\|u(t)\| \leq \|u_0\| \qquad \textit{for all} \qquad t \geq 0.$$

Moreover, if there exists $\kappa > a_1/c_1$ such that $v_0(x) > \kappa$ for all $x \in \Omega$, then

$$\begin{aligned} \|u(t)\| &\leq e^{-(\kappa c_1 - a_1)t}\|u_0\| \quad \textit{for all} \quad t \geq 0, \\ \|v(t)\| &\leq e^{\frac{b_2}{\kappa c_1 - a_1}\|u_0\|}\|v_0\| \quad \textit{for all} \quad t \geq 0. \end{aligned} \tag{44}$$

Proof. The proof is similar with the proof of Theorem 2.8 with the fact

$$v(t) \geq R_2(0, t)v_0 \geq R_2(0, t)(a_1/c_1) = a_1/c_1 \quad \textit{for all} \quad t \geq 0,$$

the operator $B(t)$ is defined by $B(t) := a_1 - c_1v(t)$ and the first equation of (1) is written by

$$u_t(t) = [k_1(t)\Delta + B(t)]u(t).$$

If $\omega := \kappa c_1 - a_1 > 0$, we have the solution

$$u(t) = R(0, t)u_0 = e^{-\omega t}G(0, t)u_0 \quad \textit{for all} \quad t \geq 0. \tag{45}$$

Substitution (45) into (35) gives

$$v(t) \leq R_2(0,t)v_0 + b_2\int_0^t R_2(s,t-s)e^{-\omega s}G(0,s)u_0v(s)ds.$$

Finally, Gronwall's equation provides

$$\|v(t)\| \leq \|v_0\|e^{\frac{b_2}{\omega}\|u_0\|}$$

that proves (44).

Remark 2.10. *Theorem 2.8 deals with system*

$$\begin{aligned} &u_t = k_1(t)\Delta u - u(b_1u + c_1v), \quad (x,t) \in \Omega \times (0,\infty), \\ &v_t = k_2(t)\Delta v + v(-a_2 + b_2u), \quad (x,t) \in \Omega \times (0,\infty), \\ &u = v = 0, \quad (x,t) \in \partial\Omega \times (0,\infty), \end{aligned} \tag{46}$$

subject to the initial conditions

$$u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x), \quad x \in \Omega. \tag{47}$$

We see that $(a_2/b_2, 0)$ *is a semi nontrivial steady state of system* (46)-(47). *Theorem 2.8 interprets that if the initial value of prey* u_0 *is less than the steady state* a_2/b_2*, then the population of predators will be extinct for a long time* ($v = 0$). *Similarly, Theorem 2.9 can be also interpreted for the related system.*

3. Stability of system

To analyze the stability, we consider system (1)–(2) subject to the no-flux boundary on the regular boundary $\partial\Omega$ with the spatial state $\Omega := [0, \ell]$.

Therefore, the Lotka-Volterra system (1)-(2) can be written by

$$\begin{aligned} u_t &= k_1(t)u_{xx} + f(u, v), \qquad (x, t) \in (0, \ell) \times (0, \infty), \\ v_t &= k_2(t)v_{xx} + g(u, v), \qquad (x, t) \in (0, \ell) \times (0, \infty), \\ u_x(0, t) &= u_x(\ell, t) = 0, \qquad v_x(0, t) = v_x(f, \ell) = 0, \qquad t > 0, \\ u(x, 0) &= u_0(x), \qquad v(x, 0) = v_0(x), \qquad x \in \Omega, \end{aligned} \tag{48}$$

where $f(u, v) = u(a_1 - b_1u - c_1v)$ and $g(u, v) = v(-a_2 + b_2u\ c_2v)$. The no-flux boundary condition indicates that the system is self-contained within the one dimensional habitat with no population flux across the boundary. Let (u_s, v_s) be the steady state to system (48) without diffusions (i.e. with $k_1 = k_2 = 0$), that is u_s, v_s satisfy $f(u_s, v_s) = g(u_s, v_s) = 0$. Straightforward computation gives four homogeneous steady states $S_i(u_s, v_s)$, i.e.,

$$S_1(0,0), S_2\left(\frac{a_1}{b_1}, 0\right), S_3\left(0, \frac{a_2}{c_2}\right), S_4\left(\frac{a_1c_2 + a_2c_1}{b_1c_2 + b_2c_1}, \frac{a_1b_2 - a_2b_1}{b_1c_2 + b_2c_1}\right). \tag{49}$$

