

Global dynamics and spatio-temporal patterns of predator–prey systems with density-dependent motion

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In this paper, we investigate the global boundedness, asymptotic stability and pattern formation of predator–prey systems with density-dependent prey-taxis in a two-dimensional bounded domain with Neumann boundary conditions, where the coefficients of motility (diffusion) and mobility (prey-taxis) of the predator are correlated through a prey density-dependent motility function. We establish the existence of classical solutions with uniform-in time bound and the global stability of the spatially homogeneous prey-only steady states and coexistence steady states under certain conditions on parameters by constructing Lyapunov functionals. With numerical simulations, we further demonstrate that spatially homogeneous time-periodic patterns, stationary spatially inhomogeneous patterns and chaotic spatio-temporal patterns are all possible for the parameters outside the stability regime. We also find from numerical simulations that the temporal dynamics between linearised system and nonlinear systems are quite different, and the prey density-dependent motility function can trigger the pattern formation.

Key words: Predator–prey system, prey-taxis, boundedness, global stability, Lyapunov functional

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1 Introduction

The foraging is the searching for wild food resources by hunting, fishing, consuming or the gathering of plant matter. It plays an important role in an organism's ability to survive and reproduce. The non-random foraging strategies in the predator–prey dynamics, such as the area-restricted search, are often observed to result in populations of predators moving (or flowing) towards regions of higher prey density (see Refs. [7, 30, 31]). Such movement is referred to as prey-taxis which has important roles in biological control or ecological balance such as regulating prey (pest) population to avoid incipient outbreaks of prey or forming large-scale aggregation for survival (cf. Refs. [10, 30, 34]). To understand the dynamics of predator–prey systems with prey-taxis, Kareiva and Odell [16] put individual foraging behaviours into a biased random walk

model which, upon passage to a continuum limit, leads to the following prey-taxis system (see

$c_1 > 0, c_2 > 0$. The function forms given in (1.2) have represented most of ecologically meaningful examples of predator–prey population interactions used in the literature by assigning appropriate expressions to $h(u), f(v)$ and $F(v)$. Typically, the predator kinetics $h(u)$ may include density-dependent death $h(u) = -u(\theta + \alpha u)$, $\theta > 0, \alpha \geq 0$, the prey kinetics $f(v)$ could be linear, logistic or Allee effect (bistable) type and $F(v)$ may be of Lotka–Volterra type [25, 41] or Holling’s type [11]. We refer the readers to the excellent surveys [29, 40] for an exhaustive list of $h(u), f(v)$ and $F(v)$. Hence, in this paper, we consider the following system:

$$\begin{cases} u_t = \nabla \cdot (d(v)\nabla u) - \nabla \cdot (u\chi(v)\nabla v) + \gamma uF(v) - \theta u - \alpha u^2, & x \in \Omega, \quad t > 0, \\ v_t = D\Delta v - uF(v) + f(v), & x \in \Omega, \quad t > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x), v(x, 0) = v_0(x), & x \in \Omega, \end{cases} \quad (1.3)$$

where $D, \gamma > 0, \theta > 0, \alpha \geq 0$ are constants, and $d(v), \chi(v), F(v)$ and $f(v)$ satisfy the following conditions:

- (H1) $d(v), \chi(v) \in C^2([0, \infty))$, $d(v) > 0, \chi(v) \geq 0$ and $d'(v) \leq 0$ on $[0, \infty)$.
- (H2) $F(v) \in C^1([0, \infty))$, $F(0) = 0, F(v) > 0$ in $(0, \infty)$ and $F'(v) > 0$.
- (H3) $f: [0, \infty) \rightarrow \mathbb{R}$ is in C^1 with $f(0) = 0$, and there exist two constants $\mu, K > 0$ such that $f(v) \leq \mu v$ for any $v \geq 0, f(K) = 0$ and $f(v) < 0$ for all $v > K$.

We remark that the above assumptions for $F(v)$ and $f(v)$ have covered a large class of interesting and meaningful examples encountered in the literature as mentioned above. Our first result on the global boundedness of solutions of (1.3) is the following.

Theorem 1.1 (Global boundedness) *Assume $(u_0, v_0) \in [W^{1,p}(\Omega)]^2$ with $p > 2$ and $u_0, v_0 \geq 0 (\not\equiv 0)$. Let $\Omega \subset \mathbb{R}^2$ be a bounded domain with smooth boundary and the hypotheses (H1)–(H3) hold. If $\alpha > 0$ or $\chi(v) = -d'(v)$, then there is a unique classical solution $(u, v) \in [C([0, \infty) \times \bar{\Omega}) \cap C^{2,1}((0, \infty) \times \bar{\Omega})]^2$ solving the problem (1.3). Moreover there is constant $C > 0$ independent of t such that*

$$\|u(\cdot, t)\|_{L^\infty} + \|v(\cdot, t)\|_{W^{1,\infty}} \leq C,$$

where in particular $0 \leq v \leq K_0$ with

$$K_0 := \max\{\|v_0\|_{L^\infty}, K\}. \quad (1.4)$$

Next, we will study the large time behaviour of solutions. One can easily compute that the system (1.3) has three homogeneous steady states (u_s, v_s) :

$$(u_s, v_s) = \begin{cases} (0, 0) \text{ or } (0, K), & \text{if } \gamma F(K) \leq \theta, \\ (0, 0) \text{ or } (0, K) \text{ or } (u_*, v_*), & \text{if } \gamma F(K) > \theta \end{cases}$$

with $u_*, v_* > 0$ determined by the following algebraic equations:

$$u_* = \frac{f(v_*)}{F(v_*)}, \quad \gamma F(v_*) = \theta + \alpha u_*, \quad (1.5)$$

where $(0, 0)$ is the extinction steady state, $(0, K)$ is the prey-only steady state and (u_*, v_*) is the coexistence steady state. As in Ref. [12], for the global stability, along with the hypotheses (H1)–(H3), we need another condition for the following compound function:

$$\phi(v) = \frac{f(v)}{F(v)},$$

as follows:

(H4) The function $\phi(v)$ is continuously differentiable on $(0, \infty)$, $\phi(0) = \lim_{v \rightarrow 0} \phi(v) > 0$ and $\phi'(v) < 0$ for any $v \geq 0$.

Then, the global stability results are given as follows:

Theorem 1.2 (Global stability) *Let the hypotheses (H1)–(H4) and assumptions in Theorem 1.1 hold. Then, the solution (u, v) obtained in Theorem 1.1 has the following properties:*

(1) *If the parameters θ, γ, K satisfy $\gamma F(K) \leq \theta$ where ‘ $=$ ’ holds iff $\alpha > 0$, then*

$$\|u\|_{L^\infty} + \|v - K\|_{L^\infty} \rightarrow 0 \text{ as } t \rightarrow \infty,$$

exponentially if $\gamma F(K) < \theta$ or algebraically if $\gamma F(K) = \theta, \alpha > 0$.

(2) *If the parameters θ, γ, K satisfy $\gamma F(K) > \theta$ and*

$$D \geq \max_{0 \leq v \leq K_0} \frac{u_* |F(v)|^2 |\chi(v)|^2}{4\gamma F(v_*) F'(v) d(v)},$$

then

$$\|u - u_*\|_{L^\infty} + \|v - v_*\|_{L^\infty} \rightarrow 0 \text{ as } t \rightarrow \infty,$$

where the convergence is exponential if $\alpha > 0$.

We remark if $d(v)$ and $\chi(v)$ are constant, the system (1.3) has been studied from various aspects (cf. Refs. [2, 6, 22, 23, 37, 46]), and in particular the global existence and stability of solutions have been established in a previous work by the authors in Ref. [12]. The results Theorems 1.1 and 1.2 extend the results of Ref. [12] to non-constant $d(v)$ and $\chi(v)$. Moreover, the proof of Theorem 1.2 uses a similar idea (method of Lyapunov functional) as in Ref. [12]. Except these analogies, we would like to stress some essential differences between the present paper and [12] below.

- The method used in Ref. [12] to prove the global existence of solutions was based on *a priori* estimate for the energy functional $\int_\Omega u \ln u dx$ to attain the L^2 -estimate of solutions. However, such *a priori* estimates are attainable only for case where the motility function $d(v)$ is constant. Hence, the method of Ref. [12] is inapplicable to the model (1.3). In this paper, we estimate L^2 -norm of solutions directly to obtain the global existence of solutions (see Section 3). With this new direct L^2 -estimate method, the concavity of $F(v)$ required in Ref. [12] is no longer needed. That is, we not only use a different method to prove the global boundedness of solutions but also remove the condition $F''(v) \leq 0$ imposed in Ref. [12].
- If $d(v)$ and $\chi(v)$ are non-constant as considered in this paper, we find that the system (1.3) can generate pattern formation as shown in Section 5. This is different from Ref. [12] where

no pattern formation can be founded for constant $d(v)$ and $\chi(v)$. Our result indicates that the density-dependent motility is a trigger for pattern formation, which is a new finding.

- In the proof of global stability shown in Section 4, we need the estimate of $\|\nabla u\|_{L^4}$ which can be easily obtained for constant $d(v)$ and $\chi(v)$ but is not clear if $d(v)$ and $\chi(v)$ are not constant. Hence, we present a new proof in Lemma 4.2.

