

LOCAL DYNAMICS OF A DIFFUSIVE PREDATOR-PREY MODEL IN SPATIALLY HETEROGENEOUS ENVIRONMENT

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ABSTRACT. We investigate the effect of dispersal and spatial heterogeneity of the environment on the dynamics of a predator-prey model. In contrast with the homogeneous environment, the dynamics of the model in spatially heterogeneous environment is more complex. For instance, for certain ranges of death and dispersal rates of the predator, the semi-trivial steady state of the model in the heterogeneous case could change its stability multiple times as the dispersal rate of the prey varies from small to large, whereas the stability of the semi-trivial steady state is unaffected by the dispersal rates of the predator and prey in the homogeneous case.

Dedicated to Professor Paul Rabinowitz on the occasion of his 77th birthday

1. INTRODUCTION

Understanding the consequences of dispersal and environmental heterogeneity on the dynamics of single species or interacting populations is an important topic in mathematical ecology [3, 6]. By dispersal, organisms are able to search for resource, avoid predations and distribute themselves more properly in space, etc. The environmental heterogeneity often affect the persistence, extinction and coexistence of populations in interesting ways. For instance, it is shown in [4] that the spatial arrangement of favorable and unfavorable habitats can influence the overall suitability of an environment for a single species. The results from [22] suggest that in two-species Lotka-Volterra competition models, the joint action of spatial heterogeneity and diffusion can drive one of the species to extinction, whereas both species can coexist everywhere in the habitat with no diffusion. We refer to [7, 23, 24, 25, 26] for surveys of recent development on the effects of dispersal and spatial heterogeneity on population dynamics; See [2, 11, 21, 18] for single species models, [9, 10, 12, 13, 14, 27] for predator-prey models, and [15, 16, 17, 19, 20] for competition models.

In this paper, we consider a diffusive predator-prey model in spatially heterogeneous environment and inquire how dispersal and spatial heterogeneity affect the dynamics of predator and prey populations. The mathematical model is given by the following

2010 *Mathematics Subject Classification.* 35B35, 35K57, 35Q92.

Key words and phrases. Predator-prey, spatial heterogeneity, diffusion, stability.

reaction-diffusion system:

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

where functions $u(x, t)$ and $v(x, t)$ account for the population density of prey and predator species, respectively, at location x and time t , and are assumed to be nonnegative, with corresponding dispersal rates μ and ν . We assume that both $u_0(x)$ and $v_0(x)$ are nonnegative and not identically zero. The function $m(x)$ represents the intrinsic growth rate of the prey population, γ is the death rate of the predator. The operator $\Delta := \sum_{i=1}^N \partial^2/\partial x_i^2$ denotes the Laplacian in \mathbb{R}^N which describe the random movement of the predator and prey species. The habitat Ω is a bounded region in \mathbb{R}^N with smooth boundary $\partial\Omega$. The zero Neumann boundary conditions are imposed for both species, which imply 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 $\partial\Omega$. The reaction term is of the Holling type II function response. We shall assume that μ, ν, l and γ are positive constants for the rest of the paper.

If the environment is spatially homogeneous, i.e. $m(x)$ is a positive constant, say, \bar{m} , then (1.1) has a semi-trivial steady state $(\bar{m}, 0)$. The following result characterizes the local stability of $(\bar{m}, 0)$ ([28, 29]):

Lemma 1. *If $\gamma < l\bar{m}/(1 + \bar{m})$, then $(\bar{m}, 0)$ is locally stable; if $\gamma > l\bar{m}/(1 + \bar{m})$, then $(\bar{m}, 0)$ is locally unstable.*

Lemma 1 implies that if $m(x)$ is a positive constant, the local stability of $(\bar{m}, 0)$ is completely determined by l, γ and m , and the diffusion rates of predator and prey are irrelevant. The goal of this paper is to show that if the environment is spatially inhomogeneous, i.e. $m(x)$ is non-constant, the local stability of semi-trivial steady state of (1.1) becomes quite subtle and thus the local dynamics of (1.1) can be complex. To this end, we make the following assumption throughout the paper:

$$(1.2) \quad m(x) > 0, \text{ non-constant, and Hölder continuous in } \bar{\Omega}.$$

If $m(x)$ satisfies (1.2), the single species equation

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

has a unique positive solution in $C^2(\bar{\Omega})$ for every $\mu > 0$, denoted by θ ; See [5]. Occasionally we write θ as $\theta(x, \mu)$ to denote its dependence on μ . It is well known that θ is a smooth function of μ from $(0, \infty)$ to $C^2(\bar{\Omega})$.

The stability of the steady state $(\theta, 0)$ is determined by the sign of the least eigenvalue (denoted as λ_1) of the problem

$$(1.4) \quad \nu \Delta \psi + \left(\frac{l\theta(x, \mu)}{1 + \theta(x, \mu)} - \gamma \right) \psi + \lambda \psi = 0 \quad \text{in } \Omega, \quad \frac{\partial \psi}{\partial n} = 0 \quad \text{on } \partial \Omega.$$

Clearly, λ_1 is a function of both μ and ν . If $m(x) = \bar{m}$ for some positive constant \bar{m} , $\lambda_1 = \gamma - l\bar{m}/(1 + \bar{m})$, which proves Lemma 1. However, when m is a non-constant function, i.e., the environment is spatially heterogenous, determining the sign of λ_1 is harder and more interesting.

It is well-known that λ_1 is strictly increasing in ν , $\lim_{\nu \rightarrow 0^+} \lambda_1 = \gamma - G(\mu)$ and $\lim_{\nu \rightarrow +\infty} \lambda_1 = \gamma - K(\mu)$, where functions $G(\mu)$ and $K(\mu)$ are given by

$$(1.5) \quad \begin{aligned} K(\mu) &:= \frac{l}{|\Omega|} \int_{\Omega} \frac{\theta}{1 + \theta}; \\ G(\mu) &:= \frac{l \max_{\bar{\Omega}} \theta}{1 + \max_{\bar{\Omega}} \theta}. \end{aligned}$$

We refer to Lemma 14 and references therein for the proofs of these behavior of $\lambda_1(\nu)$.

It is difficult to determine the exact shapes of these two functions, which are critical in our local stability analysis. Under suitable conditions of m we can show that G is monotone decreasing in μ . In general, K is not a monotone function of μ . The following result describes some key properties of functions G and K .

Theorem 2. *Suppose that m satisfies (1.2).*

(i) *For every $\mu > 0$, $K(\mu) > K(0) = \frac{l}{|\Omega|} \int_{\Omega} \frac{m}{1+m}$. For sufficiently large μ , $K(\mu) > \lim_{\mu \rightarrow \infty} K(\mu) = \frac{l\bar{m}}{1+\bar{m}}$, where \bar{m} denotes the average of m .*

(ii) *If we further assume that*

$$(1.6) \quad \Omega \text{ is an interval, } m \in C^2(\bar{\Omega}), m_x \neq 0 \text{ and } m_{xx} \neq 0 \text{ in } \bar{\Omega},$$

then $G(\mu)$ is strictly monotone decreasing in μ .

Part (i) of Theorem 2 implies that K attains the unique global minimum at $\mu = 0$ and a local minimum at $\mu = +\infty$. This means that the global maximum is attained for some $\tilde{\mu} > 0$. However, as the local maximum of function K may not be unique in general, it is fairly difficult to determine the shape of K completely.

To describe our main result, set

$$(1.7) \quad \begin{aligned} \gamma_1 &:= \frac{l}{|\Omega|} \int_{\Omega} \frac{m}{1+m}; \\ \gamma_2 &:= \frac{l\bar{m}}{1+\bar{m}}; \\ \gamma_3 &:= \sup_{\mu > 0} K(\mu); \\ \gamma_4 &:= \frac{l \max_{\bar{\Omega}} m}{1 + \max_{\bar{\Omega}} m}. \end{aligned}$$

The order of $\gamma_i, i = 1, 2, 3, 4$, is given by $\gamma_1 < \gamma_2 < \gamma_3 < \gamma_4$. See Lemma 8 for the proof.

