Modeling and Dynamics of Predator Prey Systems on a Circular Domain

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Abstract The present chapter is devoted to the mathematical modeling and the analysis of the dynamics of predator prey systems on a circular domain. We first give some reminders on the Laplace operator and spectral theory on a disc. Then, we analyze the dynamics of two mathematical models with two or three reaction diffusion equations, defined on a circular domain. The results are given in terms of local/global stability and of emergence of spatio-temporal patterns due to symmetry-breaking bifurcations. One basic type of such a phenomenon is Turing bifurcation which gives rise to pattern formation, a process by which a spatially uniform state loses stability to a non-uniform state. We derive, theoretically, the conditions for Turing diffusion driven instability to occur, and perform numerical simulations to illustrate how biological processes can affect spatiotemporal pattern formation in a spatial domain.

Keywords Dynamics · Predator prey · Spatio-temporal · Circular domain · Patterns · Turing instability

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1 Introduction

In our knowledge, the first mathematical model of predator prey interaction is given by A. Lotka [16] and V. Volterra [20]. This model is a simplified system of two ordinary differential equations which does not take into account the space variable and supposes that every individual is accessible to every other individual and produces the so-called "mean-field description of the system". One of the oldest spatio-temporal model which takes into account the movement of individuals/organisms/particules is the standard reaction diffusion system (Fisher [13], Kolmogorov et al. [15], Murray [17]):

$$\frac{\partial N(X,t)}{\partial t} = D\Delta N(X,t) + f(N(X,t)), \qquad (X,t) \in \Omega \times \mathbb{R}^+, \Omega \subseteq \mathbb{R}^n, \quad (1)$$

where N is a p components vector, Δ is the Laplacian operator, D is the diffusion matrix and f is a nonlinear term (reaction term) representing the interactions between species N (individuals/organisms/particules).

From the mathematical modeling point of view, if $N(x,t)$ is the concentration of individuals/organisms/particules at time $t > 0$ and the position x. Then the diffusion term can be regarded as:

$$\frac{\partial N(X,t)}{\partial t} = D\Delta N(X,t)$$

where D (which can depend on x) is a positive definite symmetric diffusion matrix which describes the non-homogeneous diffusion. Therefore, the local reaction process is modeled by a local dynamical system as follows:

$$\frac{\partial N(X,t)}{\partial t} = f(N(X,t))$$

To describe the interaction of both types of processes (diffusion and reaction), we suppose that they happen on a small time interval. If we let this interval to tend to zero, then this time-splitting scheme turns into the so-called reaction-diffusion system, given by system (1).

If the reaction diffusion processes occur in a spatially confined domain Ω, then boundary conditions have to be imposed, for example the Dirichlet condition when specifying the values that the solution must check on the boundaries of the field:

$$N(X,t) = \varphi(X), \;\; X \in \partial\Omega$$

or the Neumann condition when specifying the values the derivative of the solution must satisfy on the boundaries of the field :

$$\frac{\partial N}{\partial n}(X,t) = \psi(X), \;\; X \in \partial\Omega; \;\; n \text{ is outflow through the boundary of } \Omega.$$

If $\psi(X) = 0$, then, for the dynamic of the populations, there is no immigration nor emigration.

There are other possible boundary conditions. For example the Robin boundary conditions, which are a combination of Dirichlet and Neumann conditions. The dynamic boundary conditions, or the mixed boundary conditions which correspond to the juxtaposition of different boundary conditions on different parts of the border of the domain.

A lot of mathematical problems arise from reaction diffusion theory such as: existence and regularity of solutions, boundedness of solutions, stability, traveling waves etc. [3–5, 7–10, 14, 23, 24]. One of these questions is: how the diffusion term can affect the asymptotic behavior of the corresponding system without diffusion term? In 1952, Turing prove that, under certain conditions, chemical products react and diffuse to produce non constant steady state and induce spatial patterns. This property can be explained as follows: In the absence of diffusion, the stable uniform steady state of the corresponding ordinary differential equation becomes unstable in the presence of diffusion (which called diffusion driven instability or Turing instability) and spatial patterns can evolve through bifurcations [17].

2 Spectral Theory on a Circular Domain

In this section, since there exists a difference between the analysis in a rectangle domain and a circular domain (disc), we give some results on the Laplace operator on a circular domain (see, [17]).

Let us consider a disc with a radius R as follows:

$$\mathscr{D} = \{(r, \theta) : 0 \leq r < R\}.$$

Then the Laplace operator is defined in cartesian coordinates as $\Delta\varphi = \frac{\partial^2}{\partial x^2}\varphi + \frac{\partial^2}{\partial y^2}\varphi$ and in polar coordinates (r, θ) as $\Delta_{r\theta}\varphi = \frac{\partial^2}{\partial r^2}\varphi + \frac{1}{r}\frac{\partial}{\partial r}\varphi + \frac{1}{r^2}\frac{\partial^2}{\partial \theta^2}\varphi$,
with $x = r\cos(\theta)$, $y = r\sin(\theta)$ and $r = \sqrt{x^2 + y^2}$ and $\tan(\theta) = \frac{y}{x}$.

To compute the eigenvectors on the circular domain, one needs to separate variables using polar coordinates. Considering the eigenvalue problem

$$\begin{cases} \Delta_{r\theta}\varphi = -\lambda\varphi \\ \varphi(R, \theta) = 0, \ \theta \in [0, 2\pi] \\ \frac{\partial\varphi}{\partial\eta} = 0, \ \text{on } r = R \text{ and } \theta \in [0, 2\pi] \end{cases} \tag{2}$$

and looking for solutions of the form $\varphi(r, \theta) = P(r)\Phi(\theta)$. By differentiation and from the Eq. (2) we have:

$$P''(r)\Phi(\theta) + \frac{1}{r}P'(r)\Phi(\theta) + \frac{1}{r^2}P(r)\Phi''(\theta) = -\lambda P(r)\Phi(\theta) \tag{3}$$

Therefore

$$\frac{r^2}{P(r)}\{P''(r) + \frac{1}{r}P'(r) + \lambda P(r)\} = -\frac{\Phi''(\theta)}{\Phi(\theta)} \quad (4)$$

The only way for these two expressions to equal for all possible values of r and θ is to have them both equal a constant. Therefor, there exists k such that $-\Phi''(\theta) = k^2\Phi(\theta)$

The appropriate boundary conditions to apply to this problem state that the function $\Phi(\theta)$ and its first derivative with respect to θ are periodic in θ.

Then, the solution is given by:

$$\Phi_n(\theta) = a_n \sin(n\theta) + b_n \cos(n\theta) \text{ for integers } k = n \geq 1$$

where a_n and b_n are constants.

Then we have the following second order differential equation of

$$P''(r) + \frac{1}{r}P'(r) + \left(\lambda - \frac{k^2}{r^2}\right)P(r) = 0, \text{ such that } P'(R) = 0 \quad (5)$$

Let $x = \sqrt{\lambda}r$ and $P(x) = J(\frac{x}{\sqrt{\lambda}})$. Then, we have

$$J''(x) + \frac{1}{x}J'(x) + \left(1 - \frac{k^2}{x^2}\right)J(x) = 0 \text{ (called Bessel equation)} \quad (6)$$

The solution for it is the n^{th} Bessel function

$$J_n(x) = \sum_{l=0}^{+\infty} \frac{(-1)^l}{l!(n+l)!}\left(\frac{x}{2}\right)^{n+2l}$$

Since $P(r) = J_n(\sqrt{\lambda}r)$, we get:

$$\phi_n^{\lambda}(r, \theta) = \Phi_n(\theta)J_n(\sqrt{\lambda}r) \quad (7)$$

which are eigenfunctions of the Laplacian operator in polar coordinates.