In Section 5, we shall detail the results of Theorems 1.1 and 1.2 for specific and often used forms of $F(v)$. In Theorem 1.2, the conditions on parameter values are identified to ensure the global stability of homogeneous steady states. However, it is unknown whether non-homogeneous (i.e. non-constant) steady states exist outside the stability regimes found in Theorem 1.2. In the final Section 5, we shall use linear stability analysis to find the conditions on parameters for the instability of equilibria of (1.3) and then perform numerical simulations to illustrate that indeed spatially inhomogeneous patterns and time-periodic patterns can be found under certain conditions. We also demonstrate that the non-constant motility function $d(v)$ plays an important role in generating the pattern formation.

2 Local existence and Preliminaries

In what follows, we shall use c_i or $C_i (i = 1, 2, 3, \dots)$ to denote a generic constant which may vary in the context. We first state the existence of local-in-time classical solutions of system (1.3) by using the abstract theory of quasilinear parabolic systems in Ref. [5].

Lemma 2.1 (Local existence) *Let Ω be a bounded domain in $\mathbb{R}^2$ with smooth boundary and the hypotheses (H1)–(H3) hold. Assume $(u_0, v_0) \in [W^{1,p}(\Omega)]^2$ with $u_0, v_0 \geq 0$ ($\neq 0$) and $p > 2$. Then there exists $T_{\max} \in (0, \infty]$ such that the problem (1.3) has a unique classical solution $(u, v) \in [C([0, T_{\max}) \times \bar{\Omega}) \cap C^{2,1}((0, T_{\max}) \times \bar{\Omega})]^2$ satisfying $u, v \geq 0$ for all $t > 0$. Moreover, we have*

$$\text{either } T_{\max} = \infty, \text{ or } \limsup_{t \nearrow T_{\max}} (\|u(\cdot, t)\|_{L^\infty} + \|v(\cdot, t)\|_{L^\infty}) = \infty. \quad (2.1)$$

Proof We shall apply the theory developed by Amann [5] to prove this lemma. With $\omega = (u, v)$, the system (1.3) can be reformulated as

$$\begin{cases} \omega_t = \nabla \cdot (\mathbb{A}(\omega) \nabla \omega) + \Phi(\omega), & x \in \Omega, t > 0, \\ \frac{\partial \omega}{\partial \nu} = 0, & x \in \partial \Omega, t > 0, \\ \omega(\cdot, 0) = (u_0, v_0), & x \in \Omega, \end{cases}$$

where

$$\mathbb{A}(\omega) = \begin{bmatrix} d(v) & -\chi(v)u \\ 0 & 1 \end{bmatrix} \text{ and } \Phi(\omega) = \begin{bmatrix} \gamma u F(v) - \theta u - \alpha u^2 \\ f(v) - u F(v) \end{bmatrix}.$$

Since the given initial conditions satisfy $0 \leq (u_0, v_0) \in [W^{1,p}(\Omega)]^2$ with $p > 2$ and hence the matrix $\mathbb{A}(\omega)$ is positively definite at $t = 0$. Hence, the system (1.3) is normally parabolic and the local existence of solutions follows from Ref. [4, Theorem 7.3]. That is, there exists a $T_{\max} > 0$ such that the system (1.3) admits a unique solution $(u, v) \in [C([0, T_{\max}) \times \bar{\Omega}) \cap C^{2,1}((0, T_{\max}) \times \bar{\Omega})]^2$.

Next, we will use the maximum principle to prove that $u, v \geq 0$. To this end, we rewrite the first equation of (1.3) as

$$u_t = d(v)\Delta u + [d'(v)\nabla v - \chi(v)\nabla v] \cdot \nabla u - \chi'(v)u|\nabla v|^2 - \chi(v)u\Delta v + \gamma uF(v) - \theta u - \alpha u^2. \quad (2.2)$$

Then applying the strong maximum principle to (2.2) with the Neumann boundary condition asserts that $u > 0$ for all $(x, t) \in \Omega \times (0, T_{\max})$ due to $u_0 \not\equiv 0$. Similarly, we can show $v > 0$ for any $(x, t) \in \Omega \times (0, T_{\max})$ by applying the strong maximum principle to the second equation of system (1.3). Since $\mathbb{A}(\omega)$ is an upper triangular matrix, the assertion (2.1) follows from Ref. [3, Theorem 5.2] directly. Then the proof of Lemma 2.1 is completed. $\square$

Lemma 2.2 ([12]) *Under the conditions in Lemma 2.1, the solution (u, v) of (1.3) satisfies*

$$0 \leq v(x, t) \leq K_0, \quad \text{for all } x \in \Omega \text{ and } t \in (0, T_{\max}), \quad (2.3)$$

where K_0 is defined by (1.4).

Next, we present a basic boundedness property of the solutions to (1.3).

Lemma 2.3 *Let (u, v) be a solution of system (1.3). Then there exists a constant $C > 0$ such that*

$$\int_{\Omega} u dx \leq C, \quad \text{for all } t \in (0, T_{\max}). \quad (2.4)$$

Moreover, if $\alpha > 0$ or $\chi(v) = -d'(v)$, one has

$$\int_t^{t+\tau} \int_{\Omega} u^2 dx ds \leq C, \quad \text{for all } t \in (0, \tilde{T}_{\max}), \quad (2.5)$$

where

$$\tau := \min \left\{ 1, \frac{1}{2} T_{\max} \right\} \quad \text{and} \quad \tilde{T}_{\max} := \begin{cases} T_{\max} - \tau, & \text{if } T_{\max} < \infty, \\ \infty, & \text{if } T_{\max} = \infty. \end{cases} \quad (2.6)$$

Proof Multiplying the second equation (1.3) by γ and adding the resulting equation into the first equation of (1.3), then integrating the result over $\Omega \times (0, t)$, one has

$$\frac{d}{dt} \left(\int_{\Omega} u dx + \gamma \int_{\Omega} v dx \right) + \int_{\Omega} u(\theta + \alpha u) dx = \gamma \int_{\Omega} f(v) dx,$$

which, along with the hypotheses (H2) and (H3) and the fact that $0 \leq v \leq K_0$, gives

$$\begin{aligned} \frac{d}{dt} \left(\int_{\Omega} u dx + \gamma \int_{\Omega} v dx \right) + \theta \left(\int_{\Omega} u dx + \gamma \int_{\Omega} v dx \right) + \alpha \int_{\Omega} u^2 dx &\leq (\gamma \mu + \theta \gamma) \int_{\Omega} v dx \\ &\leq (\gamma \mu + \theta \gamma) K_0 |\Omega|. \end{aligned} \quad (2.7)$$

Then, the Gronwall's inequality applied to (2.7) yields (2.4). If $\alpha > 0$, then integrating (2.7) over $(t, t + \tau)$, we have (2.5) directly.

Next, we consider the case $\chi(v) = -d'(v)$. In this case, the first equation of system (1.3) can be written as

$$u_t = \Delta(d(v)u) + \gamma u F(v) - \theta u - \alpha u^2. \quad (2.8)$$

Let $0 < \delta < \frac{\theta}{d(0)}$ and let $\mathcal{A}$ denote the self-adjoint realisation of $-\Delta + \delta$ under homogeneous Neumann boundary conditions in $L^2(\Omega)$. Since $\delta > 0$, $\mathcal{A}$ possesses an order-preserving bounded inverse $\mathcal{A}^{-1}$ on $L^2(\Omega)$ and hence we can find a constant $c_1 > 0$ such that

$$\|\mathcal{A}^{-1}\psi\|_{L^2} \leq c_1 \|\psi\|_{L^2} \quad \text{for all } \psi \in L^2(\Omega), \quad (2.9)$$

and

$$\|\mathcal{A}^{-\frac{1}{2}}\psi\|_{L^2}^2 = \int_{\Omega} \psi \cdot \mathcal{A}^{-1}\psi \, dx \leq c_1 \|\psi\|_{L^2}^2 \quad \text{for all } \psi \in L^2(\Omega). \quad (2.10)$$

From the second equation of (1.3) with (2.8), we have

$$(u + \gamma v)_t = \Delta(d(v)u + D\gamma v) - \theta u - \alpha u^2 + \gamma f(v),$$

which can be rewritten as

$$\begin{aligned} (u + \gamma v)_t + \mathcal{A}(d(v)u + D\gamma v) &= \delta[d(v)u + D\gamma v] - \theta u - \alpha u^2 + \gamma f(v) \\ &= (\delta d(v) - \theta - \alpha u)u + \gamma f(v) + D\delta\gamma v. \end{aligned} \quad (2.11)$$

Noting the facts $0 < \delta < \frac{\theta}{d(0)}$ and (2.3), one can derive that

$$(\delta d(v) - \theta - \alpha u)u + \gamma f(v) + D\delta\gamma v \leq (\delta d(0) - \theta)u + c_2 \leq c_2. \quad (2.12)$$

Hence, multiplying (2.11) by $\mathcal{A}^{-1}(u + \gamma v) \geq 0$, and using the fact (2.12), one has

$$\frac{1}{2} \frac{d}{dt} \int_{\Omega} |\mathcal{A}^{-\frac{1}{2}}(u + \gamma v)|^2 \, dx + \int_{\Omega} (d(v)u + D\gamma v)(u + \gamma v) \, dx \leq c_2 \int_{\Omega} \mathcal{A}^{-1}(u + \gamma v) \, dx,$$

which together with the fact $0 < d(K_0) \leq d(v)$, gives a constant $c_3 := \min\{d(K_0), D\}$ such that

$$\frac{1}{2} \frac{d}{dt} \int_{\Omega} |\mathcal{A}^{-\frac{1}{2}}(u + \gamma v)|^2 \, dx + c_3 \int_{\Omega} (u + \gamma v)^2 \, dx \leq c_2 \int_{\Omega} \mathcal{A}^{-1}(u + \gamma v) \, dx. \quad (2.13)$$

