Electronic Journal of Qualitative Theory of Differential Equations
2017, No. **42**, 1–17; doi: 10.14232/ejqtde.2017.1.42 http://www.math.u-szeged.hu/ejqtde/

Bifurcation analysis of a diffusive predator–prey model in spatially heterogeneous environment

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Received 30 September 2016, appeared 22 May 2017
Communicated by Jeff R. L. Webb

Abstract. We investigate positive steady states of a diffusive predator–prey model in spatially heterogeneous environment. In comparison with the spatially homogeneous environment, the dynamics of the predator–prey model of spatial heterogeneity is more complicated. Our studies show that if dispersal rate of the prey is treated as a bifurcation parameter, for some certain ranges of death rate and dispersal rate of the predator, there exist multiply positive steady state solutions bifurcating from semi-trivial steady state of the model in spatially heterogeneous environment, whereas there exists only one positive steady state solution which bifurcates from semi-trivial steady state of the model in homogeneous environment.

Keywords: predator–prey, spatial heterogeneity, bifurcation.

2010 Mathematics Subject Classification: 35B35, 91B18, 35C23.

1 Introduction

Understanding the effects of dispersal and environmental heterogeneity on the dynamics of populations is a very important and challenging topic in mathematical ecology [5]. Dispersal is an important aspect of the life histories of many organisms. It allows individuals to search for resources and interact with members of their own and other species, and distribute themselves more reasonably in space, etc. The spatial heterogeneity can greatly influence the persistence, extinction and coexistence of populations, and it often give rise to certain interesting phenomena. It is demonstrated in [7] that for a Lotka–Volterra competitive model in spatially heterogeneous environment with the same resource, the slower diffuser always prevails. However, for a classical Lotka–Volterra competition system [13] with the total resource being fixed exactly at the same level, the environmental heterogeneity is usually superior to its homogeneous counterpart in the present of diffusion. Previous works [19] illustrate that for a predator–prey model in patchy environment, the spatial heterogeneity has a stabilization effects on the predator–prey interaction. There are many research results concerning the effects of dispersal and spatial heterogeneity of the environment on the dynamics of populations via predator–prey models [8, 11] and competition models [4, 13, 14, 16].

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In this paper, we study a reaction–diffusion system modelling predator–prey interactions in spatially heterogeneous environment with the following form:

$$\begin{cases} \dfrac{\partial u}{\partial t} = \mu\Delta u + u(m(x)-u) - \dfrac{uv}{1+u} & \text{in } \Omega\times(0,\infty), \\ \dfrac{\partial v}{\partial t} = \nu\Delta v + \dfrac{luv}{1+u} - \gamma v & \text{in } \Omega\times(0,\infty), \\ \dfrac{\partial u}{\partial n} = \dfrac{\partial v}{\partial n} = 0 & \text{on } \partial\Omega\times(0,\infty), \\ u(x,0)=u_0(x), v(x,0)=v_0(x) & \text{in } \Omega, \end{cases} \tag{1.1}$$

where $u(x,t)$ and $v(x,t)$ denote respectively the population density of the prey and predator with corresponding migration rates μ and ν, and are required to be nonnegative. The function $m(x)$ accounts for spatially heterogeneous carrying capacity or intrinsic growth rate of the prey population, γ is death rate of the predator. $\Delta := \sum_{i=1}^{N} \partial^2/\partial x_i^2$ is the Laplace operator in $\mathbb{R}^N (N \geq 1)$ which characterizes the random motion of the predator and prey, the habitat Ω is assumed to a bounded domain in $\mathbb{R}^N$ with smooth boundary, denoted by $\partial\Omega$. $\partial u/\partial n = \nabla u \cdot n$, where n represents the outward unit normal vector on $\partial\Omega$, and the homogeneous Neumann boundary condition means that no flux cross the boundary of the habitat. The reaction term is a Holling type II function response which describes the change in the density of prey attached per unit time per predator as the prey density changes. We shall assume that μ, ν, l and γ are all positive constants, u_0 and v_0 are nonnegative functions which are not identically to zero.

As was shown in [17], the joint action of migration and spatial heterogeneity can greatly influence the local dynamics of (1.1). To be more specific, in comparison with the homogeneous environment, for some certain ranges of death rate of the predator, the stability of semi-trivial steady state of (1.1) in spatially heterogeneous environment can change multiply times as the migration of the prey varies from small to large. In this paper, we would like to further investigate whether positive steady states of (1.1) can bifurcate from the semi-trivial steady state. Hence, the function $m(x)$ is assumed to be nonconstant for reflecting the spatial heterogeneity. Throughout this paper, we shall assume that $m(x)$ satisfies

$$m(x) > 0, \text{ and is nonconstant and Hölder continous in } \overline{\Omega}. \tag{1.2}$$

It is known [16] that under the assumption (1.2), the following logistic equation

$$\begin{cases} \mu\Delta w + w(m(x)-w) = 0 & \text{in } \Omega, \\ \dfrac{\partial w}{\partial n} = 0 & \text{on } \partial\Omega \end{cases} \tag{1.3}$$

admits a unique positive solution for every $\mu > 0$, denoted by $\theta(x,\mu)$, and $\theta(x,\mu) \in C^2(\overline{\Omega})$. We sometimes write $\theta(x,\mu)$ as θ for simplicity. By Lemma 2.3 in Section 2, the stability of semi-trivial steady state $(\theta, 0)$ of (1.1) is determined by the sign of the least eigenvalue (denoted by λ_1) of

$$\nu\Delta\psi + \left(\frac{l\theta}{1+\theta} - \gamma\right)\psi + \lambda\psi = 0 \quad \text{in } \Omega, \quad \frac{\partial\psi}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

It is well known that λ_1 is a smooth function of both μ and ν. By Lemma 2.4 in Section 2, we see that

$$\lim_{\nu\to 0} \lambda_1 = \gamma - \frac{l \max_{\overline{\Omega}} \theta}{1 + \max_{\overline{\Omega}} \theta} \quad \text{and} \quad \lim_{\nu\to\infty} \lambda_1 = \gamma - K(\mu),$$

where $K(\mu) = \frac{l}{|\Omega|}\int_\Omega \frac{\theta}{1+\theta}$. According to [17, Theorem 2], we have the following results: (1) $K(\mu) > K(0) = \frac{l}{|\Omega|}\int_\Omega \frac{m}{1+m}$ for every $\mu > 0$; (2) For sufficiently large μ, $K(\mu) > \lim_{\mu\to\infty} K(\mu) = \frac{l\overline{m}}{1+\overline{m}}$. Hence, we are able to give the possible diagram of $K(\mu)$ as figure 1.1. The exact picture

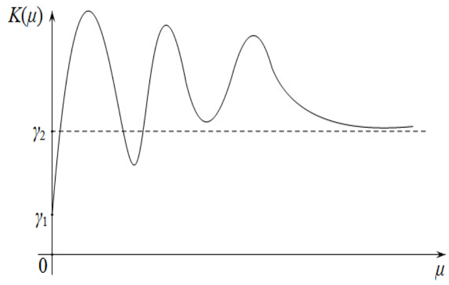

Figure 1.1: Possible shape of $K(\mu)$, where γ_1 and γ_2 are defined as in Theorem A (see below).

of $K(\mu)$ is more complex since θ is not necessarily monotone function with respect to μ.

To investigate more information about how $(\theta, 0)$ changes its stability as diffusion rate of the prey varies from small to large, Lou and Wang [17] further assumed that

$$\Omega \text{ is an interval}, \quad m(x) \in C^2(\overline{\Omega}), \quad m_x \not\equiv 0 \quad \text{and} \quad m_{xx} \not\equiv 0 \quad \text{in } \overline{\Omega}. \tag{1.4}$$

Under the assumptions (1.2) and (1.4), Lou and Wang [17] systematically investigated the stability of semi-trivial steady state $(\theta, 0)$. For five different ranges of death rate of the predator, they showed that $(\theta, 0)$ could change its stability multiply times as dispersal rate of the prey varies and obtained the following results:

Theorem A ([17])**.** *Suppose that the nonconstant function $m(x)$ satisfies (1.2), then the following conclusions hold.*

(i) If $\gamma < \gamma_1 := \frac{l}{|\Omega|}\int_\Omega \frac{m}{1+m}$, $(\theta, 0)$ is unstable for any $\mu, \nu > 0$.

(ii) If $\gamma_1 < \gamma < \gamma_2 := \frac{l\overline{m}}{1+\overline{m}}$, where $\overline{m}$ is the average of m, i.e. $\overline{m} = \frac{1}{|\Omega|}\int_\Omega m$, there exists a unique $\overline{\nu} = \overline{\nu}(\gamma, m, \Omega) > 0$ such that for every $\nu < \overline{\nu}$, $(\theta, 0)$ is unstable for any $\mu > 0$; while for every $\nu > \overline{\nu}$, $(\theta, 0)$ changes its stability at least once as μ varies from 0 to ∞.