The eigenvalues λ associated to the eigenvector ϕ_n^{λ} are determined from the boundary conditions.

From Dirichlet boundary conditions defined as follows $\phi_n^{\lambda}(R, \theta) = 0, \forall\theta \in [0, 2\pi]$ we get $J_n(\sqrt{\lambda}R) = 0$. This means that $\sqrt{\lambda}R$ is a root of J_n.

From the Neumann boundary conditions: $\partial_r\phi_n^{\lambda}(R, \theta) = 0, \forall\theta \in [0, 2\pi]$ we get $J_n'(\sqrt{\lambda}R) = 0$. This means that $\sqrt{\lambda}R$ is a root of J_n'.

We denote these roots by α_{nm} and assume they are indexed in increasing order:

$$J_n(\alpha_{nm}) = 0, \alpha_{n1} < \alpha_{n2} < \alpha_{n3} < ....$$

Therefore $\sqrt{\lambda}R = \alpha_{nm}$ for some index m and the eigenvalues will be written in the following form:

$$\lambda_{nm} = \left(\frac{\alpha_{nm}}{R}\right)^2$$

where n is the index of n^{th} Bessel function and m is the index number of their roots. If $R = 1$, then the eigenvalues of the equations $\Delta\varphi = -\lambda\varphi$ are the square of zero solution of Bessel functions.

3 Mathematical Model of Two Species

In this section, we consider a 2-D reaction diffusion model which is based on the modified Leslie-Gower model with Beddington-DeAngelis functional responses [4–6, 11, 12, 18, 19, 21, 22]:

$$\begin{cases} \frac{\partial u(t,X)}{\partial t} = D_1 \Delta u(t, X) + \left(a_1 - b_1 u(t, X) - \frac{c_1 v(t,X)}{d_1 u(t,X)+d_2 v(t,X)+k_1}\right) u(t, X) \\ \frac{\partial v(t,X)}{\partial t} = D_2 \Delta v(t, X) + \left(a_2 - \frac{c_2 v(t,X)}{u(t,X)+k_2}\right) v(t, X) \end{cases} \quad (8)$$

$u(t, X)$ and $v(t, X)$ represent population densities at time t and space $X = (x, y)$ defined on a circular domain (or disc domain) with radius R (i.e. $\Omega = \{X = (x, y) \in \mathbb{R}^2, x^2 + y^2 < R^2\}$), $r_1, a_1, b_1, k_1, r_2, a_2$, and k_2 are model parameters assuming only positive values, a_1 is the growth rate of preys u, a_2 describes the growth rate of predators v, b_1 measures the strength of competition among individuals of species u, c_1 is the maximum value of the per capita reduction of u due to v, c_2 has a similar meaning to c_1, k_1 measures the extent to which environment provides protection to prey u, k_2 has a similar meaning to k_1 relatively to the predator v, d_1 and d_2 are two positive constants, D_1 and D_2 are the terms diffusions of the preys and the predators.

Steady States and Stability

We consider the reaction diffusion system of two species (8) defined on a circular domain with Neumann boundary conditions (which means that there are no flux of species of both predator and prey on the boundary of the circular domain Ω), where $\Omega = \{(x, y) : x^2 + y^2 < R^2\}$. We can write x and y in polar coordinates as follow $x = rcos\theta$ and $y = rsin\theta$, applying the polar coordinate transformation we find $\Gamma = \{(r, \theta) : 0 < r < R,\ 0 \leq \theta < 2\pi\}$, R the radius of the disk Ω; $r = \sqrt{x^2 + y^2}$, and $\theta = \tan^{-1}(\frac{y}{x})$.

Without loss of generalities we denote also $u(t, x, y) = u(t, rcos(\theta), rsin(\theta)) = u(t, r, \theta)$ and $v(t, x, y) = v(t, rcos(\theta), rsin(\theta)) = v(t, r, \theta)$ are the densities of prey and predators respectively in polar coordinates, at $t = 0$, $u(0, r, \theta) = u_0(r, \theta) \geq 0$, $v(0, r, \theta) = v_0(r, \theta) \geq 0$. Therefore the Laplacian operator in polar coordinates is given by:

$$\Delta_{r\theta}u = \frac{\partial^2 u}{\partial r^2} + \frac{1}{r}\frac{\partial u}{\partial r} + \frac{1}{r^2}\frac{\partial^2 u}{\partial \theta^2}, \tag{9}$$

Then, the spatio-temporal system (8) in polar coordinates is written as follows:

$$\begin{cases} \frac{\partial u(t,r,\theta)}{\partial t} = D_1 \Delta_{r\theta} u(t,r,\theta) + f(u(t,r,\theta), v(t,r,\theta)) & \forall (r,\theta) \in \Gamma, t > 0 \\ \frac{\partial v(t,r,\theta)}{\partial t} = D_2 \Delta_{r\theta} v(t,r,\theta) + g(u(t,r,\theta), v(t,r,\theta)) & \forall (r,\theta) \in \Gamma, t > 0 \\ \frac{\partial u(t,r,\theta)}{\partial n} = \frac{\partial v(t,r,\theta)}{\partial n} = 0, & \forall (r,\theta) \in \partial\Gamma \end{cases} \tag{10}$$

where

$$\begin{cases} f(u(t,r,\theta), v(t,r,\theta)) = \left(a_1 - b_1 u(t,r,\theta) - \frac{c_1 v(t,r,\theta)}{d_1 u(t,r,\theta) + d_2 v(t,r,\theta) + k_1}\right) u(t,r,\theta), \\ g(u(t,r,\theta), v(t,r,\theta)) = \left(a_2 - \frac{c_2 v(t,r,\theta)}{u(t,r,\theta) + k_2}\right) v(t,r,\theta), \end{cases} \tag{11}$$

A steady state (u_e, v_e) of (10) is a solution of the following system

$$\begin{cases} D_1 \Delta_{r\theta} u_e(t,r,\theta) + f(u_e(t,r,\theta), v_e(t,r,\theta)) = 0 \\ D_2 \Delta_{r\theta} v_e(t,r,\theta) + g(u_e(t,r,\theta), v_e(t,r,\theta)) = 0 \end{cases} \tag{12}$$

Let us denote the non-negative cone by

$$\mathbb{R}^2_+ = \{(u,v) \in \mathbb{R}^2, u_0 \geq 0, v_0 \geq 0\}$$

and the positive cone by

$$int\mathbb{R}^2_+ = \{(u,v) \in \mathbb{R}^2, u_0 > 0, v_0 > 0\}.$$

The trivial steady states (belonging to the boundary of int $\mathbb{R}^2_+$, i.e. at which one or more of populations has zero density or is extinct) are in the following forms:

$$E_0 = (0,0), E_1 = \left(\frac{a_1}{b_1}, 0\right), E_2 = \left(0, \frac{a_2 k_2}{c_2}\right). \tag{13}$$

and the homogeneous steady state is given by $E^* = (u^*, v^*)$, where

$$u^* = \frac{-B + \sqrt{B^2 + 4AC}}{2A}, \tag{14}$$

$$v^* = \frac{a_2}{c_2}(u^* + k_2), \tag{15}$$

and

$$B = c_1 a_2 + b_1 c_2 k_1 + b_1 d_2 k_2 a_2 - a_1 d_1 c_2 - a_1 d_2 a_2,$$

$$A = b_1 d_2 a_2 + d_1 b_1 c_2,$$

$$C = k_1 a_1 c_2 + a_1 a_2 d_2 k_2 - c_1 a_2 k_2,$$

We will investigate the asymptotic behavior of orbits starting in the positive cone.

