

Long-time behavior and Turing instability induced by cross-diffusion in a three species food chain model with a Holling type-II functional response

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Abstract

In this paper, we study a strongly coupled reaction-diffusion system describing three interacting species in a food chain model, where the third species preys on the second one and simultaneously the second species preys on the first one. An intra-species competition b_2 among the second predator is introduced to the food chain model. This parameter produce some very interesting result in linear stability and Turing instability. We first show that the unique positive equilibrium solution is locally asymptotically stable for the corresponding ODE system when the intra-species competition exists among the second predator. The positive equilibrium solution remains linearly stable for the reaction diffusion system without cross diffusion, hence it does not belong to the classical Turing instability scheme. But it becomes linearly unstable only when cross-diffusion also plays a role in the reaction-diffusion system, hence the instability is driven solely from the effect of cross diffusion. Our results also exhibit some interesting combining effects of cross-diffusion, intra-species competitions and inter-species interactions. Numerically, we conduct a one parameter analysis which illustrate how the interactions change the existence of stable equilibrium, limit cycle, and chaos. Some interesting dynamical phenomena occur when we perform analysis of interactions in terms of self-production of prey and intra-species competition of the middle predator. By numerical simulations, it illustrates the existence of nonuniform steady solutions and new patterns such as spot patterns, strip patterns and fluctuations due to the diffusion and cross diffusion in 2-dimension.

Key word: Predator-prey models; Reaction-diffusion system; Cross-diffusions; Turing instability; Turing patterns; Food chain.

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1 Introduction

In population dynamics, the predator-prey system has been extensively studied and the analysis of food chains is an active research area in the mathematical biological science [9, 10]. A simple food chain consists of three species where the third species preys on the second one and simultaneously the second species preys on the first one. There are several interesting cases of simple food chains of three interacting species by the types of predators. It includes the case where there is a generalist predator and a specialist predator. It also includes the case where both predators are generalists or specialists. A predator is a generalist if it can change its food source in the absence of its favorite food which is very common in nature. An interesting chaotic dynamics was observed in a food chain by Hastings and Powell [5] where both the top-predator and the middle-predator are specialists.

Upadhyay, Iyengar, and Rai [17, 18] proposed a model to understand the reasons why chaos is rarely observed in natural populations of three interacting species, where the top-predator is a generalist while the middle-predator is a specialist. The model and its variants have been studied by several authors [1, 19]. Most of these studies concentrate on the original model with different functional response, which is spatially homogeneous. There are few works on pattern formation in a spatially inhomogeneous model of this type.

But spatial spread of species is more nature. The spread can lead to many interesting spatial patterns due to the dispersal of species in search for food, and also due to refuge from predators. Among the various pattern formations, Turing patterns are generated when the species in the food chain have different diffusion interactions. In [16], Wang studied an elliptic system which models the dynamics of a two-preys-one-predator ecosystem and he showed that the cross-diffusions can create the stationary patterns where cross-diffusions are included in such a way that predator chases the prey and the prey runs away from the predator. In [22], Xie studied a simple food chain model where both predators are generalists. He showed that the positive equilibrium solution for the model is globally asymptotically stable for the reaction diffusion system without cross diffusion by constructing a Lyapunov function, hence it does not belong to the classical Turing instability scheme. But it becomes linearly unstable only when cross-diffusion also plays a role in the reaction-diffusion system, hence the instability is driven solely from the effect of cross diffusion. There are numerous research papers of predator prey model, for example, [2, 3, 4, 12, 25] for two species and [6, 8, 11, 7] for three species. We just mention some of them here which are closely related to current paper and more references can be found therein.

The following simple food chain is modified from the classical Upadhyay-Iyengar-Rai model [17] by adding the self-competition ($b_2 \neq 0$) in the middle specialist predator.

$$(1) \quad \begin{cases} \frac{du_1}{dt} = u_1(a_1 - b_1 u_1 - \frac{w_0 u_2}{u_1 + D_0}), \\ \frac{du_2}{dt} = u_2(-a_2 - b_2 u_2 + \frac{w_1 u_1}{u_1 + D_1} - \frac{w_2 u_3}{u_2 + D_2}), \\ \frac{du_3}{dt} = u_3^2(a_3 - \frac{w_3}{u_2 + D_3}). \end{cases}$$

The three species in the model are denoted by u_i , $i = 1, 2, 3$. The top generalist predator u_3 preys on u_2 , which is its favorite food. In turn, the middle specialist predator u_2 preys on its only food, the prey u_1 . The interaction between the specialist predator u_2 and its prey u_1 is modeled by Volterra scheme (predator population dies out exponentially in the absence of its food). The interaction between the specialist predator u_2 and the generalist predator u_3 is modeled by the Leslie-Gower scheme. The function response is Holling type II. There are 13 nonnegative parameters in the model and their biological definitions can be found in [9, 10, 17]. a_1 is the growth rate of prey u_1 . a_2 is the rate at which u_2 dies out when there is no food u_1 and no predator u_3 . a_3 measures the growth rate of u_3 via sexual reproduction. b_1 and b_2 describe the self-competition among prey u_1 and among specialist predator u_2 respectively. w_i is the maximum value which per capita reduction rate can attain. D_0 and D_1 signifies the extent to which environment provides protection to the prey u_1 . D_2 is the value of u_2 at which its per capital removal rate becomes $w_2/2$ and D_3 represents the residual loss in u_3 population due to the severe scarcity of its favorite food u_2 . This ODE model has very rich dynamical phenomena. Simulations of this model with $b_2 = 0$ in [17] show the existence of different solutions such as the stable equilibrium, states of extinction, limit cycles, and chaotic behaviors in various ranges of the parameter space.

One of goals in this paper is to investigate the effects of the intra-species competition among the specialist predators ($b_2 \neq 0$) and the effects of diffusions between species which were not included in the previous papers [15, 17, 20]. Another goal is to understand the Turing pattern formations due to the spatial interactions in the three species food chain diffusive model.

$$(2) \quad \begin{cases} u_{1t} = \Delta [(k_{11} + k_{12}u_2)u_1] + u_1(a_1 - b_1 u_1 - \frac{w_0 u_2}{u_1 + D_0}), \\ u_{2t} = \Delta [(k_{21}u_1 + k_{22} + k_{23}u_3)u_2] + u_2(-a_2 - b_2 u_2 + \frac{w_1 u_1}{u_1 + D_1} - \frac{w_2 u_3}{u_2 + D_2}), \\ u_{3t} = \Delta [(k_{32}u_2 + k_{33})u_3] + u_3^2(a_3 - \frac{w_3}{u_2 + D_3}) \text{ in } \Omega \times (0, \infty), \\ \frac{\partial u_1}{\partial n} = \frac{\partial u_2}{\partial n} = \frac{\partial u_3}{\partial n} = 0 \text{ on } \partial\Omega \times (0, \infty), \\ u_i(x, 0) = u_{i0}(x) \text{ in } \Omega \text{ for } i = 1, 2, 3, \end{cases}$$

where Ω is a bounded domain with smooth boundary in \mathbf{R}^N ($N \geq 1$) and n is the outward unit normal vector on boundary $\partial\Omega$. The homogeneous Neumann boundary condition

means that the three species have zero flux across the boundary. k_{ii} is the diffusion rate of i -th species and k_{ij} ($i \neq j, 1 \leq i, j \leq 3$) is the cross-diffusion rate of i -th species due to the pressure of the presence of j -th species. Here k_{13} and k_{31} are missing in (2), which means that the third and first species in the simple food chain do not have direct interaction.

The role of diffusion and cross-diffusion in the modeling of many physical, chemical and biological processes has been extensively studied. A pure diffusion process usually leads to a stabilizing effect so that the system tends to a constant equilibrium state. However in [14], Alan Turing suggested that, under certain conditions, chemicals can react and diffuse in such a way as to produce non-constant equilibrium solutions, where diffusion is actually a destabilizing factor. Diffusion can destabilize an initially stable state due to inhomogeneous perturbation. Turing patterns occur when the stable homogeneous steady state of the system is broken.

In [20], Parshad etc. attempted to study the Turing instability for the positive equilibrium for a similar food chain system with self-diffusion only where all $k_{ij} = 0$ for $i \neq j$ and intra-species interaction $b_2 = 0$. They proved the existence of a finite dimensional global attractor and they also numerically found some regions where the Turing instability occurs. In [15], Tian studies a very similar model with a different third equation of top species and he presents a rigorous proof to the assumption that their model has at least one nonhomogeneous stationary solution by the Leray-Schauder degree theory. Both papers numerically found some interesting Turing patterns due to the self-diffusion or cross-diffusion.

In this paper, we will theoretically prove the existence of the Turing instability in the case $k_{ij} \geq 0$. We first find all possible equilibrium solutions to the ODE system (1). Then we conduct Turing instability analysis of the equilibrium solutions to the diffusive system (2). Finally the rich dynamical phenomena of the ODE system is studied for some given parameters. Then we investigate pattern formation and diffusion driven instability via numerical simulations in two dimension.

The paper is organized as follows. In section 2, we present the equilibrium solutions of the model and we prove that the positive coexistence equilibrium is locally asymptotically stable. In section 3, we perform Turing instability analysis and we prove that Turing instability does not happen if the conditions (7) are satisfied and only self diffusions ($k_{ii} > 0, k_{ij} = 0$) occur. In section 4, we prove that Turing instability can be induced by cross diffusion. In the last section, numerical simulation is to illustrate the rich dynamical phenomena and the existence of new patterns.

2 Stability Analysis of the Equilibriums of the ODE System

Let $\mathbf{u} = (u_1, u_2, u_3)^T$ be an equilibrium solution of the ODE system (1), i.e. $\frac{du_i}{dt} = 0$, $i = 1, 2, 3$. By solving the algebraic system,

$$(3) \quad \begin{cases} u_1 g_1(u_1, u_2, u_3) := u_1(a_1 - b_1 u_1 - \frac{w_0 u_2}{u_1 + D_0}) = 0, \\ u_2 g_2(u_1, u_2, u_3) := u_2(-a_2 - b_2 u_2 + \frac{w_1 u_1}{u_1 + D_1} - \frac{w_2 u_3}{u_2 + D_2}) = 0, \\ u_3^2 g_3(u_1, u_2, u_3) := u_3^2(a_3 - \frac{w_3}{u_2 + D_3}) = 0, \end{cases}$$

we can get the following equilibrium solutions:

$$\mathbf{u}^{(1)} = (0, 0, 0);$$

$$\mathbf{u}^{(2)} = (\frac{a_1}{b_1}, 0, 0);$$

$$\mathbf{u}^{(3)} = (0, -\frac{a_2}{b_2}, 0);$$

$$\mathbf{u}^{(4)} = (0, \frac{w_3 - a_3 D_3}{a_3}, -\frac{(a_2 + b_2 u_2)(u_2 + D_2)}{w_2});$$

$$\mathbf{u}^{(5)} = (0, 0, \alpha) \text{ if } w_3 = a_3 D_3, \text{ where } \alpha \text{ is any positive constant};$$

$$\mathbf{u}^{(6)} = (\frac{a_1}{b_1}, 0, \alpha) \text{ if } w_3 = a_3 D_3, \text{ where } \alpha \text{ is any positive constant};$$

$\mathbf{u}^{(7)} = (u_1, (a_1 - b_1 u_1)(u_1 + D_0)/w_0, 0)$, where u_1 is a real solution of a third degree polynomial from $g_2 = 0$ after $u_2 = (a_1 - b_1 u_1)(u_1 + D_0)/w_0$ and $u_3 = 0$ are substituted into g_2 .

$$\mathbf{u}^{(8)} = (u_1^-, u_2^-, u_3^-), \text{ and}$$

$$\mathbf{u}^{(9)} = (u_1^+, u_2^+, u_3^+), \text{ where } u_2^- = u_2^+ = \frac{w_3}{a_3} - D_3 \text{ by } g_3 = 0 \text{ and}$$

u_1^\pm is the two roots by the quadratic formula for the quadratic equation of u_1 resulted from $g_1 = 0$.

$$(4) \quad u_1^\pm = \frac{(a_1 - b_1 D_0) \pm \sqrt{(a_1 + b_1 D_0)^2 - 4b_1 w_0 u_2^\pm}}{2b_1}.$$

u_3^\pm can be solved for the given u_1^\pm and u_2^\pm from $g_2 = 0$ and

$$(5) \quad u_3^\pm = \frac{(u_2^\pm + D_2)}{w_2} \left(-a_2 - b_2 u_2^\pm + \frac{w_1 u_1^\pm}{u_1^\pm + D_1} \right).$$

All components of \mathbf{u} must be real and nonnegative since they are the population densities of the species. It is easy to see that solutions $\mathbf{u}^{(3)}$ and $\mathbf{u}^{(4)}$ have at least one negative component. Solutions $\mathbf{u}^{(5)}$ and $\mathbf{u}^{(6)}$ are very peculiar because they exist only when $w_3 = a_3 D_3$. Solutions $\mathbf{u}^{(8)}$ and $\mathbf{u}^{(9)}$ are the only coexistence equilibria and all others have the

extinction of one or more species. When we conduct numerical simulations to illustrate various Turing patterns, equilibrium solution $\mathbf{u}^{(8)}$ has some negative components for the parameters we used. Thus equilibrium solution $\mathbf{u}^{(9)}$ is the best choice for Turing instability analysis from the biological point view.

