

Bifurcations induced by nonlocal spatial memory versus nonlocal perception

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Abstract

Spatial memory and perception are two key mechanisms driving animal movement's decisions. In this paper, we formulate a reaction-diffusion model incorporating nonlocal spatial memory and nonlocal perception with both kernels characterized by a top-hat function. To understand the impact of species' memory and instantaneous perception on their movement, we investigate how memory-induced diffusion coefficient, perceptual strength, memory delay, and perceptual scale affect the stability and spatiotemporal dynamics of positive steady states. For spatial memory versus perception, we sketch bifurcation curves in the planes of memory delay and perception scale. When memory and perception are weak, the positive constant steady state remains locally asymptotically stable, indicating minimal impact on stability. A larger perception scale preserves stability, whereas a smaller one can induce instability through bifurcations. Specifically, when both the memory-induced diffusion coefficient and perceptual strength are large and share the same sign (or differ in sign), the system undergoes Turing bifurcation to produce spatially nonhomogeneous steady states (or spatially nonhomogeneous periodic solutions via Hopf bifurcation with increased memory delay). When one of these two parameters is large and the other is small, the stability boundary of the positive constant steady state may be governed by Turing bifurcation or a combination of Turing and Hopf bifurcations, potentially leading to higher codimension bifurcations such as Turing-Hopf and Hopf-Hopf bifurcations.

Keywords Spatial memory · Perception · Nonlocal · Top-hat · Bifurcation

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1 Introduction

Cognitive ability is a prominent feature of animals, distinguishing them remarkably from chemicals. Wang and Salmaniw (2023) summarized the cognitive behavior, categorizing it into three fundamental components: memory (Fagan et al. 2013; Shi et al. 2020, 2021), perception (Song et al. 2024; Fagan et al. 2017), and learning (Lewis et al. 2021; Shi et al. 2024). This provides a solid foundation for researchers to develop mathematical models that capture the cognition of animal movement. To incorporate spatial memory explicitly, Shi et al. (2020) introduced a reaction-diffusion equation with a delayed diffusion operator:

$$u_t = d_1 u_{xx} + d_2 (u(u_\tau)_x)_x + f(u),$$

where $d_2(u(u_{\tau})_x)_x$ characterize the memory-based diffusion. The coefficient $d_2 \in \mathbb{R}$ is the memory-induced diffusion coefficient and $u_{\tau} = u(x, t - \tau)$ with $\tau > 0$ representing the averaged memory period. They showed that the local stability of a constant steady state is completely determined by the ratio of d_1 and d_2 , but independent of τ . In this context, memory is described by a discrete time delay. More realistically, it should be characterized by spatiotemporally distributed time delays (Shi et al. 2021; Song et al. 2019; Shen et al. 2023) or at least temporally distributed time delays (Lin and Song 2023; Shi and Shi 2024). Additionally, there has been a growing interest in studying reaction-diffusion models to consider the combined effects of spatial memory and other ecological factors, such as spatial heterogeneity (Wang et al. 2022; Ji and Wu 2024), maturity delays (Shi et al. 2019), advective environments (Zhang et al. 2023), and spatial nonlocality (An et al. 2020), on movement dynamics. Many researchers have also examined scenarios involving reaction-diffusion systems with memory for predator-prey models. It can be obtained in Wang et al. (2022) that both spatial memory and pregnancy cycles can induce rich dynamics, which deepens the understanding of the influence of spatial memory on the spatiotemporal distribution of populations. The spatial memory delay and maturation delay can lead some novel spatial patterns such as the existence of stable spatially heterogeneous periodic orbits with high mode (Li et al. 2023).

Specifically, Song et al. (2024) investigated the impact of nonlocal perception on population dynamics using a consumer-resource model with nonlocal diffusion. Their findings revealed that nonlocal perception has no effect on population dynamics when the resource kernel functions are spatial average, Green, Laplace, and Gaussian. However, when the resource kernel function is a top-hat kernel function, and the perceptual strength is high with the detection scale falling within an appropriate interval, the top-hat kernel function disrupts the stability of spatially uniform steady states, leading to spatially nonhomogeneous steady states.

Recently, Xue et al. (2024) considered the reaction-diffusion model with nonlocal spatial memory:

$$\begin{cases} u_t = d_1 u_{xx} + d_2 (u(K_R * u_\tau)_x)_x + f(u), & x \in [-L, L], t > 0, \\ u(-L, t) = u(L, t), & u_x(-L, t) = u_x(L, t), & t > 0, \end{cases}$$
(1)

where $K_R * u_\tau = \int_{-L}^{L} K_R(x - y)u(y, t - \tau)dy$, and

$$K_R(x-y) = \begin{cases} \frac{1}{2R}, & -R \le x - y \le R, \\ 0, & \text{otherwise,} \end{cases}$$
(2)

is the top-hat function with 0 < R < L denoting the perception scale. The effect of memory on the spatial movement is characterized by the term $d_2(u(K_R * u_\tau)_x)_x$. Note that if $\tau = 0$, the model (1) can also describe the impact of nonlocal perception on species' movement and they found that the Turing bifurcations can occur (Ducrot et al. 2018; Xue et al. 2024). Furthermore, for $\tau > 0$, the positive constant steady state u_* is locally asymptotically stable if $-\frac{d_1}{u_*} < d_2 < 0$. However, as d_2 increases beyond a positive critical value, the system can exhibit Hopf, Turing, or Turing-Hopf bifurcations (Xue et al. 2024).

In this paper, we study the combined effects of species' memory and instantaneous perception on their movement with the new model provided by

$$\begin{cases} u_t = d_1 u_{xx} + d_2 (u(K_R * u_\tau)_x)_x + \alpha (u(K_R * u)_x)_x + f(u), & x \in [-L, L], t > 0, \\ u(-L, t) = u(L, t), & u_x(-L, t) = u_x(L, t), & t > 0, \end{cases}$$
(3)

where $K_R * u = \int_{-L}^{L} K_R(x - y)u(y, t)dy$ and K_R is defined in (2). Here, the third term on the right-hand side captures the impact of the species' perception on its spatial movement and its derivation can be found in Xue et al. (2024) and Song et al. (2024). The coefficient α represents the perception strength.

Model (3) with $\alpha = 0$ degenerates into model (1), which only focuses on the impact of memory on population diffusion. If the kernel function K is a Dirac function, it reduces to the local case in Shi et al. (2020). Model (3) with $d_2 = 0$ describes the perception effect on the species' diffusion, and it degenerates into the model (1) with $\tau = 0$. Furthermore, if $K_R * u$ in diffusion term is substituted with the forager's resource perception function, Fagan et al. (2017) demonstrated that nonlocal perception is advantageous for foragers, enhancing their spatiotemporal concentration on their resources.

In this study, we focus on the stability of the positive constant steady state of model (3) to explore the possible spatiotemporal dynamics. It is crucial to note that there exists a strong coupling between discrete time delay, spatial nonlocality, and diffusion, leading to a characteristic equation that encompasses an infinite series of transcendental equations involving integrals. Moreover, the discontinuity of the perceptual kernel function introduces further complexity in analyzing the distribution of roots for the

(**H**)
$$f'(u_*) < 0.$$

Our main findings regarding the stability and bifurcation of u_* are summarized in the following theorem.

Theorem 1.1 Assume that (**H**) holds. The stability properties of u_* are as follows:

- (I) If $-\frac{d_1}{u_*} \le \alpha \pm d_2 \le -\frac{d_1}{u_*} \frac{z_1}{\sin z_1}$, where z_1 is the smallest positive nonzero root of $\tan(z) = z$, then u_* is locally asymptotically stable for any $R \ge 0$ and $\tau \ge 0$.
- (II) If $-\frac{d_1}{u_*} \le \alpha + d_2 \le -\frac{d_1}{u_*} \frac{z_1}{\sin z_1}$, and either $\alpha d_2 < -\frac{d_1}{u_*}$ or $\alpha d_2 > -\frac{d_1}{u_*} \frac{z_1}{\sin z_1}$, there exists a threshold R_H^* of R such that
 - (a) For $R \ge R_H^*$, u_* is locally asymptotically stable for $\tau \ge 0$;
 - (b) For $0 < R < R_H^*$, there exists a threshold τ_* such that u_* is locally asymptotically stable for $0 \le \tau < \tau_*$ and becomes unstable for $\tau > \tau_*$. At $\tau = \tau_*$, the system (3) undergoes a Hopf bifurcation.
- (III) If $d_2 > 0$, $\alpha + d_2 > -\frac{d_1}{u_*} \frac{z_1}{\sin z_1}$, $\alpha d_2 \ge -\frac{d_1}{u_*}$, or $d_2 < 0$, $\alpha + d_2 < -\frac{d_1}{u_*}$, $\alpha d_2 \le -\frac{d_1}{u_*} \frac{z_1}{\sin z_1}$, there exists a critical value R_T^* of R such that
 - (a) For $R > R_T^*$, u_* is locally asymptotically stable for $\tau \ge 0$;
 - (b) For $0 < R < R_T^*$, u_* is unstable for $\tau \ge 0$;
 - (c) The system (3) undergoes Turing bifurcation at $R = R_T^*$.
- (IV) If $d_2 > 0$ and $\alpha + d_2 < -\frac{d_1}{u_*}$, or $d_2 < 0$ and $\alpha + d_2 > -\frac{d_1}{u_*}\frac{z_1}{\sin z_1}$, there exist critical values R_T^* and R_H^* of R with $R_T^* < R_H^*$ such that
 - (a) For $R \ge R_H^*$, u_* is locally asymptotically stable for $\tau \ge 0$;
 - (b) For $R_T^* < \tilde{R} < R_H^*$, there exists a threshold τ_* similar to case (II)-(b);
 - (c) For $0 < R < R_T^*$, u_* is unstable for $\tau \ge 0$;
 - (d) The system (3) undergoes Turing-Hopf bifurcation at $(R, \tau) = (R_T^*, \tau_*)$.
- (V) If $\alpha + d_2 > -\frac{d_1}{u_*} \frac{z_1}{\sin z_1}$ and $\alpha d_2 < -\frac{d_1}{u_*}$, or $\alpha + d_2 < -\frac{d_1}{u_*}$ and $\alpha d_2 > -\frac{d_1}{u_*} \frac{z_1}{\sin z_1}$, there exist two critical values of R, denoted R_T^* and R_H^* , determining the stability:
 - (a) If $R_T^* < R_H^*$, the results are similar to case (IV);
 - (b) If $R_T^* \ge R_H^*$, the results are similar to case (III).

