Research Article

Bifurcation Analysis of Gene Propagation Model Governed by Reaction-Diffusion Equations

Guichen Lu

School of Mathematics and Statistics, Chongqing University of Technology, Chongqing 400054, China

Correspondence should be addressed to Guichen Lu; bromn006@gmail.com

Received 3 April 2016; Revised 15 June 2016; Accepted 22 June 2016

Academic Editor: Andrew Pickering

Copyright © 2016 Guichen Lu. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

We present a theoretical analysis of the attractor bifurcation for gene propagation model governed by reaction-diffusion equations. We investigate the dynamical transition problems of the model under the homogeneous boundary conditions. By using the dynamical transition theory, we give a complete characterization of the bifurcated objects in terms of the biological parameters of the problem.

1. Introduction

As the field of gene technology develops, the gene propagation problems continue to be relevant. Some recent advances and problems include the following: the genetic engineering for improving crop pest and disease resistance; the bacteria have developed a tolerance to widely prescribed antibiotics; the human genome project will enable us to deduce more information on human bodies and to deduce historical patterns of migration by archaeologists. Lots of papers developed equations to describe the changes in the frequency of alleles in a population that has several possible alleles at the locus in question. Fisher [1] proposed a reaction-diffusion equation with quadratic source term that models the spread of a recessive advantageous gene through a population that previously had only one allele at the locus in question. Fisher’s equation is

\[
\frac{\partial u}{\partial t} = \theta \frac{\partial^2 u}{\partial x^2} + ru(1 - u),
\]

(1)

where \( u \) is the frequency of the new mutant gene, \( \theta \) is the diffusion coefficient, and \( r \) is the intensity of selection in favor of the mutant gene.

In [2–5], the authors have claimed that a cubic source term was more appropriate than a quadratic source term. Although the cubic source term is implicit as one possibility in the general genetic dispersion equations derived by others, its significance has not been highlighted and the difference between cubic and quadratic source terms has not been examined. Based on the Fitzhugh-Nagumo equation and Huxley equation, by using the methods of a continuum limit of a discrete generation model, direct continuum modelling, and Fick’s laws for random motion, Bradshaw-Hajek and Broadbridge [6–8] have derived a reaction-diffusion equation describing the spread of a new mutant gene; that is,

\[
\frac{\partial u}{\partial t} = \theta \frac{\partial^2 u}{\partial x^2} + ru^2(1 - u),
\]

(2)

where \( u \) is the frequency of the new mutant gene, \( \theta \) is the diffusion coefficient, and \( r \) is the intensity of selection in favor of the mutant gene.

In [9–11], the authors have discussed the two possible alleles while some others recently investigate another case in which there are more than two possible alleles at the locus in question. For three possible alleles, Littler [12] has mostly used stochastic models while Bradshaw-Hajek and Broadbridge [6–8] have developed the reaction-diffusion-convection models.

In this paper, we will follow the work of Bradshaw-Hajek et al. [7] and investigate the gene propagation model of three possible alleles at the locus. By introducing the spatial two-dimensional domains, we will give a detailed analysis of the dynamical properties for the model and consider the attractor bifurcation to show a complete characterization of
the attractors and their basins of attraction in terms of the physical parameters of the problem which is developed by Ma and Wang [13, 14].

The paper is organized as follows. In Section 2, we briefly summarize the two-dimensional spatial gene propagation model and give some mathematical settings. Section 3 states principle of exchange of stability for system. Section 4 is the main results of the phase transition theorems based on the attractor bifurcation theory. An example with the computer simulation of the pattern formation is given in the concluding remark section to illustrate our main results.

2. Modelling Analysis

In order to describe the spread of a new mutant gene, based on Skellam’s method, Bradshaw-Hajek and Broadbridge [6] have developed a one-dimensional population genetics model governed by reaction-diffusion equation describing the changes in allelic frequencies. For a population having one new mutant allele \( A_1 \) and two original alleles \( A_2, A_3 \), there are six possible genotypes:

\[
A_1A_1, A_1A_2, A_1A_3, A_2A_2, A_2A_3, A_3A_3. \tag{3}
\]

Let \( \rho_i(x_1, x_2, t), \ (i, j = 1, 2, 3) \) denote the frequency of individuals of the genotype \( A_iA_j \) on the spatial two-dimensional domain. We follow the ideas of [6] and write the genotype equations as

\[
\begin{align*}
\frac{\partial \rho_{11}}{\partial t} &= \Delta \rho_{11} - \mu \rho_{11} + \gamma_{11} u_1 \rho, \\
\frac{\partial \rho_{12}}{\partial t} &= \Delta \rho_{12} - \mu \rho_{12} + 2\gamma_{12} u_1 u_2 \rho, \\
\frac{\partial \rho_{13}}{\partial t} &= \Delta \rho_{13} - \mu \rho_{13} + 2\gamma_{13} u_1 (1 - u_1 - u_2) \rho, \\
\frac{\partial \rho_{22}}{\partial t} &= \Delta \rho_{22} - \mu \rho_{22} + 2\gamma_{22} u_2 \rho, \\
\frac{\partial \rho_{23}}{\partial t} &= \Delta \rho_{23} - \mu \rho_{23} + 2\gamma_{23} u_2 (1 - u_1 - u_2) \rho, \\
\frac{\partial \rho_{33}}{\partial t} &= \Delta \rho_{33} - \mu \rho_{33} + 2\gamma_{33} (1 - u_1 - u_2)^2 \rho,
\end{align*}
\]