We are now ready to state the main result of this paper.

Theorem 3. *Suppose that m satisfies (1.2), then the following conclusions hold:*

- (i) *If $\gamma < \gamma_1$, $(\theta, 0)$ is unstable for any $\mu, \nu > 0$.*
- (ii) *If $\gamma_1 < \gamma < \gamma_2$, there exists a unique $\nu_* = \nu_*(\gamma, m, \Omega) > 0$ such that for every $\nu < \nu_*$, $(\theta, 0)$ is unstable for any $\mu > 0$; for every $\nu > \nu_*$, $(\theta, 0)$ changes its stability at least once as μ varies from 0 to ∞ .*
- (iii) *If $\gamma_2 < \gamma < \gamma_3$ and m also satisfies (1.6), then there exists a unique $\nu_* = \nu_*(\gamma, m, \Omega) > 0$ such that for every $\nu < \nu_*$, $(\theta, 0)$ changes stability at least once as μ varies from 0 to ∞ ; for every $\nu > \nu_*$, $(\theta, 0)$ changes stability at least twice as μ varies from 0 to ∞ .*
- (iv) *If $\gamma_3 < \gamma < \gamma_4$ and m also satisfies (1.6), then there exists a unique $\nu_* = \nu_*(\gamma, m, \Omega) > 0$ such that for every $\nu < \nu_*$, $(\theta, 0)$ changes its stability at least once as μ varies from 0 to ∞ ; for every $\nu > \nu_*$, $(\theta, 0)$ is stable for any $\mu > 0$.*
- (v) *If $\gamma > \gamma_4$, $(\theta, 0)$ is stable for any $\mu, \nu > 0$.*

Biologically, part (i) means that if the death rate of the predator is small, it can always invade when rare, and the diffusion rates of predator and prey are irrelevant. In contrast, part (v) implies that if the death rate of the predator is large enough, it can not invade for any diffusion rates of the predator and prey. In spirit these results are similar as those in Lemma 1 for homogeneous environment. Indeed, when m is constant, $\gamma_1 = \gamma_2 = \gamma_3 = \gamma_4$, so Theorem 3 is reduced to Lemma 1. Therefore, parts (ii)-(iv) only make sense when m is non-constant.

The conclusions of (ii)-(iv) are illustrated in Figures 1.1-1.3, respectively. Before we discuss biological implications of these figures, we caution the readers that Figures 1.1-1.3 are for illustration purpose only as the curves separating the invasion and no-invasion regions could be more complicated than what is plotted in these figures.

Part (ii) is illustrated in Figure 1.1, where the predator can invade when rare with any diffusion rate, provided that the diffusion rate of the prey species is greater than μ_* , where μ_* is a positive root of $K(\mu) = \gamma$. For illustration purpose, in Figure 1.1 we assume that $K(\mu) = \gamma$ has exactly one positive root. This kind of unconditional invasion is similar as that in part (i). If the diffusion rate of the predator is smaller than μ_* , the invasion of the predator becomes conditional: the predator can invade when rare if only if its diffusion rate is smaller than ν_* . Hence, for the parameter region (ii), it is always advantageous to the predator to have small diffusion rate in order to invade when rare.

Part (iii) is illustrated in Figure 1.2. For illustration purpose, in Figure 1.2 we assume that $K(\mu) = \gamma$ has exactly two positive roots $\mu_* < \mu^*$. In contrast with part (ii), it can be advantageous for prey to have large diffusion rate: If the diffusion rate of the prey is larger than $\hat{\mu}$, where $\hat{\mu}$ is the unique positive root of $G(\mu) = \gamma$, the predator can never invade when rare, no matter how small its diffusion rate is. This seems to be a major difference between (ii) and (iii). If the diffusion rate of the prey is smaller than $\hat{\mu}$, the predator can invade when rare by either adopting smaller diffusion rate or any diffusion rate, depending on the diffusion rate of the prey. Therefore, only if the

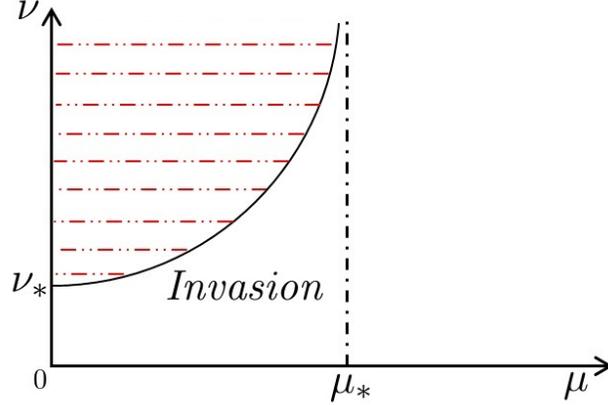


FIGURE 1.1. Illustration of part (ii), Theorem 3 for the parameter range $\gamma \in (\gamma_1, \gamma_2)$. The shaded region is where $(\theta, 0)$ is stable, i.e. the predator can not invade when rare. The unshaded region is where $(\theta, 0)$ is unstable and the predator can invade when rare. Here μ_* is a positive root of $K(\mu) = \gamma$.

diffusion rate of prey is smaller than $\hat{\mu}$, it is advantageous for predator to adopt smaller dispersal rate in order to invade.

Part (iv) is illustrated in Figure 1.3. Similar as (iii), large diffusion rate ($\mu > \hat{\mu}$) is good for the prey as the predator can never invade when rare. In contrast, if the diffusion rate of the prey is less than $\hat{\mu}$, the predator can always adopt small dispersal rate to invade. However, there is one interesting difference between (iii) and (iv), namely: For part (iv), if the dispersal rate of the predator is greater than ν_* , it can not invade for any dispersal rate of the prey. In contrast, for part (iii) if the dispersal rate of the predator is greater than ν_* , it can invade when rare for some intermediate range of diffusion rates of the prey, which corresponds to the multiple changes of stability of the semi-trivial steady state and possibly the bifurcation of positive steady states from the semi-trivial steady state.

We conclude that for the intermediate death rate of the predator, i.e. (ii)-(iv), if the diffusion rate of the prey is small, it is always advantageous for the predator to adopt small diffusion rate in order to invade, whereas if the diffusion rate of the prey is large, the predator either can always invade when rare (parameter range (ii)) or can never invade when rare (parameter ranges (iii)-(iv)).

The global dynamics of (1.1) is generally a challenging problem. For the case $\gamma > \gamma_4$, one can improve (v) in Theorem 3 by utilizing the comparison principle for the scalar parabolic equation to show that $(\theta, 0)$ is globally asymptotically stable. It is also of interest to determine the structure of positive steady states of (1.1).