Using (2.9) and (2.10), we can derive that

$$\begin{aligned} \frac{c_3}{4c_1} \int_{\Omega} |\mathcal{A}^{-\frac{1}{2}}(u + \gamma v)|^2 \, dx + c_2 \int_{\Omega} \mathcal{A}^{-1}(u + \gamma v) \, dx &\leq \frac{c_3}{4} \int_{\Omega} (u + \gamma v)^2 \, dx + c_2 |\Omega|^{\frac{1}{2}} \|u + \gamma v\|_{L^2} \\ &\leq \frac{c_3}{2} \int_{\Omega} (u + \gamma v)^2 \, dx + \frac{c_2^2 |\Omega|}{c_3}. \end{aligned} \quad (2.14)$$

Adding (2.14) and (2.13), and letting $y_1(t) := \int_{\Omega} |\mathcal{A}^{-\frac{1}{2}}(u + \gamma v)|^2$, one has

$$y_1'(t) + \frac{c_3}{2c_1} y_1(t) + c_3 \int_{\Omega} (u + \gamma v)^2 \, dx \leq \frac{2c_2^2 |\Omega|}{c_3}.$$

Then one has $y_1(t) \leq c_4$ and

$$\int_t^{t+\tau} \int_{\Omega} u^2 dx ds \leq \int_t^{t+\tau} \int_{\Omega} (u + \gamma v)^2 dx ds \leq \frac{y_1(t)}{c_3} + \frac{2c_2^2 |\Omega| \tau}{c_3^2} \leq \frac{c_4}{c_3} + \frac{2c_2^2 |\Omega|}{c_3^2} \text{ for all } t \in (0, \tilde{T}_{\max}),$$

which gives (2.5). Then the proof of this lemma is completed. $\square$

Moreover, we can thereupon deduce the following result as a consequence of Lemma 2.3.

Lemma 2.4 *Let (u, v) be the solution of system (1.3), then there exists a constant $C > 0$ independent of t such that*

$$\|\nabla v\|_{L^2} \leq C, \text{ for all } t \in (0, T_{\max}), \quad (2.15)$$

and

$$\int_t^{t+\tau} \int_{\Omega} |\Delta v|^2 dx ds \leq C, \text{ for all } t \in (0, \tilde{T}_{\max}), \quad (2.16)$$

where τ and $\tilde{T}_{\max}$ are defined by (2.6).

Proof Multiplying the second equation of system (1.3) by $-\Delta v$, integrating the result by part and using the Cauchy–Schwarz inequality and the boundedness of v in (2.3), we end up with

$$\begin{aligned} \frac{1}{2} \frac{d}{dt} \int_{\Omega} |\nabla v|^2 dx + D \int_{\Omega} |\Delta v|^2 dx &= \int_{\Omega} u F(v) \Delta v dx - \int_{\Omega} f(v) \Delta v dx, \\ &\leq \frac{D}{2} \int_{\Omega} |\Delta v|^2 dx + \frac{1}{D} \int_{\Omega} F^2(v) u^2 dx + \frac{1}{D} \int_{\Omega} f^2(v) dx \\ &\leq \frac{D}{2} \int_{\Omega} |\Delta v|^2 dx + \frac{F^2(K_0)}{D} \int_{\Omega} u^2 dx + c_1, \end{aligned}$$

which yields

$$\frac{d}{dt} \int_{\Omega} |\nabla v|^2 dx + D \int_{\Omega} |\Delta v|^2 dx \leq \frac{2F^2(K_0)}{D} \int_{\Omega} u^2 dx + 2c_1. \quad (2.17)$$

Using the Gagliardo–Nirenberg inequality and noting the fact $\|v\|_{L^2} \leq K_0 |\Omega|^{\frac{1}{2}}$, one has

$$\int_{\Omega} |\nabla v|^2 dx = \|\nabla v\|_{L^2}^2 \leq c_2 (\|\Delta v\|_{L^2} \|v\|_{L^2} + \|v\|_{L^2}^2) \leq \frac{D}{2} \|\Delta v\|_{L^2}^2 + c_3. \quad (2.18)$$

Substituting (2.18) into (2.17), we get

$$\frac{d}{dt} \int_{\Omega} |\nabla v|^2 dx + \int_{\Omega} |\nabla v|^2 dx + \frac{D}{2} \int_{\Omega} |\Delta v|^2 dx \leq \frac{2F^2(K_0)}{D} \int_{\Omega} u^2 dx + c_4. \quad (2.19)$$

Denote $y(t) := \int_{\Omega} |\nabla v(\cdot, t)|^2 dx$, $t \in [0, T_{\max})$ and $z(t) := \frac{2F^2(K_0)}{D} \int_{\Omega} u^2 dx + c_4$, from (2.19) we have

$$y'(t) + y(t) \leq z(t) \text{ for all } t \in (0, T_{\max}), \quad (2.20)$$

which gives (2.15) by noting (2.5). On the other hand, integrating (2.19) over $(t, t + \tau)$ along with (2.5) and (2.15), we obtain (2.16). $\square$

3 Boundedness of solutions

We will derive the *a priori* L^2 -estimate of the solution component u .

Lemma 3.1 *Let the conditions in Theorem 1.1 hold. Then, the solution of (1.3) satisfies*

$$\|u(\cdot, t)\|_{L^2} \leq C, \text{ for all } t \in (0, T_{\max}), \quad (3.1)$$

where $C > 0$ is a constant independent of t .

Proof Multiplying the first equation of (1.3) by $2u$, integrating the result with respect to x over Ω , one has

$$\begin{aligned} & \frac{d}{dt} \int_{\Omega} u^2 dx + 2 \int_{\Omega} d(v) |\nabla u|^2 dx + 2\alpha \int_{\Omega} u^3 dx + 2\theta \int_{\Omega} u^2 dx \\ & = 2 \int_{\Omega} u \chi(v) \nabla u \cdot \nabla v dx + 2\gamma \int_{\Omega} u^2 F(v) dx. \end{aligned} \quad (3.2)$$

With the assumptions in (H1)–(H2) and the fact (2.3), one has $d(v) \geq d(K_0) > 0$, $0 < F(v) \leq F(K_0)$ and $0 \leq \chi(v) \leq c_1$. Then using the Young's inequality and Hölder inequality, we have from (3.2) that

$$\begin{aligned} & \frac{d}{dt} \int_{\Omega} u^2 dx + 2d(K_0) \int_{\Omega} |\nabla u|^2 dx + 2\alpha \int_{\Omega} u^3 dx + 2\theta \int_{\Omega} u^2 dx \\ & \leq 2c_1 \int_{\Omega} u |\nabla u| |\nabla v| dx + 2\gamma F(K_0) \int_{\Omega} u^2 dx \\ & \leq d(K_0) \int_{\Omega} |\nabla u|^2 dx + \frac{c_1^2}{d(K_0)} \int_{\Omega} u^2 |\nabla v|^2 dx + 2\gamma F(K_0) \int_{\Omega} u^2 dx \\ & \leq d(K_0) \|\nabla u\|_{L^2}^2 + \frac{c_1^2}{d(K_0)} \|u\|_{L^4}^2 \|\nabla v\|_{L^4}^2 + 2\gamma F(K_0) \|u\|_{L^2}^2. \end{aligned} \quad (3.3)$$

Using the Gagliardo–Nirenberg inequality, one has

$$\|u\|_{L^4}^2 \leq c_2 (\|\nabla u\|_{L^2} \|u\|_{L^2} + \|u\|_{L^2}^2), \quad (3.4)$$

and the following estimate (cf. Ref. [13, Lemma 2.5]):

$$\|\nabla v\|_{L^4}^2 \leq c_3 (\|\Delta v\|_{L^2} \|\nabla v\|_{L^2} + \|\nabla v\|_{L^2}^2) \leq c_3 c_4 (\|\Delta v\|_{L^2} + c_4), \quad (3.5)$$

where the fact $\|\nabla v\|_{L^2} \leq c_4$ has been used. Combining (3.4)–(3.5) and using the Young's inequality, we obtain

$$\begin{aligned} \frac{c_1^2}{d(K_0)} \|u\|_{L^4}^2 \|\nabla v\|_{L^4}^2 &\leq c_5 (\|\nabla u\|_{L^2} \|u\|_{L^2} + \|u\|_{L^2}^2) (\|\Delta v\|_{L^2} + c_4) \\ &\leq c_5 \|\nabla u\|_{L^2} \|u\|_{L^2} \|\Delta v\|_{L^2} + c_4 c_5 \|\nabla u\|_{L^2} \|u\|_{L^2} \\ &\quad + c_5 \|u\|_{L^2}^2 \|\Delta v\|_{L^2} + c_4 c_5 \|u\|_{L^2}^2 \\ &\leq d(K_0) \|\nabla u\|_{L^2}^2 + \frac{c_5^2}{d(K_0)} \|u\|_{L^2}^2 \|\Delta v\|_{L^2}^2 + c_6 \|u\|_{L^2}^2, \end{aligned} \quad (3.6)$$

where $c_5 := \frac{c_1^2 c_2 c_3 c_4}{d(K_0)}$ and $c_6 := \frac{c_4^2 c_5^2 + d^2(K_0) + 2c_4 c_5 d(K_0)}{2d(K_0)}$. Then with (3.6), we update (3.3) as