where \( \Delta = \partial^2 / \partial x_1^2 + \partial^2 / \partial x_2^2 \), \( u_i(x_1, x_2, t) \) is the frequency of allele \( A_i \), which can be expressed as

\[
\begin{align*}
u_i &= \frac{2 \rho_{11} + \rho_{12} + \rho_{13}}{2 \rho}, \\
u_2 &= \frac{\rho_{12} + 2 \rho_{22} + \rho_{23}}{2 \rho}, \\
u_3 &= 1 - u_1 - u_2,
\end{align*}
\]

\( \rho(x, t) \) is the total population density, \( \mu \) is the common death rate, and \( \gamma_{ij} \) is the reproductive success rate of individuals with genotype \( A_iA_j \) for \( i, j = 1, 2, 3 \), respectively.

From (5), we can simplify these above six equations into the following two coupled equations describing the change in frequency of two of alleles:

\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= \Delta u_1 + \frac{2 \partial \rho}{\partial x} \frac{\partial u_1}{\partial x} + \Phi(u_1, u_2), \\
\frac{\partial u_2}{\partial t} &= \Delta u_2 + \frac{2 \partial \rho}{\partial x} \frac{\partial u_2}{\partial x} + \Psi(u_1, u_2), \tag{6}
\end{align*}
\]

where

\[
\begin{align*}
\Phi(u_1, u_2) &= (\gamma_{13} - \gamma_{33}) u_1 + (\gamma_{11} - 3\gamma_{13} + 2\gamma_{33}) u_1^2 \\
&+ (\gamma_{12} - \gamma_{13} - 2\gamma_{23} + 2\gamma_{33}) u_1 u_2 \\
&+ (-\gamma_{22} + 2\gamma_{33} - \gamma_{33}) u_2 u_2 \\
&+ (-2\gamma_{12} + 2\gamma_{13} + 2\gamma_{23} - 2\gamma_{33}) u_1^2 u_2 \\
&+ (-\gamma_{11} + 2\gamma_{13} - \gamma_{33}) u_3^3, \\
\Psi(u_1, u_2) &= (\gamma_{23} - \gamma_{33}) u_2 + (\gamma_{22} - 2\gamma_{23} + 2\gamma_{33}) u_2^2 \\
&+ (\gamma_{12} - \gamma_{13} - 2\gamma_{23} + 2\gamma_{33}) u_1 u_2 \\
&+ (-\gamma_{11} + 2\gamma_{13} - \gamma_{33}) u_3 u_3 \\
&+ (-2\gamma_{12} + 2\gamma_{13} + 2\gamma_{23} - 2\gamma_{33}) u_1 u_2^2 \\
&+ (-\gamma_{22} + 2\gamma_{23} - \gamma_{33}) u_3^3.
\end{align*}
\]

Assume that the total population density is constant across the range (so that \( \partial \rho / \partial x = 0 \)); system (6) becomes

\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= \Delta u_1 + \Phi(u_1, u_2), \tag{7} \\
\frac{\partial u_2}{\partial t} &= \Delta u_2 + \Psi(u_1, u_2).
\end{align*}
\]

One of the attractions of (8) to mathematicians is to study the diffusion induced instability introduced by Turing in his 1952 seminal paper [15]. For showing the diffusion effect on stability, we will consider a modified equation of (8):

\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= \Delta u_1 + (\gamma_{13} - \gamma_{33}) u_1 + a_1 u_1^2 + a_2 u_1 u_2 + a_3 u_1 u_2^2 \\
&+ a_4 u_1^2 u_2 + a_5 u_1^3, \\
\frac{\partial u_2}{\partial t} &= d \Delta u_2 + (\gamma_{23} - \gamma_{33}) u_2 + b_1 u_2^2 + b_2 u_1 u_2 + a_4 u_1 u_2^2 \\
&+ a_5 u_1^2 u_2 + a_5 u_1 u_3^2,
\end{align*} \tag{9}
\]

where \( a_1 = \gamma_{11} - 3 \gamma_{13} + 2 \gamma_{33}, \ a_2 = \gamma_{12} - \gamma_{13} - 2 \gamma_{23} + 2 \gamma_{33}, \ a_3 = -\gamma_{22} + 2 \gamma_{23} - \gamma_{33}, \ a_4 = -2 \gamma_{12} + 2 \gamma_{13} + 2 \gamma_{23} - 2 \gamma_{33}, \ a_5 = \gamma_{11} + 2 \gamma_{13} - 2 \gamma_{33}, \ b_1 = \gamma_{22} - 3 \gamma_{23} + 2 \gamma_{33}, \ b_2 = \gamma_{12} - 2 \gamma_{13} - 2 \gamma_{23} + 2 \gamma_{33} \) and \( a_5^2 + a_5^2 + a_5^2 \neq 0, d \) is the diffusion coefficient which measures the dispersal rate of allele \( A_2 \). On the other hand, diffusive terms can be considered as describing
the ability of the allele $A_i$ to occupy different zones in 2-
dimensional space either through the action of small-scale
mechanism or by some native transport device.