Roughly speaking, the top generalist predator u_3 can probably become blowup when $a_3 \geq \frac{w_3}{D_3}$ which makes $\frac{du_3}{dt} \geq 0$ for any time t . We should note that to make the coexistence equilibrium $\mathbf{u}^{(9)}$ happen, the parameters a_3, w_3, D_3 has to be chosen in such a way as $a_3 < \frac{w_3}{D_3}$. However, even when $a_3 < \frac{w_3}{D_3}$, the top generalist predator might still become blowup because it is possible that $\frac{w_2}{u_2 + D_3} < a_3 < \frac{w_3}{D_3}$ for some values u_2 of the middle specialist predator. Some interesting dynamics can be obtained such as stable steady states, chaotic dynamics and fast fluctuations which have been seen a lot in nature.

Now let us conduct the linear stability analysis for the biologically feasible equilibriums which are the nonnegative steady states $\mathbf{u}^{(k)}$, $k = 1, 2, 7, 9$. We first linearize the system (1) along a nonnegative equilibrium solution $\bar{\mathbf{u}} = (\bar{u}_1, \bar{u}_2, \bar{u}_3)$ and the linear stability is determined by the eigenvalues of the Jacobian matrix

$$(6) \quad \mathbf{J}|_{\bar{\mathbf{u}}} = \begin{pmatrix} g_1 + u_1 \frac{\partial g_1}{\partial u_1} & u_1 \frac{\partial g_1}{\partial u_2} & 0 \\ u_2 \frac{\partial g_2}{\partial u_1} & g_2 + u_2 \frac{\partial g_2}{\partial u_2} & u_2 \frac{\partial g_2}{\partial u_3} \\ 0 & u_3^2 \frac{\partial g_3}{\partial u_2} & 2u_3 g_3 \end{pmatrix} \bigg|_{\bar{\mathbf{u}}}.$$

For the nonnegative equilibriums $\mathbf{u}^{(k)}$, $k = 1, 2, 7$, $\bar{u}_3 = 0$ and one of the eigenvalues of the Jacobian matrix is zero. Therefore these equilibria are not linearly stable in the three dimension space. However, if we look at some subsystem, the answer may vary. For example, when we consider the subsystem of prey u_1 and middle predator u_2 while we assume $u_3 = 0$, the equilibrium $\mathbf{u}^{(7)}$ is linear stable for some parameters.

Thanks the effect of the intra-species competition $b_2 > 0$, we have a beautiful stability result and simple proof for the positive coexistence equilibrium solution $\mathbf{u}^{(9)}$. This result does not hold in paper [20].

Theorem 2.1. *Suppose that $\mathbf{u}^{(9)}$ is a positive equilibrium solution of the ODE system (1). If the parameters of the ODE system (1) satisfy*

$$(7) \quad w_0 u_2^+ < b_1 (u_1^+ + D_0)^2 \text{ and } w_2 u_3^+ < b_2 (u_2^+ + D_2)^2$$

then the positive equilibrium solution $\mathbf{u}^{(9)}$ is locally asymptotically stable.

Proof. It is sufficient to show that the characteristic value of the Jacobian matrix (6) is

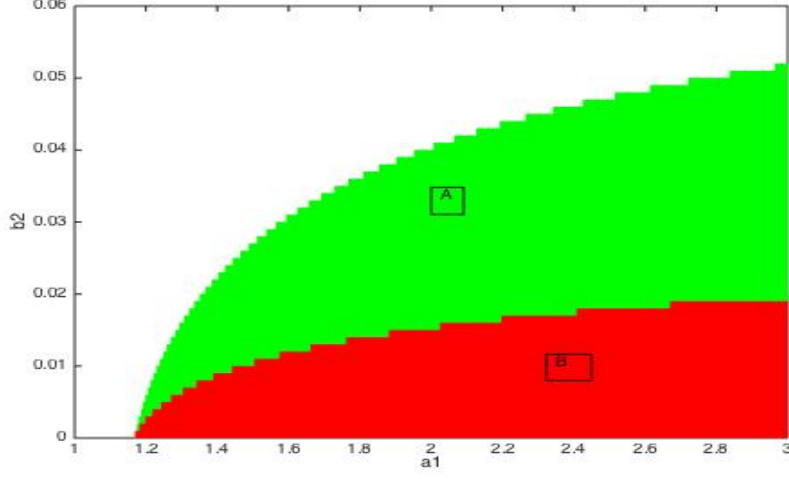


Figure 1: The linear stability space calculated in terms of the reproduction rate a_1 and intra-species competition b_2 among middle predators. All other parameters are given in (21) and (22) in section 5. The non-negative equilibrium $\mathbf{u}^{(9)}$ does not exist in the white blank region. The non-negative equilibrium $\mathbf{u}^{(9)}$ exists in the colored regions (green A and red B). The top green region A is the linear stable region which satisfies the sufficient stability condition (7).

negative when $\bar{\mathbf{u}} = \mathbf{u}^{(9)}$. Thanks $g_i(\mathbf{u}^{(9)}) = 0, i = 1, 2, 3$, a direct calculation yields

$$(8) \quad J|_{\mathbf{u}^{(9)}} = (J_{ij}) = \begin{pmatrix} u_1^+ \left(-b_1 + \frac{w_0 u_2^+}{(u_1^+ + D_0)^2} \right) & -\frac{u_1^+ w_0}{u_1^+ + D_0} & 0 \\ u_2^+ \left(\frac{w_1 D_1}{(u_1^+ + D_1)^2} \right) & u_2^+ \left(-b_2 + \frac{w_2 u_3^+}{(u_2^+ + D_2)^2} \right) & -\frac{u_2^+ w_2}{u_2^+ + D_2} \\ 0 & \frac{(u_3^+)^2 w_3}{(u_2^+ + D_3)^2} & 0 \end{pmatrix}$$

The characteristic polynomial of $J|_{\mathbf{u}^{(9)}}$ is

$$p(\lambda) = \lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3,$$

where

$$\begin{aligned} A_1 &= -J_{11} - J_{22}, \\ A_2 &= J_{11}J_{22} - J_{23}J_{32} - J_{21}J_{12}, \\ A_3 &= J_{11}J_{23}J_{32}. \end{aligned}$$

By the assumption (7), we have

$$(9) \quad J_{11} < 0, J_{12} < 0, J_{22} < 0, J_{23} < 0, J_{21} > 0, \text{ and } J_{32} > 0.$$

It is easy to check that A_1, A_2, A_3 are positive and $A_1 A_2 - A_3 = -J_{11}^2 J_{22} + J_{11} J_{21} J_{12} - J_{11} J_{22}^2 + J_{22} J_{23} J_{32} + J_{22} J_{21} J_{12} > 0$. Thus the positive coexistence equilibrium solution $\mathbf{u}^{(9)}$ is locally asymptotically stable by the Routh-Hurwitz criterion.

□

Remark 2.2. The conditions (7) in theorem (2.1) are fulfilled for a range of parameters a_1 and b_2 while keeping other parameters as constants, for example $w_0 = 1; w_1 = 2; w_2 = 0.55; w_3 = 1; D_0 = 10; D_1 = 10; D_2 = 10; D_3 = 20; a_2 = 1; b_1 = 0.05; a_3 = 0.03$. Numerically, we compute the regions of non-negative coexistence ($\mathbf{u}^{(9)} > 0$) and linear stability (Condition (7) satisfies). Figure 1 presents the stable region (green region A) for Theorem 2.1 and coexistence region (green region A and red region B).

Remark 2.3. The conditions (7) in theorem (2.1) are sufficient but not necessary. For example, $\mathbf{u}^{(9)}$ is a positive stable equilibrium solution of (1) but the conditions (7) are not satisfied when $w_0 = 0.55; w_1 = 2; w_2 = 0.5; w_3 = 1.2; D_0 = 10; D_1 = 13; D_2 = 10; D_3 = 20; a_1 = 2; a_2 = 0.8; a_3 = 0.04; b_1 = 0.15; b_2 = 0$. In fact, if $b_2 = 0$, the second inequality in (7) does not hold for any parameters. So this theorem is not applicable to the case studied in the paper [20], where $b_2 = 0$ and $k_{ij} = 0$ for $i \neq j$. Numerically, we compute the linear stable regions by Routh-Hurwitz criterion and we compare it with linear stable region by condition (7). Figure 2 presents three regions: (1) Red region B represents that non-negative equilibrium $\mathbf{u}^{(9)}$ is linearly unstable. (2) Blue region C and green region A represent that non-negative equilibrium $\mathbf{u}^{(9)}$ is linearly stable and it satisfies Routh-Hurwitz criterion. (3) Green region A represents that non-negative equilibrium $\mathbf{u}^{(9)}$ is linearly stable and it satisfies both Routh-Hurwitz criterion and stability condition (7).