Therefore, for system (48) without the diffusion, the standard analysis implies:

$$\begin{aligned} &S_1 \text{ is unstable,} \\ &S_2 \text{ is asymptotically stable if } \quad a_1/a_2 < b_1/b_2, \\ &S_3 \text{ is asymptotically stable if } \quad a_1/a_2 < c_1/c_2, \\ &S_4 \text{ is asymptotically stable if } \quad a_1/a_2 > b_1/b_2 \text{ and } c_1 > c_2. \end{aligned} \tag{50}$$

We know that each S_i is also the homogeneous steady state for system (48). Henceforth, whether the diffusion in a spatially distributed system can destabilize the stable steady states. To analyze this situation, we consider a small perturbation of the steady states,

$$u(x, t) = u_s + a(x, t), \quad v(x, t) = v_s + b(x, t) \tag{51}$$

where a, b are small. Linearizing the functions f, g in (48) at (u_s, v_s) using a Taylor series gives

$$a_t = k_1(t)a_{xx} + (a_1 - 2b_1u_s - c_1v_s)a - c_1u_sb, \tag{52}$$

$$b_t = k_2(t)b_{xx} + b_2v_sa + (-a_2 + b_2u_s - 2c_2v_s)b. \tag{53}$$

$$a_x(0, t) = a_x(f, t) = 0, \quad a(x, 0) = u_0(x) - u_s, \quad x \in \Omega, \quad t > 0, \tag{54}$$

$$b_x(0, t) = b_x(f, t) = 0, \quad b(x, 0) = v_0(x) - v_s, \quad x \in \Omega, \quad t > 0. \tag{55}$$

Since the perturbation functions have to satisfy the linear diffusion equation together with the related initial values, then the perturbations are decomposed into a set of sines and cosines functions of various spatial frequencies. Further, since system (48) has Neumann boundary conditions, we have to use cosines functions. Therefore, using Fourier series, the perturbations can be written as

$$a(x,t)=\sum_{q\in\mathbb{Z}}\alpha_q(t)\cos qx, \qquad b(x,t)=\sum_{q\in\mathbb{Z}}\beta_q(t)\cos qx \tag{56}$$

Substituting (56) into the linearized system (52)-(54) and canceling out a common factor of cos qx, for each q leads to the system

$$\begin{pmatrix}\dot{\alpha}_q(t)\\ \dot{\beta}_q(t)\end{pmatrix}=J_q\begin{pmatrix}\alpha_q(t)\\ \beta_q(t)\end{pmatrix}, \tag{57}$$

where

$$J_q=J-q^2D, \qquad J=\begin{pmatrix}\alpha_{11} & \alpha_{12}\\ \alpha_{21} & \alpha_{22}\end{pmatrix}, \qquad D=\begin{pmatrix}k_1(t) & 0\\ 0 & k_2(t)\end{pmatrix}, \tag{58}$$

and

$$a_{11}=a_1-2b_1u_s-c_1v_s, \qquad a_{12}=-c_1u_s$$
$$a_{21}=b_2v_s, \qquad a_{22}=-a_2+b_2u_s-2c_2v_s.$$