Proposition 1 ([1])
Let Θ be the set defined by

$$\Theta = \left\{ (u, v) \in \mathbb{R}_+^2,\ 0 \leq u \leq \frac{a_1}{b_1},\ 0 \leq v \leq \frac{a_2}{b_1 c_2}(a_1 + b_1 k_2) \right\}$$

(i) Θ is a positively invariant region for the flow associated to equation (10).
(ii) All solutions of (10) *initiating in Θ are ultimately bounded with respect to $\mathbb{R}_+^2$ and eventually enter the attracting set Θ.*

To study the existence of Turing instability one needs to prove the stability of spatially independent homogeneous steady state.

Proposition 2 (local stability without diffusion [1])

- *If $0 < u^* < \theta_1$ or $\theta_2 < u^* < \frac{a_1}{b_1}$, then $E^* = (u^*, v^*)$ is asymptotically stable.*
- *If $(a_2^2 d_2 + a_2 d_1 c_2 + k_1 b_1 c_2 < a_1 d_1 c_2)$ and $\theta_1 < u^* < \theta_2$, then $E^* = (u^*, v^*)$ is unstable for system* (16).
- *If $a_1 d_1 < k_1 b_1$, then the positive equilibrium $E^* = (u^*, v^*)$ is locally asymptotically stable.*

The proofs of Propositions 1 and 2 are given in [1].

4 Model with Three Species

In this section, we consider the following reaction-diffusion model [4, 5, 21, 23]

$$\begin{cases} \frac{\partial U(T,x,y)}{\partial T} = D_1 \Delta U(T,x,y) + (a_0 - b_0 U(T,x,y) - \frac{v_0 V(T,x,y)}{U(T,x,y)+d_0}) U(T,x,y), \\ \frac{\partial V(T,x,y)}{\partial T} = D_2 \Delta V(T,x,y) + (-a_1 + \frac{v_1 U(T,x,y)}{U(T,x,y)+d_0} - \frac{v_2 W(T,x,y)}{V(T,x,y)+d_2}) V(T,x,y), \\ \frac{\partial W(T,x,y)}{\partial T} = D_3 \Delta W(T,x,y) + (c_3 - \frac{v_3 W(T,x,y)}{V(T,x,y)+d_3}) W(T,x,y), \\ \frac{\partial U}{\partial n} = \frac{\partial V}{\partial n} = \frac{\partial W}{\partial n} = 0, \\ U(0,x,y) = U_0(x,y) \geq 0,\ \ V(0,x,y) = V_0(x,y) \geq 0,\ \ W(0,x,y) = W_0(x,y) \geq 0, \end{cases} \tag{16}$$

$U(T, x, y)$ the density of prey specie, $V(T, x, y)$ the density of intermediate predator specie and $W(T, x, y)$ the density of top-predator specie, at time T and position (x, y), defined on a circular domain (or disc domain) with radius R (i.e. $\Omega = \{(x, y) \in \mathbf{R}^2/x^2 + y^2 < R^2\}$. Δ is the Laplacian operator. $\frac{\partial U}{\partial \eta}$, $\frac{\partial V}{\partial \eta}$ and $\frac{\partial W}{\partial \eta}$ are respectively the normal derivatives of U, V and W on $\partial\Omega$. The three species are assumed to diffuse at rates D_i (i = 1, 2, 3). $a_0, b_0, v_0, d_0, a_1, v_1, v_2, d_2, c_3, v_3$ and d_3 are assumed to be positive parameters and are defined as follows: a_0 is the growth rate of the prey U, b_0 measures the mortality due to competition between individuals of the species U, v_0 is the maximum extent that the rate of reduction by individual U can reach, d_0 measures the protection whose prey U and intermediate predator V benefit through the environment, a_1 represents the mortality rate V in the absence of U, v_1 is the maximum value that the rate of reduction by the individual U can reach, v_2 is the maximum value that the rate of reduction by the individual V can reach, v_3 is the maximum value that the rate of reduction by the individual W can reach, d_2 is the value of V for which the rate of elimination by individual V becomes $\frac{v_2}{2}$, c_3 described the growth rate of W, assuming that there are the same number of males and females. d_3 represents the residual loss caused by high scarcity of prey V of the species W.

The initial data $U_0(x, y)$, $V_0(x, y)$ and $W_0(x, y)$ are non-negative continuous functions on Ω. The vector η is an outward unit normal vector to the smooth boundary $\partial\Omega$. The homogeneous Neumann boundary condition signifies that the system is self contained and there is no population flux across the boundary $\partial\Omega$.

Following the same algebraic computations as done in Sect. 3, firstly, we write x and y in polar coordinates as follow $x = r\cos\theta$ and $y = r\sin\theta$. By applying the polar coordinate transformation, we find $\Gamma = \{(r, \theta) : 0 < r < R,\ 0 \le \theta < 2\pi\}$. R is the radius of the disk Γ, with $r = \sqrt{x^2 + y^2}$ and $\theta = \tan^{-1}(\frac{y}{x})$.

Without loss of generalities we denote also

$$u(t, x, y) = u(t, r\cos(\theta), r\sin(\theta)) = u(t, r, \theta),$$

$$v(t, x, y) = v(t, r\cos(\theta), r\sin(\theta)) = v(t, r, \theta)$$

and

$$w(t, x, y) = w(t, r\cos(\theta), r\sin(\theta)) = w(t, r, \theta)$$

are the densities of prey, predators and top predators respectively in polar coordinates.

Therefore the Laplacian operator in polar coordinates is given by:

$$\Delta_{r\theta} u = \frac{\partial^2 u}{\partial r^2} + \frac{1}{r}\frac{\partial u}{\partial r} + \frac{1}{r^2}\frac{\partial^2 u}{\partial \theta^2}. \tag{17}$$