The rest of this paper is organized as follows: In Section 2 we present some qualitative properties of θ and prove Theorem 2. In Section 3 we give some general criteria for

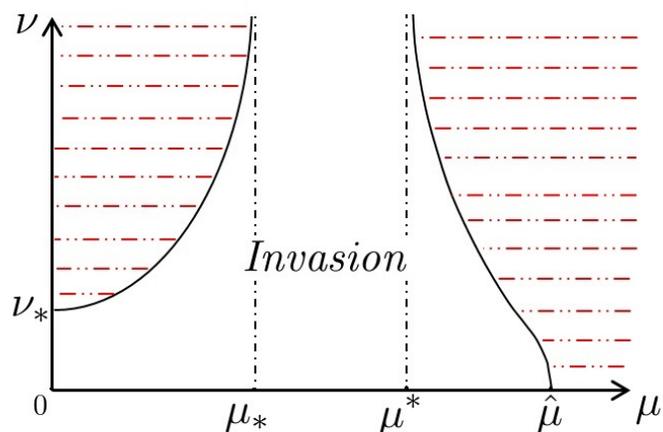


FIGURE 1.2. Illustration of part (iii), Theorem 3 for the parameter range $\gamma \in (\gamma_2, \gamma_3)$. The shaded region is where $(\theta, 0)$ is stable and it has two connected components. Here $\hat{\mu}$ is the unique positive root of $G(\mu) = \gamma$, μ_* and μ^* are two positive roots of $K(\mu) = \gamma$. As $\gamma \rightarrow \gamma_2$, $\mu^* \rightarrow \infty$ and the right shaded component will disappear so that Figure 1.2 will coincide with Figure 1.1. If $\gamma \rightarrow \gamma_3$, both μ_* and μ^* will converge to some number $\tilde{\mu} > 0$, where two shaded regions are separated by the vertical line $\mu = \tilde{\mu}$ in the $\mu - \nu$ plane.

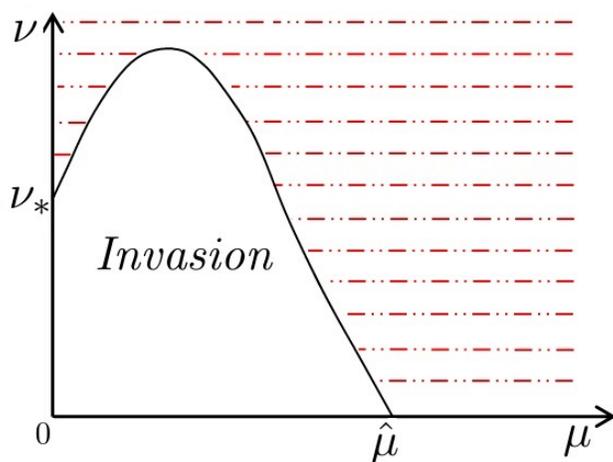


FIGURE 1.3. Illustration of part (iv), Theorem 3 for the parameter range $\gamma \in (\gamma_3, \gamma_4)$. The shaded region is where $(\theta, 0)$ is stable and the predator can not invade when rare. Here $\hat{\mu}$ is the unique positive root of $G(\mu) = \gamma$. As $\mu \rightarrow \gamma_4$, the unshaded region will approach the origin and disappear, so that (iv) is reduced to (v) in Theorem 3.

the stability of $(\theta, 0)$ and establish parts (i) and (v) of Theorem 3. Parts (ii)-(iv) of Theorem 3 are established in Sections 4-6, respectively.

2. QUALITATIVE PROPERTIES OF θ

In this section, we will present several results on properties of θ , the unique positive solution of (1.3), which shall be used in subsequence analysis.

Lemma 4. *Suppose that m satisfies (1.2).*

(i) $\mu \mapsto \theta(x, \mu)$ is a smooth mapping from \mathbb{R}^+ to $C^2(\bar{\Omega})$. Moreover, $\lim_{\mu \rightarrow 0} \theta = m$ and $\lim_{\mu \rightarrow \infty} \theta = \bar{m}$ uniformly on $\bar{\Omega}$, where $\bar{m} := \int_{\Omega} m/|\Omega|$ denotes the average of m .

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

Part (i) is an application of the implicit function theorem ([5]). The asymptotic behavior of θ as μ tends to zero or infinity is well known (See e.g. [15, Lemma 2.3]). We omit the proofs and refer to [26] for further discussions of θ .

Lemma 5. *For every $\mu > 0$, $\int_{\Omega} \theta > \int_{\Omega} m$. In particular, $\max_{\bar{\Omega}} \theta > \bar{m}$.*

Proof. Dividing (1.3) by θ and integrating in Ω , we have

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

where the last strict inequality holds as θ is non-constant. □

Lemma 6. *For any $\mu > 0$, the following inequality holds:*

$$(2.1) \quad \int_{\Omega} \frac{1}{1+\theta} < \int_{\Omega} \frac{1}{1+m}.$$

Proof. Dividing the equation of θ by $\theta(1+\theta)^2$, after some rearrangement we have

$$\frac{\mu \Delta \theta}{\theta(1+\theta)^2} + \frac{1+m}{(1+\theta)^2} - \frac{1}{1+\theta} = 0.$$

Integrating the above equation and applying the boundary condition of θ , we obtain

$$\mu \int_{\Omega} \frac{1+3\theta}{\theta^2(1+\theta)^3} |\nabla \theta|^2 + \int_{\Omega} \frac{1+m}{(1+\theta)^2} - \int_{\Omega} \frac{1}{1+\theta} = 0.$$

Hence, we have

$$(2.2) \quad \int_{\Omega} \frac{1+m}{(1+\theta)^2} < \int_{\Omega} \frac{1}{1+\theta},$$

where the strict inequality holds as θ is non-constant. Therefore, by Cauchy-Schwartz inequality we have

$$\int_{\Omega} \frac{1}{1+\theta} \leq \left(\int_{\Omega} \frac{1+m}{(1+\theta)^2} \right)^{1/2} \left(\int_{\Omega} \frac{1}{1+m} \right)^{1/2} < \left(\int_{\Omega} \frac{1}{1+\theta} \right)^{1/2} \left(\int_{\Omega} \frac{1}{1+m} \right)^{1/2},$$

from which (2.1) follows, where the last inequality follows from (2.2). □

Lemma 7. *For sufficiently large μ , the following inequality holds:*

$$\int_{\Omega} \frac{1}{1 + \theta(x; \mu)} dx < \frac{|\Omega|}{1 + \bar{m}}.$$

Proof. Set $\epsilon = 1/\mu$. Recall that $\theta \rightarrow \bar{m}$ in L^∞ as $\epsilon \rightarrow 0$. For sufficiently small positive ϵ , define $w = (\theta - \bar{\theta})/\epsilon$. Then w satisfies

$$\Delta w + \theta(m - \theta) = 0 \quad \text{in } \Omega, \quad \nabla w \cdot n = 0 \quad \text{on } \partial\Omega, \quad \int_{\Omega} w = 0.$$

Multiplying the equation of w by w and integrating in Ω we obtain

$$\int_{\Omega} |\nabla w|^2 = \int_{\Omega} \theta(m - \theta)w \leq C \int_{\Omega} |w| \leq C \left(\int_{\Omega} w^2 \right)^{1/2} \leq C \left(\int_{\Omega} |\nabla w|^2 \right)^{1/2},$$

where the last two inequalities follow from Cauchy-Schwartz inequality and Poincare inequality, respectively, and C denotes some generic positive constant which is independent of ϵ . Hence, w is uniformly bounded in $W^{1,2}$ norm for sufficiently small ϵ . Therefore, as $\theta \rightarrow \bar{m}$ in L^∞ when $\epsilon \rightarrow 0$, passing to a sequence if necessary, we see that $w \rightarrow g$ weakly in $W^{1,2}$, where g is uniquely determined by

$$\Delta g + \bar{m}(m - \bar{m}) = 0 \quad \text{in } \Omega, \quad \nabla g \cdot n = 0 \quad \text{on } \partial\Omega, \quad \int_{\Omega} g = 0.$$

By standard elliptic regularity theory we see that w is uniformly bounded in $W^{2,2}$ norm for sufficiently small ϵ . Hence by Sobolev embedding theorem, passing to a sequence if necessary, $w \rightarrow g$ in $W^{1,2}$. Since g is unique, $w \rightarrow g$ in $W^{1,2}$ as $\epsilon \rightarrow 0$.

