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PATTERN FORMATION IN DIFFUSIVE PREDATOR-PREY SYSTEMS WITH PREDATOR-TAXIS AND PREY-TAXIS

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Abstract. A reaction-diffusion predator-prey system with prey-taxis and predator-taxis describes the spatial interaction and random movement of predator and prey species, as well as the spatial movement of predators pursuing prey and prey evading predators. The spatial pattern formation induced by the prey-taxis and predator-taxis is characterized by the Turing type linear instability of homogeneous state and bifurcation theory. It is shown that both attractive prey-taxis and repulsive predator-taxis compress the spatial patterns, while repulsive prey-taxis and attractive predator-taxis help to generate spatial patterns. Our results are applied to the Holling-Tanner predator-prey model to demonstrate the pattern formation mechanism.

1. Introduction.

Systems describing predators and prey species that disperse by simple diffusion in a spatially homogeneous environment have been widely studied using well developed methods, see [21, 24, 33]. The pursuit and evasion between predators and prey (predators chasing prey and prey evading from predators) also has a strong impact on the movement pattern of predators and prey [16, 31, 45]. Such movement is not random but directed: predators move toward the gradient direction of prey distribution, and prey moves in the negative gradient direction of predator distribution. It is important to study such movement that provides reasonable descriptions that are ecologically interesting and which can provide new insights into the effects of dispersal on predators and prey.

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In this paper, we consider the following reaction-diffusion predator-prey model with both predator-taxis (prey evading predators) and prey-taxis (predators chasing prey):

$$\begin{cases} \dfrac{\partial u}{\partial t} = d\Delta u + \xi \nabla \cdot (u \nabla v) + f(u,v), & x \in \Omega,\ t > 0, \\ \dfrac{\partial v}{\partial t} = \Delta v - \eta \nabla \cdot (v \nabla u) + g(u,v), & x \in \Omega,\ t > 0, \\ \dfrac{\partial u(x,t)}{\partial \nu} = \dfrac{\partial v(x,t)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq 0, \not\equiv 0,\ v(x,0) = v_0(x) \geq 0, \not\equiv 0, & x \in \Omega. \end{cases} \tag{1}$$

Here the habitat of both species Ω is a bounded domain in $\mathbb{R}^n$ $(n \geq 1)$ with smooth boundary $\partial\Omega$; and homogeneous Neumann boundary condition is imposed to describe an enclosed domain; $u(x,t)$ and $v(x,t)$ represent the densities of prey and predator at the location x and time t, respectively; d is the rescaled diffusion coefficient for the prey and the diffusion coefficient of the predator is now rescaled as 1. The term $\xi \nabla \cdot (u \nabla v)$ shows the tendency of prey moving away from the high gradient of predator density function and $\xi \geq 0$ is the intrinsic predator-taxis rate; and the term $-\eta \nabla \cdot (v \nabla u)$ shows the tendency of predator moving toward the direction of gradient of prey density function and $\eta \geq 0$ is the intrinsic prey-taxis rate. The nonlinear functions $f(u,v)$ and $g(u,v)$ represent the interaction between predators and prey such as birth, death and predation. The model (1) was also proposed in [7, Page 1723] to consider simultaneous prey-taxis and predator-taxis.

When $\eta = \xi = 0$, system (1) reduces to the following classical reaction-diffusion system:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d\Delta u + f(u,v), & x \in \Omega,\ t > 0, \\ \dfrac{\partial v}{\partial t} = \Delta v + g(u,v), & x \in \Omega,\ t > 0, \\ \dfrac{\partial u(x,t)}{\partial \nu} = \dfrac{\partial v(x,t)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq 0,\ v(x,0) = v_0(x) \geq 0, & x \in \Omega. \end{cases} \tag{2}$$

Over the past few decades, (2) has been widely applied and extensively studied to model spatiotemporal predator-prey dynamics. Under suitable conditions, there is a positive constant equilibrium (u^*, v^*) which indicates that the predator and prey species coexist in the environment. Such coexistence state could be stable (even globally asymptotically stable) for the reaction-diffusion system (2) [5, 6, 12]; but it can also be unstable and there is a spatially homogeneous stable limit cycle which attracts all solution orbits [13, 20, 44]. On the other hand, spatial heterogeneity of the living habitat supports spatially nonhomogeneous coexistence states [11, 32, 35], and spatially nonhomogeneous time-periodic orbit may also arise from (2) [4, 15, 34, 44]. One of mechanisms of generating spatially nonhomogeneous equilibrium is due to the different diffusion coefficients of predator and prey species, which is called Turing diffusion-driven instability as it was first formulated by Alan Turing [30]. In this scenario, the positive constant equilibrium (u^*, v^*) is stable for (2) with respect to a spatially homogeneous perturbation, but becomes unstable under a spatially nonhomogeneous perturbation. Such diffusion-driven instability of a constant steady state is often accompanied by the emergence of spatially nonhomogeneous steady states (spatial patterns) through bifurcation.

Throughout the paper we assume that the functions $f(u,v)$ and $g(u,v)$ satisfy the following assumptions:

(P1) The functions f and $g : V \to \mathbb{R}$ are continuously differentiable on an open subset V of $\mathbb{R}^2_+$, $f(0,v) = g(u,0) = 0$; and there exists $(u^*,v^*) \in V$ such that $f(u^*,v^*) = g(u^*,v^*) = 0$;

(P2) (predator-prey interaction) $\dfrac{\partial f}{\partial v}(u^*,v^*) < 0$, $\dfrac{\partial g}{\partial u}(u^*,v^*) > 0$.

Our main result in this paper is that under (P1) and (P2), a diffusion-induced instability can occur for (2) and a non-constant equilibrium (spatial pattern) emerges; but the addition of attractive prey-taxis and repulsive predator-taxis annihilates the spatial pattern and the constant equilibrium regains the stability for (1). On the other hand, attractive predator-taxis and repulsive prey-taxis can drive the generation of spatial pattern. The parameter ranges of (ξ,η) which stabilizes the constant equilibrium or supports spatial patterns in (1) are found. This provides another mechanism for spatial pattern formation: introducing either an attractive predator-taxis or a repulsive prey-taxis into a reaction-diffusion system with predator-prey interaction. We also show the existence of non-constant equilibrium solutions of (1) rigorously by using the bifurcation theory. The results here also unify earlier partial results for the prey-taxis system (with $\xi = 0$ and $\eta \neq 0$) [17, 36, 38] and the predator-taxis system (with $\xi \geq 0$ and $\eta = 0$) [42]. For the prey-taxis systems, global existence and boundedness of solutions, global stability of equilibrium solutions have also been considered in, for example, [1, 14, 29, 39, 41, 43].

In Section 2, we investigate the effect of prey-taxis and predator-taxis on the stability of the constant equilibrium of (1), and we identify the parameter ranges that the constant equilibrium remains stable or becomes unstable. In Section 3, the existence of non-constant equilibrium solutions are proved via a bifurcation approach. We demonstrate the stability/instability criterion using the example of Holling-Tanner predator-prey model in Section 4 and numerical simulations confirm the theoretical predication.