To simplify system (16) we introduce some transformations of variables:

$$U = \frac{a_0}{b_0}u,\ V = \frac{a_0^2}{b_0 v_0}v,\ W = \frac{a_0^3}{b_0 v_0 v_2}w,\ T = \frac{t}{a_0},\ r = \frac{r'}{a_0},\ \theta = \theta',$$

and
$a = \frac{b_0 d_0}{a_0},\ b = \frac{a_1}{a_0},\ c = \frac{v_1}{a_0},\ d = \frac{d_2 v_0 b_0}{a_0^2},\ p = \frac{c_3 a_0^2}{v_0 b_0 v_2},\ q = \frac{v_3}{v_2},\ s = \frac{d_3 v_0 b_0}{a_0^2},\ \delta_1 = a_0 D_1,$
$\delta_2 = a_0 D_2,\ \delta_3 = a_0 D_3.$
Then the spatio-temporal system (16) in polar coordinates is written as follows:

$$\begin{cases} \frac{\partial u(t,r,\theta)}{\partial t} = \delta_1 \Delta_{r\theta} u(t,r,\theta) + f(u(t,r,\theta), v(t,r,\theta), w(t,r,\theta)), & \forall (r,\theta) \in \Gamma,\ t > 0 \\ \frac{\partial v(t,r,\theta)}{\partial t} = \delta_2 \Delta_{r\theta} v(t,r,\theta) + g(u(t,r,\theta), v(t,r,\theta), w(t,r,\theta)), & \forall (r,\theta) \in \Gamma,\ t > 0 \\ \frac{\partial w(t,r,\theta)}{\partial t} = \delta_3 \Delta_{r\theta} w(t,r,\theta) + h(u(t,r,\theta), v(t,r,\theta), w(t,r,\theta)), & \forall (r,\theta) \in \Gamma,\ t > 0 \\ \frac{\partial u(t,r,\theta)}{\partial n} = \frac{\partial v(t,r,\theta)}{\partial n} = \frac{\partial w(t,r,\theta)}{\partial n} = 0, \quad \forall (r,\theta) \in \partial\Gamma \\ u(0,r,\theta) = u_0(r,\theta) \geq 0,\ v(0,r,\theta) = v_0(r,\theta) \geq 0,\ w(0,r,\theta) = w_0(r,\theta) \geq 0. \end{cases} \tag{18}$$

where

$$\begin{cases} f(u(t,r,\theta), v(t,r,\theta), w(t,r,\theta)) = (1 - u(t,r,\theta) - \frac{v(t,r,\theta)}{u(t,r,\theta)+a})u(t,r,\theta), \\ g(u(t,r,\theta), v(t,r,\theta), w(t,r,\theta)) = (-b + \frac{cu(t,r,\theta)}{u(t,r,\theta)+a} - \frac{w(t,r,\theta)}{v(t,r,\theta)+d})v(t,r,\theta), \\ h(u(t,r,\theta), v(t,r,\theta), w(t,r,\theta)) = (p - \frac{qw(t,r,\theta)}{v(t,r,\theta)+s})w(t,r,\theta), \end{cases} \tag{19}$$

Without diffusion, system (18) becomes

$$\begin{cases} \frac{\partial u(t,r,\theta)}{\partial t} = (1 - u(t,r,\theta) - \frac{v(t,r,\theta)}{u(t,r,\theta)+a})u(t,r,\theta), \\ \frac{\partial v(t,r,\theta)}{\partial t} = (-b + \frac{cu(t,r,\theta)}{u(t,r,\theta)+a} - \frac{w(t,r,\theta)}{v(t,r,\theta)+d})v(t,r,\theta), \\ \frac{\partial w(t,r,\theta)}{\partial t} = (p - \frac{qw(t,r,\theta)}{v(t,r,\theta)+s})w(t,r,\theta), \end{cases} \tag{20}$$

A steady state (u_e, v_e, w_e) of (20) is an homogeneous steady state of (18) which is a solution of the following system

$$\begin{cases} \delta_1 \Delta_{r\theta} u_e(t,r,\theta) + f(u_e(t,r,\theta), v_e(t,r,\theta), w_e(t,r,\theta)) = 0, \\ \delta_2 \Delta_{r\theta} v_e(t,r,\theta) + g(u_e(t,r,\theta), v_e(t,r,\theta), w_e(t,r,\theta)) = 0, \\ \delta_3 \Delta_{r\theta} w_e(t,r,\theta) + h(u_e(t,r,\theta), v_e(t,r,\theta), w_e(t,r,\theta)) = 0, \end{cases} \tag{21}$$

Steady States and stability

Simple (and tedious) algebraic computations show that problem (18) has a homogeneous steady-state if and only

$$qc > bq + p \quad \text{and} \quad qc - bq - p > a(bq + p). \tag{22}$$

The homogeneous steady-state in the case when $d = s$, is uniquely given by

$$u^* = \frac{a(bq + p)}{qc - bq - p}, \quad v^* = (1 - u^*)(u^* + a) \text{ and } w^* = \frac{p(v^* + s)}{q}. \tag{23}$$

A similar study can be used when $d \neq s$.

The conditions (22) ensure that the system (18) has a positive homogeneous steady state corresponding to constant coexistence of the three species $E^* = (u^*, v^*, w^*)$.

Proposition 3 *Conditions (22) are satisfied, the set defined by*

$$\Theta \equiv [0, 1] \times [0, 1 + a] \times \left[0, \frac{p}{q}(1 + a + s)\right] \tag{24}$$

is positively invariant region, moreover all solutions of (18) initiating in Θ are ultimately bounded with respect to $\mathbb{R}^3_+$ and eventually enter the attracting set Θ.

By the same in the last section, we need the following result which states the stability of the homogeneous steady state.

Proposition 4 (local stability without diffusion) *If conditions (22) are satisfied and*

$$\frac{a + 1}{qc} > \frac{2a}{qc - bq - p},$$

and

$$b + \frac{dp((1 - u^*)(u^* + a) + s)}{q((1 - u^*)(u^* + a) + d)^2} > \frac{cu^*}{u^* + a} \tag{25}$$

and

$$\frac{p^2((1 - u^*)(u^* + a) + s)^2}{q(u^* + a)} > b + \frac{dp((1 - u^*)(u^* + a) + s)}{q((1 - u^*)(u^* + a) + d)^2}.$$

Then, the homogeneous steady state $E^* = (u^*, v^*, w^*)$ is locally asymptotically stable.

The proofs of Propositions 3 and 4 require long and tedious (albeit simple) algebraic computations, they can be found in [2].

5 Pattern Formation and Turing Instability

Pattern formation is a process by which a spatially uniform state loses stability to a non-uniform state : a pattern.

Two basic types of symmetry-breaking bifurcations, which are responsible for the emergence of spatio-temporal patterns are:

- The space-independent Hopf bifurcation breaks the temporal symmetry of a system and gives rise to oscillations that are uniform in space and periodic in time.
- The (stationary) Turing bifurcation breaks spatial symmetry, leading to the formation of patterns that are stationary in time and oscillatory in space.
  In this section, we mainly focus on this last type of bifurcation.

5.1 *Turing Instability for Two Species Model*

In this section, in order to study the diffusion driven instability for system (10), we have to analyze the stability of the homogeneous steady state $E^* = (u^*, v^*)$ which corresponds to co-existence of prey and predator. The Jacobian evaluated at the equilibrium $E^* = (u^*, v^*)$ is

$$M = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} = \begin{pmatrix} \frac{\partial}{\partial u} f(u^*, v^*) & \frac{\partial}{\partial v} f(u^*, v^*) \\ \frac{\partial}{\partial u} g(u^*, v^*) & \frac{\partial}{\partial v} g(u^*, v^*) \end{pmatrix}$$

$$= \begin{pmatrix} \frac{(a_1 d_1 - k_1 b_1)u^* - 2b_1 d_1 u^{*2} - b_1 d_2 u^* v^*}{d_1 u^* + d_2 v^* + k_1} & -\frac{c_1 u^* (k_1 + d_1 u^*)}{(d_1 u^* + d_2 v^* + k_1)^2} \\ \frac{a_2^2}{c_2} & -a_2 \end{pmatrix}$$