(iii) If $\gamma_2 < \gamma < \gamma_3 := \sup_{\mu>0} \frac{l}{|\Omega|}\int_\Omega \frac{\theta}{1+\theta}$, and m also satisfies (1.4), then there exists a unique $\overline{\nu} = \overline{\nu}(\gamma, m, \Omega) > 0$ such that for every $\nu < \overline{\nu}$, $(\theta, 0)$ changes its stability at least once as μ varies from 0 to ∞; while for every $\nu > \overline{\nu}$, $(\theta, 0)$ changes its stability at least twice as μ varies from 0 to ∞.

(iv) If $\gamma_3 < \gamma < \gamma_4 := \frac{l\max_{\overline{\Omega}} m}{1+\max_{\overline{\Omega}} m}$, and m also satisfies (1.4), then there exists a unique $\overline{\nu} = \overline{\nu}(\gamma, m, \Omega) > 0$ such that for every $\nu < \overline{\nu}$, $(\theta, 0)$ changes its stability at least once as μ varies from 0 to ∞; for every $\nu > \overline{\nu}$, $(\theta, 0)$ is stable for any $\mu > 0$.

(v) If $\gamma > \gamma_4$, $(\theta, 0)$ is stable for arbitrary $\mu, \nu > 0$.

Remark 1.1. From Theorem A, we see that Cases (i) and (v) can not have bifurcation from semi-trivial steady state $(\theta, 0)$. Therefore, it suffices to investigate Cases (ii), (iii) and (iv) in this paper. For these three cases, we have the following statements.

(a) For every $\gamma \in (\gamma_1, \gamma_2)$, if $\nu > \overline{\nu}$, $(\theta, 0)$ changes stability at least once, from stable to unstable as μ varies. Generically, we may assume that there exists some constant $\mu_1^* > 0$ such that $\lambda_1(\mu_1^*) = 0$ and $\frac{\partial \lambda_1}{\partial \mu}(\mu_1^*) < 0$, i.e., $\lambda_1(\mu_1^*)$ is nondegenerate, where λ_1 is the principal eigenvalue of (2.1).

(b) For every $\gamma \in (\gamma_2, \gamma_3)$, if $\nu > \overline{\nu}$, $(\theta, 0)$ changes stability at least twice, firstly from stable to unstable and then from unstable to stable as μ varies; If $\nu < \overline{\nu}$, $(\theta, 0)$ changes stability at least once, from unstable to stable as μ varies. Hence, we may suppose that if $\nu > \overline{\nu}$, there exist at least two positive constants $\mu_2^* < \mu_3^*$ such that $\lambda_1(\mu_2^*) = \lambda_1(\mu_3^*) = 0$ and $\frac{\partial \lambda_1}{\partial \mu}(\mu_2^*) < 0$, $\frac{\partial \lambda_1}{\partial \mu}(\mu_3^*) > 0$; If $\nu < \overline{\nu}$, there exists some constant $\mu_4^* > 0$ such that $\lambda(\mu_4^*) = 0$ and $\frac{\partial \lambda_1}{\partial \mu}(\mu_4^*) > 0$.

(c) For every $\gamma \in (\gamma_3, \gamma_4)$, if $\nu < \overline{\nu}$, $(\theta, 0)$ changes stability at least once, from unstable to stable as μ varies. Therefore, we may assume that there exists some constant $\mu_5^* > 0$ such that $\lambda_1(\mu_5^*) = 0$ and $\frac{\partial \lambda_1}{\partial \mu}(\mu_5^*) > 0$. In other words, λ_1 is nondegenerate at $\mu = \mu_5^*$, this nondegeneracy assumption is very important for applying local bifurcation theorem.

In view of Theorem A and Remark 1.1, we are able to apply bifurcation theory to inquire how many positive solutions which can bifurcate from semi-trivial steady state $(\theta, 0)$. Furthermore, we can investigate local stability of the bifurcating solutions. Our main conclusions of this paper are the following Theorems 1.2 and 1.3. If dispersal rate of the prey μ is treated as a bifurcation parameter, we have the following conclusions:

Theorem 1.2. *Suppose that $m(x)$ satisfies (1.2), then the following conclusions hold.*

(a) If $\gamma_1 < \gamma < \gamma_2$, for every $\nu > \overline{\nu}$, there exists some small $\delta_1 > 0$ such that a branch of steady state solution (u_1^*, v_1^*) of (1.1) bifurcates from $(\theta, 0)$ at $\mu = \mu_1^*$, and it can be parameterized by μ for the range $\mu \in (\mu_1^*, \mu_1^* + \delta_1)$. In addition, the bifurcating solution (u_1^*, v_1^*) is locally stable for $\mu \in (\mu_1^*, \mu_1^* + \delta_1)$.

(b) If $\gamma_2 < \gamma < \gamma_3$ and $m(x)$ satisfies (1.4) as well, then

(i) for every $\nu > \overline{\nu}$, there exists some small $\delta_2 > 0$ such that two branches of steady state solutions (u_i^*, v_i^*) $(i = 2, 3)$ of (1.1) bifurcate from $(\theta, 0)$ at $\mu = \mu_2^*, \mu_3^*$, and they can be parameterized by μ for $\mu \in (\mu_2^*, \mu_2^* + \delta_2)$ and $\mu \in (\mu_3^* - \delta_2, \mu_3^*)$, respectively. Moreover, the bifurcating solution (u_i^*, v_i^*) is locally stable for $\mu \in (\mu_2^*, \mu_2^* + \delta_2)$ and $\mu \in (\mu_3^* - \delta_2, \mu_3^*)$, respectively.

(ii) for any $\nu < \overline{\nu}$, there exists some small $\delta_3 > 0$ such that a branch of steady state solution (u_4^*, v_4^*) of (1.1) bifurcates from $(\theta, 0)$ at $\mu = \mu_4^*$, and it can be parameterized by μ for $\mu \in (\mu_4^* - \delta_3, \mu_4^*)$. Furthermore, the bifurcating solution (u_4^*, v_4^*) is locally stable for $\mu \in (\mu_4^* - \delta_3, \mu_4^*)$.

(c) If $\gamma_3 < \gamma < \gamma_4$ and $m(x)$ satisfies (1.4) as well, for every $\nu < \overline{\nu}$, there exists some small $\delta_4 > 0$ such that a branch of steady state solution (u_5^*, v_5^*) of (1.1) bifurcates from $(\theta, 0)$ at $\mu = \mu_5^*$, and it can be parameterized by μ for $\mu \in (\mu_5^* - \delta_4, \mu_5^*)$. In addition, the bifurcating solution (u_5^*, v_5^*) is locally stable for $\mu \in (\mu_5^* - \delta_4, \mu_5^*)$.

If dispersal rate of the predator ν is regarded as a bifurcation parameter, we also have the corresponding results.

Theorem 1.3. *Suppose that $m(x)$ satisfies (1.2), then the following conclusions hold.*

(a) If $\gamma_1 < \gamma < \gamma_2$, for small μ, there exists some small $\rho_1 > 0$ such that a branch of steady state solution (u_{1*}, v_{1*}) to (1.1) bifurcates from $(\theta, 0)$ at $\nu = \nu_1^*$, and it can be parameterized by ν for the range $\nu \in (\nu_1^* - \rho_1, \nu_1^*)$. In addition, the bifurcating solution (u_{1*}, v_{1*}) is locally stable for $\nu \in (\nu_1^* - \rho_1, \nu_1^*)$ and the branch of steady state solutions to (1.1) bifurcating from $(\nu_1^*, \theta, 0)$ extends to zero in ν.

(b) If $\gamma_2 < \gamma < \gamma_3$ and $m(x)$ satisfies (1.4) as well, for small or large μ, there exists some small $\rho_2 > 0$ such that two branches of steady state solutions (u_{i*}, v_{i*}) $(i = 2, 3)$ to (1.1) bifurcate from $(\theta, 0)$ at $\nu = \nu_2^*, \nu_3^*$, respectively, and they can be parameterized by ν for $\nu \in (\nu_2^* - \rho_2, \nu_2^*)$ and $\nu \in (\nu_3^* - \rho_2, \nu_3^*)$, respectively. Moreover, the bifurcating solution (u_{i*}, v_{i*}) is locally stable for $\nu \in (\nu_2^* - \rho_2, \nu_2^*)$ and $\nu \in (\nu_3^* - \rho_2, \nu_3^*)$, respectively, and the branch of steady state solutions to (1.1) bifurcating from $(\nu_i^*, \theta, 0)$ $(i = 2, 3)$ extends to zero in ν.

(c) If $\gamma_3 < \gamma < \gamma_4$ and $m(x)$ satisfies (1.4) as well, for small μ, there exists some small $\rho_3 > 0$ such that a branch of steady state solution (u_{4*}, v_{4*}) to (1.1) bifurcates from $(\theta, 0)$ at $\nu = \nu_4^*$, and it can be parameterized by ν for the range $\nu \in (\nu_4^* - \rho_3, \nu_4^*)$. Furthermore, the bifurcating solution (u_{4*}, v_{4*}) is locally stable for $\nu \in (\nu_4^* - \rho_3, \nu_4^*)$ and the branch of steady state solutions to (1.1) bifurcating from $(\nu_4^*, \theta, 0)$ extends to zero in ν.