2. Stability/Instability induced by taxis.

First we show the local existence of solutions of system (1) so the problem is well-posed at least locally.

Lemma 2.1. *Let Ω be a bounded domain in $\mathbb{R}^n$ $(n \geq 1)$ with smooth boundary. Assume that $u_0(x)$ and $v_0(x)$ are non-negative functions from $W^{1,\infty}(\Omega)$ and (P1), (P2) hold. Then there exist $\epsilon > 0$ and $T \in (0,+\infty]$ such that a pair non-negative functions $(u(x,t), v(x,t)) \in (C^0(\bar\Omega \times [0,T) \cap C^{2,1}(\bar\Omega \times (0,T))))^2$ solve (1) classically in $\bar\Omega \times [0,T)$ for $0 \leq \eta < \epsilon, 0 \leq \xi < \epsilon$.*

Proof. For that purpose, we rewrite (1) as:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d\Delta u + \xi \nabla u \cdot \nabla v + \xi u \Delta v + f(u,v), & x \in \Omega,\ t > 0, \\ \dfrac{\partial v}{\partial t} = \Delta v - \eta \nabla v \cdot \nabla u - \eta v \Delta u + g(u,v), & x \in \Omega,\ t > 0, \\ \dfrac{\partial u(x,t)}{\partial \nu} = \dfrac{\partial v(x,t)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq 0, \not\equiv 0,\ v(x,0) = v_0(x) \geq 0, \not\equiv 0, & x \in \Omega. \end{cases}$$

Then for small $\xi \geq$ and $\eta \geq 0$, by using the same argument in Theorems 4.3 and 4.4 of [10] one can show that a non-negative solution $(u(x,t), v(x,t))$ of system (1) exists locally. $\square$

It is worth noticing that the diffusion matrix of system (1) is neither symmetric nor positively definite, so the local existence of non-negative solution of (1) cannot be obtained by standard results such as [2, Theorem 1] or [3, Theorem 0.1], which is different from the case of triangular diffusion matrix in systems with only prey-taxis [14, 36, 41], only predator-taxis [42], or general chemotaxis systems [40]. Here we apply a result in [10] for a density-dependent diffusion system which does not assume the triangular diffusion matrix. On the other hand not much is known for the global solvability for (1), while such results are known for the case of systems with only prey-taxis or predator-taxis [14, 41, 42]. In this paper we focus on the question of existence and stability of steady states of the system (1) and the effect of taxis.

Suppose that (P1) and (P2) hold. Clearly (u^*, v^*) is also an equilibrium of the ODE system

$$\begin{cases} u_t = f(u,v), & t>0, \\ v_t = g(u,v), & t>0. \end{cases} \tag{3}$$

The linearized Jacobian matrix with respect to (3) at (u^*, v^*) is:

$$J = \begin{pmatrix} f_u(u^*,v^*) & f_v(u^*,v^*) \\ g_u(u^*,v^*) & g_v(u^*,v^*) \end{pmatrix} := \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}. \tag{4}$$

We assume that

$$\mathrm{Trace}(J) = f_u + g_v < 0, \quad \mathrm{Det}(J) = f_u g_v - f_v g_u > 0 \tag{5}$$

holds so that (4) has eigenvalues with negative real parts and (u^*, v^*) is locally asymptotically stable with respect to (3).

Linearizing the reaction-diffusion system with taxis (1) about the constant equilibrium (u^*, v^*) gives

$$\begin{pmatrix} \phi_t \\ \psi_t \end{pmatrix} = L(\eta,\xi) \begin{pmatrix} \phi \\ \psi \end{pmatrix}, \tag{6}$$

where

$$L(\eta,\xi) = \begin{pmatrix} d\Delta + f_u & \xi u^* \Delta + f_v \\ -\eta v^* \Delta + g_u & \Delta + g_v \end{pmatrix}.$$

Then the linear stability of (u^*, v^*) with respect to (1) is determined by the eigenvalue problem

$$\begin{cases} d\Delta\phi + \xi u^*\Delta\psi + f_u\phi + f_v\psi = \mu\phi, & x\in\Omega, \\ \Delta\psi - \eta v^*\Delta\phi + g_u\phi + g_v\psi = \mu\psi, & x\in\Omega, \\ \dfrac{\partial\psi}{\partial\nu} = \dfrac{\partial\phi}{\partial\nu} = 0, & x\in\partial\Omega. \end{cases} \tag{7}$$

Let $\{\lambda_n\}$ be the sequence of eigenvalues of $-\Delta$ with Neumann boundary condition such that $0 = \lambda_0 < \lambda_1 \le \lambda_2 \le \cdots$ and let $\phi_n(x)$ be the corresponding eigenfunctions of λ_n for $n \in \mathbb{N}_0 = \mathbb{N} \cup \{0\}$. The following lemma is fundamental but is commonly used. It shows that the eigenvalue problem (7) can be reduced to a sequence of matrix eigenvalue problems. The proof is similar to that of [19, Lemma 2.1], hence it is omitted here.

Lemma 2.2. *Let (u^*, v^*) be a positive constant equilibrium of (1). Suppose (5) holds. Define*

$$A_n = \begin{pmatrix} -d\lambda_n + f_u & -\xi u^*\lambda_n + f_v \\ \eta v^*\lambda_n + g_u & -\lambda_n + g_v \end{pmatrix}. \tag{8}$$

Then

1. *The constant equilibrium* (u^*, v^*) *is locally asymptotically stable with respect to* (1) *if and only if for every* $n \geq 1$*, all the eigenvalues of* A_n *have negative real parts.*
2. *The constant equilibrium* (u^*, v^*) *is unstable with respect to* (1) *if and only if there exists* $n \geq 1$ *such that* A_n *has at least one eigenvalue with nonnegative real part.*

It is well-known that the eigenvalues of A_n are determined by

$$\begin{aligned} &\mathrm{Trace}(A_n) = -\lambda_n(d+1) + \mathrm{Trace}(J), \\ &\mathrm{Det}(A_n) = (d + \xi\eta u^* v^*)\lambda_n^2 - F(\xi,\eta)\lambda_n + \mathrm{Det}(J), \end{aligned} \tag{9}$$

where

$$F(\xi,\eta) = f_u + dg_v + \eta v^* f_v - \xi u^* g_u. \tag{10}$$

Now we investigate how the stability of (u^*, v^*) is effected by a combination of diffusion and taxis. Since $\mathrm{Trace}(J) < 0$ and $d > 0$, we always have $\mathrm{Trace}(A_n) < 0$. Hence from Lemma 2.2, the stability /instability of (u^*, v^*) to (1) is determined by the sign of $\mathrm{Det}(A_n)$ for each $n \geq 1$; if (u^*, v^*) is unstable, then for some $n \geq 1$, A_n has an eigenvalue with positive real part, which implies that $\mathrm{Det}(A_n) < 0$ and A_n has one positive and one negative eigenvalues.