The stability of system (57) (so does (52)) can be studied from the eigen-values λ_q of the matrix J_q. Matrix J_q in (58) reduces to a quadratic characteristic equation

$$\lambda^2-\mathrm{tr}(J_q)\lambda+\det(J_q)=0, \tag{59}$$

where

$$\mathrm{tr}(J_q)=\mathrm{tr}(J)-\mathrm{tr}(D)q^2, \tag{60}$$
$$\det(J_q)=\det(D)q^4-[a_{11}k_2(t)+a_{22}k\ (t)]q^2+\det(J).$$

We note that the sufficient condition for the steady state (u_s, v_s) is asymptotically stable if all the eigenvalues λ of equation (59) have negative real parts. The basic theory gives that the real parts of the eigenvalues of equation (59) are all negative if and only if

$$\mathrm{tr}(J_q)<0 \text{ and } \det(J_q)>0. \tag{61}$$

Evaluation (60) at the steady state S_1 gives:

$$\mathrm{tr}(J_q)\,|_S1=a_1-a_2-\mathrm{tr}(D)q^2,$$
$$\det(J_q)\,|_S=\det(D)q^4-[a_1k_2(t)-a_2k_1(t)]q^2-a_1a_2.$$

The last is a quadratic form in q^2, so the requirement $\det(J_q)\,|_S>0$ forces the its discriminant is negative. However, the discriminant $d=(a_1k_2(t)+a_2k_1(t))^2$ is always positive for all $t\ge 0$. Thus, the steady state S_1 also remains unstable for system (48).

Theorem 3.1. *Points S_2, S_3 and S_4 in* (49) *under conditions* (50) *are the asymptotically stable steady states of system* (48). *Also, an additional condition to S_4 is $\dfrac{k_1(t)}{k_2(t)}<\dfrac{c_1}{c_2}$ for all $t\ge 0$.*

Proof. We simply prove that $\mathrm{tr}(J_q)\,|_{S_i}<0$ and $\det(J_q)\,|_{S_i}>0$ for all $i=2, 3, 4$. First, evaluation (60) at the steady state S_2 gives

$$\mathrm{tr}(J_q)\,|_{S_2}=-\frac{a_2b_1-a_1b_2}{b_1}-a_1-\mathrm{tr}(D)q^2,$$
$$\det(J_q)\,|_{S_2}=\left(\frac{a_1+k_1(t)q^2}{b_1}\right)\left(a_2b_1-a_1b_2+b_1k_2(t)q^2\right).$$

Condition $a_1b_2 < a_2b_1$ guarantees that $\mathrm{tr}(J_q)\,|_S 2 < 0$ and $\det(J_q)\,|_S 2 > 0$.

Evaluation (60) at the steady state S_3 provides

$$\mathrm{tr}(J_q)\,|_{S_3} = -\frac{a_2c_1 - a_1c_2}{c_2} - 3a_2 - \mathrm{tr}(D)q^2,$$

$$\det(J_q)\,|_{S_3} = \left(a_2c_1 - a_1c_2 + c_2k_1(t)q^2\right)\left(\frac{3a_2 + k_2(t)q^2}{c_2}\right).$$

Condition $a_1c_2 < a_2c_1$ implies that $\mathrm{tr}(J_q)_{S_3} < 0$ and $\det(J_q)_{S_3} > 0$.

Finally, evaluation (60) at the steady state S_4 gives

$$\mathrm{tr}(J_q)\,|_{S_4} = -\frac{a_1c_2(b_1 + b_2) + a_2b_1(c_1 - c_2)}{b_1c_2 + b_2c_1} - \mathrm{tr}(D)q^2,$$

$$\det(J_q)\,|_{S_4} = \det(D)q^4 + \frac{1}{b_1c_2 + b_2c_1}\Big[a_2b_1(c_1k_2(t) - c_2k_1(t))q^2 + a_1c_2(b_1k_2(t) + b_2k_1(t)) + (a_1b_2 - a_2b_1)(a_1c_2 + a_2c_1)\Big].$$

Condition $c_1 > c_2$ ensures that $\mathrm{tr}(J_q)\,|_{S_4} < 0$. Since $a_1b_2 > a_2b_1$, the requirement $\det(J_q)\,|_{S_4} > 0$ leads $\dfrac{k_1(t)}{k_2(t)} < \dfrac{c_1}{c_2}$ for all $t \geq 0$.