For predator–prey models in spatially homogeneous environment, there have been many works concerning the local or global bifurcation results [1,2,9,10,21], we here use bifurcation theory to examine a predator prey model in spatial heterogeneity of the environment and demonstrate that positive steady state solutions could bifurcate from semi-trivial steady state of the model. Theorem 1.3 tells us that the bifurcation branch of positive solutions to (1.1) can be extended from $(\nu_i^*, \theta, 0)$ $(i = 1, 2, 3, 4)$ to zero in ν. However, it is quite difficult to extend the results of Theorem 1.2 to global bifurcation. One of the main reasons is that the limit behavior of positive steady states as dispersal rate of the prey approaches to zero is not clear. A deep understanding of the limit behavior of positive steady states of the model with small dispersal rate seems to be a very interesting and challenging problem, awaiting for further investigation.

The rest of this paper is organized as follows: In Section 2 we present Lemmas 2.1–2.4. Section 3 is devoted to the proof of Lemmas 3.1–3.9, Theorems 1.2, 1.3 and Theorem 3.10.

2 Preliminaries

In this section, we will present several lemmas which shall be used in subsequence analysis.

Lemma 2.1. *Suppose that $m(x)$ satisfies (1.2), then*

(i) $\mu \mapsto \theta(x, \mu)$ is a smooth mapping from $\mathbb{R}^+$ to $C^2(\overline{\Omega})$. Moreover, $\lim_{\mu \to 0} \theta = m$ and $\lim_{\mu \to \infty} \theta = \overline{m}$ uniformly on $\overline{\Omega}$, where $\overline{m}$ is defined as in Theorem A.

(ii) For any $\mu > 0$, $\max_{\overline{\Omega}} \theta < \max_{\overline{\Omega}} m$ and $\min_{\overline{\Omega}} \theta > \min_{\overline{\Omega}} m$. In particular, $\|\theta\|_{L^\infty(\Omega)} < \|m\|_{L^\infty(\Omega)}$.

Proof. (i) To prove that $\mu \mapsto \theta(x, \mu)$ is a smooth mapping from $\mathbb{R}^+$ to $C^2(\overline{\Omega})$, it suffices to verify that $\theta(x, \mu)$ is differentiable with respect to μ. Let $X = \mathbb{R}^+, Y = W_0^{2,p}(\Omega)$ and $Z = L^p(\Omega)$. Define the operator

$$F = F(\lambda, u) = -\lambda \Delta u - u(m - u),$$

then

$$F_u(\mu,\theta)\phi = -\mu\Delta\phi - (m-2\theta)\phi$$

with $\phi \in Y$. Clearly, $F(\mu,\theta)=0$. It is not hard to see that F is a continuous map from $X \times Y$ into Z and F_u is also a continuous map from Y into Z. By (1.3) and the positivity of θ, we see that zero is the smallest eigenvalue of the operator $-\mu\Delta - (m-\theta)$. By the comparison principle for eigenvalues and the positivity of θ, the smallest eigenvalue of the operator $F_u(\mu,\theta)$ is strictly positive, hence $F_u(\mu,\theta)$ is invertible. By the implicit function theorem [5], $\theta(x,\mu)$ is differentiable with respect to μ.

The limiting behavior of θ as μ goes to zero or infinity is well known, for instance, see [16]. As for (ii), the proof is standard. See e.g. [18]. □

Lemma 2.2. *For any $\mu > 0$, we have $\frac{1}{|\Omega|}\int_\Omega m < \max_{\overline{\Omega}}\theta$.*

Proof. Dividing both sides of the equation of θ of (1.3) and integrating by parts, after some reorganization, we find

$$\int_\Omega m < \int_\Omega m + \mu\int_\Omega \frac{|\nabla\theta|^2}{\theta^2} = \int_\Omega \theta.$$

Hence $\frac{1}{|\Omega|}\int_\Omega m < \max_{\overline{\Omega}}\theta$ for any $\mu > 0$. □

Lemma 2.3. *The semi-trivial steady state $(\theta,0)$ is stable/unstable if and only if the following eigenvalue problem, for $(\lambda_1,\psi)\in\mathbb{R}\times C^2(\overline{\Omega})$, has a positive/negative principle eigenvalue (denoted by λ_1):*

$$\begin{cases} \nu\Delta\psi + \left(\dfrac{l\theta}{1+\theta} - \gamma\right)\psi + \lambda\psi = 0 & \text{in } \Omega, \\ \dfrac{\partial\psi}{\partial n} = 0 \quad \text{on } \partial\Omega, \quad \psi > 0 & \text{in } \overline{\Omega}. \end{cases} \tag{2.1}$$

Proof. It follows from similar argument to that of [3, Lemma 5.5]. □

Lemma 2.4. *The smallest eigenvalue λ_1 of (2.1) depends smoothly on $\nu > 0$. Moreover,*

(i) λ_1 is strictly monotone increasing in ν.

(ii) λ_1 satisfies the following properties:

$$\lim_{\nu\to 0}\lambda_1 = \gamma - \frac{l\max_{\overline{\Omega}}\theta}{1+\max_{\overline{\Omega}}\theta}, \qquad \lim_{\nu\to\infty}\lambda_1 = \gamma - \frac{1}{|\Omega|}\int_\Omega \frac{l\theta}{1+\theta}.$$

Proof. The smooth dependence of λ_1 on ν can be found in [5]. Part (i) can be established by the variational characterization of λ_1. Part (ii) can be proved by using Part (i) of Lemma 2.1, we skip it here. □

3 Local bifurcation of steady states

In this section, by applying local bifurcation theory [6,20], we will choose dispersal rates of the prey and predator as bifurcation parameters, respectively, and prove its corresponding local bifurcation conclusions. To this end, we write positive steady states of (1.1) as:

$$\begin{cases} \mu\Delta u + u(m(x)-u) - \dfrac{uv}{1+u} = 0 & \text{in } \Omega, \\ \nu\Delta v + \dfrac{luv}{1+u} - \gamma v = 0 & \text{in } \Omega, \\ \dfrac{\partial u}{\partial n} = \dfrac{\partial v}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{3.1}$$

Set $X = \{(u,v) \in W^{2,p}(\Omega) \times W^{2,p}(\Omega) : \partial u/\partial n = \partial v/\partial n = 0 \text{ on } \partial\Omega\}$ and $Y = L^p(\Omega) \times L^p(\Omega)$ with $p > N$. Define the operator $F(\mu,u,v) : (0,\infty) \times X \to Y$ by

$$F(\mu,u,v) = \begin{pmatrix} \mu\Delta u + u(m(x) - u) - \dfrac{uv}{1+u} \\ \nu\Delta v + \dfrac{luv}{1+u} - \gamma v \end{pmatrix}.$$

We observe that $F(\mu,\theta,0) = 0$ and the derivatives $D_\mu F(\mu,u,v)$, $D_{(u,v)}F(\mu,u,v)$ and $D_\mu D_{(u,v)}F(\mu,u,v)$ exist and are continuous close to $(\mu,\theta,0)$.

3.1 The proof of Theorem 1.2.

Lemma 3.1. *Suppose that* (1.2) *holds. If $\gamma_1 < \gamma < \gamma_2$, for every $\nu > \overline{\nu}$, there exists some small $\delta_1 > 0$, some function $\mu_1(s) \in C^2(-\delta_1,\delta_1)$ with $\mu_1(0) = \mu_1^*$ such that all nonnegative steady state solutions of* (1.1) *near $(\mu_1^*,\theta,0)$ can be parameterized as*

$$(\mu,u_1^*,v_1^*) = (\mu_1(s),\theta + s\varphi_1^* + s^2\phi_1^*(s), s\psi_1^* + s^2\omega_1^*(s)), \quad 0 < s < \delta_1, \tag{3.2}$$

where (φ_1^*,ψ_1^*) is defined as (3.6) *and* (3.3)*, and $(\phi_1^*(s),\omega_1^*(s))$ lies in the complement of the kernel of $D_{(u,v)}F|_{(\mu_1^*,\theta(x,\mu_1^*),0)}$ in X.*

Proof. By Remark 1.1 (a), we see that for every $\gamma \in (\gamma_1,\gamma_2)$, if $\nu > \overline{\nu}$, there exists some $\mu_1^* > 0$ such that the linearized system of (1.1) at $(\theta(x,\mu_1^*),0)$ satisfies

$$\nu\Delta\psi_1^* + \left(\frac{l\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)} - \gamma\right)\psi_1^* = 0 \quad \text{in } \Omega, \qquad \frac{\partial\psi_1^*}{\partial n} = 0 \quad \text{on } \partial\Omega, \tag{3.3}$$

i.e., $\lambda_1(\mu_1^*) = 0$ is the principal eigenvalue of (3.3), where $\psi_1^* > 0$ is its corresponding eigenfunction. Moreover, we have $\frac{\partial\lambda_1}{\partial\mu}(\mu_1^*) < 0$. Denote $\psi' = \frac{\partial\psi}{\partial\mu}, \theta' = \frac{\partial\theta}{\partial\mu}$, differentiate (2.1) with regard to μ, we obtain

$$\nu\Delta\psi' + \left(\frac{l\theta}{1+\theta} - \gamma\right)\psi' + \lambda_1\psi' + \frac{l\theta'}{(1+\theta)^2}\psi + \frac{\partial\lambda_1}{\partial\mu}\psi = 0.$$