To track the determinant of A_n, we define

$$D(\xi,\eta,p) = (d + \xi\eta u^* v^*)p^2 - (f_u + dg_v + \eta v^* f_v - \xi u^* g_u)p + \mathrm{Det}(J), \tag{11}$$

for $p > 0$ and (ξ, η) belongs to

$$U = \{(\xi,\eta) \in \mathbb{R}^2 : d + \xi\eta u^* v^* > 0\}. \tag{12}$$

Note that the region U allows $\xi < 0$ or $\eta < 0$ mathematically, though that is not reasonable biologically. We only consider (ξ, η) satisfying $d + \xi\eta u^* v^* > 0$ as only under this condition, the second order differential operator defined in (7) is strongly elliptic and the corresponding parabolic differential operator is strongly parabolic.

The following results show that (u^*, v^*) remains stable for system (1) if (ξ, η) is in a stable parameter region on the $\xi - \eta$ parameter plane.

Theorem 2.3. *Suppose that* $d > 0$ *and (P1), (P2),* (5) *hold. Define*

$$S := \{(\xi,\eta) \in U : f_u + dg_v + \eta v^* f_v - \xi u^* g_u < 2\sqrt{d + \xi\eta u^* v^*}\sqrt{DetJ}\}. \tag{13}$$

1. *If* $(\xi, \eta) \in S$*, then* (u^*, v^*) *is locally asymptotically stable with respect to* (1).
2. *Assume* $(\xi_0, \eta_0) \in S$ *for some* $\xi_0 \geq 0, \eta_0 \geq 0$*. If* $\xi \geq \xi_0$ *and* $\eta \geq \eta_0$*, then* (u^*, v^*) *is also locally asymptotically stable with respect to* (1).

Proof. 1. Since $D(\xi, \eta, p) > 0$ for $p > 0$ if $(\xi, \eta) \in S$ by the definition of S, which implies that $\mathrm{Det}(A_n) > 0$ for all $n \geq 1$.

2. Under the conditions given here, it is clear that

$$\begin{aligned} &\frac{\partial D(\xi,\eta,p)}{\partial \xi}|_{\xi=\xi_0} = \eta u^* v^* p^2 + g_u(u^*, v^*)u^* p \geq 0, \\ &\frac{\partial D(\xi,\eta,p)}{\partial \eta}|_{\eta=\eta_0} = \xi u^* v^* p^2 - f_v(u^*, v^*)u^* p \geq 0, \end{aligned}$$

for $\xi \geq \xi_0, \eta \geq \eta_0$. Hence $D(\xi_0, \eta_0, p) > 0$ implies that $D(\xi, \eta, p) > 0$. This proves that if $(\xi_0, \eta_0) \in S$, then $(\xi, \eta) \in S$ if $\xi \geq \xi_0$ and $\eta \geq \eta_0$. $\square$

Remark 1. (1) A special case in Part 1 of Theorem 2.3 is $\xi = \eta = 0$, which means that if (u^*, v^*) is locally asymptotically stable for the ODE system (3), then (u^*, v^*) remains locally asymptotically stable with respect to the reaction diffusion system (2) if $f_u + dg_v < 2\sqrt{dDetJ}$.

(2) We also point out that $(\xi, \eta) \in S$ is a sufficient condition for the locally asymptotical stability of (u^*, v^*), and the definition of S is independent of the spatial domain Ω. For a specific bounded domain Ω, we define

$$S_\Omega = \{(\xi, \eta) \in U : \min_{n\in\mathbb{N}} D(\xi, \eta, \lambda_n) > 0\}, \tag{14}$$

then $S \subset S_\Omega$, and (u^*, v^*) is still stable for system (1) when $(\xi, \eta) \in S_\Omega$. To see that $S \subset S_\Omega$, we note that S can also be defined by

$$S = \{(\xi, \eta) \in U : \min_{p>0} D(\xi, \eta, p) > 0\}. \tag{15}$$

From Theorem 2.3, we can immediately conclude that if (u^*, v^*) is stable with respect to the reaction-diffusion system (2), then the addition of attractive prey-taxis and/or repulsive predator-taxis does not change the stability of (u^*, v^*).

Corollary 1. *Suppose $d > 0$ and (P1), (P2), (5) hold. If $(0, 0) \in S$, then $\mathbb{R}^2_+ \subset S$. That is, if (u^*, v^*) is locally asymptotically stable equilibrium with respect with ODE system (3) and reaction-diffusion system (2), then it is also a locally asymptotically stable equilibrium with respect to the reaction diffusion system with taxis (1) for any $\xi \geq 0, \eta \geq 0$.*

Proof. This follows directly from part 2 of Theorem 2.3 with $\xi_0 = \eta_0 = 0$. □

Corollary 1 indicates that attractive prey-taxis ($\eta > 0$) or repulsive predator-taxis ($\xi > 0$) cannot induce the instability of (u^*, v^*) in the reaction-diffusion system with taxis (1) if (u^*, v^*) is locally asymptotically stable with respect with reaction-diffusion system (2), thus these mechanism cannot generate spatial patterns. Therefore taxis-induced instability only occurs when there is repulsive prey-taxis ($\xi < 0$) or attractive predator-taxis ($\eta < 0$). In fact, similar stability/instability analysis have also been considered for cross-diffusion models [27, 37].

On the other hand, if $(0, 0) \notin S$, then a Turing diffusion-induced instability can occur for the reaction-diffusion system (2), and such instability persists for some weak attractive prey-taxis ($\eta > 0$ small) or repulsive predator-taxis ($\xi > 0$ small). It is more precisely characterized in the following results.

We recall the following classical Turing instability induced by diffusion when $\xi = \eta = 0$:

Lemma 2.4. *Suppose that $(0, 0) \notin S$ (or equivalently $2\sqrt{dDet(J)} < f_u + dg_v$) in the system (1) and (5) holds. If*

$$0 < d < \max_{j\geq 1} \frac{f_u\lambda_j - \mathrm{Det}(J)}{\lambda_j(\lambda_j - g_v)}, \tag{16}$$

then (u^*, v^*) is unstable with respect to the reaction diffusion system (2). In this case, the Turing instability is caused by a small prey diffusion coefficient d.