Remark 3.2. *Theorem 3.1 confirms that the sufficiency for the stability of steady state S_4 is the ratio of the diffusivity of system is uniformly bounded by c_1/c_2.*

Theorem 3.3. *If (u_s, v_s) is the asymptotically stable steady state of system* (48) *and (u, v) is the solution of the system, then* $\lim_{t\to\infty}(u(x, t), v(x, t)) = (u_s, v_s)$.

Proof. From (51), we sufficiently prove that $\lim_{t\to\infty}(a(x, t), b(x, t)) = (0, 0)$. Since we focus on the nonnegative solution (u, v), (51) implies that a and b are nonnegative. In virtue (6) and (7), the solutions of problems (52)-(53) and (54)-(55) can be presented by

$$a(t) = e^{\alpha_{11}t}R_1(0,t)(u_0 - u_s) - c_1u_s\int_0^t e^{\alpha_{11}(t-\tau)}R_1(\tau, t-\tau)b(\tau)d\tau, \tag{62}$$

$$b(t) = e^{\alpha_{22}t}R_2(0,t)(v_0 - v_s) + b_2u_s\int_0^t e^{\alpha_{22}(t-\tau)}R_2(\tau, t-\tau)a(\tau)d\tau, \tag{63}$$

respectively. The contraction of $R_1(t, s)$ and the nonnegativity of a, b, (62) gives

$$\|a(t)\| \leq e^{\alpha_{11}t}\|u_0 - u_s\| \qquad \text{for all} \qquad t \geq 0. \tag{64}$$

Moreover, by the contraction of $R_2(t, s)$, (63) together with (64) give

$$\|b(t)\| \leq e^{\alpha_{22}t}\|v_0 - v_s\| + b_2u_s\left(e^{\alpha_{11}t} - e^{\alpha_{22}t}\right)\frac{\|u_0 - u_s\|}{|\alpha_{11} - \alpha_{22}|} \tag{65}$$

for all $t \geq 0$. Since α_{11} and α_{22} are negative under the stability conditions (50) for each the steady states S_i, $i = 2, 3, 4$, equations (64) and (65) prove that $\lim_{t\to\infty} a(x, t) = 0$ and $\lim_{t\to\infty} b(x, t) = 0$, respectively.

Alternative proof. We use directly the assumptions in (56). First, solving the homogeneous equation of (52) subject to the initial and boundary value (53) using the variable separation method and the Duhamel principle, we obtain the solution of problem (52)–(53)

$$a(x,t) = \sum_{n=0}^{\infty}\left(w_n(t) - c_1u_s\int_0^t w_n(t-\tau)b(x,\tau)d\tau\right)\cos\lambda_n x,$$

where

$$\lambda_n = \frac{n\pi}{\ell}, \quad w_n(t) = \omega_n e^{-\lambda_n^2 g_1(t)+\alpha_{11}t}, \quad \omega_n = \frac{2}{\ell}\int_0^\ell (u_0 - u_s)\cos\lambda_n x dx.$$

Form (56), the positivity of c_1, u_s and b gives $\alpha_\lambda n\ (t)\ w_n(t)$ for all $t \le 0$. Further, since α_{11} is negative under the stability conditions (50) for each the steady states S_i, $i = 2, 3, 4$, we have $\lim_{t\to\infty} w_n(t) = 0$ for all n. Therefore, $\lim_{t\to\infty} \alpha_\lambda n\ (t) = 0$ for all n which provides

$$\lim_{t\to\infty} a(x,t) = 0. \tag{66}$$

Analogue to system (54)–(55), we have the solution

$$b(x,t) = \sum_{n=0}^{\infty}\left(z_n(t) + b_2 u_s \int_0^t z_n(t-\tau)a(x,\tau)d\tau\right)\cos\lambda_n x,$$

where

$$z_n(t) = d_n e^{-\lambda_n^2 g_2(t)+\alpha_{22}t}, \quad d_n = \frac{2}{\ell}\int_0^\ell (v_0 - v_s)\cos\lambda_n x dx.$$