Multiplying both sides of above equation by ψ with $\|\psi\|_{L^\infty(\Omega)} = 1$, integrating by parts and applying the boundary condition of ψ, we have

$$\frac{\partial\lambda_1}{\partial\mu}\int_\Omega \psi^2 = -\int_\Omega \frac{l\theta'}{(1+\theta)^2}\psi^2.$$

By regularity theory of elliptic equations [12], we have $\psi \to \psi_1^* \in C^2(\overline{\Omega})$ as $\mu \to \mu_1^*$. Hence, passing to the limit we have

$$\int_\Omega \frac{l\theta'(x,\mu_1^*)}{(1+\theta(x,\mu_1^*))^2}(\psi_1^*)^2 = -\frac{\partial\lambda_1}{\partial\mu}(\mu_1^*)\int_\Omega(\psi_1^*)^2 > 0. \tag{3.4}$$

Since

$$D_{(u,v)}F|_{(\mu_1^*,\theta(x,\mu_1^*),0)}\begin{pmatrix}\varphi\\ \psi\end{pmatrix} = \begin{pmatrix} \mu_1^*\Delta\varphi + [m - 2\theta(x,\mu_1^*)]\varphi - \dfrac{\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)}\psi \\ \nu\Delta\psi + \Big(\dfrac{l\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)} - \gamma\Big)\psi \end{pmatrix},$$

it is not difficult to verify that the kernel of $D_{(u,v)}F|_{(\mu_1^*,\theta(x,\mu_1^*),0)}$ is spanned by (φ_1^*, ψ_1^*) and $\dim \mathcal{N}(D_{(u,v)}F|_{(\mu_1^*,\theta(x,\mu_1^*),0)}) = 1$, where ψ_1^* is the unique positive solution of (3.3) up to a constant multiplier, and φ_1^* is uniquely determined by

$$\mu_1^*\Delta\varphi_1^* + [m - 2\theta(x,\mu_1^*)]\varphi_1^* - \frac{\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)}\psi_1^* = 0 \quad \text{in } \Omega, \qquad \frac{\partial \varphi_1^*}{\partial n} = 0 \quad \text{on } \partial\Omega. \tag{3.5}$$

By (1.3) and the positivity of θ, we see that zero is the smallest eigenvalue of the operator $-\mu_1^*\Delta - (m - \theta(x,\mu_1^*))$ with homogeneous Neumann boundary condition. By the comparison principle for eigenvalues and the positivity of θ, the smallest eigenvalue of the operator $-\mu_1^*\Delta - (m - 2\theta(x,\mu_1^*))$ with homogeneous Neumann boundary condition is strictly positive, thus

$$\varphi_1^* = [-\mu_1^*\Delta - (m - 2\theta(x,\mu_1^*))]^{-1}\left[-\frac{\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)}\psi_1^*\right]. \tag{3.6}$$

Moreover, it follows from the Fredholm alternative that $\operatorname{codim}\mathcal{R}\big(D_{(u,v)}F|_{(\mu_1^*,\theta(x,\mu_1^*),0)}\big) = 1$. In order to apply the bifurcation theory due to Crandall and Rabinowitz [6], it suffices to check the following transversality condition:

$$D_\mu D_{(u,v)}F|_{(\mu_1^*,\theta(x,\mu_1^*),0)}\begin{pmatrix}\varphi_1^*\\ \psi_1^*\end{pmatrix} \notin \mathcal{R}(D_{(u,v)}F|_{(\mu_1^*,\theta(x,\mu_1^*),0)}).$$

We argue by contradiction. If not, since

$$D_\mu D_{(u,v)}F|_{(\mu_1^*,\theta(x,\mu_1^*),0)}\begin{pmatrix}\varphi_1^*\\ \psi_1^*\end{pmatrix} = \begin{pmatrix}\Delta\varphi_1^* - 2\theta'(x,\mu_1^*)\varphi_1^* - \dfrac{\theta'(x,\mu_1^*)}{[1+\theta(x,\mu_1^*)]^2}\psi_1^*\\ \dfrac{l\theta'(x,\mu_1^*)}{[1+\theta(x,\mu_1^*)]^2}\psi_1^*\end{pmatrix},$$

there exists some function $(\varphi,\psi) \in X$ such that

$$\begin{cases}\mu_1^*\Delta\varphi + [m - 2\theta(x,\mu_1^*)]\varphi - \dfrac{\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)}\psi = \Delta\varphi_1^* - 2\theta'(x,\mu_1^*)\varphi_1^* - \dfrac{\theta'(x,\mu_1^*)}{[1+\theta(x,\mu_1^*)]^2}\psi_1^*,\\ \nu\Delta\psi + \left(\dfrac{l\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)} - \gamma\right)\psi = \dfrac{l\theta'(x,\mu_1^*)}{[1+\theta(x,\mu_1^*)]^2}\psi_1^*,\\ \dfrac{\partial\varphi}{\partial n}\Big|_{\partial\Omega} = \dfrac{\partial\psi}{\partial n}\Big|_{\partial\Omega} = 0.\end{cases} \tag{3.7}$$

Multiplying the equation of ψ in (3.7) by ψ_1^*, integrating by parts and applying the boundary condition of ψ_1^*, we have

$$\int_\Omega \frac{l\theta'(x,\mu_1^*)}{[1+\theta(x,\mu_1^*)]^2}(\psi_1^*)^2 = 0.$$

Obviously, this is a contradiction. □

Lemma 3.2. *The bifurcation direction of the solution* $(\mu_1^*, \theta(x,\mu_1^*), 0)$ *can be characterized by* $\mu_1'(0) > 0$.

Proof. Substituting the expansion (3.2) into the equation of v in (3.1), applying (3.3) and dividing both sides by s, we have

$$\begin{aligned}\frac{1}{s}\left(\frac{l\theta}{1+\theta} - \frac{l\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)}\right)\psi_1^* + \nu\Delta\omega_1^* + \left(\frac{l\theta}{1+\theta} - \gamma\right)\omega_1^* + \frac{l\varphi_1^*\psi_1^*}{(1+\theta)^2}&\\ = s\left[\frac{(\varphi_1^*)^2\psi_1^* - \varphi_1^*\omega_1^* - \phi_1^*\psi_1^*}{(1+\theta)^2} - \frac{\theta(\varphi_1^*)^2\psi_1^*}{(1+\theta)^3}\right]l + o(s).&\end{aligned} \tag{3.8}$$

Multiplying both sides of (3.8) by ψ_1^*, integrating by parts, and finally passing to the limit we have

$$\mu_1'(0)\int_\Omega \frac{l\theta'(x,\mu_1^*)}{[1+\theta(x,\mu_1^*)]^2}(\psi_1^*)^2 = -\int_\Omega \frac{l\varphi_1^*(\psi_1^*)^2}{(1+\theta(x,\mu_1^*))^2}. \tag{3.9}$$

By (3.6), we easily see that $\varphi_1^* < 0$. This fact together with the positivity of ψ_1^*, (3.4) and (3.9) imply that $\mu_1'(0) > 0$. □

Now we investigate the linear stability of (u_1^*, v_1^*) which bifurcates from semi-trivial steady state $(\theta, 0)$. Firstly, we need to make some preparation.

Lemma 3.3. *As $s \to 0$, we have $(u_1^*, v_1^*) \to (\theta(x,\mu_1^*), 0)$, $v_1^*/\|v_1^*\|_{L^\infty(\Omega)} \to \psi_1^*$, and $\psi \to \psi_1^*$ in $C^1(\overline{\Omega})$, where ψ is the corresponding eigenfunction of the principal eigenvalue λ_1 of* (2.1) *with $\|\psi\|_{L^\infty(\Omega)} = 1$.*

Proof. By (3.2), we may assume that $\|u_1^* - \theta\|_{L^\infty(\Omega)} + \|v_1^*\|_{L^\infty(\Omega)} \le \|\theta\|_{L^\infty(\Omega)}/2$ for small s. By elliptic regularity theory, passing to a subsequence if necessary, we suppose that $(u_1^*, v_1^*) \to (u_0, v_0)$ in $C^2(\overline{\Omega})$ as $s \to 0$, where u_0 and v_0 satisfy

$$\begin{cases} \mu_1^*\Delta u_0 + u_0(m(x) - u_0) - \dfrac{u_0 v_0}{1+u_0} = 0 & \text{in } \Omega, \\ \nu\Delta v_0 + \dfrac{l u_0 v_0}{1+u_0} - \gamma v_0 = 0 & \text{in } \Omega, \\ \dfrac{\partial u_0}{\partial n} = \dfrac{\partial v_0}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases}$$

Since $\|u_0 - \theta\|_{L^\infty(\Omega)} \le \|\theta\|_{L^\infty(\Omega)}/2$, we see that $u_0 \not\equiv 0$ in $\overline{\Omega}$. If $v_0 \not\equiv 0$, by the Harnack inequality [15], we have $\min_{x\in\overline{\Omega}} v_0 \ge C \cdot \max_{x\in\overline{\Omega}} v_0$ for some constant $C > 0$. Hence $v_0 > 0$ in $\overline{\Omega}$. By the equation of u_0 and [13], we obtain $u_0 < \theta(x,\mu_1^*)$ in $\overline{\Omega}$. Multiplying the equation of v_0 by ψ_1^*, (3.3) by v_0, integrating by parts and subtracting the result, we have

$$\int_\Omega v_0\psi_1^*\left(\frac{l u_0}{1+u_0} - \frac{l\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)}\right) = 0.$$

Since $v_0 > 0, \psi_1^* > 0$ and $u_0 < \theta$, this is impossible. Hence $v_0 \equiv 0$ in $\overline{\Omega}$. It follows that $u_0 \equiv \theta(x,\mu_1^*)$ in $\overline{\Omega}$.