3 No Turing instability without cross-diffusion

For simplicity we denote

$$\mathbf{K}(\mathbf{u}) = \begin{pmatrix} (k_{11} + k_{12}u_2)u_1 \\ (k_{21}u_1 + k_{22} + k_{23}u_3)u_2 \\ (k_{32}u_2 + k_{33})u_3 \end{pmatrix}, \quad \mathbf{G}(\mathbf{u}) = \begin{pmatrix} u_1 g_1 \\ u_2 g_2 \\ u_3^2 g_3 \end{pmatrix},$$

where g_1, g_2, g_3 are defined in the system of algebraic (3). Then the reaction-diffusion system (2) can be rewritten in matrix notation as:

$$(10) \quad \begin{cases} \frac{\partial \mathbf{u}}{\partial t} = \Delta \mathbf{K}(\mathbf{u}) + \mathbf{G}(\mathbf{u}) \text{ in } \Omega \times (0, \infty), \\ \frac{\partial \mathbf{u}}{\partial n} = 0 \text{ on } \partial\Omega \times (0, \infty), \\ \mathbf{u}(x, 0) = (u_{10}(x), u_{20}(x), u_{30}(x))^T \text{ in } \Omega. \end{cases}$$

Linearizing the reaction-diffusion system (10) about a nonnegative equilibrium $\bar{\mathbf{u}} = (\bar{u}_1, \bar{u}_2, \bar{u}_3)$, we have

$$(11) \quad \frac{\partial \Psi}{\partial t} = \mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}) \Delta \Psi + \mathbf{G}_{\mathbf{u}}(\bar{\mathbf{u}}) \Psi,$$

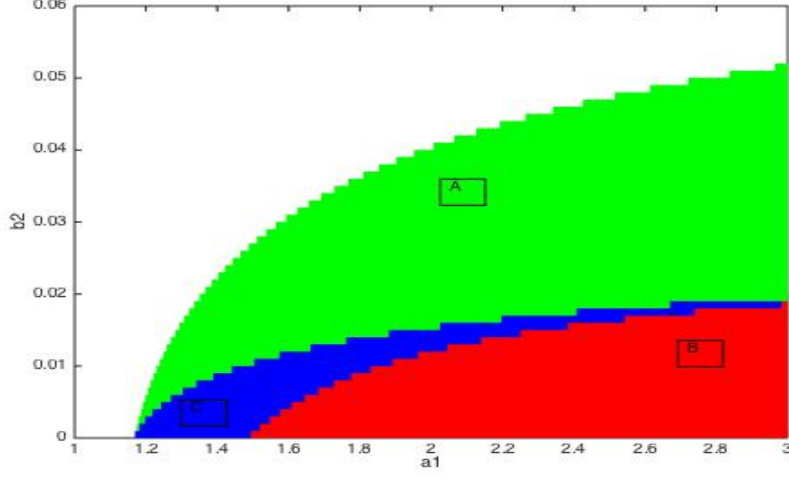


Figure 2: The linear stability space calculated in terms of the reproduction rate a_1 and intra-species competition b_2 among middle predators. All other parameters are given in (21) and (22) in section 5. The top green region A is the linear stable region which satisfies the sufficient stability condition (7). Both the top green region A and the blue region C are the linear stable regions which satisfy the Routh-Hurwitz criterion. The non-negative equilibrium $\mathbf{u}^{(9)}$ is linear unstable in red region B.

where $\Psi = (\Psi_1, \Psi_2, \Psi_3)^T$ and

$$\mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}) = \begin{pmatrix} k_{11} + k_{12}\bar{u}_2 & k_{12}\bar{u}_1 & 0 \\ k_{21}\bar{u}_2 & k_{21}\bar{u}_1 + k_{22} + k_{23}\bar{u}_3 & k_{23}\bar{u}_2 \\ 0 & k_{32}\bar{u}_3 & k_{33} + k_{32}\bar{u}_2 \end{pmatrix}, \quad \mathbf{G}_{\mathbf{u}}(\bar{\mathbf{u}}) = \mathbf{J}|_{\bar{\mathbf{u}}} \text{ in (6).}$$

Let $0 = \mu_1 < \mu_2 < \mu_3 < \dots$ be the eigenvalues of the operator $-\Delta$ on Ω with the homogeneous Neumann boundary condition, and $E(\mu_i)$ be the eigenspace corresponding to μ_i in $C^2(\Omega)$. Let $\mathbf{X} = \{\mathbf{u} \in [C^1(\bar{\Omega})]^3 | \partial_n \mathbf{u} = 0 \text{ on } \partial\Omega\}$, $\{\phi_{ij}\}_{j=1,2,\dots,\dim E(\mu_i)}$ be an orthonormal basis of $E(\mu_i)$, and $\mathbf{X}_{ij} = \{\mathbf{c}\phi_{ij} | \mathbf{c} \in \mathbf{R}^3\}$. Then

$$\mathbf{X} = \bigoplus_{i=1}^{\infty} \mathbf{X}_i \quad \text{and} \quad \mathbf{X}_i = \bigoplus_{j=1}^{\dim E(\mu_i)} \mathbf{X}_{ij}.$$

For each $i \geq 1$, \mathbf{X}_i is invariant under the operator $\mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}})\Delta + \mathbf{G}_{\mathbf{u}}(\bar{\mathbf{u}})$. Then problem (11) has a non trivial solution of the form $\Psi = \mathbf{c}\phi \exp(\lambda t)$ if and only if (λ, \mathbf{c}) is an eigenpair for the matrix $-\mu_i \mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}) + \mathbf{G}_{\mathbf{u}}(\bar{\mathbf{u}})$, where \mathbf{c} is a constant vector. Then the equilibrium $\bar{\mathbf{u}}$ is unstable if at least one eigenvalue λ has a positive real part for some μ_i .

For $\bar{\mathbf{u}} = \mathbf{u}^{(9)}$, $\mathbf{G}_{\mathbf{u}}(\bar{\mathbf{u}}) = \mathbf{J}|_{\mathbf{u}^{(9)}}$ in (8) and the characteristic polynomial of $-\mu_i \mathbf{K}_{\mathbf{u}}(\bar{\mathbf{u}}) + \mathbf{G}_{\mathbf{u}}(\bar{\mathbf{u}})$ for each μ_i is given by

$$(12) \quad \rho_i(\lambda) = \lambda^3 + B_{2i}\lambda^2 + B_{1i}\lambda + B_{0i},$$

where

$$(13) \quad B_{2i} = -g_{22} - g_{11} + (k_{11} + k_{12} u_2^+ + k_{21} u_1^+ + k_{32} u_2^+ + k_{33} + k_{22} + k_{23} u_3^+) \mu_i$$

$$(14) \quad B_{1i} = -J_{21} J_{12} + J_{11} J_{22} - J_{23} J_{32} + (-J_{11} k_{32} u_2^+ + k_{23} u_2^+ J_{32} - k_{12} u_2^+ J_{22} + k_{21} u_2^+ J_{12} - J_{22} k_{32} u_2^+ - J_{11} k_{21} u_1^+ + J_{23} k_{32} u_3^+ - k_{11} J_{22} - J_{22} k_{33} + J_{21} k_{12} u_1^+ - J_{11} k_{23} u_3^+ - J_{11} k_{33} - J_{11} k_{22}) \mu_i + (k_{11} k_{23} u_3^+ + k_{21} u_1^+ k_{33} + k_{21} u_1^+ k_{32} u_2^+ + k_{12} u_2^+ k_{23} u_3^+ + k_{12} u_2^{+2} k_{32} + k_{12} u_2^+ k_{22} + k_{11} k_{21} u_1^+ + k_{22} k_{33} + k_{12} u_2^+ k_{33} + k_{11} k_{32} u_2^+ + k_{11} k_{22} + k_{22} k_{32} u_2^+ + k_{23} u_3^+ k_{33} + k_{11} k_{33}) \mu_i^2$$

$$(15) \quad B_{0i} = J_{11} J_{23} J_{32} + (J_{11} J_{22} k_{33} - J_{21} J_{12} k_{32} u_2^+ - k_{11} J_{23} J_{32} + J_{11} J_{22} k_{32} u_2^+ - J_{21} J_{12} k_{33} - J_{11} J_{23} k_{32} u_3^+ - J_{11} k_{23} u_2^+ J_{32} - k_{12} u_2^+ J_{23} J_{32}) \mu_i + (-J_{11} k_{22} k_{33} + J_{21} k_{12} u_1^+ k_{33} - J_{11} k_{22} k_{32} u_2^+ + k_{11} J_{23} k_{32} u_3^+ + k_{21} u_2^{+2} J_{12} k_{32} - k_{11} J_{22} k_{33} - k_{12} u_2^{+2} J_{22} k_{32} + k_{12} u_2^{+2} k_{23} J_{32} - J_{11} k_{21} u_1^+ k_{33} + J_{21} k_{12} u_1^+ k_{32} u_2^+ - J_{11} k_{23} u_3^+ k_{33} - k_{11} J_{22} k_{32} u_2^+ + k_{11} k_{23} u_2^+ J_{32} + k_{21} u_2^+ J_{12} k_{33} + k_{12} u_2^+ J_{23} k_{32} u_3^+ - k_{12} u_2^+ J_{22} k_{33} - J_{11} k_{21} u_1^+ k_{32} u_2^+) \mu_i^2 + (k_{11} k_{22} k_{33} + k_{11} k_{23} u_3^+ k_{33} + k_{12} u_2^+ k_{22} k_{33} + k_{11} k_{21} u_1^+ k_{32} u_2^+ + k_{12} u_2^+ k_{23} u_3^+ k_{33} + k_{12} u_2^{+2} k_{22} k_{32} + k_{11} k_{21} u_1^+ k_{33} + k_{11} k_{22} k_{32} u_2^+) \mu_i^3$$

Let $\lambda_{1i}, \lambda_{2i}, \lambda_{3i}$ be the three roots of (12)

$$\rho_i(\lambda) = \lambda^3 + B_{2i}\lambda^2 + B_{1i}\lambda + B_{0i} = 0.$$

In order to obtain the stability of $\bar{\mathbf{u}}$, we need to show that there exists a positive constant δ such that

$$(16) \quad \text{Re}\{\lambda_{1i}\}, \text{Re}\{\lambda_{2i}\}, \text{Re}\{\lambda_{3i}\} < -\delta \text{ for all } i \geq 1.$$

Next we use the Routh-Hurwitz criterion to study the stability [9]. For a third-order polynomial to be linearly stable, i.e. to have all its roots with negative real parts, it is necessary and sufficient that

$$(17) \quad B_{ji} > 0, \text{ and } B_{1i}B_{2i} > B_{0i}, \text{ for } j = 1, 2, 3 \text{ and all } i.$$

The aim of the following theorem is to prove that the diffusion alone (without cross-diffusion, i.e. $k_{21} = k_{12} = k_{32} = k_{23} = 0$) can not drive instability for this food chain model, i.e., Turing instability does not occur in the three species food chain model without cross-diffusion.

Theorem 3.1. *Suppose that (7) holds and $k_{21} = k_{12} = k_{32} = k_{23} = 0$. Then the positive coexistence equilibrium solution $\bar{\mathbf{u}} = \mathbf{u}^{(9)}$ of (10) is locally asymptotically stable.*

Proof. Substituting $k_{21} = k_{12} = k_{32} = k_{23} = 0$ into B_{2i} , B_{1i} and B_{0i} , we have

$$\begin{aligned} B_{2i} &= -J_{22} - J_{11} + (k_{11} + k_{33} + k_{22}) \mu_i \\ B_{1i} &= -J_{21} J_{12} + J_{11} J_{22} - J_{23} J_{32} + (-J_{11} k_{33} - J_{22} k_{33} - k_{11} J_{22} - J_{11} k_{22}) \mu_i \\ &\quad + (k_{11} k_{33} + k_{22} k_{33} + k_{11} k_{22}) \mu_i^2 \\ B_{0i} &= J_{11} J_{23} J_{32} + (-J_{21} J_{12} k_{33} - k_{11} J_{23} J_{32} + J_{11} J_{22} k_{33}) \mu_i \\ &\quad + (-k_{11} J_{22} k_{33} - J_{11} k_{22} k_{33}) \mu_i^2 + k_{11} k_{22} k_{33} \mu_i^3 \end{aligned}$$

By simply applying the sign of J_{ij} in (9) and $k_{ij} > 0$, we have $B_{2i} > 0$, $B_{1i} > 0$, $B_{0i} > 0$. A direct calculation shows that

$$\begin{aligned} B_{2i} B_{1i} - B_{0i} &= (-J_{22} - J_{11}) (-J_{21} J_{12} + J_{11} J_{22} - J_{23} J_{32}) - J_{11} J_{23} J_{32} \\ &\quad + ((-J_{22} - J_{11}) (-J_{11} k_{33} - J_{22} k_{33} - k_{11} J_{22} - J_{11} k_{22}) + (k_{11} + k_{33} + k_{22}) (-J_{21} J_{12} \\ &\quad + J_{11} J_{22} - J_{23} J_{32}) + J_{21} J_{12} k_{33} + k_{11} J_{23} J_{32} - J_{11} J_{22} k_{33}) \mu_i + ((-J_{22} - J_{11}) (k_{11} k_{33} \\ &\quad + k_{22} k_{33} + k_{11} k_{22}) + (k_{11} + k_{33} + k_{22}) (-J_{11} k_{33} - J_{22} k_{33} - k_{11} J_{22} - J_{11} k_{22}) \\ &\quad + k_{11} J_{22} k_{33} + J_{11} k_{22} k_{33}) \mu_i^2 \\ &\quad + ((k_{11} + k_{33} + k_{22}) (k_{11} k_{33} + k_{22} k_{33} + k_{11} k_{22}) - k_{11} k_{22} k_{33}) \mu_i^3 > 0 \end{aligned}$$

for all $i \geq 1$. It follows from Routh-Hurwitz criterion (17) that, all the three roots λ_{1i} , λ_{2i} , λ_{3i} of $\rho_i(\lambda) = 0$ have negative real parts for each $i \geq 1$.