Dividing (1.3) by θ and integrating the resulting equation we obtain

$$\int_{\Omega} \frac{|\nabla \theta|^2}{\theta^2} + \epsilon |\Omega| (\bar{m} - \bar{\theta}) = 0.$$

Dividing the above equation by ϵ^2 and by the definition of w , we have

$$0 < \frac{\bar{\theta} - \bar{m}}{\epsilon} = \frac{1}{|\Omega|} \int_{\Omega} \frac{|\nabla w|^2}{\theta^2}.$$

Since $w \rightarrow g$ in $W^{1,2}$ and $\theta \rightarrow \bar{m}$ as $\epsilon \rightarrow 0$, we have

$$\lim_{\epsilon \rightarrow 0} \frac{\bar{\theta} - \bar{m}}{\epsilon} = \frac{1}{\bar{m}^2 |\Omega|} \int_{\Omega} |\nabla g|^2.$$

Therefore, as $\epsilon \rightarrow 0$, we obtain

$$\begin{aligned} & \frac{1}{\epsilon} \left(\int_{\Omega} \frac{1}{1 + \theta} - \int_{\Omega} \frac{1}{1 + \bar{m}} \right) \\ &= \int_{\Omega} \frac{(\bar{m} - \bar{\theta})/\epsilon}{(1 + \theta)(1 + \bar{m})} - \int_{\Omega} \frac{w}{(1 + \theta)(1 + \bar{m})} \\ &\rightarrow -\frac{\int_{\Omega} |\nabla g|^2}{\bar{m}^2 (1 + \bar{m})^2 |\Omega|} - \frac{\int_{\Omega} g}{(1 + \bar{m})^2} \\ &= -\frac{\int_{\Omega} |\nabla g|^2}{\bar{m}^2 (1 + \bar{m})^2 |\Omega|} < 0. \end{aligned}$$

This completes the proof. \square

The order of $\gamma_i, i = 1, 2, 3, 4$, is given in the following result:

Lemma 8. *Suppose that m satisfies (1.2). Then $\gamma_1 < \gamma_2 < \gamma_3 < \gamma_4$.*

Proof. The inequality $\gamma_1 < \gamma_2$ follows from

$$\int_{\Omega} \frac{m}{1+m} - \frac{|\Omega|\bar{m}}{1+\bar{m}} = -\frac{1}{(1+\bar{m})^2} \int_{\Omega} \frac{(m-\bar{m})^2}{1+m} < 0.$$

Note that $\gamma_2 < \gamma_3$ and $\gamma_3 < \gamma_4$ follow from Lemmas 6 and 4, respectively. \square

We refer the following two results to Lemmas 5.13 and 5.14 in [1], respectively.

Lemma 9. *Suppose that Ω is an interval and $m \in C^1(\bar{\Omega})$. If $m_x > 0$ in $\bar{\Omega}$, then $\theta_x > 0$ in Ω ; If $m_x < 0$ in $\bar{\Omega}$, then $\theta_x < 0$ in Ω .*

Lemma 10. *Suppose that Ω is an interval, $m \in C^2(\bar{\Omega})$, $m_x \neq 0$ and $m_{xx} \neq 0$ in $\bar{\Omega}$. Then $\theta - m$ changes sign exactly once in $\bar{\Omega}$.*

The following result seems to be of independent interest.

Lemma 11. *Suppose that Ω is an interval, $m \in C^2(\bar{\Omega})$, $m_x \neq 0$ and $m_{xx} \neq 0$ in $\bar{\Omega}$. Then $\max_{\bar{\Omega}} \theta$ is strictly decreasing in μ .*

Proof. Without loss of generality, assume that $\Omega = (0, 1)$, $m_x > 0$ and $m_{xx} > 0$ in $[0, 1]$. It follows from Lemma 9 that $\theta_x > 0$ in $(0, 1)$, i.e. θ is strictly increasing in $[0, 1]$. Hence, $\max_{\bar{\Omega}} \theta(\cdot, \mu) = \theta(1, \mu)$. Therefore, it suffices to show that $\theta'(1, \mu) < 0$ for any $\mu > 0$, where $\theta'(x, \mu) := \partial\theta/\partial\mu(x, \mu)$. We argue by contradiction: Suppose that $\theta'(1, \bar{\mu}) \geq 0$ for some $\bar{\mu} > 0$. For simplicity we drop the bar and write $\bar{\mu}$ as μ .

Differentiate (1.3) with respect to μ , we find

$$\mu\theta'_{xx} + (m - 2\theta)\theta' + \theta_{xx} = 0, \quad 0 < x < 1.$$

Set $\theta' = \theta w$. Then w satisfies

$$(2.3) \quad \mu(\theta w_{xx} + 2\theta_x w_x) - \theta^2 w + \theta_{xx} = 0, \quad 0 < x < 1.$$

Furthermore, as $\theta'_x = \theta_x = 0$ at $x = 0, 1$, w also satisfies $w_x = 0$ at $x = 0, 1$. By Lemma 10, $m_{xx} > 0$ and $m_x > 0$ imply that $\theta - m > 0$ changes sign exactly once, from positive to negative. That is, there exists some $x_0 \in (0, 1)$ such that

$$\theta_{xx} \begin{cases} > 0, & 0 \leq x < x_0; \\ = 0, & x = x_0; \\ < 0, & x_0 < x \leq 1. \end{cases}$$

This implies that

$$(2.4) \quad \mu(\theta w_{xx} + 2\theta_x w_x) - \theta^2 w > 0, \quad x_0 < x \leq 1.$$

As $\theta'(1, \mu) \geq 0$, $w(1) \geq 0$. Hence, as $w_x(1) = 0$, we have $w_{xx}(1) > 0$. Therefore, there exists some $\delta_1 > 0$ such that $w_{xx} > 0$ for $x \in [1 - \delta_1, 1]$. Since $w_x(1) = 0$, $w_x < 0$ in $[1 - \delta_1, 1]$. As $w(1) \geq 0$, $w > 0$ in $[1 - \delta_1, 1]$.

Claim. w must be negative somewhere in $(0, 1)$.

To establish our assertion, multiplying (2.3) by θ we find

$$\mu(\theta^2 w_x)_x - \theta^3 w + \theta \theta_{xx} = 0 \quad \text{in } (0, 1).$$

Integrating the above equation and applying the boundary condition of θ we obtain

$$\int_0^1 \theta^3 w = \int_0^1 \theta \theta_{xx} = - \int_0^1 \theta_x^2 < 0,$$

where the last strict inequality holds since m is non-constant, thus θ is also non-constant. This shows that w must be negative somewhere in $(0, 1)$.