The results of Theorem 1.1 are visualized in Fig. 1, where local dynamics of u_* are characterized in (d_2, α) plane. When both $|d_2|$ and $|\alpha|$ are small (Region I), the non-local spatial memory and nonlocal perception exert minimal influence on the stability of u_* , resulting in u_* maintaining its locally asymptotically stable state. However, in other scenarios, the stability of u_* may be compromised. On the one hand, when $|d_2|$ is large, our results reveal distinct patterns based on the relationship between d_2 and α . Specifically, if d_2 and α share the same sign (Region III), a spatial nonhomogeneous steady state emerges through a Turing bifurcation. This implies that when the memory



information of the species aligns with the perceived information, the species maintains a particular spatial distribution. Conversely, if the signs of d_2 and α differ, particularly for α and d_2 demonstrating comparable magnitudes (Region II), a Hopf bifurcation occurs, leading to spatial nonhomogeneous periodic solutions. This phenomenon can be attributed to the mismatch between memory and perception information of species, which tends to induce periodic variations in their spatial distribution. For other values of α (Region IV), both Turing and Hopf bifurcations impact system stability, indicating that when memory factor is dominant, the system is more prone to exhibiting spatiotemporal patterns, with species displaying spatial distributions characterized by temporal oscillations. On the other hand, when $|\alpha|$ surpasses $|d_2|$ (Region V), the stability boundary of u_* can be delineated by either the Turing bifurcation curve alone or a combination of both Turing and Hopf bifurcations. This indicates that discrepancies between memory and perceived information can result in either a stable spatial distribution or periodic variations.

In addition, Theorem 1.1 established that the constant steady state u_* is locally asymptotically stable if the perceptual scale *R* is large enough, regardless of d_2 , α and τ values. This stability arises due to the transformation of the perceptual kernel function *K* into an average kernel function as *R* approaches infinity. Conversely, when the perceptual scale *R* is small, u_* may lose its stability and lead to the emergence of spatial patterns. This finding contrasts with the result reported in Song et al. (2024), where two population models possessing perceptual abilities exhibited a stable u_* irrespective of whether *R* is sufficiently large or small. Besides, we provide scenarios $(d_2 < -\frac{d_1}{u_*}$ for (1)) that were not addressed in Xue et al. (2024). We not only establish that u_* is unstable, as previously noted in Shi et al. (2020) where *K* is Dirac function and $\alpha = 0$ in (3), but also offer an explanation for the underlying cause of this instability, which was previously unknown in Shi et al. (2020).

The paper is organized as follows: In Section 2, we rigorously show the stability and bifurcation phenomena induced by memory-induced diffusion and nonlocal perception for the positive constant steady state of model (3). In Section 3, we present numerical simulations for a logistic model encapsulated by model (3), followed by a concise

2 Stability and bifurcation

The linearization of (3) around u_* yields the equation

$$u_t = d_1 u_{xx} + d_2 u_* (K_R * u_\tau)_{xx} + \alpha u_* (K_R * u)_{xx} + f'(u_*)u.$$

The corresponding characteristic equation is given by

$$\Pi_k(\lambda) = \lambda + d_1 k^2 + d_2 u_* k^2 H(k, R) e^{-\lambda \tau} + \alpha u_* k^2 H(k, R) - f'(u_*) = 0, \quad (4)$$

where $k = \frac{n\pi}{L}$ with $n \in \mathbb{N}_0$, and the function H(R, k) is defined as

$$H(k, R) = \begin{cases} \frac{\sin(kR)}{kR}, & k \neq 0, \\ 1, & k = 0. \end{cases}$$

The analysis of the stability of u_* will be conducted in three sequential steps. First, we examine the distribution of the roots of the characteristic equation (4) when the parameters R and τ are set to zero. This not only enables us to determine the stability of u_* under specific parameter regimes but also identifies the critical conditions for the emergence of zero roots in the characteristic equation (4). Second, We analyze the existence of purely imaginary roots in the characteristic equation under the condition that u_* is locally asymptotically stable when $\tau = 0$. Finally, by synthesizing the results from the above two steps, we analyze the distribution of the characteristic equation's roots to classify the dynamic behavior of the system (3).

Note that hypothesis (**H**) ensures the local asymptotic stability of u_* in the absence of nonlocal effects ($d_2 = \alpha = 0$). We now present several results pertaining to specific instances of *R* and τ within the context of (3), where d_2 and α are nonzero.

Proposition 2.1 Under the assumption of (**H**), the following stability properties of u_* hold:

- (1) For $R = \tau = 0$, u_* is locally asymptotically stable if $d_1 + \alpha u_* + d_2 u_* \ge 0$ and unstable if $d_1 + \alpha u_* + d_2 u_* < 0$.
- (II) For R = 0, u_* is locally asymptotically stable for all $\tau \ge 0$ if $d_1 + \alpha u_* |d_2|u_* \ge 0$ and unstable if $d_1 + \alpha u_* |d_2|u_* < 0$ with $\tau > 0$.
- (III) For $\tau = 0$, we have the following results:
 - (i) If $-\frac{d_1}{u_*} d_2 \le \alpha \le -\frac{d_1}{u_*} \frac{z_1}{\sin z_1} d_2$, then u_* is locally asymptotically stable for any R > 0.
 - (ii) If $\alpha < -\frac{d_1}{u_*} d_2$ or $\alpha > -\frac{d_1}{u_*} \frac{z_1}{\sin z_1} d_2$, there exists a critical value R_T^* such that
 - (a) u_* is locally asymptotically stable for $R > R_T^*$,
 - (b) u_* is unstable for $0 < R < R_T^*$,

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(c) The system (3) undergoes a Turing bifurcation at $R = R_T^*$.

Remark 1 When either R = 0 or $\tau = 0$, the corresponding terms in the model reduce to $\nabla \cdot (u \nabla u)$ representing density-dependent diffusion where species movement depends on local population density. For $R = \tau = 0$, the result (I) reveals that species tend to diffuse from high density to low density regions due to intraspecific competition or local overcrowding, thereby enhancing ecosystem stability. Conversely, aggregation behaviors (for enhanced defense, foraging efficiency, or reproduction) destabilize the intrinsic constant steady state mechanism of ecosystems. For R = 0, the memory effect introduced. The finding (II) demonstrates that sufficiently strong memory capabilities (even with minimal memory period) disrupt the intrinsic constant steady state mechanism, leading to novel dynamic patterns. This suggests memory-driven behavioral adjustments can fundamentally alter ecosystem equilibria. For $\tau = 0$, considering perception effect, the system undergoes a Turing bifurcation, indicating that perceptual abilities drive spatial self-organization into stable patterns with spatial periodic. This phenomenon likely corresponds to habitat formation mechanisms, where species redistribute themselves to establish structured spatial configurations. However, when species possess sufficiently large-scale perception capabilities (R exceeding critical thresholds), the system reverts to its original equilibrium state determined by environmental carrying capacity.

Remark 2 When $R = \tau = 0$, the characteristic equation (4) will be simplified and transformed into an algebraic equation that permits a straightforward evaluation of the stability of u_* . In the scenario where R = 0, the model (3) simplifies to equation (2.4) as detailed in Shi et al. (2020), with the pertinent results encapsulated in Corollary 3.9 of that study. Moreover, when $\tau = 0$, the model (3) degenerates into a classical reaction-diffusion equation under the condition $\alpha + d_2 = 0$, ensuring the local asymptotic stability of u_* . For the case where $\alpha + d_2 \neq 0$, the analytical methodology closely resembles that presented in Section 3.2.1 of Xue et al. (2024), and thus, a detailed discussion is omitted here for brevity.

Now we delve into the analysis of the asymptotic stability of u_* for R > 0 and $\tau > 0$. First we focus on the emergence of Hopf bifurcation by manipulating the parameter $\tau > 0$, premised on the assumption that u_* is locally asymptotically stable when $\tau = 0$. Let $\lambda = i\omega$ with $\omega > 0$ be a root of (4), we have

$$\omega i = -d_1 k^2 - d_2 u_* k^2 \frac{\sin kR}{kR} e^{-\omega \tau i} - \alpha u_* k^2 \frac{\sin kR}{kR} + f'(u_*).$$

Separating the real and imaginary parts produces

$$\begin{cases} d_2 u_* k^2 \frac{\sin kR}{kR} \cos \omega \tau &= -d_1 k^2 - \alpha u_* k^2 \frac{\sin kR}{kR} + f'(u_*), \\ d_2 u_* k^2 \frac{\sin kR}{kR} \sin \omega \tau &= \omega, \end{cases}$$
(5)

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which yields to

$$\omega^{2} = \left[d_{2}u_{*}k^{2} \frac{\sin kR}{kR} - f'(u_{*}) + d_{1}k^{2} + \alpha u_{*}k^{2} \frac{\sin kR}{kR} \right]$$

$$\cdot \left[d_{2}u_{*}k^{2} \frac{\sin kR}{kR} + f'(u_{*}) - d_{1}k^{2} - \alpha u_{*}k^{2} \frac{\sin kR}{kR} \right]$$

$$= g(k, R),$$
(6)

where

$$g(k, R) = \begin{cases} (d_2 + \alpha)u_*k^2 \left[f_1(k, R) - f_2^T(k) \right] \left[f'(u_*) - d_1k^2 \right], & d_2 - \alpha = 0, \\ (d_2 - \alpha)u_*k^2 \left[-f'(u_*) + d_1k^2 \right] \left[f_1(k, R) - f_2^H(k) \right], & d_2 + \alpha = 0, \\ (d_2 + \alpha)(d_2 - \alpha)u_*^2k^4 \left[f_1(k, R) - f_2^T(k) \right] \left[f_1(k, R) - f_2^H(k) \right], & d_2 \pm \alpha \neq 0, \end{cases}$$

$$(7)$$

and $f_1(k, R)$, $f_2^T(k)$ and $f_2^H(k)$ are defined as

$$\begin{cases} f_1(k, R) = \frac{\sin kR}{kR}, \\ f_2^T(k) = -\frac{d_1}{(\alpha + d_2)u_*} + \frac{f'(u_*)}{(\alpha + d_2)u_*k^2}, \\ f_2^H(k) = -\frac{d_1}{(\alpha - d_2)u_*} + \frac{f'(u_*)}{(\alpha - d_2)u_*k^2}. \end{cases}$$
(8)

An immediate consequence of (6) is the following lemma.

