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擴散跟有向流在競爭物種演化下的效應

一個關於 Lotka-Volterra 競爭模型的回顧

The Effects of Diffusion and Advection on the Evolution of Competing Species: a Survey on the Lotka-Volterra Competition Model

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致謝

一份論文書寫的過程，也是認識自己的過程。

大三某天早起時，我決定法律系畢業後要轉讀數學研究所。那時，我相信如果大學畢業後不讀數學，一輩子也不會再讀了。對於這個理想與現實之間的決斷，父母和妹妹一直默默地支持，給我靜定的力量。後來，我才明白自己多麼任性又多麼幸福。如今，我想獻上這篇他們或許永遠讀不懂的論文，但在這些奇形怪狀的數學符號背後，有我這兩年成長的足跡，有我最真摯的感激。

碩一入學時，在畢業留學講座認識了後來的指導教授：夏俊雄老師。那場講座，老師透過古典詩文分享出國留學與生活的點滴，讓我印象十分深刻。因爲這個機緣，他成爲我的指導教授。不久，老師提供一篇極具啓發性的文章（參考文獻〔7〕)，確立我的論文研究方向。在研究過程中，老師不斷展現新銳學者的創意與品味，並給我及時的解惑與鼓勵，感謝老師！

轉讀數學研究所的原因或許是林紹雄老師，七年來，老師開授的課程，我共修習 37 學分（加旁聽爲 46 學分）。老師律己的教學風範以及嚴謹的治學態度，一直是我心目中理想數學家的典型。研究所兩年來的許多假日，老師帶領我徜徉北台灣的山林之美，我們天南地北聊著數學、文學、電影、音樂、生活點滴，還有那些真摯而現實的經驗。感謝老師，帶給我一輩子難忘的研究所生活。

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如今，一路走來，這篇論文已承載了許多故事，而我深深感謝⋯

在論文內容方面：
每週 Meeting 時，老師和同門哲瑋、明佑、仲麟和峻銘細膩地爬梳論文的每個論證與細節。我曾感到困難的 Lemma 2.5，硯仁五分鐘就提供絕妙無比的證明。愉生學長分享變分法的相關知識。一鴻幫忙克服困擾我許久的 maximum principles 關卡。知芃分享生態學相關期刊，她的生態學視角帶給我不少方法論上的反省。

在論文撰寫方面：
人文提供 LaTex 模板，讓我快速上手。晉宏總是熱心地幫我解決 LaTex 各種疑難雜症。彥穎教我使用 TeXworks，大幅節省校對及排版時間。立昌學長提供投影片的精美模板。君羊和哲瑋分享製作投影片的寶貴經驗。

在論文修訂方面：
正維、人文和旭唐撥冗認真讀過，分享不少數學與英文上的意見。勳育在英文用詞與摘要翻譯方面提供許多專業的意見。

在口試準備方面：
易璁幫忙潤飾連繫外國學者的信件。人文幫我第一次預演，針對論文內容提出相當敏銳的問題。硯仁、彥穎和君羊幫我第二次預演，提醒我修正演講速度。正維和哲瑋幫我最後一次預演，讓我臨場時不會緊張。旭唐跟人文提供英文演講的要點。薇儒和正維幫忙採購茶點，還有正維製作的精美海報。

論文之外的數學研究所生活，我要感謝彥穎和硯仁，我們一起舉辦代數讀書會，寫出 T. Hungerford 代數課本八成習題的解答，讓我從此不再害怕代數。之後君羊也加入的〈Proofs from the Book〉讀書會，大幅提升了我的數學品味。週二下午偶爾和旭唐的午聚，激發出許多美妙想法。撰寫論文時，感謝旭唐、育齡和恩臨的幫助與討論，我才能兼顧偏微分方程式這門吃重的必修課。

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最後，這四年多，陪伴我，當我面對未來而徬徨時、問題難解而沮喪時、名實不符而憤世時，始終願意傾聽、包容與分享，是我的女孩正維。而這一切一切，不只是刻骨銘心的感謝而已。

擴散跟有向流在競爭物種演化下的效應

一個關於 Lotka-Volterra 競爭模型的回顧[1]

戴佳原[2]

摘要

本論文完整地回顧了一個具有生態學意義的問題：兩個競爭物種在資源異質分布的孤立環境中將如何演化？本研究透過再分布機制由相互競爭、隨機擴散跟有向移動組成的假設建立一個特別的 Lotka-Volterra 競爭模型，用以分析競爭物種的長期演化結果，亦即決定該模型均衡解的穩定性。本研究以標準程序應用諸如最大值原則（maximum principles）、變分法（calculus of variation）和單調動力系統理論（the theory of monotone dynamical systems）等數學方法。主要結論是隨機擴散和有向移動共同決定了演化結果，因此不同擴散速率和有向流傾向的組合可能影響演化結果。據此，研究者建立了一個初步的分歧圖以提供理論上可信賴的預測。

[1] 關鍵字：Lotka-Volterra 競爭模型、隨機擴散、有向移動、均衡解、局部穩定性、全域穩定性

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The Effects of Diffusion and Advection on the Evolution of Competing Species: a Survey on the Lotka-Volterra Competition Model *

Jia Yuan Dai †

Abstract

This thesis is a rather complete survey concerning an ecologically meaningful problem: how would two competing species evolve in a given spatially heterogeneous and isolated environment? A special kind of the Lotka-Volterra competition model is derived by assuming that the mechanisms of redistribution consist of mutual competition, random diffusion, and advective motion. The main task is to analyze the evolutionary results of the competing species in the long run, or equivalently, to determine the stability of equilibria of the model. The mathematical methods such as maximum principles, calculus of variation, and the theory of monotone dynamical systems are utilized as the standard procedure. The main conclusion is that both random diffusion and advective motion decide the evolutionary results; thus different combinations of diffusion rates and advective tendencies may influence the evolutionary results. Accordingly, a preliminary bifurcation diagram can be established to provide certain theoretically reliable predictions.

*Keywords: Lotka-Volterra competition model, random diffusion, advective motion, equilibria, local stability, global stability

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1 Introduction

In 1910, Alfred J. Lotka proposed the article *"In the Theory of Autocatalytic Chemical Reactions"* which was effectively the logistic model. In 1920, Lotka extended the model to analyze predator-prey interaction in his book on biomathematics. In 1926, Vito Volterra derived the model independently for the purpose to make a statistical analysis of fish catches in the Adriatic. Today, being a special kind of *reaction-diffusion-advection model* which is proved to be mathematically meaningful and challenging, the so-called *Lotka-Volterra model* has been widely and deeply investigated both by ecologists and mathematicians, and indeed it can provide theoretically reliable predictions on the complicated interaction among different species in an ecological system.

In this thesis, a rather detailed survey concerning a special kind of the *Lotka-Volterra competition model* is presented. To state the problem more precisely, we utilize the common-used approach based on fluxes to derive the model. Firstly, we consider N species or N different pheotypes of a species which are mutually competing in a given environment $\Omega \subset \mathbb{R}^l$ with boundary $\partial\Omega$ (in reality, l=3) and each has the density $u_i(x,t)$ at location x and time t. There are some factors concerning

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the reasonable setting:

(a) *Environment*

In reality, the environment Ω is surely bounded, but for mathematical reasons we require it to be a domain with smooth boundary. Since resources are not uniformly distributed, the heterogeneity of the environment can be reflected by the *intrinsic growth rate* $m(x,t)$. Nevertheless, we assume two rather particular constraints: ***(C1) All species or*** N ***different phenotypes of a species have the same intrinsic growth rate***. ***(C2) The environment is homogeneous in time***, that is, $m(x,t) = m(x)$.

(b) *Mechenisms of Redistribution*

There are two basic mechanisms that make the densities vary in time: one is the *local process* such as birth, death, competition etc.; the other mechanism is the *motion of individuals* which can be understood as a combination of the random motion and the advective motion, that is, *conditional dispersal.* Now, we take $u_i(x,t)$ for example and let $u(x,t) = (u_1(x,t), u_2(x,t), ..., u_N(x,t))$, then the rate of change of the total population of u_i is given by

$$\frac{\partial}{\partial t}\int_\Omega u_i(x,t)dx = -\int_{\partial\Omega} J_i \cdot n ds + \int_\Omega F_i(u(x,t))dx \tag{1}$$

where J_i is the density flux of u_i through the boundary, n is the unit outer normal on $\partial\Omega$. and $F_i(u) = u_i f_i(u)$ with $f_i(u)$ being the *per-capita growth rate* of the i-th species.

How can we describe the density flux? Since the effects of the random motion in the flux is usually assumed to be proportional to the density gradient ∇u_i, and it is reasonable to assume that all species move toward more favorable habitats, we derive

$$J_i = -d_i \nabla u_i + \alpha_i u_i \nabla m$$

where $d_i > 0$ is the *diffusion rate* of u_i, and $\alpha_i \geq 0$ is the *advective tendency* of u_i toward the resource gradient ∇m. To describe the per-capita growth rate, we need to take into account not only the birth rate and death rate, but the interaction with all other species; hence

$$f_i(u(x,t)) = m(x) + \sum_{j=1}^{N} t_{ij} u_j(x,t)$$

where t_{ij} measures the intensity of mutual interaction between u_i and u_j. Here for mathematical simplicity we assume another constraint: ***(C3) All diffusion rates and advective tendencies are constants***. Since the divergence theorem implies

$$\int_{\partial\Omega} J_i \cdot n ds = \int_{\Omega} \nabla \cdot J_i dx$$

we obtain the equation:

$$\frac{\partial u_i}{\partial t} = \nabla \cdot (d_i \nabla u_i - \alpha_i u_i \nabla m) + u_i(m + \sum_{j=1}^{N} t_{ij} u_j)$$

Let $T = [t_{ij}]$ be the $N \times N$ interaction matrix, t_{ii} should be negative for all i because the living space and resources are limited, and concepts of cooperation and competition are defined as:

Definition. *Two species u_i and u_j ($i \neq j$) are called cooperative if $\frac{\partial f_i}{\partial u_j} > 0$ and $\frac{\partial f_j}{\partial u_i} > 0$; competitive if $\frac{\partial f_i}{\partial u_j} < 0$ and $\frac{\partial f_j}{\partial u_i} < 0$.*

In particular, our model is competitive if $t_{ij} < 0$ and $t_{ji} < 0$ for $i \neq j$. However, in this thesis we make a further constraint: ***(C4)*** $t_{ij} = -1$ ***for all*** i, j [1], in other words, all species have the same competing ability. In ecological fields, the scenery could occur if they were different phenotypes of the same species, or they were different species but they had gained mutation from the same ancestral species, and the result of mutation is not effective.

Finally, we assume that the ecological system is isolated; hence each equation is equipped with the *no-flux boundary condition.* Owing to assumptions from (C1) to (C4), we derive a special kind of the Lotka-Volterra competition system:

$$\begin{cases} \dfrac{\partial u_i}{\partial t} = \nabla \cdot (d_i \nabla u_i - \alpha_i u_i \nabla m) + u_i(m - \displaystyle\sum_{j=1}^{N} u_j) & \text{in } \Omega \times (0, \infty) \\ B[u_i] = J_i \cdot n = d_i \partial_n u_i - \alpha_i u_i \partial_n m = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases} \quad (2)$$

[1] See Lemma 3.5 for the mathematical reason of the constraint.

where $\partial_n u_i = \dfrac{\partial u_i}{\partial n}$ is the normal derivative.

It is obvious that the diffusion rate and the advective tendency are two important parameters of the full system (2). An interesting question is: ***How would competing species evolve under a given combination of diffusion rates and advective tendencies?*** Even though there are only two biological consequences in the long run: only one species *wins* (or equivalently, all other species extinct) or some species *coexist*, it is not easy to answer the above question by rough observations. For writing strategies, the ranges of diffusion rates and advective tendencies are classified into three types:

Type A: general N, $\alpha_i = 0$ for all i, and $0 < d_1 < d_2 < ... < d_N$.

Type B: $N = 2$, $\alpha_2 = 0$, and Ω is convex.

Type C: $N = 2$, and $\alpha_i \geq 0$ for $i = 1, 2$.

and we make a notational convention whenever there are only two competing species: **(Notation)** $(u_1, \alpha_1, d_1) = (u, \alpha, \mu)$ and $(u_2, \alpha_2, d_2) = (v, \beta, \nu)$ whenever $N = 2$. At the first glance, the differences between the types may be slight, but the approaches to analyze the full system (2) become quite different as we will later see.

To study the full system (2), the first crucial task is to show that for any non-negative continuous initial data $u_0(x) \equiv u(x, 0)$, there exists a unique classical solution $u(x, t)$ in $\Omega \times (0, T(u_0))$ where $T(u_0) > 0$ is the existing time for u_0. This task is achieved by [15], Corollary 4.1 which proved that the full system (2) generates a continuous local semiflow (or local semi-dynamical system):

$$S : (0, T(u_0)) \times [C(\overline{\Omega})]^N \to [C(\overline{\Omega})]^N, \; S(t, u_0)(\cdot) = u(\cdot, t)$$

where $[C(\overline{\Omega})]^N = \{u : u : \overline{\Omega} \to \mathbb{R}^N \text{ is continuous}\}$. However, the full system (2) is biological meaningful only if the existing time $T(u_0) = \infty$. For Type A, this requirement is fulfilled with some a priori L^∞ estimates (ref.[1], Lemma 2.3). For Type B and C, it is obvious that positive constants $K > \max\{\|u_0\|_{L^\infty(\overline{\Omega})}, \|v_0\|_{L^\infty(\overline{\Omega})}, \|m\|_{L^\infty(\overline{\Omega})}\}$ are supersolutions for *each equation*; hence by the Parabolic Comparison Principle (see Appendix), the solution $u(x, t)$ with initial data u_0 exists for all $t \geq 0$. That is, $T(u_0) = \infty$.

Now that obtaining exact solutions of the full system (2) is unlikely, it is wise to consider the scalar equation:

$$\begin{cases} \dfrac{\partial \theta}{\partial t} = \nabla \cdot (d_i \nabla \theta - \alpha_i \theta \nabla m) + \theta(m - \theta) & \text{in } \Omega \times (0, \infty) \\ B[\theta] = d_i \partial_n \theta - \alpha_i \theta \partial_n m = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases} \tag{3}$$

Under some suitable assumptions on the intrinsic growth rate $m(x)$, especially

$$\textbf{(A1)}\ m(x) \in C^{2+\delta}(\overline{\Omega}) \text{ is not a constant function and } \int_\Omega m(x)dx > 0$$

where $0 < \delta < 1$, we can prove that for any $d_i > 0$ and $\alpha_i \geq 0$, there exists a unique positive steady-state $\theta = \theta(x; \alpha_i, d_i)$ of (3) (see Theorem 1.6) and the solution $(0, ..., 0, \theta(x; \alpha_i, d_i), 0, ..., 0)$ to the full system (2) is often called a *semi-trivial equilibrium* [2]. Beside the semi-trivial equilibria, we call $w(x)$ a *positive equilibrium* if it is an equilibrium of the full system (2) and all components are positive. For each equilibrium, we define several kinds of the stability as:

Definition. *Let $w(x)$ be an equilibrium of the full system (2), then*

(1) $w(x)$ is locally stable if for given $\epsilon > 0$, there exists $r > 0$ such that for any non-negative continuous initial data u_0 with $\|u_0 - w\|_{L^\infty(\overline{\Omega})} < r$, the solution $u(x,t)$ satisfies $\|u(\cdot,t) - w\|_{L^\infty(\overline{\Omega})} < \epsilon$ for sufficiently large t. Furthermore, such $w(x)$ is locally asymptotically stable if $\lim_{t\to\infty} \|u(\cdot,t) - w\|_{L^\infty(\overline{\Omega})} = 0$.