Proof. The assumption (5) guarantees the stability of (u^*, v^*) for the ODE system, and $\mathrm{Det}(A_n)$ is negative under the assumption (16). □

To compare taxis-induced instability with the results in Lemma 2.4, we give the following properties:

Lemma 2.5. *Suppose $d > 0$ and (P1), (P2), (5) hold. If $(0,0) \notin S$, then there is a smooth decreasing curve $\Gamma = \{(\xi(\eta), \eta) : 0 \le \eta \le \eta^*\}$ connecting $(0, \eta^*)$ to $(\xi^*, 0)$ in first quadrant of $\xi - \eta$ plane, such that $S_+ = S \cap \mathbb{R}^2_+$ is bounded by the ξ-axis, η-axis and Γ, where*

$$\eta^* = \frac{(f_u + dg_v) - 2\sqrt{dDet(J)}}{-v^* f_v} > 0, \qquad \xi^* = \frac{(f_u + dg_v) - 2\sqrt{dDet(J)}}{u^* g_u} > 0,$$

and $\xi(\eta) \ge 0$ satisfies

$$f_u + dg_v + \eta v^* f_v - \xi(\eta) u^* g_u = 2\sqrt{d + \xi(\eta)\eta u^* v^*}\sqrt{DetJ}. \tag{17}$$

Proof. Since $(0,0) \notin S$, $f_u + dg_v > 2\sqrt{d\mathrm{Det}(J)}$, then η^* and ξ^* are well defined. It is obvious that the boundary of S is defined by (17), which is implicitly defined for ξ and η. Differentiating (17) in ξ, we obtain that

$$v^* f_v - \frac{d\xi}{d\eta} u^* g_u - \sqrt{\frac{\mathrm{Det}(J)}{d + \xi\eta u^* v^*}} \left(\frac{d\xi}{d\eta} \eta u^* v^* + \xi u^* v^* \right) = 0, \tag{18}$$

which holds if and only if $\dfrac{d\xi}{d\eta} < 0$ otherwise each term is negative in (18). So $\xi(\eta)$ is strictly decreasing in η. □

Proposition 1. *Suppose that (P1), (P2), (5) hold and $(0,0) \notin S$. For any $\eta \ge 0$ fixed,*

1. *if $\xi > \max\{0, \xi(\eta)\}$, then (u^*, v^*) is asymptotically stable with respect to (1).*
2. *if $\xi < \xi(\eta)$, then (u^*, v^*) is unstable with respect to (1).*

That is, if (u^*, v^*) is locally asymptotically stable with respect with ODE system (3) but unstable with respect with reaction-diffusion system (2), then it is still unstable when $(\xi, \eta) \in S_+$ is under the curve Γ in the first quadrant of ξ-η plane and there exists some $n \ge 1$ such that $Det(A_n) < 0$.

Proof. It is from the definition of $\mathrm{Det}(A_n)$ directly. □

In general, the linear stability results in this section show that a large attractive prey-taxis ($\eta > 0$) or a large repulsive predator-taxis ($\xi > 0$) stabilizes the constant equilibrium, while a large repulsive prey-taxis ($\xi < 0$) or a large attractive predator-taxis ($\eta < 0$) destabilizes it. These results include earlier partial results in [17, 38, 42] in which only one of prey-taxis or predator-taxis is presented in the model. Corollary 1 and Proposition 1 give a precise description of the boundary of the stability parameter region. Figure 1 shows the stable parameter region S in the case of $(0,0) \in S$ (left) and $(0,0) \notin S$ (right). In both cases, the upper right side of region U is the stable one, while the lower left side of U is the unstable one. In the unstable parameter region, a Turing type taxis-induced instability exists and spatially non-constant equilibria are expected. We prove the existence of such patterns in the next section by using bifurcation theory.

3. **Bifurcation of nontrivial spatial pattern.** In this section we consider the bifurcation of non-constant equilibrium solutions of (1) from the positive constant equilibrium (u^*, v^*) using ξ as the bifurcation parameter while $d > 0$ and $\eta \ge 0$ are fixed. One can also use d or η as bifurcation parameter and similar results can be obtained.

For simplicity of presentation, we only consider the case that (u^*, v^*) is unstable for (1) when $(\xi, \eta) = (0, 0)$, which is considered in Proposition 1, and we only

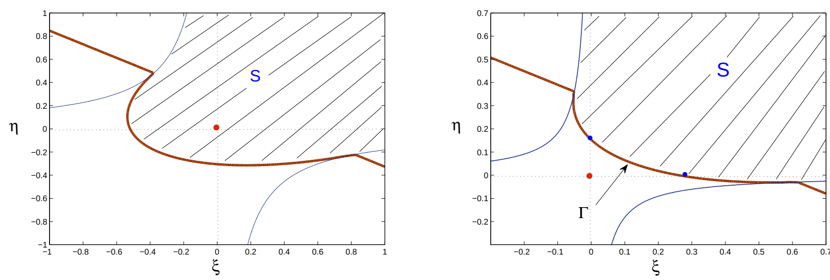

FIGURE 1. The stable region/unstable region of equilibrium (u^*, v^*) of system (1) in $\xi-\eta$ parameter plane. Here f, g and other parameters are taken from (25) in Section 4. (Left): $d = 0.06$, $(0,0) \in S$; (Right): $d = 0.01$, $(0,0) \notin S$. The thick solid curve is $f_u + dg_v + \eta v^* f_v - \xi u^* g_u - 2\sqrt{d + \xi\eta u^* v^*}\sqrt{DetJ} = 0$, the thin solid curve is $d + \xi\eta u^* v^* = 0$ in both panels.

consider the bifurcation value $\xi > 0$. Note that the switch of stability still occurs for some parameters when $\xi < 0$ or $\eta < 0$ as shown in Figure 1 (right), and the boundary curve Γ can be in the second, third or fourth quadrant. Here we consider the case that the bifurcation point (ξ, η) is in the first quadrant.

From $D(\eta, \xi, p) = 0$, we define a function

$$\xi(p) = \frac{dp^2 - (\eta v^* f_v + f_u + dg_v)p + Det(J)}{-u^* g_u p - \eta u^* v^* p^2}, \quad p > 0. \tag{19}$$

Notice that the positivity of $\xi(p)$ is guaranteed when $\eta > 0$ satisfies $(0, \eta) \notin S$. We summarize the properties of the function $\xi(p)$ as follows.

Lemma 3.1. *Suppose that $d > 0$, $\eta \geq 0$, and (P1), (P2), (5) hold. Assume that $(0, \eta) \notin S$ where S is defined in (13) and $\xi(p)$ is defined as in (19). Define*

$$\begin{aligned} p_\pm &= \frac{f_u + dg_v + \eta v^* f_v \pm \sqrt{(f_u + dg_v + \eta v^* f_v)^2 - 4dDet(J)}}{2d}, \\ p^* &= \frac{\eta v^* Det(J) + \sqrt{\eta^2 (v^*)^2 Det^2(J) + dg_u^2 Det(J) + (f_u + dg_v + \eta v^* f_v)\eta v^* g_u Det(J)}}{dg_u + (f_u + dg_v + \eta v^* f_v)\eta v^*}. \end{aligned} \tag{20}$$

Then

1. *Only when $p_- < p < p_+$, we have $\xi(p) > 0$, and $\xi(p_\pm) = 0$;*
2. *$\xi'(p) > 0$ for $p_- < p < p^*$, $\xi'(p) < 0$ for $p^* < p < p_+$, and $\xi(p^*) := M^*$ is the maximum point of $\xi(p)$ on $p \in [p_-, p_+]$.*