By setting

$$S = \begin{pmatrix} u - u^* \\ v - v^* \end{pmatrix} \varphi(r, \theta) e^{\lambda t + ikr}$$

where $\phi(r, \theta)$ is a eigenfunction of the Laplacian operator on a disc domain with zero flux boundary, i.e.:

$$\begin{cases} \Delta_{r\theta} \phi = -k^2 \phi, \\ \phi_r(R, \theta) = 0 \end{cases}$$

k is the wave number and λ is the perturbation growth rate. Then by linearizing around (u^*, v^*), we have the following equation:

$$\frac{dS}{dt} = MS + D\Delta S \tag{26}$$

where

$$D = \begin{pmatrix} D_1 & 0 \\ 0 & D_2 \end{pmatrix}$$

by substituting S by $\phi e^{\lambda t}$ in Eq. (26) and canceling $e^{\lambda t}$, we get:

$$\lambda\phi = M - Dk^2\phi \tag{27}$$

We obtain the characteristic equation for the growth rate λ as determinant of

$$det(\lambda I_2 - M + k^2 D) = 0 \Leftrightarrow \begin{vmatrix} \lambda - f_u + D_1 k^2 & -f_v \\ -g_u & \lambda - g_v + D_2 k^2 \end{vmatrix} = 0, \tag{28}$$

By computation we have the expression of the characteristic equation $\Theta(k^2)$:

$$\Theta(k^2) = \lambda^2 + R(k^2)\lambda + B(k^2) \tag{29}$$

where

$$R(k^2) = k^2(D_1 + D_2) - tr(M) \tag{30}$$

and

$$B(k^2) = D_1 D_2 k^4 - (D_2 f_u + D_1 g_v)k^2 + \det(M). \tag{31}$$

Therefore, the eigenvalues are the roots of (29) are given by

$$\lambda_{\pm}(k) = \frac{-R(k^2) \pm \sqrt{(R(k^2))^2 - 4B(k^2)}}{2} \tag{32}$$

Let

$$\theta_{1,2} = \frac{-z_2 \pm \sqrt{z_2^2 - 4z_1 z_3}}{z_1^2}, \tag{33}$$

and

$$z_1 = 2b_1 d_1 c_2 + b_1 d_2 a_2,$$

$$z_2 = a_2^2 d_2 + a_2 d_1 c_2 + k_1 b_1 c_2 - a_1 d_1 c_2,$$

$$z_3 = a_2^2 d_2 k_2 + b_1 d_2 k_2 a_2 + k_1 a_2 c_2.$$

Proposition 5 *If $a_2^2 d_2 + a_2 d_1 c_2 + k_1 b_1 c_2 > a_1 d_1 c_2$ or $0 < u^* < \theta_1$ or $\theta_2 < u^*$, θ_1 and θ_2 are defined in Eq. (33) and if $D_2 < (D_2)_c$, then $E^* = (u^*, v^*)$ is asymptotically stable for system (10). If $D_2 > (D_2)_c$ then $E^* = (u^*, v^*)$ is unstable for system (10), where,*

$$(D_2)_c = \frac{-(2D_1 f_v g_u - D_1 f_u g_v)}{f_u^2}$$

$$+\frac{\sqrt{(2D_1 f_v g_u - D_1 f_u g_v)^2 - D_1^2 f_u^2 g_v^2}}{f_u^2}$$

Now, we study the conditions leading to Turing instability for the two-species model. These conditions are given by:

$$Tr(M) = f_u + g_v < 0 \tag{34}$$

$$\det(M) = f_u g_v - f_v g_u > 0 \tag{35}$$

$$D_2 f_u + D_1 g_v > 0 \tag{36}$$

$$(D_2 f_u + D_1 g_v)^2 - 4D_1 D_2 \det(A) > 0 \tag{37}$$

For a predator-prey model, the necessary condition to have the instability of Turing is that the predator spreads faster than the prey, namely $D_2 > D_1$. Turing instability corresponds to the onset of patterns periodic in space and stationary in time. Mathematically speaking, the case when $Im(\lambda(k)) = 0$ for $k = k_c$ is called Turing instability.

The conditions $R(k^2) > 0$ and $B(k^2) > 0$ are equivalent to the stability criterion $R(k^2 = 0) > 0$ and $B(k^2 = 0) > 0$ for the local dynamic. In particular this means that $R(k^2) > 0$ for all k, ($tr(M) < 0$ and $k^2(D_1 + D_2) > 0$, then $R(k^2) > 0$), therefore the only choice for $Re(\lambda(k)) > 0$ is $B(k^2) < 0$ for some $k \neq 0$. Thus the instability of the homogeneous solution can occur when $B(k^2)$ is zero for some k. It means that the instability occur at the point where the equation $B(k^2) = 0$ has a multiple root. We find that $B(k^2)$ is a quadratic polynomial with respect to k^2. Its extremum is a minimum at some k^2 [17].

$$B^{'}(k^2) = 4D_1 D_2 k^3 - 2(D_2 f_{ull} + D_1 g_v)k = 0 \Longrightarrow k_{min}^2 = \frac{1}{2}\left(\frac{D_2 f_u + D_1 g_v}{D_1 D_2}\right). \tag{38}$$

Equation (29) is defined if

$$D_2 f_u + D_1 g_v > 0. \tag{39}$$

Then,

$$B_{min} = B(k^2_{min}) = det(M) - \frac{(D_2 f_u + D_1 g_v)^2}{4D_1 D_2}. \qquad (40)$$

If $det(M) < \frac{(D_2 f_u + D_1 g_v)^2}{4D_1 D_2}$, then there exists $k^2 \neq 0$ such that $B(k^2) < 0$.

The bifurcation for which $B_{min} = 0$ that is $det(M) = \frac{(D_2 f_u + D_1 g_v)^2}{4D_1 D_2}$ occurs for a critical value $(D_2)_T$ of the diffusion coefficient D_2, which is a solution of the equation:

$$f_u^2 D_2^2 + 2(2D_1 f_v g_u - D_1 f_u g_v) D_2 + D_1^2 g_v^2 = 0 \qquad (41)$$

Then the critical value k_c of the wave number k associated with the critical value $(D_2)_T$ is given by

$$k^2_{min} = \frac{1}{2}\left(\frac{(D_2)_T f_u - D_1 a_2}{D_1 (D_2)_T}\right)$$

and the wavelength w_T associated also with the critical value $(D_2)_T$ is given by

$$w_T = \frac{2\pi}{k_T} = 2\pi\sqrt{\frac{2D_1 (D_2)_T}{(D_2)_T f_u - D_1 a_2}}$$

Then, the resolution of Eq. (31) gives us the region of wavenumbers of unstable modes

$$k_1^2 = \frac{D_2 f_u + D_1 g_v - \sqrt{(D_2 f_u + D_1 g_v)^2 - 4D_1 D_2 \det(M)}}{2D_1 D_2}$$

$$k_2^2 = \frac{D_2 f_u + D_1 g_v + \sqrt{(D_2 f_u + D_1 g_v)^2 - 4D_1 D_2 \det(M)}}{2D_1 D_2}$$

