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Convective instability in a diffusive predator–prey system

Hui Chen[*1] and **Xuelian Xu**[✉2]

[1]School of Science, Heilongjiang University of Science and Technology, Harbin, 150022, China
[2]School of Mathematical Sciences, Harbin Normal University, Harbin, 150025, China

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Abstract. It is well known that biological pattern formation is the Turing mechanism, in which a homogeneous steady state is destabilized by the addition of diffusion, though it is stable in the kinetic ODEs. However, steady states that are unstable in the kinetic ODEs are rarely mentioned. This paper concerns a reaction diffusion advection system under Neumann boundary conditions, where steady states that are unstable in the kinetic ODEs. Our results provide a stabilization strategy for the same steady state, the combination of large advection rate and small diffusion rate can stabilize the homogeneous equilibrium. Moreover, we investigate the existence and stability of nonconstant positive steady states to the system through rigorous bifurcation analysis.

Keywords: diffusion, advection, predator–prey, instability.

2020 Mathematics Subject Classification: 92D40, 35K57, 35B40, 35B35.

1 Introduction

The central player in mathematical biology models is the stability of steady states. It is well known that biological pattern formation is the Turing mechanism, in which a homogeneous steady state that is stable in the kinetic ODEs is destabilised by the addition of diffusion terms. However, steady states that are unstable in the kinetic ODEs are almost never mentioned. As a result, there is a widespread assumption that unstable steady states are not biologically significant as PDE solutions.

The objective of this paper is to explain how diffusion and advection can turn an unstable steady state of kinetic ODEs to a stable one, to illustrate their implications for PDE models of biological systems. For that purpose, we investigate the spatially extended Rosenzweig–

[*]Co-corresponding author. Email: chenhuialena@163.com
[✉]Corresponding author. Email: xuelian632@163.com

MacArthur model for predator–prey interaction in river, which was proposed in [3]:

$$\begin{cases} P_t = d_1(P_{xx} - \alpha P_x) + P\left(1 - P - \dfrac{mN}{a+P}\right), & (0,L)\times(0,+\infty), \\ N_t = N_{xx} - \alpha N_x - dN + \dfrac{mPN}{a+P}, & (0,L)\times(0,+\infty), \\ P_x(0,t) = P_x(L,t) = N_x(0,t) = N_(L,t) = 0, & t>0, \\ P(x,0) = P_0(x) \geq 0, N(x,0) = N_0(x) \geq 0, & x \in (0,L), \end{cases} \tag{1.1}$$

where $P(x,t)$ and $N(x,t)$ denote predator and prey densities, which depend on space x and time t. Here, and throughout this paper, we restrict attention to one space dimension $(0,L)$, though our analysis carries over to multi-dimensions. Most predator–prey studies do not include advection terms, advection of this type arises naturally in river-based predator–prey systems [3] and α is the convective rate of unidirectional flow. The parameter d_1 is the random diffusion rate of the prey and the random diffusion rate of the predator is rescaled to 1. The prey consumption rate per predator is an increasing saturating function of the prey density with Holling type II form: m reflects how quickly the consumption rate saturates as prey density increases, a is the density of prey necessary to achieve one half the rate. d is the death rate of the predator, also see [9].

Here the zero Neumann boundary conditions correspond to a long river in which the downstream boundary has little influence, see e.g., [3,7]. For the same parameter values as used ODEs, the stability of constant steady states does not change in diffusive systems under zero Neumann boundary conditions, see e.g., [12]. We will find a distinguished result for the reaction-diffusion-advection system (1.1): the coexistence steady state of (1.1) becomes stable for large advection rates though it is unstable for the corresponding diffusive system.

Over the past few decades, reaction-diffusion systems have been widely applied and extensively studied to model the spatial-temporal predator–prey dynamics, which can greatly explain the invasion of a prey by predators (e.g., [8]). For the spatial model with advection, there are some recent related works to understand how the diffusion and advection jointly effect population persist over large temporal scales and resist washout in such environment [5,6,13]. Our purpose is to investigate the stabilization effect of advection.