Lemma 2.1 If g(k, R) > 0 (defined in (7)), then there exists a positive ω_k given by

$$\omega_k = \sqrt{g(k, R)}$$

such that (6) holds.

Define the critical values of τ as follows:

$$\tau_{k,j} = \begin{cases} \frac{1}{\omega_k} \left\{ \arccos\left(\frac{f'(u_*) - \alpha u_* k^2 \frac{\sin kR}{kR} - d_1 k^2}{d_2 u_* k^2 \frac{\sin kR}{kR}}\right) + 2j\pi \right\}, & \text{if } d_2 \sin(kR) > 0, \end{cases}$$

$$(9)$$

$$\frac{1}{\omega_k} \left\{ 2\pi - \arccos\left(\frac{f'(u_*) - \alpha u_* k^2 \frac{\sin kR}{kR} - d_1 k^2}{d_2 u_* k^2 \frac{\sin kR}{kR}}\right) + 2j\pi \right\}, & \text{if } d_2 \sin(kR) < 0, \end{cases}$$

for which the characteristic equation (4) admits purely imaginary roots $\pm i\omega_k$ when $\tau = \tau_{k,j}$ for some k > 0 and $j \in \mathbb{N}_0$. Furthermore, the transversality conditions at these critical values can be verified.

Lemma 2.2 Let $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ be a root of the characteristic equation (4) such that $\alpha(\tau_{k,j}) = 0$ and $\omega(\tau_{k,j}) = \omega_k$. Then,

$$\frac{\mathrm{d}\mathrm{Re}\lambda(\tau)}{\mathrm{d}\tau}\bigg|_{\tau=\tau_{k,j}}>0.$$

Proof Differentiating (4) with respect to τ , we obtain

$$\frac{\mathrm{d}\lambda}{\mathrm{d}\tau} = \frac{\lambda d_2 u_* k^2 \frac{\sin kR}{kR} e^{-\lambda\tau}}{1 - \tau d_2 u_* k^2 \frac{\sin kR}{kR} e^{-\lambda\tau}}.$$

Evaluating this derivative at $\lambda = i \omega_k$ and $\tau = \tau_{k,j}$, we find

$$\operatorname{Re}\left\{\frac{\mathrm{d}\tau}{\mathrm{d}\lambda}\Big|_{\lambda=i\omega_{k},\tau=\tau_{k,j}}\right\} = \operatorname{Re}\left\{\frac{1}{i\omega_{k}d_{2}u_{*}k^{2}\frac{\sin kR}{kR}(\cos\omega_{k}\tau_{k,j}-i\sin\omega_{k}\tau_{k,j})} - \frac{\tau_{k,j}}{i\omega_{k}}\right\}$$
$$= \frac{1}{\left(d_{2}u_{*}k^{2}\frac{\sin kR}{kR}\right)^{2}} > 0,$$

where the second equation in (5) has been utilized. The proof is completed. \Box

Before analyzing the stability of u_* , we first provide some properties of the function f_1 defined in (8). Let z = kR, then $f_1(z) = \frac{\sin z}{z}$. We have the following lemma which can be found in Proposition 3.3 of Xue et al. (2024).

Lemma 2.3 The function $f_1(z)$ obtains its local extremum at $z = z_j$, where $f_1(0) = 1$ and $z_j \ge 0$ are the countable number of roots of $\tan(z) = z$ satisfying $z_0 = 0$ and $z_j < z_{j+1}, j \in \mathbb{N}_0$. Moreover, we have

(i) $f_1(z)$ obtains its local minimum at $z = z_j$, j = 2(m - 1) + 1, and

$$f_1(z_{2m-1}) < f_1(z_{2m+1}) < 0, m \in \mathbb{N}.$$

(ii) $f_1(z)$ obtains its local maximum at $z = z_j$, j = 2m, and

$$f_1(z_{2m}) > f_1(z_{2(m+1)}) > 0, m \in \mathbb{N}_0.$$

Denote

$$\begin{cases} \alpha_{T_{2m}} = -\frac{d_1}{u_*} \frac{z_{2m}}{\sin z_{2m}} - d_2, m \in \mathbb{N}_0, \quad \alpha_{T_{2m-1}} = -\frac{d_1}{u_*} \frac{z_{2m-1}}{\sin z_{2m-1}} - d_2, m \in \mathbb{N}, \\ \alpha_{H_{2m}} = -\frac{d_1}{u_*} \frac{z_{2m}}{\sin z_{2m}} + d_2, m \in \mathbb{N}_0, \quad \alpha_{H_{2m-1}} = -\frac{d_1}{u_*} \frac{z_{2m-1}}{\sin z_{2m-1}} + d_2, m \in \mathbb{N}. \end{cases}$$
(10)

Notably, $\alpha_{T_0} = -\frac{d_1}{u_*} - d_2$ and $\alpha_{T_1} = -\frac{d_1}{u_*}\frac{z_1}{\sin z_1} - d_2$ represent the critical values of the stability boundary for u_* as stipulated in Proposition 2.1-(III).

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It is essential to know that if $\lambda = 0$ is a root of the characteristic equation (4) when $\tau = 0$, it remains a root for all positive values of τ as well. Consequently, by integrating the aforementioned analysis with Proposition 2.1-(III), we derive a series of proposition presented below.

Proposition 2.2 Assuming that $\alpha \pm d_2 > 0$ (or $\alpha \pm d_2 < 0$) and condition (**H**) holds, we have the following results.

- (*I*) For $d_2 > 0$ (or $d_2 < 0$):
 - (i) If $\alpha \leq \alpha_{T_1}$ (or $\alpha \geq \alpha_{T_0}$), where α_{T_1} and α_{T_0} are defined in (10), then u_* is locally asymptotically stable for any $R \geq 0$.
 - (ii) If $\alpha > \alpha_{T_1}$ (or $\alpha < \alpha_{T_0}$), there exists a critical value R_T^* of R such that:
 - (a) u_* is locally asymptotically stable for $R > R_T^*$;
 - (b) u_* is unstable for $0 < R < R_T^*$;
 - (c) The system (3) undergoes Turing bifurcation at $R = R_T^*$.

(II) For
$$d_2 < 0$$
 (or $d_2 > 0$):

- (i) If $\alpha \leq \alpha_{H_1}$ (or $\alpha \geq \alpha_{H_0}$), then u_* is locally asymptotically stable for any $R \geq 0$ and $\tau \geq 0$.
- (ii) If $\alpha_{H_1} < \alpha \le \alpha_{T_1}$ (or $\alpha_{T_0} \le \alpha < \alpha_{H_0}$), there exists a threshold R_H^* of R such that:
 - (a) For $R \ge R_H^*$, u_* is locally asymptotically stable for $\tau \ge 0$;
 - (b) For $0 < R < R_H^*$, there exists a threshold τ_* such that u_* is locally asymptotically stable for $0 \le \tau < \tau_*$ and unstable for $\tau > \tau_*$, with the system (3) undergoing Hopf bifurcation at $\tau = \tau_*$.
- (iii) If $\alpha > \alpha_{T_1}$ (or $\alpha < \alpha_{T_0}$), there exist critical values R_T^* and R_H^* of R with $R_T^* < R_H^*$ such that:
 - (a) For $R \ge R_H^*$, u_* is locally asymptotically stable for $\tau \ge 0$;
 - (b) For $R_T^* < R < R_H^*$, there exists a threshold τ_* similar to case (II)-(ii)-(b).
 - (c) For $0 < R < R_T^*$, u_* is unstable for $\tau \ge 0$;
 - (d) The system (3) undergoes Turing-Hopf bifurcation at $(R, \tau) = (R_T^*, \tau_*)$.

Proof We initially investigate the scenario where $\alpha \pm d_2 > 0$. It is established that both $f_2^T(k)$ and $f_2^H(k)$ exhibit an increasing trend with respect to k and

$$\lim_{k \to 0^+} f_2^T(k) = -\infty, \quad \sup f_2^T(k) = \lim_{k \to +\infty} f_2^T(k) = -\frac{d_1}{(\alpha + d_2)u_*} < 0, \quad (11)$$

$$\lim_{k \to 0^+} f_2^H(k) = -\infty, \quad \sup f_2^T(k) = \lim_{k \to +\infty} f_2^H(k) = -\frac{d_1}{(\alpha - d_2)u_*} < 0.$$
(12)

In addition, invoking Lemma 2.3, we derive

$$\min f_1(z) = \frac{\sin z_1}{z_1} < 0, \quad \lim_{z \to +\infty} f_1(z) = 0, \quad z = kR.$$
(13)



Fig. 2 The curves $f_1(k, R)$, and $f_2^T(k)$, $f_2^H(k)$ for different conditions of d_2 and α . (a)-(b): $\alpha \pm d_2 > 0$. (c)-(d): $\alpha \pm d_2 < 0$. Here, r = 0.8, $d_1 = 0.2$, R = 1

This implies the analogous behavior of $f_1(k, R)$ for k, R > 0:

$$\min_{k,R>0} f_1(k,R) = \frac{\sin z_1}{z_1}, \quad \lim_{k \to \infty} f_1(k,R) = 0.$$
(14)

Notably, the local minimum of $f_1(k, R)$ remains invariant under variations in both R and k.

The occurrence of zero roots is determined by the condition $f_1(k, R) < f_2^T(k)$, while the emergence of pure imaginary roots depends on the inequality $f_2^H(k) < f_1(k, R) < f_2^T(k)$ for $d_2 > 0$, or $f_2^T(k) < f_1(k, R) < f_2^H(k)$ for $d_2 < 0$. To determine the distribution of roots of the characteristic equation (4), we systematically analyze the relative positions of the curves $f_1(k, R)$, $f_2^T(k)$ and $f_2^H(k)$ for both cases $d_2 > 0$ and $d_2 < 0$, respectively.

Case I: For $d_2 > 0$, we observe that $f_2^H(k) < f_2^T(k) < 0$ holds for all k > 0, see Fig. 2-(a).