Let $\lambda = \mu_i \xi$, then

$$\rho_i(\lambda) = \mu_i^3 \xi^3 + B_{2i} \mu_i^2 \xi^2 + B_{1i} \mu_i \xi + B_{0i} \equiv \bar{\rho}_i(\xi).$$

Since $\mu_i \rightarrow \infty$ as $i \rightarrow \infty$, we have

$$\bar{\rho}(\xi) = \lim_{i \rightarrow \infty} \frac{\bar{\rho}_i(\xi)}{\mu_i^3} = \xi^3 + (k_{33} + k_{22} + k_{11}) \xi^2 + (k_{22} k_{33} + k_{11} k_{33} + k_{11} k_{22}) \xi + k_{11} k_{22} k_{33}.$$

Applying the Routh-Hurwitz criterion it follows that the three roots ξ_1, ξ_2, ξ_3 of $\bar{\rho}(\xi) = 0$ all have negative real parts. Thus, there exists a positive constant $\bar{\delta}$ such that $Re\{\xi_1\}, Re\{\xi_2\}, Re\{\xi_3\} \leq -2\bar{\delta}$. By continuity, we see that there exists $i_0 \geq 1$ such that $\mu_{i_0} > 1$ and the three roots $\xi_{i1}, \xi_{i2}, \xi_{i3}$ of $\bar{\rho}_i(\xi) = 0$ satisfy $Re\{\xi_{i1}\}, Re\{\xi_{i2}\}, Re\{\xi_{i3}\} \leq -\bar{\delta}$ for any $i \geq i_0$. Then $Re\{\lambda_{i1}\}, Re\{\lambda_{i2}\}, Re\{\lambda_{i3}\} \leq -\mu_i \bar{\delta} \leq -\mu_{i_0} \bar{\delta} \leq -\bar{\delta}$ for any $i \geq i_0$. Let $-\bar{\delta} = \max_{1 \leq i \leq i_0} \{Re\{\lambda_{i1}\}, Re\{\lambda_{i2}\}, Re\{\lambda_{i3}\}\}$ and $\delta = \min\{\bar{\delta}, \bar{\delta}\}$. Then

$$Re\{\lambda_{1i}\}, Re\{\lambda_{2i}\}, Re\{\lambda_{3i}\} < -\delta \text{ for all } i \geq 1.$$

Consequently the positive equilibrium $\mathbf{u}^{(9)}$ is locally asymptotically stable. □

Note that $B_{2i} > 0$ in (13), $B_{1i} > 0$ in (14), $B_{0i} > 0$ in (15), and $B_{2i} B_{1i} - B_{0i} > 0$ if $k_{21} = k_{32} = 0$ since the possible negative terms all involve either k_{21} or k_{32} . By the same arguments as in Theorem 3.1, we have

Theorem 3.2. *Suppose that (7) holds and $k_{21} = k_{32} = 0$. Then the positive equilibrium $\bar{\mathbf{u}} = \mathbf{u}^{(9)}$ of (10) is locally asymptotically stable.*

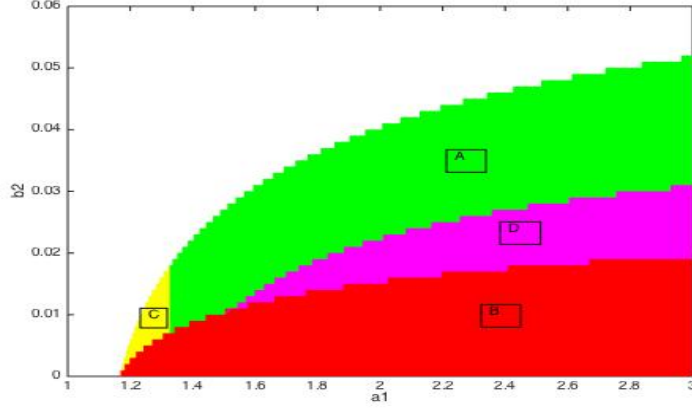


Figure 3: The Turing instability conditions are calculated in terms of the reproduction rate a_1 and intra-species competition b_2 among middle predators. All other parameters are given in (21) and (22) in section 5. The non-negative equilibrium $\mathbf{u}^{(9)}$ exists in all four colored regions (A, B, C, and D). The non-negative equilibrium $\mathbf{u}^{(9)}$ is linear stable in the top three regions (green A, yellow C, and magenta D) where conditions (7) are satisfied. Turing instability conditions (7) and (18) are satisfied in the yellow region C. Turing instability conditions (7) and (19) are satisfied only in the magenta region D.

4 Turing Instability driven by cross-diffusion

The Turing instability [14] refers to “diffusion-driven instability, ”i.e., the stability of the positive equilibrium $\bar{\mathbf{u}} = \mathbf{u}^{(9)}$ changing from stable, for the ODE dynamics (1), to unstable, for the PDE dynamics (10). From Theorem 3.1 we see that only adding self-crossing diffusion to the ODE system (1), the positive equilibrium is also locally stable, which means that Turing instability has not happened. From Theorem 3.2, crossing diffusion between middle specialist predator and prey ($k_{12} > 0, k_{23} > 0$) can not drive instability either. Here we are going to give sufficient conditions on cross-diffusion which drives the instability. k_{21} and k_{32} can be chosen as variation parameters, whereas the other constants are fixed.

Theorem 4.1. (1) Suppose that the condition (7) and the following inequality are satisfied

$$(18) \quad b_1(u_1^+ + D_0)^2 < w_0 u_2^+ \frac{(2u_1^+ + D_0)}{u_1^+}.$$

Let k_{21} be the variation parameter. Then there exists a positive constant δ_{21} such that when $k_{21} > \delta_{21}$, the equilibrium $\mathbf{u}(x, t) = \mathbf{u}^{(9)}$ is linearly unstable for some domain Ω .

(2) Suppose that the condition (7) and the following inequality are satisfied

$$(19) \quad (J_{11} J_{22} - J_{21} J_{12})u_2^+ < J_{11} J_{23} u_3^+$$

Let k_{32} be the variation parameter. Then there exists a positive constant δ_{32} such that when $k_{32} > \delta_{32}$, the equilibrium $\mathbf{u}(x, t) = \mathbf{u}^{(9)}$ is linearly unstable for some domain Ω .

Remark 4.2. (A) k_{21} and k_{32} can be chosen as variation parameters because the number of sign of change for the polynomial (20) could be bigger than one for large values of k_{21} or k_{32} . By Descartes' Rule, the polynomial (20) could have positive roots which lead to linear instability.

(B) The condition (7) is compatible with the condition (18). The condition (7) is also compatible with the condition (19). We refer those conditions satisfying either (7) and (18) or (7) and (19) as the *Turing instability conditions*. We will use examples to illustrate the existence of parameters which satisfy the Turing instability conditions.

(C) In fact, if the parameters are given in (21) and (22) in section 5 except a_1 and b_2 , with the assumption of the condition (7), the region of a_1, b_2 satisfying the Turing instability conditions (7) and (18) is shown in the region C in Figure 3.

Proof. We will use an argument similar to those in paper [22] to prove the existence of Turing instability. By the assumption (7) and the sign of J_{ij} in (9), we have $B_{2i} > 0$ and $B_{1i} > 0$. By Routh-Hurwitz criteria (17), the stable equilibrium \mathbf{u}^9 will be destabilized by diffusion if $B_{0i} < 0$ for some i .

Denote $A(\mu) = -\mu \mathbf{K}_u(\bar{\mathbf{u}}) + \mathbf{G}_u(\bar{\mathbf{u}})$. We have $B_{0i} = -\det(A(\mu_i))$. By the direct computations we have

$$(20) \quad \det(A(\mu)) = -(C_3 \mu^3 + C_2 \mu^2 + C_1 \mu + C_0),$$

where

$$C_0 = J_{11} J_{23} J_{32};$$

$$C_1 = (J_{11} J_{22} u_2^+ - J_{21} J_{12} u_2^+ - J_{11} J_{23} u_3^+) k_{32} + J_{11} J_{22} k_{33} - k_{11} J_{23} J_{32} - J_{21} J_{12} k_{33} - J_{11} k_{23} u_2^+ J_{32} - k_{12} u_2^+ J_{23} J_{32};$$

$$C_2 = ((J_{12} u_2^+ - J_{11} u_1^+) k_{32} u_2^+ + (J_{12} u_2^+ - J_{11} u_1^+) k_{33}) k_{21} - J_{11} k_{22} k_{32} u_2^+ + k_{11} J_{23} k_{32} u_3^+ - k_{12} u_2^{+2} J_{22} k_{32} + J_{21} k_{12} u_1^+ k_{32} u_2^+ - k_{11} J_{22} k_{32} u_2^+ - J_{11} k_{22} k_{33} + J_{21} k_{12} u_1^+ k_{33} - k_{11} J_{22} k_{33} + k_{12} u_2^{+2} k_{23} J_{32} - J_{11} k_{23} u_3^+ k_{33} + k_{11} k_{23} u_2^+ J_{32} + k_{12} u_2^+ J_{23} k_{32} u_3^+ - k_{12} u_2^+ J_{22} k_{33};$$

$$C_3 = k_{11} k_{22} k_{33} + k_{11} k_{23} u_3^+ k_{33} + k_{12} u_2^+ k_{22} k_{33} + k_{11} k_{21} u_1^+ k_{32} u_2^+ + k_{12} u_2^+ k_{23} u_3^+ k_{33}$$

$$+k_{12} u_2^{+2} k_{22} k_{32} + k_{11} k_{21} u_1^+ k_{33} + k_{11} k_{22} k_{32} u_2^+.$$

By using the assumption (7) and the sign of J_{ij} in (9), it is easy to know that $C_0 > 0$ and $C_3 > 0$.

CASE 1: k_{21} is the variation parameter.

Because each root of the algebraic equation (20) is a continuous function of the variation parameter k_{21} . It is easy to prove that equation (20) has three real roots $\mu_1^{(i)} = \mu_1^{(i)}(k_{21})$, $i = 1, 2, 3$ when k_{21} goes to infinity and they are $\lim_{k_{21} \rightarrow \infty} \mu_1^{(1)}(k_{21}) = \lim_{k_{21} \rightarrow \infty} \mu_1^{(2)}(k_{21}) = 0$ and

$$\lim_{k_{21} \rightarrow \infty} \mu_1^{(3)}(k_{21}) = \frac{J_{11}u_1^+ - J_{12}u_2^+}{k_{11}u_1^+}.$$

The inequality (18) implies that $J_{11}u_1^+ - J_{12}u_2^+ > 0$. Therefore, the root $\lim_{k_{21} \rightarrow \infty} \mu_1^{(3)}(k_{21})$ is positive. By continuation, there exists a positive constant δ_{21} such that when $k_{21} > \delta_{21}$, $C_2 < 0$ and $\det(A(\mu)) = 0$ has three real roots. Because $C_3 > 0$ and $C_0 > 0$, the number of sign changes of (20) is exactly two. Therefore by Descartes' rule, the three real roots have the following properties:

- (i) $-\infty < \mu_1^{(1)} < 0 < \mu_1^{(2)} < \mu_1^{(3)} < \infty$;
- (ii) $\det(A(\mu)) > 0$ if $\mu \in (-\infty, \mu_1^{(1)}) \cup (\mu_1^{(2)}, \mu_1^{(3)})$;
- (iii) $\det(A(\mu)) < 0$ if $\mu \in (\mu_1^{(1)}, \mu_1^{(2)}) \cup (\mu_1^{(3)}, \infty)$.

