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Stability and bifurcation of a diffusive predator-prey model in a spatially heterogeneous environment

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Abstract. We consider a diffusive predator-prey model in a spatially heterogeneous environment. In contrast to existing models that operate in spatially homogeneous environments, our model can describe natural environments that are basically heterogeneous. We explain how the linearly stability of semi-trivial steady state of our model changes from stable to unstable step-wise as the death rate of the predator decreases. Based on the results of stability of the semi-trivial steady state, we regard the dispersal rates of the predator and prey as bifurcation parameters, and deduce corresponding bifurcation conclusions. In particular, considering the dispersal rate of the predator as a bifurcation parameter, the bifurcation result can be extended to the global bifurcation case.

Contents

1. Introduction

It is important to investigate interactions between biological species and their environment because these interactions can significantly influence the spatial distribution of the species' populations and the structure of their communities [3]. Mathematical models can be used to investigate the effect of the environment on the dynamics of the populations of biological species.

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Reaction-diffusion models can be used to inquire about relationships such as the persistence and extinction of populations and the coexistence of interacting species. In general, these models are used in spatially homogeneous environments, that is, the coefficients of these models are assumed to be positive constants. In reality, natural environments for most biological species are spatially inhomogeneous. If certain coefficients of the reaction-diffusion models are to be positive functions of a space variable x to make the environment spatially heterogeneous, the dynamics of populations of biological species will change significantly by the Lotka-Volterra competition models [5, 11, 12, 13, 17, 18, 20, 21, 29]. However, research using these predator-prey models is scarce [6, 9, 22, 28]. Therefore, we study the effect of spatial heterogeneity of an environment on the dynamics of the populations of biological species via a diffusive predator-prey model.

In this study, we assume that the intrinsic growth rate of the prey population is a positive function of the space variable x and examine the dynamics of the diffusive predator-prey model in a spatially heterogeneous environment. Specifically, we examine the effect of the joint action of the dispersal rates of the predator and prey and the spatial heterogeneity on the population dynamics using the following model:

$$\begin{cases} u_t = \mu\Delta u + u(m(x) - u) - uv & \text{in } \Omega \times (0,\infty), \\ v_t = \nu\Delta v + kuv - dv & \text{in } \Omega \times (0,\infty), \\ \partial u/\partial n = \partial v/\partial n = 0 & \text{on } \partial\Omega \times (0,\infty), \\ u(x,0) = u_0(x), v(x,0) = v_0(x) & \text{in } \Omega, \end{cases} \tag{1.1}$$

where $u(x,t)$ and $v(x,t)$ represent the population density of the prey and predator, at time t and position x. They are therefore assumed to be nonnegative, with corresponding migration rates $\mu, \nu > 0$. The function $m(x)$ denotes the intrinsic growth rate of the prey population. The constant d is the death rate of the predator. $\Delta := \sum_{i=1}^{N} \partial^2/\partial x_i^2$ is the Laplace operator in $\mathbb{R}^N$ that characterizes the random motion of the prey and predator, the habitat Ω is a bounded region in $\mathbb{R}^N$ with a smooth boundary $\partial\Omega$. The homogeneous Neumann boundary condition implies that no individual crosses the boundary of the habitat, $\partial u/\partial n = \nabla u \cdot n$, where n denotes the outward unit normal vector on $\partial\Omega$. For simplicity we assume that $u_0(x)$ and $v_0(x)$ are nonnegative and not identically zero. Moreover, we shall suppose that k and d are nonnegative constants.

The function $m(x)$ is assumed to be non-constant to indicate spatial heterogeneity of the environment. In addition, we assume that $m(x)$ satisfies

$$m(x) > 0, \text{ is non-constant, and Hölder continous on } \bar{\Omega}. \tag{1.2}$$

Therefore, the logistic equation [3, 20]

$$\mu\Delta\theta + \theta(m(x) - \theta) = 0 \text{ in } \Omega, \quad \partial\theta/\partial n = 0 \text{ on } \partial\Omega \tag{1.3}$$

has a unique positive solution for every $\mu > 0$, denoted as $\theta(x,\mu)$, and $\theta(x,\mu) \in C^2(\bar{\Omega})$. For brevity, we write $\theta(x,\mu)$ as θ. Therefore, if $m(x)$

satisfies (1.2), then the system (1.1) has only one semi-trivial steady state $(\theta, 0)$ for any $\mu > 0$.

Compared to the spatially homogeneous case where stability of the semi-trivial steady state is trivial, the stability of the semi-trivial steady state of (1.1) is significant. For every range of the death rate of the predator, we will determine the linearly stability of $(\theta, 0)$. In particular, for certain death rates of the predator, we describe the corresponding stability variations of $(\theta, 0)$ with variations of the dispersal rates of the predator and prey.

The first main result of this study is as follows:

Theorem 1.1. *Suppose the non-constant function m satisfies (1.2). Then the following results hold.*

(i) *If $d > k \max_{\bar{\Omega}} m$, then $(\theta, 0)$ is linearly stable for $\mu > 0$ and $\nu > 0$.*

(ii) *If $k \sup_{\mu>0} \bar{\theta} < d < k \max_{\bar{\Omega}} m$, and m also satisfies (2.1), then there exists a unique $\nu^* = \nu^*(d, m, \Omega) > 0$ such that for every $\nu > \nu^*$, $(\theta, 0)$ is linearly stable; whereas for every $\nu < \nu^*$, $(\theta, 0)$ changes its stability at least once as μ varies from 0 to ∞, where $\bar{\theta}$ is the average of θ.*

(iii) *If $k\bar{m} < d < k \sup_{\mu>0} \bar{\theta}$, then there exists a unique $\nu^* = \nu^*(d, m, \Omega) > 0$ such that for every $\nu > \nu^*$, $(\theta, 0)$ changes its stability at least twice as μ varies from 0 to ∞; whereas for every $\nu < \nu^*$, $(\theta, 0)$ changes its stability at least once as μ varies from 0 to ∞.*

(iv) *If $d < k\bar{m}$, then $(\theta, 0)$ is linearly unstable for any $\mu > 0$ and $\nu > 0$.*

From the biological perspective, Theorem 1.1 (i) indicates that if the death rate of the predator is larger than some constant, the predator cannot invade when rare and it is independent of the dispersal rates of the prey and predator. Furthermore, Theorem 1.1 (ii) implies that for some death rates of the predator, the predator cannot invade when rare if and only if the dispersal rate of the predator is larger than some critical constant. However, if the dispersal rate of the predator is less than the critical constant, the predator can invade if scarce for some ranges of the dispersal rate of the prey. Theorem 1.1 (iii) can be explained similarly. Theorem 1.1 (iv) means that the predator can invade if scarce if the death rate of the predator is less than some constant, and it is irrelevant to the dispersal rates of the prey and predator.

Remark 1.2. *By Theorem 1.1, Cases (i) and (iv) cannot generate bifurcation from $(\theta, 0)$. Therefore, Cases (ii) and (iii) need to be investigated. We make the following hypotheses:*

(a) *For every $d \in (k \sup_{\mu>0} \bar{\theta}, k \max_{\bar{\Omega}} m)$, if $\nu < \nu^*$, then $(\theta, 0)$ changes stability at least once, from unstable to stable as μ varies. In particular, we assume that there exists some $\hat{\mu}_1 > 0$ such that $\lambda_1(\hat{\mu}_1) = 0$ and $\partial\lambda_1/\partial\mu(\hat{\mu}_1) > 0$, that is, $\lambda_1(\hat{\mu}_1)$ is non-degenerate, where λ_1 is the least eigenvalue of (2.2). Herein, the non-degeneracy assumption is vital to apply the local bifurcation theorem.*

(b) *For every* $d \in (k\bar{m}, k\sup_{\mu>0}\bar{\theta})$, *if* $\nu > \nu^*$, *then* $(\theta, 0)$ *changes stability at least twice, initially from stable to unstable and thereafter from unstable to stable as* μ *varies. If* $\nu < \nu^*$, *then* $(\theta, 0)$ *changes stability at least once, from unstable to stable as* μ *varies. Therefore, we assume that if* $\nu > \nu^*$, *then there exist some* $\hat{\mu}_3 > \hat{\mu}_2 > 0$ *such that* $\lambda_1(\hat{\mu}_2) = \lambda_1(\hat{\mu}_3) = 0$ *and* $\partial\lambda_1/\partial\mu(\hat{\mu}_2) < 0, \partial\lambda_1/\partial\mu(\hat{\mu}_3) > 0$. *If* $\nu < \nu^*$, *then there exists some* $\hat{\mu}_4 > 0$ *such that* $\lambda_1(\hat{\mu}_4) = 0$ *and* $\partial\lambda_1/\partial\mu(\hat{\mu}_4) > 0$.