(i) Notably, the condition $\alpha \le \alpha_{T_1}$ is equivalent to $\frac{\sin z_1}{z_1} \ge -\frac{d_1}{(\alpha+d_2)u_*}$. Under this premise, it follows that $f_1(k, R) > f_2^T(k) > f_2^H(k)$ for any k, R > 0, see Fig. 2-(a). Consequently, all roots of the characteristic equation (4) possess strictly negative real parts, ensuring that u_* is locally asymptotically stable when $\alpha \le \alpha_{T_1}$.

(ii) Alternatively, when $\alpha > \alpha_{T_1}$, the situation becomes more intricate. According to Proposition 2.1-(III), $\lambda_k = 0$ is a root of the characteristic equation (4) when $f_1(k, R) = f_2^T(k)$. Furthermore, for certain values of k and R, if $f_1(k, R) < f_2^T(k)$, then $\lambda_k > 0$, indicating potential instability.

Crucially, the existence of $\omega_k > 0$ is governed by the condition $f_2^H(k) < f_1(k, R) < f_2^T(k)$ for some k and R, as established in Lemma 2.1. Notably, whenever the existence condition for ω_k is satisfied, Turing instability ensues, as stipulated by Proposition 2.1-(III). Thus, the conclusions regarding stability and the onset of Turing instability can be directly derived from these conditions and propositions.

Case II: For $d_2 < 0$, we have $f_2^T(k) < f_2^H(k) < 0$ for for all k > 0, see Fig. 2-(b).

(i) When $\alpha \leq \alpha_{H_1}$ (which is equivalent to the condition $\frac{\sin z_1}{z_1} \geq -\frac{d_1}{(\alpha - d_2)u_*}$), we have $f_1(k, R) > f_2^H(k) > f_2^T(k)$ for any k, R > 0, see Fig. 2-(b). Following a similar reasoning as in Case I-(i), we conclude that u_* is locally asymptotically stable for any R > 0.

(ii) For the intermediate range of α satisfying $\alpha_{H_1} < \alpha \leq \alpha_{T_1}$, we know from Proposition 2.1-(III) that u_* is locally asymptotically stable at $\tau = 0$. Consequently,

 $\lambda = 0$ is not a root of the characteristic equation (4), precluding the occurrence of Turing bifurcation.

Furthermore, the existence of $\omega_k > 0$ is contingent upon satisfying $f_2^T(k) < f_1(k, R) < f_2^H(k)$ for some specific values of k and R. Given that $\alpha_{H_1} < \alpha \leq \alpha_{T_1}$, it is guaranteed that $f_1(k, R) > f_2^T(k)$ for all positive k and R. Therefore, our focus shifts to identifying the conditions on R that ensure $f_1(k, R) < f_2^H(k)$ for some k > 0, which we proceed to explore in the subsequent analysis.

It is noteworthy that the sequence $\alpha_{H_1} < \alpha_{H_3} < \alpha_{H_5} < \cdots$ allow us to refine the interval $\alpha_{H_1} < \alpha \leq \alpha_{T_1}$ as follows

$$\alpha_{H_{2m-1}} < \alpha \leqslant \min\{\alpha_{H_{2m+1}}, \alpha_{T_1}\}, m \in \mathbb{N}.$$

Specifically, the condition $\alpha_{H_{2m-1}} < \alpha < \alpha_{H_{2m+1}}$ is equivalent to

$$\frac{\sin z_{2m-1}}{z_{2m-1}} < -\frac{d_1}{(\alpha - d_2)u_*} < \frac{\sin z_{2m+1}}{z_{2m+1}}.$$
(15)

According to (12) and Lemma 2.3, as *R* varies from large to small, $f_1(k, R)$ and $f_2^H(k)$ become tangent *m* times. We first consider the case when m = 1. In this scenario, there exists a unique $(k_H^{(1)}, R_H^{(1)})$ such that $f_1(k, R_H^{(1)})$ and $f_2^H(k)$ are tangent at $k = k_H^{(1)}$, which satisfies

$$f_1(k_H^{(1)}, R_H^{(1)}) = f_2^H(k_H^{(1)}), \quad \frac{\partial f_1(k, R_H^{(1)})}{\partial k} \bigg|_{k=k_H^{(1)}} = \frac{\mathrm{d} f_2^H(k)}{\mathrm{d} k} \bigg|_{k=k_H^{(1)}}$$

Notably, for m = 1, $R_H^* = R_H^{(1)}$. We now analyze two subcases:

(a) For $R \ge R_H^{(1)}$, $f_1(k, R) \ge f_2^H(k)$ for any k > 0. By Lemma 2.1, all roots of (4) have strictly negative real parts, implying that u_* is locally asymptotically stable.

(**b**) Fix $R < R_H^{(1)}$. In this case, there exist two distinct positive values $k_{H_{c_1}}^{(1)}$ and $k_{H_{c_2}}^{(1)}$ such that $f_1(k, R)$ intersects $f_2^H(k)$ at these points, and $f_1(k, R) < f_2^H(k)$ for $k \in (k_{H_{c_1}}^{(1)}, k_{H_{c_2}}^{(1)})$. According to Lemma 2.1, the characteristic equation (4) admits a pair of purely imaginary root $\pm i\omega_k^{(1)}$ at $\tau = \tau_{k,j}^{(1)}$ for $j \in \mathbb{N}_0$ and fixed $k \in (k_{H_{c_1}}^{(1)}, k_{H_{c_2}}^{(1)})$. Let $\tau_* = \min_{k \in (k_{H_{c_1}}^{(1)}, k_{H_{c_2}}^{(1)}) \{\tau_{k,0}^{(1)}\}$. Consequently, u_* is locally asymptotically stable for $0 \le \tau < \tau_*$ and becomes unstable for $\tau > \tau_*$. Moreover, the system (3) undergoes a Hopf bifurcation at $\tau = \tau_*$.

For all instances where *m* ranges from 2 up to a specified value \tilde{m} , there exist \tilde{m} pairs $(k_H^{(m)}, R_H^{(m)})$ such that, as *R* varies from large to small, the functions $f_1(k, R_H^{(m)})$ and $f_2^H(k)$ are tangent to each other at the point $k = k_H^{(m)}$ for $m = 1, 2, ..., \tilde{m}$. Analogous to the proof devised for the special case where $m = \tilde{m} = 1$, we can demonstrate that the characteristic equation (4) possesses purely imaginary roots denoted by $\omega_k^{(m)}$ at specific delays $\tau = \tau_{k,j}^{(m)}$ for all non-negative integers $j \in \mathbb{N}_0$. Subsequently, we define

two critical parameters:

$$R_{H}^{*} = \max\left\{R_{H}^{(1)}, R_{H}^{(2)}, \dots, R_{H}^{(\tilde{m})}\right\}, \quad \tau_{*} = \min_{k \in I_{H}}\{\tau_{k,0}^{(m)}\},$$

where I_H represents a bounded set of positive k values that satisfy the following conditions:

$$I_H = \left\{ k > 0 : f_1(k, R) > f_2^T(k) \text{ and } f_1(k, R) < f_2^H(k) \right\}.$$
 (16)

With these definitions, the corresponding results can be systematically derived and presented.

(iii) For $\alpha > \alpha_{T_1}$, which is equivalent to $\frac{\sin z_1}{z_1} < -\frac{d_1}{(\alpha+d_2)u_*}$, we note the following inequalities from the expression in (10): $\alpha_{H_1} < \alpha_{H_3} > \alpha_{H_5} < \cdots, \alpha_{T_1} < \alpha_{T_3} < \cdots$ $\alpha_{T_5} < \cdots$, and $\alpha_{H_{2m-1}} < \alpha_{T_{2m-1}}$ for each $m \in \mathbb{N}$. Using the same approach as in (ii), $\alpha > \alpha_{T_1}$ can be divided as $\alpha_{H_{2m-1}} < \alpha < \alpha_{H_{2m+1}}$ and $\alpha_{T_{2n-1}} < \alpha < \alpha_{T_{2n+1}}$, which is equivalent to the following inequalities, respectively:

$$\frac{\sin z_{2m-1}}{z_{2m-1}} < -\frac{d_1}{(\alpha - d_2)u_*} \le \frac{\sin z_{2m+1}}{z_{2m+1}}, \quad m \in \mathbb{N},$$
$$\frac{\sin z_{2n-1}}{z_{2n-1}} < -\frac{d_1}{(\alpha + d_2)u_*} \le \frac{\sin z_{2n+1}}{z_{2n+1}}, \quad n \in \mathbb{N}.$$

As R varies from large to small, $f_1(k, R)$ and $f_2^H(k)$ are tangent m times, and $f_1(k, R)$ and $f_2^T(k)$ are tangent *n* times.

We first consider the case where m = n = 1. There exist $(k_H^{(1)}, R_H^{(1)})$ and $(k_T^{(1)}, R_T^{(1)})$ such that $f_1(k, R_H^{(1)})$ and $f_2^H(k)$ are tangent at $k = k_H^{(1)}$, and $f_1(k, R_T^{(1)})$ and $f_2^T(k)$ are tangent at $k = k_T^{(1)}$ (as derived from (11)-(13)). Additionally, $R_H^{(1)} > R_T^{(1)}$ since $f_2^H(k) > f_2^T(k)$ for any k > 0.

- For R ≥ R_H⁽¹⁾, f₁(k, R) > f₂^H(k) > f₂^T(k) for any k > 0. Consequently, all roots of the characteristic equation (4) have strictly negative real parts.
 For a fixed R such that R_T⁽¹⁾ < R < R_H⁽¹⁾, f₁(k, R) > f₂^T(k) for all k > 0. Furthermore, there exist k_{H_{c1}}⁽¹⁾, k_{H_{c2}}⁽¹⁾ > 0 such that f₁(k, R) and f₂^H(k) intersect at $k = k_{H_{c_1}}^{(1)}$ and $k = k_{H_{c_2}}^{(1)}$. Therefore, the characteristic equation (4) has no zero roots but has a purely imaginary root $\pm i\omega_k^{(1)}$ at $\tau = \tau_{k,j}^{(1)}$ for $j \in \mathbb{N}_0$ and a fixed $k \in (k_{H_{c_1}}^{(1)}, k_{H_{c_2}}^{(1)}).$
- 3) For $R = R_T^{(1)} < R_H^{(1)}$, $f_1(k_T^{(1)}, R_T^{(1)}) = f_2^T(k_T^{(1)})$ for any $\tau \ge 0$. This implies that the characteristic equation (4) has a zero root at $(k, R) = (k_T^{(1)}, R_T^{(1)})$. Additionally, there exist $k_{H_{c_1}}^{(1)}, k_{H_{c_2}}^{(1)} > 0$ such that $f_1(k, R)$ and $f_2^H(k)$ intersect at $k = k_{H_{c_1}}^{(1)}$ and $k = k_{H_{c_2}}^{(1)}$. Then $f_1(k, R) > f_2^H(k)$ for $k \in (0, k_{H_{c_1}}^{(1)}) \cup (k_{H_{c_2}}^{(1)}, \infty)$ and $f_1(k, R) > k_{H_{c_2}}^H(k)$ $f_2^T(k), f_1(k, R) < f_2^H(k)$ for $k \in (k_{H_{c_1}}^{(1)}, k_{H_{c_2}}^{(1)}) \setminus k_T^{(1)}$. Therefore, the characteristic

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equation (4) has a zero root and a pair of purely imaginary roots $\pm i\omega_k^{(1)}$, and all other roots have strictly negative real parts derived from Lemma 2.1.