(2) $w(x)$ is globally asymptotically stable if for any non-negative and not identically zero continuous initial data u_0 which is not an equilibrium, the solution $u(x,t)$ satisfies $\lim_{t\to\infty} \|u(\cdot,t) - w\|_{L^\infty(\overline{\Omega})} = 0$.

It is known that the study on the local stability of semi-trivial equilibria can obtain some rather strong implications on the dynamics of the full system (2). From both mathematical and ecological points of view, a species will invade (or not invade) even when it is rare if its corresponding semi-trivial equilibrium is unstable (or locally stable). Mathematically, the local stability (and equivalently *invasibility*) of a semi-trivial equilibrium is often determined by the sign of principal eigenvalues of the

[2]The terminology "semi-trivial equilibrium" is in comparison with the "trivial equilibrium" 0.

linearized system around it; thus we need to deal with eigenvalue problems.

The most difficult part is perhaps to determine the global stability of semi-trivial equilibria, but the result is quite decisive since a species will win in the long run if its corresponding semi-trivial equilibrium is globally asymptotically stable. The main difficulties are rooted in the lack of sufficiently powerful mathematical tools such as the maximum principles if $N > 2$, whereas in the quite restrictive case $N = 2$, the full system (2) which is competitive can be *cooperative* via a change of variables (see the proof of Lemma 1.8). After performing this change of variables, most mathematical tools, especially *the theory of monotone dynamical systems* becomes applicable (see Theorem 1.9 and Theorem 4.9).

Main Results

In section 2, we deal with the main result of the Type A which comes from *Dockery, Hutson, Mischaikow, and Pernarowski [1]*:

***Theorem* 1.1.** *(c.f.[1]) Suppose that (A1) holds. Let $U_i(x)$ be the semi-trivial equilibrium of the i-th species, then*

- *(a) (local stability) $U_1(x)$ is locally asymptotically stable, whereas $U_i(x)$ ($i \geq 2$) is unstable.*
- *(b) (global stability) if $N = 2$, $U_1(x)$ is globally asymptotically stable.*

When N competing species move randomly and compete mutually, Theorem 1.1 shows that the difference of the diffusion rates principally drives the dynamics of the full system (2), and the slower-diffusing species will win if $N = 2$.

In section 3, the main result of the Type B comes from *Cantrell, Cosner, and Lou [3][4]*.

***Theorem* 1.2.** *(c.f.[3][4]) Suppose that $N = 2$ and (A1) holds. Let $(\theta(x;\alpha,\mu), 0)$ and $(0, \theta(x; 0, \nu))$ be the semi-trivial equilibria of the 1st and 2nd species respectively. If Ω is convex and $\mu \approx \nu$, then $(\theta(x;\alpha,\mu), 0)$ is globally asymptotically stable provided that α is sufficiently small but not too small relative to the difference $\mu - \nu$.*

Here $\mu \approx \nu$ means $\mu - \nu = O(\epsilon)$ for sufficiently small $\epsilon > 0$. When two species compete in a *convex environment* and *the advective tendency of the 1st species is sufficiently small*, Theorem 1.2 generalizes the result of Theorem 1.1 in the case $\mu < \nu$. The new implication is for the case $\mu > \nu$ that the faster-diffusing species can overcome the disadvantage caused by far rapider diffusion via directed movement toward more favorable habitats.

In section 4, we deal with the main result of Type C which comes from *Hambrock and Lou [6]*. Before dealing with the main result, we need other technical assumptions on $m(x)$ to restrict the distribution of resources in the environment:

(A2) $|\nabla m(x)| > 0$ for almost $x \in \Omega$. In other words, the set of critical points of $m(x)$ has Lebesgue measure zero.

(A3) $\partial_n m < 0$ on $\partial\Omega$, $m(x)$ has only one critical point in $\overline{\Omega}$ denoted by x_0, and $x_0 \in \Omega$ satisfies $D^2 m(x_0)$ is negative-definite, where $D^2 m(x_0)$ is the Hessian matrix of $m(x)$ at $x = x_0$.

***Theorem* 1.3.** *(c.f.[6]) Suppose that $N = 2$ and (A1) holds. Let $(\theta(x;\alpha,\mu), 0)$ and $(0, \theta(x;\beta,\nu))$ be the semi-trivial equilibria of the 1st and 2nd species respectively:*

(a) if (A2) holds. then given any $0 \le \beta/\nu \le 1/\max_{\overline{\Omega}} m$, both semi-trivial equilibria are unstable and the full system (2) has at least one locally stable positive equilibrium provided that α is sufficiently large.

(b) if (A3) holds and $m > 0$ in $\overline{\Omega}$, given any $\beta/\nu \ge 1/\min_{\overline{\Omega}} m$, then $(0, \theta(x;\beta,\nu))$ is globally asymptotically stable provided that α is sufficiently large.

When both the diffusion rates and advective tendencies occur and *the advective tendency of the 1st species is sufficiently large*, Theorem 1.3 shows that neither the diffusion rate ν nor the advective tendency β, but the ***ratio of dispersal*** β/ν plays an important role in the dynamics of the full system (2). It is in strong contrast to Theorem 1.2 that as α increases, Theorem 1.3(a) shows that the 1st species which is *smarter* may not win the competition and coexistence becomes possible. Such coexistence is called an *advection-induced coexistence.* An explanation for such phenomenon is that the smarter species concentrates on the most favorable habitats, leaving enough room for the other species to survive there. However, if every habitat is favorable ($m > 0$ in $\overline{\Omega}$) and both species strongly pursue favorable habitats, Theorem 1.3(b) shows that they will lead to *overcrowd*, causing an *advection-induced extinction* of the 1st species which has the larger advective tendency.

In the last section, we establish a bifurcation diagram to organize the main results and provide some further interesting problems.

Frequently-applied Theorems and the Main Scheme

In this subsection, three basic and frequently-applied theorems (see Theorem 1.6, 1.7, and 1.9) in our subsequent analysis are presented. The first theorem concerns about the existence and the uniqueness of the semi-trivial equilibrium. Here we denote $\mu = d_i$ and $\alpha = \alpha_i$ in (3) for notational convenience. To change the no-flux boundary condition into the Neumann boundary condition, we set $w = e^{-(\alpha/\mu)m}\theta$ to obtain the *equivalent form* of (3):

$$\begin{cases} \dfrac{\partial w}{\partial t} = \mu \Delta w + \alpha \nabla m \cdot \nabla w + w(m - e^{(\alpha/\mu)m} w) & \text{in } \Omega \times (0, \infty) \\ B[w] = \partial_n w = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases} \tag{4}$$

Since 0 is a trivial equilibrium of (4), we linearize (4) around 0 and then consider the eigenvalue problem:

$$\begin{cases} \mu \Delta \phi + \alpha \nabla m \cdot \nabla \phi + \phi m = \lambda \phi & \text{in } \Omega \\ B[\phi] = \partial_n \phi = 0 & \text{on } \partial\Omega \end{cases} \tag{5}$$

***Lemma* 1.4.** *For each $m \in C^{2+\delta}(\overline{\Omega})$, $\alpha \geq 0$, and $\mu > 0$, there exists a unique simple principal eigenvalue $\lambda(m, \alpha, \mu)$ such that the correpsonding principal eigenfunction is strictly positive.*

Proof. Since $\overline{\Omega}$ is compact and $m \in C^{2+\delta}(\overline{\Omega})$, it is well-known (ref.[9], p.340, Theorem 3) that the eigenvalue problem

$$\begin{cases} \mu \Delta \phi + \alpha \nabla m \cdot \nabla \phi + \phi(m - \max_{\overline{\Omega}} m) = \tilde{\lambda} \phi & \text{in } \Omega \\ B[\phi] = \partial_n \phi = 0 & \text{on } \partial\Omega \end{cases}$$

has a unigue simple principal eigenvalue $\tilde{\lambda}(m,\alpha,\mu)$ such that the corresponding principal eigenfunction is strictly positive; hence the original eigenvalue problem has $\lambda(m,\alpha,\mu) = \tilde{\lambda}(m,\alpha,\mu) + max_{\overline{\Omega}} m$ as the simple principal eigenvalue and the corresponding principal eigenfunction is strictly positive. □

In fact, owing to the assumption (A1), the following lemma shows that the principal eigenvalue of (5) is positive; hence 0 is unstable.

***Lemma* 1.5.** *Suppose that (A1) holds, then*

(a) $\displaystyle\int_\Omega m e^{(\alpha/\mu)m} dx > 0.$

(b) $\displaystyle\lambda(m,\alpha,\mu) \downarrow \hat{m} \equiv \frac{\int_\Omega m e^{(\alpha/\mu)m} dx}{\int_\Omega e^{(\alpha/\mu)m} dx} > 0$ *as* $\mu \to \infty$*; hence* 0 *is unstable.*

Proof. The mapping $\alpha \in \mathbb{R} \mapsto \displaystyle\int_\Omega m e^{(\alpha/\mu)m} dx$ is strictly increasing; hence (A1) implies $\displaystyle\int_\Omega m e^{(\alpha/\mu)m} dx > 0$ for all $\alpha \geq 0$.

To prove the part (b), the main idea is to analyze the variational characterization of the principal eigenvalue. We let $\sigma(m,\alpha,\mu) = -\lambda(m,\alpha,\mu)$ for notational convenience and it suffices to consider the case $\phi > 0$ by Lemma 1.4. Multiplying (5) by $e^{(\alpha/\mu)m}\phi$, integrating over Ω, and utilizing the divergence theorem and the Neumann boundary condition, we obtain

$$\sigma(m,\alpha,\mu) = \inf_{\phi \in H^1(\overline{\Omega}), \phi \neq 0} \frac{\mu \int_\Omega e^{(\alpha/\mu)m} |\nabla\phi|^2 dx - \int_\Omega m e^{(\alpha/\mu)m} \phi^2 dx}{\int_\Omega e^{(\alpha/\mu)m} \phi^2 dx} \tag{6}$$

Take $\phi \equiv 1$, then $\sigma(m,\alpha,\mu) \leq -\hat{m}$. Now, given $\epsilon > 0$, we want to show $\sigma(m,\alpha,\mu) \geq -\hat{m} - \epsilon$ if μ is large enough, but it is only required to obtain

$$\mu \int_\Omega e^{(\alpha/\mu)m} |\nabla\phi|^2 dx - \int_\Omega (m - \hat{m}) e^{(\alpha/\mu)m} \phi^2 dx + \epsilon \int_\Omega e^{(\alpha/\mu)m} \phi^2 dx \geq 0$$

for all $\phi \in H^1(\overline{\Omega})$ if μ is large enough.

Since $\sigma(m,\alpha,\mu)$ is invariant under $\phi \mapsto c\phi$ for any nonzero constant c, it suffices to consider the case ϕ with $\dfrac{\int_\Omega \phi dx}{|\Omega|} = 1$. Define $\phi(x) = 1 + \psi(x)$ and apply the Poincaré inequality, then there exists a constant $K > 0$ which is independent of ϕ such that

$$\|\psi\|_{L^2(\overline{\Omega})} \leq K \|\nabla\psi\|_{L^2(\overline{\Omega})} = K \|\nabla\phi\|_{L^2(\overline{\Omega})}$$

Applying the Hölder inequality, we obtain

$$\begin{aligned}\left|\int_\Omega (m-\hat{m})e^{(\alpha/\mu)m}\phi^2 dx\right| &= \left|\int_\Omega (m-\hat{m})e^{(\alpha/\mu)m}(1+2\psi+\psi^2)dx\right| \\ &\le 2\|me^{(\alpha/\mu)m}-\hat{m}e^{(\alpha/\mu)m}\|_{L^2(\overline{\Omega})}\|\psi\|_{L^2(\overline{\Omega})}+M\|\psi\|^2_{L^2(\overline{\Omega})} \\ &= 2M|\Omega|^{\frac{1}{2}}K\|\nabla\phi\|_{L^2(\overline{\Omega})}+MK^2\|\nabla\phi\|^2_{L^2(\overline{\Omega})}\end{aligned}$$

where $M = \|me^{(\alpha/\mu)m} - \hat{m}e^{(\alpha/\mu)m}\|_{L^\infty(\overline{\Omega})} < \infty$. This inequality implies

$$\begin{aligned}&\mu\int_\Omega e^{(\alpha/\mu)m}|\nabla\phi|^2dx - \int_\Omega (m-\hat{m})e^{(\alpha/\mu)m}\phi^2dx + \epsilon\int_\Omega e^{(\alpha/\mu)m}\phi^2dx \\ &\ge (\mu\min_{\overline{\Omega}} e^{(\alpha/\mu)m} - Mk^2)\|\nabla\phi\|^2_{L^2(\overline{\Omega})} - 2M|\Omega|^{\frac{1}{2}}K\|\nabla\phi\|_{L^2(\overline{\Omega})} + \epsilon\int_\Omega e^{(\alpha/\mu)m}\phi^2dx \ge 0\end{aligned}$$

if μ is large enough. $\square$

The unstability of 0 makes the single species invade even when it is rare. We see that in the logistic model ($\alpha_i = d_i = 0$ in (3)), 0 is unstable, and there exists a unique global attractor among all non-negative and not identically zero continuous initial data. The following theorem shows that (3) shares this key feature of the logistic model.

***Theorem* 1.6.** *(c.f.[8]) Suppose that (A1) holds, then for any $\alpha \ge 0$ and $\mu > 0$, there exists a unique positive steady-state $\theta = \theta(x;\alpha,\mu)$ of (4), that is, θ is the unique positive solution to the scalar equation*

$$\begin{cases}\nabla\cdot(\mu\nabla\theta - \alpha\theta\nabla m) + \theta(m-\theta) = 0 & \text{in } \Omega \\ B[\theta] = \mu\partial_n\theta - \alpha\theta\partial_n m = 0 & \text{on } \partial\Omega\end{cases}$$

In addition, θ is the global attractor among all non-negative and not identically zero continuous initial data.