For a predator-prey system in a spatially homogeneous environment, several significant outcomes have been reported in [1, 2, 15, 16, 24, 25, 26, 27, 30]. In this paper, by Theorem 1.1 and bifurcation theory [4], if the dispersal rate of the prey is considered as a bifurcation parameter, we can deduce the following local bifurcation conclusion.

Theorem 1.3. *Suppose the non-constant function* m *satisfies (*1.2*). Then the following statements hold.*

(i) *If* $k\sup_{\mu>0}\bar{\theta} < d < k\max_{\bar{\Omega}} m$ *and* m *also satisfies* (2.1), *then for every* $\nu < \nu^*$, *there exists some* $\delta_1 > 0$ *such that a branch of the steady state solution* $(\hat{u}_1, \hat{v}_1)$ *of* (1.1) *bifurcates from* $(\theta, 0)$ *at* $\mu = \hat{\mu}_1$, *that can be characterized by* μ *for* $\mu \in (\hat{\mu}_1 - \delta_1, \hat{\mu}_1)$. *Furthermore, the bifurcating solution* $(\hat{u}_1, \hat{v}_1)$ *is locally stable for* $\mu \in (\hat{\mu}_1 - \delta_1, \hat{\mu}_1)$.

(ii) *If* $k\bar{m} < d < k\sup_{\mu>0}\bar{\theta}$, *then*

(a) *For any* $\nu > \nu^*$, *there exists some* $\delta_2 > 0$ *such that two branches of the steady state solutions* $(\hat{u}_i, \hat{v}_i)$ $(i = 2, 3)$ *of* (1.1) *bifurcate from* $(\theta, 0)$ *at* $\mu = \hat{\mu}_2, \hat{\mu}_3$, *which can be described by* μ *for* $\mu \in (\hat{\mu}_2, \hat{\mu}_2 + \delta_2)$ *and* $\mu \in (\hat{\mu}_3 - \delta_2, \hat{\mu}_3)$, *respectively. Moreover, the bifurcating solution* $(\hat{u}_i, \hat{v}_i)$ *is locally stable for* $\mu \in (\hat{\mu}_2, \hat{\mu}_2 + \delta_2)$ *and* $\mu \in (\hat{\mu}_3 - \delta_2, \hat{\mu}_3)$, *respectively.*

(b) *For any* $\nu < \nu^*$, *there exists some* $\delta_3 > 0$ *such that a branch of the steady state solution* $(\hat{u}_4, \hat{v}_4)$ *of* (1.1) *bifurcates from* $(\theta, 0)$ *at* $\mu = \hat{\mu}_4$, *which can be parameterized by* μ *for* $\mu \in (\hat{\mu}_4 - \delta_3, \hat{\mu}_4)$. *In addition, the bifurcating solution* $(\hat{u}_4, \hat{v}_4)$ *is locally stable for* $\mu \in (\hat{\mu}_4 - \delta_3, \hat{\mu}_4)$.

If the dispersal rate of the predator is considered as a bifurcation parameter, we can similarly obtain the following global bifurcation result.

Theorem 1.4. *Suppose the non-constant function* m *satisfies (*1.2*). Then the following conclusions hold.*

(i) *If* $k\sup_{\mu>0}\bar{\theta} < d < k\max_{\bar{\Omega}} m$ *and* m *satisfies* (2.1), *then for small* μ, *there exists some* $\eta_1 > 0$ *such that a branch of the steady state solution* $(\tilde{u}_1, \tilde{v}_1)$ *to* (1.1) *bifurcates from* $(\theta, 0)$ *at* $\nu = \tilde{\nu}_1$, *which can be parameterized by* ν *for the range* $\nu \in (\tilde{\nu}_1 - \eta_1, \tilde{\nu}_1)$. *Moreover, the bifurcating solution* $(\tilde{u}_1, \tilde{v}_1)$ *is locally stable for* $\nu \in (\tilde{\nu}_1 - \eta_1, \tilde{\nu}_1)$ *and the branch of the steady state solutions of* (1.1) *bifurcating from* $(\tilde{\nu}_1, \theta, 0)$ *extend to zero in* ν.

(ii) *If $k\bar{m} < d < k \sup_{\mu>0} \bar{\theta}$, then for small or large μ, there exists some $\eta_2 > 0$ such that two branches of the steady state solutions $(\tilde{u}_i, \tilde{v}_i)$ $(i = 2,3)$ to* (1.1) *bifurcate from $(\theta, 0)$ at $\nu = \tilde{\nu}_2, \tilde{\nu}_3$, which can be characterized by ν for $\nu \in (\tilde{\nu}_2 - \eta_2, \tilde{\nu}_2)$ and $\nu \in (\tilde{\nu}_3 - \eta_2, \tilde{\nu}_3)$, respectively. Furthermore, the bifurcating solution $(\tilde{u}_i, \tilde{v}_i)$ is locally stable for $\nu \in (\tilde{\nu}_2 - \eta_2, \tilde{\nu}_2)$ and $\nu \in (\tilde{\nu}_3 - \eta_2, \tilde{\nu}_3)$, respectively, and the branch of the steady state solutions of* (1.1) *bifurcating from $(\tilde{\nu}_i, \theta, 0)(i = 2, 3)$ extend to zero in ν.*

Remark 1.5. *Because θ is not necessarily monotone with respect to μ, we cannot obtain the monotonicity of the principal eigenvalue λ_1 of* (2.2) *about μ. In addition, it is difficult to determine the limiting behaviors of positive steady states of* (1.1) *as μ approach zero and infinity, respectively. Hence, we cannot generalize the local bifurcation result to a global one.*

Remark 1.6. *For the predator-prey model studied in this paper, there are at least two remaining questions unanswered:*

(i) *By Theorem* 1.4, *the branch bifurcating from $(\tilde{\nu}_i, \theta, 0)(i = 1, 2, 3)$ approaches zero in ν. However, the global structure of the branch as ν varies remains unclear. Specifically, it is relevant to determine if there exist multiple solutions for some ranges of ν. See* [7, 8] *for related research.*

(ii) *The dynamics of the following model offers scope for further research: When $m(x, t+1) = m(x, t)$* [14], *that is, the intrinsic growth rate of the prey not only depends on spatial variable x, but also time t, and m is periodic.*

The rest of this paper is organized as follows: In Section 2 we present Lemmas 2.1-2.5. Section 3 is devoted to the proof of Theorem 1.1. In Section 4 we prove Theorems 1.3 and 1.4.

2. Preliminaries

In this section, we present some lemmas that are useful for later analysis.