In Section 2, we perform linear stability of the unique equilibrium (P^*, N^*) with respect to (1.1). Our results in Theorem 2.4 indicate that advection and diffusion stabilize the homogeneous equilibrium when the advection is large and diffusion is small, while it still destabilizes predator–prey interactions when the advection is small. This extends the work of [9]. Section 3 is devoted to the steady state bifurcation analysis of (1.1) which establishes the existence of its nonconstant steady states, with advection rate α being the bifurcation parameter, see Theorem 3.2.

2 Linearized stability driven by advection

The system (1.1) has three non-negative constant equilibrium solution $(0,0)$, $(1,0)$, (P^*, N^*), where

$$(P^*, N^*) = \left(\frac{ad}{m-d}, \frac{(a+P^*)(1-P^*)}{m}\right).$$

The coexistence equilibrium (P^*, N^*) is in the first quadrant if and only if $0 < \frac{ad}{m-d} < 1$. First we recall some well known results on the ODE dynamics of (1.1), see for example [4,11]:

$$\begin{cases} P_t = P\left(1 - P - \dfrac{mN}{a+P}\right), \\ N_t = -dN + \dfrac{mPN}{a+P}. \end{cases} \tag{2.1}$$

Lemma 2.1. *The following statements hold for system (2.1):*

1. *when $P^* \geq 1$, $(1,0)$ is globally asymptotically stable, see [4];*
2. *when $1 - a < P^* < 1$, (P^*, N^*) is globally asymptotically stable, see [4];*
3. *$P^* = \frac{1-a}{2}$ is the unique bifurcation point where a Hopf bifurcation occurs, and the Hopf bifurcation is supercritical and backward;*
4. *when $0 < P^* < \frac{1-a}{2}$, (P^*, N^*) is unstable and there is a globally asymptotically stable periodic orbit, see [11];*
5. *when $\frac{1-a}{2} < P^* < 1$, then (2.1) has no closed orbits in the first quadrant and the positive equilibrium (P^*, N^*) is globally asymptotically stable in the first quadrant, see [11].*

Based on this, we always assume that the constants satisfy $0 < a < 1, P^* > 0$ and $N^* > 0$ throughout the paper. Following the same process of Theorem 2.1 in [12], we have the existence of solution and *a priori* bound of the solution to the dynamical equation (1.1).

Lemma 2.2. *The following statements hold:*

(a) If $P_0(x) \geq 0 (\not\equiv 0)$, $N_0(x) \geq 0 (\not\equiv 0)$, then (1.1) has a unique solution $(P(x,t), N(x,t))$ such that $P(x,t) > 0$, $N(x,t) > 0$ for $t \in (0,\infty)$ and $x \in [0, L]$;

(b) For any solution $(P(x,t), N(x,t))$ of (1.1),

$$\limsup_{t\to\infty} P(x,t) \leq 1, \qquad \int_0^L N(x,t)dx \leq \left(1 + \frac{(a+1)L}{4d}\right).$$

Moreover, there exists $C > 0$ such that

$$\limsup_{t\to+\infty} N(x,t) \leq C,$$

where C is independent of P_0, N_0, d_1, α. If $d_1 = 1$, then $N(x,t) \leq \left(1 + \frac{(a+1)L}{4d}\right)$ for all $t > 0$, $x \in [0, L]$.

In the following, we investigate the effect of diffusion and advection on the stability of (P^*, N^*). For the convenience, we denote

$$\begin{cases} f(P,N) = P\left(1 - P - \dfrac{mN}{a+P}\right), \\ g(P,N) = -dN + \dfrac{mPN}{a+P}. \end{cases}$$