From (56), (57) and (66), we can write $a_{\lambda_n}(t) = e_n e^{-\gamma n t}$ for some $\gamma_n > 0$ and e_n. Therefore, by the orthogonality of $\cos\lambda_n x$, the solution $b(x, t)$ can be written by

$$b(x,t) = \sum_{n=0}^{\infty}\left(z_n(t) + b_2 u_s \int_0^t z_n(t-\tau)e_n e^{-\gamma_n \tau} d\tau\right)\cos\lambda_n x,$$

Let $f_n(t) = z_n(t) + b_2 u_s e_n \int_0^t z_n(t-\tau)e^{-\gamma_n\tau} d\tau$, by a slightly computations of the integral, we obtain

$$f_n(t) = z_n(t) + \frac{b_2 u_s e_n}{-\lambda_n^2 k_2(t) + \alpha_{22} + \gamma_n}\left[e^{-\lambda_n^2 g_2(t)+\alpha_{22}t} - e^{-\gamma_n t}\right].$$

Since $a_{22} < 0$, we have $f_n(t)$ 0 as t . This proves $\lim_{t\to\infty} b(x,t) = 0$.

Remark 3.4. *We see that Theorem 3.3 holds only when* (u_s, v_s) *is stable. In fact,* S_1 *is unstable steady state and from* (64) *and* (65)*, we have* $(a(t), b(t)) \to (\infty, \infty)$ *as* $t \to \infty$.

4. Bifurcation analysis

In this section we will briefly review the bifurcation analysis of system (48). The results in (61) imply that the steady state of system (48) is unstable if

$$\mathrm{tr}(J_q) \ge 0 \quad \text{or} \quad \det(J_q) \le 0 \quad \text{for some} \quad q.$$

In this context, we shall investigate the existence of Turing instability and Hopf bifurcation at the non trivial steady state. From (60) if the steady state is asymptotically stable, then the addition of diffusion cannot change the condition $\mathrm{tr}(J_q) < 0$. Therefore, the diffusion-driven instability (Turing instability) only depends on the change of sign of the determinant $\det(J_q)$. Thus, Turing instability occurs under two conditions: (i) The steady state is stable in the absence of diffusion; (ii) The presence of diffusion destabilize the stable steady state ($\det(J_q) < 0$ for some q). On the other hand, Hopf bifurcation occurs under the condition $\mathrm{tr}(J_q) = 0$ and $\det(J_q) > 0$ for some q.

The critical condition of Turing instability is $\det(J_q) = 0$ for some q. The determinant $\det(J_q)$ is a quadratic polynomial in q^2 which attains a minimum if

$$q^2_{\min} = \frac{\alpha_{11}k_2(t) + \alpha_{22}k_1(t)}{2\det(D)}, \quad t \geq 0$$

with the minimum

$$\det(J_q)\,|_{q^2_{\min}} = -\frac{\left(\alpha_{11}k_2(t) + \alpha_{22}k_1(t)\right)^2}{4\det(D)} + \det(J), \quad t \geq 0.$$

Therefore, the critical condition for Turing instability is

$$q^2_T = \sqrt{\frac{\det(J)}{\det(D)}}. \tag{67}$$

Substituting q^2_T into $\det(J_q) < 0$ gives

$$(a_{11}k_2(t) + a_{22}k_1(t))^2 \geq 4\det(J)\det(D), \qquad t \geq 0.$$

This result can be simplified as

$$(a_{11} + a_{22}k(t))^2 \geq 4k(t)\det(J), \qquad t \geq 0,$$

where $k(t) := k_1(t)/k_2(t)$. This gives Turing curve defined by

$$(a_{11} + a_{22}k(t))^2 = 2k(t)\det(J), \qquad t \geq 0. \tag{68}$$

The critical threshold of the ratio of diffusions $k_{cr}(t)$ is found by solving this equation for $k(t)$, which the Turing instability starts.