$$\frac{d}{dt} \|u\|_{L^2}^2 \leq \frac{c_5^2}{d(K_0)} \|u\|_{L^2}^2 \|\Delta v\|_{L^2}^2 + (2\gamma F(K_0) + c_6) \|u\|_{L^2}^2 \leq c_7 \|u\|_{L^2}^2 (\|\Delta v\|_{L^2}^2 + 1), \quad (3.7)$$

with $c_7 := \frac{c_5^2}{d(K_0)} + 2\gamma F(K_0) + c_6$. For any $t \in (0, T_{\max})$ and in the case of either $t \in (0, \tau)$ or $t \geq \tau$ with $\tau = \min \left\{ 1, \frac{1}{2} T_{\max} \right\}$, from (2.5) we can find a $t_0 = t_0(t) \in ((t - \tau)_+, t)$ such that $t_0 \geq 0$ and

$$\int_{\Omega} u^2(x, t_0) dx \leq c_8. \quad (3.8)$$

On the other hand, from (2.16) in Lemma 2.4, we can find a constant $c_9 > 0$ such that

$$\int_{t_0}^{t_0 + \tau} \int_{\Omega} |\Delta v(x, s)|^2 dx ds \leq c_9 \quad \text{for all } t_0 \in (0, \tilde{T}_{\max}). \quad (3.9)$$

Then integrating (3.7) over (t_0, t) , and using (3.8), (3.9) and the fact $t \leq t_0 + \tau \leq t_0 + 1$, we derive

$$\|u(\cdot, t)\|_{L^2}^2 \leq \|u(\cdot, t_0)\|_{L^2}^2 \cdot e^{c_7 \int_{t_0}^t (\|\Delta v(\cdot, s)\|_{L^2}^2 + 1) ds} \leq c_8 e^{c_7(c_9 + 1)},$$

which yields (3.1) and completes the proof of Lemma 3.1. $\square$

Next, we will derive the boundedness of $\|u(\cdot, t)\|_{L^\infty}$ by the Moser iteration.

Lemma 3.2 *Let the conditions in Theorem 1.1 hold. Then the solution of system (1.3) satisfies*

$$\|u(\cdot, t)\|_{L^\infty} \leq C \quad \text{for all } t \in (0, T_{\max}), \quad (3.10)$$

where the constant $C > 0$ independent of t .

Proof First, we claim that if $\|u(\cdot, t)\|_{L^p} \leq M_0(p \geq 1)$, then it holds that

$$\|\nabla v(\cdot, t)\|_{L^r} \leq c_1, \quad \text{for all } t \in (0, T_{\max}), \quad (3.11)$$

with

$$r \in \begin{cases} [1, \frac{np}{n-p}), & \text{if } p < n, \\ [1, \infty), & \text{if } p = n, \\ [1, \infty], & \text{if } p > n. \end{cases} \quad (3.12)$$

In fact, from the second equation of system (1.3), we know that v solves the following problem:

$$v_t = D\Delta v - v + g(u, v) \text{ in } \Omega, \quad \frac{\partial v}{\partial \nu} = 0, \quad (3.13)$$

where $g(u, v) := v - uF(v) + f(v)$. Noting the properties of $F(v), f(v)$ and the fact that $0 \leq v(x, t) \leq K_0$ in (2.3), one has

$$\|g(u, v)\|_{L^p} \leq c_2(\|u\|_{L^p} + 1) \leq c_2(M_0 + 1) := c_3. \quad (3.14)$$

Then applying the results of Ref. [19, Lemma 1] (see also Ref. [39, Lemma 1.2]) to the problem (3.13) with (3.14), we obtain (3.11) with (3.12).

Using u^{p-1} with $p \geq 2$ as a test function for the first equation in (1.3), and integrating the resulting equation by parts, we obtain

$$\begin{aligned} & \frac{1}{p} \frac{d}{dt} \int_{\Omega} u^p dx + (p-1) \int_{\Omega} d(v) u^{p-2} |\nabla u|^2 dx + \alpha \int_{\Omega} u^{p+1} dx + \theta \int_{\Omega} u^p dx \\ &= (p-1) \int_{\Omega} \chi(v) u^{p-1} \nabla u \cdot \nabla v dx + \gamma \int_{\Omega} F(v) u^p dx. \end{aligned} \quad (3.15)$$

Using the facts $0 \leq \chi(v) \leq c_4$, $d(v) \geq d(K_0) > 0$, $0 < F(v) \leq F(K_0)$, $\alpha \geq 0$ and applying the Young's inequality, from (3.15) we obtain

$$\begin{aligned} & \frac{1}{p} \frac{d}{dt} \int_{\Omega} u^p dx + (p-1) d(K_0) \int_{\Omega} u^{p-2} |\nabla u|^2 dx + \theta \int_{\Omega} u^p dx \\ & \leq c_4 (p-1) \int_{\Omega} u^{p-1} |\nabla u| |\nabla v| dx + \gamma F(K_0) \int_{\Omega} u^p dx \\ & \leq \frac{(p-1) d(K_0)}{2} \int_{\Omega} u^{p-2} |\nabla u|^2 dx + \frac{c_4^2 (p-1)}{2 d(K_0)} \int_{\Omega} u^p |\nabla v|^2 dx + \gamma F(K_0) \int_{\Omega} u^p dx, \end{aligned}$$

which along with the fact

$$\frac{p(p-1) d(K_0)}{2} \int_{\Omega} u^{p-2} |\nabla u|^2 dx = \frac{2(p-1) d(K_0)}{p} \int_{\Omega} |\nabla u^{\frac{p}{2}}|^2 dx,$$

gives

$$\begin{aligned} & \frac{d}{dt} \int_{\Omega} u^p dx + p\theta \int_{\Omega} u^p dx + \frac{2(p-1) d(K_0)}{p} \int_{\Omega} |\nabla u^{\frac{p}{2}}|^2 dx \\ & \leq \frac{c_4^2 p (p-1)}{2 d(K_0)} \int_{\Omega} u^p |\nabla v|^2 dx + \gamma F(K_0) \int_{\Omega} u^p dx, \end{aligned} \quad (3.16)$$

for all $t \in (0, T_{\max})$ and for all $p \geq 2$. From Lemma 3.1, one has $\|u(\cdot, t)\|_{L^2} \leq c_5$ and hence $\|\nabla v(\cdot, t)\|_{L^4} \leq c_6$ by noting (3.11). Then using the Hölder inequality and the Gagliardo–Nirenberg inequality with the fact $\|u^{\frac{p}{2}}(\cdot, t)\|_{L^{\frac{4}{p}}}^{\frac{p}{2}} = \|u(\cdot, t)\|_{L^2}^{\frac{p}{2}} \leq c_5^{\frac{p}{2}}$, one has for all $t \in (0, T_{\max})$

$$\begin{aligned}
\frac{c_4^2 p(p-1)}{2d(K_0)} \int_{\Omega} u^p |\nabla v|^2 dx &\leq \frac{c_4^2 p(p-1)}{2d(K_0)} \left(\int_{\Omega} u^{2p} dx \right)^{\frac{1}{2}} \left(\int_{\Omega} |\nabla v|^4 dx \right)^{\frac{1}{2}} \\
&\leq \frac{c_4^2 c_6^2 p(p-1)}{2d(K_0)} \|u^{\frac{p}{2}}\|_{L^4}^2 \\
&\leq c_7 \left(\|\nabla u^{\frac{p}{2}}\|_{L^2}^{2(1-\frac{1}{p})} \|u^{\frac{p}{2}}\|_{L^{\frac{4}{p}}}^{\frac{2}{p}} + \|u^{\frac{p}{2}}\|_{L^{\frac{4}{p}}}^2 \right) \\
&\leq c_7 c_5 \|\nabla u^{\frac{p}{2}}\|_{L^2}^{2(1-\frac{1}{p})} + c_7 c_5^p \\
&\leq \frac{(p-1)d(K_0)}{p} \|\nabla u^{\frac{p}{2}}\|_{L^2}^2 + \frac{d(K_0)}{p} \left(\frac{c_7 c_5}{d(K_0)} \right)^p + c_7 c_5^p,
\end{aligned} \tag{3.17}$$

and

$$\begin{aligned}
\gamma F(K_0) \int_{\Omega} u^p dx &= \gamma F(K_0) \|u^{\frac{p}{2}}\|_{L^2}^2 \\
&\leq c_8 \left(\|\nabla u^{\frac{p}{2}}\|_{L^2}^{2(1-\frac{2}{p})} \|u^{\frac{p}{2}}\|_{L^{\frac{4}{p}}}^{\frac{4}{p}} + \|u^{\frac{p}{2}}\|_{L^{\frac{4}{p}}}^2 \right) \\
&\leq c_8 c_5^2 \|\nabla u^{\frac{p}{2}}\|_{L^2}^{2(1-\frac{2}{p})} + c_8 c_5^p \\
&\leq \frac{(p-1)d(K_0)}{p} \|\nabla u^{\frac{p}{2}}\|_{L^2}^2 + \frac{d(K_0)}{p} \left(\frac{c_8 c_5^2}{d(K_0)} \right)^p + c_8 c_5^p.
\end{aligned} \tag{3.18}$$