Proof. It suffices to consider the equivalent form of the scalar equation:

$$\begin{cases}\mu\Delta w + \alpha\nabla m\cdot\nabla w + w(m - e^{(\alpha/\mu)m}w) = 0 & \text{in } \Omega \\ B[w] = \partial_n w = 0 & \text{on } \partial\Omega\end{cases} \tag{7}$$

By Lemma 1.4, we let $\phi_1 > 0$ be the principal eigenfunction of (5) with the corresponding principal eigenvalue $\lambda_1 > 0$, then we can choose sufficiently small $\epsilon > 0$

such that

$$\begin{aligned}
&\mu\Delta(\epsilon\phi_1) + \alpha\nabla m\cdot\nabla(\epsilon\phi_1) + \epsilon\phi_1(m - e^{(\alpha/\mu)m}\epsilon\phi_1)\\
&= \epsilon(\mu\Delta\phi_1 + \alpha\nabla m\cdot\nabla\phi_1 + m\phi_1) - \epsilon^2 e^{(\alpha/\mu)m}\phi_1^2\\
&= \epsilon\lambda_1\phi_1 - \epsilon^2 e^{(\alpha/\mu)m}\phi_1^2 = \epsilon\phi_1(\lambda_1 - \epsilon e^{(\alpha/\mu)m}\phi_1) > 0
\end{aligned}$$

hence $\epsilon\phi_1$ is a subsolution of (7). If $\underline{u}(x,t)$ is a solution of (4) with $\underline{u}(x,0) = \epsilon\phi_1$, then

$$\frac{\partial\underline{u}(x,0)}{\partial t} = \mu\Delta(\epsilon\phi_1) + \alpha\nabla m\cdot\nabla(\epsilon\phi_1) + \epsilon\phi_1(m - e^{(\alpha/\mu)m}\epsilon\phi_1) > 0$$

and general properties of sub- and supersolutions imply that $\underline{u}(x,t)$ is increasing in t (ref.[8], Proposition 3.2) [3]. Since any constant $K > \dfrac{\max_{\overline{\Omega}} m}{\min_{\overline{\Omega}} e^{(\alpha/\mu)}m}$ is a supersolution of (4), we can conclude that there exists a minimal positive steady-state of (4), denoted by $u^*(x)$, such that $\underline{u}(x,t)\uparrow u^*(x)$ as $t\to\infty$.

If u^{**} is another positive steady-state of (4) with $u^{**}\neq u^*$, then since u^* is minimal, we have $u^{**}\geq u^*$ and $u^{**} > u^*$ somewhere in Ω. Since u^* is a *positive solution* of

$$\begin{cases}\mu\Delta\psi + \alpha\nabla m\cdot\nabla\psi + \psi(m - e^{(\alpha/\mu)m}u^*) = \lambda^*\psi & \text{in } \Omega\\ B[\psi] = \partial_n\psi = 0 & \text{on } \partial\Omega\end{cases}$$

with $\lambda^* = 0$, and in the above eigenvalue problem, eigenfunctions belonging to distinct eigenvalues are orthogonal; hence the principal eigenvalue $\lambda_1^* = 0$. Similarly, u^{**} is a *positive solution* of

$$\begin{cases}\mu\Delta\psi + \alpha\nabla m\cdot\nabla\psi + \psi(m - e^{(\alpha/\mu)m}u^{**}) = \lambda^{**}\psi & \text{in } \Omega\\ B[\psi] = \partial_n\psi = 0 & \text{on } \partial\Omega\end{cases}$$

with $\lambda^{**} = 0$; hence the principal eigenvalue $\lambda_1^{**} = 0$. However, given $h\in C^{2+\delta}(\overline{\Omega})$, the principal eigenvalue λ_1 of the eigenvalue problem:

$$\begin{cases}\mu\Delta\psi + \alpha\nabla m\cdot\nabla\psi + \psi(m - h) = \lambda\psi & \text{in } \Omega\\ B[\psi] = \partial_n\psi = 0 & \text{on } \partial\Omega\end{cases}$$

has a variational characterization:

$$\lambda_1 = \sup_{\psi\in H^1(\overline{\Omega}),\psi\neq 0}\frac{-\mu\int_\Omega e^{(\alpha/\mu)m}|\nabla\psi|^2dx + \int_\Omega e^{(\alpha/\mu)m}(m-h)\psi^2dx}{\int_\Omega e^{(\alpha/\mu)m}\psi^2dx} \tag{8}$$

[3] Honestly speaking, I have not found the way to prove such general properties.

hence $m-e^{(\alpha/\mu)m}u^{**} \leq m-e^{(\alpha/\mu)m}u^{*}$ and $m-e^{(\alpha/\mu)m}u^{**} < m-e^{(\alpha/\mu)m}u^{*}$ somewhere in Ω imply $\lambda_1^{**} < \lambda_1^{*}$, which is a contradiction.

If $u(x,t)$ is a solution of (4) with non-negative and not identically zero continuous initial data, then $u(x,t) > 0$ in $\overline{\Omega} \times (0,\infty)$ by the Parabolic Strong Maximum Principle (see Appendix). For any $t_0 > 0$, we can choose sufficiently small $\epsilon > 0$ such that $\underline{u}(x,0) = \epsilon\phi_1(x) < u(x,t_0)$ for all $x \in \overline{\Omega}$, then $\underline{u}(x,t-t_0) < u(x,t)$ for all $t > t_0$ by the Parabolic Comparison Principle (see Appendix). Thus, $u(x,t)$ is bounded from below by $\underline{u}(x,t-t_0)$ and $\underline{u}(x,t-t_0) \uparrow u^*(x)$ as $t \to \infty$. Since u^* is the *unique* positive steady-state of (4) and $u(x,t)$ is bounded in $\overline{\Omega} \times [0,\infty)$, we have $u(x,t) \to u^*(x)$ as $t \to \infty$. □

Even though the full system (2) is non-linear (indeed, semi-linear), the local stability of semi-trivial equilibria can be determined by the spectrum of the linearized system around them (ref.[15], Theorem 4.2). In paricular, if $N = 2$, the second theorem provides a manipulable criterion for the local stability:

***Theorem* 1.7.** *(c.f.[6]) If $N = 2$, then the semi-trivial equilibrium $(0,\theta(x;\beta,\nu))$ is locally stable/unstable if and only if the following eigenvalue problem for $(\lambda,\phi) \in \mathbb{R} \times C^{2+\delta}(\overline{\Omega})$:*

$$\begin{cases} \nabla \cdot (\mu\nabla\phi - \alpha\phi\nabla m) + \phi[m - \theta(\cdot;\beta,\nu)] = \lambda\phi & \text{in } \Omega \\ B[\phi] = \mu\partial_n\phi - \alpha\phi\partial_n m = 0 \text{ on } \partial\Omega,\ \phi > 0 \text{ in } \overline{\Omega} \end{cases}$$

has a negative/positive principal eigenvalue λ_1. The criterion for the local stability of $(\theta(x;\alpha,\mu),0)$ is analogous.

Proof. If $N = 2$, then the linearization of the full system (2) around $(0,\theta(x;\beta,\nu))$ leads to the eigenvalue problem:

$$\begin{cases} L_1[\phi] \equiv \nabla \cdot (\mu\nabla\phi - \alpha\phi\nabla m) + \phi[m - \theta(\cdot;\beta,\nu)] = \lambda\phi & \text{in } \Omega \\ L_2[\psi] \equiv \nabla \cdot (\nu\nabla\psi - \beta\phi\nabla m) + \psi[m - 2\theta(\cdot;\beta,\nu)] = \lambda\psi - \theta(\cdot;\beta,\nu)\phi & \text{in } \Omega \end{cases} \tag{9}$$

The main observation is that the principal eigenvalue of L_2 is always negative. To see this observation, we let (λ,ψ) be a solution pair of $L_2[\psi] = \lambda\psi$ with $\psi > 0$

and $\theta \equiv \theta(\cdot;\beta,\nu)$. Multiplying $L_2[\psi] = \lambda\psi$ by $e^{-(\beta/\nu)m}\theta$, integrating over Ω, and utilizing the equation of θ:

$$\begin{cases} \nabla\cdot(\nu\nabla\theta - \beta\theta\nabla m) + \theta(m-\theta) = 0 & \text{in } \Omega \\ B[\theta] = \partial_n\theta = 0 & \text{on } \partial\Omega \end{cases}$$

we can derive

$$\begin{aligned} \lambda\int_\Omega e^{-(\beta/\nu)m}\theta\psi dx &= \int_\Omega \nu e^{-(\beta/\nu)m}\theta\nabla[e^{-(\beta/\nu)m}\nabla(e^{-(\beta/\nu)m}\psi)] + (m-2\theta)e^{-(\beta/\nu)m}\theta\psi dx \\ &= \int_\Omega \nu e^{-(\beta/\nu)m}\psi\nabla[e^{-(\beta/\nu)m}\nabla(e^{-(\beta/\nu)m}\theta)] + (m-2\theta)e^{-(\beta/\nu)m}\theta\psi dx \\ &= -\int_\Omega e^{-(\beta/\nu)m}\theta^2\psi dx < 0 \end{aligned}$$

Let λ_1 be the principal eigenvalue of L_1. Suppose that $(0, \theta(x;\beta,\nu))$ is stable, and if (9) has a solution pair with $\lambda_1 \geq 0$. Since the principal eigenvalue of L_2 is negative, which implies that λ_1 lies in the resolvent set of L_2; hence there exists a unique solution ψ of $(L_2 - \lambda_1\mathbb{I})[\psi] = -\theta\phi$. In other words, (9) has a non-trivial solution with $\lambda_1 \geq 0$, which contradicts the local stability of $(0, \theta(x;\beta,\nu))$.

Suppose that $(0, \theta(x;\beta,\nu))$ is unstable, then there exists a non-trivial solution pair (λ, ϕ, ψ) with $Re(\lambda) > 0$. If $\phi \equiv 0$, then L_2 has an eigenvalue with positive real parts; hence its principal eigenvalue is positive, which is a contradiction. Consequently, $\phi \neq 0$ implies that L_1 has an eigenvalue with positive real parts; hence its principal eigenvalue is positive. $\square$

To determine the global stability of semi-trivial equilibria, the first step is to show that the full system (2) is a *strongly monotone dynamical system* if $N = 2$:

***Lemma* 1.8.** *Let $(u_1(x,t), v_1(x,t))$ and $(u_2(x,t), v_2(x,t))$ be two solutions of the full system (2) with $u_1(x,0) \geq u_2(x,0)$ and $v_1(x,0) \leq v_2(x,0)$ for $x \in \overline{\Omega}$, then $u_1(x,t) \geq u_2(x,t)$ and $v_1(x,t) \leq v_2(x,t)$ for $x \in \overline{\Omega}$ and $t > 0$. Furthermore, if $u_1(x,0) \neq u_2(x,0)$ and $v_1(x,0) \neq v_2(x,0)$ for some $x \in \overline{\Omega}$, then $u_1(x,t) > u_2(x,t)$ and $v_1(x,t) < v_2(x,t)$ for $x \in \overline{\Omega}$ and $t > 0$.*

Proof. We set $(u_i, v_i) \mapsto (e^{-(\alpha/\mu)m}u_i, e^{-(\beta/\nu)m}v_i)$ to get the equivalent form:

$$\begin{cases} \dfrac{\partial u_i}{\partial t} = \mu\Delta u_i + \alpha\nabla m \cdot \nabla u_i + u_i(m - e^{(\alpha/\mu)m}u_i - e^{(\beta/\nu)m}v_i) & \text{in } \Omega \times (0,\infty) \\ \dfrac{\partial v_i}{\partial t} = \nu\Delta v_i + \beta\nabla m \cdot \nabla v_i + v_i(m - e^{(\alpha/\mu)m}u_i - e^{(\beta/\nu)m}v_i) & \text{in } \Omega \times (0,\infty) \\ B[u_i] = \partial_n u_i = 0,\ B[v_i] = \partial_n v_i = 0 & \text{on } \partial\Omega \times (0,\infty) \end{cases} \tag{10}$$

Since $v_i(x,t)$ is bounded in $\overline{\Omega} \times [0,\infty)$ for any given initial data $v_i(x,0)$, we can choose a constant $K > 0$ (which may be dependent on the initial data) such that $v_i(x,t) < K$ for all $(x,t) \in \overline{\Omega} \times [0,\infty)$. Consequently, (10) becomes *cooperative* via the change of variables $(u_i, v_i) \mapsto (u_i, K - v_i)$. Since $u_1(x,0) \geq u_2(x,0)$ and $K - v_1(x,0) \geq K - v_2(x,0)$ for all $x \in \overline{\Omega}$, by the Parabolic Comparison Principle (see Appendix), we have $u_1(x,t) \geq u_2(x,t)$ and $K - v_1(x,t) \geq K - v_2(x,t)$ for all $x \in \overline{\Omega}$ and $t > 0$. The last part of the Lemma follows from the Parabolic Hopf Boundary Lemma and the Parabolic Strong Maximum Principle (see Appendix). □

Combining with Lemma 1.5(b), Theorem 1.6, and Lemma 1.8, we can apply the following theorem which provides a criterion to determine the global stability.

***Theorem* 1.9.** *(c.f. [14], Theorem B) Suppose that $N = 2$ and (A1) holds. Let $(\theta(x;\alpha,\mu),0)$ and $(0,\theta(x;\beta,\nu))$ be the semi-trivial equilibria of the 1st and 2nd species respectively. If $(\theta(x;\alpha,\mu),0)$ is locally stable, $(0,\theta(x;\beta,\nu))$ is unstable, and the full system (2) has no positive equilibria, then $(\theta(x;\alpha,\mu),0)$ is globally asymptotically stable. The criterion for the global stability of $(0,\theta(x;\beta,\nu))$ is analogous.*

We establish the following scheme to close this subsection.

	Problems	Main Ideas	Related Theorems
Local Stability	eigenvalue problems	determine the sign of principal eigenvalues	Theorem 1.7
No Coexistence		argue by contradiction	Lemma 3.5 Lemma 4.10
Global Stability			Theorem 1.9

Briefly speaking, the first task is to determine the local stability via the sign of principal eigenvalues. The second task is to rule out the possibility of positive equilibria. This may be the most difficult part because we need to compare with some integral identities which are not a priori known (see Lemma 3.5) or to control the asymptotic behavior of principal eigenvalues with respect to some parameters (see Theorem 4.5 and Lemma 4.10). As long as all the conditions in Theorem 1.9 are fulfilled, the global stability follows directly.