5.2 Turing Instability for Three Species Model

Let us now analyze this symmetry breaking bifurcation for system (18). We know that Turing instability occurs from a finite number of wave vectors producing stable spatial patterns depending essentially on the initial condition. Let

$$W = \begin{pmatrix} u - u^* \\ v - v^* \\ w - w^* \end{pmatrix} \varphi(r, \theta) e^{\lambda t + ikr} \qquad (42)$$

where k is the wave number and $\varphi(r, \theta)$ is an eigenfunction of the Laplacian operator on a disc domain with zero flux on the boundary, i.e.:

$$\begin{cases} \Delta_{r\theta}\varphi = -k^2\varphi, \\ \varphi_r(R,\theta) = 0 \end{cases}$$

Then, by linearizing around (u^*, v^*, w^*), we have the following equation:

$$\frac{dW}{dt} = D\Delta W + L_E(E^*)W. \tag{43}$$

where $E = (u, v, w)^T$ and

$$L(E) = \begin{pmatrix} f(u,v,w) \\ g(u,v,w) \\ h(u,v,w) \end{pmatrix} = \begin{pmatrix} (1 - u - \frac{v}{u+a})u \\ (-b + \frac{cu}{u+a} - \frac{w}{v+d})v \\ (p - \frac{qw}{v+s})w \end{pmatrix}$$

Then, problem (20) can be written as: Consider now the system with diffusion (18) and let us substitute W by $\varphi e^{\lambda t}$ in Eq. (43) and canceling $e^{\lambda t}$, we get:

$$\lambda\varphi = L_E(E^*) - Dk^2\varphi. \tag{44}$$

We obtain the characteristic equation for the growth rate λ as the determinant of

$$det(\lambda I_3 - L_E(E^*) + K^2 D) = 0 \Longleftrightarrow$$

$$det\begin{pmatrix} \lambda - a_{11} + \delta_1 k^2 & -a_{12} & -a_{13} \\ -a_{21} & \lambda - a_{22} + \delta_2 k^2 & -a_{23} \\ -a_{31} & -a_{32} & \lambda - a_{33} + \delta_3 k^2 \end{pmatrix} = 0. \tag{45}$$

The characteristic polynomial from (45) is

$$H(k^2) = \lambda^3 + \Phi_1(k^2)\lambda^2 + \Phi_2(k^2)\lambda + \Phi_3(k^2) = 0, \tag{46}$$

with

$$\Phi_1(k^2) = k^2(\delta_1 + \delta_2 + \delta_3) + B_1,$$

$$\Phi_2(k^2) = k^4(\delta_1\delta_2 + \delta_1\delta_3 + \delta_2\delta_3)$$

$$-k^2(\delta_1(a_{22} + a_{33}) + \delta_2(a_{11} + a_{33}) + \delta_3(a_{11} + a_{22})) + B_2,$$

$$\Phi_3(k^2) = k^6\delta_1\delta_2\delta_3 - k^4(\delta_1\delta_2 a_{33} + \delta_1\delta_3 a_{22} + \delta_2\delta_3 a_{11})$$

$$+k^2(\delta_3(a_{11}a_{22} - a_{12}a_{21}) + \delta_2 a_{11}a_{33}) + B_3.$$

For the stability of the equilibrium point, according to the Routh–Hurwitz criteria, $Re(\lambda) < 0$ if

$$\Phi_1(k^2) > 0, \tag{47}$$

$$\Phi_2(k^2) > 0, \tag{48}$$

$$\Phi_1(k^2)\Phi_2(k^2) - \Phi_3(k^2) > 0. \tag{49}$$

The Turing instability requires that the stable homogeneous steady state becomes unstable due to the interaction and diffusion of species.

Under the conditions of Turing:

$$Re(\lambda(k^2 = 0)) < 0, \;\; Re(\lambda(k^2 > 0)) > 0, \;\; \text{for a} \quad k^2 > 0 \tag{50}$$

We have the following Theorem.

Proposition 6 *If one of the following conditions holds:*

$$\Phi_1(k^2) < 0,$$

$$\Phi_2(k^2) < 0,$$

$$\Phi_1(k^2)\Phi_2(k^2) - \Phi_3(k^2) < 0$$

then, the homogeneous steady state $E^* = (u^*, v^*, w^*)$ of system (18) drives instability.

Proof For $k^2 \neq 0$ we have $\Phi_1(k^2) = -(a_{11} + a_{22} + a_{33}) + k^2(\delta_1 + \delta_2 + \delta_3)$. If $a_{11} + a_{22} + a_{33} < 0$, then $\Phi_1(k^2) > 0$ and instability of Turing does not occur. Thereafter, we suppose in Eq. (48) $\rho = k^2 > 0$, to get:

$$\Phi_2(\rho) = \rho^2 p_1 - \rho p_2 + p_3, \tag{51}$$

where

$$p_1 = \delta_1\delta_2 + \delta_1\delta_3 + \delta_2\delta_3,$$

$$p_2 = \delta_1 a_{22} + \delta_1 a_{33} + \delta_2 a_{11} + \delta_2 a_{33} + \delta_3 a_{11} + \delta_3 a_{22},$$

$$p_3 = a_{11}a_{22} + a_{11}a_{33} + a_{22}a_{33} - a_{12}a_{11} - a_{23}a_{23},$$

a necessary condition for $E^* = (u^*, v^*, w^*)$ of (18) becomes unstable is that

$$\Phi_2(\rho) = \rho^2 p_1 - \rho p_2 + p_3 < 0. \tag{52}$$

For the instability, we need that $p_2 > 0$ and $p_2^2 - 4p_1p_3 > 0$ for some ρ. The equation $p_1\rho^2 - p_2\rho + p_3$ has two positive roots given by:

$$\rho_1 = \frac{p_2 - \sqrt{p_2^2 - 4p_1p_3}}{2p_1} \text{ and } \rho_2 = \frac{p_2 - \sqrt{p_2^2 + 4p_1p_3}}{2p_1}. \tag{53}$$

The constant positive steady state $E^* = (u^*, v^*, w^*)$ of (18) is unstable and so (18) experiences Turing instability provided that $\rho_1 < \rho < \rho_2$.

The expressions $\Phi_3(k^2)$ and $\Phi_1(k^2)\Phi_2(k^2) - \Phi_3(k^2)$ are a cubic function of k^2 of the form

$$\Phi_3(k^2) = q_1(k^2)^3 + q_2(k^2)^2 + q_3k^2 + q_4, \tag{54}$$

$$q_1 = \delta_1\delta_2\delta_3,$$

$$q_2 = -(\delta_1\delta_2a_{33} + \delta_1\delta_3a_{22} + \delta_2\delta_3a_{11}),$$

$$q_3 = \delta_1a_{22}h_w + \delta_2a_{11}a_{33} + \delta_3a_{11}a_{22} - \delta_1a_{23}a_{32} - \delta_3a_{22}a_{21}$$

$$= \delta_1(a_{22}a_{33} - a_{23}a_{32}) + \delta_2a_{11}a_{33} + \delta_3(a_{11}a_{22} - a_{12}a_{21}),$$

$$q_4 = \Phi_3(0) = a_{12}a_{21}a_{33} + a_{11}a_{23}a_{32} - a_{11}a_{22}a_{33},$$

with $q_1 = det(D) \geq 0$ and $q_4 = -det(L_E(E^*)) > 0$.

If Φ_3 has a minimum, one finds by simple computation that

$$\frac{d\Phi_3}{d(k^2)} = 3q_1(k^2)^2 + 2q_2(k^2) + q_3 = 0 \tag{55}$$

and $\frac{d^2\Phi_3}{d^2(k^2)} > 0$, this minimum is reached for the solution of (55) at

$$k_{inf}^2 = \frac{-q_2 + \sqrt{q_2^2 - 3q_1q_3}}{3q_1}. \tag{56}$$

If $a_{11} > 0$, $a_{22} > 0$ and $a_{33} > 0$ then $q_2 < 0$.