The above analysis gives the conditions for Turing instability.

Lemma 4.1. *System* (48) *around the steady states* S_i, $i = 2, 3, 4$ *occurs Turing instability if*

(a) $\mathrm{tr}(J) < 0$,
(b) $\det(J) > 0$,
(c) $(a_{11} + a_{22}k(t))^2\ 4k(t)\det(J)$, $t \geq 0$.

Henceforth, substituting q^2_T in (67) into $\mathrm{tr}(J_q)$ in (60) gives

$$\mathrm{tr}(J_q) = \mathrm{tr}(J) - (k(t)+1)\sqrt{\frac{\det(J)}{k(t)}}. \tag{69}$$

Therefore, by keeping any two parameters (for example a_1 and $k(t)$) and taking fixed for the others, then solving the equations of (68) and $\mathrm{tr}(J_q) = 0$ in (69), we have the critical conditions of Hopff bifurcation a_{1H} and Turing bifurcation $k_T(t)$.

Now, we give the numerical simulation results of the spatiotemporal model (48) for parameter values within the Turing and Turing-Hopf domain.

Example 4.2. *Set the parameter values* $a_1 = 1$, $a_2 = 0.25$, $b_1 = 0.3$, $b_2 = 0.1$, $c_1 = 0.4$, *and* $c_2 = 0.1$ *in system* (48). *There is Turing instability around the homogeneous steady state.*

We obtain the coexisting homogeneous steady state $S_4(2.8571, 0.3571)$. Since the first two conditions of Lemma 4.1 are satisfied, S_4 is asymptotically stable for the temporal counterpart. For the chosen parameter values, we find two critical thresholds $k_{cr_1}(t) = 3.3360$ (approx) and $k_{cr_2}(t) = 172.6640$ (approx) for all $t \geq 0$. However, Theorem 3.1 implies that the feasible critical point is k_{cr_1}.

Therefore, if $0 < k(t) \leq k_{cr_1}$ for all t 0, the third condition of Lemma 4.1 is satisfied. It means that the diffusivity of prey and predator destabilize the homogeneous steady state S_4. In other words, for $0 < k(t) \leq k_{cr_1}$ for all $t \geq 0$, the heterogeneous perturbations lead to Turing bifurcation. Further, from Theorem 3.1, the diffusions to destabilize the stable steady state S_4 in interval $0 < k(t) < 3.3360$ for all $t \geq 0$ and $a_1 = 1$, see Fig. 1.

The existence and non-existence of Turing bifurcation depend solely on the values of chosen parameters under the model consideration. In the following example, we will construct the Turing bifurcation diagram choosing a_1 and $k(t)$ as the bifurcation parameters, i.e. as the controlling parameters to obtain different spatiotemporal patterns.

Example 4.3. *Turing bifurcation diagram in* $(a_1, k(t))$*-plane of system* (48) *for the parameter values* a_2, b_1, b_2, c_1, c_2 *as in Example 4.2 consists of four regions bounded by the Turing bifurcation and Hopf bifurcation curves. See Fig. 1.*

A little computation gives the critical conditions of Hopf bifurcation $a_{1_H} = 2.0017$ (approx) and Turing bifurcation $k_T(t) = 1$ (approx). The bifurcation diagram consists of two bifurcation curves, namely Turing bifurcation curve (blue curve) and temporal Hopf bifurcation curve (red line), see Fig. 1. The coexisting steady state S_4 for the temporal and spatiotemporal perturbations of system (48) is stable when $(a_1, k(t)) \in D_1$ and losing the stability through the Hopf-bifurcation at a_{1_H}. The Hopf region is given by D_2 which the temporal perturbation is unstable. The Turing instability region is the region lying below the Turing bifurcation curve (i.e. $D_3 \cup D_4$). Region D_4, the Turing region lying in the region $a_1 > a_{1_H}$ is the Turing-Hopf region where temporal and spatiotemporal perturbations