Proof. Part 1 is clear by setting $dp^2 - (\eta v^* f_v + f_u + dg_v)p + \mathrm{Det}(J) = 0$. For part 2, differentiating $\xi(p)$, we obtain

$$\xi'(p) = \frac{[-dg_u - (\eta v^* f_v + f_u + dg_v)\eta v^*]p^2 + 2\eta v^* Det(J)p + g_u Det(J)}{u^*(-g_u p - \eta v^* p^2)^2}.$$

Since $(0, \eta) \in \mathbb{R}_+^2 \backslash S$ means that $-\eta v^* f_v - f_u - dg_v < -2\sqrt{d\mathrm{Det}(J)} < 0$. Combining $g_u > 0$, $2\eta v^* \mathrm{Det}(J) > 0$ and $g_u \mathrm{Det}(J) > 0$, we obtain there is a unique $p^* > 0$ (defined as in (20)) such that $\xi'(p) > 0$ for $0 < p < p^*$ and $\xi'(p) < 0$ for $p > p^*$. $\square$

From Lemma 3.1, if there exists $n \in \mathbb{N}$ such that $p_- < \lambda_n < p_+$, there is a corresponding steady state bifurcation value $\xi_S^n = \xi(\lambda_n) \in (0, M^*]$ such that $D(\xi_S^n, \eta, \lambda_n) = 0$. Figure 2 shows the steady state bifurcation values ξ_S^n at the

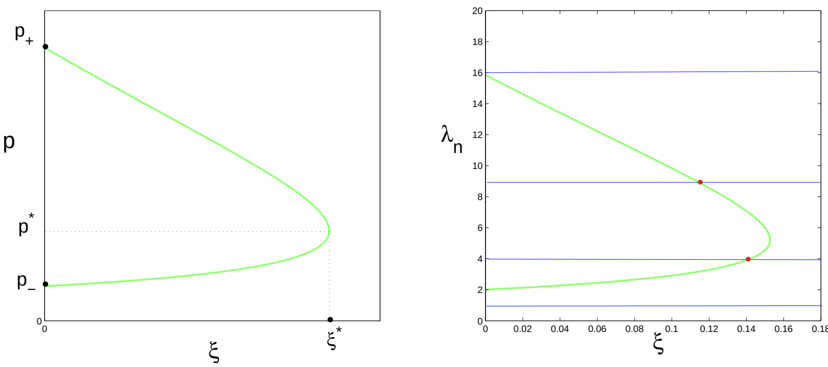

FIGURE 2. (Left): $D(\eta, \xi, p) = 0$ in $\xi - p$ plane for fixed η; (right): there are two bifurcation value ξ_S^2(corresponding to $\lambda_2 = 4$) and ξ_S^3(corresponding to $\lambda_3 = 9$), here f, g and other parameters are taken from (25) in Section 4 with $\eta = 0.02$, $d = 0.01$, $\Omega = (0, \pi)$.

intersection of $p = \lambda_n$ and $D(\xi, \eta, p) = 0$. For a one dimensional spatial domain $(0, l\pi)$, it is possible there is no steady state bifurcation value ξ_S^n if the length $l\pi$ is too small, and when $l\pi$ is large enough, there are finitely many $n \in \mathbb{N}$ such that $\lambda_n \in (p_-, p_+)$; the constant equilibrium (u^*, v^*) is locally asymptotically stable when $\xi > \max\limits_{n\in\mathbb{N}} \xi_S^n$, and it is unstable when $0 \le \xi < \max\limits_{n\in\mathbb{N}} \xi_S^n$.

Next we show that if the system (1) satisfies certain transversality condition at $\xi = \xi_S^n$, then a bifurcation of non-constant equilibrium solutions of (1) occurs at $\xi = \xi_S^n$. The equilibrium equation of (1) is

$$\begin{cases} d\Delta u + \xi\nabla \cdot (u\nabla v) + f(u, v) = 0, & \xi \ge 0, \quad x \in \Omega, \\ \Delta v - \eta\nabla \cdot (v\nabla u) + g(u, v) = 0, & \eta \ge 0, \quad x \in \Omega, \\ \dfrac{\partial u(x)}{\partial \nu} = \dfrac{\partial v(x)}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases} \tag{21}$$

For that purpose, we apply a local bifurcation theorem of Crandall and Rabinowitz [8, Theorem 1.7] (see also [26]), which we recall here for reader's convenience.

Theorem 3.2. *Let X and Y be Banach spaces and let V be an open connected subset of $X \times R$; Suppose $(\omega_0, \lambda_0) \in V$, and F is a continuously differentiable mapping from V into Y. Assume that*

1. *$F(\omega_0, \lambda) = 0$ for $(\omega_0, \lambda) \in V$;*
2. *The mixed partial derivative $D_{\lambda\omega}F(\omega, \lambda)$ exists and is continuous in (ω, λ) near (ω_0, λ_0);*
3. *The dimension of the null space $N(D_\omega F(\omega_0, \lambda_0))$ is 1, and the codimension of the range space $R(D_\omega F(\omega_0, \lambda_0))$ is 1;*
4. *$D_{\lambda\omega}F(\omega_0, \lambda_0)[\Phi_0] \notin R(D_\omega F(\omega_0, \lambda_0))$, where $\Phi_0(\neq 0) \in N(D_\omega F(\omega_0, \lambda_0))$.*

Let Z be any complement of span$\{\Phi_0\}$ in X. Then there exist an open interval $(-\delta, \delta)$ and continuous functions $\lambda : (-\delta, \delta) \to \mathbb{R}, \psi : (-\delta, \delta) \to Z$, such that $\lambda(0) = \lambda_0$, $\psi(0) = 0$, and, if $\omega(s) = \omega_0 + s\Phi_0 + s\psi(s)$ for $s \in (-\delta, \delta)$, then $F(\omega(s), \lambda(s)) = 0$. Moreover, if $(\omega, \lambda) \in V$ is a solution of $F = 0$ and is near (ω_0, λ_0), then either $\omega = \omega_0$ or (ω, λ) is on the curve $\Gamma = \{(\lambda(s), \omega(s)) : s \in (-\delta, \delta)\}$.