2 The Main Result of Type A

In Type A, all advective tendencies are zero; hence the full system (2) becomes

$$\begin{cases} \dfrac{\partial u_i}{\partial t} = d_i \Delta u_i + u_i(m - \displaystyle\sum_{j=1}^{N} u_j) & \text{in } \Omega \times (0, \infty) \\ B[u_i] = \partial_n u_i = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases} \tag{11}$$

and the scalar equation (3) becomes

$$\begin{cases} \dfrac{\partial u_i}{\partial t} = d_i \Delta u_i + u_i(m - u_i) & \text{in } \Omega \times (0, \infty) \\ B[u_i] = \partial_n u_i = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases}$$

We note that Theorem 1.6 guarantees the existence and uniqueness of the positive steady-state of (11) which is a global attractor among all non-negative and not identically zero continuous initial data. In this section, the i-th semi-trivial equilibrium is denoted by $U_i(x) = (0, ..., \tilde{u_i}(x), ..., 0)$ with $\tilde{u_i}(x) > 0$ in $\overline{\Omega}$. To understand the local stability of $U_i(x)$, we need to determine the sign of principal eigenvalues of the linearization operator of the full system around $U_i(x)$ [4]:

$$\begin{cases} \dfrac{\partial v_i}{\partial t} = L_2[\tilde{u_i}; d_i] v_i - \tilde{u_i} \displaystyle\sum_{j \neq i} v_j \\ \dfrac{\partial v_k}{\partial t} = L_1[\tilde{u_i}; d_k] v_k & \text{for } k \neq i \end{cases} \tag{12}$$

where L_1,L_2 : $\mathbb{D} = \{u \in C^{2+\delta}(\overline{\Omega}) : B[u] = 0 \text{ on } \partial\Omega\} \to C^{\delta}(\overline{\Omega})$ are two linear operators defined by

$$\begin{cases} L_1[\tilde{u_i}; d_k] = d_k \Delta + (m - \tilde{u_i}) & \text{for } k \neq i \\ L_2[\tilde{u_i}; d_i] = d_i \Delta + (m - 2\tilde{u_i}) \end{cases}$$

Even though (12) is a coupled system, we will show that it suffices to discuss the sign of principal eigenvalues of $L_1[\tilde{u_i}; d_k]$ $(k \neq i)$ and $L_2[\tilde{u_i}; d_i]$. Since both $m - \tilde{u_i}$ and $m - 2\tilde{u_i}$ lie in $C^{2+\delta}(\overline{\Omega})$, we investigate the eigenvalue problem:

$$\begin{cases} \mu \Delta \phi + h\phi = \lambda \phi & \text{in } \Omega \\ B[\phi] = \partial_n \phi = 0 & \text{on } \partial\Omega \end{cases}$$

[4] We note that Theorem 1.7 deals with the case $N = 2$, not general N.

for any given $\mu > 0$ and $h \in C^{2+\delta}(\overline{\Omega})$.

By Lemma 1.4, we denote the principal eigenvalue of $L_1[\tilde{u}_i; d_k]$ by $\lambda(m - \tilde{u}_i, d_k)$, and the principal eigenvalue of $L_2[\tilde{u}_i; d_i]$ by $\lambda(m - 2\tilde{u}_i, d_i)$. The following lemmas provide more characterizations of the principal eigenvalues:

***Lemma* 2.1.** *(c.f.[9]) $\lambda(h, \mu)$ satisfies the following properties*

(a) $\lambda(h, \mu)$ is continuous and non-increasing in μ, and strictly decreasing in μ if h is not a constant function.

(b) If $h_1(x) \geq h_2(x)$ for all $x \in \Omega$, then $\lambda(h_1, \mu) \geq \lambda(h_2, \mu)$. Strict inequality occurs if $h_1(x) \neq h_2(x)$ for some $x \in \Omega$.

Proof. Put $\alpha = 0$ and $m = h$ into (6), we have

$$\sigma(h, \mu) = \inf_{\phi \in H^1(\overline{\Omega}), \phi \neq 0} \frac{\mu \int_\Omega |\nabla \phi|^2 dx - \int_\Omega h \phi^2 dx}{\int_\Omega \phi^2 dx}$$

hence (a) and (b) follow immediately. □

***Lemma* 2.2.** *(c.f.[1])*

$$\lambda(m - \tilde{u}_i, d_k) \begin{cases} > 0 & \text{if } i > k \\ < 0 & \text{if } i < k \end{cases}$$

$$\lambda(m - 2\tilde{u}_i, d_i) < 0 \text{ for } i = 1, 2, ...N$$

L_1, L_2 have bounded inverses whenever the corresponding principal eigenvalue is less than zero, and $(-L_1)^{-1}$, $(-L_2)^{-1}$ are positive operators in the sense that $v \geq 0$ implies $(-L_1)^{-1}v \geq 0$ and $(-L_2)^{-1}v \geq 0$, and the inequalities are strict if $v \neq 0$ somewhere in Ω.

Proof. By definition, $\tilde{u}_i$ is a positive function that satisfies

$$d_i \Delta \tilde{u}_i + \tilde{u}_i(m - \tilde{u}_i) = 0$$

hence $\tilde{u}_i$ is the principal eigenfunction with the corresponding principal eigenvalue $\lambda(m - \tilde{u}_i, d_i) = 0$. Since $d_i > d_k$ for $i > k$, Lemma 2.1(a) implies $\lambda(m - \tilde{u}_i, d_k) > \lambda(m - \tilde{u}_i, d_i) = 0$. The case $i < k$ follows similarly. Also, Lemma 2.1(b) implies

$\lambda(m-2\tilde{u}_i, d_i) < \lambda(m-\tilde{u}_i, d_i) = 0$.

To prove the second assertion, we apply the Schauder interior estimates (ref.[10], Theorem 6.2) to get a constant $c>0$ which is independent of u such that

$$\|u\|_{C^{2+\delta}(\Omega)} \leq c(\|L_i\|_{C^\delta(\Omega)} + \|u\|_{C^\delta(\Omega)}) \text{ (i=1,2)}$$

Now that $C^{2+\delta} \overset{compact}{\hookrightarrow} C^\delta$ and 0 is not an eigenvalue of L_i whenever the corresponding principal eigenvalue is less than zero, by the Fredholm alternative (ref.[10], Theorem 5.3), L_i^{-1} exists and it is bounded. The positivity of $(-L_1)^{-1}$ and $(-L_2)^{-1}$ follows from maximum principles (ref.[12], Lemma 14.3 and Theorem 16.6). □

Theorem 2.3. *(c.f.[1])* $U_1(x)$ *is hyperbolic and locally asymptotically stable, whereas* $U_i(x)$ *for* $i \geq 2$ *is unstable. Except the zero function, there are no other equlibria in the biological feasible region* $K^+ = \{u \in C^{2+\delta}(\overline{\Omega}) : u \geq 0\}$

Proof. For fixed i and $1 \leq i \leq N$, it is biologically reasonable to consider the linearized system of (11) around $U_i(x)$ in K^+; thus we consider (12):

$$\begin{cases} \dfrac{\partial v_i}{\partial t} = L_2[\tilde{u}_i; d_i]v_i - \tilde{u}_i \displaystyle\sum_{j \neq i} v_j & \\ \dfrac{\partial v_k}{\partial t} = L_1[\tilde{u}_i; d_k]v_k & \text{for } k \neq i \end{cases}$$

with $v_k \geq 0$ for $k \neq i$. It is known that the local stability can be determined by the spectrum of the linearized system (ref. [15], Theorem 4.2). Since

$$L_2[\tilde{u}_i; d_i]v_i - \tilde{u}_i \sum_{j \neq i} v_j \leq L_2[\tilde{u}_i; d_i]v_i$$

we can conclude that the largest real parts of eigenvalues of the linearized system is smaller than

$$\max\{\lambda(m-\tilde{u}_i, d_k), \lambda(m-2\tilde{u}_i, d_i) : k \neq i\}$$

If $i=1$, then all eigenvalues have negative real parts by Lemma 2.2. Consequently, $U_1(x)$ is hyperbolic and locally aymptotically stable. If $i \geq 2$, then $\lambda(m-\tilde{u}_i, d_{i-1}) > 0$, which implies the unstability.

Suppose that the final assertion of the theorem is false; hence another nonzero equilibrium exists in K^+. By a rearrangement of indices if necessary, the equilibrium can be of the form $(u'_1, u'_2, ..., u'_i, 0, ..., 0)$, $2 \leq i \leq N$ and $u_j \geq 0$ is not identically zero for all $1 \leq j \leq i$. Put the equilibrium into the system (11), we get

$$d_j \Delta u'_j + u'_j (m - \sum_{k=1}^{i} u'_k) = 0$$

for all $1 \leq j \leq i$; hence $\lambda(m - \sum_{k=1}^{i} u'_k, d_j) = 0$ for all $1 \leq j \leq i$. But $\sum_{k=1}^{i} u'_k$ is not a constant function; hence Lemma 2.1(b) implies

$$0 = \lambda(m - \sum_{k=1}^{i} u'_k, d_i) < \lambda(m - \sum_{k=1}^{i} u'_k, d_{i-1}) = 0$$

which is a contradiction. □

Proof of Theorem 1.1

Proof. The part (a) follows from Theorem 2.3. The part (b) follows from Theorem 2.3 and Theorem 1.9. □

An Interlude: Type A Under Effects of Mutation

In this subsection, the genetics of N species or N different phenotypes of the same species are assumed to be *haploid*; hence their process of mutation is simple enough that we can take the effects of mutation into account:

$$\begin{cases} \dfrac{\partial u_i}{\partial t} = d_i \Delta u_i + u_i (m - \sum_{j=1}^{N} u_j) + \epsilon \sum_{j=1} M_{ij} u_j & \text{in } \Omega \times (0, \infty) \\ B[u_i] = \partial_n u_i = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases} \tag{13}$$

where $M_{ij} u_j$ is the density converted from u_j into u_i via mutation. The effects of mutation is represented by the *mutation matrix* $M = [M_{ij}]_{N \times N}$. Even though it is believed that mutation happens randomly, but for mathematical simplicity, we assume that M is a constant matrix satisfying:

$$M_{ij} \begin{cases} < 0 & \text{if } i = j \quad \text{self-mutation is harmful} \\ \geq 0 & \text{if } i \neq j \end{cases}$$

and we focus on the case of small mutation rate $0 < \epsilon \ll 1$.

What are behaviors of semi-trivial equilibria under effects of mutation? A standard method is to utilize the implicit function theorem to describe the perturbation of $U_i(x)$, but ***the fairly interesting part is to show that after perturbation*** $U_1(x)$ ***still lies in the biological feasible region*** K^+***, even in*** $intK^+$.

For notational correctness, we consider u as *column vectors*. To utilize the implicit function theorem, we define the operator $F : \mathbb{D}^N \times \mathbb{R} \to [C^\delta(\overline{\Omega})]^N$ by

$$F(u, \epsilon) = D(\Delta u) + u(m - \mathbf{1} \cdot u) + \epsilon M u$$

where $D = diag[d_1, d_2, ..., d_N]$ and $\mathbf{1} = [1, 1, ..., 1]^T$. Equilibria of the perturbed system (13) are solutions of $F(u, \epsilon) = 0$, and we try to solve u in terms of ϵ such that $F(u(\epsilon), \epsilon) = 0$ for all small $\epsilon > 0$. The Frechét derivative of F at $(U_1(x), 0)$ is the linear operator $L : \mathbb{D}^N \to [C^\delta(\overline{\Omega})]^N$ given by

$$L[u] = D(\Delta u) + u(m - \mathbf{1} \cdot U_1) - (\mathbf{1} \cdot u)U_1 \tag{14}$$

The components of L are

$$\begin{cases} (L[u])_1 = L_2[\tilde{u_1}; d_1]u_1 - \sum_{j=2}^{N} \tilde{u_1} u_j \\ (L[u])_i = L_1[\tilde{u_1}; d_i]u_i \qquad \text{for } i \geq 2 \end{cases}$$

hence L can be written as

$$L = \begin{bmatrix} L_2[\tilde{u_1}; d_1] & -\tilde{u_1} & \dots & -\tilde{u_1} & -\tilde{u_1} \\ 0 & L_1[\tilde{u_1}; d_2] & \dots & 0 & 0 \\ \vdots & & & & \vdots \\ 0 & 0 & \dots & L_1[\tilde{u_1}; d_{N-1}] & 0 \\ 0 & 0 & \dots & 0 & L_1[\tilde{u_1}; d_N] \end{bmatrix}$$

Similar arguments of Lemma 2.2 can prove that L has a bounded inverse, but the structure of L^{-1} can be described explicitly:

$$-L^{-1} = \begin{bmatrix} -L_2^{-1} & -L_2^{-1}(\tilde{u_1} L_1^{-1}[\tilde{u_1}; d_2]) & \dots & -L_2^{-1}(\tilde{u_1} L_1^{-1}[\tilde{u_1}; d_N]) \\ 0 & -L_1^{-1}[\tilde{u_1}; d_2] & \dots & 0 \\ \vdots & & & \vdots \\ 0 & 0 & \dots & 0 \\ 0 & 0 & \dots & -L_1^{-1}[\tilde{u_1}; d_N] \end{bmatrix} \tag{15}$$

where $-L_2^{-1} = -L_2^{-1}[\tilde{u_1}; d_1]$. By Lemma 2.2, each diagonal entry of $-L^{-1}$ is a positive operator and other nonzero off-diagonal entry is a bounded operator.

Theorem 2.4. *(c.f.[1]) There exists* $\epsilon_0 > 0$ *such that the perturbed system (13) has an equilibrium* $U_1(x;\epsilon) \in [C^{2+\delta}(\overline{\Omega})]^N$ *for* $0 < \epsilon < \epsilon_0$ *with* $U_1(x;0) = U_1(x)$*, and* $U_1(x;\cdot)$ *is real analytic, hyperbolic and locally asymptotically stable.*

Proof. (c.f.[11], p.15) F is linear in ϵ, quadratic in u, and it has partial Frechét derivatives up to infinitely many order of which power series converges in some neighborhood of $(U_1, 0)$; hence F is analytic. We define $G : \mathbb{D}^N \times \mathbb{R} \to [C^\delta(\overline{\Omega})]^N$ by

$$G(u,\epsilon) = u - L^{-1}F(u,\epsilon)$$

then G is analytic and $G(U_1, 0) = U_1$. Let $D_uG(u,\epsilon)$ be the partial Frechét derivative of G at (u,ϵ), then $D_uG(U_1,0) = 0$; thus there exists $0 < \kappa < 1$ such that $\|D_uG(u,\epsilon)\| \leq \kappa$ in some neighborhood of $(U_1, 0)$. By the Contraction Mapping Theorem, some $\epsilon_0 > 0$ exists such that there exists $f : (0,\epsilon_0) \to [C^{2+\delta}(\overline{\Omega})]^N$ which is analytic and satisfies $f(0) = U_1$, and $F(f(\epsilon),\epsilon) = 0$. Denote $f(\epsilon) = U_1(\cdot;\epsilon)$, and from Theorem 2.3 we can choose smaller $\epsilon_0 > 0$ to maintain the local stability and hyperbolicity. □