Lemma 2.1. *Suppose m satisfies* (1.2). *Then the following properties hold.*

(i) *$\mu \mapsto \theta$ is a smooth mapping from $\mathbb{R}^+$ to $C^2(\bar{\Omega})$. Furthermore, $\lim_{\mu\to 0} \theta = m$ and $\lim_{\mu\to\infty} \theta = \bar{m}$ uniformly on $\bar{\Omega}$.*

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

Proof. Part (i) follows from the implicit function theorem [3]. The limiting behaviors of θ as μ approaches 0 or ∞ is well known (see e.g.[11, 20]). Part (ii) can be derived from the maximum principle (see [11, 23] for details). $\square$

Lemma 2.2. *For every $\mu > 0$, we obtain $\bar{m} < \bar{\theta}$. In particular, $\bar{m} < \max_{\bar{\Omega}} \theta$.*

Proof. Dividing (1.3) by θ, applying integration by parts, and simplifying yields

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

In particular, $\int_\Omega m < \int_\Omega \theta \le \max_{\bar\Omega} \theta / |\Omega|$. □

In general, we cannot determine if $\max_{\bar\Omega} \theta$ is strictly decreasing in μ. However, this conclusion is true for certain special cases. The following result describes the monotonicity of $\max_{\bar\Omega} \theta$ with respect to μ. The proof can be found in [22].

Lemma 2.3. *Suppose*

$$\Omega \textit{ is an interval }, m \in C^2(\bar\Omega), m_{xx} \neq 0 \textit{ and } m_x \neq 0 \textit{ on } \bar\Omega. \tag{2.1}$$

Then $\max_{\bar\Omega} \theta$ *is strictly decreasing in* μ.

Lemma 2.4. *The semi-trivial steady state* $(\theta, 0)$ *is stable/unstable if and only if the following eigenvalue problem, for* $(\lambda_1, \phi) \in \mathbb{R} \times C^2(\bar\Omega)$, *has a positive /negative principal eigenvalue (denoted by* λ_1*)*

$$\nu\Delta\phi + (k\theta - d)\phi + \lambda\phi = 0 \textit{ in } \Omega, \quad \partial\phi/\partial n = 0 \textit{ on } \partial\Omega. \tag{2.2}$$

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

$$F(u, v) = \begin{pmatrix} -\mu\Delta u - u(m - u - v) \\ -\nu\Delta v - v(ku - d) \end{pmatrix}.$$

Then we obtain

$$D_{(u,v)}F|_{(\theta,0)} = \begin{pmatrix} -\mu\Delta - (m - 2\theta) & \theta \\ 0 & -\nu\Delta - (k\theta - d) \end{pmatrix}.$$

By (1.2) and the positivity of θ, zero is the smallest eigenvalue of the operator $-\mu\Delta - (m - \theta)$ with homogeneous Neumann boundary condition. By the comparison principle for eigenvalues, the least eigenvalue of the operator $-\mu\Delta - (m - 2\theta)$ is strictly positive. Therefore, to investigate the stability of semi-trivial steady state $(\theta, 0)$, it remains to inquire about the sign of the smallest eigenvalue of (2.2). □

Lemma 2.5. *The least eigenvalue* λ_1 *of (2.2) depends smoothly on* $\nu > 0$. *Moreover,*

(i) λ_1 *is strictly increasing and concave in* ν.
(ii) λ_1 *has the following limiting behaviors:*

$$\lim_{\nu\to 0} \lambda_1 = d - k \max_{\bar\Omega} \theta, \quad \lim_{\nu\to\infty} \lambda_1 = d - k\bar\theta.$$

Proof. Part (i) can be easily deduced from the variational characterization of λ_1. See [22, 23] for the proof of Part (ii). □

3. Local stability of semi-trivial steady state

By Lemmas 2.1 and 2.2, we can show that $\bar{m} < \sup_{\mu>0} \bar{\theta} < \max_{\bar{\Omega}} m$ and $\lim_{\mu\to 0} \bar{\theta} = \lim_{\mu\to\infty} \bar{\theta} = \bar{m}$. By Lemma 2.4, the stability of $(\theta, 0)$ is determined by the sign of the principal eigenvalue of

$$\nu\Delta\phi + (k\theta - d)\phi + \lambda\phi = 0 \text{ in } \Omega, \quad \partial\phi/\partial n = 0 \text{ on } \partial\Omega. \tag{3.1}$$

It follows from Lemmas 2.1 and 2.5 that the principal eigenvalue λ_1 of (3.1) is a smooth function of μ and ν. We shall consider the following four cases to examine the changes in sign of λ_1 relative to variation in μ and ν.

Proof of Theorem 1.1. (i) Herein, $d > k \max_{\bar{\Omega}} m$. By Lemma 2.5, we obtain

$$\lim_{\nu\to 0} \lambda_1 = d - k \max_{\bar{\Omega}} \theta > 0, \quad \lim_{\nu\to\infty} \lambda_1 = d - k\bar{\theta} > 0$$

for every $\mu > 0$. Furthermore, λ_1 is strictly increasing with respect to ν. Therefore, $\lambda_1 > 0$ for any $\mu > 0$ and $\nu > 0$.

(ii) For $k \sup_{\mu>0} \bar{\theta} < d < k \max_{\bar{\Omega}} m$, $\int_\Omega (k\theta - d) < 0$ for every $\mu > 0$. Because

$$\begin{aligned} &k \max_{\bar{\Omega}} \theta - d \to k \max_{\bar{\Omega}} m - d > 0 \text{ as } \mu \to 0, \\ &k \max_{\bar{\Omega}} \theta - d \to k\bar{m} - d < 0 \text{ as } \mu \to \infty, \end{aligned}$$

and $\max_{\bar{\Omega}} \theta$ is strictly decreasing in μ (by Lemma 2.3), $k \max_{\bar{\Omega}} \theta - d$ admits a unique positive root $\tilde{\mu}$. Moreover, $k\theta - d$ is positive at some point in Ω for every $\mu < \tilde{\mu}$ and $k\theta < d$ for any $\mu > \tilde{\mu}$. Therefore, for every $\mu < \tilde{\mu}$, the eigenvalue problem [3]:

$$\Delta\varphi + \sigma(k\theta - d)\varphi = 0 \text{ in } \Omega, \quad \partial\varphi/\partial n = 0 \text{ on } \partial\Omega \tag{3.2}$$

has a positive principal eigenvalue, denoted by σ_1. Set $\tilde{\nu} = 1/\sigma_1(\mu)$. Because the smallest eigenvalue λ_1 of (3.1) is strictly increasing in ν, we have $\lambda_1 > 0$ for any $\nu > \tilde{\nu}$, $\lambda_1 = 0$ at $\nu = \tilde{\nu}$ and $\lambda_1 < 0$ for any $\nu < \tilde{\nu}$.

Claim. For the smallest eigenvalue σ_1 of (3.2), $\lim_{\mu\to\tilde{\mu}^-} \sigma_1 = +\infty$.

We argue by contradiction. Suppose the claim is not true; we pass to a subsequence if necessary, and assume $\sigma_1 \to \tilde{\sigma} \le \hat{C}$ as $\mu \to \tilde{\mu}^-$, where $\hat{C} > 0$. By elliptic regularity theory and the Sobolev embedding theorem [10], we obtain the associated eigenfunction $\varphi \to \varphi^*$ in $C^2(\bar{\Omega})$ as $\mu \to \tilde{\mu}^-$. Furthermore, $\varphi^* > 0$ and satisfies

$$\Delta\varphi^* + \tilde{\sigma}(k\theta(x,\tilde{\mu}) - d)\varphi^* = 0 \text{ in } \Omega, \quad \partial\varphi^*/\partial n = 0 \text{ on } \partial\Omega. \tag{3.3}$$

Integrating (3.3) and applying the boundary condition, we obtain

$$\tilde{\sigma} \int_\Omega (k\theta(x,\tilde{\mu}) - d)\varphi^* = 0.$$

Because $k\theta(x,\tilde{\mu}) - d \le 0$ and $\varphi^* > 0$, $\tilde{\sigma} \equiv 0$. We note that φ^* will be a positive constant. Integrating (3.2), we obtain $\int_\Omega (k\theta - d)\varphi = 0$. If $\mu \to \tilde{\mu}^-$, then $\int_\Omega (k\theta(x,\tilde{\mu}) - d)\varphi^* = 0$, that is a contradiction.