Then the linearization of (1.1) at (P^*, N^*) can be expressed by:

$$\begin{pmatrix} \phi_t \\ \psi_t \end{pmatrix} = L(\alpha)\begin{pmatrix} \phi \\ \psi \end{pmatrix} := D\begin{pmatrix} \phi_{xx} - \alpha\phi_x \\ \psi_{xx} - \alpha\psi_x \end{pmatrix} + J_{(P,N)}\begin{pmatrix} \phi \\ \psi \end{pmatrix} \tag{2.2}$$

with domain $X = \{(\phi, \psi) \in H^2((0, L)) \times H^2((0, L)) : \phi_x = \psi_x = 0, x = 0, L\}$, where

$$D = \begin{pmatrix} d_1 & 0 \\ 0 & 1 \end{pmatrix}, \qquad J_{(P,N)} = \begin{pmatrix} f_P & f_N \\ g_P & g_N \end{pmatrix},$$

and

$$f_P = \frac{P^*(1 - a - 2P^*)}{(a + P^*)}, \qquad f_N = -\frac{mP^*}{(a + P^*)},$$
$$g_P = \frac{a(1 - P^*)}{(a + P^*)}, \qquad g_N = 0.$$

From Theorem 5.1.1 of [2], it is known that if all the eigenvalues of the operator L have negative real parts, then (P^*, N^*) is asymptotically stable, otherwise, (P^*, N^*) is unstable.

Thus λ is an eigenvalue of L if and only if λ is an eigenvalue of the matrix $J_k = -\mu_k D + J_{(P,N)}$ for some $k \geq 0$, where $\mu_k (k = 0, 1, 2, \ldots)$ is the kth eigenvalue of the following eigenvalue problem:

$$\begin{cases} \phi_{xx} - \alpha\phi_x = -\mu_k \phi, & x \in (0, L), \\ \phi_x(0) = \phi_x(L) = 0. \end{cases} \tag{2.3}$$

Since $x \in (0, L)$, we can directly calculate the eigenvalue μ_k and eigenfunction $\phi_k(x)$ as following:

$$\begin{cases} \mu_k = \left(\frac{k\pi}{L}\right)^2 + \frac{\alpha^2}{4}, \ k = 0, 1, 2, \ldots, \\ \phi_k(x) = \alpha e^{\frac{\alpha x}{2}} \cos\left(\frac{k\pi x}{L}\right) + \frac{2k\pi}{L} e^{\frac{\alpha x}{2}} \sin\left(\frac{k\pi x}{L}\right), \ k = 0, 1, 2, \ldots \end{cases} \tag{2.4}$$

So the stability is reduced to consider the characteristic equation

$$\lambda^2 - \mathrm{Trace}(J_k)\lambda + \mathrm{Det}(J_k) = 0, \qquad k = 0, 1, 2, \ldots \tag{2.5}$$

with

$$\begin{aligned} &\mathrm{Trace}(J_k) = -(d_1 + 1)\mu_k + f_P + g_N := -(d_1 + 1)\mu_k + \mathrm{Trace}(J), \\ &\mathrm{Det}(J_k) = d_1 {\mu_k}^2 - (d_1 g_N + f_P)\mu_k + f_P g_N - f_N g_P := d_1 {\mu_k}^2 - (d_1 g_N + f_P)\mu_k + \mathrm{Det}(J). \end{aligned} \tag{2.6}$$

We take α as the main bifurcation parameter to observe its effect on the local stability (P^*, N^*). First of all, we list four conditions for the sake of following discussion.

$(A1)$ $f_P^2 + 4d_1 f_N g_P < 0$,

$(A2)$ $f_P^2 + 4d_1 f_N g_P > 0$,

$(A3)$ $d_1 \mu_0^2 - f_P \mu_0 - f_N g_P \leq 0$,

$(A4)$ $d_1 \mu_0^2 - f_P \mu_0 - f_N g_P > 0$.

Theorem 2.3. *Suppose $P^* \geq \frac{1-a}{2}$. Then (P^*, N^*) is always locally asymptotically stable for any advection rate $\alpha > 0$.*

Proof. It can find that $f_P \leq 0$ when $P^* \geq \frac{1-a}{2}$. Thus $\mathrm{Trace}(J_k) < 0$ and $\mathrm{Det}(J_k) > 0$ for all $k = 0, 1, 2, \ldots$, which implies the desired results. □

Theorem 2.4. *Suppose* $P^* < \dfrac{1-a}{2}$.