System (9) has seven constant solutions: $(u_1, u_2) =
(0,0),(0,1),(1,0),(0,a),(\beta,a, b^*, a^*), (a,b)$, where $\alpha, \beta, a, b^*, a^*,$
and $b$ are complicated expressions of the reproductive
success rate $\gamma_{ij}$ and $a, b$ are given by

$$a = \frac{\Delta_1}{\Delta_0},$$
$$b = \frac{\Delta_2}{\Delta_0},$$  \hspace{1cm} (10)

where

$$\Delta_1 = -\gamma_{13} \gamma_{23} + \gamma_{13} \gamma_{22} - \gamma_{12} \gamma_{23} + \gamma_{12} \gamma_{33} - \gamma_{22} \gamma_{33}$$
$$+ \gamma_{23}^2,$$
$$\Delta_2 = -\gamma_{12} \gamma_{13} + \gamma_{13} \gamma_{12} - \gamma_{11} \gamma_{33} + \gamma_{11} \gamma_{23}$$
$$+ \gamma_{12}^2,$$
$$\Delta_0 = \gamma_{12}^2 + \gamma_{13}^2 + \gamma_{23}^2 - 2\gamma_{12} \gamma_{13} + 2\gamma_{12} \gamma_{23} - 2\gamma_{13} \gamma_{23}$$
$$+ 2\gamma_{12} \gamma_{33} - \gamma_{11} \gamma_{22} + 2\gamma_{12} \gamma_{22} + 2\gamma_{13} \gamma_{33}$$
$$+ 2\gamma_{12} \gamma_{23} + 2\gamma_{13} \gamma_{23},$$  \hspace{1cm} (11)

Considering the biological context, we assume that the steady
state solution $(a, b)$ is positive and $0 < u_1, u_2 < 1.$

In the present paper, we focus on the bifurcation from the
constant solution $(a, b).$ Let

$$u_1 = a + u_1',$$
$$u_2 = b + u_2'.$$  \hspace{1cm} (12)

Omitting the primes, then system (9) becomes

$$\frac{\partial u_1}{\partial t} = \Delta u_1 + a (\gamma_{11} - \gamma_{13}) u_1 + a (\gamma_{12} - \gamma_{13}) u_2$$
$$+ G_1 (u_1, u_2),$$
$$\frac{\partial u_2}{\partial t} = d \Delta u_2 + b (\gamma_{12} - \gamma_{23}) u_1 + b (\gamma_{13} - \gamma_{23}) u_2 + G_2 (u_1, u_2),$$  \hspace{1cm} (13)

where

$$G_1 (u_1, u_2) = (a_1 b + 3a_1 a + a_1) u_1^2$$
$$+ (a_1 + 3a_2 b + 2a_1 a) u_1 u_2 + aa_2 u_2^2$$
$$+ a_3 u_1^3 + u_1 a_3 u_2^2 + a_4 u_1^2 u_2,$$
$$G_2 (u_1, u_2) = b a_4 u_1^2 + (2a_1 a + b_1 + 3a_3 b + a_4 a) u_2 + a_3 u_2^3$$
$$+ a_4 u_1 u_2^2 + a_5 u_2 u_2^2.$$  \hspace{1cm} (14)

We assume that system (13) is satisfied on an open
bounded domain $\Omega \subset R^2.$ There are two types of biologically
sound boundary conditions: the Dirichlet boundary condition,

$$u_1|_{\partial \Omega} = 0,$$
$$u_2|_{\partial \Omega} = 0,$$  \hspace{1cm} (15)

which means that the frequency is extinct in the boundary of
range and the Neumann boundary condition:

$$\frac{\partial u_1}{\partial n}|_{\partial \Omega} = 0,$$
$$\frac{\partial u_2}{\partial n}|_{\partial \Omega} = 0,$$  \hspace{1cm} (16)

which means that the frequency is invariant in the boundary of
range in biological significant.

Define the function spaces

$$H = L^2 (\Omega, R^2),$$

$$H_1 = \left\{ u \in H^2 (\Omega, R^2) \mid \frac{\partial u}{\partial n}|_{\partial \Omega} = 0 \right\}$$  \hspace{1cm} (17)

for boundary conditions (15)

$$H_2 = \left\{ u \in H^2 (\Omega, R^2) \mid \frac{\partial u}{\partial n}|_{\partial \Omega} = 0 \right\}$$  \hspace{1cm} (18)

for boundary conditions (16).