Substituting (3.17) and (3.18) into (3.16), and letting $c_9 := \frac{d(K_0)}{p} \left(\frac{c_7 c_5}{d(K_0)} \right)^p + \frac{d(K_0)}{p} \left(\frac{c_8 c_5^2}{d(K_0)} \right)^p + (c_7 + c_8) c_5^p$, we obtain

$$\frac{d}{dt} \int_{\Omega} u^p dx + p\theta \int_{\Omega} u^p dx \leq c_9,$$

which, combined with the Gronwall's inequality, yields

$$\|u(\cdot, t)\|_{L^p}^p \leq e^{-p\theta t} \|u_0\|_{L^p}^p + \frac{c_9}{p\theta} (1 - e^{-p\theta t}) \leq \|u_0\|_{L^p}^p + \frac{c_9}{p\theta}. \tag{3.19}$$

Then choosing $p = 4$ in (3.19) and using (3.11) again, one can find a constant $c_{10} > 0$ independent of p such that $\|\nabla v(\cdot, t)\|_{L^\infty} \leq c_7$. Then using the Moser iteration procedure (cf. Ref. [1]), one has (3.10). Hence, we complete the proof of Lemma 3.2. $\square$

Proof of Theorem 1.1 Theorem 1.1 is a consequence of Lemmas 2.1 and 3.2. $\square$

4 Globally asymptotic stability of solutions

Based on some ideas in Ref. [12], we shall prove the global stability results in Theorem 1.2 in this section by the method of Lyapunov functionals with the help of LaSalle's invariant principle under the hypotheses (H1)–(H4). Here, we employ the same Lyapunov functionals as

Lemma 4.2 Suppose the conditions in Lemma 4.1 hold. Then we can find a constant $C > 0$ such that

$$\|\nabla u\|_{L^4} \leq C \text{ for all } t > 1. \quad (4.5)$$

Proof From the first equation of system (1.3), we have

$$\begin{aligned} \frac{1}{4} \frac{d}{dt} \int_{\Omega} |\nabla u|^4 dx &= \int_{\Omega} |\nabla u|^2 \nabla u \cdot \nabla u_t dx \\ &= \int_{\Omega} |\nabla u|^2 \nabla u \cdot \nabla (\nabla \cdot (d(v) \nabla u)) dx - \int_{\Omega} |\nabla u|^2 \nabla u \cdot \nabla (\nabla \cdot (\chi(v) u \nabla v)) dx \\ &\quad + \int_{\Omega} \nabla (\gamma F(v) u - \theta u - \alpha u^2) \cdot \nabla u |\nabla u|^2 dx \\ &=: I_1 + I_2 + I_3. \end{aligned} \quad (4.6)$$

With the integration by parts, the term I_1 becomes

$$\begin{aligned} I_1 &= - \int_{\Omega} (|\nabla u|^2 \Delta u) \nabla \cdot (d(v) \nabla u) dx - \int_{\Omega} (\nabla |\nabla u|^2 \cdot \nabla u) \nabla \cdot (d(v) \nabla u) dx \\ &= \int_{\Omega} d(v) |\nabla u|^2 (\nabla \Delta u \cdot \nabla u) dx - \int_{\Omega} d'(v) (\nabla |\nabla u|^2 \cdot \nabla u) (\nabla u \cdot \nabla v) dx, \end{aligned}$$

which, combined with the fact $\nabla \Delta u \cdot \nabla u = \frac{1}{2} \Delta |\nabla u|^2 - |D^2 u|^2$ where $D^2 u$ denotes the Hessian matrix of u , gives

$$\begin{aligned} I_1 &= \frac{1}{2} \int_{\Omega} d(v) |\nabla u|^2 \Delta |\nabla u|^2 dx - \int_{\Omega} d(v) |\nabla u|^2 |D^2 u|^2 dx - \int_{\Omega} d'(v) (\nabla |\nabla u|^2 \cdot \nabla u) (\nabla u \cdot \nabla v) dx \\ &= \frac{1}{2} \int_{\partial \Omega} d(v) |\nabla u|^2 \frac{\partial |\nabla u|^2}{\partial \nu} dS - \frac{1}{2} \int_{\Omega} d'(v) |\nabla u|^2 \nabla v \cdot \nabla |\nabla u|^2 dx - \frac{1}{2} \int_{\Omega} d(v) |\nabla |\nabla u|^2|^2 dx \\ &\quad - \int_{\Omega} d(v) |\nabla u|^2 |D^2 u|^2 dx - \int_{\Omega} d'(v) (\nabla |\nabla u|^2 \cdot \nabla u) (\nabla u \cdot \nabla v) dx \\ &\leq \frac{1}{2} \int_{\partial \Omega} d(v) |\nabla u|^2 \frac{\partial |\nabla u|^2}{\partial \nu} dS - \frac{1}{2} \int_{\Omega} d(v) |\nabla |\nabla u|^2|^2 dx - \int_{\Omega} d(v) |\nabla u|^2 |D^2 u|^2 dx \\ &\quad + \frac{3}{2} \int_{\Omega} |d'(v)| |\nabla |\nabla u|^2| |\nabla u|^2 |\nabla v| dx. \end{aligned} \quad (4.7)$$

With the facts $\|u(\cdot, t)\|_{L^\infty} + \|v(\cdot, t)\|_{W^{1,\infty}} \leq c_1$ and (4.1), we have

$$\begin{aligned} \nabla \cdot (\chi(v) u \nabla v) &= \chi'(v) u |\nabla v|^2 + \chi(v) \nabla u \cdot \nabla v + \chi(v) u \Delta v \\ &\leq c_2 (1 + |\nabla u|) \text{ for all } t > 1, \end{aligned}$$

which updates I_2 as

$$\begin{aligned} I_2 &= \int_{\Omega} \nabla |\nabla u|^2 \cdot \nabla u \nabla \cdot (\chi(v) u \nabla v) dx + \int_{\Omega} |\nabla u|^2 \Delta u \nabla \cdot (\chi(v) u \nabla v) dx \\ &\leq c_2 \int_{\Omega} |\nabla u| |\nabla |\nabla u|^2| (1 + |\nabla u|) dx + c_2 \int_{\Omega} |\nabla u|^2 |\Delta u| (1 + |\nabla u|) dx. \end{aligned} \quad (4.8)$$

Substituting (4.11)–(4.13) into (4.10), we end up with

$$\begin{aligned} & \frac{d}{dt} \int_{\Omega} |\nabla u|^4 dx + d(K_0) \int_{\Omega} |\nabla |\nabla u|^2|^2 dx + 2d(K_0) \int_{\Omega} |\nabla u|^2 |D^2 u|^2 dx \\ & \leq c_8 \int_{\Omega} |\nabla u|^4 dx + c_9, \end{aligned} \quad (4.14)$$

where $c_8 := 4 \left(c_3 + c_5 + c_7 + \frac{4c_2^2}{d(K_0)} \right)$ and $c_9 := 4 \left(c_4 + c_7 + \frac{c_2^2 |\Omega|}{2d(K_0)} \right)$. On the other hand, integrating by parts, noting $\|u(\cdot, t)\|_{L^\infty} \leq c_{10}$ and using the Young's inequality, one has

$$\begin{aligned} (c_8 + 2) \int_{\Omega} |\nabla u|^4 dx &= c_{11} \int_{\Omega} |\nabla u|^2 \nabla u \cdot \nabla u dx \\ &= -c_{11} \int_{\Omega} u \nabla |\nabla u|^2 \cdot \nabla u dx - c_{11} \int_{\Omega} u |\nabla u|^2 \Delta u dx \\ &\leq c_{10} c_{11} \int_{\Omega} |\nabla |\nabla u|^2| |\nabla u| dx + c_{10} c_{11} \sqrt{2} \int_{\Omega} |\nabla u|^2 |D^2 u| dx \\ &\leq d(K_0) \int_{\Omega} |\nabla |\nabla u|^2|^2 dx + 2d(K_0) \int_{\Omega} |\nabla u|^2 |D^2 u|^2 dx + \frac{c_{10}^2 c_{11}^2}{2} \int_{\Omega} |\nabla u|^2 dx \\ &\leq d(K_0) \int_{\Omega} |\nabla |\nabla u|^2|^2 dx + 2d(K_0) \int_{\Omega} |\nabla u|^2 |D^2 u|^2 dx \\ &\quad + \int_{\Omega} |\nabla u|^4 dx + \frac{|\Omega| c_{10}^4 c_{11}^4}{16}, \end{aligned}$$

which updates (4.14) to

$$\frac{d}{dt} \int_{\Omega} |\nabla u|^4 dx + \int_{\Omega} |\nabla u|^4 dx \leq c_9 + \frac{c_{10}^4 c_{11}^4 |\Omega|}{16}. \quad (4.15)$$

Applying the Gronwall's inequality to (4.15) along with the fact $\|\nabla u(\cdot, 1)\|_{L^\infty} \leq c_{12}$, one obtains

($\|\nabla$

4.1 Global stability of the prey-only steady state

In this subsection, we shall prove that (u, v) converges to $(0, K)$ in L^∞ as $t \rightarrow \infty$ when $\gamma F(K) \leq \theta$ and further show that the convergence rate is exponential if $\gamma F(K) < \theta$ and algebraic if $\gamma F(K) = \theta$ and $\alpha > 0$.

Lemma 4.4 *Let the assumptions in Theorem 1.2 hold. If $\gamma F(K) \leq \theta$, then the solution (u, v) of (1.3) satisfies*

$$\|u\|_{L^\infty} + \|v - K\|_{L^\infty} \rightarrow 0 \text{ as } t \rightarrow \infty,$$

where the convergence rate is exponential if $\gamma F(K) < \theta$ and algebraic if $\gamma F(K) = \theta$ and $\alpha > 0$.