1. *If* $-(d_1+1)\mu_0 + f_P > 0$, *then* (P^*, N^*) *is unstable.*
2. *If there is some* $k \geq 0$ *such that* $-(d_1+1)\mu_k + f_P = 0$, *then system* (1.1) *generates a heterogeneous Hopf bifurcation at* (P^*, N^*) *provided either (A1) holds or (A2), (A4) and* $\mu_0 > \frac{f_P}{2}$ *holds.*
3. *If* $-(d_1+1)\mu_0 + f_P < 0$, *then* (P^*, N^*) *is locally asymptotically stable provided either (A1) holds or (A2), (A4) and* $\mu_0 > \frac{f_P}{2}$ *holds; and* (P^*, N^*) *is unstable provided (A3) holds,*

Proof. It just notices that $\mathrm{Det}(J_k) > 0$ for all $k = 0, 1, 2, \ldots$ if either (A1) or (A2) holds; and $\mathrm{Det}(J_0) < 0$ if (A3) holds. □

Remark 2.5. Theorem 2.3 and Theorem 2.4 imply that the advection rate α makes (P^*, N^*) more stable compared with that for the corresponding ODE system in Lemma 2.1. The periodic solution bifurcating from (P^*, N^*) will disappear when introducing the advection and diffusion; Moreover under the same condition that (P^*, N^*) is unstable for (2.1), there is newborn homogeneous/heterogeneous Hopf bifurcation solutions at (P^*, N^*) or (P^*, N^*) even becomes stable for small diffusion rate d_1 or large advection rate α.

3 Existence of non-constant positive steady state

In this section we show that when (P^*, N^*) is unstable, there exist positive non-constant steady state solutions of (1.1). In order to show that we use bifurcation theory to prove the existence of positive non-constant steady state solutions. The bifurcations can be shown with parameter α_k(or μ_k) as shown in Theorem 2.4. From the relation given in (2.6), we define the potential bifurcation points:

$$\alpha_{k,\pm}^2 = \frac{2f_P \pm 2\sqrt{{f_P}^2 + 4d_1 f_N g_P}}{d_1} - 4\left(\frac{k\pi}{L}\right)^2, \qquad k = 0, 1, 2, \ldots \tag{3.1}$$

We have the following properties of $\alpha_{k,\pm}$:

Lemma 3.1. *Assume that (A2) holds. Then*

1. $\lim_{k\to\infty} \alpha_{k,\pm} = -\infty$;
2. *Both* $\alpha_{k,+}$ *and* $\alpha_{k,-}$ *are monotonically decreasing with respect to* k, *there exists* m, n *such that* $\alpha_{0,+} > \alpha_{1,+} > \cdots > \alpha_{m,+} \geq 0$ *and* $\alpha_{0,-} > \alpha_{1,-} > \cdots > \alpha_{m,-} \geq 0$.

Theorem 3.2. *Assume that (A2) holds. Let* $\alpha_{k,\pm}$ *be defined as in* (3.1) *such that* $\alpha_{i,+} \neq \alpha_{j,-}$ *for any* $0 \leq i \leq m$ *and* $0 \leq j \leq n$. *Then*

1. *Near* $(\alpha_{i,\pm}, P^*, N^*)$, *the set of positive non-constant steady state solutions of* (1.1) *is a smooth curve* $\Sigma_i = \{\alpha_i(s), P_i(s), N_i(s) : s \in (-\varepsilon, \varepsilon)\}$, *where where* $P_i(s) = P^* + sa_i\phi_i(x) + s^2\psi_{1,i}(s) + O(s^3)$, $N_i(s) = N^* + sb_i\phi_i(x) + s^2\psi_{2,i}(s) + O(s^3)$ *for some smooth functions* $\psi_{1,i}, \psi_{2,i}$ *such that* $\alpha_i(s) = \alpha_{i,\pm} + O(s)$ *and* $\psi_{1,i}(0) = \psi_{2,i}(0) = 0$; *Here* (a_i, b_i) *satisfies*

$$L(\alpha_i)[(a_i, b_i)^T\phi_i(x)] = (0, 0)^T.$$

2. *The smooth curve Σ_i in part (1) is contained in a connected component C_i of Γ, which is the closure of the set of positive non-constant steady state solutions of* (1.1)*, and either C_i is unbounded or C_i contains another $(\alpha_{j,\pm}, P^*, N^*)$ with $\alpha_{i,\pm} \neq \alpha_{j,\pm}$.*

Proof. The existence and uniqueness of $\alpha_{i,\pm}$ follows from discussions above. Then the local bifurcation result follows the bifurcation theorem in [1], and it is an application of a more general result Theorem 4.3 in [10].