Define

$$\nu^* = 1/\inf_{0<\mu<\tilde{\mu}} \sigma_1(\mu).$$

We consider the following two cases to finish the proof.

Case 1. For every $\nu > \nu^*$, we find $\nu > 1/\sigma_1(\mu)$ for every $\mu \in (0, \tilde{\mu})$. Because λ_1 is strictly increasing with respect to ν, $\lambda_1 > 0$ for every $\mu \in (0, \tilde{\mu})$. By contrast, because $k\theta - d \leq 0$ for every $\mu \geq \tilde{\mu}$, we have $\lambda_1 > 0$ for every $\mu \geq \tilde{\mu}$. That is, $\lambda_1 > 0$ for any $\mu > 0$ and $\nu > \nu^*$.

Case 2. For every $\nu < \nu^*$, we have $1/\nu > \inf_{0<\mu<\tilde{\mu}} \sigma_1(\mu)$. Because $\sigma_1(\mu) \to +\infty$ as $\mu \to \tilde{\mu}^-$, $1/\nu - \sigma_1(\mu)$ changes sign at least once in $(0, \tilde{\mu})$. Therefore, λ_1 changes sign at least once as μ varies from zero to infinity.

(iii) If $k\bar{m} < d < k \sup_{\mu>0} \bar{\theta}$, then there exist two points $\mu_* \leq \mu^*$ such that $d > k\bar{\theta}$ for every $\mu \in (0, \mu_1) \cup (\mu_2, \infty)$, and $d < k\bar{\theta}$ for any $\mu \in (\mu_1, \mu_*) \cup (\mu^*, \mu_2)$, where μ_1 and μ_2 are the smallest and largest positive roots of $d = k\bar{\theta}$, respectively. It may occur that $\mu_* = \mu^*$.

For every $\mu \in (\mu_1, \mu_*) \cup (\mu^*, \mu_2)$, $\int_\Omega (k\theta - d) > 0$. Dividing (3.1) by ϕ, applying integration by parts, and simplifying yields

$$\lambda_1 = -\frac{\nu}{|\Omega|} \int_\Omega \frac{|\nabla \phi|^2}{\phi^2} - \frac{1}{|\Omega|} \int_\Omega (k\theta - d) < 0.$$

Therefore, $(\theta, 0)$ is unstable for arbitrary $\mu \in (0, \mu_1) \cup (\mu_2, \infty)$ and $\nu > 0$.

For every $\mu \in (0, \mu_1) \cup (\mu_2, \infty)$, we obtain $\int_\Omega (k\theta - d) < 0$. Consider the following eigenvalue problem

$$\Delta \psi + \zeta (k\theta - d)\psi = 0 \text{ in } \Omega, \quad \partial \psi / \partial n = 0 \text{ on } \partial \Omega. \tag{3.4}$$

We can show that $k \max_{\bar{\Omega}} \theta - d \geq k \sup_{\mu>0} \bar{\theta} - d > 0$. That is, there exists some $x^* \in \Omega$ such that $k\theta - d$ is positive. Therefore, the eigenvalue problem (3.4) has a positive principal eigenvalue, denoted by ζ_1, that can be characterized by

$$\zeta_1 = \inf_{\psi \in H^1(\Omega), \int_\Omega (k\theta - d)\psi^2 > 0} \frac{\int_\Omega |\nabla \psi|^2}{\int_\Omega (k\theta - d)\psi^2}.$$

Set $\nu_* = 1/\zeta_1(\mu)$. Because the principal eigenvalue λ_1 of (3.1) is strictly increasing in ν, we obtain $\lambda_1 > 0$ for any $\nu > \nu_*$, $\lambda_1 = 0$ at $\nu = \nu_*$ and $\lambda_1 < 0$ for any $\nu < \nu_*$.

Claim. For the smallest eigenvalue ζ_1 of (3.4), $\lim_{\mu \to \mu_1^-} \zeta_1 = \lim_{\mu \to \mu_2^+} \zeta_1 = 0$.

We argue by contradiction. Suppose the claim is not true; we pass to a subsequence if necessary, and assume $\zeta_1 \to \bar{\zeta} \neq 0$ as $\mu \to \mu_1^-$. By elliptic regularity theory and the Sobolev embedding theorem [10], we obtain the associated eigenfunction $\psi \to \psi^*$ in $C^2(\bar{\Omega})$ as $\mu \to \mu_1^-$. Moreover, $\psi^* > 0$ and satisfies

$$\Delta \psi^* + \bar{\zeta}(k\theta(x, \mu_1) - d)\psi^* = 0 \text{ in } \Omega, \quad \partial \psi^* / \partial n = 0 \text{ on } \partial \Omega. \tag{3.5}$$

Dividing (3.5) by ψ^*, applying integration by parts and the boundary condition, we obtain

$$\int_\Omega \frac{|\nabla\psi^*|^2}{\psi^{*2}} + \bar{\zeta}\int_\Omega (k\theta(x,\mu_1) - d) = 0 \text{ in } \Omega, \quad \partial\psi^*/\partial n = 0 \text{ on } \partial\Omega.$$

Because $\int_\Omega (k\theta(x,\mu_1) - d) = 0$, ψ^* must be a positive constant. This together with $\bar{\zeta} \neq 0$ means that $k\theta(x,\mu_1) - d = 0$, which is a contradiction. By a similar argument, we can show that $\lim_{\mu\to\mu_2^+} \zeta_1 = 0$.

By the definition of ν_*, we can conclude that $\lim_{\mu\to\mu_1^-} \nu_* = \lim_{\mu\to\mu_2^+} \nu_* = +\infty$. Define $\nu^* = \inf_{\mu\in(0,\mu_1)\cup(\mu_2,\infty)} 1/\zeta_1(\mu)$. For every $\nu < \nu^*$, we have $\nu < 1/\zeta_1(\mu)$. In addition, $\lambda_1 < 0$ for any $\mu \in (0,\mu_1)\cup(\mu_2,\infty)$. However, as $\mu \to \infty$, we have

$$\lim_{\nu\to 0} \lambda_1 = d - k\max_{\bar{\Omega}} \theta \to d - k\bar{m} > 0, \lim_{\nu\to\infty} \lambda_1 = d - k\bar{\theta} \to d - k\bar{m} > 0.$$

That is, $\lambda_1 > 0$ for sufficiently large μ and every $\nu > 0$. Therefore, for every $\nu < \nu^*$, λ_1 changes sign at least once, from negative to positive as μ varies from zero to infinity. If $\nu > \nu^*$, because $\nu^* \to +\infty$ as $\mu \to \mu_1^-$ and $\mu \to \mu_2^+$, we observe that $\nu - \nu^*$ changes sign at least twice, initially from positive to negative, and thereafter from negative to positive as μ varies from zero to infinity. Because λ_1 is strictly increasing in ν, its sign also changes at least twice as μ varies from zero to infinity.

(iv) For this case, we can show that

$$\lim_{\nu\to 0} \lambda_1 = d - k\max_{\bar{\Omega}} \theta < 0, \quad \lim_{\nu\to\infty} \lambda_1 = d - k\bar{\theta} < 0$$

for every $\mu > 0$. Therefore $\lambda_1 < 0$ for any $\mu > 0$ and $\nu > 0$.