To ensure $U_1(\epsilon)$ ($\equiv U_1(x;\epsilon)$) has any biological meaning, we must show that it lies in K^+. Since $\tilde{u_1}(x) > 0$ in $\overline{\Omega}$, it suffices to prove the other i-th ($i \geq 2$) components of $U_1(\epsilon)$ remain non-negative under the perturbation. Define $\widehat{U}(\epsilon) = U_1(\epsilon) - U_1$ and fix i with $2 \leq i \leq N$. To investigate the Taylor series of $\widehat{U}(\epsilon)$, we put $\widehat{U}(\epsilon)$ into (14) to get

$$\begin{aligned}
L\widehat{U}(\epsilon) &= D\Delta[U_1(\epsilon) - U_1] + [m - \mathbf{1}\cdot U_1][U_1(\epsilon) - U_1] - \{\mathbf{1}\cdot[U_1(\epsilon) - U_1]\}U_1 \\
&= D\Delta U_1(\epsilon) + [m - \mathbf{1}\cdot U_1(\epsilon)]U_1(\epsilon) + \epsilon M U_1(\epsilon) - \epsilon M U_1(\epsilon) + [\mathbf{1}\cdot\widehat{U}(\epsilon)]\widehat{U}(\epsilon) \\
&= -\epsilon M[U_1 + \widehat{U}(\epsilon)] + [\mathbf{1}\cdot\widehat{U}(\epsilon)]\widehat{U}(\epsilon)
\end{aligned}$$

Denote $\partial_\epsilon^k \widehat{U}(0) = \dfrac{\partial^k \widehat{U}(\epsilon)}{\partial \epsilon^k}|_{\epsilon=0}$. A direct computation and induction show

$$\begin{cases}
L\partial_\epsilon^1 \widehat{U}(0) = -MU_1 \\
L\partial_\epsilon^k \widehat{U}(0) = \displaystyle\sum_{j=1}^{k-1}[\mathbf{1}\cdot\partial_\epsilon^{k-j}\widehat{U}(0)]\partial_\epsilon^j\widehat{U}(0) - kM\partial_\epsilon^{k-1}\widehat{U}(0) \quad \text{for } k \geq 2
\end{cases}$$

Since L^{-1} exists, we substitute backward to obtain $\partial_\epsilon^1 \widehat{U}(0) = (-L^{-1}M)U_1$ and

$$\partial_\epsilon^k \widehat{U}(0) = k!(-L^{-1}M)^k U_1 + \text{ lower order term in } (-L^{-1}M)$$

If the principal term is of order k, then $[\partial_\epsilon^j \widehat{U}(0)]_i = 0$ for $j = 1, ..., k-1$. From the special form of $-L^{-1}$ (see (15)) and $U_1(x) = (\tilde{u_1}(x), 0, ..., 0)$, we observe

$$[\partial_\epsilon^k \widehat{U}(0)]_i \neq 0 \text{ if and only if } [M\partial_\epsilon^{k-1}\widehat{U}(0)]_i \neq 0 \text{ if and only if } [M^k U_1]_i \neq 0$$

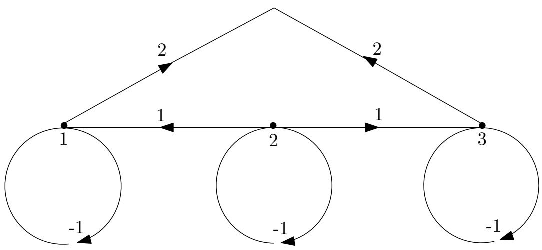
hence the sign of the principal term is determined by the $(i, 1)$-entry of M^k, denoted by $[M^k]_{i1}$, which is characterized by the following lemma:

***Lemma* 2.5.** *(c.f.[1]) For each i with $2 \leq i \leq N$, there are two possibilities: either $[M^k]_{i1} = 0$ for all $k \geq 1$ or there exists $p = p(i)$ with $1 \leq p(i) \leq N-1$ such that*

$$[M^k]_{i1} \begin{cases} = 0 & \text{if } 1 \leq k < p \\ > 0 & \text{if } k = p \end{cases}$$

Proof. [5] Suppose that $[M^j]_{i1} \neq 0$ for some j, then we can always choose $p = p(i)$ such that $[M^k]_{i1} = 0$ for $1 \leq k < p$ and $[M^p]_{i1} \neq 0$. If $p \geq N$, then by the Cayley-Hamilton theorem, $[M^k]_{i1} = 0$ for all $k \geq 1$, which is a contradiction. If $1 \leq p \leq N-1$, then we must utilize the structure of M to guarantee $[M^p]_{i1} > 0$.

Define an *oriented-graph* on the vertices $\{1, 2, ..., N\}$ as following: Two vertices i and j are connected by an oriented-path $p_{i,j}$ started from i into j if $M_{ij} \neq 0$, and we define M_{ij} to be the weight on $p_{i,j}$. An example is given by



and its corresponding matrix is

$$\begin{bmatrix} -1 & 0 & 2 \\ 1 & -1 & 1 \\ 2 & 0 & -1 \end{bmatrix}$$

[5]The fairly simple and beautiful proof comes from Y. J. Cheng: R97221014@ntu.edu.tw

Let $P_{j_0,j_k} : p_{j_0,j_1} \to p_{j_1,j_2} \to ... \to p_{j_{k-1},j_k}$ be a total oriented-path of length $|P_{j_0,j_k}| = k$ connecting j_0 and j_k. Define the weight of P_{j_0,j_k} as $\omega(P_{j_0,j_k}) = M_{j_0 j_1} M_{j_1 j_2} ... M_{j_{k-1} j_k}$, then an inductive argument shows that

$$[M^k]_{i1} = \sum_{|P_{i,1}|=k} \omega(P_{i,1})$$

Let $p = p(i)$ be the *least length* of total oriented-paths connecting i and 1, then $[M_k]_{i1} = 0$ for all $1 \leq k < p$, but each of them has no cycles $p_{r,r}$ $(r = 1, ..., N)$ of which weight is negative. Consequently, $[M^p]_{i1} > 0$. $\square$

Lemma 2.5 implies that either $[\partial_\epsilon^k \widehat{U}(0)]_i = 0$ for all $k \geq 1$ or $[\partial_\epsilon^j \widehat{U}(0)]_i = 0$ for $1 \leq j < p$ and $[\partial_\epsilon^p \widehat{U}(0)]_i = p![(-L^{-1}M)^p U_1]_i > 0$ *which is independent of* ϵ. Thus, we have proved the following theorem which concludes that $U_1(x;\epsilon)$ lies in K^+, even in $intK^+$ under the effects of small mutation.

***Theorem* 2.6.** *(c.f.[1]) Let* $\widehat{U}(\epsilon) = U_1(\epsilon) - U_1$*, and fix* i *with* $2 \leq i \leq N$*, then for* $0 < \epsilon < \epsilon_0$*, either* $\widehat{U}(\epsilon)_i = 0$ *in* $\overline{\Omega}$ *or*

$$\widehat{U}(\epsilon)_i = \epsilon^{p(i)} v_i(x) + O(\epsilon^{p(i)+1})$$

where $v_i(x) > 0$ *for all* $x \in \overline{\Omega}$.

3 The Main Result of Type B

In Type B, there are two competing species and only the 1st species pursues more favorable habitats; hence the full system (2) becomes

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot (\mu \nabla u - \alpha u \nabla m) + u(m-u-v) & \text{in } \Omega \times (0,\infty) \\ \dfrac{\partial v}{\partial t} = \nu \Delta v + v(m-u-v) & \text{in } \Omega \times (0,\infty) \\ B[u] = \mu \partial_n u - \alpha u \partial_n m = 0, B[v] = \partial_n v = 0 & \text{on } \partial\Omega \times (0,\infty) \end{cases} \tag{16}$$

and the scalar equation (3) becomes

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot (\mu \nabla u - \alpha u \nabla m) + u(m-u) & \text{in } \Omega \times (0,\infty) \\ B[u] = \mu \partial_n u - \alpha u \partial_n m = 0 & \text{on } \partial\Omega \times (0,\infty) \end{cases} \tag{17}$$

$$\begin{cases} \dfrac{\partial v}{\partial t} = \nu \Delta v + v(m-v) & \text{in } \Omega \times (0,\infty) \\ B[v] = \partial_n v = 0 & \text{on } \partial\Omega \times (0,\infty) \end{cases} \tag{18}$$

We note that for each $\alpha \geq 0$ and $\mu, \nu > 0$, Theorem 1.6 guarantees the existence and uniqueness of the positive steady-state $\tilde{u} \equiv \tilde{u}(\alpha,\mu) \equiv \theta(\cdot;\alpha,\mu)$ of (17), $\tilde{v} \equiv \tilde{v}(\nu) \equiv \theta(\cdot;0,\nu)$ of (18) respectively, and each of them is a global attractor among all non-negative and not identically zero continuous initial data.

To determine the local stability, we know from Theorem 1.7 that the semi-trivial equilibrium $(\tilde{u}, 0)$ is locally stable/unstable if and only if the principal eigenvalue of the problem

$$\begin{cases} \nu \Delta \psi + \psi(m - \tilde{u}) = \sigma \psi & \text{in } \Omega \\ B[\psi] = \partial_n \psi = 0 & \text{on } \partial\Omega \end{cases} \tag{19}$$

is negative/positive. Similarly, $(0, \tilde{v})$ is locally stable/unstable if and only if the principal eigenvalue of the problem

$$\begin{cases} \nabla \cdot (\mu \nabla \phi - \alpha \phi \nabla m) + \phi(m - \tilde{v}) = \tau \phi & \text{in } \Omega \\ B[\phi] = \mu \partial_n \phi - \alpha \phi \partial_n m = 0 & \text{on } \partial\Omega \end{cases}$$

or the equivalent form by taking $\phi \mapsto e^{-(\alpha/\mu)m}\phi$

$$\begin{cases} \mu \Delta \phi + \alpha \nabla \phi \cdot \nabla m + \phi(m - \tilde{v}) = \tau \phi & \text{in } \Omega \\ B[\phi] = \partial_n \phi = 0 & \text{on } \partial\Omega \end{cases} \tag{20}$$

is negative/positive. In the subsequent analysis, we always consider the equivalent form because it is equipped with the Neumann boundary condition.

How can we investigate the effects of diffusion and small advective tendency on the evolution of competition? The main idea is to examine the results by the *perturbation analysis* of parameters (α, μ, ν) in (16) from $(0, \mu_0, \mu_0)$ for some $\mu_0 > 0$. For readers' convenience, we collect a version of the implicit function theorem (ref. [8], Theorem 3.5) :

***Theorem* 3.1.** *(c.f.[8]) Let X, Y and Z be Banach spaces and $F : U \subset X \times Y \to Z$ where U is an open subset. Suppose $F(x, y)$ and $F_y(x, y)$ are continuous in U and $F(x_0, y_0) = 0$ for some $(x_0, y_0) \in U$. If the linear map $F_y(x_0, y_0) : Y \to Z$ has a continuous inverse, then some neighborhood V of x_0 exists such that for each $x \in V$, there exists a unique $y(x) \in Y$ satisfying $F(x, y(x)) = 0$ and the mapping $x \mapsto y(x)$ is differentiable.*

***Lemma* 3.2.** *(c.f.[3]) Suppose that $\alpha_0 \geq 0$ and μ_0, $\nu_0 > 0$. The map from $\mathbb{R}^2$ to $C^{2+\delta}(\overline{\Omega})$ given by $(\alpha, \mu) \mapsto \tilde{u}(\alpha, \mu)$ is differentiable in some neighborhood of (α_0, μ_0). The map from $\mathbb{R}$ to $C^{2+\delta}(\overline{\Omega})$ given by $\nu \mapsto \tilde{v}(\nu)$ is differentiable in some neighborhood of ν_0. Let $\sigma_0(\alpha, \mu, \nu)$ and $\tau_0(\alpha, \mu, \nu)$ be the principal eigenvalues of (19) and (20) respectively, then $\sigma_0(\alpha, \mu, \nu)$, $\tau_0(\alpha, \mu, \nu)$ and their corresponding normalized eigenfunctions depend differentiably on α, μ, and ν in some neighborhood of (α_0, μ_0, ν_0).*

Proof. The main idea is to utilize Theorem 3.1 via comparison of principal eigenvalues. To show that $\tilde{u}$ depends differentiably on α and μ, we set $\tilde{w} = e^{-(\alpha/\mu)m}\tilde{u}$ in (17) and multiply $e^{(\alpha/\mu)m}$, then

$$\begin{cases} \mu\nabla \cdot (e^{(\alpha/\mu)m}\nabla\tilde{w}) + e^{(\alpha/\mu)m}\tilde{w}(m - e^{(\alpha/\mu)m}\tilde{w}) = 0 & \text{in } \Omega \\ B[\tilde{w}] = \partial_n \tilde{w} = 0 & \text{on } \partial\Omega \end{cases}$$

Define $Y = \{w \in C^{2+\delta}(\overline{\Omega}) : \partial_n w = 0 \text{ on } \partial\Omega\}$ and $F : \mathbb{R} \times \mathbb{R} \times Y \to C^{\delta}(\overline{\Omega})$ by

$$F(\alpha, \mu, w) = \mu\nabla \cdot (e^{(\alpha/\mu)m}\nabla w) + e^{(\alpha/\mu)m}w(m - e^{(\alpha/\mu)m}w)$$

For any $v \in Y$, we calculate

$$D_w F(\alpha, \mu, w)v = \frac{d}{d\epsilon}F(\alpha, \mu, w + \epsilon v)|_{\epsilon=0} = \mu\nabla \cdot (e^{(\alpha/\mu)m}\nabla v) + e^{(\alpha/\mu)m}v(m - 2e^{(\alpha/\mu)m}w)$$

To show that $D_wF(\alpha_0, \mu_0, \tilde{w})$ is invertible, we must prove that for any $h(x) \in C^\delta(\overline{\Omega})$, the equation for $v \in Y$

$$\mu_0 \nabla \cdot (e^{(\alpha_0/\mu_0)m} \nabla v) + e^{(\alpha_0/\mu_0)m} v(m - 2e^{(\alpha_0/\mu_0)m} \tilde{w}) = h(x) \text{ in } \Omega$$

has a unique solution. Since $F(\alpha_0, \mu_0, \tilde{w}) = 0$ implies that $\psi = \tilde{w}$ is the positive solution of the eigenvalue problem

$$\begin{cases} \mu_0 \nabla \cdot (e^{(\alpha_0/\mu_0)m} \nabla \psi) + e^{(\alpha_0/\mu_0)m} \psi(m - e^{(\alpha_0/\mu_0)m}) = \lambda \psi & \text{in } \Omega \\ B[\psi] = \partial_n \psi = 0 & \text{on } \partial\Omega \end{cases}$$

with $\lambda = 0$; hence the principal eigenvalue $\lambda_1 = 0$. By the variational characterization of principal eigenvalues (8), the fact $m - 2e^{(\alpha_0/\mu_0)m}\tilde{w} < m - e^{(\alpha_0/\mu_0)m}\tilde{w}$ implies that the eigenvalue problem

$$\begin{cases} \mu_0 \nabla \cdot (e^{(\alpha_0/\mu_0)m} \nabla \psi) + e^{(\alpha_0/\mu_0)m} \psi(m - 2e^{(\alpha_0/\mu_0)m}) = \lambda^* \psi & \text{in } \Omega \\ B[\psi] = \partial_n \psi = 0 & \text{on } \partial\Omega \end{cases}$$

has the principal eigenvalue $\lambda_1^* < \lambda_1 = 0$; hence all other eigenvalues have negative real parts. Now that 0 lies in the resolvent set of $D_wF(\alpha_0, \mu_0, \tilde{w})$, we can conclude that $D_wF(\alpha_0, \mu_0, \tilde{w})$ has a continuous inverse; hence the differentiable dependence of $\tilde{u}$ on α and μ follows from Theorem 3.1. The proof for the differentiable dependence of $\tilde{v}$ on μ is an analogy.