By the above assertion, there exists $x_1 \in (0, 1)$ such that $w > 0$ in $(x_1, 1)$ and $w(x_1) = 0$. Hence, there exists $x_2 \in (x_1, 1)$ such that w attains a positive, local maximum at x_2 . Therefore $w_{xx}(x_2) \leq 0$, $w_x(x_2) = 0$ and $w(x_2) > 0$. Evaluating (2.3) at x_2 we find that $\theta_{xx}(x_2) > 0$, which implies that $x_1 < x_2 < x_0$. Therefore, $\theta_{xx} > 0$ in $(0, x_2]$. Hence,

$$(2.5) \quad \begin{aligned} \mu(\theta w_{xx} + 2\theta_x w_x) - \theta^2 w &< 0, \quad 0 < x \leq x_1; \\ w_x(0) = 0, \quad w_x(x_1) &\geq 0, \quad w(x_1) = 0. \end{aligned}$$

Since $w(x_1) = 0$, $w_x(x_1) \geq 0$ and $\theta_x(x_1) > 0$, we have $w_{xx}(x_1) < 0$. This implies that $w_{xx} < 0$ in a neighborhood of x_1 , and thus w_x is strictly decreasing in a neighborhood of x_1 . Since $w_x(x_1) \geq 0$, we see that $w_x > 0$ for $x < x_1$ and x close to x_1 . As $w(x_1) = 0$, we find $w < 0$ for $x < x_1$ and x close to x_1 . We claim that $w < 0$ in $[0, x_1)$: if not, suppose that $w(x_3) \geq 0$ for some $x_3 \in [0, x_1)$. Then there exists some $x_4 \in (x_3, x_1)$ such that w attains a negative, local minimum at x_4 . Thus $w(x_4) < 0$, $w_x(x_4) = 0$, and $w_{xx}(x_4) \geq 0$. But this contradicts (2.5). Therefore, $w < 0$ in $[0, x_1)$. This together with (2.5) imply that

$$(2.6) \quad \begin{aligned} \theta w_{xx} + 2\theta_x w_x &< 0, \quad 0 < x \leq x_1; \\ w_x(0) = 0, \quad w(x_1) &= 0, \quad w_x(x_1) \geq 0. \end{aligned}$$

Hence, $(\theta^2 w_x)_x < 0$ in $(0, x_1)$, which implies that $\theta^2 w_x$ is strictly decreasing in $(0, x_1)$. As $w_x(0) = 0$, we obtain $w_x(x_1) < 0$, which is a contradiction. This proves that $\max_{\bar{\Omega}} \theta$ is strictly decreasing in μ . \square

Remark 12. For general Ω and m we do not know whether $\max_{\bar{\Omega}} \theta$ is strictly decreasing in μ . It is also unknown whether $\min_{\bar{\Omega}} \theta$ is strictly increasing in μ . Biologically it is of interest to know whether $\max_{\bar{\Omega}} \theta - \min_{\bar{\Omega}} \theta$ is strictly decreasing in μ , as $\max_{\bar{\Omega}} \theta - \min_{\bar{\Omega}} \theta$ is a measurement of the variation of the spatial population distributions.

In the end of this section we establish Theorem 2.

Proof of Theorem 2. Part (i) follows from Lemmas 4, 6 and 7. Part (ii) is a consequence of Lemmas 4 and 11. \square

3. GENERAL CRITERIA FOR STABILITY OF $(\theta, 0)$

In this section we collect several criteria for determining the local stability of $(\theta, 0)$. Parts (i) and (v) of Theorem 3 are established in this section. It is well known that the local stability of $(\theta, 0)$ is determined by its linear stability. The following result gives the criteria for determining the linear stability of $(\theta, 0)$.

Lemma 13. *The semi-trivial steady state $(\theta, 0)$ is stable/unstable if and only if the following eigenvalue problem, for $(\lambda, \psi) \in \mathbb{R} \times C^2(\overline{\Omega})$, has a positive/negative eigenvalue (denoted as λ_1):*

$$(3.1) \quad \begin{cases} \nu \Delta \psi + \left(\frac{l\theta}{1+\theta} - \gamma \right) \psi + \lambda \psi = 0 & \text{in } \Omega, \\ \frac{\partial \psi}{\partial n} = 0 & \text{on } \partial\Omega, \quad \psi > 0 \quad \text{on } \overline{\Omega}. \end{cases}$$

Proof. It follows from arguments similar to that of [8, Lemma 5.5]. \square

We occasionally write λ_1 as $\lambda_1(\mu, \nu)$ to denote its dependence on μ, ν . The following result characterizes the dependence of λ_1 on ν .

Lemma 14. *The smallest eigenvalue λ_1 of (3.1) depends smoothly on $\nu > 0$. Moreover,*

- (i) λ_1 is strictly increasing in ν ;
- (ii) It has the following properties:

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

Proof. The proof of the smooth dependence of λ_1 on ν can be found in [5]. The proof of (i) follows from the variational characterization of λ_1 and the fact that θ is non-constant. We refer the proof of (ii) to [26]. \square

The following result is a corollary of Lemma 14:

Theorem 15. *Suppose that m satisfies (1.2).*

- (i) *If $\gamma \leq \gamma_1$, then $(\theta, 0)$ is unstable for any $\mu, \nu > 0$.*
- (ii) *If $\gamma \geq \gamma_4$, then $(\theta, 0)$ is stable for any $\mu, \nu > 0$.*

Proof. If $\gamma \leq \gamma_1$, by Lemma 6 we have $\gamma < \frac{l}{|\Omega|} \int_{\Omega} \frac{\theta}{1+\theta}$ for every $\mu > 0$. By Lemma 14, $\lambda_1 < 0$ for every $\mu > 0$ and $\nu > 0$. Hence, by Lemma 13, $(\theta, 0)$ is unstable for any $\mu, \nu > 0$. This proves part (i).

By Lemma 4, $\max_{\overline{\Omega}} \theta < \max_{\overline{\Omega}} m$ for every $\mu > 0$. Therefore, if $\gamma \geq \gamma_4$, then $\gamma > \frac{l \max_{\overline{\Omega}} \theta}{1 + \max_{\overline{\Omega}} \theta}$ for every $\mu > 0$. By Lemma 14, $\lambda_1 > 0$ for every $\mu, \nu > 0$. Hence, by Lemma 13, $(\theta, 0)$ is stable for any $\mu, \nu > 0$. This proves part (ii). \square

In general, it is difficult to completely determine the sign of λ_1 in terms of μ, ν . Our idea is to connect λ_1 with another eigenvalue problem with indefinite weight. To this end, set

$$(3.2) \quad \lambda^* := \inf_{\{\varphi \in H^1(\Omega) : \int_{\Omega} (\frac{l\theta}{1+\theta} - \gamma) \varphi^2 > 0\}} \frac{\int_{\Omega} |\nabla \varphi|^2}{\int_{\Omega} (\frac{l\theta}{1+\theta} - \gamma) \varphi^2}.$$

Throughout this paper we sometimes write λ^* as $\lambda^*(\mu)$ to indicate its dependence on μ . It is easy to see that if λ^* is well defined, then it is non-negative. The following result is well known ([5]):

Lemma 16. *If $l\theta/(1+\theta) - \gamma$ is positive somewhere in Ω , then λ^* is well defined, i.e., λ^* is non-negative and finite, and there exists $\psi \in C^2(\bar{\Omega})$ such that*

$$(3.3) \quad \begin{cases} \Delta\psi + \lambda^* \left(\frac{l\theta}{1+\theta} - \gamma \right) \psi = 0 & \text{in } \Omega, \\ \frac{\partial\psi}{\partial n} = 0 & \text{on } \partial\Omega, \quad \psi > 0 & \text{on } \bar{\Omega}. \end{cases}$$

Moreover, $\lambda^*(\mu) = 0$ if $K(\mu) \geq \gamma$ and $\lambda^*(\mu) > 0$ if $K(\mu) < \gamma$.

Since θ is smooth in μ , we see that λ^* is also a smooth function of $\mu \in (0, \infty)$ (but not necessarily analytic for all $\mu > 0$). In view of Theorem 15, it suffices to consider the parameter region

$$(3.4) \quad \frac{l}{|\Omega|} \int_{\Omega} \frac{m}{1+m} < \gamma < \frac{l \max_{\bar{\Omega}} m}{1 + \max_{\bar{\Omega}} m}.$$

Our next result characterizes the asymptotic behavior of λ^* near $\mu = 0$.