Proof We start with the following functional:

$$V_1(u(t), v(t)) =: V_1(t) = \frac{1}{\gamma} \int_{\Omega} u dx + \int_{\Omega} \int_K^v \frac{F(\sigma) - F(K)}{46456.0351 \text{SBT}/F11Tf9.9626009.9626320.} d\sigma dv$$

which together with (4.18) yields the decay rate of u . Similarly, with $\|\nabla v\|_{L^4} \leq c_5$ (cf. (3.11)), we obtain

$$\begin{aligned}\|v - K\|_{L^\infty} &\leq c_6 \|\nabla v\|_{L^4}^{\frac{2}{3}} \|v - K\|_{L^2}^{\frac{1}{3}} + c_6 \|v - K\|_{L^2} \\ &\leq c_6 c_5^{\frac{2}{3}} \|v - K\|_{L^2}^{\frac{1}{3}} + c_6 \|v - K\|_{L^2},\end{aligned}\quad (4.20)$$

which combined with (4.18) gives the decay rate of v . This completes the proof of Lemma 4.4. $\square$

4.2 Global stability of the coexistence steady state

Now we turn to the case $\gamma F(K) > \theta$ and prove the homogeneous coexistence steady state (u_*, v_*) is globally asymptotically stable under certain conditions. We shall prove our result based on the following Lyapunov functional as in Ref. [12]:

$$V_2(u(t), v(t)) =: V_2(t) = \frac{1}{\gamma} \int_{\Omega} \left(u - u_* - u_* \ln \frac{u}{u_*} \right) dx + \int_{\Omega} \int_{v_*}^v \frac{F(\sigma) - F(v_*)}{F(\sigma)} d\sigma dx.$$

Lemma 4.5 Assume the assumptions in Theorem 1.2 hold. If $\gamma F(K) > \theta$ and

$$D \geq \max_{0 \leq v \leq K_0} \frac{u_* |F(v)|^2 |\chi(v)|^2}{4\gamma F(v_*) F'(v) d(v)}$$

where u_* and v_* are determined by (1.5) and independent of D , then the solution (u, v) of (1.3) satisfies

$$\|u - u_*\|_{L^\infty} + \|v - v_*\|_{L^\infty} \rightarrow 0 \text{ as } t \rightarrow \infty$$

where the convergence is exponential when $\alpha > 0$.

Proof First by the same argument as the proof of Ref. [12, Lemma 4.3], we have that $V_2(t) \geq 0$ for all $u, v \geq 0$. Next we differentiate $V_2(t)$ with respect to t and use the equations of (1.3) to obtain that

$$\begin{aligned}\frac{d}{dt} V_2(t) &= \frac{1}{\gamma} \int_{\Omega} \left(1 - \frac{u_*}{u} \right) u_t dx + \int_{\Omega} \frac{F(v) - F(v_*)}{F(v)} v_t dx \\ &= \underbrace{-\frac{u_*}{\gamma} \int_{\Omega} \frac{d(v) |\nabla u|^2}{u^2} dx - DF(v_*) \int_{\Omega} F'(v) \left| \frac{\nabla v}{F(v)} \right|^2 dx + \frac{u_*}{\gamma} \int_{\Omega} \frac{\chi(v) \nabla u \cdot \nabla v}{u} dx}_{I_1} \\ &\quad + \underbrace{\frac{1}{\gamma} \int_{\Omega} \left(1 - \frac{u_*}{u} \right) (\gamma u F(v) - \theta u - \alpha u^2) dx + \int_{\Omega} (F(v) - F(v_*)) \left(\frac{f(v)}{F(v)} - u \right) dx}_{I_2}.\end{aligned}$$

I_1 can be rewritten as

$$I_1 = - \int_{\Omega} \Theta^T A \Theta, \quad \Theta = \begin{bmatrix} \nabla u \\ \nabla v \end{bmatrix}, \quad A = \begin{bmatrix} \frac{u_* d(v)}{\gamma u^2} & -\frac{\chi(v) u_*}{2\gamma u} \\ -\frac{\chi(v) u_*}{2\gamma u} & \frac{DF(v_*) F'(v)}{|F(v)|^2} \end{bmatrix}.$$

where Θ^T denotes the transpose of Θ . Then, it can be easily checked with Sylvesters criterion that the matrix A is non-negative definite (and hence $I_1 \leq 0$) if and only if

$$\frac{DF(v_*)F'(v)u_*d(v)}{\gamma|F(v)|^2u^2} \geq \frac{|\chi(v)|^2u_*^2}{4\gamma^2u^2} \quad \text{or} \quad D \geq \frac{u_*|F(v)|^2|\chi(v)|^2}{4\gamma F(v_*)F'(v)d(v)},$$

where u_* and v_* do not depend on D , see (1.5). Note that the above I_2 is exactly the same as the I_2 in the proof of Ref. [12, Lemma 4.3]. Hence, we can follow the same procedure for the proof of Ref. [12, Lemma 4.3] to show the homogeneous coexistence state (u_*, v_*) is globally asymptotically stable and satisfies

$$\|u - u_*\|_{L^2} + \|v - v_*\|_{L^2} \leq c_1 e^{-c_2 t} \quad \text{for } t > t_0, \quad (4.21)$$

with some $t_0 > 1$ for $\alpha > 0$. Using the Gagliardo–Nirenberg inequality and the boundedness of $\|\nabla u\|_{L^4}$ and $\|\nabla v\|_{L^\infty}$ (see Lemmas 4.1 and 4.2), we use a similar procedure as for (4.19)–(4.20) to finally obtain the exponential decay rate in L^∞ -norm from (4.21). $\square$

4.3 Proof of Theorem 1.2

Theorem 1.2 is directly obtained from Lemmas 4.4 and 4.5.

5 Applications and spatio-temporal patterns

The first purpose of this section is to apply our general results obtained in Theorems 1.1 and 1.2 to two most widely used predator–prey interactions: Lotka–Volterra type (i.e. $F(v) = v$) and Rosenzweig–MacArthur type (i.e. $F(v) = \frac{v}{\lambda + v}$ and $\alpha = 0$) [33]. Note that these results only give the global existence of solutions (by Theorem 1.1) and global stability of constant steady states (by Theorem 1.2), the distribution of the predator and the prey in space and the time-asymptotic dynamics of the population outside the parameter regimes found in Theorem 1.2 are unclear, but indeed they are more interesting from the application point of view in ecology though hard to study analytically. Hence, the second purpose of this section is to numerically exploit the spatio-temporal patterns generated by the Lotka–Volterra and Rosenzweig–MacArthur predator–prey systems, which not only display the distribution patterns of the predator and the prey in space or evolution of population in time but also provide useful sources for the future research.

5.1 Application of our results

In this subsection, we shall give some examples to illustrate the applications of Theorems 1.1 and 1.2. The first example is the Lotka–Volterra predator–prey system [25] with prey-taxis

$$\left\{ \begin{array}{l} u_t = \nabla \cdot (d(v)\nabla u) - \nabla \cdot (u\chi(v)\nabla v) + \gamma uv - \theta u - \alpha u^2, \quad x \in \Omega, \quad u \\ \end{array} \right.$$

Then, the application of the results in Theorems 1.1 and 1.2 yields the following results on the system (5.1).

Proposition 5.1 *Let $\Omega \subset \mathbb{R}^2$ be a bounded domain with smooth boundary and assume $(u_0, v_0) \in [W^{1,p}(\Omega)]^2$ with $u_0, v_0 \geq 0$ ($\neq 0$) and $p > 2$. Assume $\alpha > 0$, then the problem (5.1) has a unique global classical solution $(u, v) \in [C([0, \infty) \times \bar{\Omega}) \cap C^{2,1}((0, \infty) \times \bar{\Omega})]^2$ such that:*

- If $\gamma K \leq \theta$, then

$$\|u\|_{L^\infty} + \|v - K\|_{L^\infty} \rightarrow 0 \text{ as } t \rightarrow \infty,$$

where the convergence is exponential if $\gamma K < \theta$ and algebraic if $\gamma K = \theta$.

- If $\gamma K > \theta$ and

$$\frac{4D\gamma K(\mu\alpha + \theta)}{\mu(\gamma K - \theta)K_0^2} \geq M_0,$$

with $M_0 = \max_{0 \leq v \leq K_0} \frac{|\chi(v)|^2}{d(v)}$, then

$$\|u - u^*\|_{L^\infty} + \|v - v^*\|_{L^\infty} \rightarrow 0 \text{ exponentially as } t \rightarrow \infty,$$

where

$$(u_*, v_*) = \left(\frac{\mu(\gamma K - \theta)}{\gamma K + \mu\alpha}, \frac{K(\mu\alpha + \theta)}{\gamma K + \mu\alpha} \right). \quad (5.2)$$

The second example is the Rosenzweig–MacArthur type predator–prey interaction. From Theorem 1.1 with $\alpha = 0$, we only have the results for the special case $\chi(v) = -d'(v)$ (density suppressed motility) which leads to the following system:

$$\begin{cases} u_t = \Delta(d(v)u) + \frac{\gamma uv}{\lambda + v} - \theta u, & x \in \Omega, \quad t > 0, \\ v_t = D\Delta v - \frac{uv}{\lambda + v} + \mu v \left(1 - \frac{v}{K}\right), & x \in \Omega, \quad t > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x), v(x, 0) = v_0(x), & x \in \Omega. \end{cases} \quad (5.3)$$

In this case, the hypothesis (H4) is satisfied by requiring $\lambda > K$. Then, the interpretation of our results of Theorems 1.1 and 1.2 into (5.3) yields the following results.