Define $\widetilde{v} = v_1^*/\|v_1^*\|_{L^\infty(\Omega)}$. By elliptic regularity theory [12], we may suppose that $\widetilde{v} \to \widehat{v}$, where $\widehat{v} \ge 0, \|\widehat{v}\|_{L^\infty(\Omega)} = 1$ and satisfies

$$\nu\Delta\widehat{v} + \left(\frac{l\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)} - \gamma\right)\widehat{v} = 0 \quad \text{in } \Omega, \qquad \frac{\partial\widehat{v}}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

Therefore, we have $\widehat{v} \equiv \psi_1^*$, i.e., $v_1^*/\|v_1^*\|_{L^\infty(\Omega)} \to \psi_1^*$ in $C^1(\overline{\Omega})$ as $s \to 0$. A similar argument shows that $\lambda_1 \to 0$ and $\psi \to \psi_1^*$ in $C^1(\overline{\Omega})$ as $s \to 0$. □

Lemma 3.4. *For every small $s > 0$, the bifurcating solution $(\mu, u_1^*, v_1^*) = (\mu_1(s), \theta + s\varphi_1^* + s^2\phi_1^*(s), s\psi_1^* + s^2\omega_1^*(s))$ is linearly stable.*

Proof. To study the stability of bifurcating solution (u_1^*, v_1^*) for small s, we consider the following linear eigenvalue problem

$$\begin{cases} \mu\Delta\varphi_1 + \left(m - 2u_1^* - \dfrac{v_1^*}{(1+u_1^*)^2}\right)\varphi_1 - \dfrac{u_1^*}{1+u_1^*}\psi_1 + \lambda\varphi_1 = 0, \\ \nu\Delta\psi_1 + \left(\dfrac{lu_1^*}{1+u_1^*} - \gamma\right)\psi_1 + \dfrac{lv_1^*}{(1+u_1^*)^2}\varphi_1 + \lambda\psi_1 = 0, \\ \dfrac{\partial\varphi_1}{\partial n}\Big|_{\partial\Omega} = \dfrac{\partial\psi_1}{\partial n}\Big|_{\partial\Omega} = 0. \end{cases} \tag{3.10}$$

Define operators Π_s and $\Pi_0 : X \to Y$ by

$$\Pi_s\begin{pmatrix}\varphi_1\\ \psi_1\end{pmatrix} = \begin{pmatrix} \mu_1(s)\Delta\varphi_1 + \left(m - 2u_1^* - \dfrac{v_1^*}{(1+u_1^*)^2}\right)\varphi_1 - \dfrac{u_1^*}{1+u_1^*}\psi_1 \\ \nu\Delta\psi_1 + \left(\dfrac{lu_1^*}{1+u_1^*} - \gamma\right)\psi_1 + \dfrac{lv_1^*}{(1+u_1^*)^2}\varphi_1 \end{pmatrix}$$

and

$$\Pi_0\begin{pmatrix}\varphi_1\\ \psi_1\end{pmatrix} = \begin{pmatrix} \mu_1^*\Delta\varphi_1 + (m - 2\theta(x,\mu_1^*))\varphi_1 - \dfrac{\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)}\psi_1 \\ \nu\Delta\psi_1 + \left(\dfrac{l\theta(x,\mu_1^*)}{1+\theta(x,\mu_1^*)} - \gamma\right)\psi_1 \end{pmatrix}.$$

By Lemma 3.3, we have $(u_1^*, v_1^*) \to (\theta, 0)$ in $C^1(\overline{\Omega})$ as $s \to 0$. Thus $\Pi_s \to \Pi_0$ uniformly in operator norm as $s \to 0$. Moreover, it is not difficult to verify that the kernel of Π_0 is spanned by (φ_1^*, ψ_1^*), and zero is a K-simple eigenvalue of Π_0 (where the operator K is the canonical injection from X to Y). Hence, for small s, there exists a unique K-simple eigenvalue $\eta_1 = \eta_1(s)$ of Π_s with $\eta_1 \to 0$ as $s \to 0$. Let η_1 be an eigenvalue of (3.10) with associated eigenfunction (φ_1, ψ_1). Furthermore, we have $\eta_1 = -\lambda$.

We separate the following proof into two cases.

Case 1. $\psi_1 \not\equiv 0$ in $\overline{\Omega}$. After scaling we may assume that $\|\psi_1\|_{L^\infty(\Omega)} = 1$ and ψ_1 is positive somewhere in Ω. Since $(u_1^*, v_1^*) \to (\theta, 0)$ and $\eta_1 \to 0$, we can argue similarly as before to conclude that $(\varphi_1, \psi_1) \to (\varphi_1^*, \psi_1^*)$ in $C^1(\overline{\Omega})$ as $s \to 0$, where φ_1^* is unique solution of (3.5). Multiplying the equation of ψ_1 by v_1^*, the equation of v_1^* by ψ_1, integrating by parts and applying the boundary conditions of ψ_1 and v_1^*, after some reorganization we have

$$\eta_1 \int_\Omega \psi_1 v_1^* = \int_\Omega \frac{l(v_1^*)^2}{(1+u_1^*)^2}\varphi_1.$$

Dividing the above equation by $\|v_1^*\|^2_{L^\infty(\Omega)}$ and applying the fact $v_1^*/\|v_1^*\|_{L^\infty(\Omega)} \to \psi_1^*, u_1^* \to \theta, v_1^* \to 0, \varphi_1 \to \varphi_1^*$ and $\psi_1 \to \psi_1^*$ in $C^1(\overline{\Omega})$ as $s \to 0$, we obtain

$$\lim_{s\to 0} \frac{\eta_1}{\|v_1^*\|_{L^\infty(\Omega)}} = \frac{\int_\Omega \frac{l(\psi_1^*)^2\varphi_1^*}{(1+\theta(x,\mu_1^*))^2}}{\int_\Omega (\psi_1^*)^2}.$$

By (3.6), we find that $\varphi_1^* < 0$ in Ω. Hence $\eta_1 < 0$ for small s.

Case 2. $\psi_1 \equiv 0$ in $\overline{\Omega}$. Then $\varphi_1 \not\equiv 0$ and satisfies

$$\mu_1(s)\Delta\varphi_1 + \left(m - 2u_1^* - \frac{v_1^*}{(1+u_1^*)^2}\right)\varphi_1 = \eta_1\varphi_1 \quad \text{in } \Omega, \qquad \frac{\partial\varphi_1}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

Since $(u_1^*, v_1^*) \to (\theta, 0)$ as $s \to 0$, the least eigenvalue of the operator $-\mu_1^*\Delta - (m - 2\theta(x, \mu_1^*))$ with homogeneous Neumann boundary condition is strictly positive, we have $\eta_1 < 0$. In other words, all eigenvalues of (3.10) must have positive real part, i.e., (u_1^*, v_1^*) is linearly stable. □

The proof of Theorem 1.2. Theorem 1.2 (a) follows from Lemmas 3.1, 3.2 and Lemma 3.4. Cases (b) and (c) can be proved by similar argument to that of Case (a), we skip it here. □

3.2 The proof of Theorem 1.3.

Before establishing the conclusions of Theorem 1.3, we need to make some preparations. Firstly, define the operator $G(\nu, u, v) : (0, \infty) \times X \to Y$ by

$$G(\nu, u, v) = \begin{pmatrix} \mu\Delta u + u(m(x) - u) - \dfrac{uv}{1+u} \\ \nu\Delta v + \dfrac{luv}{1+u} - \gamma v \end{pmatrix}.$$

It is easy to see that $G(\nu, \theta, 0) = 0$ and the derivatives $D_\nu G(\nu, u, v), D_{(u,v)}G(\nu, u, v)$ and $D_\nu D_{(u,v)}G(\nu, u, v)$ exist and are continuous close to $(\nu, \theta, 0)$.