4. Local bifurcation from semi-trivial steady state

Using bifurcation theory [4], we select the migration rates of the prey and predator as bifurcation parameters and determine their corresponding bifurcation consequences. Accordingly, we write the positive steady states of (1.1) as follows:

$$\begin{cases} \mu\Delta u + u(m(x) - u) - uv = 0 & \text{in } \Omega, \\ \nu\Delta v + (ku - d)v = 0 & \text{in } \Omega, \\ \partial u/\partial n = \partial v/\partial n = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.1}$$

4.1. μ is considered as a bifurcation parameter. Let $X = \{(u,v) \in W^{2,p}(\Omega) \times W^{2,p}(\Omega) : \partial u/\partial n = \partial v/\partial n = 0 \text{ on } \partial\Omega\}$ and $Y = L^p(\Omega) \times L^p(\Omega)$ with $p > N$. Define the operator $G(\mu,u,v) : (0,\infty) \times X \to Y$ by

$$G(\mu,u,v) = \begin{pmatrix} \mu\Delta u + u(m(x) - u) - uv \\ \nu\Delta v + (ku - d)v \end{pmatrix}.$$

We observe that $G(\mu,\theta,0) = 0$ and the derivatives $D_\mu G(\mu,u,v)$, $D_{(u,v)}G(\mu,u,v)$ and $D_\mu D_{(u,v)}G(\mu,u,v)$ exist and are continuous in the neighborhood of $(\mu,\theta,0)$.

Lemma 4.1. *Suppose* (1.2) *holds. If* $k\sup_{\mu>0}\bar{\theta} < d < k\max_{\bar{\Omega}} m$ *and* m *also satisfies* (2.1)*, then for every* $\nu < \nu^*$*, there exist some* $\delta_1 > 0$ *and* $\mu_1(s) \in C^2(-\delta_1, \delta_1)$ *with* $\mu_1(0) = \hat{\mu}_1$ *such that all nonnegative steady state solutions of* (1.1) *in the neighborhood of* $(\hat{\mu}_1, \theta, 0)$ *can be parameterized as*

$$(\mu, \hat{u}_1, \hat{v}_1) = (\mu_1(s), \theta + s\hat{\varphi}_1 + s^2\hat{\phi}_1(s), s\hat{\psi}_1 + s^2\hat{\chi}_1(s)), \quad 0 < s < \delta_1, \tag{4.2}$$

where $(\hat{\varphi}_1, \hat{\psi}_1)$ *is determined by* (4.6) *and* (4.3)*, and* $(\hat{\phi}_1(s), \hat{\chi}_1(s))$ *lies in the complement of the kernel of* $D_{(u,v)}G|_{(\hat{\mu}_1,\theta(x,\hat{\mu}_1),0)}$ *in* X*.*

Proof. Herein, by Remark 1.2 (a), there exists some $\hat{\mu}_1 > 0$ such that

$$\nu\Delta\hat{\psi}_1 + (k\theta(x,\hat{\mu}_1) - d)\hat{\psi}_1 + \lambda_1(\hat{\mu}_1)\hat{\psi}_1 = 0 \text{ in } \Omega, \quad \partial\hat{\psi}_1/\partial n = 0 \text{ on } \partial\Omega, \tag{4.3}$$

where $\lambda_1(\hat{\mu}_1) = 0$ and $\hat{\psi}_1 > 0$ is its associated eigenfunction. In addition, $\partial\lambda_1/\partial\mu(\hat{\mu}_1) > 0$. Define $\psi' = \partial\psi/\partial\mu, \theta' = \partial\theta/\partial\mu$, and $\lambda_1' = \partial\lambda_1/\partial\mu$. Differentiating (2.2) with respect to μ yields

$$\nu\Delta\psi' + (k\theta - d)\psi' + k\theta'\psi + \lambda_1\psi' + \lambda_1'\psi = 0.$$

Multiplying the aforementioned equation by ψ with $\|\psi\|_{L^\infty(\Omega)} = 1$ and applying integration by parts yields

$$\lambda_1' \int_\Omega \psi^2 = -\int_\Omega k\theta'\psi^2.$$

By elliptic regularity theory [10], $\psi \to \hat{\psi}_1$ in $C^2(\bar{\Omega})$ as $\mu \to \hat{\mu}_1$. Therefore,

$$\int_\Omega k\theta'(x,\hat{\mu}_1)(\hat{\psi}_1)^2 = -\lambda_1'(\hat{\mu}_1)\int_\Omega (\hat{\psi}_1)^2 < 0. \tag{4.4}$$

By the operator $G(\mu, u, v)$, we deduce

$$D_{(u,v)}G|_{(\hat{\mu}_1,\theta(x,\hat{\mu}_1),0)} \begin{pmatrix} \varphi \\ \psi \end{pmatrix} = \begin{pmatrix} \hat{\mu}_1\Delta\varphi + (m - 2\theta(x,\hat{\mu}_1))\varphi - \theta(x,\hat{\mu}_1)\psi \\ \nu\Delta\psi + (k\theta(x,\hat{\mu}_1) - d)\psi \end{pmatrix}.$$

The kernel of $D_{(u,v)}G|_{(\hat{\mu}_1,\theta(x,\hat{\mu}_1),0)}$ is spanned by $(\hat{\varphi}_1, \hat{\psi}_1)$, where $\hat{\psi}_1$ is defined as in (4.3), and $\hat{\varphi}_1$ is uniquely determined by

$$\hat{\mu}_1\Delta\hat{\varphi}_1 + (m - 2\theta(x,\hat{\mu}_1))\hat{\varphi}_1 - \theta(x,\hat{\mu}_1)\hat{\psi}_1 = 0 \text{ in } \Omega, \quad \partial\hat{\varphi}_1/\partial n = 0 \text{ on } \partial\Omega. \tag{4.5}$$

By the comparison principle of eigenvalues and the positivity of θ, the principal eigenvalue of the operator $-\hat{\mu}_1\Delta - (m - 2\theta(x,\hat{\mu}_1))$ with homogeneous Neumann boundary condition is strictly positive. Therefore,

$$\hat{\varphi}_1 = (-\hat{\mu}_1\Delta - (m - 2\theta(x,\hat{\mu}_1)))^{-1}(-\theta(x,\hat{\mu}_1)\hat{\psi}_1). \tag{4.6}$$

In addition, it follows from the Fredholm alternative that

$$\operatorname{codim}\mathcal{R}(D_{(u,v)}G|_{(\hat{\mu}_1,\theta(x,\hat{\mu}_1),0)}) = \dim\mathcal{N}(D_{(u,v)}G|_{(\hat{\mu}_1,\theta(x,\hat{\mu}_1),0)}) = 1.$$

Therefore, it suffices to examine the following transversality condition:

$$D_\mu D_{(u,v)}G|_{(\hat{\mu}_1,\theta(x,\hat{\mu}_1),0)} \begin{pmatrix} \hat{\varphi}_1 \\ \hat{\psi}_1 \end{pmatrix} \notin \mathcal{R}(D_{(u,v)}G|_{(\hat{\mu}_1,\theta(x,\hat{\mu}_1),0)}).$$

Otherwise, because

$$D_\mu D_{(u,v)} G|_{(\hat{\mu}_1, \theta(x,\hat{\mu}_1),0)} \begin{pmatrix} \hat{\varphi}_1 \\ \hat{\psi}_1 \end{pmatrix} = \begin{pmatrix} \Delta\hat{\varphi}_1 - 2\theta'(x,\hat{\mu}_1)\hat{\varphi}_1 - \theta'(x,\hat{\mu}_1)\hat{\psi}_1 \\ k\theta'(x,\hat{\mu}_1)\hat{\psi}_1 \end{pmatrix},$$

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

$$\begin{cases} \hat{\mu}_1 \Delta\varphi + (m - 2\theta(x,\hat{\mu}_1))\varphi - \theta(x,\hat{\mu}_1)\psi = \Delta\hat{\varphi}_1 - 2\theta'(x,\hat{\mu}_1)\hat{\varphi}_1 - \theta'(x,\hat{\mu}_1)\hat{\psi}_1, \\ \nu\Delta\psi + (k\theta(x,\hat{\mu}_1) - d)\psi = k\theta'(x,\hat{\mu}_1)\hat{\psi}_1. \end{cases} \tag{4.7}$$

Multiplying ψ in (4.7) by $\hat{\psi}_1$ and thereafter applying integration by parts, we obtain

$$\int_\Omega k\theta'(x,\hat{\mu}_1)(\hat{\psi}_1)^2 = 0.$$

This contradicts (4.4). □

Lemma 4.2. *The bifurcation direction of the solution from Lemma* 4.1 *can be characterized by* $\mu_1'(0) < 0$.