However, the proof for the differentiable dependences of σ_0 and τ_0 on α, μ and ν need some modification. Multiplying (20) by $e^{(\alpha/\mu)m}$ yields

$$\begin{cases} \mu \nabla \cdot (e^{(\alpha/\mu)m} \nabla \phi) + e^{(\alpha/\mu)m} \phi(m - \tilde{v}) = \tau e^{(\alpha/\mu)m} \phi & \text{in } \Omega \\ B[\phi] = \partial_n \phi = 0 & \text{on } \partial\Omega \end{cases}$$

Define $G : (\mathbb{R}^2 \times Y) \times (Y \times \mathbb{R}) \to C^\delta(\overline{\Omega}) \times \mathbb{R}$ by

$$G(\alpha, \mu, \tilde{v}, \phi, \tau) = (\mu \nabla \cdot (e^{(\alpha/\mu)m} \nabla \phi) + e^{(\alpha/\mu)m} \phi(m - \tilde{v}) - \tau e^{(\alpha/\mu)m} \phi, \int_\Omega e^{(\alpha/\mu)m} \phi^2 dx - 1)$$

The linearization of G with respect to ϕ and τ is $D_{(\phi,\tau)}G(\alpha, \mu, \tilde{v}, \phi, \tau)(v, \rho) =$

$$(\mu \nabla \cdot (e^{(\alpha/\mu)m} \nabla v) + e^{(\alpha/\mu)m} v(m - \tilde{v}) - \tau e^{(\alpha/\mu)m} v - \rho e^{(\alpha/\mu)m} \phi, 2 \int_\Omega e^{(\alpha/\mu)m} \phi v dx)$$

where $(v, \rho) \in Y \times \mathbb{R}$. Let $\tau_0^* = \tau_0(\alpha_0, \mu_0, \nu_0)$ and $\tilde{v} = \tilde{v}(\nu_0)$. To show that $D_{(\phi,\tau)}G(\alpha_0, \mu_0, \tilde{v}, \phi_0, \tau_0^*)$ is invertible, we should prove that for any $(g, r) \in C^\delta(\overline{\Omega}) \times \mathbb{R}$, the equations

$$\begin{cases} \mu_0 \nabla \cdot (e^{(\alpha_0/\mu_0)m} \nabla v) + e^{(\alpha_0/\mu_0)m} v(m - \tilde{v}) - \tau_0^* e^{(\alpha_0/\mu_0)m} v - \rho e^{(\alpha_0/\mu_0)m} \phi_0 = g(x) \\ 2 \int_\Omega e^{(\alpha_0/\mu_0)m} \phi_0 v dx = r \end{cases} \tag{21}$$

in Ω have a unique solution $(v, \rho) \in Y \times \mathbb{R}$. By a special version of the Fredholm alternative (ref.[8], Theorem 1.10), $v \in Y$ can be solved for given $g \in C^\delta(\overline{\Omega})$ if

$$\int_\Omega (\rho e^{(\alpha_0/\mu_0)m} \phi_0 + g) \phi_0 dx = 0$$

We normalize ϕ_0 as $\int_\Omega e^{(\alpha_0/\mu_0)m} \phi_0^2 dx = 1$, then ρ is uniquely determined by $\rho = -\int_\Omega \phi_0 g dx$. To show that v is uniquely determined, we observe that v has the form $v = v_0 + s\phi_0$ where v_0 is a given particular solution of the first equation of (21) and $s \in \mathbb{R}$. Substituting this form into the second equation of (21) and utilizing the normalization of ϕ_0 yield

$$2 \int_\Omega e^{(\alpha_0/\mu_0)m} \phi_0 v_0 dx + 2s = r$$

hence s is uniquely determined by $s = r/2 - \int_\Omega e^{(\alpha_0/\mu_0)m} \phi_0 v_0 dx$. By the Schauder interior estimates (ref.[10], Theorem 6.2) the solution mapping from (g, r) to (v, ρ) is continuous; thus the differentiable dependence of τ_0 on α, μ and ν follows from Theorem 3.1. The proof for the differentiable dependence of σ_0 on α, μ and ν is an analogy. □

When $(\alpha, \mu, \nu) = (0, \mu_0, \mu_0)$, we know $\tilde{u} = \tilde{v} = \theta$ where θ is the unique positive steady-state of

$$\begin{cases} \mu_0 \Delta \theta + \theta(m - \theta) = 0 & \text{in } \Omega \\ B[\theta] = \partial_n \theta = 0 & \text{on } \partial\Omega \end{cases} \tag{22}$$

By Lemma 3.2, we let $(\alpha, \mu, \nu) = (\alpha(s), \mu(s), \nu(s))$ where $\alpha(s)$, $\mu(s)$, and $\nu(s)$ are differentiable functions in a neighborhood of 0 with $(\alpha(0), \mu(0), \nu(0)) = (0, \mu_0, \mu_0)$. When $s = 0$, $\psi = p_0\theta$ is a positive solution of (19) with $\sigma = 0$ and $\psi = p_0\theta$ is a positive solution of the equivalent form (20) with $\tau = 0$ where p_0 is any positive constant; hence $\sigma_0(0, \mu_0, \mu_0) = \tau_0(0, \mu_0, \mu_0) = 0$. To be consistent with Lemma 3.2, we choose $p_0 = 1/\int_\Omega \theta^2 dx$ and require that the eigenfunctions ψ_0 and ϕ_0 corresponding to σ_0 and τ_0 respectively satisfy

$$\int_\Omega \psi_0^2 dx = 1, \quad \int_\Omega e^{(\alpha/\mu)m} \phi_0^2 dx = 1$$

We express the parameters (α, μ, ν), the positive steady-state $\tilde{u}$ and $\tilde{v}$, the principal eigenvalues σ_0 and τ_0, and the normalized eigenfunctions ψ_0 and ϕ_0 as

$$\alpha = 0 + \alpha_1 s + o(s), \ \mu = \mu_0 + \mu_1 s + o(s), \ \nu = \mu_0 + \nu_1 s + o(s)$$

$$\tilde{u} = \theta + u_1 s + o(s), \ \tilde{v} = \theta + v_1 s + o(s)$$

$$\sigma_0 = 0 + \sigma_1 s + o(s), \ \tau_0 = 0 + \tau_1 s + o(s)$$

$$\psi_0 = p_0\theta + \psi_1 s + o(s), \ \phi_0 = p_0\theta + \phi_1 s + o(s)$$

Substituting the above expressions into (17), (18), (19) and (20), dividing by s and letting $s \to 0$, we obtain the following relations:

$$\mu_1 \Delta\theta + \mu_0 \Delta u_1 - \nabla \cdot (\alpha_1 \theta \nabla m) + u_1(m - 2\theta) = 0 \text{ in } \Omega \tag{23}$$

$$\nu_1 \Delta\theta + \mu_0 \Delta v_1 v_1 + (m - 2\theta) = 0 \text{ in } \Omega \tag{24}$$

$$p_0 \nu_1 \Delta\theta + \mu_0 \Delta\psi_1 + \psi_1(m - \theta) - p_0 u_1 \theta = \sigma_1 p_0 \theta \text{ in } \Omega \tag{25}$$

$$p_0 \mu_1 \Delta\theta + \mu_0 \Delta\phi_1 + \alpha_1 p_0 \nabla\theta \cdot \nabla m + \phi_1(m - \theta) - p_0 v_1 \theta = \tau_1 p_0 \theta \text{ in } \Omega \tag{26}$$

where θ, u_1, v_1, ψ_1 and ϕ_1 satisfy the boundary conditions:

$$\partial_n \theta = \partial_n v_1 = \partial_n \psi_1 = \partial_n \phi_1 = 0, \ \mu_0 \partial_n u_1 - \alpha_1 \theta \partial_n m = 0 \text{ in } \partial\Omega$$

Since the sign of the principal eigenvalue σ_0 (resp. τ_0) is determined by the sign of σ_1 (resp. τ_1), our next goal is to express σ_1 and τ_1 in terms of α_1, μ_1, and ν_1.

Multiplying (25) by θ, integrating over Ω, and utilizing the divergence theorem, we have

$$\int_\Omega \psi_1[\mu_0 \Delta\theta + \theta(m - \theta)]dx - p_0 \nu_1 \int_\Omega |\nabla\theta|^2 dx - p_0 \int_\Omega u_1 \theta^2 dx = p_0 \sigma_1 \int_\Omega \theta^2 dx$$

The first term vanishes according to (22). Dividing by p_0 yields

$$-\nu_1 \int_\Omega |\nabla\theta|^2 dx - \int_\Omega u_1 \theta^2 dx = \sigma_1 \int_\Omega \theta^2 dx \tag{27}$$

To evaluate the second integral in (27), we multiply (23) by θ, integrate over Ω and utilize the divergence theorem and (23), then

$$\int_{\partial\Omega} \theta(\mu_0 \partial_n u_1 - \alpha_1 \theta \partial_n m) ds - \mu_1 \int_\Omega |\nabla\theta|^2 dx + \alpha_1 \int_\Omega \theta \nabla\theta \cdot \nabla m dx = \int_\Omega u_1 \theta^2 dx$$

By the boundary condition of u_1, we have

$$-\mu_1 \int_\Omega |\nabla\theta|^2 dx + \alpha_1 \int_\Omega \theta \nabla\theta \cdot \nabla m dx = \int_\Omega u_1 \theta^2 dx \tag{28}$$

Substituting (28) into (27), we can express σ_1 as

$$\sigma_1 = \frac{(\mu_1 - \nu_1) \int_\Omega |\nabla\theta|^2 dx - \alpha_1 \int_\Omega \theta \nabla\theta \cdot \nabla m dx}{\int_\Omega \theta^2 dx}$$

The process to obtain the expression of τ_0 is roughly analogous. Multiplying (26) by θ, integrating over Ω, utilizing the divergence theorem and (22), and dividing by p_0 yield

$$-\mu_1 \int_\Omega |\nabla\theta|^2 dx + \alpha_1 \int_\Omega \theta \nabla\theta \cdot \nabla m dx - \int_\Omega v_1 \theta^2 dx = \tau_1 \int_\Omega \theta^2 dx$$

Multiplying (24) by θ, integrating over Ω, and utilizing (22) yield

$$-\nu_1 \int_\Omega |\nabla\theta|^2 dx + \alpha_1 \int_\Omega \theta \nabla\theta \cdot \nabla m dx = \int_\Omega v_1 \theta^2 dx$$

Substitution yields

$$\tau_1 = -\sigma_1 = \frac{(\nu_1 - \mu_1) \int_\Omega |\nabla\theta|^2 dx + \alpha_1 \int_\Omega \theta \nabla\theta \cdot \nabla m dx}{\int_\Omega \theta^2 dx} \tag{29}$$

We note that $\nabla\theta$ is not identically zero since $m(x)$ is not a constant function. The signs of σ_1 and τ_1 can be determined and *independent of* θ if we can guarantee that $\int_\Omega \theta \nabla\theta \cdot \nabla m dx$ is always of the same sign. This is not obvious, but the following lemma which may be surprising proves that $\int_\Omega \theta \nabla\theta \cdot \nabla m dx$ is always positive if the shape of the environment is convex.

Lemma 3.3. *(c.f.[3]) Suppose that $\Omega \subset \mathbb{R}^l$ is convex, then* $\int_\Omega \theta \nabla\theta \cdot \nabla m dx > 0$.

Proof. Differentiating the equation [6]

$$\begin{cases} \Delta\theta + \theta(m-\theta) = 0 & \text{in } \Omega \\ B[\theta] = \partial_n \theta = 0 & \text{on } \partial\Omega \end{cases} \tag{30}$$

and taking dot product with $\nabla\theta$, we have

$$\nabla\theta \cdot \nabla(\Delta\theta) + |\nabla\theta|^2(m-2\theta) + \theta\nabla\theta\cdot\nabla m = 0 \text{ in } \Omega$$

A straightforward computation yields the identity

$$\nabla\theta \cdot \nabla(\Delta\theta) + |D^2\theta|^2 = \frac{1}{2}\Delta(|\nabla\theta|^2)$$

hence we have

$$\frac{1}{2}\Delta(|\nabla\theta|^2) - |D^2\theta|^2 + |\nabla\theta|^2(m-2\theta) + \theta\nabla\theta\cdot\nabla m = 0 \text{ in } \Omega \tag{31}$$

Integrating (31) over Ω and utilizing the divergence theorem, we have

$$\int_\Omega \theta\nabla\theta\cdot\nabla m dx = \int_\Omega |D^2\theta|^2 - |\nabla\theta|^2(m-2\theta)dx - \frac{1}{2}\int_{\partial\Omega} \partial_n(|\nabla\theta|^2)ds \tag{32}$$

Since θ is a positive solution of (30); hence the eigenvalue problem

$$\begin{cases} \Delta\phi + \phi(m-\theta) = \lambda\phi & \text{in } \Omega \\ B[\theta] = \partial_n \phi = 0 & \text{on } \partial\Omega \end{cases}$$

has the principal eigenvalue $\lambda_1 = 0$. However, by the variational characterization of the principal eigenvalue, we know

$$\lambda_1 = \sup_{\phi\in H^1(\overline{\Omega}),\phi\neq 0} \frac{\int_\Omega[-|\nabla\phi|^2 + \phi^2(m-\theta)]dx}{\int_\Omega \phi^2 dx}$$

hence

$$\int_\Omega [-|\nabla\phi|^2 + \phi^2(m-\theta)]dx \le \lambda_1 \int_\Omega \phi^2 dx = 0$$

for any $\phi \in H^1(\overline{\Omega})$ and $\phi \neq 0$. Since $\theta \in C^{2+\delta}(\overline{\Omega})$, we have $\theta_{x_i} \in H^1(\overline{\Omega})$ for each i and

$$\int_\Omega [-|\nabla\theta_{x_i}|^2 + \theta_{x_i}^2(m-\theta)]dx \le 0$$

---

[6] θ may not be three-times differentiable, but (32) still holds.