4) For $R < R_T^{(1)}$, there exist $k_{T_{c_1}}^{(1)}, k_{T_{c_2}}^{(1)} > 0$ such that $f_1(k, R)$ and $f_2^T(k)$ intersect at $k = k_{T_{c_1}}^{(1)}$ and $k = k_{T_{c_2}}^{(1)}$. For $k \in (0, k_{T_{c_1}}^{(1)}) \cup (k_{T_{c_2}}^{(1)}, \infty)$, we have $f_1(k, R) > f_2^T(k)$. Consequently, the characteristic equation (4) has at least one root with a positive real part for $k \in (k_{T_{c_1}}^{(1)}, k_{T_{c_2}}^{(1)})$.

Let $R_T^* = R_T^{(1)}$, $R_H^* = R_H^{(1)}$, and $\tau_* = \min\{\tau_{k,0}^{(1)}, k \in I_H\}$, where I_H is defined in (16). Based on the above analysis, the results can be confirmed for m = n = 1.

For other cases where $m, n \in \mathbb{N}$, there exist pairs $(k_H^{(m)}, R_H^{(m)})$ for $m = 1, 2, ..., \tilde{m}$ such that $f_1(k, R_H^{(m)})$ and $f_2^H(k)$ are tangent at $k = k_H^{(m)}$. Similarly, there exist pairs $(k_T^{(n)}, R_T^{(n)})$ for $n = 1, 2, ..., \tilde{n}$ such that $f_1(k, R_T^{(n)})$ and $f_2^T(k)$ are tangent at $k = k_T^{(n)}$. Following a similar line of proof as for the case where m = n = 1, the characteristic equation (4) possesses purely imaginary roots $\omega_k^{(m)}$ at $\tau = \tau_{k,j}^{(m)}$ for $j \in \mathbb{N}_0$. We define

$$R_{H}^{*} = \max\left\{R_{H}^{(1)}, \dots, R_{H}^{(\tilde{m})}\right\}, \quad R_{T}^{*} = \max\left\{R_{T}^{(1)}, \dots, R_{T}^{(\tilde{m})}\right\}, \quad \tau_{*} = \min_{k \in I_{H}}\{\tau_{k,0}^{(m)}\},$$

where I_H is a set defined in (16) and is bounded. Since $f_2^H(k) > f_2^T(k)$ for any k > 0, it follows that $R_H^* > R_T^*$.

The proof for the case where $\alpha \pm d_2 > 0$ is thus completed.

For $\alpha \pm d_2 < 0$, both $f_2^T(k)$ and $f_2^H(k)$ decrease with respect to k and

$$\lim_{k \to 0^+} f_2^T(k) = +\infty, \quad \sup f_2^T(k) = \lim_{k \to +\infty} f_2^T(k) = -\frac{d_1}{(\alpha + d_2)u_*} > 0,$$
$$\lim_{k \to 0^+} f_2^H(k) = +\infty, \quad \sup f_2^T(k) = \lim_{k \to +\infty} f_2^H(k) = -\frac{d_1}{(\alpha - d_2)u_*} > 0.$$

The curves of $f_2^T(k)$ and $f_2^H(k)$ are shown in Fig. 2-(c) for $d_2 < 0$ and in Fig. 2-(d) for $d_2 > 0$. The remainder of the proof follows a similar analysis to the case where $\alpha \pm d_2 > 0$ and we omit the detailed discussion for brevity.

Remark 3 For the specific scenarios where either $\alpha - d_2 = 0$ or $\alpha + d_2 = 0$, by adopting an analytical methodology akin to that presented in Proposition 2.2 and invoking Lemma 2.1, we can conclude that the results (which we omit here for brevity) are consistent with those outlined in Proposition 2.2-(I) and Proposition 2.2-(II)(i-ii), respectively.

Proposition 2.3 Suppose that $\alpha + d_2 > 0$ and $\alpha - d_2 < 0$ (or vice versa), and further assume that (**H**) holds. The stability properties of u_* are as follows:

- (I) If $\alpha \leq \alpha_{T_1}, \alpha \geq \alpha_{H_0}$ (or $\alpha \geq \alpha_{T_0}, \alpha \leq \alpha_{H_1}$), then u_* is locally asymptotically stable for any $R \geq 0$ and $\tau \geq 0$.
- (II) If $\alpha \leq \alpha_{T_1}$, $\alpha < \alpha_{H_0}$ (or $\alpha \geq \alpha_{T_0}$, $\alpha > \alpha_{H_1}$), there exists a threshold R_H^* of R such that



Fig. 3 The curves $f_1(k, R)$, and $f_2^T(k)$, $f_2^H(k)$ for different conditions of d_2 and α . (a): $\alpha + d_2 > 0$ and $\alpha - d_2 < 0$. (b): $\alpha + d_2 < 0$ and $\alpha - d_2 > 0$. Here, r = 0.8, $d_1 = 0.2$, R = 1

- (a) For $R \ge R_H^*$, u_* is locally asymptotically stable for all $\tau \ge 0$.
- (b) For $0 < R < R_H^*$, there exists a threshold τ_* where u_* is locally asymptotically stable for $0 \le \tau < \tau_*$ and becomes unstable for $\tau > \tau_*$. At $\tau = \tau_*$, the system (3) undergoes a Hopf bifurcation.
- (III) If $\alpha > \alpha_{T_1}, \alpha < \alpha_{H_0}$ (or $\alpha < \alpha_{T_0}, \alpha > \alpha_{H_1}$), there exists two critical values of R, denoted R_T^* and R_H^* , determining the stability.
 - (*i*) If $R_T^* < R_H^*$, then
 - (a) For $R \ge R_H^*$, u_* is locally asymptotically stable.
 - (b) For $R_T^* < R < R_H^*$, there exists a critical delay τ_* similar to case (II)-(b).
 - (c) For $0 < R < R_T^*$, u_* is unstable for all $\tau \ge 0$.
 - (d) At the point $(R, \tau) = (R_T^*, \tau_*)$, the system (3) undergoes a Turing-Hopf bifurcation.
 - (ii) If $R_T^* \ge R_H^*$, then
 - (a) u_* is locally asymptotically stable for $R > R_T^*$.
 - (b) u_* is unstable for $0 < R < R_T^*$.
 - (c) The system (3) undergoes a Turing bifurcation at $R = R_T^*$.
- (IV) If $\alpha > \alpha_{T_1}, \alpha > \alpha_{H_0}$ (or $\alpha < \alpha_{T_0}, \alpha < \alpha_{H_1}$), there exists a critical value R_T^* of R similar to the case (III) $R_T^* \ge R_H^*$.

Proof We only consider the case where $\alpha + d_2 > 0$ and $\alpha - d_2 < 0$, with the corresponding curves of $f_2^T(k)$ and $f_2^H(k)$ shown in Fig. 3-(a). Similarly, the curves for the alternative case where $\alpha + d_2 < 0$ and $\alpha - d_2 > 0$ are depicted in Fig.(3)-(b). The proof for this case follows a similar approach to the previous one and is omitted here for brevity.

Similarly, we will derive the distribution of the roots of characteristic equation (4) by examining the positional relationships among the curves $f_1(k, R)$, $f_2^T(k)$, and $f_2^H(k)$.

When $\alpha + d_2 > 0$ and $\alpha - d_2 < 0$, $f_2^T(k)$ increases with k while $f_2^H(k)$ decreases with k. Furthermore,

$$\lim_{k \to 0^+} f_2^T(k) = -\infty, \quad \sup f_2^T(k) = \lim_{k \to +\infty} f_2^T(k) = -\frac{d_1}{(\alpha + d_2)u_*} < 0, \quad (17)$$

$$\lim_{k \to 0^+} f_2^H(k) = +\infty, \quad \sup f_2^T(k) = \lim_{k \to +\infty} f_2^H(k) = -\frac{d_1}{(\alpha - d_2)u_*} > 0.$$
(18)

Additionally, according to Lemma 2.3, we have

$$\sup f_1(z) = \lim_{z \to 0^+} f_1(z) = 1, \quad \min f_1(z) = \frac{\sin z_1}{z_1} < 0, \quad \lim_{z \to +\infty} f_1(z) = 0, \quad (19)$$

where z = kR. It follows that

$$\sup_{k>0} f_1(k, R) = \lim_{k \to 0} f_1(k, R) = 1, \quad \min_{k, R>0} f_1(k, R) = \frac{\sin z_1}{z_1}, \quad \lim_{k \to \infty} f_1(k, R) = 0,$$
(20)

and the local maxima and minima of $f_1(k, R)$ are invariant with respect to both R and k.

Notice that $\lambda_k = 0$ is a root of (4) when $f_1(k, R) = f_2^T(k)$, and $\omega_k > 0$ exists if and only if either $f_1(k, R) < f_2^T(k)$ and $f_1(k, R) < f_2^H(k)$, or $f_1(k, R) > f_2^T(k)$ and $f_1(k, R) < f_2^H(k)$ for some k and R, as stated in Lemma 2.1.