Let $X = W_N^{2,p}(\Omega) = \left\{u \in W^{2,p}(\Omega) : \frac{\partial u}{\partial \nu} = 0 \text{ on } \partial\Omega\right\}$, and $Y = L^p(\Omega)$ where $p > n$. Fix $\eta \geq 0$. Define a nonlinear mapping $F : \mathbb{R}^+ \times X \times X \to Y \times Y$ by

$$F(\xi, u, v) = \left(\begin{array}{c} d\Delta u + \xi\nabla \cdot (u\nabla v) + f(u, v) \\ \Delta v - \eta\nabla \cdot (v\nabla u) + g(u, v) \end{array} \right).$$

By using the assumptions (P1), (P2), it is observed that

(1) F is a continuously differentiable mapping in an open subset V of $\mathbb{R}^+ \times X \times X$;
(2) $F(\xi, u^*, v^*) = 0$ for all $\xi \in \mathbb{R}^+$;
(3) For any fixed $(\xi, u_1, v_1) \in \mathbb{R}^+ \times X \times X$, the Fréchet derivative is given by

$$\begin{aligned} &D_{(u,v)}F(\xi, u_1, v_1)[(u, v)] \\ =& \left(\begin{array}{c} -d\Delta u - \xi\nabla v_1 \cdot \nabla u - M_1 u - \xi u_1 \Delta v - \xi\nabla u_1 \cdot \nabla v - M_2 v \\ \eta v_1 \Delta u + \eta\nabla v_1 \cdot \nabla u - M_3 u - \Delta v + \eta\nabla u_1 \cdot \nabla v - M_4 v \end{array} \right), \end{aligned} \tag{22}$$

where

$$\begin{aligned} M_1(u_1, v_1) &= \nabla \cdot (u_1\nabla v_1) + \xi\Delta v_1 + f_u(u_1, v_1), \\ M_2(u_1, v_1) &= \nabla \cdot (u_1\nabla v_1) + f_v(u_1, v_1), \\ M_3(u_1, v_1) &= -\nabla \cdot (v_1\nabla u_1) + g_u(u_1, v_1), \\ M_4(u_1, v_1) &= -\nabla \cdot (v_1\nabla u_1) - \eta(u_1, v_1)\Delta u_1 + g_v(u_1, v_1). \end{aligned}$$

We show that all conditions in Theorem 3.2 are satisfied in the following lemmas. First we prove the simple eigenvalue assumption which is based on an assumption on the eigenvalues of $-\Delta$.

Lemma 3.3. *Suppose that $d > 0$, $\eta \geq 0$, and (P1), (P2), (5) hold. Assume that $(0, \eta) \notin S$ where S is defined in (13) and $\xi_S^j = \xi(\lambda_j)$ is defined as in (19). Assume that*

(E1) for some $j \in \mathbb{N}$, λ_j is a simple eigenvalue of $-\Delta$ in Ω with Neumann boundary condition, and the corresponding eigenfunction is $\phi_j(x)$.

Then $dim N(D_{(u,v)}F(\xi_S^j, u^*, v^*)) = 1$.

Proof. Let $(\phi, \psi)(\neq 0) \in N(D_{(u,v)}F(\xi_S^j, u^*, v^*))$, then 0 is an eigenvalue of $L(\xi_S^j, \eta)$. From Lemma 2.2, $\mu = 0$ is an eigenvalue of A_j (defined in (8)), and a direct calculation shows that the corresponding eigenfunction is

$$\overrightarrow{V_j} = \left(\begin{array}{c} a_j \\ b_j \end{array} \right) \phi_j = \left(\begin{array}{c} f_v - \xi_S^j u^* \lambda_j \\ d\lambda_j - f_u \end{array} \right) \phi_j. \tag{23}$$

From the condition $(E1)$, the eigenfunction is unique up to a constant multiple. Hence we have $N(D_{(u,v)}F(\xi_S^j, u^*, v^*)) = span\{\overrightarrow{V_j}\}$, which is one-dimensional. □

Lemma 3.4. *Suppose that the conditions of Lemma 3.3 are satisfied. Then codim $R(D_{(u,v)}F(\xi_S^j, u^*, v^*)) = 1$.*

Proof. From the proof of Lemma 3.3, we have $D_{(u,v)}F(\xi_S^j, u^*, v^*) = L(\xi_S^j, \eta)$. Its adjoint operator is defined by

$$L^*(\xi_S^j, \eta) \left(\begin{array}{c} \phi \\ \psi \end{array} \right) = \left(\begin{array}{c} d_1\Delta\phi - \eta v^*\Delta\psi + f_u\phi + g_u\psi \\ \xi_S^j u^*\Delta\phi + \Delta\psi + f_v\phi + g_v\psi \end{array} \right).$$

Since 0 is a simple eigenvalue of $L(\xi_S^j,\eta)$, it is also a simple eigenvalue of $L^*(\xi_S^j,\eta)$ with eigenfunction

$$\overrightarrow{V_j^*} = \begin{pmatrix} a_j^* \\ b_j^* \end{pmatrix} \phi_j = \begin{pmatrix} \eta v^* \lambda_j + g_u \\ d\lambda_j - f_u \end{pmatrix} \phi_j.$$

If $(h_1,h_2) \in R(D_{(u,v)}F(\xi_S^j,u^*,v^*))$, then there exists $(\phi_1,\psi_1) \in Z \times Z$ such that

$$D_{(u,v)}F(\xi_S^j,u^*,v^*) \begin{pmatrix} \phi_1 \\ \psi_1 \end{pmatrix} = L(\xi_S^j,\eta) \begin{pmatrix} \phi_1 \\ \psi_1 \end{pmatrix} = \begin{pmatrix} h_1 \\ h_2 \end{pmatrix}.$$

Then we have

$$\begin{aligned} &\langle (h_1,h_2),(a_j^*,b_j^*)\phi_j\rangle = \langle L(\xi_S^j,\eta)[(\phi_1,\psi_1)],(a_j^*,b_j^*)\phi_j\rangle \\ =&\langle(\phi_1,\psi_1),L^*(\xi_S^j,\eta)[(a_j^*,b_j^*)\phi_j]\rangle = \langle(\phi_1,\psi_1),0\rangle = 0, \end{aligned}$$

where $\langle\cdot,\cdot\rangle$ is the inner-product in $[L^2(\Omega)]^2$. This proves that if $(h_1,h_2) \in R(D_{(u,v)} F(\xi_S^j,u^*,v^*))$, then

$$\int_\Omega (a_j^* h_1 + b_j^* h_2)\phi_j dx = 0. \tag{24}$$

This shows that $codim R(D_{(u,v)}F(\xi_S^j,u^*,v^*)) = 1$. □

Finally we show that the transversality condition holds.

Lemma 3.5. *Suppose that the conditions of Lemma 3.3 are satisfied. Then*

$$D_{(u,v)\xi}F(\xi_S^j,u^*,v^*)(\overrightarrow{V_j}) \notin R(D_{(u,v)}F(\xi_S^j,u^*,v^*)),$$

where $\overrightarrow{V_j}(\neq 0) \in N(D_{(u,v)}F(\xi_S^j,u^*,v^*))$.