If $\mu_i \in (\mu_1^{(2)}, \mu_1^{(3)})$ for some i , then $\det(A(\mu_i)) > 0$ by (ii), and consequently $B_{0i} = -\det(A(\mu_i)) < 0$. The number of sign changes of the characteristic polynomial (12) $\rho(\lambda) = \lambda^3 + B_{2i}\lambda^2 + B_{1i}\lambda + B_{0i}$ is either one or three. By Descartes' rule, the characteristic polynomial (12) has at least one positive root. Hence, the equilibrium $\mathbf{u}^{(9)}$ of (10) is linearly unstable for any domain Ω on which at least one eigenvalue μ_i of $-\Delta$ is in the interval $(\mu_1^{(2)}, \mu_1^{(3)})$.

CASE 2: k_{32} is the variation parameter.

Note that the inequality (19) implies that $C_1 < 0$ for large k_{32} . Because each root of the algebraic equation (20) is a continuous function of the variation parameter k_{32} . It is easy to prove that equation (20) has three real roots $\mu_2^{(i)} = \mu_2^{(i)}(k_{32})$, $i = 1, 2, 3$ when k_{32} goes to infinity and they are $\lim_{k_{32} \rightarrow \infty} \mu_2^{(1)}(k_{32}) < 0$ and $\lim_{k_{32} \rightarrow \infty} \mu_2^{(2)}(k_{32}) = 0$ and $\lim_{k_{32} \rightarrow \infty} \mu_2^{(3)}(k_{32}) > 0$. This is done by applying Descartes' Rule to the limit case when $k_{32} \rightarrow \infty$.

By continuation, there exists a positive constant δ_{32} such that when $k_{32} > \delta_{32}$, $C_1 < 0$ and $\det(A(\mu)) = 0$ has three real roots. Because $C_3 > 0$ and $C_0 > 0$, the number of sign changes

of (20) is exactly two. Therefore by Descartes' rule, the three real roots have the following properties:

- (i) $-\infty < \mu_2^{(1)} < 0 < \mu_2^{(2)} < \mu_2^{(3)} < \infty$;
- (ii) $\det(A(\mu)) > 0$ if $\mu \in (-\infty, \mu_2^{(1)}) \cup (\mu_2^{(2)}, \mu_2^{(3)})$;
- (iii) $\det(A(\mu)) < 0$ if $\mu \in (\mu_2^{(1)}, \mu_2^{(2)}) \cup (\mu_2^{(3)}, \infty)$.

If $\mu_i \in (\mu_2^{(2)}, \mu_2^{(3)})$ for some i , then $\det(A(\mu_i)) > 0$, and consequently $B_{0i} = -\det(A(\mu_i)) < 0$ and $\rho_i(0) = B_{0i} < 0$. By similar argument as in case 1, the characteristic polynomial (12) has at least one positive root. Hence, the equilibrium $\mathbf{u}^{(9)}$ of (10) is linearly unstable for any domain Ω on which at least one eigenvalue μ_i of $-\Delta$ is in the interval $(\mu_2^{(2)}, \mu_2^{(3)})$.

□

Remark 4.3. Biological interpretation: In our three-species food chain model, the third species (the generalist predator) preys on the second species (the specialist predator) and simultaneously the second one preys on the first one (the prey). Biologically, a cross diffusion coefficient k_{12} in the system (2) means that the prey u_1 intends to keep away from its predators u_2 . The cross diffusion k_{21} represents the tendency of the predator u_2 to chase its prey. Positive cross diffusion coefficient implies that one species takes advantage of the strategies that they tends to move in the direction of lower concentration of another species. However, negative cross diffusion coefficient means that one species would take advantage of moving in the direction of higher concentration of another species. Similar biological meaning is applied to the cross diffusion coefficients k_{23} and k_{32} . In this paper, we only study the case when the species move in the direction of lower concentration of another species, i.e. $k_{ij} \geq 0$.

Predator u_2 can be treated as a prey with respect to the predator u_3 . When the positive equilibrium solution $\mathbf{u}^{(9)}$ satisfies the condition (7), the strategies (k_{12} or k_{23}) that the prey u_1 and the prey u_2 used are not able to affect the stability of the equilibrium (long term population distribution), i.e. k_{12} or k_{23} can not destabilize the stability of the equilibrium. Keeping away from predators can not break the stability of the equilibrium. However, the changing of the strategies of predators chasing prey may affect the stability of the equilibrium. We discover that the positive steady state of the three species food chain can be broken by the reaction diffusion among two species on the chain.

When the positive equilibrium solution $\mathbf{u}^{(9)}$ satisfies the conditions (7) and (18), the cross diffusion k_{21} can drive the stable equilibrium away. In this case, the first species (the prey) are assumed to reproduce exponentially unless subject to intra-species competition and predation. The exponential growth is modeled by the term $a_1 u_1$ in the system (2). The level of intra-species competition among the first species is proportional to its population size by the term $b_1 u_1$. The functional response of the first species (the prey) to the specialist predator is the Holling type II functional response which takes the environment protection

into consideration. At the positive equilibrium solutions, if the population of the second species u_2^+ is bounded by a function of u_1^+ , i.e. $b_1(u_1^+ + D_0)^2 \frac{u_1^+}{(2u_1^+ + D_0)} < w_0 u_2^+ < b_1(u_1^+ + D_0)^2$, the large cross-diffusion of the second species due to the first species (k_{21}) can break the stability. In other words, if the predator (second species) has a dominate effect on the decreasing of the prey (first species) such as the maximum per capita reduction rate w_0 is appropriate, then the predator (the second species) with large cross-diffusion can destabilize the stable equilibrium.

5 Numerical Results

In this section, we use numerical simulations to study the long-time behavior of the solutions to our three species food chain model.

5.1 Diversity of Solutions for ODE system (1) without Competition among the Specialist Predators ($b_2 = 0$)

The ODE system (1) was studied by Upadhyay, Iyengar and Rai [17] in the case $b_2 = 0$. It was shown that the system has a very diversity of dynamical behaviors. Chaotic solutions occur in various ranges of the parameter space. In addition to chaotic solutions, there are states of extinction for certain species, stable equilibrium solutions, and limit cycles. We want to illustrate how the long time behavior of the solution can vary from one state to another state when the growth rate of prey changes. A bifurcation curve is described in table 1 on a_1 .

In this subsection, the numerical simulation is carried out by using ODE45 function in MATLAB (R2014b). Since there are 13 parameters, the search for the diversity of solutions was found by fixing some common parameters and varying the growth rate a_1 of the prey. In addition to $b_2 = 0$, the other common parametric values for this subsection are

$$(21) \quad a_2 = 1; a_3 = 0.03; b_1 = 0.05; w_0 = 1; w_1 = 2; w_2 = 0.55; w_3 = 1;$$

$$(22) \quad D_0 = 10; D_1 = 10; D_2 = 10; D_3 = 20.$$

Then there are at most four nonnegative equilibriums which depends on a_1 . They are

$$\mathbf{u}^{(1)} = (0, 0, 0); \mathbf{u}^{(2)} = (20a_1, 0, 0) \text{ for } a_1 > 0; \mathbf{u}^{(7)} = (10, 20a_1 - 10, 0) \text{ for } a_1 > 0.5;$$

and when $a_1 \geq \frac{7}{6}$

$$\mathbf{u}^{(9)} = \left(10a_1 - 5 + 10\sqrt{a_1^2 + a_1 - \frac{29}{12}}, \frac{40}{3}, -\frac{1400}{33} + \frac{2800 \left(10a_1 - 5 + 10\sqrt{a_1^2 + a_1 - \frac{29}{12}} \right)}{33 \left(10a_1 + 5 + 10\sqrt{a_1^2 + a_1 - \frac{29}{12}} \right)} \right).$$

In table 1, we list the detailed information about the nonnegative equilibriums and the corresponding parameter spaces. A typical solution is computed for a specific growth rate of the prey. All solutions start the same initial point $\mathbf{u} = (15, 13, 9)$. We use ODE45 with error tolerance less than 10^{-4} to solve the initial value problem of ODE system (1). The time interval is chosen appropriately for the better display of the solution behaviors. We put them into the following cases and they are illustrated in table 1.

- $(0, 0, 0)$ is always a trivial equilibrium but no solution will converge to it when the growth rate a_1 of prey is great than zero. Not all species will extinct.
- When $0 < a_1 \leq \frac{1}{2}$, solutions starting from any positive initial condition converge to the nonnegative equilibrium $\mathbf{u}^{(2)}$. For $a_1 = 0.45$, $\mathbf{u} \rightarrow \mathbf{u}^{(2)} = (9, 0, 0)$. Only prey survives after a long time.
- When $\frac{1}{2} < a_1 \leq \frac{7}{6}$, solutions of ODE system converge to the nonnegative equilibrium $\mathbf{u}^{(7)}$. For $a_1 = 1$, $\mathbf{u} \rightarrow \mathbf{u}^{(7)} = (10, 10, 0)$. Only the top generalist predator extinct.
- When $\frac{7}{6} < a_1 \leq 1.492$, solutions of ODE system converge to the nonnegative equilibrium $\mathbf{u}^{(9)}$ which is linearly stable. For $a_1 = 1.3$, $\mathbf{u} \rightarrow \mathbf{u}^{(9)} = (15.5719, 13.3333, 9.2439)$. Three species coexist and the population is stable after a long time. But when a_1 is near 1.492, it may takes a long time to approach the equilibrium solution.
- When $1.492 < a_1$, the solutions of ODE system experience a fluctuation. Limit cycles and chaotic solutions can occur. Numerically, limit cycles happen clearly for $1.5 \leq a_1 < 1.6$. Chaotic solutions occur clearly for $1.6 < a_1 < 2.1$. Then limit cycles come back again. Some blow-up solution can happen when a_1 is large.