Lemma 17. *Suppose that (3.4) holds. Then $\lim_{\mu \rightarrow 0^+} \lambda^*(\mu) = \lambda_0$, where λ_0 is some positive constant.*

Proof. As $\theta \rightarrow m$ uniformly as $\mu \rightarrow 0^+$, we see that $\lambda^*(\mu) \rightarrow \lambda_0$, where

$$(3.5) \quad \lambda_0 := \inf_{\{\varphi \in H^1(\Omega) : \int_{\Omega} (\frac{lm}{1+m} - \gamma) \varphi^2 > 0\}} \frac{\int_{\Omega} |\nabla\varphi|^2}{\int_{\Omega} (\frac{lm}{1+m} - \gamma) \varphi^2}.$$

By assumption (3.4), we have $\int_{\Omega} \frac{lm}{1+m} < \gamma$ and $lm/(1+m) - \gamma$ is positive somewhere. Hence, similar as in Lemma 16 we have $\lambda_0 > 0$. \square

Finally, the following result is critical for our proofs as it provides a connection between the signs of $\lambda_1 = \lambda_1(\mu, \nu)$ and $\lambda^* = \lambda^*(\mu)$.

Lemma 18. *Suppose that $l\theta/(1+\theta) - \gamma$ is positive somewhere in Ω . Then $\lambda^* - 1/\nu > 0$ if $\lambda_1 > 0$, and $\lambda^* - 1/\nu < 0$ if $\lambda_1 < 0$.*

The proof of Lemma 18 can be found in [5, 26].

4. PROOF OF (II), THEOREM 3

In this section we consider the parameter range

$$(4.1) \quad \gamma_1 := \frac{l}{|\Omega|} \int_{\Omega} \frac{m}{1+m} < \gamma < \gamma_2 := \frac{l\bar{m}}{1+\bar{m}}.$$

For this range of γ , there exist positive constants $\mu_* \leq \mu^*$ such that $\gamma > K(\mu)$ for $\mu \in (0, \mu_*)$ and $\gamma < K(\mu)$ for $\mu > \mu^*$, where μ_*, μ^* are the smallest and largest positive roots of $K(\mu) = \gamma$, respectively. It is possible that $\mu_* = \mu^*$.

When $\mu > \mu^*$, we can argue similarly as in the proof of part (i) of Theorem 15 to conclude that $(\theta, 0)$ is unstable for any $\nu > 0$.

If $\mu < \mu_*$, by Lemma 5 and Lemma 14 we have

$$\lim_{\nu \rightarrow 0} \lambda_1 = \gamma - \frac{l \max_{\bar{\Omega}} \theta}{1 + \max_{\bar{\Omega}} \theta} < \gamma - \frac{l\bar{m}}{1 + \bar{m}} < 0,$$

where the last inequality follows from (4.1). By Lemma 14 and (4.1) we have

$$\lim_{\nu \rightarrow \infty} \lambda_1 = \gamma - \frac{l}{|\Omega|} \int_{\Omega} \frac{\theta}{1 + \theta} > 0.$$

Since λ_1 is strictly monotone increasing in ν , for every $\mu < \mu_*$ there exists a unique $\bar{\nu} = \bar{\nu}(\mu) > 0$ such that $(\theta, 0)$ is unstable for any $\nu < \bar{\nu}$ and stable for $\nu > \bar{\nu}$.

In general we can not rule out the possibility $\mu_* < \mu^*$. If we fix $\nu > 0$ and let μ vary from small to large, can we conclude that $(\theta, 0)$ changes stability at least once? It turns out that this is not true: Part (ii) of Theorem 3 claims that there exists some $\nu_* > 0$ (independent of μ and ν) such that when $\nu \in (0, \nu_*)$, then $(\theta, 0)$ is unstable for any $\mu > 0$; If $\nu > \nu_*$, then $(\theta, 0)$ changes stability at least once as μ varies from zero to infinity. If $\mu_* = \mu^*$, then we see that such ν_* exists as it is the minimum value of $\bar{\nu}(\mu)$ for $\mu \in [0, \mu_*]$. In order to establish the existence of such ν_* in general situation, we need to consider the possibility $\mu_* < \mu^*$.

Proof of (ii), Theorem 3. We note that $K(\mu) = \gamma$ has at least one positive root. From the above discussions, we denote μ_* and μ^* as the smallest and largest positive roots of $K(\mu) = \gamma$, respectively.

We first show that if $\gamma < \gamma_2 := l\bar{m}/(1 + \bar{m})$, then for every $\mu > 0$, $l\theta/(1 + \theta) - \gamma$ is positive somewhere in Ω . By Lemma 5, we have $\max_{\bar{\Omega}} \theta > \bar{m}$. Therefore,

$$\frac{l \max_{\bar{\Omega}} \theta}{1 + \max_{\bar{\Omega}} \theta} > \frac{l\bar{m}}{1 + \bar{m}} > \gamma.$$

Hence, $l\theta/(1 + \theta) - \gamma$ is always positive somewhere.

Recall that λ^* is defined in (3.2). Since $K(\mu) > \gamma$ for every $\mu > \mu^*$, $\lambda^* \equiv 0$ for $\mu \geq \mu^*$. Since $K(\mu) < \gamma$ for $\mu \in (0, \mu_*)$ and $l\theta/(1 + \theta) - \gamma$ is positive somewhere, $\lambda^*(\mu) > 0$ for every $\mu \in (0, \mu_*)$. Furthermore, by Lemma 17, $\lim_{\mu \rightarrow 0+} \lambda^*(\mu)$ exists and is positive. Hence, $\lambda^*(\mu)$ is continuous, non-negative, and not identically zero in $[0, \mu^*]$, and vanishes in $[\mu^*, +\infty)$.

Define

$$\nu_* := \frac{1}{\sup_{\mu > 0} \lambda^*(\mu)}.$$

By our above discussions, we have $\bar{\nu} > 0$.

(a) $\nu < \nu_*$. For this case, $\lambda^*(\mu) - 1/\nu < 0$ for every $\mu > 0$. Since $l\theta/(1 + \theta) - \gamma$ is positive somewhere, Lemma 18 implies that $\lambda_1 < 0$ for any $\mu > 0$.

(b) $\nu > \nu_*$. For this case, $1/\nu < \sup_{\mu > 0} \lambda^*(\mu)$. We claim that $\lambda^*(\mu) - 1/\nu$ changes sign at least once in $(0, \mu^*)$. Since $\lambda^*(\mu)$ is continuous in μ , $\lim_{\mu \rightarrow 0} \lambda^*$ exists and $\lambda^*(\mu) = 0$ for $\mu \geq \mu^*$, $\sup_{\mu > 0} \lambda^*(\mu) = \lambda^*(\bar{\mu})$ for some $\bar{\mu} \geq 0$. We consider two cases:

Case 1. $\bar{\mu} \in [0, \mu_*)$, then $\lambda^* - 1/\nu$ changes sign at least once in $(0, \mu_*)$.

Case 2. If $\bar{\mu} \in (\mu_*, \mu^*)$, then there exist positive constants μ_1, μ_2 such that $\mu_* \leq \mu_1 < \bar{\mu} < \mu_2 \leq \mu^*$, $\lambda^*(\mu_1) = \lambda^*(\mu_2) = 0$ and $\lambda^*(\mu) > 0$ for $\mu \in (\mu_1, \mu_2)$. Therefore, $\lambda^* - 1/\nu$ changes sign at least once in (μ_1, μ_2) .

Hence in both cases, $\lambda^* - 1/\nu$ changes sign at least once in $(0, \mu^*)$. By Lemma 18, λ_1 also changes sign at least once in $(0, \mu^*)$. This completes the proof. \square

5. PROOF OF (III), THEOREM 3

In this section we focus on the range

$$(5.1) \quad \gamma_2 := \frac{l\bar{m}}{1+\bar{m}} < \gamma < \gamma_3 := \sup_{\mu>0} K(\mu).$$

For this range of γ , there exist positive constants $\mu_* \leq \mu_{**} < \mu^{**} \leq \mu^*$ such that $K(\mu) < \gamma$ for $\mu \in (0, \mu_*) \cup (\mu^*, +\infty)$, and $K(\mu) > \gamma$ for $\mu \in (\mu_{**}, \mu^{**})$, where $\mu_*, \mu_{**}, \mu^*, \mu^{**}$ are positive roots of $K(\mu) = \gamma$. It is possible that $\mu_* = \mu_{**}$ and $\mu^* = \mu^{**}$.