It is clear that $H$ and $H_1$ are two Hilbert space and $H_1 \hookrightarrow H$
is dense and compact inclusion.

Later, we choose the bifurcation parameter $\lambda$ to be the
diffusion coefficient $d; \text{ that is, } \lambda = d.$ Let $L_\lambda : H_1 \rightarrow H$
be defined by

$$L_\lambda := -A_\lambda + B,$$  \hspace{1cm} (19)

where

$$-A_\lambda u = (\Delta u_1, \lambda \Delta u_2)^T,$$
$$Bu = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} u_1,$$

where $u = (u_1, u_2)^T \in H_1,$ $a_{11} = a(\gamma_{11} - \gamma_{13}),$
$a_{12} = a(\gamma_{12} - \gamma_{13}),$ $a_{21} = b(\gamma_{12} - \gamma_{23}),$
and $a_{22} = b(\gamma_{22} - \gamma_{23}).$
Furthermore, let $G(u_1, u_2)$ be given by
\[
G(u_1, u_2) = \begin{pmatrix} G^2_1 (u_1, u_2) + G^3_1 (u_1, u_2), G^2_2 (u_1, u_2) \\
+ G^3_2 (u_1, u_2) \end{pmatrix},
\]
where
\[
\begin{align*}
G^2_1 (u_1, u_2) &= (a_1 + 3a_1 u_1^2 + a_2) u_1 u_2 + a_3 u_2^2, \\
G^2_2 (u_1, u_2) &= (a_2 + b + 3a_1 b + a_3) u_1 u_2 + b_1 + 3a_1 b + a_3) u_2^2, \\
G^3_1 (u_1, u_2) &= (a_1 u_1^3 + a_2 u_2^2 + a_3 u_1^1 u_2^2), \\
G^3_2 (u_1, u_2) &= (a_2 u_1^3 + a_4 u_1^2 u_2^2 + a_5 u_1^1 u_2^2).
\end{align*}
\]

Then (13) can be written in the following operator form:
\[
\frac{du}{dt} = L \Delta u + G(u).
\]

3. Principle of Exchange of Stability

From the theoretical ecology, it is interesting to study the bifurcation of system (9) at steady state $(a, b)$. Bifurcation means that a change in the stability or in the types of steady state which occurs as a parameter is varied in a dissipative dynamic system; that is, the state changes during steady state which occurs as a parameter is varied in a dissipative dynamic system; therefore, in this section, we consider the attractor bifurcation of system (9) at steady state.

Firstly, we consider the linear system of (13),
\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= \Delta u_1 + a_1 u_1 + a_2 u_2, \\
\frac{\partial u_2}{\partial t} &= \lambda \Delta u_2 + a_3 u_1 + a_4 u_2,
\end{align*}
\]
and its eigenvalue problem
\[
L \phi = \beta (\lambda) \phi, \quad \phi \in H_1,
\]
\[
-\Delta \phi = \rho \phi
\]
with the Dirichlet boundary condition (15) or the Neumann boundary condition (16). Let $M_k$ be defined by
\[
M_k = \begin{pmatrix} a_{11} - \rho_k & a_{12} \\
a_{21} & a_{22} - \lambda \rho_k \end{pmatrix},
\]
It is easy to see that any eigenvector $\phi_k$ and eigenvalue $\beta_k$ of (24) can be expressed as
\[
\phi_k = \begin{pmatrix} \xi_k_1 e_k \\
\xi_k_2 e_k \end{pmatrix},
\]
where $e_k$ is as in (25) and $\beta_k$ is also the eigenvalue of $B_k$. By (24), $\beta_k$ can be written as
\[
\beta_{ik} = -\frac{1}{2} \left( (\rho_k - a_{11}) + (\lambda \rho_k - a_{22}) \right)
+ \frac{1}{2} \sqrt{\left( (\rho_k - a_{11}) - (\lambda \rho_k - a_{22}) \right)^2 + 4a_{12} a_{21}},
\]
\[
\beta_{2k} = -\frac{1}{2} \left( (\rho_k - a_{11}) + (\lambda \rho_k - a_{22}) \right)
- \frac{1}{2} \sqrt{\left( (\rho_k - a_{11}) - (\lambda \rho_k - a_{22}) \right)^2 + 4a_{12} a_{21}}.
\]


Theorem 1. Let $\lambda_0$ be the number given in (30) such that (29) is satisfied and let $K \geq 1$ be the integer such that the minimum is achieved at $\rho_K$. Then $\beta_{1K}(\lambda)$ is the first real eigenvalue of $L_\lambda$ near $\lambda = \lambda_0$ satisfying that
\[
\begin{align*}
\beta_{1K}(\lambda) &= \begin{cases} < 0, & \lambda \in \Lambda^+_K, \\
= 0, & \lambda = \lambda_0, \\
> 0, & \lambda \in \Lambda^-_K,
\end{cases}
\end{align*}
\]
\[
\text{Re} \beta_{2k}(\lambda_0) < 0, \quad \forall k \in \mathbb{N},
\]
\[
\text{Re} \beta_{ik}(\lambda_0) < 0, \quad \forall k \neq K.
\]
\[
\text{Here } \Lambda^+_K = \{ \lambda \mid \chi_K(\lambda) > 0 \} \text{ and } \Lambda^-_K = \{ \lambda \mid \chi_K(\lambda) < 0 \}.
\]