Proof. Notice that

$$D_{(u,v)\xi}F(\xi_S^j,u^*,v^*) \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \begin{pmatrix} u^*\Delta\phi \\ 0 \end{pmatrix}.$$

Now we have

$$D_{(u,v)\xi}F(\xi_S^j,u^*,v^*)(\overrightarrow{V_j}) = \begin{pmatrix} u^* a_j \Delta\phi_j \\ 0 \end{pmatrix} = \begin{pmatrix} -\lambda_j u^* a_j \phi_j \\ 0 \end{pmatrix}.$$

Hence from (P2),

$$\begin{aligned} &\int_\Omega \left(-a_j^* \cdot \lambda_j u^* a_j \phi_j + b_j^* \cdot 0\right)\phi_j dx = -\int_\Omega \lambda_j u^* a_j a_j^* \phi_j^2 dx \\ =& -\lambda_j u^*(\eta v^* \lambda_j + g_u)(f_v - \xi_S^j u^* \lambda_j)\int_\Omega \phi_j^2 dx > 0. \end{aligned}$$

From (24), we obtain that $D_{(u,v)\xi}F(\xi_S^j,u^*,v^*)(\overrightarrow{V_j}) \notin R(D_{(u,v)}F(\xi_S^j,u^*,v^*))$. □

Now we have the following existence of non-constant equilibrium solutions of (1) by using the local bifurcation theorem (Theorem 3.2), as Lemma 3.3-Lemma 3.5 guarantee that the conditions 1-4 in Theorem 3.2 are satisfied.

Theorem 3.6. *Suppose that $d > 0$, $\eta \geq 0$, and (P1), (P2), (5) hold. Assume that $(0,\eta) \notin S$ where S is defined in (13), $\xi_S^j = \xi(\lambda_j)$ is defined as in (19), and the condition $(E1)$ holds. Then there is a continuous curve Γ_j of positive solutions of (21) bifurcating from the branch of the trivial branch $\{(\xi,u^*,v^*) : \xi > 0\}$ at $\xi = \xi_S^j > 0$; and $\Gamma_j = \{(\xi(s),u(s),v(s)) : s \in (-\varepsilon,\varepsilon)\}$, where $u(s) = u^* + sa_j\phi_j + sh_{1,j}(s)$,*

$v(s) = v^* + sb_j\phi_j + sh_{2,j}(s)$ for some continuous functions $h_{1,j}(s)$, $h_{2,j}(s)$ such that $h_{1,j}(0) = h_{2,j}(0) = 0$, and $A_j(a_j, b_j)^T = (0,0)^T$ where A_j is defined in (8).

Remark 2.

1. If the nonlinearities $f(u,v)$ and $g(u,v)$ are more smooth, one can determine the direction of bifurcation and stability of bifurcating solutions by computing $\xi'(0)$, see [9, 15, 25]. When the bifurcating solutions are locally asymptotically stable, it shows the spatial profile of $(a_j, b_j)\phi_j$ as in Theorem 3.6. This usually occurs at $\xi_S^* = \max_{n\in\mathbb{N}} \xi_S^n$, and the eigen-mode ϕ_j is selected as the spatial pattern.
2. The strength of the attractive prey-taxis ξ is used as the bifurcation parameter, hence the non-constant equilibrium solutions obtained in Theorem 3.6 are spatial pattern induced by the attractive prey-taxis. Here these spatial pattern emerge when ξ decreases.

4. **Application to Holling-Tanner model.** In this section, we apply the stability/instability and bifurcation analysis to the well known Holling-Tanner model:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d\Delta u + \xi\nabla\cdot(u\nabla v) + u(1-\beta u) - \dfrac{muv}{u+1}, & x\in\Omega,\ t>0, \\ \dfrac{\partial v}{\partial t} = \Delta v - \eta\nabla\cdot(v\nabla u) + sv\left(1 - \dfrac{v}{u}\right), & x\in\Omega,\ t>0, \\ \dfrac{\partial u(x,t)}{\partial\nu} = \dfrac{\partial v(x,t)}{\partial\nu} = 0, & x\in\partial\Omega,\ t>0, \\ u(x,0) = u_0(x)\geq 0,\ v(x,0) = v_0(x)\geq 0, & x\in\Omega. \end{cases} \tag{25}$$

The Holling-Tanner system is one of prototypical predator-prey models. The (non-spatial) kinetic equation of system (25) was first proposed in [20, 28], and the ODE model has been completely analyzed in [13]. For diffusive system (25) with $\xi = \eta = 0$, the global stability of the positive constant steady state was proved in [5, 22, 23], and Turing and Hopf bifurcations have been considered in [18].

System (25) has two non-trivial constant equilibria: a boundary equilibrium $E_1 = (1/\beta, 0)$ and a positive equilibrium $E_2 = (u^*, v^*)$, where

$$u^* = v^* = \frac{1}{2\beta}(\sqrt{R^2 + 4\beta} - R), \quad R = \beta + m - 1.$$

We recall the following results on the stability of E_2 for the corresponding ODE system and reaction-diffusion system (see [18, Theorem 2.1, 3.1]).

Theorem 4.1. *Suppose that $\beta, m, s, d > 0$ satisfy*

$$\beta < 1, \quad \text{and} \quad m > \frac{(1+\beta)^2}{2(1-\beta)}, \tag{26}$$

and define

$$s_0 = 1 - 2\beta u^* - \frac{mu^*}{(1+u^*)^2}, \quad b = -\frac{mu^*}{1+u^*}.$$

1. *When $0 < s < s_0$, E_2 is unstable for the corresponding ODE system of (25);*
2. *When $s > s_0$, E_2 is locally asymptotically stable for the corresponding ODE system of (25);*
3. *When $\eta = \xi = 0$ and $s > s_0$, then E_2 is unstable for (25) if d satisfies $0 < d < \min\{s_0/s, h(\lambda^*)\}$, where*

$$h(p) = \frac{s_0 p + s(s_0 + b)}{p(p+s)}, \quad \text{and} \quad \lambda^* = \frac{-s(s_0+b) + \sqrt{b^2 + s_0 b}}{s_0}. \tag{27}$$

Part 2 and 3 in Theorem 4.1 show a typical Turing type diffusion-induced instability. Next we consider the effect of prey-taxis and predator-taxis.

Theorem 4.2. *Suppose $\beta, m, s, d > 0$ satisfy (26), and $s > s_0$. Define*

$$\xi(p) = \frac{dp^2 - (\eta u^* b + s_0 - ds)p - s(s_0 + b)}{-u^* sp - \eta(u^*)^2 p^2},$$

and let $\xi^* = \max_{j\in\mathbb{N}} \xi(\lambda_j)$ where λ_j are eigenvalues of $-\Delta$ in Ω with Neumann boundary condition.