(I) When $\alpha \leq \alpha_{T_1}$ and $\alpha \geq \alpha_{H_0}$, which is equivalent to $\frac{\sin z_1}{z_1} \geq -\frac{d_1}{(\alpha+d_2)u_*}$ and $1 \leq -\frac{d_1}{(\alpha-d_2)u_*}$, respectively, it follows that $f_1(k, R) > f_2^T(k)$ and $f_1(k, R) < f_2^H(k)$ for any k, R > 0, see Fig. 3-(a). Therefore, all the roots of (4) have strictly negative real parts, implying that u_* is locally asymptotically stable.

(II) When $\alpha \leq \alpha_{T_1}$, u_* is locally asymptotically stable for $\tau = 0$ according to Proposition 2.1-(III). Consequently, $\lambda = 0$ is not a root of (4), and Turing bifurcation cannot occur. Given that $\alpha \leq \alpha_{T_1}$ implies $f_1(k, R) > f_2^T(k)$ for all k, R > 0, the existence of $\omega_k > 0$ is contingent upon $f_1(k, R) > f_2^H(k)$ for some k and R. Therefore, we focus solely on identifying the condition for R such that $f_1(k, R) > f_2^H(k)$ for some k > 0. Noting that $\alpha_{H_0} > \alpha_{H_2} > \alpha_{H_4} > \cdots$, the interval $\alpha \leq \alpha_{T_1}, \alpha < \alpha_{H_0}$ can be partitioned as:

$$[\alpha_{H_{2(m+1)}}, \alpha_{H_{2m}}) \cap [\alpha_{T_1}, \infty), \quad m \in \mathbb{N}.$$

The remaining analysis follows similarly to the proof of Proposition 2.2-(II)-(iii) and is therefore omitted for brevity.

(III) When $\alpha > \alpha_{T_1}$ and $\alpha < \alpha_{H_0}$, this implies that

$$\min f_1(k, R) < \sup f_2^T(k)$$
 and $\max f_1(k, R) > \inf f_2^H(k)$.

Noting that $\alpha_{H_0} > \alpha_{H_2} > \alpha_{H_4} > \cdots$ and $\alpha_{T_1} < \alpha_{T_3} < \alpha_{T_5} < \cdots$, we can divide the interval of α as follows:

$$\alpha_{H_{2(m+1)}} < \alpha < \alpha_{H_{2m}}$$
 and $\alpha_{T_{2n-1}} < \alpha < \alpha_{T_{2n+1}}$,

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which is equivalent to

$$\frac{\sin z_{2(m+1)}}{z_{2(m+1)}} < -\frac{d_1}{(\alpha - d_2)u_*} \le \frac{\sin z_{2m}}{z_{2m}}, \quad m \in \mathbb{N},$$
$$\frac{\sin z_{2n-1}}{z_{2n-1}} < -\frac{d_1}{(\alpha + d_2)u_*} \le \frac{\sin z_{2n+1}}{z_{2n+1}}, \quad n \in \mathbb{N},$$

respectively. As *R* varies from large to small, $f_1(k, R)$ and $f_2^H(k)$ become tangent m + 1 times, and $f_1(k, R)$ and $f_2^T(k)$ become tangent *n* times.

We first consider the case where m = 0 and n = 1. Then, from (17)-(19), there exist $(k_H^{(0)}, R_H^{(0)})$ and $(k_T^{(1)}, R_T^{(1)})$ such that $f_1(k, R_H^{(0)})$ and $f_2^H(k)$ are tangent at $k = k_H^{(0)}$, and $f_1(k, R_T^{(1)})$ and $f_2^T(k)$ are tangent at $k = k_T^{(1)}$. Specifically,

$$\begin{aligned} f_1(k_H^{(0)}, R_H^{(0)}) &= f_2^H(k_H^{(0)}), \quad \frac{\partial f_1(k, R)}{\partial k} \bigg|_{k_H^{(0)}} = \frac{\mathrm{d} f_2^H(k)}{\mathrm{d} k} \bigg|_{k_H^{(0)}}, \\ f_1(k_T^{(1)}, R_T^{(1)}) &= f_2^T(k_T^{(1)}), \quad \frac{\partial f_1(k, R)}{\partial k} \bigg|_{k_T^{(1)}} = \frac{\mathrm{d} f_2^T(k)}{\mathrm{d} k} \bigg|_{k_T^{(1)}}. \end{aligned}$$

Notice that $R_T^* = R_T^{(1)}$ and $R_H^* = R_H^{(0)}$.

When $R_H^{(0)} > R_T^{(1)}$, by following a similar analysis to the proof of Proposition 2.2-(II)-(iii), we have

- 1) For $R \ge R_H^{(0)} > R_T^{(1)}$, $f_1(k, R) > f_2^T(k)$ and $f_1(k, R) < f_2^H(k)$ for any k > 0. Consequently, all the roots of the characteristic equation (4) have strictly negative real parts.
- 2) For a fixed *R* such that $R_T^{(1)} < R < R_H^{(0)}$, we have $f_1(k, R) > f_2^T(k)$ for all k > 0. Additionally, there exist $k_{H_{c_1}}^{(0)}, k_{H_{c_2}}^{(0)} > 0$ such that $f_1(k, R)$ and $f_2^H(k)$ intersect at $k = k_{H_{c_1}}^{(0)}$ and $k = k_{H_{c_2}}^{(0)}$. It follows that the characteristic equation (4) has no zero roots but does have a purely imaginary root $\pm i\omega_k^{(0)}$ at $\tau = \tau_{k,j}^{(0)}$ for $j \in \mathbb{N}_0$ and a fixed $k \in (k_{H_{c_1}}^{(0)}, k_{H_{c_2}}^{(0)})$.
- 3) For $R = R_T^{(1)} < R_H^{(0)}$, we have $f_1(k_T^{(1)}, R_T^{(1)}) = f_2^T(k_T^{(1)})$ for any $\tau \ge 0$, which implies that the characteristic equation (4) has a zero root at $(k, R) = (k_T^{(1)}, R_T^{(1)})$. Furthermore, there exist $k_{H_{c_1}}^{(0)}, k_{H_{c_2}}^{(0)} > 0$ such that $f_1(k, R)$ and $f_2^H(k)$ intersect at $k = k_{H_{c_1}}^{(0)}$ and $k = k_{H_{c_2}}^{(0)}$. Additionally, $f_1(k, R) > f_2^H(k)$ for $k \in (0, k_{H_{c_1}}^{(0)}) \cup$ $(k_{H_{c_2}}^{(0)}, \infty)$, and $f_1(k, R) > f_2^T(k)$, $f_1(k, R) < f_2^H(k)$ for $k \in (k_{H_{c_1}}^{(0)}, k_{H_{c_2}}^{(0)}) \setminus k_T^{(1)}$. Therefore, the characteristic equation (4) has a zero root and a pair of purely imaginary roots $\pm i\omega_k^{(1)}$, with all other roots having strictly negative real parts according to Lemma 2.1.
- 4) For $R < R_T^{(1)}$, there exist $k_{T_{c_1}}^{(1)}, k_{T_{c_2}}^{(1)} > 0$ such that $f_1(k, R)$ and $f_2^T(k)$ intersect at $k = k_{T_{c_1}}^{(1)}$ and $k = k_{T_{c_2}}^{(1)}$. Additionally, $f_1(k, R) > f_2^T(k)$ for $k \in (0, k_{T_{c_1}}^{(1)}) \cup$

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 $(k_{T_{c_2}}^{(1)}, \infty)$. It follows that the characteristic equation (4) has at least one root with a positive real part for $k \in (k_{T_{c_1}}^{(1)}, k_{T_{c_2}}^{(1)})$.

Let $\tau_* = \min\{\tau_{k,0}^{(1)}, k \in I_H\}$, where I_H is defined in (16).

When $R_H^{(0)} < R_T^{(1)}$, by applying a similar analysis to the proof of Proposition 2.2-(II)-(iii), the following conclusions can be drawn:

- For R ≥ R_T⁽¹⁾ > R_H⁽⁰⁾, it holds that f₁(k, R) > f₂^T(k) and f₁(k, R) < f₂^H(k) for any k > 0. Consequently, all the roots of (4) possess strictly negative real parts.
 When R = R_T⁽¹⁾, we observe that f₁(k_T⁽¹⁾, R_T⁽¹⁾) = f₂^T(k_T⁽¹⁾) for any τ ≥ 0. This
- implies that (4) admits a zero root at $(k, R) = (k_T^{(1)}, R_T^{(1)})$.
- 3) For $R < R_T^{(1)}$, there exist positive values $k_{T_{c_1}}^{(1)}$ and $k_{T_{c_2}}^{(1)}$ such that $f_1(k, R)$ and $f_2^T(k)$ intersect at $k = k_{T_{c_1}}^{(1)}$ and $k = k_{T_{c_2}}^{(1)}$. Furthermore, $f_1(k, R) > f_2^T(k)$ for $k \in (0, k_{T_{c_1}}^{(1)}) \cup (k_{T_{c_2}}^{(1)}, \infty)$. As a result, (4) possesses at least one root with a positive real part for $k \in (k_{T_{c_1}}^{(1)}, k_{T_{c_2}}^{(1)})$.

Based on the above analysis, the results can be confirmed for the case where m = 0and n = 1.

For the other cases of m and n, a similar analysis can be applied, but we omit the details here.

(IV) Since $\alpha \ge \alpha_{H_0}$ implies that $f_1(k, R) < f_2^H(k)$ for any k and R > 0, it follows from Lemma 2.1 that there exists $\omega_k > 0$ if and only if $f_1(k, R) < f_2^T(k)$ for some k and R. This inevitably leads to the occurrence of Turing instability. Consequently, the results can be directly inferred from Proposition 2.1-(III).

The proof is now complete.

Theorem 1.1 can be directly derived from Propositions 2.2, 2.3, and Remark 3.

3 An application to a logistic model

In this section, we will apply the findings to the following model:

$$\begin{cases} u_t = d_1 u_{xx} + d_2 (u(K_R * u_\tau)_x)_x + \alpha (u(K_R * u)_x)_x + ru(1-u), \\ u(-L,t) = u(L,t), \ u_x(-L,t) = u_x(L,t), \end{cases}$$
(21)

where r > 0 represents the intrinsic growth rate. It is evident that the equation (21) possesses a unique constant steady state $u_* = 1$.