In the absence of diffusion, system (23) becomes the spatial homogeneous system
\[
\frac{du}{dt} = a_1 u_1 + a_2 u_2,
\]
\[
\frac{du}{dt} = a_3 u_1 + a_4 u_2.
\]
System (33) is local asymptotic stability if
\[ a_{11} + a_{22} < 0, \]
\[ a_{11}a_{22} - a_{12}a_{21} > 0, \]
and the Hopf bifurcation occurs when
\[ a_{11} + a_{22} = 0, \]
\[ a_{11}a_{22} - a_{12}a_{21} < 0. \]

From Theorem 1, we can infer that if condition (34) and \( \lambda \in \Lambda_{K} \) hold, then the homogeneous attracting equilibrium loses stability due to the interaction of diffusion processes and system (23) undergoes a Turing bifurcation.

### 4. Phase Transition on Homogeneous State

Hereafter, we always assume that the eigenvalue \( \beta_{IK}(\lambda) \) in (24) is simple. Based on Theorem 1, as \( \lambda \in \Lambda_{K} \), the transition of (22) occurs at \( \lambda = \lambda_{0} \), which is from real eigenvalues.

The following is the main theorem in this paper, which provides not only a precise criterion for the transition types of (22) but also globally dynamical behaviors.

**Theorem 2.** Let \( \rho_{K} \) be defined in Theorem 1, and \( e_{K} \) is the corresponding eigenvector to \( \rho_{K} \) of (25) satisfying
\[ \int_{\Omega} e_{K}^{3} dx \neq 0. \]  

For system (22), we have the following assertions.

(1) Equation (22) has a mixed transition from \((0, \lambda_{0})\); more precisely, there exists a neighborhood \( U \subset X \) of \( u = 0 \), such that \( U \) is separated into two disjoint open sets \( U_1^{\lambda} \) and \( U_2^{\lambda} \) by the stable manifold \( \Gamma_{\lambda} \) of \( u = 0 \), satisfying the following.

(a) \( U = U_1^{\lambda} + U_2^{\lambda} + \Gamma_{\lambda} \), \( b \) The transition in \( U_1^{\lambda} \) is jump. \( c \) The transition in \( U_2^{\lambda} \) is continuous.

(2) Equation (22) bifurcates in \( U_1^{\lambda} \) to a unique singular point \( v^{\lambda} \) on \( \lambda \in \Lambda_{K} \), which is attractor such that, for any \( \phi \in U_2^{\lambda} \),
\[ \lim_{t \to \infty} \| u(t, \phi) - v^{\lambda} \|_{K} = 0. \]  

(3) Equation (22) bifurcates on \( \lambda \in \Lambda_{K} \) to a unique saddle point with morse index 1.

(4) The bifurcated singular point \( v^{\lambda} \) can be expressed by
\[ v^{\lambda} = - \frac{\beta_{IK}(\lambda)}{b} \phi_{K} + o \left( \| \beta_{IK}(\lambda) \| \right). \]

Here
\[ b = \frac{1}{a_{12}a_{21} + (a_{11} - \rho_{K})^{2}} \left[ -b (b_{2} + a_{1}b + 2a_{2}a) \right. \]
\[ \cdot \left( a_{a} (a_{1} + a_{2}b + 2a_{2}a) - \rho_{K}^{2} \right. \]
\[ - (a_{1} + a_{2}b + 2a_{2}a) a (a_{1} + a_{2}b + a_{4}) \]
\[ \cdot \left. (a_{1} + a_{2}b + 2a_{2}a) (a_{1} + a_{2}b + 2a_{2}a) - \rho_{K} \right) \]
\[ + (a_{2} + 2a_{b} + a_{4}) (a_{1} + a_{2}b + 2a_{2}a) \]
\[ - \rho_{K} \left( b_{2} + 3a_{3}b + a_{4} \right) \]
\[ - (a_{1} + a_{2}b + 2a_{2}a) \]
\[ - (2a_{2}a + b_{2} + 2a_{4}b) \]
\[ \cdot (a_{2} + 2a_{b} + a_{4}) (a_{1} + a_{2}b + 2a_{2}a) - \rho_{K} \]
\[ + b_{2}a_{4}a^{2} (a_{2} + 2a_{b} + a_{4}a^{2}) \].