If $a_{22}a_{33} < a_{23}a_{32}$, $a_{11}a_{33} < 0$, $a_{11}a_{22} < a_{12}a_{21}$ or $a_{22}a_{33} < 0$, $a_{11}a_{33} < 0$ and $a_{11}a_{22} < 0$ then, $q_3 < 0$.

To verify condition (49) let us denote

$$\Psi(k^2) = \Phi_1(k^2)\Phi_2(k^2) - \Phi_3(k^2) = r_1(k^2)^3 + r_2(k^2)^2 + r_3k^2 + r_4, \tag{57}$$

where

$$r_1 = 2\delta_1\delta_2\delta_3 + \delta_1^2\delta_3 + \delta_1^2\delta_2 + \delta_1\delta_2^2 + \delta_1\delta_3^2 + \delta_3\delta_2^2 + \delta_2\delta_3^2$$
$$= (\delta_2 + \delta_3)(\delta_1^2 + \delta_2\delta_3 + \delta_1\delta_2 + \delta_1\delta_3),$$

$$r_2 = -(\delta_1^2 a_{22} + \delta_1^2 a_{33} + \delta_2^2 a_{11} + \delta_2^2 a_{33} + \delta_3^2 a_{11} + \delta_3^2 a_{22} + 2\delta_1\delta_2 a_{11} + 2\delta_1\delta_2 a_{33}$$
$$+2\delta_1\delta_3 a_{11} + 2\delta_1\delta_3 a_{22} + 2\delta_1\delta_2 a_{22} + 2\delta_1\delta_3 a_{33}, +2\delta_2\delta_3 a_{11} + 2\delta_2\delta_3 a_{22} + 2\delta_2\delta_3 a_{33})$$
$$= -a_{11}(\delta_3 + \delta_2)(2\delta_1 + \delta_2 + \delta_3) - a_{22}(\delta_3 + \delta_1)(\delta_1 + 2\delta_2 + \delta_3)$$
$$-a_{33}(\delta_1 + \delta_2)(\delta_1 + \delta_2 + 2\delta_3),$$

$$r_3 = \delta_1 a_{22}^2 + \delta_1 a_{33}^2 + \delta_2 a_{11}^2 + \delta_2 a_{33}^2 + \delta_3 a_{11}^2 + \delta_3 a_{22}^2 + 2\delta_1 a_{11} a_{22}$$
$$+2\delta_1 a_{11} a_{33} + 2\delta_1 a_{22} a_{33} - \delta_1 f_v g_u - \delta_1 f_w h_u + 2\delta_2 f_u g_v$$
$$+2\delta_2 a_{11} a_{33} + 2\delta_2 a_{22} a_{33} - \delta_2 a_{12} a_{21} - \delta_2 a_{23} a_{32} + 2\delta_3 a_{11} a_{22}$$
$$+2\delta_3 a_{11} a_{33} + 2\delta_1 a_{22} a_{33} - \delta_3 a_{23} a_{32}$$
$$= \delta_1 a_{22}^2 + \delta_1 a_{33}^2 + \delta_2 a_{11}^2 + \delta_2 a_{33}^2 + \delta_3 a_{11}^2 + \delta_3 a_{22}^2 + 2(\delta_1 + \delta_2$$
$$+\delta_3)(a_{11} a_{22} + a_{11} a_{33} + 2a_{33} a_{22}) - \delta_1 a_{12} a_{21}$$
$$-\delta_2(a_{12} a_{21} + a_{23} a_{32}) - \delta_3 a_{23} a_{32},$$

$$r_4 = \Psi(0)$$
$$= -(a_{11}^2 a_{22} + a_{11}^2 a_{33} + 2a_{11} a_{22} a_{33} + a_{11} a_{33}^2 + a_{11} a_{22}^2$$
$$+a_{22}^2 a_{33} + a_{22} a_{33}^2) + a_{12} a_{21} a_{22} + a_{22} a_{23} a_{32}.$$

$r_4 > 0$ if

$$a_{11}^2 a_{22} + a_{11}^2 a_{33} + 2a_{11} a_{22} a_{33} + a_{11} a_{33}^2 + a_{11} a_{22}^2$$
$$+a_{22}^2 a_{33} + a_{22} a_{33}^2 < a_{12} a_{12} a_{22} + a_{22} a_{23} a_{32}.$$

If Ψ has a minimum, by simple algebraic computation we get

$$\frac{d\Psi}{d(k^2)} = 3r_1(k^2)^2 + 2r_2(k^2) + r_3 = 0 \tag{58}$$

and $\frac{d^2\Psi}{d^2(k^2)} > 0$, this minimum is reached for the solution of (58) at

$$k_{1inf}^2 = k_{inf}^2 = \frac{-r_2 + \sqrt{r_2^2 - 3r_1 r_3}}{3r_1} \tag{59}$$

$r_2 < 0$ if $a_{11} > 0$, $a_{22} > 0$ and $a_{33} > 0$.

$r_3 < 0$ if $a_{12}a_{21} > 0$, $(a_{12}a_{21} + a_{23}a_{32}) > 0$, $a_{23}a_{32}) > 0$ and $\delta_1 a_{22}^2 + \delta_1 a_{33}^2 + \delta_2 a_{11}^2 + \delta_2 a_{33}^2 + \delta_3 a_{11}^2 + \delta_3 a_{22}^2 + 2(\delta_1 + \delta_2 + \delta_3)(a_{11}a_{22} + a_{11}a_{33} + 2a_{33}a_{22}) < \delta_1 a_{12}a_{21} + \delta_2(a_{12}a_{21} + a_{23}a_{32}) + \delta_3 a_{23}a_{32}$.

By using the conditions for the existence of the homogeneous steady state of the system without diffusion to be stable ($\Phi_1(0) > 0, \Phi_2(0) > 0, \Phi_3(0) > 0\Phi_1(0)$ $\Phi_2(0) - \Phi_3(0) > 0$) and the necessary condition for the homogeneous steady state of the system with diffusion to be instable that is to say, at least one of the following conditions, ($\Phi_1(k^2) < 0, \Phi_2(k^2) < 0, \Phi_3(k^2) < 0, \Phi_1(k^2)\Phi_2(k^2) - \Phi_3(k^2) < 0$) is satisfied for a certain $k^2 \neq 0$, we can prove the following proposition which gives a necessary condition (not sufficient) for the instability for the homogeneous steady state of the reaction-diffusion system with three species.