Summing over i yields

$$\int_\Omega [-|D^2\theta|^2 + |\nabla\theta|^2(m-\theta)]dx \le 0$$

Thus, (32) can be rewritten as

$$\begin{aligned}\int_\Omega \theta\nabla\theta\cdot\nabla m dx &= \int_\Omega \theta|\nabla\theta|^2 dx - \frac{1}{2}\int_{\partial\Omega} \partial_n(|\nabla\theta|^2)ds \\ &+ \int_\Omega |D^2\theta|^2 - |\nabla\theta|^2(m-\theta)dx \\ &\ge \int_\Omega \theta|\nabla\theta|^2 dx - \frac{1}{2}\int_{\partial\Omega} \partial_n(|\nabla\theta|^2)ds\end{aligned}$$

which is positive if

$$\int_{\partial\Omega} \partial_n(|\nabla\theta|^2)ds \le 0$$

To prove the above inequality, it suffices to show that $\partial_n(|\nabla\theta|^2) \le 0$ on $\partial\Omega$. Fix $x^* \in \partial\Omega$, and let $x^* = 0$ without any loss of generality. Since Ω is convex, we can choose a local coordinate system, still denoted by x, such that Ω can be expressed by $x_l = f(x_1, ..., x_{l-1})$ where $f(x_1, ..., x_{l-1})$ is a concave function with $f(0) = 0$, $\nabla f(0) = 0$, and $D^2 f(0)$ is non-positive definite. Near $x^* = 0$, the unit outer normal is given by $n = \frac{(-\nabla f, 1)}{\sqrt{1+|\nabla f|^2}}$; hence $\partial_n\theta = 0$ implies $\theta_{x_l} = \sum_{j=1}^{l-1}\theta_{x_j} f_{x_j}$. Differentiating the equation with respect to x_k $(k = 1, ..., l-1)$ and putting $x_1 = ... = x_{l-1} = 0$ yield $\theta_{x_l x_k} = \sum_{j=1}^{l-1}\theta_{x_j}(0) f_{x_j x_k}(0)$. Since $(0, ..., 0, 1)$ is the unit outer normal at $x^* = 0$, we have $\theta_{x_l}(0) = 0$ and

$$\begin{aligned}\partial_n(|\nabla\theta|^2)(0) = (|\nabla\theta|^2)_{x_l}(0) &= 2\sum_{j=1}^{l}\theta_{x_j}(0)\theta_{x_j x_l}(0) = 2\sum_{j=1}^{l}\theta_{x_j}(0)\theta_{x_l x_j}(0) \\ &= 2\sum_{j=1}^{l-1}\theta_{x_j}(0)\sum_{k=1}^{l-1}\theta_{x_k}(0) f_{x_k x_j}(0) + 2\theta_{x_l}(0)\theta_{x_l x_l}(0) \\ &= 2\sum_{j,k=1}^{l-1}\theta_{x_k}(0) f_{x_k x_j}(0)\theta_{x_j}(0) \le 0\end{aligned}$$

□

By (29) and Lemma 3.3, we can derive the following theorem which concludes that $(\tilde{u}, 0)$ is locally stable if α is sufficiently small, but not too small relative to the difference $\mu - \nu$.

***Theorem* 3.4.** *(c.f.[3]) Suppose that $\Omega \subset \mathbb{R}^l$ is convex. Let*

$$(\alpha, \mu, \nu) = (\alpha_1 s + o(s), \mu_0 + \mu_1 s + o(s), \mu_0 + \nu_1 s + o(s))$$

then for sufficiently small $s > 0$, we have

$$\sigma_0(\alpha, \mu, \nu) < 0 < \tau_0(\alpha, \mu, \nu)$$

provided that

$$\alpha_1 > (\mu_1 - \nu_1)\frac{\int_\Omega |\nabla\theta|^2 dx}{\int_\Omega \theta\nabla\theta \cdot \nabla m dx}$$

Theorem 3.4 shows that the quantity $\frac{\int_\Omega |\nabla\theta|^2 dx}{\int_\Omega \theta\nabla\theta \cdot \nabla m dx}$ may play an important role in studying the dynamics of the full system (16). Hence, for $\mu > 0$, since $\nabla\theta$ is not identically zero, its reciprocal

$$\alpha^*(\mu) = \frac{\int_\Omega \theta(x;\mu)\nabla\theta(x;\mu) \cdot \nabla m(x) dx}{\int_\Omega |\nabla\theta(x;\mu)|^2 dx}$$

is always well-defined, and $\alpha^*(\mu) > 0$ if Ω is convex by Lemma 3.3. To determine the global stability of $(\tilde{u}, 0)$, we need to rule out the possibility of positive equilibria.

***Lemma* 3.5.** *(c.f.[4]) Suppose that $m(x)$ is not a constant function. Let $(\alpha, \mu, \nu) = (\alpha_1 s + o(s), \mu_0 + \mu_1 s + o(s), \mu_0 + \nu_1 s + o(s))$. If $\alpha^*(\mu_0) \neq 0$ and $\alpha_1 \neq (\mu_1 - \nu_1)/\alpha^*(\mu_0)$, then the full system (16) has no positive equilibria for sufficiently small $s > 0$.*

***Remark*.** *In Lemma 3.5, Ω is not necessarily convex.*

Proof. Suppose that (16) has a family of positive equilibria $\{(u_s, v_s)\}$ where $s > 0$ is sufficiently small. By *elliptic regularity*, that is, a process consists of an a priori global Schauder estimate (ref.[10], Theorem 6.30), the uniform boundedness of the family in $[C^{2+\delta}(\overline{\Omega})]^2$, and the precompactness result (ref.[10], Lemma 6.36), then passing to a subsequence if necessary, we have $(u_s, v_s) \to (u^*, v^*)$ in $[C^2(\overline{\Omega})]^2$ as $s \to 0$ and $u^*, v^* \geq 0$ in $\overline{\Omega}$ satisfy

$$\begin{cases} \mu_0 \Delta u^* + u^*(m - u^* - v^*) = 0 & \text{in } \Omega \\ \mu_0 \Delta v^* + v^*(m - u^* - v^*) = 0 & \text{in } \Omega \\ B[u^*] = \partial_n u^*, B[v^*] = \partial_n v^* = 0 & \text{on } \partial\Omega \end{cases} \tag{33}$$

hence $u^* + v^*$ satisfies

$$\begin{cases} \mu_0\Delta(u^* + v^*) + (u^* + v^*)[m - (u^* + v^*)] = 0 & \text{in } \Omega \\ B[u^* + v^*] = \partial_n(u^* + v^*) = 0 & \text{on } \partial\Omega \end{cases}$$

(***This is the crucial mathematical reason to assume (C4)***). [7] By the uniqueness of (22), either $u^* + v^* \equiv 0$ or $u^* + v^* \equiv \theta(\cdot; \mu_0)$. If $u^* + v^* \equiv 0$, then $(u_s, v_s) \to (0, 0)$ uniformly in x as $s \to 0$. Setting $\hat{v_s} = v_s/\|v_s\|_{L^\infty(\Omega)}$, by *elliptic regularity*, $\hat{v_s} \to \hat{v}$ in $C^2(\overline{\Omega})$ as $s \to 0$ where $\hat{v} \geq 0$ is not identically zero and satisfies

$$\begin{cases} \mu_0\Delta\hat{v} + m\hat{v} = 0 & \text{in } \Omega \\ B[\hat{v}] = \partial_n\hat{v} = 0 & \text{on } \partial\Omega \end{cases}$$

Multiplying the above equation by $\theta(\cdot; \mu_0)$, integrating over Ω, and utilizing (22) yield $\displaystyle\int_\Omega \theta^2(x; \mu_0)\hat{v}(x)dx = 0$, which is a contradiction. Hence $u^* + v^* \equiv \theta(\cdot; \mu_0)$.

If $u^* \equiv 0$ and $v^* \equiv \theta(\cdot; \mu_0)$, we set $\hat{u_s} = u_s/\|u_s\|_{L^\infty(\Omega)}$, then $\hat{u_s}$ satisfies

$$\begin{cases} \nabla \cdot (\mu\nabla\hat{u_s} - \alpha\hat{u_s}\nabla m) + \hat{u_s}(m - u_s - v_s) = 0 & \text{in } \Omega \\ B[\hat{u_s}] = \mu\partial_n\hat{u_s} - \alpha\hat{u_s}\partial_n m = 0 & \text{on } \partial\Omega \end{cases}$$

By *elliptic regularity*, $\hat{u_s} \to \hat{u}$ in $C^2(\overline{\Omega})$ as $s \to 0$ where $\hat{u} \geq 0$ satisfies $\max\limits_{\overline{\Omega}} \hat{u} = 1$ and

$$\begin{cases} \mu_0\Delta\hat{u} + \hat{u}[m - \theta(\cdot; \mu_0)] = 0 & \text{in } \Omega \\ B[\hat{u}] = \partial_n\hat{u} = 0 & \text{on } \partial\Omega \end{cases}$$

Therefore, $\hat{u} \equiv \theta(\cdot; \mu_0)/\|\theta(\cdot; \mu_0)\|_{L^\infty(\Omega)}$ by the uniqueness of (22).

Since u_s and v_s satisfy

$$\begin{cases} \nabla \cdot (\mu\nabla u_s - \alpha u_s\nabla m) + u_s(m - u_s - v_s) = 0 & \text{in } \Omega \\ \nu\Delta v_s + v_s(m - u_s - v_s) = 0 & \text{in } \Omega \\ B[u_s] = \mu\partial_n u_s - \alpha u_s\partial_n m = 0, B[v_s] = \partial_n v_s = 0 & \text{on } \partial\Omega \end{cases}$$

Multiplying the equation of u_s by v_s, the equation of v_s by u_s, subtracting and integrating over Ω yield

$$\alpha \int_\Omega u_s\nabla v_s \cdot \nabla m dx = (\mu - \nu) \int_\Omega \nabla u_s \cdot \nabla v_s dx \tag{34}$$

[7] Here, we see that the full system (2) has a rather special *"2 in 1" structure*, that is, two equations with the same parameters can be added into one equation.

Dividing both sides by s and $\|u_s\|_{L^\infty(\Omega)}$, we have

$$(\alpha_1 + o(1)) \int_\Omega \hat{u}_s \nabla v_s \cdot \nabla m dx = (\mu_1 - \nu_1 + o(1)) \int_\Omega \nabla \hat{u}_s \cdot \nabla v_s dx$$

Letting $s \to 0$, we obtain

$$\alpha_1 \int_\Omega \theta(x;\mu_0)\nabla\theta(x;\mu_0) \cdot \nabla m(x) dx = (\mu_1 - \nu_1) \int_\Omega |\nabla\theta(x;\mu_0)|^2 dx$$

Hence, $\alpha_1 = (\mu_1 - \nu_1)/\alpha^*(\mu_0)$ which is a contradiction. The case for $v^* \equiv 0$ and $u^* \equiv \theta(\cdot;\mu_0)$ is analogous.

If $u^*, v^* \geq 0$ are not identically zero and satisfy $u^* + v^* \equiv \theta(\cdot;\mu_0)$, then from (33), $(u^*, v^*) = (\kappa\theta(\cdot;\mu_0), (1-\kappa)\theta(\cdot;\mu_0))$ for some $\kappa \in (0,1)$. Dividing (34) by s and letting $s \to 0$, then again $\alpha_1 = (\mu_1 - \nu_1)/\alpha^*(\mu_0)$ which is a contradiction. □

Proof of Theorem 1.2

Proof. By Theorem 3.4, $(\tilde{u}, 0)$ is locally stable, whereas $(0, \tilde{v})$ is unstable. Lemma 3.5 rules out the possibility of positive equilibria; hence $(\tilde{u}, 0)$ is globally aymptotically stable by Theorem 1.9. □

Remark. *We note that the assumption on the convexity in Theorem 1.2 is necessary. In other words, for any $\mu > 0$, we can construct a non-convex domain $\Omega \subset \mathbb{R}^2$ and smooth function $m(x)$ such that $\alpha^*(\mu) < 0$; hence by Theorem 3.4, Lemma 3.5 and Theorem 1.9, $(0, \tilde{v})$ is globally asymptotically stable. See the section 3 of [3] and the section 2.2 of [4].*

4 The Main Result of Type C

In Type C, both competing species move toward more favorable habitats; hence the full system (2) becomes

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot (\mu \nabla u - \alpha u \nabla m) + u(m-u-v) & \text{in } \Omega \times (0,\infty) \\ \dfrac{\partial v}{\partial t} = \nabla \cdot (\nu \nabla v - \beta v \nabla m) + v(m-u-v) & \text{in } \Omega \times (0,\infty) \\ B[u] = \mu \partial_n u - \alpha u \partial_n m = 0, B[v] = \nu \partial_n v - \beta v \partial_n m = 0 & \text{on } \partial\Omega \times (0,\infty) \end{cases} \tag{35}$$

and the scalar equation (3) becomes

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot (\mu \nabla u - \alpha u \nabla m) + u(m-u) & \text{in } \Omega \times (0,\infty) \\ B[u] = \mu \partial_n u - \alpha u \partial_n m = 0 & \text{on } \partial\Omega \times (0,\infty) \end{cases} \tag{36}$$

$$\begin{cases} \dfrac{\partial v}{\partial t} = \nabla \cdot (\nu \nabla v - \beta v \nabla m) + v(m-v) & \text{in } \Omega \times (0,\infty) \\ B[v] = \nu \partial_n v - \beta v \partial_n m = 0 & \text{on } \partial\Omega \times (0,\infty) \end{cases} \tag{37}$$

We note that for each $\alpha, \beta \geq 0$ and $\mu, \nu > 0$, Theorem 1.6 guarantees the existence and uniqueness of the positive steady-state $\theta(\cdot;\alpha,\mu)$ of (36), $\theta(\cdot;\beta,\nu)$ of (37) respectively, and each of them is a global attractor among all non-negative and not identically zero continuous initial data.

To determine the local stability, we know from Theorem 1.7 that the semi-trivial equilibrium $(\theta(x;\alpha,\mu),0)$ is locally stable/unstable if and only if the principal eigenvalue σ_1 of the problem

$$\begin{cases} \nabla \cdot (\nu \nabla \psi - \beta \psi \nabla m) + \psi[m - \theta(\cdot;\alpha,\mu)] = \sigma \psi & \text{in } \Omega \\ B[\psi] = \nu \partial_n \psi - \beta \psi \partial_n m = 0 & \text{on } \partial\Omega \end{cases} \tag{38}$$

is negative/positive. Similarly, $(0,\theta(x;\beta,\nu))$ is locally stable/unstable if and only if the principal eigenvalue τ_1 of the problem

$$\begin{cases} \nabla \cdot (\mu \nabla \phi - \alpha \phi \nabla m) + \phi[m - \theta(\cdot;\beta,\nu)] = \tau \phi & \text{in } \Omega \\ B[\phi] = \mu \partial_n \phi - \alpha \phi \partial_n m = 0 & \text{on } \partial\Omega \end{cases} \tag{39}$$

is negative/positive.

In Type B, the assumptions of similar diffustion ($\mu \approx \nu$), small advective tendency, and the convexity of the environment determine the sign of principal eigenvalues (see Theorem 3.4). In Type C, the situation becomes more complicated because the convexity assumption is dropped out and each species may have quite different conditional dispersal. To deal with the situation, ***the main idea is to search suitable ranges of parameters*** $(\alpha, \beta, \mu, \nu)$ ***where some important inequalities are applicable***.