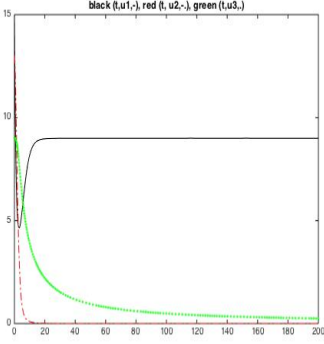
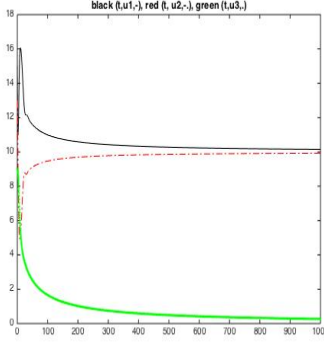
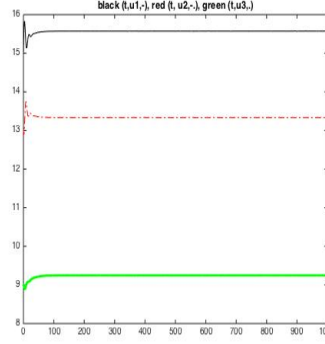
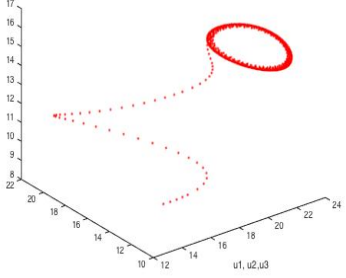
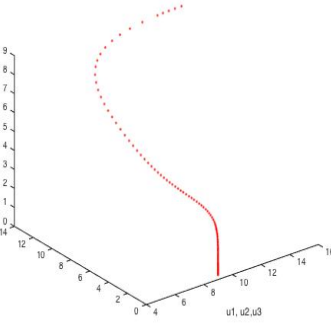
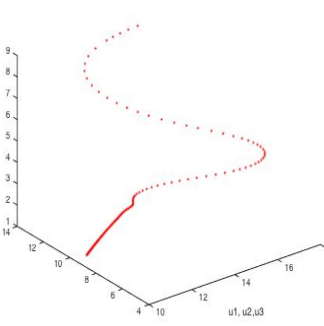
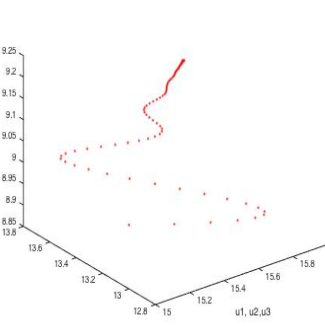
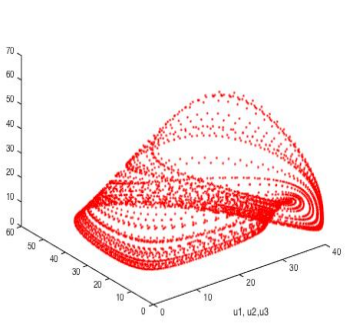
$b_2 = 0$			
$0 < a_1 \leq \frac{1}{2}$	$\frac{1}{2} < a_1 \leq \frac{7}{6}$	$\frac{7}{6} < a_1 \leq 1.492$	$1.492 < a_1$
$\mathbf{u}^{(2)} = (20a_1, 0, 0)$	$\mathbf{u}^{(2)} = (20a_1, 0, 0),$ $\mathbf{u}^{(7)} = (10, 20a_1 - 10, 0)$	$\mathbf{u}^{(2)} = (20a_1, 0, 0),$ $\mathbf{u}^{(7)} = (10, 20a_1 - 10, 0)$ $\mathbf{u}^{(9)} = (u_1^+, \frac{40}{3}, -\frac{1400}{33} + \frac{2800u_1^+}{33(u_1^+ + 10)})$	$\mathbf{u}^{(2)} = (20a_1, 0, 0),$ $\mathbf{u}^{(7)} = (10, 20a_1 - 10, 0)$ $\mathbf{u}^{(9)} = (u_1^+, \frac{40}{3}, -\frac{1400}{33} + \frac{2800u_1^+}{33(u_1^+ + 10)})$
Converges to $\mathbf{u}^{(2)}$	Converges to $\mathbf{u}^{(7)}$	Converges to $\mathbf{u}^{(9)}$	Chaos, limit cycle and others
Predators extinct	Top generalist predators extinct	Stable coexistence	chaotic or periodic fluctuation
$a_1 = 0.45, \mathbf{u} \rightarrow (9, 0, 0)$	$a_1 = 1, \mathbf{u} \rightarrow (10, 10, 0)$	$a_1 = 1.3, \mathbf{u} \rightarrow (15.57, 13.33, 9.24)$	$a_1 = 1.5$ limit cycle, $a_1 = 2$ chaos.
			
			

Table 1: The values of other parameters are given in (21) and (22). $u_1^+ = 10a_1 - 5 + 10\sqrt{a_1^2 + a_1 - \frac{29}{12}}$ in $\mathbf{u}^{(9)}$. Solutions converge to an equilibrium, a limit cycle or they experience chaotic. Graphs are either solution curves over time or phase portrait.

5.2 Affect of the Intra-species Competition among the Specialist Predators ($b_2 \neq 0$)

In this subsection, we are going to illustrate numerically how the intra-species competition among the specialist predators will change the long time behavior of a solution. We consider three cases: (1) the stable coexistence for $a_1 = 1.3$; (2) the limit cycle for $a_1 = 1.5$; (3) the chaos for $a_1 = 2$. By the continuation of solutions on parameters, when b_2 is very small, the behavior of solution will similar to those solutions in table (1) for $b_2 = 0$. The numerical values of the parameters are taken from (21) and (22). To have a better view of simulation, the initial conditions are chosen appropriately (close the ending point). The numerical graphs are illustrated in table 2 for the following cases.

- When $a_1 = 1.3$, the solutions converge to the stable equilibrium $\mathbf{u}^{(9)}$ for $0 \leq b_2 < 0.016$. The solutions converge to equilibrium $\mathbf{u}^{(7)}$ for $b_2 > 0.017$. In particular, when $b_2 = 0.01$, $\mathbf{u}^{(9)} = [15.5719, 13.3333, 3.5873]$; when $b_2 = 0.2$, $\mathbf{u}^{(7)} = [24.7782, 2.1246, 0]$; when $b_2 = 2$, $\mathbf{u}^{(7)} = [25.8767, 0.2213, 0]$. As the intra-species competition among specialist predator b_2 increase, the stability of equilibrium changes and the population density of specialist predator is decreasing.
- When $a_1 = 1.5$, the equilibrium $\mathbf{u}^{(9)}$ is unstable and limit cycle occurs for $b_2 = 0$. When b_2 increase from 0 to a small positive number, the unstable equilibrium $\mathbf{u}^{(9)}$ becomes to a stable equilibrium. For example, when $b_2 = 0.01$, the equilibrium $\mathbf{u}^{(9)} = [21.5470, 13.3333, 9.8718]$ is stable. While the intra-species competition among specialist predator b_2 keep increase, the positive equilibrium $\mathbf{u}^{(9)}$ will disappear and solutions will converge to $\mathbf{u}^{(7)}$. For example when $b_2 = 0.1$, solutions will converge to $\mathbf{u}^{(7)} = [27.5110, 4.6682, 0]$.
- When $a_1 = 2$, the equilibrium $\mathbf{u}^{(9)}$ is unstable and chaos occurs for $b_2 = 0$. When b_2 increase from 0 to a small positive number, chaos changes to limit cycle while the equilibrium $\mathbf{u}^{(9)}$ is still unstable. For example, when $b_2 = 0.01$, the equilibrium $\mathbf{u}^{(9)} = [33.9297, 13.3333, 17.4531]$ is still unstable. However, when b_2 increase a little bit, the equilibrium $\mathbf{u}^{(9)}$ becomes stable and solutions will converge to it. For example the equilibrium $\mathbf{u}^{(9)} = [33.9297, 13.3333, 6.1399]$ becomes stable and solutions will converge to it.

In summary, the intra-species competition among specialist predator b_2 can stabilize the system by making the unstable equilibrium $\mathbf{u}^{(9)}$ stable. With the help of intra-species competition, large fluctuations of the population distribution such as limit cycle or chaos can be reduced and they can become to stable steady states.

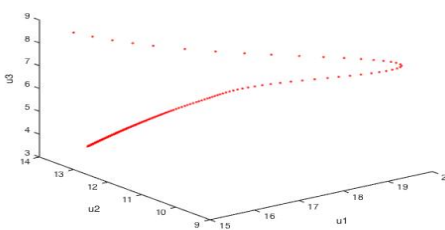
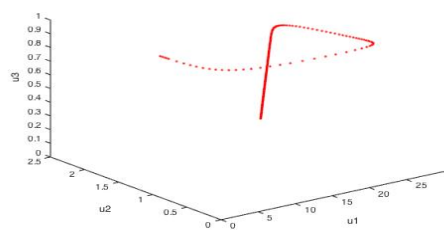
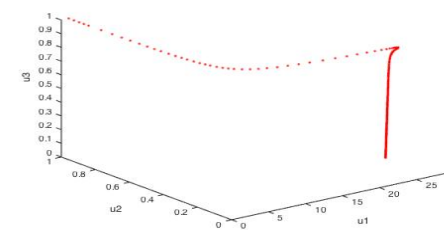
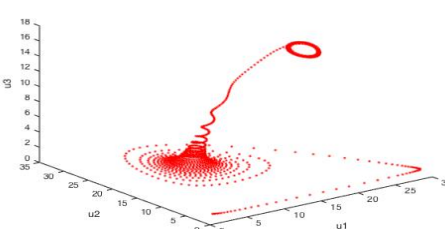
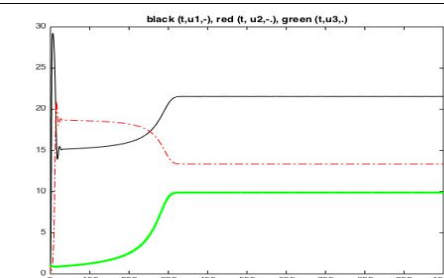
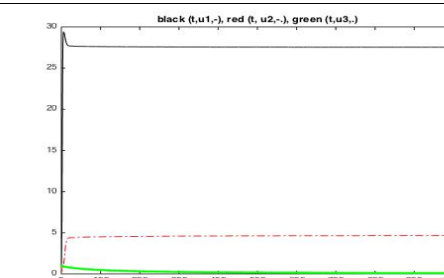
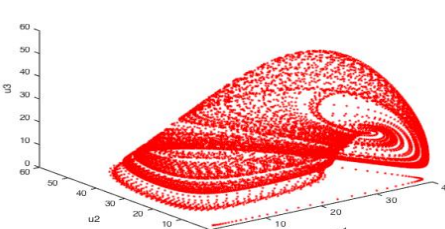
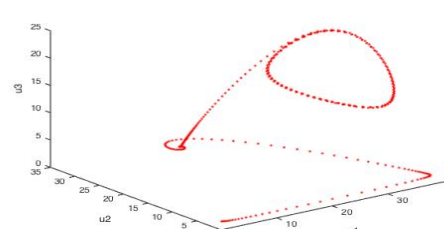
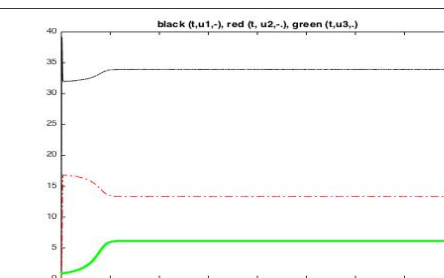
$a_1 = 1.3$		
$b_2 = 0.01$; Converges to $\mathbf{u}^{(9)}$	$b_2 = 0.2$; Converges to $\mathbf{u}^{(7)}$	$b_2 = 2$; Converges to $\mathbf{u}^{(7)}$
		
$a_1 = 1.5$		
$b_2 = 0.0001$; Converges to a limit cycle	$b_2 = 0.01$; Converges to $\mathbf{u}^{(9)}$	$b_2 = 0.1$; Converges to $\mathbf{u}^{(7)}$
		
$a_1 = 3$		
$b_2 = 0.001$; Chaos	$b_2 = 0.01$; Converges to a limit cycle	$b_2 = 0.4$; Converges to $\mathbf{u}^{(9)}$
		

Table 2: The values of other parameters are given in (21) and (22). Graphs are either solution curves over time or phase portrait.

5.3 Turing instability induced by cross diffusion and Turing patterns

In the above subsections, we fixed the parameters in (21) and (22) and the reproduce rate a_1 and intra-species competition b_2 can induce the stable coexistence equilibrium, partial extinction, limit cycle, and chaos in the ODE system. In this subsection, using numerical methods, we illustrate that the cross-diffusion induce spatial patterns.