**Proof.** First, we need to get the reduced equation of (22) near \( \lambda = \lambda_{0} \).

Let \( u = x \cdot \phi_{K} + y \), where \( y = \sum_{i=1}^{n} y_{i} \phi_{i} \) and \( \phi_{K} \) is the eigenvector of (24) corresponding to \( \beta_{IK}(\lambda) \) at \( \lambda = \lambda_{0} \). Then the reduced equation of (22) reads
\[ \frac{dx}{dt} = \beta_{IK}(\lambda_{0}) x + \frac{1}{\langle \phi_{K}, \phi_{K} \rangle} \langle G(x \cdot \phi_{K} + y), \phi_{K} \rangle. \]

Here \( \phi_{K}^{*} \) is the conjugate eigenvector of \( \phi_{K} \). By Implicit Function Theorem, we can obtain that
\[ y = \Phi(x, \lambda) = o(\|x\|). \]

Substituting (41) into (40), we get the bifurcation equation of (22) as follows:
\[ \frac{dx}{dt} = \beta_{IK}(\lambda_{0}) x + \frac{1}{\langle \phi_{K}, \phi_{K} \rangle} \langle G(x \cdot \phi_{K} + y), \phi_{K} \rangle + o(2). \]

By (27), \( \phi_{K} \) is written as
\[ \phi_{K} = (\xi_{1} e_{K}, \xi_{2} e_{K})^{T}, \]
with \( (\xi_{1}, \xi_{2}) \) satisfying
\[ \left( \begin{array}{cc} a_{11} - \rho_{K} & a_{12} \\ a_{21} & a_{22} - \lambda_{0} \rho_{K} \end{array} \right) \left( \begin{array}{c} \xi_{1} \\ \xi_{2} \end{array} \right) = \beta_{IK}(\lambda_{0}) \left( \begin{array}{c} \xi_{1} \\ \xi_{2} \end{array} \right), \]
from which we get
\[ (\xi_{1}, \xi_{2}) = (-a_{21}, a_{11} - \rho_{K}). \]
Likewise, \( \phi_{K}^{*} \) is
\[ \phi_{K}^{*} = (\xi_{1}^{*} e_{K}, \xi_{2}^{*} e_{K})^{T}, \]
with \((\xi_1^*, \xi_2^*)\) satisfying
\[
\begin{pmatrix}
a_{11} - \rho_K & a_{21} \\
a_{22} - \lambda \rho_K
\end{pmatrix}
\begin{pmatrix}
\xi_1^* \\
\xi_2^*
\end{pmatrix}
= \beta_{1K} \begin{pmatrix}
\lambda_0 \\
\xi_1^*
\end{pmatrix},
\]
(47)
which yields
\[
(\xi_1^*, \xi_2^*) = (-a_{21}, a_{11} - \rho_K).
\]
By (22), the nonlinear operator \(G\) is
\[
\begin{pmatrix}
G_1^*(u_1, u_2) \\
G_2^*(u_1, u_2)
\end{pmatrix}
= \begin{pmatrix}
(a_0 + a_1 a + a_2) u_1^2 + (a_1 + 2 a_2 b + a_3 a) u_1 u_2 + a_4 a u_2^2 \\
a_5 u_1^2 + (2 a_6 + 2 a_7 b) u_1 u_2 + (a_8 + a_9 b) a u_2^2
\end{pmatrix},
\]
(49)
Then, in view of (45) and (48), by direct computation we derive that
\[
\langle G(x \xi_1 e_K, x \xi_2 e_K), \phi_K^* \rangle = \begin{pmatrix}
a_0 + a_1 x + a_2 x^2 \\
2 a_1 x + 2 a_2 b
\end{pmatrix} \begin{pmatrix}
\xi_1^* \\
\xi_2^*
\end{pmatrix}
+ (b_1 + a_3 a) \begin{pmatrix}
\xi_1^* \\
\xi_2^*
\end{pmatrix}
+ (2 a_6 + 2 a_7 b) \begin{pmatrix}
\xi_1^* \\
\xi_2^*
\end{pmatrix}
\cdot \int_\Omega e_k^2 dx + o(x^2).
\]
(50)
By (45) and (48), we have
\[
\langle \phi, \phi^* \rangle = \left[ a_{12} a_{21} - (a_1 - \rho_k)^2 \right] \int_\Omega e_k^2 dx, \quad (51)
\]
Hence, by (50) the reduced equation (13) is expressed as
\[
\frac{dx}{dt} = \beta_{1K}(\lambda) x + b x^2 + o(x^2),
\]
(52)
where \(b\) is the parameter as in (39). Based on Theorem A.2 in [16], this theorem follows from (52). The proof is complete. \(\square\)

**Remark 3.** If the domain \(\Omega \neq (0, L) \times D\) with \(D \in R\) being a bounded open set, then condition (36) holds true for boundary conditions (15) and (16).

If the domain \(\Omega = (0, L) \times D\) with \(D \in R\) being a bounded open set, then
\[
\int_\Omega e_k^2 dx = 0
\]
(53)
holds true for Neumann condition (16) and Dirichlet condition (15) when the number \(m\) in \(\| \rho_k \| = m^2 \pi^2 / L^2 + \rho_k^2\) is even.

Hereafter, we consider the Neumann condition (16) and let the domain \(\Omega = (0, L_1) \times (0, L_2)\) with \(L_1 \neq L_2\).