In part (ii) we have shown that for every $\mu > 0$, $l\theta/(1+\theta) - \gamma$ must be positive somewhere when $\gamma \in (\gamma_1, \gamma_2)$. Some different phenomenon occurs for part (iii).

Lemma 19. *Suppose that Ω is an interval, $m_x \neq 0$ and $m_{xx} \neq 0$ in Ω . If $l\bar{m}/(1+\bar{m}) < \gamma < l \max_{\bar{\Omega}} m/(1 + \max_{\bar{\Omega}} m)$, then there exists some $\hat{\mu} > 0$ such that $l\theta/(1+\theta) - \gamma$ is positive somewhere in Ω for every $\mu < \hat{\mu}$, and $l\theta/(1+\theta) - \gamma < 0$ in $\bar{\Omega}$ for every $\mu > \hat{\mu}$.*

Proof. By Lemma 13, $\max_{\bar{\Omega}} \theta/(1 + \max_{\bar{\Omega}} \theta)$ is strictly decreasing in μ . As

$$\lim_{\mu \rightarrow 0} \frac{l \max_{\bar{\Omega}} \theta}{1 + \max_{\bar{\Omega}} \theta} - \gamma = \frac{l \max_{\bar{\Omega}} m}{1 + \max_{\bar{\Omega}} m} - \gamma > 0$$

and

$$\lim_{\mu \rightarrow \infty} \frac{l \max_{\bar{\Omega}} \theta}{1 + \max_{\bar{\Omega}} \theta} - \gamma = \frac{l\bar{m}}{1 + \bar{m}} - \gamma < 0,$$

we see that $l \max_{\bar{\Omega}} \theta/(1 + \max_{\bar{\Omega}} \theta) - \gamma$ has a unique positive root, denoted as $\hat{\mu}$. In particular, $l\theta/(1+\theta) - \gamma$ is positive somewhere in Ω for $\mu < \hat{\mu}$, and $l\theta/(1+\theta) - \gamma < 0$ in $\bar{\Omega}$ for $\mu > \hat{\mu}$. \square

Proof of (iii), Theorem 3. If $\mu \geq \hat{\mu}$, Lemma 13 and Lemma 19 imply that $(\theta, 0)$ is stable for any $\nu > 0$.

For $\mu < \hat{\mu}$, Lemma 19 implies that $\lambda^*(\mu)$ is well defined and is non-negative. From previous discussions we see that $K(\mu) = \gamma$ has at least two positive roots. Denote μ_* and μ^* as the smallest and largest positive roots of $K(\mu) = \gamma$, respectively. It is easy to see that for any positive root μ of $K(\mu) = \gamma$, we have $\mu < \hat{\mu}$. In particular, $\mu_* < \mu^* < \hat{\mu}$. By Lemmas 6 and 7, $K(\mu) < \gamma$ for every $\mu < \mu_*$ and $\mu > \mu^*$. Hence, $\lambda^*(\mu) > 0$ for $\mu \in (0, \mu_*) \cup (\mu^*, \hat{\mu})$, and $\lambda^*(\mu_*) = \lambda^*(\mu^*) = 0$. Lemma 17 ensures that $\lim_{\mu \rightarrow 0} \lambda^*$ exists and the limit is positive.

Define

$$\nu_* := \frac{1}{\sup_{0 < \mu \leq \mu^*} \lambda^*(\mu)}.$$

By our above discussions, we have $\nu_* > 0$.

We first consider the sign change of λ_1 in $(\mu^*, \hat{\mu})$. Similarly as in Section 4, if $\nu > \nu_*$, $\lambda^*(\mu) - 1/\nu$ changes sign at least once in $(0, \mu_*)$. By Lemma 18, for $\nu > \nu_*$, λ_1 changes sign at least once in $(0, \mu_*)$.

Next we study the sign change of λ_1 in $(\mu^*, \hat{\mu})$. To this end, we first show that $\lambda^*(\mu) \rightarrow +\infty$ as $\mu \rightarrow \hat{\mu}-$. To establish this assertion, we argue by contraction: Passing to a sequence if necessary, we may assume that there exists some positive constant C

such that $\lambda^*(\mu) \leq C$ for every $\mu \in (\mu^*, \hat{\mu})$. By the definition of $\lambda^*(\mu)$, there exists some positive function $\varphi \in C^2(\bar{\Omega})$ such that

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

Passing to a sequence if necessary we may assume that as $\mu \rightarrow \hat{\mu}-$, $\lambda^*(\mu) \rightarrow \lambda_0$ for some $\lambda_0 \geq 0$, and $\varphi \rightarrow \varphi_0$ in $C^2(\bar{\Omega})$, where φ_0 satisfies

$$\Delta\varphi_0 + \lambda_0 \left(\frac{l\theta(x, \hat{\mu})}{1+\theta(x, \hat{\mu})} - \gamma \right) \varphi_0 = 0 \quad \text{in } \Omega, \quad \frac{\partial\varphi_0}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

If $\lambda_0 > 0$, integrating the equation of φ_0 in Ω we find

$$\int_{\Omega} \left(\frac{l\theta(x, \hat{\mu})}{1+\theta(x, \hat{\mu})} - \gamma \right) \varphi_0 = 0.$$

Since $\varphi_0 > 0$ and $\frac{l\theta(x, \hat{\mu})}{1+\theta(x, \hat{\mu})} - \gamma$ is non-positive and not identically zero, we reach the contradiction.

If $\lambda_0 = 0$, we see that φ_0 must be a positive constant. Integrating the equation of φ in Ω we find

$$\int_{\Omega} \left(\frac{l\theta(x, \mu)}{1+\theta(x, \mu)} - \gamma \right) \varphi = 0.$$

Let $\mu \rightarrow \hat{\mu}-$ in the above equation, as φ tends to some positive constant, we have

$$\int_{\Omega} \left(\frac{l\theta(x, \hat{\mu})}{1+\theta(x, \hat{\mu})} - \gamma \right) = 0,$$

which is also a contradiction. This proves $\lambda^*(\mu) \rightarrow +\infty$ as $\mu \rightarrow \hat{\mu}-$.

As $\lambda^*(\mu^*) = 0$ and $\lim_{\mu \rightarrow \hat{\mu}-} \lambda^*(\mu) = +\infty$, we see that for any $\nu > 0$, $\lambda(\mu) - 1/\nu$ changes sign at least once in $(\mu^*, \hat{\mu})$. By Lemma 18, for any $\nu > 0$, λ_1 changes sign at least once in $(\mu^*, \hat{\mu})$.

Summarizing these discussions we conclude that for any $\nu < \nu_*$, λ_1 changes sign at least once as μ varies from zero to μ^* ; If $\nu > \nu_*$, λ_1 changes sign at least twice as μ varies from zero to μ^* . This completes the proof. \square

6. PROOF OF (IV), THEOREM 3

In this section we consider the parameter range

$$\gamma_3 < \gamma < \gamma_4 := \frac{l \max_{\bar{\Omega}} m}{1 + \max_{\bar{\Omega}} m}.$$

Proof of (iv), Theorem 3. In this case, $K(\mu) = \gamma$ has no positive root and $K(\mu) < \gamma$ for any $\mu > 0$. By Lemma 19, there exists some $\hat{\mu} > 0$ such that $l\theta/(1+\theta) - \gamma$ is positive somewhere in Ω for every $\mu < \hat{\mu}$, and $l\theta/(1+\theta) - \gamma < 0$ in $\bar{\Omega}$ for every $\mu > \hat{\mu}$. Hence, $\lambda^*(\mu) > 0$ for every $\mu \in (0, \hat{\mu})$. Arguing similarly as in previous section, as $\mu \rightarrow \hat{\mu}-$, we have $\lambda^*(\mu) \rightarrow +\infty$.