Throughout this subsection we assume the region of PDE system (2) is a fixed rectangular domain $\Omega = [0, L] \times [0, L] \subset \mathbf{R}^2$. We modify the numerical method in [15] to solve the PDE system (2). We found the numerical solution of the PDE system on a grid with $100L \times 100L$ nodes by a simple standard Euler method with a time step of Δt .

We discretize the Laplacian in the grid with lattice sites denoted by (i, j) . The form is

$$(23) \quad \Delta w|_{(i,j)} = \frac{1}{s^2} (a_l(i, j)w(i-1, j) + a_r(i, j)w(i+1, j) + a_d(i, j)w(i, j-1) + a_u(i, j)w(i, j+1) - 4w(i, j)),$$

where s is the lattice constant and the matrix elements of a_l, a_r, a_d, a_u are unity except at the boundary. When (i, j) is at the left boundary, that is $i = 0$, in order to have zero-flux of reactants in the left boundary, we define

$$a_l(i, j)w(i-1, j) \equiv w(i+1, j).$$

Similarly we define $a_r(i, j), a_d(i, j), a_u(i, j)$ such that the boundary is no flux. Notice that approximation formula for the Laplacian operator (23) can be used to approximate Laplacian u_1, u_2 , and $k_{12}u_1u_2$ etc.

Parshad, Kumari, Kasimov, and Abderrahmane [20] conduct numerical simulations to explore the spatiotemporal dynamics in two dimensional spatial domain. Some beautiful Turing patterns such as spots, or a mix of spot and labyrinth are numerically simulated. To compare our results with theirs, some parameters we used here are same as theirs. We choose a rectangle domain $[3.14, 3.14]$ with a grid of $\Delta x = \Delta y = 0.01$ and a time step of $\Delta t = 0.001$. The common parameters are taken as

$$(24) \quad \begin{aligned} a_1 &= 2; a_2 = 0.8; a_3 = 0.04; b_1 = 0.15; w_0 = 0.55; w_1 = 2; \\ w_2 &= .5; w_3 = 1.2; D_0 = 10; D_1 = 13; D_2 = 10; D_3 = 20. \end{aligned}$$

We first reconstruct the spot pattern (Fig. 5 in [20]) by using the following parameters

$$(25) \quad b_2 = 0; k_{11} = 0.01; k_{22} = 0.00001; k_{33} = 0.01; k_{ij} = 0 \text{ for } i \neq j.$$

The initial distribution of the species is considered to be a small spatial perturbation of the form $0.1 \cos^2(10x) \cos^2(10y)$ about the coexistence steady state. The result of the simulation is presented as contour plot in Figure 4 and as surface plot in Figure 5. The pattern may also depend on the initial distribution of the species. If the initial distribution of the species is taken as a small perturbation of the form $0.1 \cos^2(10x)$, the result of the simulation shows the strip patterns in Figure 6 as contour plot and in Figure 7 as surface plot.

If $b_2 = 0$ is replaced by $b_2 = 0.005$ in (25), the equilibrium $\mathbf{u}^{(9)}$ is linearly stable when $k_{ij} = 0$ for $i \neq j$ by theorem 3.1. No new pattern is generated and solutions are convergent to homogenous equilibrium solution in our numerical simulations. In order to have new patterns, the parameter k_{ij} shall not be all zeros.

$$(26) \quad \begin{aligned} b_2 &= 0.005; k_{11} = 0.01; k_{22} = 0.00001; k_{33} = 0.01; \\ k_{21} &= 0.0001; k_{23} = 0; k_{32} = 0.0039. \end{aligned}$$

When the parameters in (25) are replaced by (26), the coexistence equilibrium $\mathbf{u}^{(9)}$ is (11.6389, 10, 3.7902) and it is linearly stable for the ODE system (1) by theorem 2.1. Condition (7) in theorem 2.1 and condition (19) in theorem 4.1 are both satisfied. By theorem 4.1, Turing instability may occur when cross-diffusion k_{21} or k_{32} are not zero and larger than certain values. New pattern is found numerically (see Figure 8 and Figure 9) and it is very different from patterns in Pashad's paper [20]. The stable steady state $\mathbf{u}^{(9)}$ is destabilized by cross-diffusion. But the new pattern is not a stable steady spatial pattern and it is almost periodically fluctuation like a wave over the time. In order to show the differences of the patterns, Figure 10 presents three solution curves starting at the same space point (1, 1) over a long time period. The convergence of top row graphs in Figure 10 implies that the spot pattern (Figure 4) and strip pattern (Figure 6) are steady patterns. But the almost periodically varying pattern in the lower row graph in Figure 10 show that the pattern in Figure 8 keeps periodically changing. If the parameter k_{32} takes smaller value while unchanging other parameters in (24) and (26), spatial solutions converge to flat equilibrium. If the parameter k_{32} takes larger value, spatial solutions may not exist any more and they become unbounded.

6 Conclusion and Discussion

In this paper, we have analytically and numerically studied a coupled three-species food chain model (2). We extend the results in paper [20] by introducing the intra-species competition b_2 and cross-diffusions. The model of ODE system (1) exhibits very rich dynamics including stable steady states, limit cycles, and chaos (see table 1 and 2). The main goal of the paper is to study the spatial pattern formation of the system (2). We show that classical Turing instability induced by self-diffusion does not occur for a stable region when condition (7) is satisfied. But under some conditions, the model generates spatial patterns only in the presence of cross-diffusion. The phenomenon can be regarded as the extension of Turing patterns and it is called Turing instability induced by cross-diffusion. Moreover, numerical simulation of Turing patterns in 2d is given to illustrate some spatial patterns such as the spot pattern (Figure 4 and 5), strip pattern (Figure 6 and 7), and almost periodically fluctuation pattern. Hence, we illustrate numerically the existence of nonuniform steady state solutions.

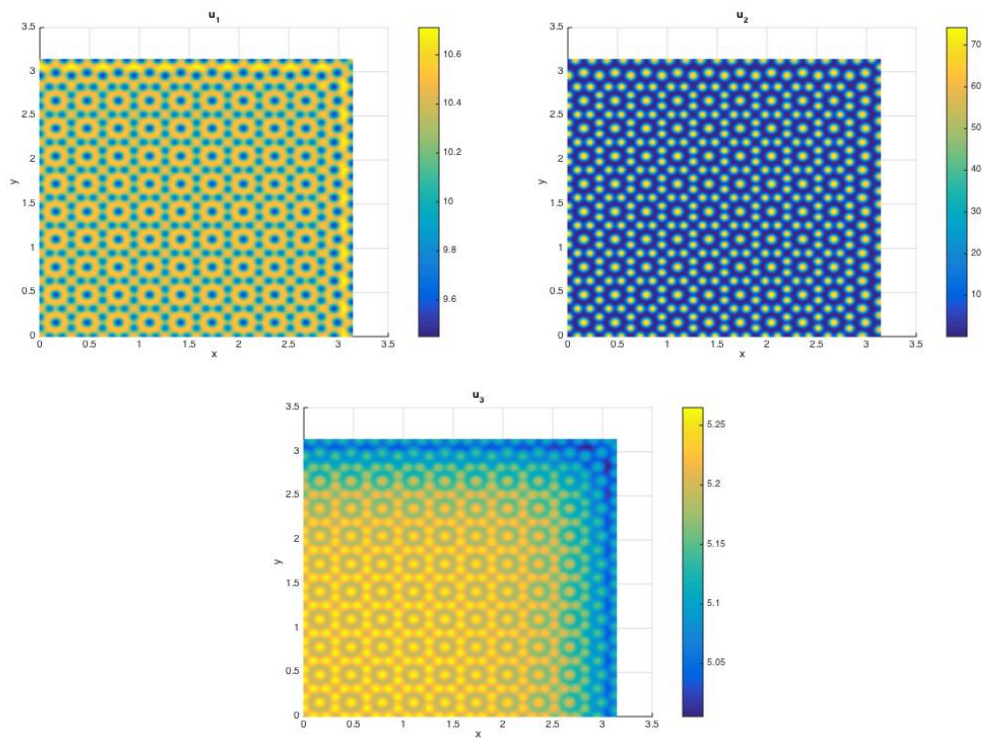


Figure 4: The densities of the three species are shown as contour plots in the xy -plane. Parameters are given in (24) and (25). The long-time is seen to be spot Turing patterns which have been seen in the paper [20].

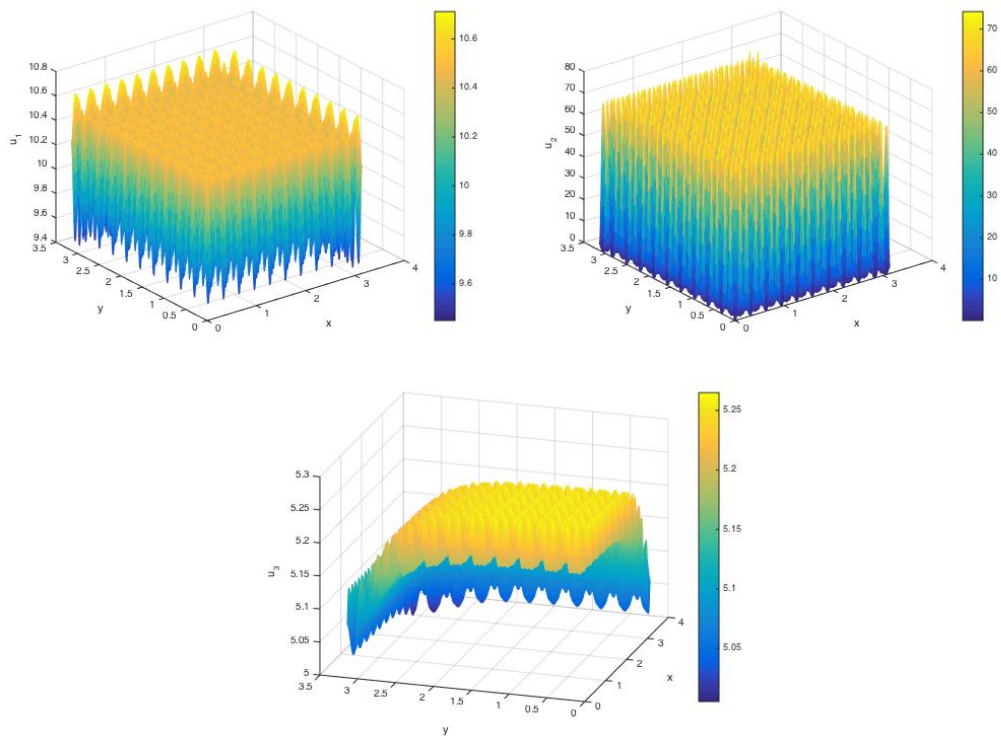


Figure 5: Spatial distributions of the species as surfaces are shown, matching with the contour plot of Figure 4 .