The following eigenvalue problem (24) with the equation
\[
-\Delta e_k = \rho_k e_k, \quad \frac{\partial e_k}{\partial n} \bigg|_{x_1} = 0
\]
(54)
has eigenfunctions \(e_k\) and eigenvalues \(\rho_k\) as follows:
\[
e_k = \cos \frac{k_1 \pi x_1}{L_1} \cos \frac{k_2 \pi x_2}{L_2}, \quad \rho_k = \pi^2 \left( \frac{k_1^2}{L_1^2} + \frac{k_2^2}{L_2^2} \right),
\]
(55, 56)
Here \(\rho_0 = 0\) and \(e_0 = 1\).

Denote \(K = (K_1, K_2)\), the pair of integers satisfying (30), and simply denote \(K_1 = (K_1, 0)\) and \(K_2 = (0, K_2)\); then we have the following.

**Theorem 4.** Let \(\eta\) be the parameter defined by
\[
\eta = \frac{(9/16) \bar{H}(\xi, \xi^*) + (1/4) H(\xi, \xi^*)}{a_{12} a_{21} + (a_1 - \rho_k)^2},
\]
where \(H(\xi, \xi^*) = a_1 \xi_1^* \xi_1 + a_2 \xi_2^* \xi_2 + a_3 \xi_1 \xi_1^* + a_4 \xi_2 \xi_2^* + b_1 \xi_1^* \xi_2 + a_5 \xi_1 \xi_2^* + a_6 \xi_2 \xi_1^*\) and \(\bar{H}(\xi, \xi^*)\) is in Appendix and \(\xi, \xi^*\) are defined in the proof.

Assume that the eigenvalue \(\beta_{1K}(\lambda)\) satisfying (28) is simple; then for system (22), we have the following assertions:

(1) This system has a transition from \((0, \lambda_0)\); that is, \(u = 0\) is asymptotically stable in \(\lambda \in \Lambda_K^*\) and unstable for \(\lambda \in \Lambda_K^*\); which transits to a stable equilibrium at \(\lambda = \lambda_0\).

(2) If \(\eta > 0\), then (22) has a jump transition from \((0, \lambda_0)\) and bifurcates on \(\lambda \in \Lambda_K^*\) to exactly two saddle points \(v_1^*\) and \(v_2^*\) with the Morse index one.

(3) If \(\eta < 0\), then (22) has a continuous transition from \((0, \lambda_0)\), which is an attractor bifurcation.

(4) The bifurcated singular points \(v_1^*\) and \(v_2^*\) in the above cases can be expressed in the following form:
\[
v_{1,2}^* = \left[ \beta_{1K}(\lambda) \right] \frac{1}{\eta} e_k + o \left( \frac{\| \rho_k \|}{\eta} \right),
\]
(58)
**Proof.** Assertion (1) follows from (32). To prove assertions (2) and (3), we need to get the reduced equation of (22) to the center manifold near \(\lambda = \lambda_0\).

Let \(u = x \cdot \varphi_K + \Phi\), where \(\varphi_K\) is the eigenvector of (25) corresponding to \(\beta_{1K}(\lambda)\) at \(\lambda = \lambda_0\) and \(\Phi(x)\) the center manifold function of (22). Then the reduced equation of (22) takes the following form:
\[
\frac{dx}{dt} = \beta_{1K}(\lambda_0) x + \frac{1}{\langle \varphi_K, \varphi_K^* \rangle} \langle G(x \cdot \varphi_K + \Phi), \varphi_K^* \rangle.
\]
(59)
Here \(\varphi_K^*\) is the conjugate eigenvector of \(\varphi_K\).

By (27), \(\varphi_K\) is written as
\[
\varphi_K = (\xi_1 e_K, \xi_2 e_K)^T,
\]
(60)
with \((\xi_1, \xi_2)\) satisfying (45).
Likewise, \( \varphi_K^* \) is

\[
\varphi_K^* = (\xi_1^* e_K, \xi_2^* e_K)^T,
\]

with \( (\xi_1^*, \xi_2^*) \) satisfying (46).

It is known that the center manifold function

\[
\Phi(x) = (\Phi_1(x), \Phi_2(x)) = o(x^3).
\]

By using the formula for center manifold functions in [13, 14, 16], \( \Phi \) satisfies

\[
\Phi = \Phi_0 + \cdots + \Phi_4 \text{ where } \Phi_4 \text{ satisfies } \eta \cdot \Phi = o(x^3).
\]

Inserting (66) into (59), by (60) and (61) we get

\[
\langle G(x \varphi_K^* + \Phi), \varphi_K^* \rangle = \frac{9L_1 L_2}{64} x^3 \overline{H}(\xi, \xi^*) + \frac{L_1 L_2}{16} x^3 H(\xi, \xi^*) + o(x^3),
\]

where \( \overline{H}(\xi, \xi^*) = a_3 \xi_1^* \xi_1^* + a_4 \eta_1 \xi_1^* \xi_2^* + a_5 \xi_1^* \xi_1^* \xi_1^* + b_3 \eta_2 \xi_2^* \xi_2^* + b_3 \xi_1^* \xi_1^* \xi_1^* + b_3 \xi_1^* \xi_1^* \xi_1^* \)

and \( H(\xi, \xi^*) \) is in Appendix.