Let

$$\Phi_3(k_{inf}^2) = \frac{2q_2^3 - 9q_1q_2q_3 + 27q_1^2q_4 - 2(q_2^2 - 3q_1q_3)^{\frac{3}{2}}}{27q_1^3}$$

$$\Psi(k_{1inf}^2) = \frac{2r_2^3 - 9r_1r_2r_3 + 27r_1^2r_4 - 2(r_2^2 - 3r_1r_3)^{\frac{3}{2}}}{27r_1^3}$$

Therefore, in the following assumptions:
$(H_0) : q_2 < 0$
$(H_1) : q_3 < 0$
$(H_2) : q_2^2 - 3q_1q_3 > 0$
$(H_3) : r_2 < 0, r_3 < 0$ and $q_2^2 - 3q_1q_3 > 0$
$(H_4) : r_2^2 - 3r_1r_3 > 0$
$(H_5) : 2q_2^3 - 9q_1q_2q_3 + 27q_1^2q_4 - 2(q_2^2 - 3q_1q_3)^{\frac{3}{2}} < 0$
$(H_6) : 2r_2^3 - 9r_1r_2r_3 + 27r_1^2r_4 - 2(r_2^2 - 3r_1r_3)^{\frac{3}{2}} < 0$
and using

Lemma 1 *(i)- If (H_0) or (H_1) and (H_2) are verified, then k_{inf}^2 is a positive real.*
(ii)- If (H_0), (H_2) and (H_3) (Resp (H_4)) are verified, then k_{inf}^2 is a positive real (Resp k_{1inf}^2 is a positive real).
(iii)- If (H_5) (Resp (H_6)), then $\Phi_3(k_{inf}^2) < 0$ (Resp $\Psi(k_{1inf}^2) < 0$).

we can easily prove the final result:

Proposition 7 *Suppose*
1—[(H_0) or (H_1) and (H_2)] or [(H_0), (H_2) and (H_3)] or [(H_0), (H_2) and (H_4)].
2—(H_5) or (H_6).
If conditions 1 and 2 are satisfied, then we have emergence of Turing instability for system (18).

5.3 Numerical Simulations

In this subsection, we perform numerical simulations to illustrate the theoretical results given in the previous sections. In Figs. 1 and 2, Patterns formation are shown for systems (10) and (18).

Initial conditions for system (10) have been chosen as

$$u(0, r, \theta) = u^*((rcos\theta)^2 + (rsin\theta)^2) < 400 \tag{60}$$

$$v(0, r, \theta) = v^*((rcos\theta)^2 + (rsin\theta)^2) < 400 \tag{61}$$

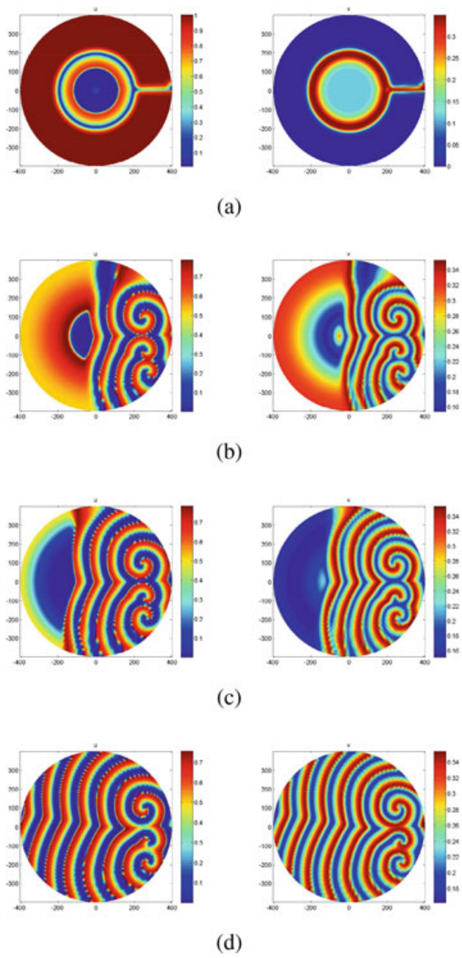

Fig. 1 Spatial distribution of species for system (10) with $D_1 = D_2 = 1, a_1 = 1, a_2 = 0.02, b_1 = 1, k_1 = 0.2, k_2 = 0.1, d_1 = 0.9, d_2 = 0.1, c_1 = 1.1, c_2 = 0.02$ and time varying **a** for $t = 100$, **b** for $t = 2800$, **c** for $t = 3500$, **d** for $t = 6000$. The left figures are spatial evolutions of the prey and the right are for predator

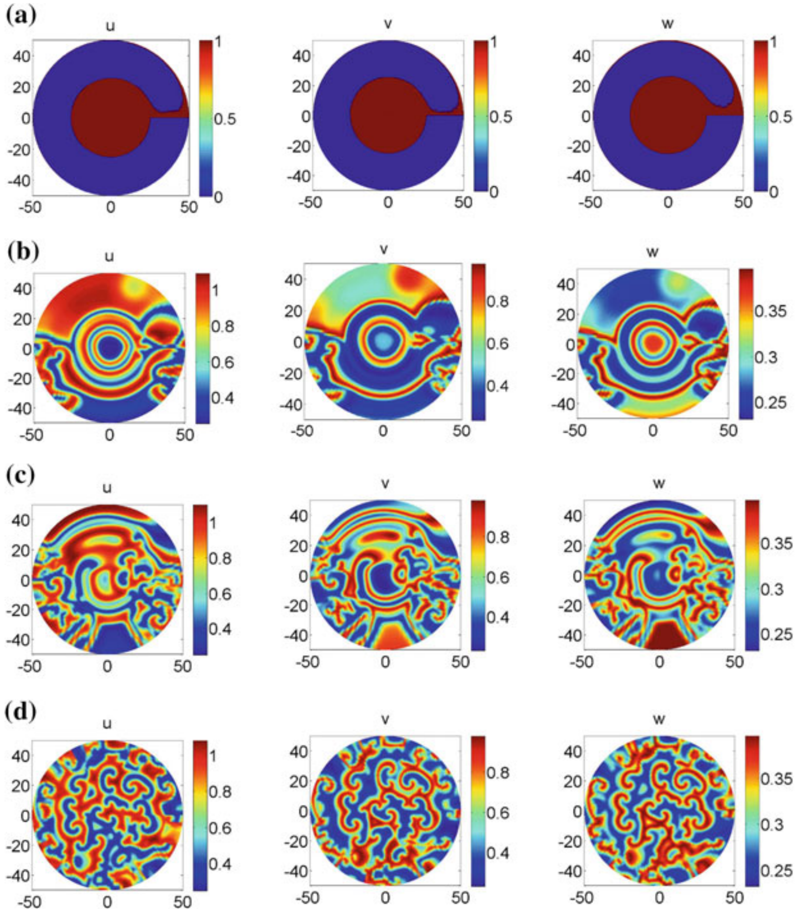

Fig. 2 Spatial distribution of prey (first column), predator (second column) and top predator (third column) for system (18). Spatial patterns are obtained with diffusivity coefficients $\delta_1 = 0.02$, $\delta_2 = 0.01$ and $\delta_3 = 0.05$, $a_0 = 0.5$, $a_1 = 0.4$, $b_0 = 0.36$, $c_3 = 0.2$, $d_0 = 0.3$, $d_2 = 0.4$, $d_3 = 0.4$, $v_0 = 0.4$, $v_1 = 0.8$, $v_2 = 0.4$, $v_3 = 0.6$ at different time levels: for t = 0 (a), t = 1000 (b), t = 2000 (c), t = 20000 (d)

Initial conditions for system (18) have been chosen as,

$$u(0, r, \theta) = u^*((rcos\theta)^2 + (rsin\theta)^2) < 50,$$

$$v(0, r, \theta) = v^*((rcos\theta)^2 + (rsin\theta)^2) < 50,$$

$$w(0, r, \theta) = w^*((rcos\theta)^2 + (rsin\theta)^2) < 50.$$

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