Define a nonlinear mapping

$$F(\alpha, P, N) = \begin{pmatrix} d_1(P_{xx} - \alpha P_x) + f(P, N) \\ N_x x - \alpha N_x + g(P, N) \end{pmatrix}$$

with domain $V = \{(\alpha, P, N) : 0 < \alpha < \alpha_{0,+}, (P, N) \in X \times X\}$, where $X = \{\omega \in H^2((0, L)) : \omega'(0) = \omega'(L) = 0\}$. Then $F(\alpha, P, N) = 0$ is equivalent to the steady state system of (1.1):

$$\begin{cases} d_1(P_{xx} - \alpha P_x) + P\left(1 - P - \dfrac{mN}{a + P}\right) = 0, & x \in (0, L), \\ N_{xx} - \alpha N_x - dN + \dfrac{mPN}{a + P} = 0, & x \in (0, L), \\ P_x(0) = P_x(L) = N_x(0) = N_x(L) = 0. \end{cases} \tag{3.2}$$

It is observed that $F(\alpha, P, N) = 0$ for all $\alpha > 0$. For any $(\alpha, P^*, N^*) \in V$, the The Fréchet derivative of F is given by

$$D_{(P,N)}F(\alpha, P^*, N^*)(P, N) = \begin{pmatrix} d_1(P_{xx} - \alpha P_x) + f_P P + f_N N \\ N_{xx} - \alpha N_x + g_P P + g_N N \end{pmatrix}.$$

Then $D_{(P,N)}F(\alpha_{i,\pm}, P^*, N^*)(P, N)$ is a Fredholm operator with index zero by Corollary 2.11 in [10].

We show that the conditions for Theorem 4.3 in [10] are satisfied in several steps.

Step 1. $\dim N(D_{(P,N)}F(\alpha_{i,\pm}, P^*, N^*)) = 1$.

From the definition of $\alpha_{i,\pm}$, it is easy to verify that $\mathrm{Det}(J_i) = 0$, hence zero is an eigenvalue of J_i with an eigenvector $(a_i, b_i) = (g_P, d_1\mu_i)$. Then $V_i = (g_P, d_1\mu_i)\phi_i(x)$ is an eigenfunction of $L(\alpha_{i,\pm})$ defined in (2.2) and evaluated at (P^*, N^*) with eigenvalue zero. Since μ_i $(i = 0, 1, 2 \dots)$ is a simple eigenvalue from (2.4), then the eigenvector is unique up to a constant multiple. Thus one has $N(D_{(P,N)}F(\alpha_{i,\pm}, P^*, N^*)) = \mathrm{span}\{V_i\}$ which is one-dimensional. Note that we also have that $\mathrm{codim}\, R(D_{(P,N)}F(\alpha_{i,\pm}, P^*, N^*)) = 1$ as $D_{(P,N)}F(\alpha_{i,\pm}, P^*, N^*)$ is Fredholm with index zero.

Step 2. $D_{(P,N)\alpha}F(\alpha_{i,\pm}, P^*, N^*)(V_i) \notin R(D_{(P,N)}F(\alpha_{i,\pm}, P^*, N^*))$.