Proposition 5.2 *Assume $(u_0, v_0) \in [W^{1,p}(\Omega)]^2$ with $u_0, v_0 \geq 0$ ($\neq 0$) and $p > 2$. If $\lambda > K$, then the problem (5.3) has a unique global classical solution in $\Omega \subset \mathbb{R}^2$ such that*

- If $\frac{\gamma K}{\lambda + K} < \theta$, then

$$\|u\|_{L^\infty} + \|v - K\|_{L^\infty} \rightarrow 0 \text{ exponentially as } t \rightarrow \infty.$$

- If $\frac{\gamma K}{\lambda + K} > \theta$ and $\frac{4D\theta\lambda}{K_0^2 u_*} \geq M_1$ with $M_1 = \max_{0 \leq v \leq K_0} \frac{|d'(v)|^2}{d(v)}$, it follows that

$$\|u - u^*\|_{L^\infty} + \|v - v^*\|_{L^\infty} \rightarrow 0 \text{ as } t \rightarrow \infty,$$

where

$$(u_*, v_*) = \left(\frac{\gamma \lambda \mu [(\gamma - \theta)K - \theta \lambda]}{(\gamma - \theta)^2 K}, \frac{\theta \lambda}{\gamma - \theta} \right).$$

5.2 Linear instability analysis

In this section, we will study the possible pattern formation generated by the system (1.3) under the assumptions (H1)–(H3). We begin with the space-absent ordinary differential equation (ODE) system of (1.3):

$$\begin{cases} u_t = \gamma u F(v) - \theta u - \alpha u^2, \\ v_t = -u F(v) + f(v), \end{cases} \quad (5.4)$$

which has three possible equilibria: $(0, 0)$, $(0, K)$ and (u_*, v_*) . One can easily check that the steady state $(0, 0)$ is linearly unstable and $(0, K)$ is linearly stable for both Lotka–Volterra and Rosenzweig–MacArthur type predator–prey interactions. For the homogeneous coexistence steady state (u_*, v_*) , it is linearly stable for the Lotka–Volterra type interaction. While for the Rosenzweig–MacArthur type interaction, one can easily find that all the eigenvalues of the linearised system of (5.4) at (u_*, v_*) have negative real part (hence (u_*, v_*) is stable) if $v_* > \frac{K-\lambda}{2}$, and are complex with zero real part if $v_* = \frac{K-\lambda}{2}$, and are complex with positive real part (hence (u_*, v_*) is unstable) if $0 < v_* < \frac{K-\lambda}{2}$.

Next we proceed to consider the stability of equilibria $(0, K)$ and (u_*, v_*) in the presence of spatial structure. To this end, we first linearise the system (1.3) at an equilibrium (u_s, v_s) and write the linearised system as

$$\begin{cases} \Phi_t = \mathcal{A} \Delta \Phi + \mathcal{B} \Phi, & x \in \Omega, \ t > 0, \\ (\nu \cdot \nabla) \Phi = 0, & x \in \partial \Omega, \ t > 0, \\ \Phi(x, 0) = (u_0 - u_s, v_0 - v_s)^T, & x \in \Omega, \end{cases} \quad (5.5)$$

where $\mathcal{T}$ denotes the transpose and

$$\Phi = \begin{pmatrix} u - u_s \\ v - v_s \end{pmatrix}, \quad \mathcal{A} = \begin{pmatrix} d(v_s) & -u_s \chi(v_s) \\ 0 & D \end{pmatrix},$$

as well as

$$\mathcal{B} = \begin{pmatrix} -\alpha u_s & \gamma u_s F'(v_s) \\ -F(v_s) & -u_s F'(v_s) + f'(v_s) \end{pmatrix} = \begin{pmatrix} B_1 & B_2 \\ B_3 & B_4 \end{pmatrix}.$$

Let $W_k(x)$ denote the eigenfunction of the following eigenvalue problem:

$$\Delta W_k(x) + k^2 W_k(x) = 0, \quad \frac{\partial W_k(x)}{\partial \nu} = 0,$$

where k is called the wavenumber. Since the system (5.5) is linear, the solution $\Phi(x, t)$ has the form of

$$\Phi(x, t) = \sum_{k \geq 0} c_k e^{\rho t} W_k(x), \quad (5.6)$$

where the constants c_k are determined by the Fourier expansion of the initial conditions in terms of $W_k(x)$ and ρ is the temporal eigenvalue. Substituting (5.6) into (5.5), one has

$$\rho W_k(x) = -k^2 A W_k(x) + B W_k(x),$$

which implies ρ is the eigenvalue of the following matrix:

$$\begin{aligned} M_k &= \begin{pmatrix} -d(v_s)k^2 - \alpha u_s & u_s \chi(v_s)k^2 + \gamma u_s F'(v_s) \\ -F(v_s) & -Dk^2 - u_s F'(v_s) + f'(v_s) \end{pmatrix}, \\ &= \begin{pmatrix} -d(v_s)k^2 + B_1 & u_s \chi(v_s)k^2 + B_2 \\ B_3 & -Dk^2 + B_4 \end{pmatrix}. \end{aligned}$$

Calculating the eigenvalue of matrix M_k , we get the eigenvalues $\rho(k^2)$ as functions of the wavenumber k as the roots of

$$\rho^2 + a(D, k^2)\rho + b(D, k^2) = 0,$$

where

$$\begin{aligned} a(D, k^2) &= (d(v_s) + D)k^2 + (\alpha + F'(v_s))u_s - f'(v_s), \\ &= (d(v_s) + D)k^2 - (B_1 + B_4), \end{aligned}$$

and

$$b(D, k^2) = d(v_s)Dk^4 - (d(v_s)B_4 + u_s \chi(v_s)B_3 + B_1 D)k^2 + B_1 B_4 - B_2 B_3.$$

Then, it can be easily verified that the eigenvalue ρ for the prey-only steady state $(0, K)$ has negative real part for both Lotka–Volterra and Rosenzweig–MacArthur type predator–prey interactions and hence $(0, K)$ is linearly stable. Thus, the pattern (if any) can only arise from the homogeneous coexistence steady state (u_*, v_*) . In the following results, we first show that the Lotka–Volterra type predator–prey system (5.1) indeed has no pattern bifurcated from (u_*, v_*) .

Lemma 5.3 *The homogeneous coexistence steady state (u_*, v_*) of system (5.1) is linearly stable if $\gamma K > \theta$.*

Proof Since $F(v) = v$ and $f(v) = \mu v(1 - v/K)$, we can easily check that

$$B_1 = -\alpha u_* < 0, B_2 = \gamma u_* > 0, B_3 = -v_* < 0, B_4 = -\frac{\mu}{K} v_* < 0.$$

Hence, $B_1 + B_4 < 0$ and $B_1 B_4 - B_2 B_3 > 0$ as well as

$$d(v_*) \text{Hence,}$$

Therefore, we are left to consider the possibility of the patterns bifurcated from (u_*, v_*) for the Rosenzweig–MacArthur type predator–prey system (5.3) and hence hereafter $\alpha = 0$. In this case, the corresponding characteristic equation is

$$\rho^2 + a(D, k^2)\rho + b(D, k^2) = 0, \quad (5.7)$$

with

$$a(D, k^2) = (d(v_*) + D)k^2 - \beta_1, \quad b(D, k^2) = d(v_*)Dk^4 - \beta_2k^2 + \beta_3, \quad (5.8)$$

where

$$\begin{cases} \beta_1 = \frac{\mu v_*(K - \lambda - 2v_*)}{K(\lambda + v_*)}, \\ \beta_2 = \frac{\mu v_*(K - \lambda - 2v_*)d(v_*)}{K(\lambda + v_*)} - \frac{\mu v_*(K - v_*)\chi(v_*)}{K}, \\ \beta_3 = \frac{\lambda\theta\mu(K - v_*)}{K(\lambda + v_*)}. \end{cases} \quad (5.9)$$

If $K > v_* > \frac{K-\lambda}{2}$, one has $K - \lambda - 2v_* < 0$ which yields $a(D, k^2) > 0$ and $b(D, k^2) > 0$ for all $k \geq 0$. Hence, all the eigenvalues have negative real parts and the homogeneous coexistence steady state (u_*, v_*) is linearly stable. This implies that the pattern formation is possible only when

$$0 < v_* \leq \frac{K - \lambda}{2}. \quad (5.10)$$

First, if $v_* = \frac{K-\lambda}{2}$, one has $a(D, 0) = 0$ and $b(D, 0) = \beta_3 > 0$, which corresponds to the spatially homogeneous periodic solutions. Moreover, for any $k > 0$, one has $a(D, k) > 0$ and $b(D, k) > 0$, which indicates that all the eigenvalues of (5.7) have negative real part and hence no spatially inhomogeneous patterns arise in this case. Next, we shall exploit whether the spatially inhomogeneous patterns may arise in the case $0 < v_* < \frac{K-\lambda}{2}$.