Proof. Substituting (4.2) into v in (4.1), applying (4.3) and dividing the result by s, we obtain

$$\begin{aligned} &\frac{k\theta - k\theta(x,\hat{\mu}_1)}{s}\hat{\psi}_1 + \nu\Delta\hat{\chi}_1 + (k\theta - d)\hat{\chi}_1 + k\hat{\varphi}_1\hat{\psi}_1 \\ &= -k(\hat{\varphi}_1\hat{\chi}_1 + \hat{\phi}_1\hat{\psi}_1)s + o(s). \end{aligned} \tag{4.8}$$

Multiplying (4.8) by $\hat{\psi}_1$, applying integration by parts, and taking the limit, we obtain

$$\mu_1'(0)\int_\Omega \theta'(x,\hat{\mu}_1)(\hat{\psi}_1)^2 = -\int_\Omega \hat{\varphi}_1(\hat{\psi}_1)^2. \tag{4.9}$$

By (4.6), $\hat{\varphi}_1 < 0$. It follows from the positivity of $\hat{\psi}_1$, (4.4) and (4.9) that $\mu_1'(0) < 0$. □

To investigate the linear stability of $(\hat{u}_1, \hat{v}_1)$ from Lemma 4.1, we present the following preliminary results.

Lemma 4.3. *As* $s \to 0$, *we have* $(\hat{u}_1, \hat{v}_1) \to (\theta(x,\hat{\mu}_1), 0)$, $\hat{v}_1/\|\hat{v}_1\|_{L^\infty(\Omega)} \to \hat{\psi}_1$, *and* $\psi \to \hat{\psi}_1$ *in* $C^1(\bar{\Omega})$, *where* ψ *is the corresponding eigenfunction of the least eigenvalue* λ_1 *of* (2.2) *with* $\|\psi\|_{L^\infty(\Omega)} = 1$.

Proof. By (4.2), we may suppose that $\|\hat{u}_1 - \theta\|_{L^\infty(\Omega)} + \|\hat{v}_1\|_{L^\infty(\Omega)} \le \|\theta\|_{L^\infty(\Omega)}/2$ for small s. By elliptic regularity theory, and passing to a subsequence if necessary, we may assume that $(\hat{u}_1, \hat{v}_1) \to (u^*, v^*)$ in $C^2(\bar{\Omega})$ as $s \to 0$, where u^* and v^* satisfy

$$\begin{cases} \hat{\mu}_1 \Delta u^* + u^*(m(x) - u^*) - u^* v^* = 0 & \text{in } \Omega, \\ \nu\Delta v^* + (ku^* - d)v^* = 0 & \text{in } \Omega, \\ \partial u^*/\partial n = \partial v^*/\partial n = 0 & \text{on } \partial\Omega. \end{cases}$$

Because $\|u^* - \theta\|_{L^\infty(\Omega)} \le \|\theta\|_{L^\infty(\Omega)}/2$, $u^* \not\equiv 0$ on $\bar{\Omega}$. If $v^* \not\equiv 0$, it follows from the strong maximum principle that $v^* > 0$ on $\bar{\Omega}$. By the equation of u^*, we obtain $u^* < \theta(x, \hat{\mu}_1)$ on $\bar{\Omega}$. Multiplying the equation of v^* by $\hat{\psi}_1$, and (4.3) by v^*, applying integration by parts and subtracting the results, we obtain

$$\int_\Omega v^* \hat{\psi}_1 (u^* - \theta(x, \hat{\mu}_1)) = 0.$$

This is a contradiction. Consequently, $v^* \equiv 0$. It follows that $u^* \equiv \theta(x, \hat{\mu}_1)$ on $\bar{\Omega}$.

Set $\tilde{v} = \hat{v}_1 / \|\hat{v}_1\|_{L^\infty(\Omega)}$. By elliptic regularity theory [10], we may assume that $\tilde{v} \to \bar{v}$ as $s \to 0$, where $\bar{v} \geq 0, \|\bar{v}\|_{L^\infty(\Omega)} = 1$ and satisfies

$$\nu \Delta \bar{v} + (k\theta(x, \hat{\mu}_1) - d)\bar{v} = 0 \text{ in } \Omega, \quad \partial \bar{v} / \partial n = 0 \text{ on } \partial\Omega.$$

Therefore, $\bar{v} \equiv \hat{\psi}_1$, that is, $\hat{v}_1 / \|\hat{v}_1\|_{L^\infty(\Omega)} \to \hat{\psi}_1$ in $C^1(\bar{\Omega})$ as $s \to 0$. We can use a similar argument to deduce that $\lambda_1 \to 0$ and $\psi \to \hat{\psi}_1$ in $C^1(\bar{\Omega})$ as $s \to 0$. □

Lemma 4.4. *For small $s > 0$, the bifurcating solution from Lemma* 4.1 *is linearly stable.*

Proof. Linearizing the system (1.1) for the bifurcating solution $(\hat{u}_1, \hat{v}_1)$, we have

$$\begin{cases} \mu_1(s)\Delta\varphi + (m - 2\hat{u}_1 - \hat{v}_1)\varphi - \hat{u}_1\psi + \lambda\varphi = 0 & \text{in } \Omega, \\ \nu\Delta\psi + (k\hat{u}_1 - d)\psi + k\hat{v}_1\varphi + \lambda\psi = 0 & \text{in } \Omega, \\ \partial\varphi/\partial n = \partial\psi/\partial n = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.10}$$

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

$$\Gamma_s \begin{pmatrix} \varphi \\ \psi \end{pmatrix} = \begin{pmatrix} \mu_1(s)\Delta\varphi + (m - 2\hat{u}_1 - \hat{v}_1)\varphi - \hat{u}_1\psi \\ \nu\Delta\psi + (k\hat{u}_1 - d)\psi + k\hat{v}_1\varphi \end{pmatrix}$$

and

$$\Gamma_0 \begin{pmatrix} \varphi \\ \psi \end{pmatrix} = \begin{pmatrix} \hat{\mu}_1\Delta\varphi + (m - 2\theta)\varphi - \theta\psi \\ \nu\Delta\psi + (k\theta - d)\psi \end{pmatrix}.$$

By Lemma 4.3, $(\hat{u}_1, \hat{v}_1) \to (\theta, 0)$ in $C^1(\bar{\Omega})$ as $s \to 0$. It follows that $\Gamma_s \to \Gamma_0$ uniformly in operator norm as $s \to 0$. Furthermore, the kernel of Γ_0 is spanned by $(\hat{\varphi}_1, \hat{\psi}_1)$, and zero is a K-simple eigenvalue of Γ_0, where the operator K is the canonical injection from X to Y. Therefore, there exists a unique K-simple eigenvalue $\sigma_1 = \sigma_1(s)$ of Γ_s with $\sigma_1 \to 0$ as $s \to 0$. If σ_1 is an eigenvalue of (4.10) with associated eigenfunction (φ, ψ), then $\sigma_1 = -\lambda$.

The remaining arguments of the proof are considered in the following two cases.