Set

$$\nu_* = \frac{1}{\inf_{0 < \mu < \hat{\mu}} \lambda^*(\mu)}.$$

By the above discussions and Lemma 17, we see that ν_* is finite and positive. We consider two cases:

(a) $\nu > \nu_*$. For this case, $1/\nu < \lambda^*(\mu)$ for every $\mu \in (0, \hat{\mu})$. By Lemma 14, $\lambda_1 > 0$ for every $\mu \in (0, \hat{\mu})$. As $\lambda_1 > 0$ for every $\mu \geq \hat{\mu}$ and $\nu > 0$, we see that $\lambda_1 > 0$ for every $\mu > 0$.

(b) $\nu < \nu_*$. For this case, $1/\nu > \inf_{0 < \mu < \hat{\mu}} \lambda^*(\mu)$. Since $\lim_{\mu \rightarrow \hat{\mu}^-} \lambda^*(\mu) = +\infty$, we see that $\lambda^*(\mu) - 1/\nu$ changes sign at least once in $(0, \hat{\mu})$. By Lemma 18, λ_1 also changes sign at least once in $(0, \hat{\mu})$. \square

Acknowledgement. We thank the referee for his helpful comments and suggestions. We thank Dr. Renhao Cui for his help with the figures and Ms. Rui Li for her helpful comments. This research is partially supported by NSFC grants No. 11571364 and 11571363 (YL), NSF grant DMS-1411476 (YL) and China Scholarship Council (BW). Part of this work was done during the visit of YL to Tokyo Institute of Technology and the visit of BW to Ohio State University. We thank both institutions for the hospitality.

REFERENCES

- [1] I. Averill, K.-Y. Lam, Y. Lou, The role of advection in a two-species competition model: a bifurcation approach, Mem. Amer. Math. Soc., In press: Vol. 245, No. 1161, 2017.
- [2] X.L. Bai, X.Q. He, F. Li, An optimization problem and its application in population dynamics. Proc. AMS, 144 (2016) 2161-2170.
- [3] R.S. Cantrell, C. Conser, Diffusive logistic equations with indefinite weights: population models in disrupted environments. Proc. Roy. Soc. Edin. Sect. A 112 (1989) 293-318.
- [4] R.S. Cantrell, C. Conser, The effects of spatial heterogeneity in population dynamics. J. Math. Biol. 29 (1991) 315-338.
- [5] R.S. Cantrell, C. Conser, Spatial Ecology via Reaction-diffusion Equations, Series in Mathematical and Computational Biology, John Wiley and Sons, Chichester, UK, 2003.
- [6] R.S. Cantrell, C. Conser, V. Hutson, Permanence in ecological systems with spatial heterogeneity. Proc. Roy. Soc. Edin. Sect. A 123 (1993) 533-559.
- [7] C. Cosner, Reaction-diffusion-advection models for the effects and evolution of dispersal. Discr. Cont. Dyn. Syst. 34 (2014) 1701-1745.
- [8] X.F. Chen, R. Hambrock, Y. Lou, Evolution of conditional: a reaction-diffusion-advection model. J. Math. Biol. 57 (2008) 3687-3703.
- [9] R.H. Cui, Y. Lou, Spatial SIS epidemic models in advective environments. J. Differential Equations 261 (2016) 3305-3343.
- [10] E.N. Dancer, Y.H. Du, Effects of certain degeneracies in the predator-prey model. SIAM J. Math. Anal. 34 (2002) 292-314.
- [11] D. DeAngelis, W.-M. Ni, B. Zhang, Dispersal and spatial heterogeneity: single species. J. Math. Biol. 72 (2016) 239-254.
- [12] Y.H. Du, S.B. Hsu, A diffusive predator-prey model in heterogeneous environment. J. Differential Equations 203 (2004) 331-364.
- [13] Y.H. Du, J.P. Shi, Some recent results on diffusive predator-prey models in spatially heterogeneous environment, in: Nonlinear Dynamics and Evolution Equations, in: Fields Inst. Commun., vol. 48, Amer. Math. Soc., 2006, pp. 95-135.
- [14] Y.H. Du, J.P. Shi, Allee effect and bistability in a spatially heterogeneous predator-prey model. Trans. Amer. Math. Soc. 359 (2007) 4557-4593.
- [15] X.Q. He, W.M. Ni, The effects of diffusion and spatial variation in Lotka-Volterra competition-diffusion system I: Heterogeneity vs. homogeneity. J. Differential Equations 254 (2013) 528-546.

- [16] X.Q. He, W.-M. Ni, The effects of diffusion and spatial variation in Lotka-Volterra competition-diffusion system II: The general case. *J. Differential Equations* 254 (2013) 4088-4108.
- [17] X.Q. He, W.-M. Ni, Global dynamics of the Lotka-Volterra competition-diffusion system: Diffusion and spatial heterogeneity, I. *Comm. Pure Appl. Math.* 69 (2016) 981-1014.
- [18] K.-Y. Lam, Y. Lou, F. Lutscher, The emergence of range limits in advective environments. *SIAM J. Appl. Math.* 76 (2016) 641-662
- [19] K.-Y. Lam, Y. Lou, F. Lutscher, Evolution of dispersal in closed advective environments. *J. Biological Dynamics* 9 (2015) Supplement 1, 188-212.
- [20] K.-Y. Lam, W.-M. Ni, Uniqueness and complete dynamics of the Lotka-Volterra competition diffusion system. *SIAM J. Appl. Math.* 72 (2012) 1695-1712.
- [21] S. Liang, Y. Lou, On the dependence of population size upon random dispersal rate. *Discr. Cont. Dyn. Syst. Series B.* 17 (2012) 2771-2788.
- [22] Y. Lou, On the effects of migration and spatial heterogeneity on single and multiple species. *J. Differential Equations* 223 (2006) 400-426.
- [23] Y. Lou, Some challenging mathematical problems in evolution of dispersal and population dynamics, Pp.171-205 in: Friedman, A. (Ed.), *Tutor. Math. Biosci. vol IV: Evolution and Ecology*, Lect. Notes Mathematics Vol. 1922, Springer, 2007.
- [24] Y. Lou, Some reaction diffusion models in spatial ecology. *Scientia Sinica Mathematica*, 2015, 45(10): 1619-1634.
- [25] A.B. Medvinsky, S.V. Petrovskii, I.A. Tikhonova, H. Malchow and B.-L. Li, Spatiotemporal complexity of plankton and fish dynamics. *SIAM Rev.* 44 (2002) 311-370.
- [26] W.-M. Ni, *The Mathematics of Diffusion*, CBMS-NSF Regional Conf. Ser. in Appl. Math. 82, SIAM, Philadelphia, 2011.
- [27] R. Peng, J.P. Shi, Non-existence of non-constant positive steady states of two Holling type-II predator-prey systems: strong interaction case. *J. Differential Equations* 247 (2009) 866-886.
- [28] J.F. Wang, J.J. Wei, J.P. Shi, Global bifurcation analysis and pattern formation in homogeneous diffusive predator-prey systems. *J. Differential Equations* 260 (2016) 3495-3523.
- [29] F.Q. Yi, J.J. Wei, J.P. Shi, Bifurcation and spatiotemporal patterns in a homogeneous diffusive predator-prey system. *J. Differential Equations* 246 (2009) 1944-1977.

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