It is easy to see that an eigenvector of $L^*(\alpha_{i,\pm})$ corresponding to zero eigenvalue is $V_i^* = (a_i^*, b_i^*) = (-\mu_i + f_P, g_P)\phi(x)$, here $L^*(\alpha_{i,\pm})$ is the adjoint matrix of $-L(\alpha_{i,\pm})$. If $(h_1, h_2) \in R(D_{(P,N)}F(\alpha_{i,\pm}, P^*, N^*))$, then there exists (φ_1, φ_2) such that $D_{(P,N)\alpha}F(\alpha_{i,\pm}, P^*, N^*)(\varphi_1, \varphi_2)^T = -L(\alpha_{i,\pm})(\varphi_1, \varphi_2)^T = (h_1, h_2)^T$. Thus

$$\int_0^L (a_i^* h_1 + b_i^* h_2)\phi_i(x)dx = 0.$$

It is noticed that $D_{(P,N)\alpha}F(\alpha_{i,\pm}, P^*, N^*)(V_i) = (0, -\mu_i b_i \phi_i(x))^T$, and

$$\int_0^L a_i^* \cdot 0 + b_i^* \cdot (-\mu_i b_i \phi_i(x))dx = \int_0^L d_1 \mu_i^2 g_P \phi_i^2(x)dx > 0.$$

Thus $D_{(P,N)\alpha}F(\alpha_{i,\pm}, P^*, N^*)(V_i) \notin R(D_{(P,N)}F(\alpha_{i,\pm}, P^*, N^*))$.

Step 3. It is noticed that $\{(\alpha, P^*, N^*) : 0 < \alpha < \alpha_{0,+}\}$ is a line of trivial solutions for $F = 0$, thus Theorem 4.3 in [10] can be applied to each continuum C_i bifurcated from $(\alpha_{i,\pm}, P^*, N^*)$. The solutions of (3.2) on C_i near the bifurcation point are apparently positive. For each continuum C_i, either $\bar{C}_i$ contains another $(\alpha_{j,\pm}, P^*, N^*)$ or C_i is not compact. (Here we do not make an extinction between the solutions of (3.2) and $F = 0$ as they are essentially same, hence we use C_i for solution continuum for both equations.) Therefore, either C_i is unbounded or C_i contains another $(\alpha_{j,\pm}, P^*, N^*)$ with $\alpha_{i,\pm} \neq \alpha_{j,\pm}$. □

4 Conclusions and numerical simulations

It is a general result that a steady state that is unstable as a solution of the kinetic ODEs is also unstable as a PDE solution on a finite domain under zero Neumann conditions [12]. Our results in Theorem 2.4 indicate that the combination of advection and diffusion can stabilize the homogeneous equilibrium. For the constant steady state that are unstable in the kinetic ODEs, it becomes stable when the advection is large and diffusion is small, while it keeps instability when the advection is small. Moreover, we obtain non-constant steady states by bifurcation theory when the constant steady state is unstable. These results extend the work of [9]. Our analysis and methods are also suitable for higher dimensional systems, we can obtain the concrete bifurcation value in one dimensional interval. From a theoretical point of view, this paper introduces a new class of reaction-diffusion models with advection, which may be of independent interest.

Consider system (3.2) and fix $d = 0.5, m = 1, a = 0.6$. Then $P^* > \frac{1-a}{2}$. Lemma 2.1 says that $(P^*, N^*) = (0.6, 0.48)$ is locally asymptotically stable for any $d_1 > 0$ and $\alpha = 0$, and Theorem 2.3 shows that $(P^*, N^*) = (0.6, 0.48)$ keeps stable for $\alpha > 0$, see Figure 4.1.

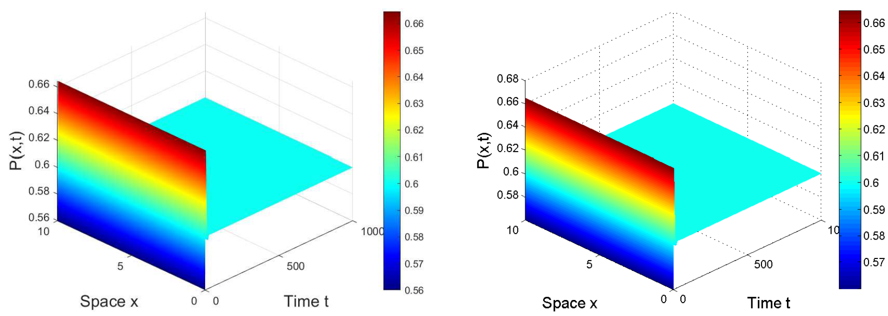

Figure 4.1: (Left): $d_1 = 1$, $\alpha = 0$, and (P^*, N^*) is locally asymptotically stable; (Right): $d_1 = 1$, $\alpha = 10$, and (P^*, N^*) is still locally asymptotically stable, the same initial value $(P_0, N_0) = (0.56, 0.4)$.