(a) $\psi \not\equiv 0$ on $\bar{\Omega}$. After scaling we may suppose that $\|\psi\|_{L^\infty(\Omega)} = 1$ and ψ is positive at some point in Ω. Because $(\hat{u}_1, \hat{v}_1) \to (\theta, 0)$ and $\sigma_1 \to 0$, analogous to Lemma 4.3, we can show that $(\varphi, \psi) \to (\hat{\varphi}_1, \hat{\psi}_1)$ in $C^1(\bar{\Omega})$ as $s \to 0$, where $\hat{\varphi}_1$ is uniquely determined by (4.6). Multiplying the equation of ψ by $\hat{v}_1$, and the equation of $\hat{v}_1$ by ψ, applying integration by parts and the boundary conditions, we have

$$\sigma_1 \int_\Omega \psi \hat{v}_1 = \int_\Omega k(\hat{v}_1)^2 \varphi.$$

Dividing by $\|\hat{v}_1\|^2_{L^\infty(\Omega)}$, applying Lemma 4.3 and taking the limit gives

$$\lim_{s\to 0} \frac{\sigma_1}{\|\hat{v}_1\|_{L^\infty(\Omega)}} = \int_\Omega k(\hat{\psi}_1)^2 \hat{\varphi}_1 / \int_\Omega (\hat{\psi}_1)^2.$$

By (4.6), $\hat{\varphi}_1 < 0$ on $\bar{\Omega}$. Therefore, $\sigma_1 < 0$ for small s.

(b) If $\psi \equiv 0$ on $\bar{\Omega}$, then $\varphi \not\equiv 0$ and it satisfies

$$\mu_1(s)\Delta\varphi + (m - 2\hat{u}_1 - \hat{v}_1)\varphi = \sigma_1 \varphi \text{ in } \Omega, \quad \partial\varphi/\partial n = 0 \text{ on } \partial\Omega.$$

Because $(\hat{u}_1, \hat{v}_1) \to (\theta, 0)$ as $s \to 0$, the smallest eigenvalue of the operator $-\hat{\mu}_1\Delta - (m - 2\theta(x, \hat{\mu}_1))$ with homogeneous Neumann boundary condition is strictly positive, we have $\sigma_1 < 0$. That is, all eigenvalues of (4.10) must have positive real part, hence, $(\hat{u}_1, \hat{v}_1)$ is linearly stable. $\square$

Proof of Theorem 1.3. The conclusions of Case (i) follows from Lemmas 4.1, 4.2 and 4.4. Case (ii) can be deduced from the similar argument that are, omitted here.

4.2. $\boldsymbol{\nu}$ is considered as a bifurcation parameter. Before proving Theorem 1.4, we present some preliminary results. We define the operator $H(\nu, u, v) : (0, \infty) \times X \to Y$ by

$$H(\nu, u, v) = \begin{pmatrix} \mu\Delta u + u(m(x) - u) - uv \\ \nu\Delta v + (ku - d)v \end{pmatrix}.$$

It is noted that $H(\nu, \theta, 0) = 0$, the derivatives $D_\nu H(\nu, u, v)$, $D_{(u,v)}H(\nu, u, v)$ and $D_\nu D_{(u,v)}H(\nu, u, v)$ exist and are continuous in the neighborhood of $(\nu, \theta, 0)$.

Lemma 4.5. *Suppose* (1.2) *holds. If* $k \sup_{\mu>0} \bar{\theta} < d < k \max_{\bar{\Omega}} m$ *and* m *also fulfills* (2.1)*, then for sufficiently small* μ*, there exists some* $\tau_1 > 0$ *and* $\nu_1(s) \in C^2(-\tau_1, \tau_1)$ *with* $\nu_1(0) = \tilde{\nu}_1$ *such that all nonnegative steady state solutions of* (1.1) *in the neighborhood of* $(\tilde{\nu}_1, \theta, 0)$ *can be parameterized as*

$$(\nu, \tilde{u}_1, \tilde{v}_1) = (\nu_1(s), \theta + s\tilde{\varphi}_1 + s^2\tilde{\phi}_1(s), s\tilde{\psi}_1 + s^2\tilde{\chi}_1(s)), \quad 0 < s < \tau_1, \ (4.11)$$

where $(\tilde{\phi}_1(s), \tilde{\chi}_1(s))$ *lies in the complement of the kernel of* $D_{(u,v)}H|_{(\tilde{\nu}_1,\theta,0)}$ *in* X*. Moreover, the bifurcation direction of the solution* $(\tilde{\nu}_1, \theta, 0)$ *can be characterized by* $\nu_1'(0) < 0$.

Proof. Because $\lim_{\nu\to 0} \lambda_1 = d - k \max_{\bar{\Omega}} \theta \to d - k \max_{\bar{\Omega}} m < 0$ and $\lim_{\nu\to\infty} \lambda_1 = d - k\bar{\theta} \to d - k\bar{m} > 0$ as $\mu \to 0$, there exists a unique $\tilde{\nu}_1 = \tilde{\nu}_1(\mu) > 0$ such that for sufficiently small μ, $\lambda_1 < 0$ if $\nu < \tilde{\nu}_1$, $\lambda_1 = 0$ at

$\nu = \tilde{\nu}_1$ and $\lambda_1 > 0$ if $\nu > \tilde{\nu}_1$. Therefore, there is some function $\psi \to \tilde{\psi}_1$ in $C^2(\bar{\Omega})$ as $\nu \to \tilde{\nu}_1$, and $\tilde{\psi}_1 > 0$ satisfies

$$\tilde{\nu}_1 \Delta \tilde{\psi}_1 + (k\theta - d)\tilde{\psi}_1 + \lambda_1 \tilde{\psi}_1 = 0 \text{ in } \Omega, \quad \partial \tilde{\psi}_1/\partial n = 0 \text{ on } \partial\Omega, \tag{4.12}$$

that is, $\lambda_1 = 0$ is the least eigenvalue of (4.12) and $\tilde{\psi}_1$ is its corresponding eigenfunction. In addition, $\tilde{\varphi}_1$ is uniquely determined by

$$\mu \Delta \tilde{\varphi}_1 + (m - 2\theta)\tilde{\varphi}_1 - \theta \tilde{\psi}_1 = 0 \text{ in } \Omega, \quad \partial \tilde{\varphi}_1/\partial n = 0 \text{ on } \partial\Omega. \tag{4.13}$$

Because

$$D_{(u,v)} H|_{(\tilde{\nu}_1,\theta,0)} \begin{pmatrix} \varphi \\ \psi \end{pmatrix} = \begin{pmatrix} \mu\Delta\varphi + (m - 2\theta)\varphi - \theta\psi \\ \tilde{\nu}_1 \Delta\psi + (k\theta - d)\psi \end{pmatrix},$$

we can show that the kernel of $D_{(u,v)}H|_{(\tilde{\nu}_1,\theta,0)}$ is spanned by $(\tilde{\varphi}_1, \tilde{\psi}_1)$ and $\dim \mathcal{N}(D_{(u,v)}H|_{(\tilde{\nu}_1,\theta,0)}) = \operatorname{codim} \mathcal{R}(D_{(u,v)}H|_{(\tilde{\nu}_1,\theta,0)}) = 1$. Now we begin to examine the transversality condition:

$$D_\nu D_{(u,v)} H|_{(\tilde{\nu}_1,\theta,0)} \begin{pmatrix} \tilde{\varphi}_1 \\ \tilde{\psi}_1 \end{pmatrix} = \begin{pmatrix} 0 \\ \Delta\tilde{\psi}_1 \end{pmatrix} \notin \mathcal{R}(D_{(u,v)}H|_{(\tilde{\nu}_1,\theta,0)}).$$

Because $\int_\Omega |\nabla \tilde{\psi}_1|^2 \neq 0$, $\tilde{\nu}_1 \Delta\psi + (k\theta - d)\psi = \Delta\tilde{\psi}_1$ is not solvable. The transversality condition follows.