1. *For fixed $\eta \geq 0$, E_2 is unstable for (25) if $0 \leq \xi < \xi^*$, and it is locally asymptotically stable for (25) if $\xi > \xi^*$. In particular E_2 is locally asymptotically stable if $\xi > \dfrac{b\eta v^* + s_0 - ds}{su^*} \geq \xi^*$.*
2. *Suppose that $\xi^* = \xi(\lambda_k)$ for some $k \in \mathbb{N}$. Then near $\xi = \xi^*$, there is a smooth curve of non-constant equilibrium solutions of (25): $\Gamma_k = \{(\xi(s), u(s), v(s)) : s \in (-\varepsilon, \varepsilon)\}$ such that $\xi(0) = \xi^*$, and $(u(0), v(0)) = (u^*, v^*)$.*

Proof. Part 1 is from Proposition 1 and Theorem 2.3, as one can solve the threshold value $\dfrac{b\eta v^* + s_0 - ds}{su_0}$ from the definition of S in (13). Part 2 follows from Theorem 3.6. □

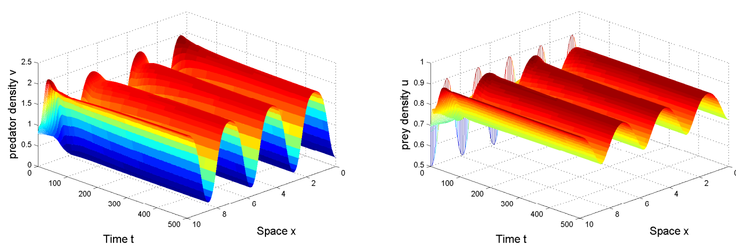

FIGURE 3. Turing instability for (25) with $\beta = 0.2$, $m = 2$, $s = 0.5$, $\Omega = (0, 10\pi)$, $d = 0.01$, $\xi = \eta = 0$ and initial value $(0.7 + 0.1\sin(2x), 0.7 + 0.2\sin(3x))$.

We use some numerical simulations to illustrate our analysis. We choose $\beta = 0.2$, $m = 2$, $s = 0.5$ in (25). Then the constant equilibrium is $(u^*, v^*) = (0.7417, 0.7417)$ and $s_0 = 0.2143$. So from Theorem 4.1 part 2, the equilibrium (u^*, v^*) is locally asymptotically stable for the corresponding ODE system as $s > s_0$. For the reaction-diffusion system (25) with $\eta = \xi = 0$, we use $l = 10$ with $\Omega = (0, l\pi)$. In this case, $\lambda^* = 4.3305$ and $h(\lambda^*) = 0.0367$. By Theorem 4.1 part 3, the homogeneous equilibrium (u^*, v^*) is unstable for (25) with $\xi = \eta = 0$ when $d = 0.01 < h(\lambda^*)$ (see Figure 3 for the spatial pattern). But for $d = 0.06 > h(\lambda^*)$, (u^*, v^*) is locally asymptotically stable for (25) with $\xi = \eta = 0$, which is depicted in Figure 4.

If an attractive prey-taxis and a repulsive predator-taxis are added to (25) when $d = 0.01$: we choose $\xi = 0.9$, $\eta = 0.4$, then from Theorem 4.2, the constant equilibrium (u^*, v^*) becomes locally asymptotically stable for system (25), (see Figure 5). This is the taxis-induced stability, and the attractive prey-taxis and repulsive predator-taxis have a stabilizing effect. On the other hand, if a repulsive prey-taxis and an attractive predator-taxis are added to (25) when $d = 0.06$: we choose

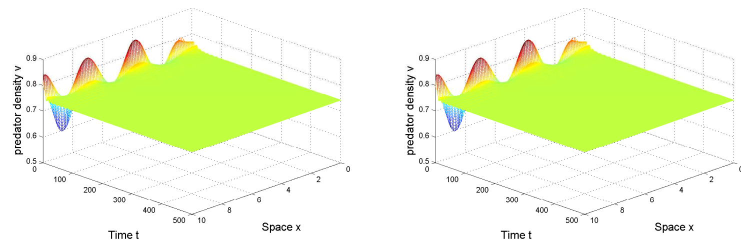

FIGURE 4. Stable constant equilibrium for (25) with $\beta = 0.2$, $m = 2$, $s = 0.5$, $\Omega = (0, 10\pi)$, $d = 0.06$, $\xi = \eta = 0$ and initial value $(0.7 + 0.1\sin(2x), 0.7 + 0.2\sin(3x))$.

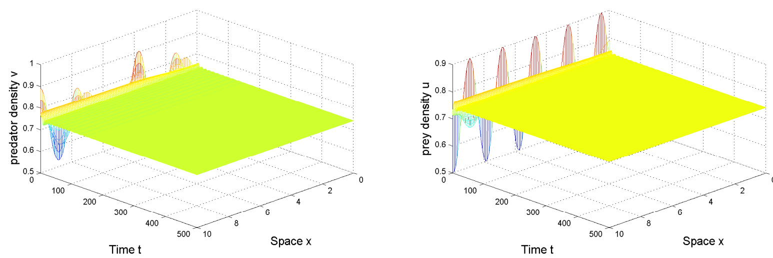

FIGURE 5. Turing pattern in (25) is stabilized when $\xi = 0.9$ and $\eta = 0.4$, and the same initial value $(0.7 + 0.1\sin(2x), 0.7 + 0.2\sin(3x))$. Other parameters are also same as in Figure 3.

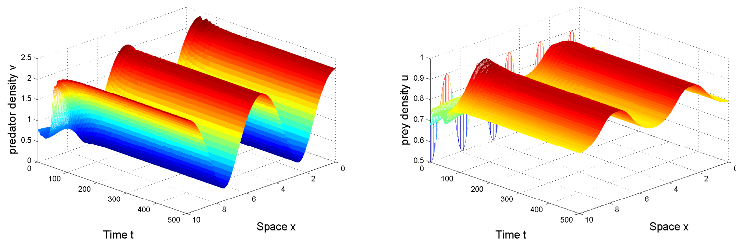

FIGURE 6. Instability induced by taxis in (25) when $\xi = -0.5$ and $\eta = -0.4$ and initial condition $(0.7+0.1\sin(2x), 0.7+0.2\sin(3x))$. Other parameters are same as in Figure 4.

$(\xi, \eta) = (-0.5, -0.4) \notin S$, then the constant equilibrium (u^*, v^*) becomes unstable and a spatial pattern is generated (see Figure 6).

Finally the prey-taxis and predator-taxis not only determine whether spatial patterns are generated but also affect the amplitude of the patterns. Figure 7 shows the amplitude (difference of maximum and minimum values) of the non-constant equilibrium solutions. It is apparent that an increase of either the strength of prey-taxis ξ or the strength of predator-taxis η will decrease the amplitude of the pattern, and the amplitude becomes zero (constant equilibrium with no pattern) when ξ or η is large enough.

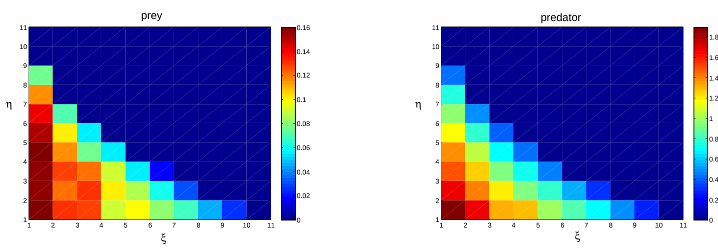

FIGURE 7. The amplitude change of non-constant equilibrium solutions of (25) for different (ξ, η). Here the value is the difference of maximum and minimum values of the non-constant equilibrium solution; the initial value is $(0.7+0.1\sin(2x), 0.7+0.2\sin(3x))$ and other parameters are the same as Figure 3.

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