Set

$$r = 0.8, d_1 = 0.2.$$

Based on Proposition 2.1 and Theorem 1.1, we establish the stability of the constant steady state u_* within the (d_2, α) -plane, as depicted in Fig. 4. Notably, when R = 0 (i.e., in the absence of a perception scale), the introduction of a time delay τ alters the stability boundary of u_* from a single line defined by $\alpha = -\frac{d_1}{u_*} - d_2$ to a more intricate configuration involving two lines: $\alpha = -\frac{d_1}{u_*} - d_2$ and $\alpha = -\frac{d_1}{u_*} + d_2$. Importantly, despite the introduction of τ , the stability of u_* remains solely dependent on the coefficients d_2 and α , with τ having no direct influence. Conversely, when $\tau = 0$ (no time delay), the perception scale R, alongside d_2 and α , emerges as a crucial factor influencing the stability of u_* . Specifically, a small value of R can destabilize an otherwise stable u_* , whereas a larger R may stabilize previously unstable regions. This underscores the sensitivity of the system's stability to variations in the perception scale. Furthermore, in the scenario where both R and τ are positive, the system's dynamics become profoundly intricate. The stability of the constant steady state u_* is intricately tied to the specific region within the (d_2, α) -plane where the parameters d_2 and α reside. In these circumstances, u_* may manifest stability or undergo dynamical transitions such as Hopf, Turing, or even Turing-Hopf bifurcations, with R and τ playing pivotal roles as tuning parameters. To provide a deeper understanding of these complexities, we shall subsequently present detailed numerical analyses, exploring the behavior of u_* across diverse regions of the (d_2, α) -plane, while systematically varying the parameters R and τ .

Choosing $d_2 = -0.8$ and according to (10), we derive the following coefficients:

$$\alpha_{H_0} = -1, \quad \alpha_{H_1} \doteq 0.1207, \quad \alpha_{H_2} \doteq -2.3579, \quad \alpha_{H_3} \doteq 1.3900, \\ \alpha_{T_0} = 0.6, \quad \alpha_{T_1} \doteq 1.7207, \quad \alpha_{T_2} \doteq -0.7579, \quad \alpha_{T_3} \doteq 2.9900.$$

By selecting $\alpha = 1.5$ (Q_1 in Fig. 4-(d)), which satisfies the conditions $\alpha \pm d_2 > 0$ and $\alpha_{H_3} < \alpha < \alpha_{T_1}$, we proceed to compute the functions:

$$f_2^T(k) = -\frac{8}{7k^2} - \frac{2}{7}, \quad f_2^H(k) = -\frac{8}{23k^2} - \frac{2}{23}$$

Subsequently, it is determined that $f_1(k, R)$ and $f_2^T(k)$ do not intersect, whereas $f_1(k, R)$ tangentially intersects $f_2^H(k)$ at points $(k_H^{(1)}, R_H^{(1)}) \doteq (1.6784, 2.8295)$ and $(k_H^{(2)}, R_H^{(2)}) \doteq (8.9265, 1.2225)$. Invoking Proposition 2.2-(II)-(ii) (or Theorem 1.1-(II)), we establish:

$$R_H^* = \max\{R_H^{(1)}, R_H^{(2)}\} = R_H^{(1)} \doteq 2.8295.$$

Setting L = 5, the bifurcation curves in the (d_2, α) -plane are depicted in Fig. 5. Consequently, the constant steady state u_* is asymptotically stable for $R > R_H^*$ and $\tau > 0$, as illustrated in Fig. 6-(a). Moving on, we consider the interval $R_H^{(2)} < R < R_H^*$, within which the characteristic equation (4) possesses precisely one pair of purely imaginary roots. By selecting R = 2.4, which falls within this interval, we determine that the characteristic equation yields a pair of purely imaginary roots $\pm i\omega_n$, with $\omega_n \doteq 0.5060$ for n = 3. The corresponding critical delay $\tau_* \doteq 4.3091$ is derived from (9). Consequently, the stability of u_* transitions from asymptotic stability when $\tau = 3.8 < \tau_*$ to instability when $\tau = 4.5 > \tau_*$, as evidenced by Fig. 6-(b) and (c).



Fig. 4 The local dynamics of (3) near u_* in the (d_2, α) -plane are explored for all R and τ cases. Panel (d) is same as Fig. 1, categorizing regions I to V with absolute stability, Hopf bifurcation, Turing instability, Turing-Hopf bifurcation, and Turing/Turing-Hopf bifurcations, respectively. Specific points Q_1 to Q_5 are identified within these regions, highlighting the diversity of dynamical behaviors. $Q_1 = (-0.8, 1.5), Q_2 = (-0.2, -0.483), Q_3 = (-0.2, 1.725), Q_4 = (0.8, 0.1622), Q_5 = (0.8, 0.5)$

Notably, Fig. 5-(b) highlights the intersection point $O_{H_4H_5}$ of the curves $\tau_{4,0}$ and $\tau_{5,0}$, marking a double Hopf bifurcation point where Hopf bifurcation curves associated with distinct wave numbers intersect. The intricate dynamical behavior in the vicinity of this double Hopf bifurcation point $O_{H_4H_5}$ is further illuminated in Fig. 6-(d) to (f).

Choosing $d_2 = -0.2$, from (10), we derive the following critical values:

$$\alpha_{H_1} \doteq 0.7207, \ \alpha_{H_3} \doteq 1.9900, \ \alpha_{T_0} = 0,$$

 $\alpha_{T_1} \doteq 1.1207, \ \alpha_{T_2} \doteq -1.3579, \ \alpha_{T_3} \doteq 2.3900.$

Selecting $\alpha = -0.483$ (Q_2 in Fig. 4-(d)) such that the conditions $\alpha \pm d_2 < 0$ and $\alpha_{T_2} < \alpha < \alpha_{T_0}$ hold, we obtain

$$f_2^T(k) = \frac{800}{683k^2} + \frac{200}{683}.$$



Fig. 5 The bifurcation diagrams of model (3) in the (R, τ) -plane at Q_1 (Fig. 4-(d)). The left panel offers an overview, and the right panel magnifies the solid line for clarity. Key features include the Hopf bifurcation threshold $R_H^* \doteq 2.8295$



Fig. 6 Solutions of system (3) exhibited for varying (R, τ) combinations. Upper row (a)-(c) illustrates the response with initial condition $u_0(x, t) = 1 + 0.1 \cos((3\pi x/5))$ for $t \in [-\tau, 0]$. The lower row (d)-(f) shows the results for initial condition $u_0(x, t) = 1 + 0.1 \cos((4\pi x/5))$ over the same time interval

Subsequently, we identify the tangency point between $f_2^T(k)$ and $f_1(k, R)$ at

$$(k_T^*, R_T^*) \doteq (1.8867, 0.8517).$$

This leads to the bifurcation curves depicted in Fig. 7-(a) from Proposition 2.2-(I) (or Theorem 1.1-(III)). When *R* exceeds R_T^* , $f_1(k, R)$ and $f_2^T(k)$ do not intersect. Conversely, selecting R = 0.8 (which is less than R_T^*), we find intersection points at $k_{T_{c_1}} \doteq 1.6069$ and $k_{T_{c_2}} \doteq 2.3606$. Assuming L = 10, we compute $n_T^* = \frac{k_T^* L}{\pi} \doteq 6.0057$ and determine $n = \{6, 7\}$ from the range $k_{T_{c_1}} < n < k_{T_{c_2}}$. Consequently, for any positive τ , at least one characteristic roots of (4) possess positive real parts, indicating that u_* is unstable and a spatial nonhomogeneous steady



Fig. 7 Left (a): Bifurcation curve of u_* in the (d_2, α) -plane at Q_2 from Fig. 4-(d). Right (b)-(e): Solutions of model (3) for varying (R, τ) combinations, with initial condition $u_0(x, t) = 1 + 0.1 \cos(0.6\pi x)$ for $t \in [-\tau, 0]$. Key parameters: $R_T^* \doteq 0.8517$, $n_T^* \doteq 6.0057$

state emerges, as illustrated in Fig. 7-(e). Furthermore, in Fig. 7-(a), it is discernible that the stability of the system remains unaffected by variations in the time delay τ , whether it is zero or non-zero. Importantly, regardless of the presence or absence of τ , a decrease in the parameter *R* consistently destabilizes u_* , triggering the emergence of spatially nonhomogeneous steady states see Fig. 7-(b) to (e). This is consistent with the theoretical results.

Subsequently, we select $\alpha = 1.725$ (Q_3 in Fig. 4-(d)) to ensure it lies within the interval defined by $\alpha_{T_1} < \alpha < \alpha_{H_3}$. This choice leads to the explicit forms of the functions $f_2^T(k)$ and $f_2^H(k)$ as

$$f_2^T(k) = -\frac{32}{61k^2} - \frac{8}{61}, \quad f_2^H(k) = -\frac{32}{77k^2} - \frac{8}{77}.$$

At the tangency points between $f_1(k, R)$ and these functions, we obtain

$$(k_T^*, R_T^*) \doteq (2.5140, 1.8553), \quad (k_H^*, R_H^*) \doteq (1.9606, 2.4058),$$

with the crucial observation that $R_T^* < R_H^*$. The bifurcation behavior of the model (3) in the (R, τ) -plane is depicted in Fig. 8. This figure is in congruence with the theoretical predictions outlined in Proposition 2.2-(II)-(iii) (or Theorem 1.1-(IV)), reinforcing the validity of our analytical and numerical findings. Assuming a domain length of L = 10, we calculate the critical mode number associated with the Turing instability as $n_T^* = \frac{k_T^* L}{\pi} \doteq 8.0023$. When R is chosen such that $R_T^* < R < R_H^*$, a Hopf bifurcation occurs as τ traverses the stability boundary. Consequently, spatial nonhomogeneous periodic solutions emerge, as evidenced in Fig. 9-(d), (e), and (h). In contrast, for $R < R_T^*$, the steady state u_* becomes unstable, giving rise to spatial nonhomogeneous steady states and intricate spatiotemporal dynamics, as illustrated in Fig. 9-(a), (b) and (c). Notably, the intersection points $O_{T_8H_8}$ and $O_{H_7H_8}$ represent



Fig. 8 The bifurcation diagrams of model (3) in the (R, τ) -plane at Q_3 from Fig. 4-(d) illustrate the dynamical transitions. The left diagram presents an overview, while the right image provides a magnified view of the solid line, revealing the Turing-Hopf $(O_{T_8H_8})$ and Hopf-Hopf $(O_{H_7H_8})$ bifurcation points. Here, $R_T^* \doteq 1.8553$ and $R_H^* \doteq 2.4058$



Fig. 9 Solutions of model (3) at $P^{21} - P^{28}$. (a)-(b): $u_0 = 1 + 0.1 \cos(0.8\pi x)$ for $t \in [-\tau, 0]$. (c)-(d): $u_0 = 1 + 0.1 \cos(0.84\pi x)$ for $t \in [-\tau, 0]$. (e)-(f): $u_0 = 1 + 0.1 \cos(0.75\pi x)$ for $t \in [-\tau, 0]$. (g)-(h): $u_0 = 1 + 0.1 \cos(0.7\pi x)$ for $t \in [-\tau, 0]$

significant bifurcation events. Specifically, $O_{T_8H_8}$ is the intersection of the R_T^* curve for mode-8 and $\tau_{8,0}$, marking a Turing-Hopf bifurcation point. Furthermore, Fig. 9-(b) depicts the connecting trajectories from spatially nonhomogeneous periodic solutions to spatially nonhomogeneous steady state solutions. Additionally, Fig. 9-(c) showcases the connecting trajectories from spatially nonhomogeneous periodic solutions to other spatially nonhomogeneous periodic solutions. Similarly, $O_{H_7H_8}$ represents the intersection of $\tau_{7,0}$ and $\tau_{8,0}$, indicating a Hopf-Hopf bifurcation point. These points signify regions where high codimensional bifurcations may lead to even more complex spatiotemporal dynamics as observed in Fig. 9.