Lemma 3.5. *Suppose that $m(x)$ satisfies (1.2). If $\gamma_1 < \gamma < \gamma_2$, for small μ, there exists some small $\rho_1 > 0$, some function $\nu_1(s) \in C^2(-\rho_1, \rho_1)$ with $\nu_1(0) = \nu_1^*$ such that all nonnegative steady state solutions of (1.1) close to $(\nu_1^*, \theta, 0)$ can be parameterized as*

$$(\nu, u_{1*}, v_{1*}) = (\nu_1(s), \theta + s\varphi_1^* + s^2\phi_1^*(s), s\psi_1^* + s^2\omega_1^*(s)), \qquad 0 < s < \rho_1, \tag{3.11}$$

where (φ_1^*, ψ_1^*) is defined as in (3.13) and (3.12), and $(\phi_1^*(s), \omega_1^*(s))$ lies in the complement of the kernel of $D_{(u,v)}G|_{(\nu_1^*,\theta,0)}$ in X. In addition, the bifurcation direction of the solution $(\nu_1^*, \theta, 0)$ can be characterized by $\nu_1'(0) < 0$.

Proof. For this case, there exist positive constants $\mu_* \le \mu^*$ such that $\gamma > K(\mu)$ for every $\mu \in (0, \mu_*)$ and $\gamma < K(\mu)$ for any $\mu > \mu^*$. It may occur that $\mu_* < \mu^*$ (See Figure 1.1).

Dividing the equation of ψ in (2.1), integrating by parts and after some reorganization, we have

$$\lambda_1|\Omega| = -\nu \int_\Omega \frac{|\nabla\psi|^2}{\psi^2} + \int_\Omega \left(\gamma - \frac{l\theta}{1+\theta}\right).$$

Hence, for any $\mu > \mu^*$, we conclude $\lambda_1 < 0$ for any $\nu > 0$. For every $\mu < \mu_*$, since $\lim_{\nu\to 0}\lambda_1 = \gamma - \frac{l\max_{\overline{\Omega}}\theta}{1+\max_{\overline{\Omega}}\theta} < \gamma - \frac{l\overline{m}}{1+\overline{m}} < 0$ (by Lemma 2.2) and $\lim_{\nu\to\infty}\lambda_1 = \gamma - K(\mu) > 0$, by Lemma 2.4, we see that there exists a unique $\nu_1^* = \nu_1^*(\mu) > 0$ such that $\lambda_1 > 0$ if $\nu > \nu_1^*$, $\lambda_1 = 0$ at $\nu = \nu_1^*$ and $\lambda_1 < 0$ if $\nu < \nu_1^*$. Hence, there exists some function $\psi \to \psi_1^* \in C^2(\overline{\Omega})$ as $\nu \to \nu_1^*$, and $\psi_1^* > 0$ satisfies

$$\nu_1^*\Delta\psi_1^* + \left(\frac{l\theta}{1+\theta} - \gamma\right)\psi_1^* = 0 \quad \text{in } \Omega, \qquad \frac{\partial\psi_1^*}{\partial n}\Big|_{\partial\Omega} = 0, \tag{3.12}$$

i.e., $\lambda_1 = 0$ is the smallest eigenvalue of (2.1) with $\nu = \nu_1^*$ and ψ_1^* is its corresponding eigenfunction. Since

$$D_{(u,v)}G|_{(\nu_1^*,\theta,0)}\begin{pmatrix}\varphi \\ \psi\end{pmatrix} = \begin{pmatrix} \mu\Delta\varphi + (m - 2\theta)\varphi - \dfrac{\theta}{1+\theta}\psi \\ \nu_1^*\Delta\psi + \left(\dfrac{l\theta}{1+\theta} - \gamma\right)\psi \end{pmatrix},$$

it is easy to testify that the kernel of $D_{(u,v)}G|_{(\nu_1^*,\theta,0)}$ is spanned by (φ_1^*, ψ_1^*) and that $\dim \mathcal{N}(D_{(u,v)}G|_{(\nu_1^*,\theta,0)}) = 1$, where ψ_1^* is the unique positive solution of (3.12) up to a constant multiplier, and φ_1^* is uniquely determined by

$$\mu\Delta\varphi_1^* + (m-2\theta)\varphi_1^* - \frac{\theta}{1+\theta}\psi_1^* = 0 \quad \text{in } \Omega, \qquad \left.\frac{\partial\varphi_1^*}{\partial n}\right|_{\partial\Omega} = 0.$$

By (1.3) and the positivity of θ, we see that zero is the smallest eigenvalue of the operator $-\mu\Delta - (m-\theta)$ with homogeneous Neumann boundary condition. By the comparison principle for eigenvalues, the smallest eigenvalue of the operator $-\mu\Delta - (m-2\theta)$ with homogeneous Neumann boundary condition is strictly positive, hence

$$\varphi_1^* = [-\mu\Delta - (m-2\theta)]^{-1}\left(-\frac{\theta}{1+\theta}\psi_1^*\right). \tag{3.13}$$

Furthermore, it follows from the Fredholm alternative that $\operatorname{codim} \mathcal{R}(D_{(u,v)}G|_{(\nu_1^*,\theta,0)}) = 1$. For the transversality condition,

$$D_\nu D_{(u,v)}G|_{(\nu_1^*,\theta,0)}\begin{pmatrix}\varphi_1^*\\ \psi_1^*\end{pmatrix} = \begin{pmatrix}0\\ \Delta\psi_1^*\end{pmatrix} \notin \mathcal{R}(D_{(u,v)}G|_{(\nu_1^*,\theta,0)}),$$

because the equation $\nu_1^*\Delta\psi + (\frac{l\theta}{1+\theta} - \gamma)\psi = \Delta\psi_1^*$ is not solvable since $\int_\Omega |\nabla\psi_1^*|^2 \neq 0$.

Substituting the expansion (3.11) into the equation of v and dividing both sides by s, we have

$$\begin{aligned}\frac{\nu-\nu_1^*}{s}\Delta\psi_1^* + \nu\Delta\omega_1^* &+ \left(\frac{l\theta}{1+\theta} - \gamma\right)\omega_1^* + \frac{l\varphi_1^*\psi_1^*}{(1+\theta)^2}\\ &= s\left[\frac{(\varphi_1^*)^2\psi_1^* - \varphi_1^*\omega_1^* - \phi_1^*\psi_1^*}{(1+\theta)^2} - \frac{\theta\psi_1^*(\varphi_1^*)^2}{(1+\theta)^3}\right] l + o(s).\end{aligned} \tag{3.14}$$

Multiplying (3.14) by ψ_1^*, integrating by parts, applying the boundary condition of ψ_1^*, and finally passing to the limit we have

$$\nu_1'(0)\int_\Omega |\nabla\psi_1^*|^2 = \int_\Omega \frac{l\varphi_1^*(\psi_1^*)^2}{(1+\theta)^2}.$$

By (3.13), we see that $\varphi_1^* < 0$. This fact together with the positivity of ψ_1^* imply that $\nu_1'(0) < 0$. □

Lemma 3.6. *For any small $s > 0$, the bifurcating solution $(\nu, u_{1*}, v_{1*}) = (\nu_1(s), \theta + s\varphi_1^* + s^2\phi_1^*(s), s\psi_1^* + s^2\omega_1^*(s))$ is linearly stable.*

Proof. Now we are ready to investigate the stability of bifurcating solutions (u_{1*}, v_{1*}). To this end, we study the following linear eigenvalue problem

$$\begin{cases}\mu\Delta\varphi_1 + \left(m - 2u_{1*} - \dfrac{v_{1*}}{(1+u_{1*})^2}\right)\varphi_1 - \dfrac{u_{1*}}{1+u_{1*}}\psi_1 + \lambda\varphi_1 = 0,\\ \nu\Delta\psi_1 + \left(\dfrac{lu_{1*}}{1+u_{1*}} - \gamma\right)\psi_1 + \dfrac{lv_{1*}}{(1+u_{1*})^2}\varphi_1 + \lambda\psi_1 = 0,\\ \left.\dfrac{\partial\varphi_1}{\partial n}\right|_{\partial\Omega} = \left.\dfrac{\partial\psi_1}{\partial n}\right|_{\partial\Omega} = 0.\end{cases} \tag{3.15}$$

Define operators Γ_s and $\Gamma_0 : X \to Y$ by

$$\Gamma_s \begin{pmatrix} \varphi_1 \\ \psi_1 \end{pmatrix} = \begin{pmatrix} \mu\Delta\varphi_1 + \left(m - 2u_{1*} - \dfrac{v_{1*}}{(1+u_{1*})^2}\right)\varphi_1 - \dfrac{u_{1*}}{1+u_{1*}}\psi_1 \\ \nu_1(s)\Delta\psi_1 + \left(\dfrac{lu_{1*}}{1+u_{1*}} - \gamma\right)\psi_1 + \dfrac{lv_{1*}}{(1+u_{1*})^2}\varphi_1 \end{pmatrix}$$

and

$$\Gamma_0 \begin{pmatrix} \varphi_1 \\ \psi_1 \end{pmatrix} = \begin{pmatrix} \mu\Delta\varphi_1 + (m-2\theta)\varphi_1 - \dfrac{\theta}{1+\theta}\psi_1 \\ \nu_1^*\Delta\psi_1 + \left(\dfrac{l\theta}{1+\theta} - \gamma\right)\psi_1 \end{pmatrix}.$$

Similarly as the proof of Lemma 3.3, we can show that $(u_{1*}, v_{1*}) \to (\theta, 0)$ in $C^1(\overline{\Omega})$ as $s \to 0$. Hence $\Gamma_s \to \Gamma_0$ uniformly in operator norm as $s \to 0$. In addition, it is easy to check that the kernel of Γ_0 is spanned by (φ_1^*, ψ_1^*), and zero is a K-simple eigenvalue of Γ_0 (where the operator K is the canonical injection from X to Y). Therefore, for small s, there exists a unique K-simple eigenvalue $\eta_1 = \eta_1(s)$ of Γ_s with $\eta_1 \to 0$ as $s \to 0$. Let η_1 be an eigenvalue of (3.15) with associated eigenfunction (φ_1, ψ_1). Furthermore, we have $\eta_1 = -\lambda$.