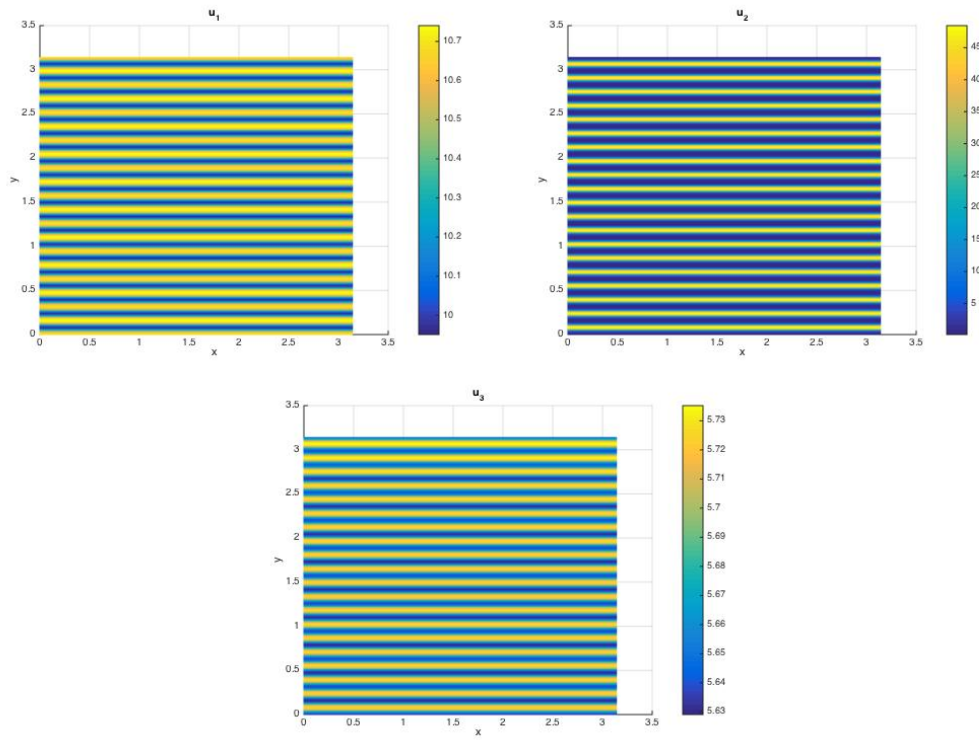


Figure 6: Spatial distributions of the species as contour plot are shown with parameters are given in (24) and (25). Strip patterns are presented and they are not appeared in reference [?].

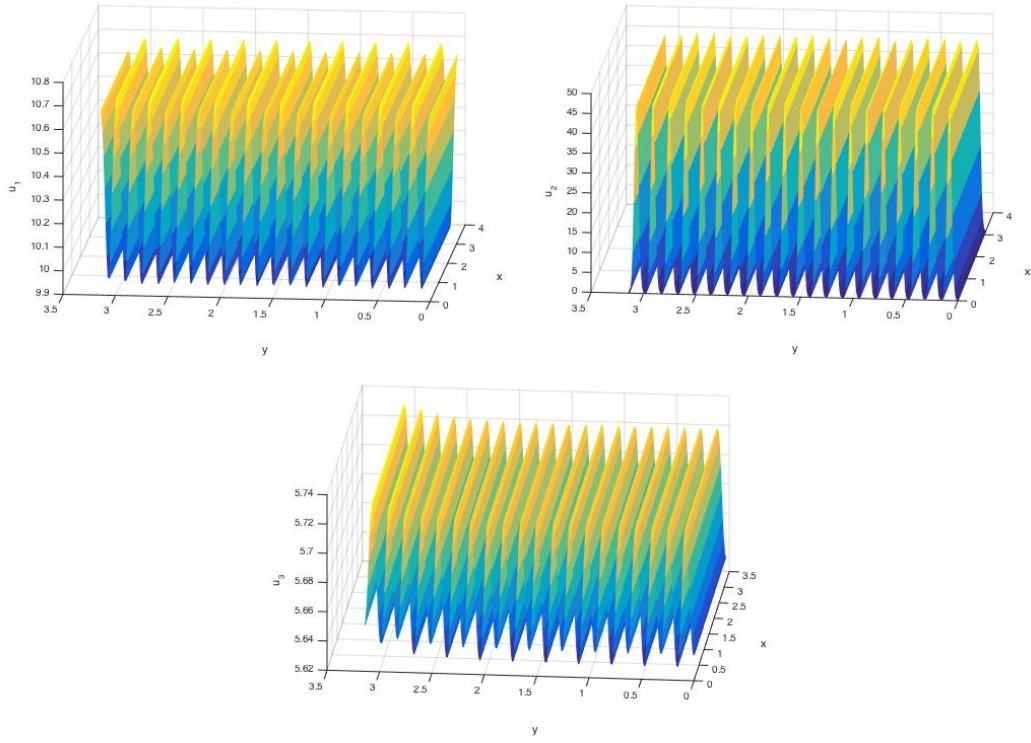


Figure 7: Spatial distributions of the species as surfaces are shown with parameters are given in (24) and (25), matching with the contour plot of Figure 6 .

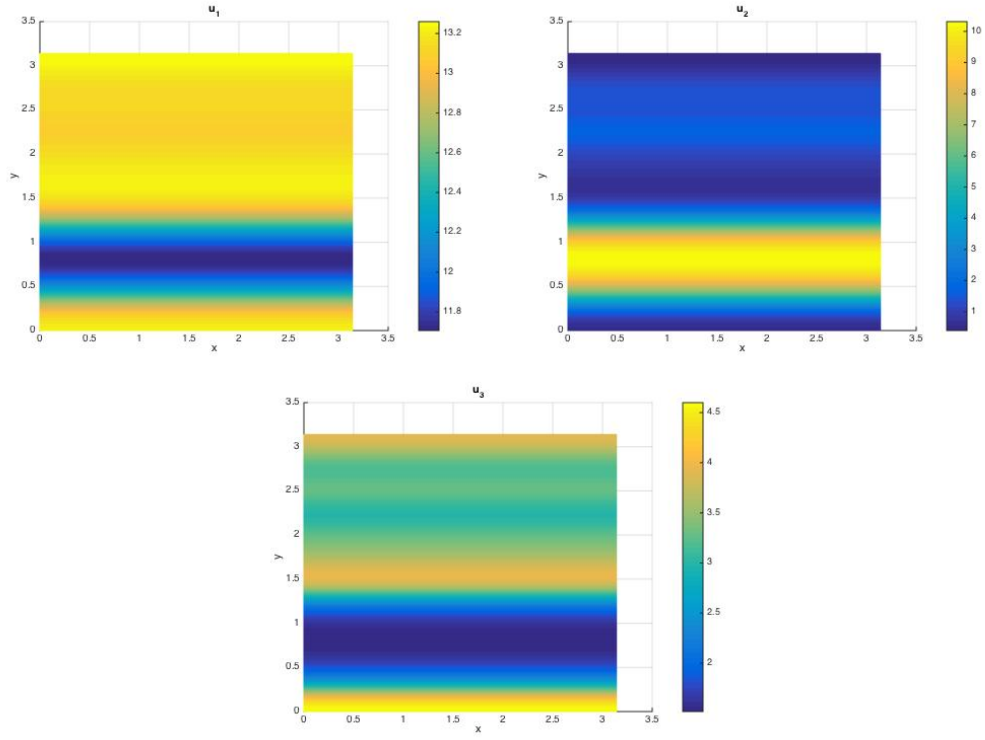


Figure 8: Spatial distributions of the species as contour plot are shown with parameters are given in (24) and (26). This is not a steady state pattern and spatial distributions are almost periodically fluctuated over time. It is different to the steady spot patterns and strip patterns.

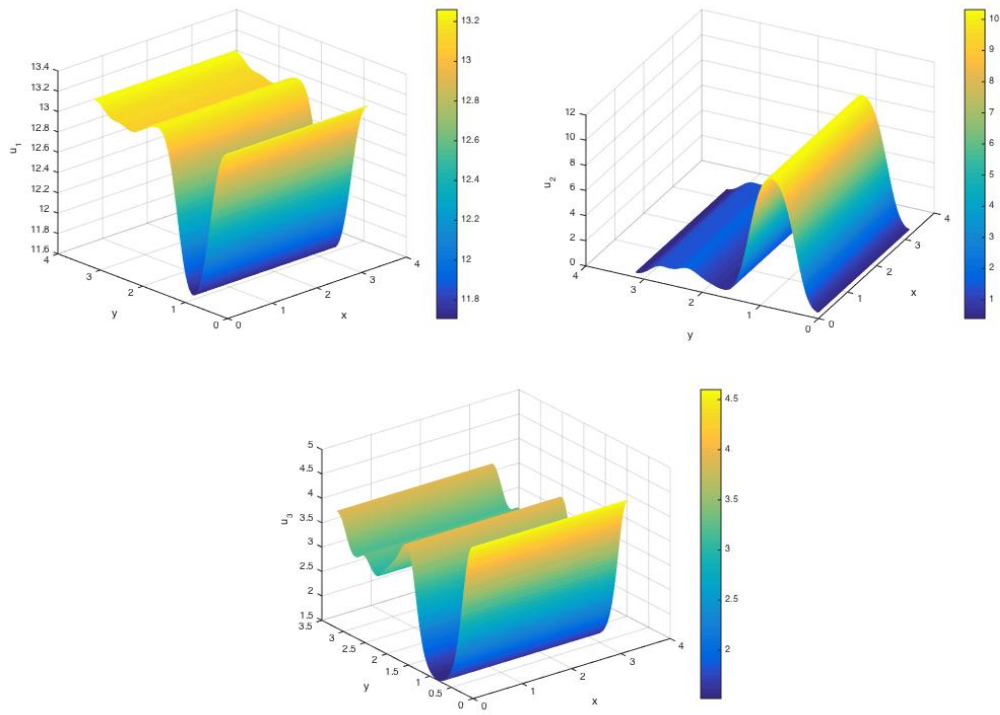


Figure 9: Spatial distributions of the species as surfaces are shown with parameters are given in (24) and (26), matching the contour plot 8.

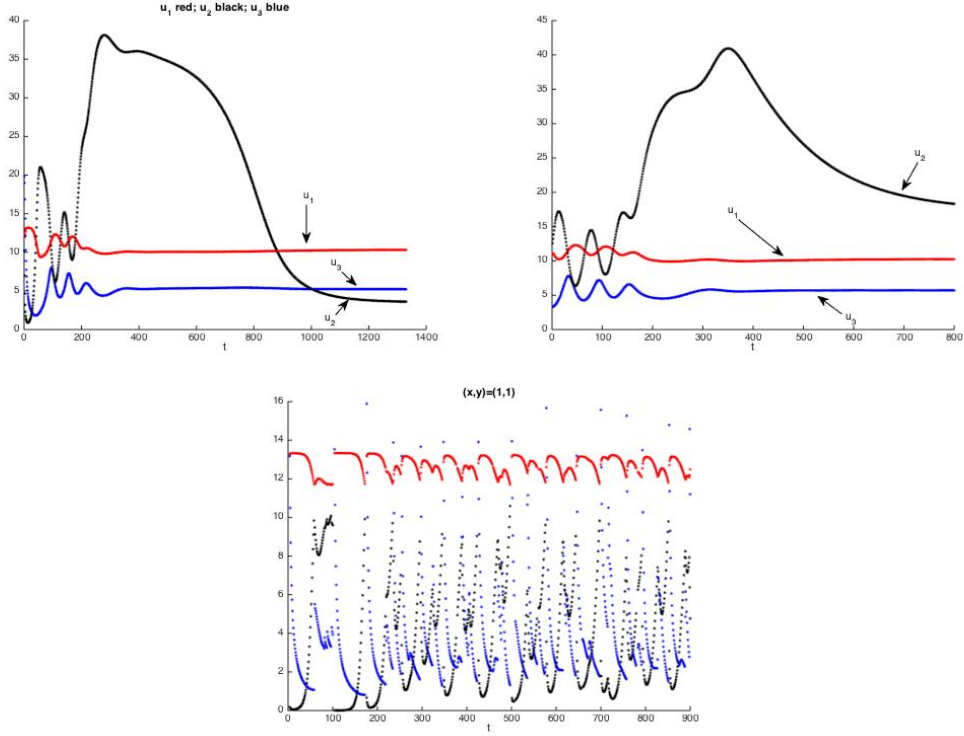


Figure 10: The curves in graph are the density function $u_i(t)$ starting from a same space location over time t . The convergence of the curves in the top two graphs shows that the spot pattern (Figure 4) and strip pattern (Figure 7) are steady state. But the periodically changing of the curves in the low graph shows that the pattern in Figure 9 is not a steady state and the spatial distributions are fluctuated periodically over time.

Acknowledgements

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