For the specific case where $d_2 = 0.8$, we systematically evaluate the critical parameters using expression (10), which yields

$$\alpha_{H_0} = 0.6, \quad \alpha_{H_2} \doteq -0.7579, \quad \alpha_{T_1} \doteq 0.1207, \quad \alpha_{T_3} \doteq 1.3900.$$



Fig. 10 Left (a): Bifurcation diagram of u_* in the (d_2, α) -plane at Q_4 from Fig. 4-(d). Right (b)-(e): Solutions of model (3) for various (R, τ) configurations, with $O_{T_3H_1}$ marking the Turing-Hopf point. Parameters: $R_T^* \doteq 0.4782$, $n_T^* \doteq 3.0037$, $R_H^* \doteq 0.7972$, and initial condition $u_0(x, t) = 1 + 0.1 \cos(\pi x)$ for $t \in [-\tau, 0]$

It is noteworthy that these values exhibit a distinct ordering: $\alpha_{H_2} < \alpha_{T_1} < \alpha_{H_0} < \alpha_{T_3}$.

Subsequently, we judiciously select $\alpha = 0.1622$ (Q_4 in Fig. 4-(d)) to satisfy the constraints $\alpha + d_2 > 0$, $\alpha - d_2 < 0$, and $\alpha_{T_1} < \alpha < \alpha_{H_0}$. This choice facilitates the determination of the tangency points between $f_1(k, R)$ and the functions $f_2^T(k)$ and $f_2^H(k)$, located at

$$(k_T^*, R_T^*) \doteq (9.4365, 0.4782), \quad (k_H^*, R_H^*) \doteq (1.9789, 0.7972),$$

respectively. Notably, $R_T^* < R_H^*$ in this configuration. Setting L = 1, we derive $n_T^* \doteq 3.0037$. Leveraging Proposition 2.3-(III) (or Theorem 1.1-(V)-(a)), we map out the bifurcation curves in the (d_2, α) -plane, as depicted in Fig. 10-(a). Here, a crucial observation is that $O_{T_3H_1}$ serves as the intersection point between the R_T^* curve associated with mode-3 and the $\tau_{1,0}$ curve, thereby identifying $O_{T_3H_1}$ as a Turing-Hopf bifurcation point. The solutions of this point can be found in Fig. 10-(b) to (e).

Choosing $\alpha = 0.5$ (Q_5 in Fig. 4-(d)), which also indeed satisfies the constraints $\alpha + d_2 > 0$, $\alpha - d_2 < 0$, and $\alpha_{T_1} < \alpha < \alpha_{H_0}$, we can further analyze the system dynamics. Specifically, we determine the tangency points between $f_1(k, R)$ and the functions $f_2^T(k)$ and $f_2^H(k)$ to be

$$(k_T^*, R_T^*) \doteq (3.1587, 1.4627), \quad (k_H^*, R_H^*) \doteq (4.0571, 0.2568).$$

In this scenario, $R_T^* > R_H^*$ indicates a reversal in the relative magnitudes of these critical perception scales compared to the previous case. With L = 10, we compute $n_T^* \doteq 10.054$. According to Proposition 2.3-(III) (or Theorem 1.1-(V)-(b)), we understand that the constant steady state u_* exhibits local asymptotic stability for $R > R_T^*$ and becomes unstable for $R < R_T^*$. This transition in stability is illustrated in Fig. 11.



Fig. 11 (a): Bifurcation curve of u_* in the (d_2, α) -plane at Q_5 from Fig. 4-(d). (b)-(c): Solutions of model (3) for varying (R, τ) , with initial $u_0(x, t) = 1 + 0.1 \cos \pi x$ for $t \in [-\tau, 0]$. Critical parameters: $(n_T^*, R_T^*) \doteq (10.054, 1.4627)$

4 Discussion

In this study, we developed a reaction-diffusion model integrating nonlocal spatial memory and instantaneous perception to explore how these cognitive mechanisms shape species movement dynamics. By analyzing the root distribution of the characteristic equation, we characterized the local stability of the positive constant steady state u_* in the parameter plane spanned by the memory-induced diffusion coefficient d_2 and perceptual strength α . Our findings demonstrate that both nonlocal memory and perception profoundly reshape system dynamics, mediating transitions from constant steady state to complex spatiotemporal configurations through bifurcation-driven instabilities.

When the memory-induced diffusion coefficient dominates, the system exhibits contrasting behaviors depending on the alignment between memory and perception. If memory and perceptual cues reinforce one another (i.e., d_2 and α share the same sign), Turing bifurcation destabilizes the homogeneous steady state u_* , favoring spatially heterogeneous structures. Ecologically, this corresponds to the formation of "hotspot" regions, where animals exhibit clustered distributions in localized areas while maintaining sparser densities in adjacent zones. For example, in enclosed environments, tracking the movement of honeybees reveals the spontaneous formation of structured spatial distributions, as they navigate using map-like spatial memory (Menzel et al. 2005). Similarly, North American elk rely on memory to establish migratory corridors (Merkle et al. 2019), a behavior aligning with spatially periodic solutions predicted by our model. Conversely, antagonistic memory-perception interactions (d_2 and α with opposing signs) induce oscillatory dynamics. When these parameters are comparable in magnitude, a Hopf bifurcation generates temporal periodicity, reflecting cyclical behaviors such as avian seasonal migration or "site fidelity" (the tendency to return to previously visited locations)-phenomena critical to habitat conservation (Morrison et al. 2021). Intermediate perceptual strength triggers Turing-Hopf bifurcations, producing spatiotemporal patterns that manifest as periodic oscillations in both space and time. This phenomenon mirrors the migratory behavior of certain avian species, such as the long-distance movements of songbirds tracked via geolocators (e.g., nocturnal flight phases interspersed with transient stopovers at intermediate latitudes) (Stutchbury et al. 2009). These cyclical movements-featuring brief stopovers

punctuating sustained migratory phases-reflect the coexistence of spatial periodicity and temporal synchronization predicted by the bifurcation framework, where localized aggregations (analogous to stopover sites) alternate rhythmically with dispersal episodes across spatially structured habitats.

Enhanced perceptual capacity enables species to precisely detect conspecific densities, stabilizing migratory routes or aggregation zones. However, the interplay between perception rang and memory period introduces nuanced effects: while broad spatial perception promotes Turing patterns, limited perception ranges amplify Turing-Hopf interactions, driving cyclical spatiotemporal reorganizations. This dichotomy is exemplified by songbirds, which maintain territorial fidelity during breeding seasons yet engage in collective migratory movements, balancing localized resource optimization with large-scale navigation (Kristensen et al. 2013).

Our theoretical framework highlights the complexity of animal movement when memory and perception act synergistically. Instantaneous perception enables the extraction of real-time local cues, while memory synthesizes historical data to optimize adaptive movement strategies. Mathematically, this synergy corresponds to higher-order bifurcations (e.g., Turing-Hopf), suggesting rich nonlinear phenomena awaiting further exploration. Empirical studies corroborate these insights: GPS-tracked terrestrial mammals like caribou and wildebeest optimize migration efficiency by combining memory-guided route retention with perception-driven adjustments (Bracis and Mueller 2017). Similarly, blue whales utilize long-term memory along-side real-time oceanic cues to navigate marine environments (Abrahms et al. 2019), underscoring the biological relevance of our model's predictions.

A key limitation of our model stems from its assumption of spatial homogeneity-a simplification that enhances analytical tractability at the cost of neglecting environmental heterogeneity, a critical driver of animal movement dynamics. Extending the framework to incorporate spatial variability would render the steady state dependent on spatial coordinates, necessitating the analysis of characteristic equations involving non-self-adjoint elliptic operators with delay and spatial integral terms. Such extensions pose formidable mathematical challenges, as standard stability analysis techniques for constant steady state become inapplicable. While in data-driven movement ecology, such as agent-based models parameterized with GPS tracking data (Bastille-Rousseau et al. 2018), offer promising pathways to integrate realistic habitat variability. In the future, we are committed to obtaining corresponding results theoretically.

In conclusion, our study establishes a mechanistic framework for understanding animal movement as a dynamic interplay between memory-guided historical navigation and instantaneous perceptual adjustments. By analyzing these cognitive processes through bifurcation theory, we identify fundamental principles that regulate both spatial patterning and adaptive temporal behaviors-a perspective with direct relevance to conservation challenges. For instance, this framework could predict how habitat fragmentation disrupts species' ability to reconcile past migratory routes with current sensory cues, leading to maladaptive movements. As advances in biologging technologies and dynamical systems theory converge, embedding cognitive mechanisms into ecological models will become increasingly vital for deciphering the intricate interplay of memory, perception, and movement-a synthesis critical for preserving biodiversity in rapidly changing ecosystems.

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Conflict of interest The authors declare that they have no conflict of interest. All authors satisfy ethical responsibilities.

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