For convenience, we split the following proof into two cases.

Case 1. $\psi_1 \not\equiv 0$ in $\overline{\Omega}$. By some scaling, we may suppose that ψ_1 such that $\|\psi_1\|_{L^\infty(\Omega)} = 1$. Since $(u_{1*}, v_{1*}) \to (\theta, 0)$ and $\eta_1 \to 0$, we can argue similarly as before to conclude that $(\varphi_1, \psi_1) \to (\varphi_1^*, \psi_1^*)$ in $C^1(\overline{\Omega})$ as $s \to 0$, where φ_1^* is uniquely determined by (3.13). Multiplying the equation of ψ_1 by v_{1*}, the equation of v_{1*} by ψ_1, integrating by parts and applying the boundary conditions of ψ_1 and v_{1*}, after some reorganization we have

$$\eta_1 \int_\Omega \psi_1 v_{1*} = (\nu - \nu_1(s)) \int_\Omega \nabla\psi_1 \cdot \nabla v_{1*} + \int_\Omega \frac{l(v_{1*})^2}{(1+u_{1*})^2}\varphi_1.$$

Dividing the above equation by $\|v_{1*}\|_{L^\infty(\Omega)}$ and applying the fact $v_{1*}/\|v_{1*}\|_{L^\infty(\Omega)} \to \psi_1^*, u_{1*} \to \theta, v_{1*} \to 0, \varphi_1 \to \varphi_1^*$ and $\psi_1 \to \psi_1^*$ in $C^1(\overline{\Omega})$ as $s \to 0$, we obtain

$$\lim_{s\to 0} \eta_1 = \frac{(\nu - \nu_1^*) \int_\Omega |\nabla\psi_1^*|^2}{\int_\Omega (\psi_1^*)^2}.$$

By Lemma 3.5, we have $\nu_1'(0) < 0$. Hence $\eta_1 < 0$ for small s.

Case 2. $\psi_1 \equiv 0$ in $\overline{\Omega}$. Then $\varphi_1 \not\equiv 0$ and satisfies

$$\mu\Delta\varphi_1 + \left(m - 2u_{1*} - \frac{v_{1*}}{(1+u_{1*})^2}\right)\varphi_1 = \eta_1\varphi_1 \quad \text{in } \Omega, \qquad \frac{\partial\varphi_1}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

Since $(u_{1*}, v_{1*}) \to (\theta, 0)$ as $s \to 0$, the smallest eigenvalue of the operator $-\mu\Delta - (m - 2\theta)$ with homogeneous Neumann boundary condition is strictly positive, we have $\eta_1 < 0$. That is to say, all eigenvalues of (3.15) must have positive real part. Hence (u_{1*}, v_{1*}) is linearly stable for small s. □

Lemma 3.7. *If $\gamma_2 < \gamma < \gamma_3$, and $m(x)$ satisfies (1.2) and (1.4), then for small or large μ, there exists some small $\rho_2 > 0$, some function $\nu_i(s) \in C^2(-\delta_2, \delta_2)$ with $\nu_i(0) = \nu_i^*$ $(i = 2, 3)$ such that all nonnegative steady state solutions of (1.1) near $(\nu_i^*, \theta, 0)$ can be parameterized as*

$$(\nu, u_{i*}, v_{i*}) = (\nu_i(s), \theta + s\varphi_i^* + s^2\phi_i^*(s), s\psi_i^* + s^2\omega_i^*(s)), \qquad 0 < s < \rho_2,$$

where $(\phi_i^*(s), \omega_i^*(s))$ $(i = 2, 3)$ lies in the complement of the kernel of $D_{(u,v)}F|_{(\nu_i^*, \theta, 0)}$ in X. Moreover, the bifurcation direction of the solution $(\nu_i^*, \theta, 0)$ can be characterized by $\nu_i'(0) < 0$.

Proof. For this case, there exist two positive constants $\mu_{**} < \mu^{**}$ such that $K(\mu) < \gamma$ for every $\mu < \mu_{**}$ and $K(\mu) < \gamma$ for any $\mu > \mu^{**}$. For any $\mu < \mu_{**}$ or $\mu > \mu^{**}$, since $\lim_{\nu\to 0}\lambda_1 = \gamma - \frac{l\max_{\overline{\Omega}}\theta}{1+\max_{\overline{\Omega}}\theta} < \sup_{\mu>0}\frac{1}{|\Omega|}\int_\Omega \frac{l\theta}{1+\theta} - \frac{l\max_{\overline{\Omega}}\theta}{1+\max_{\overline{\Omega}}\theta} \le 0$, $\lim_{\nu\to\infty}\lambda_1 = \gamma - K(\mu) > 0$, then there exists a unique $\nu_i^* = \nu_i^*(\mu) > 0$ $(i = 2,3)$ such that $\lambda_1 < 0$ if $\nu < \nu_i^*$, $\lambda_1 = 0$ at $\nu = \nu_i^*$ and $\lambda_1 > 0$ if $\nu > \nu_i^*$. It is easy to see that the kernel of $D_{(u,v)}G|_{(\nu_i^*,\theta,0)}$ is spanned by (φ_i^*, ψ_i^*) and $\dim\mathcal{N}(D_{(u,v)}G|_{(\nu_i^*,\theta,0)}) = 1$, where ψ_i^* is the unique positive solution (up to a constant multiplier) of

$$\nu_i^*\Delta\psi_i^* + \left(\frac{l\theta}{1+\theta} - \gamma\right)\psi_i^* = 0 \quad \text{in } \Omega, \qquad \frac{\partial\psi_i^*}{\partial n}\bigg|_{\partial\Omega} = 0$$

and φ_i^* is uniquely determined by

$$\mu\Delta\varphi_i^* + (m-2\theta)\varphi_i^* - \frac{\theta}{1+\theta}\psi_i^* = 0 \quad \text{in } \Omega, \qquad \frac{\partial\varphi_i^*}{\partial n}\bigg|_{\partial\Omega} = 0.$$

Moreover, it follows from Fredholm Alternative that $\operatorname{codim}\mathcal{R}(D_{(u,v)}G|_{(\nu_i^*,\theta,0)}) = 1$. We can argue similarly as in the proof of Lemma 3.5 to conclude that the transversality condition holds. In addition, it is easy to check that $\nu_i'(0) < 0$. □

Lemma 3.8. *If $\gamma_3 < \gamma < \gamma_4$ and $m(x)$ satisfies (1.2) and (1.4), for sufficiently small μ, there exists some small $\rho_3 > 0$, some function $\nu_4(s) \in C^2(-\rho_3, \rho_3)$ with $\nu_4(0) = \nu_4^*$ such that all nonnegative steady state solutions of (1.1) close to $(\nu_4^*, \theta, 0)$ can be parameterized as*

$$(\nu, u_{4*}, v_{4*}) = (\nu_4(s), \theta + s\varphi_4^* + s^2\phi_4^*(s), s\psi_4^* + s^2\omega_4^*(s)), \qquad 0 < s < \rho_3,$$

where $(\phi_4^*(s), \omega_4^*(s))$ lies in the complement of the kernel of $D_{(u,v)}G|_{(\nu_4^*,\theta,0)}$ in X. Furthermore, the bifurcation direction of the solution $(\nu_4^*, \theta, 0)$ can be characterized by $\nu_4'(0) < 0$.