Define the set

$$\mathcal{H} = \{(D, \eta) \in \mathbb{R}_+^2 : a(D, \eta) = 0\},$$

as the Hopf bifurcation curve, and

$$\mathcal{S} = \{(D, \eta) \in \mathbb{R}_+^2 : b(D, \eta) = 0\},$$

as the steady-state bifurcation curve, where the linearised system around the homogeneous coexistence steady state has an eigenvalue with zero real part on the curves $\mathcal{S}$ or $\mathcal{H}$. Furthermore, if we define

$$D_{\mathcal{H}}(\eta) = \frac{\mu v_*(K - \lambda - 2v_*)}{K(\lambda + v_*)\eta} - d(v_*), \quad (5.11)$$

and

$$D_{\mathcal{S}}(\eta) = \left(\frac{\mu v_*(K - \lambda - 2v_*)}{K(\lambda + v_*)} - \frac{\mu v_*(K - v_*)\chi(v_*)}{d(v_*)K} \right) \frac{1}{\eta} - \frac{\lambda\theta\mu(K - v_*)}{Kd(v_*)(\lambda + v_*)} \frac{1}{\eta^2}, \quad (5.12)$$

then, we have the following stability results for the coexistence steady state (u_*, v_*) .

Lemma 5.4 Assume the parameters $\theta, \gamma, \mu, \lambda$ and $K > \lambda$ are fixed. Let $D_{\mathcal{H}}(\eta)$ and $D_{\mathcal{S}}(\eta)$ be defined in (5.11) and (5.12). Then, the homogeneous coexistence steady state is locally asymptotically stable provided the parameter D satisfies

$$D > \max_{\eta \geq 0} \{D_{\mathcal{H}}(\eta), D_{\mathcal{S}}(\eta)\}. \quad (5.13)$$

Remark 5.1 In one dimension, say $\Omega = [0, \ell]$, $\eta = k^2 = (\frac{n\pi}{\ell})^2$ where $n = 0, 1, 2, \dots$, and ℓ is the length of the domain. For fixed $D > 0$, the condition (5.13) can be satisfied if ℓ is small enough. Hence, no pattern formation will develop if ℓ is sufficient small.

Next we explore the possible (local) bifurcation by treating D as a bifurcation parameter. Under (5.10), we see that the sign of $a(D, k^2)$ and $b(D, k^2)$ could be generic and different type bifurcation may arise. In particular, the discriminant of (5.7) $\Delta = |a(D, k^2)|^2 - 4b(D, k^2)$ has not determined sign. Therefore, there are two possibilities: $\Delta < 0$ and $\Delta \geq 0$, where the former will lead to a Hopf bifurcation (periodic patterns) and the latter may lead to a steady-state bifurcation (aggregation patterns). Note the allowable wavenumbers k are discrete in a bounded domain, for instance, if $\Omega = (0, \ell)$, then $k = \frac{n\pi}{\ell}$ ($n = 0, 1, 2, \dots$). It can be easily verified that

$$\Delta = |a(D, k^2)|^2 - 4b(D, k^2) = (D - d(v_*))^2 k^4 - 2[(D + d(v_*))\beta_1 - 2\beta_2]k^2 + \beta_1^2 - 4\beta_3.$$

Hence, the Hopf bifurcation may occur (i.e. $\Delta < 0$) if $[(D + d(v_*))\beta_1 - 2\beta_2]^2 - (\beta_1^2 - 4\beta_3)(D - d(v_*))^2 > 0$ and there is allowable wavenumber k such that

$$k_1^- < k^2 < k_1^+,$$

where $k_1^\pm = \frac{(D+d(v_*))\beta_1-2\beta_2 \pm \sqrt{[(D+d(v_*))\beta_1-2\beta_2]^2 - (\beta_1^2-4\beta_3)(D-d(v_*))^2}}{(D-d(v_*))^2}$ if $D \neq d(v_*)$.

If $\Delta > 0$, steady-state bifurcation may occur but the possibility can be generic. Indeed one can readily verify that the steady-state bifurcation will occur if there is allowable wavenumber k such that one of the following cases holds:

$$\begin{aligned} (i) & \ b(D, k^2) < 0; \\ (ii) & \ b(D, k^2) = 0, a(D, k^2) < 0; \\ (iii) & \ b(D, k^2) > 0, a(D, k^2) < 0 \text{ and } |a(D, k^2)|^2 - 4b(D, k^2) > 0. \end{aligned} \quad (5.14)$$

The corresponding parameter regime guaranteeing each of (i), (ii) and (iii) can be found with easy calculations. For example, under (5.10), it follows that $\beta_3 > 0$. Hence, condition (i) is ensured if

$$\beta_2 > 0, \text{ namely } \frac{K - \lambda - 2v_*}{(\lambda + v_*)(K - v_*)} > \frac{\chi(v_*)}{d(v_*)}, \quad (5.15)$$

and the allowable wavenumber k satisfies

$$k_2^- < k^2 < k_2^+, \quad k_2^\pm = \frac{\beta_2 \pm \sqrt{\Lambda}}{2Dd(v_*)} \text{ with } \Lambda = \beta_2^2 - 4\beta_3Dd(v_*). \quad (5.16)$$

Conditions of ensuring (ii) or (iii) can be derived similarly and will not be detailed here since these conditions can be easily inspected when the parameter values and the motility function $d(v)$, $\chi(v)$ are specified, as shown in the next subsection.

5.3 Spatio-temporal patterns

In this subsection, we shall present some examples to illustrate the periodic and steady-state patterns. As discussed in the previous section, the Lotka–Volterra type predator–prey system (5.1) does not generate any spatially inhomogeneous patterns while the Rosenzweig–MacArthur type predator–prey system (5.3) with $\chi(v) = -d'(v)$ may generate periodic or steady-state patterns in appropriate parameter regimes. Therefore, we only consider the Rosenzweig–MacArthur type predator–prey system (5.3) with $\chi(v) = -d'(v)$. We fix the value of the parameters in all simulations as follows:

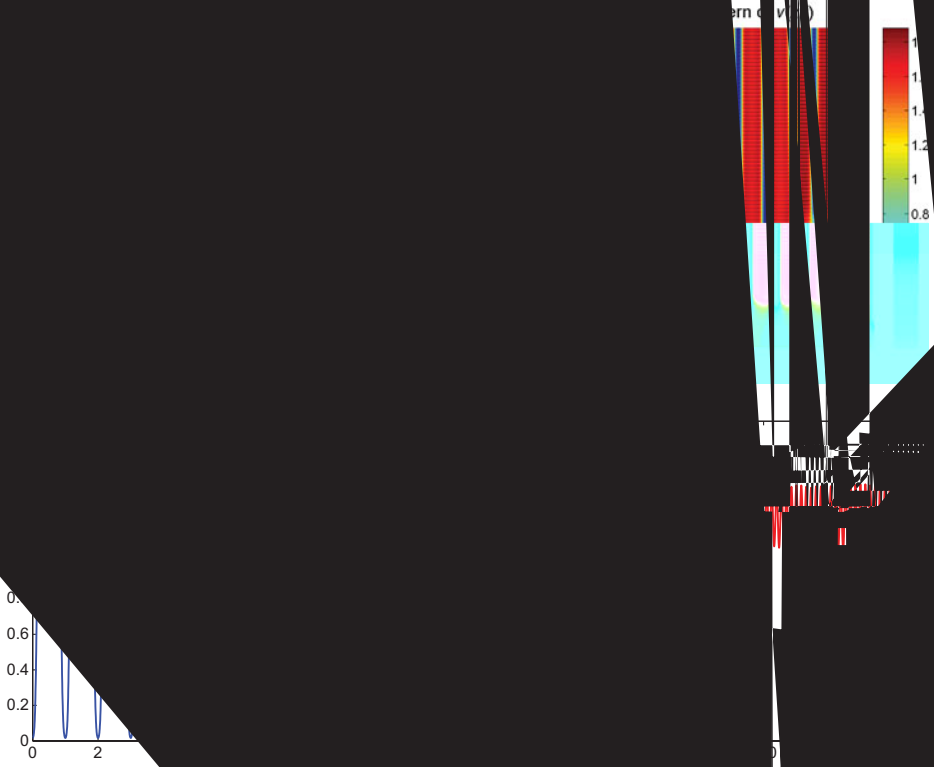
$$K = 4, \gamma = 2, \theta = 1, \lambda = 1, \mu = 1. \quad (5.17)$$

Then, it can be checked from (5.2) that the coexistence steady state $(u_*, v_*) = (3/2, 1)$. Furthermore, it can be verified from (5.9) that

$$\beta_1 = \frac{1}{8}, \quad \beta_3 = \frac{3}{8},$$

where the value of β_2 depends on the specific form of $d(v)$. In this paper, we shall test three-motility function $d(v)$ as follows:

$$d_1(v) = \frac{1}{1 + e^{h_2 v}}, \quad h_2 = 0.61 \text{ Tm } (())\text{T(d)Tj}, \text{F1 1 Tf 1.7544 Tc 3 (d)Tj /F2 1 Tf 0.5408 0 0 6.9738 262.3217..71067 Tm (1)}$$



1 and 3 lies in the choice of motility function $d(v)$. This observation hints us that the motility function $d(v)$ of the predator plays an important role in determining the spatial distribution of the predator and the prey. In particular, the random motion ($d(v)$ is constant) and non-random motion ($d(v)$ is non-constant) will result in different patterns (i.e. spatial distribution of the predator and the prey). Hence, how does the motility function $d(v)$ affects the dynamics of nonlinear predator–prey systems launches an interesting question for the future.

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Conflict of Interest

None.

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