Substituting the expansion (4.11) into the equation of v and dividing the result by s yields

$$\begin{aligned} &\frac{\nu_1(s) - \tilde{\nu}_1}{s} \Delta\tilde{\psi}_1 + \nu_1(s)\Delta\tilde{\chi}_1 + (k\theta - d)\tilde{\chi}_1 + k\tilde{\varphi}_1\tilde{\psi}_1 \\ &= -k(\tilde{\varphi}_1\tilde{\chi}_1 + \tilde{\phi}_1\tilde{\psi}_1)s + o(s). \end{aligned} \tag{4.14}$$

Multiplying (4.14) by $\tilde{\psi}_1$, and applying integration by parts and the boundary condition, and thereafter taking the limit, we obtain

$$\nu_1'(0) \int_\Omega |\nabla\tilde{\psi}_1|^2 = \int_\Omega k\tilde{\varphi}_1(\tilde{\psi}_1)^2.$$

By (4.13), $\tilde{\varphi}_1 < 0$. It follows that $\nu_1'(0) < 0$. □

Lemma 4.6. *For small $s > 0$, the bifurcating solution from Lemma 4.5 is linearly stable.*

Proof. To study the stability of the bifurcating solution $(\tilde{u}_1, \tilde{v}_1)$, we consider the following linear eigenvalue problem:

$$\begin{cases} \mu\Delta\varphi + (m - 2\tilde{u}_1 - \tilde{v}_1)\varphi - \tilde{u}_1\psi + \lambda\varphi = 0 & \text{in } \Omega, \\ \nu_1(s)\Delta\psi + (k\tilde{u}_1 - d)\psi + k\tilde{v}_1\varphi + \lambda\psi = 0 & \text{in } \Omega, \\ \partial\varphi/\partial n = \partial\psi/\partial n = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.15}$$

Define the operators Λ_s and $\Lambda_0 : X \to Y$ by

$$\Lambda_s \begin{pmatrix} \varphi \\ \psi \end{pmatrix} = \begin{pmatrix} \mu\Delta\varphi + (m - 2\tilde{u}_1 - \tilde{v}_1)\varphi - \tilde{u}_1\psi \\ \nu_1(s)\Delta\psi + (k\tilde{u}_1 - d)\psi + k\tilde{v}_1\varphi \end{pmatrix}$$

and

$$\Lambda_0 \begin{pmatrix} \varphi \\ \psi \end{pmatrix} = \begin{pmatrix} \mu\Delta\varphi + (m-2\theta)\varphi - \theta\psi \\ \tilde{\nu}_1\Delta\psi + (k\theta - d)\psi \end{pmatrix}.$$

By similar arguments as in Lemma 4.3, we can deduce that $(\tilde{u}_1, \tilde{v}_1) \to (\theta, 0)$ $\tilde{v}_1/\|\tilde{v}_1\|_{L^\infty(\Omega)} \to \tilde{\psi}_1, \varphi \to \tilde{\varphi}_1$ and $\psi \to \tilde{\psi}_1$ in $C^1(\bar{\Omega})$ as $s \to 0$. Therefore, $\Lambda_s \to \Lambda_0$ uniformly in operator norm as $s \to 0$. Moreover, we observe that the kernel of Λ_0 is spanned by $(\tilde{\varphi}_1, \tilde{\psi}_1)$, and zero is a K-simple eigenvalue of Λ_0, where the operator K is the canonical injection from X to Y. Therefore, there exists a unique K-simple eigenvalue $\zeta_1 = \zeta_1(s)$ of Λ_s with $\zeta_1 \to 0$ as $s \to 0$. Let ζ_1 be an eigenvalue of (4.15) with associated eigenfunction (φ, ψ). Then $\zeta_1 = -\lambda$.

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

(a) $\psi \not\equiv 0$ on $\bar{\Omega}$. We normalize ψ such that $\|\psi\|_{L^\infty(\Omega)} = 1$. Multiplying the equation of ψ by $\tilde{v}_1$, and the equation of $\tilde{v}_1$ by ψ, and thereafter applying integration by parts and the boundary conditions, we obtain

$$\zeta_1 \int_\Omega \psi\tilde{v}_1 = \int_\Omega k(\tilde{v}_1)^2\varphi.$$

Dividing by $\|\tilde{v}_1\|^2_{L^\infty(\Omega)}$ and applying $\tilde{v}_1/\|\tilde{v}_1\|_{L^\infty(\Omega)} \to \tilde{\psi}_1, \varphi \to \tilde{\varphi}_1$ and $\psi \to \tilde{\psi}_1$ in $C^1(\bar{\Omega})$ as $s \to 0$, we have

$$\lim_{s\to 0} \frac{\zeta_1}{\|\tilde{v}_1\|_{L^\infty(\Omega)}} = \int_\Omega k(\tilde{\psi}_1)^2\tilde{\varphi}_1 / \int_\Omega (\tilde{\psi}_1)^2.$$

By (4.13), $\tilde{\varphi}_1 < 0$. Therefore, $\zeta_1 < 0$ for small s.

(b) $\psi \equiv 0$ on $\bar{\Omega}$. Therefore, $\varphi \not\equiv 0$ and satisfies

$$\mu\Delta\varphi + (m - 2\tilde{u}_1 - \tilde{v}_1)\varphi = \zeta_1\varphi \text{ in } \Omega, \quad \partial\varphi/\partial n = 0 \text{ on } \partial\Omega.$$

Because $(\tilde{u}_1, \tilde{v}_1) \to (\theta, 0)$ as $s \to 0$, the least eigenvalue of the operator $-\mu\Delta - (m - 2\theta)$ with homogeneous Neumann boundary condition is strictly positive, thus $\zeta_1 < 0$. That is, all eigenvalues of (4.15) have positive real part. Therefore $(\tilde{u}_1, \tilde{v}_1)$ is linearly stable for small s. □

Lemma 4.7. *Suppose* (1.2) *holds. There exists $\eta_* > 0$ such that if $\nu > \eta_*$, then any nonnegative solution of* (4.1) *satisfies*

$$0 \le u(x) \le \max_{\bar{\Omega}} m, \quad 0 \le v(x) \le \hat{C}, \quad x \in \bar{\Omega}$$

for every $\mu > 0$, where $\hat{C} > 0$ is some constant depending on d, k, η_*, m and Ω.

Proof. By the sub/super-solution method, θ is a super-solution of u. In particular, $u \le \theta$ for every $\mu > 0$. The upper bound of u follows from Lemma 2.1. Integrating the product of u and k, and the equation of v, we obtain

$$d \int_\Omega v = k \int_\Omega u(m-u) \le \frac{k}{4} \int_\Omega m^2.$$

By the Harnack inequality [19], there exists $\eta > 0$ such that if $\nu > \eta$, then $\max_{\bar{\Omega}} v \leq C^* \min_{\bar{\Omega}} v$ for some positive constant C^* depending on d, η and Ω. The upper bound of v follows. □

Proof of Theorem 1.4. Herein, it suffices to prove Case (i) because other cases can be obtained by similar arguments. For Case (i), by Lemmas 4.5, 4.6 and 4.7, it suffices to show that (4.1) has no positive solution for large ν. By Lemma 4.7, u and v are uniformly bounded above for every $\mu, \nu > 0$. Let $\nu \to \infty$ in (4.1), v will converge to some constant, denoted by c. We have $c \int_\Omega (ku - d) = 0$. Because θ is a super-solution of u in (4.1), $k\bar{u} \leq k\bar{\theta} \leq k \sup_{\mu > 0} \bar{\theta} < d$ for every $\mu > 0$. Furthermore, $c \equiv 0$ for large ν. That is, $(u, v) \to (\theta, 0)$ as $\nu \to \infty$. Therefore (4.1) has no positive solution for large ν. This finishes the proof.

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