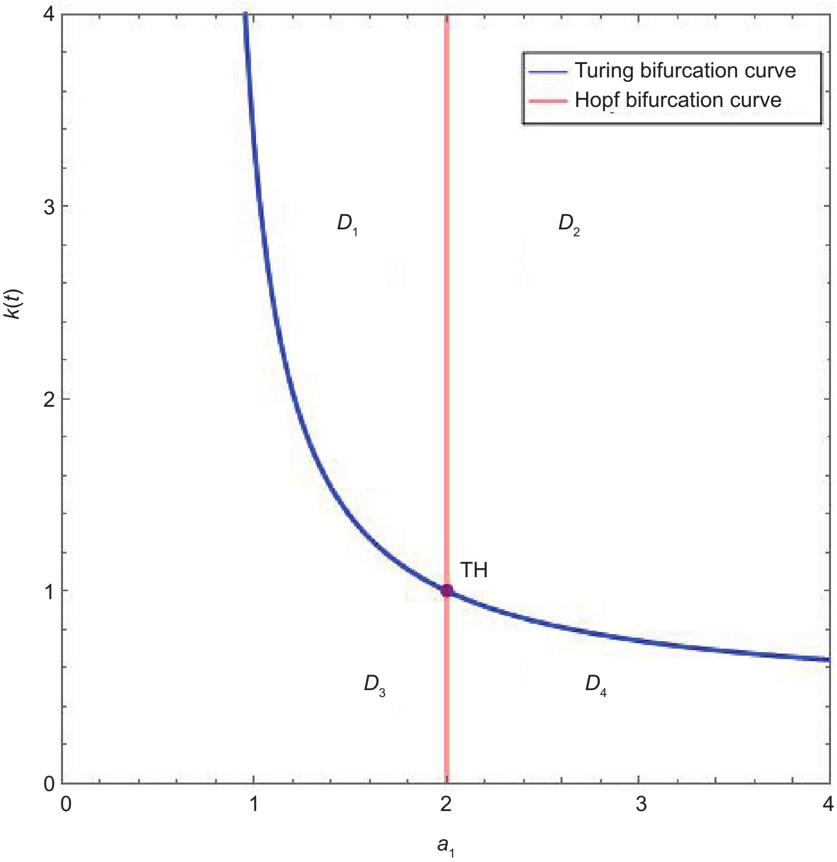

Figure 1. Bifurcation diagram of system (48) in $(a_1, k(t))$-plane for $a_2 = 0.25$, $b_1 = 0.3$, $b_2 = 0.1$, $c_1 = 0.4$, and $c_2 = 0.1$. The stable region is denoted by D_1, which is bounded by the blue and red curves; D_2-Hopf region; D_3-Turing region; D_4-Turing-Hopf region; *TH* is the critical Turing–Hopf bifurcation point.

are both unstable. The Turing–Hopf bifurcation occurs at the intersection point *TH*. From Theorem 3.1, the interval of stability of the diffusion for $k(t)$ is (1, 4). Therefore, the diffusion-driven instability occurs when $0 < k(t) < 1$ for all $t \geq 0$.

Remark 4.4. *(a) In Example 4.3, we actually have another critical condition of Hopf bifurcation, namely* $a_{1_H} = 0.75$ *(approx). However, for* $a_1 < 0.75$, $\mathrm{tr}(J_q)|_{a_1}$ *has a negative real part, so the steady state* S_4 *remains stable.*

(b) We note that the critical functions of Turing bifurcation k_{cr} *and* k_T *are constant (independent of time) due to other parameters as well. Also, the diffusion-driven instability occurs, if the ratio of diffusivity* $k(t)$ *is uniform bounded.*

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