Fix $d = 0.5, m = 1, a = 0.33$. Then $P^* = \frac{1-a}{2}$. Lemma 2.1 says that (3.2) has a homogeneous Hopf bifurcation solution at $(P^*, N^*) = (0.33, 0.44)$ for any $d_1 > 0$ and $\alpha = 0$, while Theorem 2.3 shows that the homogeneous periodic solutions disappears for $\alpha > 0$, see Figure 4.2.

Fix $d = 0.5, m = 1, a = 0.32$. Then $P^* < \frac{1-a}{2}$. Lemma 2.1 says that $(P^*, N^*) = (0.32, 0.44)$ is unstable for any $d_1 > 0$ and $\alpha = 0$, while Theorem 2.3 shows that $(P^*, N^*) = (0.32, 0.44)$ becomes stable for large $d_1 > 0$ and large $\alpha > 0$, see Figure 4.3.

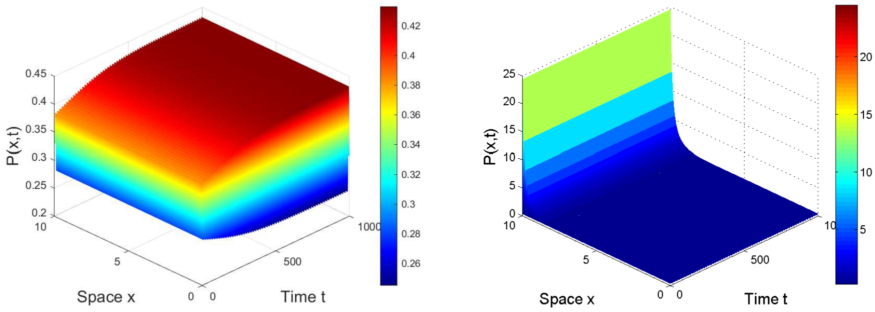

Figure 4.2: (Left): $d_1 = 1$, $\alpha = 0$, and (3.2) has a homogeneous Hopf bifurcation solution at (P^*, N^*); (Right): $d_1 = 0.3$, $\alpha = 1$, and the periodic solution disappears, the same initial value $(P_0, N_0) = (0.33, 0.4)$.

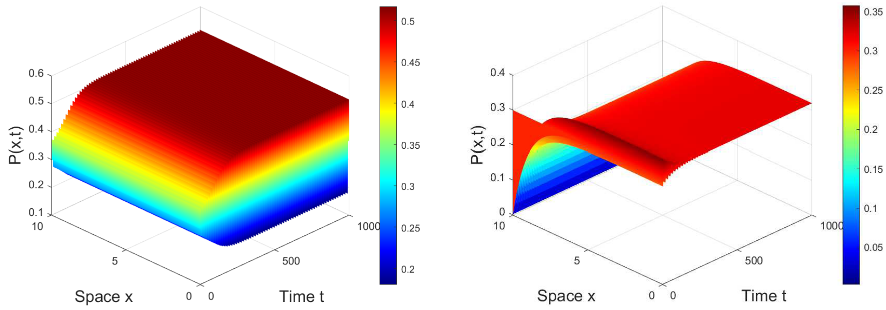

Figure 4.3: (Left): $d_1 = 1$, $\alpha = 0$, and and (P^*, N^*) is unstable; (Right): $d_1 = 1500$, $\alpha = 1$, and (P^*, N^*) becomes locally asymptotically stable, the same initial value $(P_0, N_0) = (0.3, 0.4)$.

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