In view of (70), it follows that

\[
\langle \phi_K, \varphi_K^* \rangle = [a_{12} a_{21} + (a_{11} - \rho_K)^2] \int_\Omega x^2 d\Omega
\]

\[
= \frac{L_1 L_2}{4} [a_{12} a_{21} + (a_{11} - \rho_K)^2].
\]

Hence, by (73) the reduced equation (13) is expressed as

\[
\frac{dx}{dt} = \beta_{1K} (\lambda) x + \eta x^3 + o(x^3).
\]

Based on Theorem A.1 in [16], this theorem follows from (73). The proof is complete. \( \square \)

5. Concluding Remarks and Example

In this paper, we have studied the Turing bifurcation introduced by Alan Turing and attractor bifurcation developed by Ma and Wang [13] of gene propagation population model governed by reaction-diffusion equation.

Theorems 2 and 4 tell us that the critical value \( \lambda_0 \) of diffusion constant given by

\[
\lambda_0 = \frac{a_{22} \rho_K - (a_{11} a_{22} - a_{12} a_{21})}{(\rho_K - a_{11}) \rho_K}
\]
By Theorem 1, we obtain that the transition conditions are satisfied.

From Theorem 4, \( \eta \approx -4527.181405 < 0 \), and system (22) has a continuous transition from \((0, \lambda_0)\), which is an attractor bifurcation.

Since \( \rho_K + a_1 < 0 \), we infer that if \( \lambda < \lambda_0 \), then \( \beta_1(\lambda) > 0 \), and the Turing instability occurs. By numerical simulation, we have shown that the gene population model is able to sustain Turing patterns (Figure 1).

**Appendix**

**The Expressions of** \( H(\xi, \xi^*) \)

The Expressions of \( H(\xi, \xi^*) \) are as follows:

\[
H(\xi, \xi^*) = 4a_3\xi^*_1b\Phi_1^{2K+1}\xi_2 + 4b\xi^*_2\Phi_1^{2K+1}a_3\xi_2 \\
+ 4\xi^*_2a_3b\Phi_1^{2K}\xi^*_1 + 4\xi^*_3a_4b\Phi_1^{2K}\xi^*_2 \\
+ 4\xi^*_3a_2b\Phi_1^{2K}\xi^*_1 + 4\xi^*_3a_4b\Phi_1^{2K}\xi^*_2 \\
+ 4\xi^*_3a_2b\Phi_1^{2K}\xi^*_1 + 4\xi^*_3a_4b\Phi_1^{2K}\xi^*_2
\]

plays a crucial role in determining the attractor bifurcation and Turing bifurcation when the diffusion parameter \( \lambda \) crosses the critical value \( \lambda_0 \), and the uniform stationary state \((a, b)\) loses its stability, which yields the Turing or attractor bifurcation.

We give some examples to illustrate our main theories.

**Example 5.** In system (9), we let

\[
\begin{align*}
\gamma_1 &= \frac{2773376069253}{499999999994} \\
\gamma_2 &= \frac{3789926287167}{499999999994} \\
\gamma_3 &= \frac{810843220017}{499999999994} \\
\gamma_4 &= \frac{45454545454}{499999999994} \\
\gamma_5 &= \frac{4789523227559}{499999999994} \\
\gamma_6 &= \frac{249999999997}{499999999994} \\
\gamma_7 &= \frac{43625576135}{249999999997} \\
\gamma_8 &= \frac{3109.685536}{249999999997}
\end{align*}
\]

and then the steady state \((a, b)\) of system (9) is

\[
\begin{align*}
a &= \frac{732070686076807741207077}{1417067211664436233221844} \\
b &= \frac{380119934758603124485687}{708533605832218116610922}
\end{align*}
\]

where \( 0 < a < b < 1 \).

If we set \( \Omega = (0, 40\pi) \times (0, 60\pi) \), then \( \rho_K = 13/14400 \), where \( K = (1,1) \), and then

\[
\lambda_0 = \frac{814910923617150223684573395768233809936382690140395479526347826117214934665200}{262055733351368170238516966160634367981740699395562313482933174917881678669} \approx 3109.685536.
\]
Acknowledgments

This paper was partially supported by National Natural Science Foundation of China (Grants no. 11401062 and no. 11371386), Research Fund for the National Natural Science Foundation of Chongqing CSTC (Grant no. cstc2014jcyA0080), Scientific and Technological Research Program of Chongqing Municipal Education Commission (Grant no. KJ1400937), and the Scientific Research Foundation of CQUT (Grant no. 2012ZZD37).

References


Competing Interests

The author declares that there is no conflict of interests regarding the publication of this paper.