Proof. Since $\lim_{\nu\to 0}\lambda_1 = \gamma - \frac{l\max_{\overline{\Omega}}\theta}{1+\max_{\overline{\Omega}}\theta} \to \gamma - \frac{l\max_{\overline{\Omega}} m}{1+\max_{\overline{\Omega}} m} < 0$ as $\mu \to 0$ (by Lemma 2.1), and $\lim_{\nu\to\infty}\lambda_1 = \gamma - K(\mu) > \sup_{\mu>0}\frac{1}{|\Omega|}\int_\Omega\frac{l\theta}{1+\theta} - \frac{1}{|\Omega|}\int_\Omega\frac{l\theta}{1+\theta} \ge 0$, there exists a unique $\nu_4^* = \nu_4^*(\mu) > 0$ such that for sufficiently small μ, $\lambda_1 < 0$ if $\nu < \nu_4^*$, $\lambda_1 = 0$ at $\nu = \nu_4^*$ and $\lambda_1 > 0$ if $\nu > \nu_4^*$. It is not hard to verify that the kernel of $D_{(u,v)}G|_{(\nu_4^*,\theta,0)}$ is spanned by (φ_4^*, ψ_4^*) and $\dim\mathcal{N}(D_{(u,v)}G|_{(\nu_4^*,\theta,0)}) = \operatorname{codim}\mathcal{R}(D_{(u,v)}G|_{(\nu_4^*,\theta,0)}) = 1$, where ψ_4^* is the unique positive solution (up to a constant multiplier) of

$$\nu_4^*\Delta\psi_4^* + \left(\frac{l\theta}{1+\theta} - \gamma\right)\psi_4^* = 0 \quad \text{in } \Omega, \qquad \frac{\partial\psi_4^*}{\partial n}\bigg|_{\partial\Omega} = 0$$

and φ_4^* is uniquely determined by

$$\mu\Delta\varphi_4^* + (m-2\theta)\varphi_4^* - \frac{\theta}{1+\theta}\psi_4^* = 0 \quad \text{in } \Omega, \qquad \frac{\partial\varphi_4^*}{\partial n}\bigg|_{\partial\Omega} = 0.$$

By similar argument to that of Lemma 3.5, we still can check that the transversality condition holds here. Moreover, we have $\nu_4'(0) < 0$. □

Lemma 3.9. *(a) Let $\widehat{\delta}$ be a fixed positive constant. For every $\mu > 0$, there exists some constant $\widehat{C} = \widehat{C}(\gamma, l, m, \Omega, \widehat{\delta}) > 0$ such that if $\nu \ge \widehat{\delta}$, any positive solution (u, v) of (3.1) satisfies*

$$0 < u(x) \le \max_{x\in\overline{\Omega}} m(x), \qquad 0 < v(x) \le \widehat{C} \quad \text{in } \overline{\Omega}. \tag{3.16}$$

(b) Assume that $\gamma_1 < \gamma < \gamma_2$. For small μ, there exists some $M > 0$ such that if $\nu > M$, (3.1) has no positive solution.

Proof. (a) Applying the maximum principle to the equation of u in (3.1), we have $\max_{x\in\overline{\Omega}} u \le \max_{x\in\overline{\Omega}} m$. Then the boundedness of u follows. Integrating the equations of u and v in (3.1), applying the boundary condition and after some rearrangement, we have

$$\frac{\gamma}{l}\int_\Omega v = \int_\Omega u(m-u).$$

Hence,

$$\int_\Omega v \le \frac{l}{4\gamma}\int_\Omega m^2. \tag{3.17}$$

By Harnack inequality [15] and the equation of v in (3.1), we see that there exists some constant $\widetilde{C} = \widetilde{C}(l,\gamma,\widehat{\delta},\Omega) > 0$ such that if $\nu \ge \widehat{\delta}$, $\max_{x\in\overline{\Omega}} v \le \widetilde{C}\min_{x\in\overline{\Omega}} v$. This together with (3.17) implies the second inequality of (3.16).

(b) Suppose that (u,v) is a positive solution to (3.1). For Case (a), we find that $\frac{l}{|\Omega|}\int_\Omega \frac{m}{1+m} < \gamma < \frac{l}{|\Omega|}\int_\Omega \frac{\overline{m}}{1+\overline{m}}$. By Lemma 3.9, we see that u and v are uniformly bounded from above for every $\mu,\nu > 0$. Standard elliptic regularity theory implies that $v \to \overline{v}$ in $C^2(\overline{\Omega})$ as $\nu \to \infty$. On the other hand, taking into account homogeneous Neumann boundary condition, v must converge to a constant $\widetilde{c}$. Integrating over Ω and passing to the limit, we have $\widetilde{c}\int_\Omega(\frac{lu}{1+u}-\gamma) = 0$. Then $\widetilde{c} = 0$ or $\int_\Omega(\frac{lu}{1+u}-\gamma) = 0$. We claim that $\int_\Omega(\frac{lu}{1+u}-\gamma) \ne 0$. By the equation of u, we see that θ is a super-solution. Hence, $\frac{l}{|\Omega|}\int_\Omega \frac{u}{1+u} \le \frac{l}{|\Omega|}\int_\Omega \frac{\theta}{1+\theta}$. By Lemma 2.1, we have $\frac{l}{|\Omega|}\int_\Omega \frac{u}{1+u} \le \frac{l}{|\Omega|}\int_\Omega \frac{\theta}{1+\theta} \to \frac{l}{|\Omega|}\int_\Omega \frac{m}{1+m}$ as $\mu \to 0$. Then our assertion follows. Therefore, $\widetilde{c} = 0$, i.e., for small μ, $(u,v) \to (\theta,0)$ in $C^2(\overline{\Omega})$ as $\nu \to \infty$. □

The proof of Theorem 1.3. Local bifurcation results of Case (a) follows from Lemma 3.5, the linear stability of the bifurcating solution follows from Lemma 3.6. While local bifurcation results of Cases (b) and (c) can be found in Lemmas 3.7 and 3.8, and their linear stability of the bifurcating solution can be proved by similar argument to that of Case (a). Now it remains to investigate whether local bifurcation conclusions can be extended to global one, our following proof shows that it is true. By Lemma 3.9 and global bifurcation theory [20], we see that the bifurcating solution (ν, u_1^*, v_1^*) can be extended from $(\nu_1^*,\theta,0)$ to zero in ν. A similar argument yields that global bifurcation conclusions of Cases (b) and (c) also hold. □

In contrast with the heterogeneous environment, if m is a positive constant, then (1.1) has a semi-trivial steady state $(m,0)$ which is independent of μ. For this case, we can choose m as a bifurcation parameter, utilize local bifurcation theory and obtain the following theorem.

Theorem 3.10. *Suppose that m is constant and $\gamma < l$. For any $\mu,\nu > 0$, there exists some small $\delta > 0$, some function $m(s) \in C^2(-\delta,\delta)$ with $m(0) = m^*$ such that all nonnegative steady state solutions of (1.1) close to $(m^*,m,0)$ can be parameterized as*

$$(m,u,v) = (m(s), m + s\varphi_1 + s^2\varphi_1^*(s), s\psi_1 + s^2\psi_1^*(s)), \qquad 0 < s < \delta,$$

where ψ_1 is some positive constant, φ_1 is determined by (3.18), and $(\varphi_1^*(s),\psi_1^*(s))$ lies in the complement of the kernel of $D_{(u,v)}F|_{(m^*,m,0)}$ in X. Moreover, the bifurcation direction of the solution $(m^*,m,0)$ can be characterized by $m'(0) > 0$. In addition, the bifurcating solution (m,u,v) is locally stable for small s.

Proof. By Lemma 2.3, the stability of $(m,0)$ is determined by the sign of the smallest eigenvalue (denoted as λ_1) of the eigenvalue problem:

$$\nu\Delta\psi + \left(\frac{lm}{1+m}-\gamma\right)\psi + \lambda\psi = 0 \quad \text{in } \Omega, \qquad \frac{\partial\psi}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

Since m is constant, we have $\lambda_1 = \gamma - lm/(1+m)$. Thus λ_1 is strictly decreasing with respect to m. As $\lim_{m\to 0}\lambda_1 = \gamma > 0$ and $\lim_{m\to\infty}\lambda_1 = \gamma - l < 0$, there exists a unique constant $m^* > 0$ such that $\lambda_1 < 0$ if $m > m^*$, $\lambda_1 = 0$ at $m = m^*$ and $\lambda_1 > 0$ if $m < m^*$.

Since

$$D_{(u,v)}F|_{(m^*,m,0)}\begin{pmatrix}\varphi\\ \psi\end{pmatrix} = \begin{pmatrix}\mu\Delta\varphi - m^*\varphi - \dfrac{m^*}{1+m^*}\psi\\ \nu\Delta\psi\end{pmatrix},$$

we see that the kernel of $D_{(u,v)}F|_{(m^*,m,0)}$ is spanned by (φ_1,ψ_1) and $\dim\mathcal{N}(D_{(u,v)}F|_{(m^*,m,0)}) = 1$, where φ_1 is uniquely determined by

$$\mu\Delta\varphi_1 - m^*\varphi_1 - \frac{m^*}{1+m^*}\psi_1 = 0 \quad \text{in } \Omega, \qquad \left.\frac{\partial\varphi_1}{\partial n}\right|_{\partial\Omega} = 0. \tag{3.18}$$

It is not difficult to see that $\operatorname{codim}\mathcal{R}(D_{(u,v)}F|_{(m^*,m,0)}) = 1$. For the transversality condition,

$$D_m D_{(u,v)}F|_{(m^*,m,0)}\begin{pmatrix}\varphi_1\\ \psi_1\end{pmatrix} = \begin{pmatrix}\varphi_1\\ 0\end{pmatrix} \notin \mathcal{R}(D_{(u,v)}F|_{(m^*,m,0)}),$$

because the equation $\mu\Delta\varphi - m^*\varphi - \frac{m^*}{1+m^*}\psi = \varphi_1$ is not solvable since $\int_\Omega \varphi_1^2 \neq 0$. Furthermore, we have $m'(0) > 0$. □

Acknowledgements

We would like to thank the referee for his/her careful reading and valuable suggestions, which contribute to improving the exposition of Theorems 1.2 and 1.3, and also thank Prof. Yi Li for his helpful discussions. This work was supported by the National Natural Science Foundation of China (Nos. 11371286, 11401458).

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