Local Stability of $(0, \theta(x; \beta, \nu))$

To take the sign of τ_1 for example. Let $\phi > 0$ be the principal eigenfunction with the corresponding principal eigenvalue τ_1. We set $\phi \mapsto e^{-(\alpha/\mu)m}\phi$ to change (39) into the equivalent form:

$$\begin{cases} \mu\nabla \cdot (e^{(\alpha/\mu)m}\nabla\phi) + e^{(\alpha/\mu)m}\phi[m - \theta(\cdot; \beta, \nu)] = \tau_1 e^{(\alpha/\mu)m}\phi & \text{in } \Omega \\ B[\phi] = \partial_n\phi = 0 & \text{on } \partial\Omega \end{cases}$$

Dividing the above equation by ϕ and integrating over Ω, we obtain

$$\mu \int_\Omega \frac{e^{(\alpha/\mu)m}|\nabla\phi|^2}{\phi^2} dx + \int_\Omega e^{(\alpha/\mu)m}[m - \theta(\cdot; \beta, \nu)]dx = \tau_1 \int_\Omega e^{(\alpha/\mu)m} dx \tag{40}$$

Since the first integral in left-hand side of (40) is positive, it is natural to expect that the inequality

$$\int_\Omega e^{(\alpha/\mu)m}[m - \theta(\cdot; \beta, \nu)]dx > 0 \tag{41}$$

holds, then we can conclude that $(0, \theta(x; \beta, \nu))$ is unstable. To prove (41), it suffices to show

$$\int_\Omega e^{(\alpha/\mu)(m - \|\theta_2\|_\infty)}[m - \theta(\cdot; \beta, \nu)]dx > 0$$

where $\|\theta_2\|_\infty = \|\theta(\cdot; \beta, \nu)\|_{L^\infty(\overline{\Omega})}$. Define

$$\Omega_+ = \{x \in \overline{\Omega} : m(x) \le \|\theta_2\|_\infty\},\ \Omega_- = \{x \in \overline{\Omega} : m(x) > \|\theta_2\|_\infty\}$$

$$m^* = \max_{\overline{\Omega}} m$$

The main observation is that if $\|\theta_2\|_\infty < m^*$ ***holds*** [8] ***provided that*** β/ν ***lies in some compact interval*** R, then

$$\left|\int_{\Omega_+} e^{(\alpha/\mu)(m-\|\theta_2\|_\infty)}[m-\theta(\cdot;\beta,\nu)]dx\right| \le \int_{\Omega_+} e^{(\alpha/\mu)(m-\|\theta_2\|\|_\infty)}|m-\theta(\cdot;\beta,\nu)|dx$$
$$\le \int_{\Omega_+} |m-\theta(\cdot;\beta,\nu)|dx \le 2\|m\|_\infty|\Omega| < \infty$$

holds whenever β/ν lies in R. Since $\theta(\cdot;\beta,\nu)$ depends continuously on β (see Lemma 3.2), we can define

$$\epsilon \equiv \frac{1}{2}\min_{\beta/\nu\in R}(m^* - \|\theta_2\|_\infty) > 0$$

and there exists $r > 0$ which is independent of β such that

$$m(x) - \|\theta_2\|_\infty \ge \frac{1}{2}(m^* - \|\theta_2\|_\infty) \ge \epsilon, \text{ if } x \in B(x_0;r)\cap\overline{\Omega} \subset \Omega_-$$

where $m(x_0) = m^*$. Hence

$$\int_{\Omega_-} e^{(\alpha/\mu)(m-\|\theta_2\|_\infty)}[m-\theta(\cdot;\beta,\nu)]dx \ge \int_{B(x_0;r)\cap\overline{\Omega}} e^{(\alpha/\mu)(m-\|\theta_2\|_\infty)}[m-\theta(\cdot;\beta,\nu)]dx$$
$$\ge \int_{B(x_0;r)\cap\overline{\Omega}} e^{(\alpha/\mu)\epsilon}\epsilon \to \infty$$

as $\alpha \to \infty$. As a result, we find that there exists a constant $C_1 = C_1(\mu,\nu,m,\Omega) > 0$ which is *independent of* α *and* β such that (41) holds. Consequently, $(0, \theta(x;\beta,\nu))$ is unstable provided that $\alpha \ge C_1$ and $\beta/\nu \in R$.

What is the compact interval R? Before answering the question, we shall utilize the maximum principles to gain some useful information.

Lemma 4.1. *(c.f.[6]) Suppose that m is not a constant function, then the inequalities*

$$\min_{\overline{\Omega}}(me^{-(\beta/\nu)m}) < e^{-(\beta/\nu)m}\theta(\cdot;\beta,\nu) < \max_{\overline{\Omega}}(me^{-(\beta/\nu)m}) \tag{42}$$

hold in $\overline{\Omega}$.

[8] We note that the inequality $\|\theta_2\|_\infty < m^*$ is a direct consequence of the Hopf Boundary Lemma and the Strong Maximum Principle if $\alpha = 0$; hence this inequality is not beyond our experience.

Proof. Setting $w = e^{-(\beta/\nu)m}\theta(\cdot;\beta,\nu)$, then w satisfies

$$\begin{cases} \nu\Delta w + \beta\nabla w \cdot \nabla m + w(m - e^{(\beta/\nu)m}w) = 0 & \text{in } \Omega \\ B[w] = \partial_n w = 0 & \text{on } \partial\Omega \end{cases} \tag{43}$$

Let $w(x_0) = \max_{\overline{\Omega}} w > 0$. If $x_0 \in \Omega$, then $\nabla w(x_0) = 0$ and $\Delta w(x_0) \le 0$; hence we have $m(x_0) - e^{(\beta/\nu)m(x_0)}w(x_0) \ge 0$. If $x_0 \in \partial\Omega$ and suppose $m - e^{(\beta/\nu)m}w \le 0$ near x_0, then the Hopf Boundary Lemma (ref.[10], Lemma 3.4) implies $\partial_n w > 0$ which is a contradiction. Consequently, from (43) and $w > 0$, we obtain

$$w(x_0) \le m(x_0)e^{-(\beta/\nu)m(x_0)} \le \max_{\overline{\Omega}}(me^{-(\beta/\nu)m})$$

To show that the second inequality is strict, we let $M_1 = \max_{\overline{\Omega}}(me^{-(\beta/\nu)m})$ and $w_1(x) = M_1 - w(x)$, then w_1 satisfies

$$\nu\Delta w_1 + \beta\nabla w_1 \cdot \nabla m - e^{(\beta/\nu)m}(M_1 - w_1)[me^{-(\beta/\nu)m} - M_1 + w_1] = 0 \text{ in } \Omega$$

Multiplying the above identity out and utilizing the definition of M_1, we obtain

$$\nu\Delta w_1 + \beta\nabla w_1 \cdot \nabla m + e^{(\beta/\nu)m}w_1(w_1 - 2M_1 + me^{-(\beta/\nu)m}) = e^{(\beta/\nu)m}(me^{-(\beta/\nu)m} - M_1) \le 0$$

where the last inequality is not identically zero since m is not a constant function. Since $w_1 \ge 0$ in $\overline{\Omega}$, $\partial_n w_1 = 0$ on $\partial\Omega$, and $w_1 - 2M_1 + me^{-(\beta/\nu)m} \le 0$, by the Hopf Boundary Lemma (ref.[10], Lemma 3.4) and the Strong Maximum Principle (ref.[10], Theorem 3.5) we have $w_1 = M_1 - w(x) > 0$ in $\overline{\Omega}$. The proof for the first inequality is an analogy. □

From Lemma 4.1, we may suspect that the mapping $y \mapsto ye^{-(\beta/\nu)y}$ plays an important role. Since

$$\frac{d}{dy}(ye^{-(\beta/\nu)y}) = e^{-(\beta/\nu)y}(1 - \frac{\beta}{\nu}y)$$

we know that $ye^{-(\beta/\nu)y}$ is increasing for $y \le \nu/\beta$. If we consider $m^* \le \nu/\beta$, then

$$\max_{\overline{\Omega}}(me^{-(\beta/\nu)m}) \le m^* e^{-(\beta/\nu)m^*}$$

Combining with (42), we derive

$$\theta(x;\beta,\nu) < m^* e^{(\beta/\nu)[m(x) - m^*]} \le m^*$$

for all $x \in \overline{\Omega}$ if $\beta/\nu \leq 1/m^*$; hence the suitable compact interval $R = [0, 1/\max_{\overline{\Omega}} m]$.

In addtion, we know that $ye^{-(\beta/\nu)y}$ is decreasing for $y \geq \nu/\beta$. If we consider

$$\min_{\overline{\Omega}} m \geq \nu/\beta$$

(here we see the reason to assume $m > 0$ in $\overline{\Omega}$), then

$$\min_{\overline{\Omega}} (me^{-(\beta/\nu)m}) \geq m^* e^{-(\beta/\nu)m^*}$$

and by (42) we obtain

$$\theta(x; \beta, \nu) > m^* e^{(\beta/\nu)[m(x) - m^*]}$$

for all $x \in \overline{\Omega}$ if $\beta/\nu \geq 1/\min_{\overline{\Omega}} m$.

As a consequence, we have proved the following lemmas:

***Lemma* 4.2.** *(c.f.[6])*

(a) If $\beta/\nu \leq 1/\max_{\overline{\Omega}} m$, *then*

$$\theta(x; \beta, \nu) < m^* e^{(\beta/\nu)[m(x) - m^*]} \leq m^*$$

for all $x \in \overline{\Omega}$.

(b) If $m > 0$ *in* $\overline{\Omega}$ *and* $\beta/\nu \geq 1/\min_{\overline{\Omega}} m$, *then*

$$\theta(x; \beta, \nu) > m^* e^{(\beta/\nu)[m(x) - m^*]}$$

for all $x \in \overline{\Omega}$. *In particular,* $\theta(x_0; \beta, \nu) > m^*$ *if* $m(x_0) = m^*$ *for some* $x_0 \in \overline{\Omega}$.

***Lemma* 4.3.** *(c.f.[6]) Suppose that (A1) holds. If* $\beta/\nu \leq 1/\max_{\overline{\Omega}} m$, *then some constant* $C_1 = C_1(\mu, \nu, m, \Omega) > 0$ *exists such that* $(0, \theta(x; \beta, \nu))$ *is unstable provided that* $\alpha \geq C_1$.

We note that in Lemma 4.2, the inequality $\theta(\cdot; \beta, \nu) < m^*$ may not hold *for all* β, but under the assumption (A3), we can establish an upper bound for $\theta(\cdot; \beta, \nu)$ which is uniform in β.

***Lemma* 4.4.** *(c.f.[6]) Suppose that (A3) holds, then there exists a constant $K > 0$ which is independent of β such that*

$$\theta(x;\beta,\nu) \le K e^{(\beta/\nu)[m(x)-m^*]} \le K \tag{44}$$

for all $x \in \overline{\Omega}$.

Proof. We assume $\nu = 1$ without any loss of generality. From the proof of Lemma 4.1, (44) holds uniformly for $\beta \in [0,2]$ by choosing $K \ge e^{\beta m^*} \max_{\overline{\Omega}} m e^{-\beta m}$. For $\beta \ge 2$, we set $w(x;\beta) = e^{(\beta-1)m(x)}\theta(x;\beta)$ with $\theta(x;\beta) = \theta(x;\beta,1)$, then w satisfies

$$\Delta w + (\beta-2)\nabla m \cdot \nabla w - w[(\beta-1]|\nabla w|^2 + \Delta m + \theta(\cdot;\beta) - m] = 0 \text{ in } \Omega$$

Define $z = z(\beta) \in \overline{\Omega}$ with $w(z) = \max_{\overline{\Omega}} w$. By the no-flux boundary condition and (A3), we have $\partial_n w = w\partial_n m < 0$ on $\partial\Omega$; hence the Hopf Boundary Lemma (ref.[10], Lemma 3.4) implies $\nabla w(z) = 0$ and $\Delta w(z) \le 0$. Consequently,

$$(\beta-1)|\nabla w(z)|^2 + \Delta m(z) + \theta(z;\beta) \le m(z)$$

Hence, we have

$$(\beta-1)|\nabla w(z)|^2 \le m^* - \Delta m(z) \le \|m\|_{C^2(\overline{\Omega})} \tag{45}$$

and

$$\theta(z;\beta) \le m^* - \Delta m(z) \le \|m\|_{C^2(\overline{\Omega})}$$

Since $x_0 \in \Omega$ is the *unique* point such that $m^* = m(x_0)$, there exist κ_1, κ_2, and κ_3 satisfying

$$|\nabla m(x)| \ge \kappa_1 |x - x_0|,\ \kappa_2|x-x_0|^2 \ge m^* - m(x) \ge \kappa_3|x-x_0|^2 \tag{46}$$

for all $x \in \overline{\Omega}$. By (45) and (46), we can derive

$$(\beta-1)[m^* - m(z)] \le \frac{\kappa_2(\beta-1)}{\kappa_1^2}|\nabla m(z)|^2 \le \frac{\kappa_2\|m\|_{C^2(\overline{\Omega})}}{\kappa_1^2}$$

Since $w(x) \le w(z)$ implies $\theta(x;\beta) \le \theta(z;\beta)e^{(\beta-1)[m(x)-m(z)]}$, we have

$$\begin{aligned} e^{-\beta[m(x)-m^*]}\theta(x;\beta) &\le e^{-\beta[m(x)-m^*]}\theta(z;\beta)e^{(\beta-1)[m(x)-m(z)]} \\ &= \theta(z;\beta)e^{[m^*-m(x)]+(\beta-1)[m^*-m(z)]} \\ &\le \|m\|_{C^2(\overline{\Omega})} e^{2m^* + (\kappa_2/\kappa_1^2)\|m\|_{C^2(\overline{\Omega})}} \equiv K \end{aligned}$$

for all $x \in \overline{\Omega}$. □

We set $\phi \mapsto e^{-(\alpha/\mu)m}\phi$ to change (39) into the equivalent form:

$$\begin{cases} \mu\Delta\phi + \alpha\nabla\phi\cdot\nabla m + \phi[m - \theta(\cdot;\beta,\nu)] = \tau\phi & \text{in } \Omega \\ B[\phi] = \partial_n\phi = 0 & \text{on } \partial\Omega \end{cases} \tag{47}$$

hence it is natural to investigate the principal eigenvalue $\lambda_1(\alpha)$ of the eigenvalue problem:

$$\begin{cases} \mu\Delta\phi + \alpha\nabla\phi\cdot\nabla m + \phi c = \lambda(\alpha)\phi & \text{in } \Omega \\ B[\phi] = \partial_n\phi = 0 & \text{on } \partial\Omega \end{cases} \tag{48}$$

where $m \in C^2(\overline{\Omega})$, $c \in C(\overline{\Omega})$, and $\phi > 0$ on $\overline{\Omega}$. The following theorem characterizes the asymptotic behavior of principal eigenvalues of which proof is given in the next subsection.

***Theorem* 4.5.** *(c.f.[5]) Suppose that all critical points of m are non-degenerate. Let $\mathbb{M}$ be the set of points of local maximum of m, then*

$$\lim_{\alpha\to\infty} \lambda_1(\alpha) = \max_{x\in\mathbb{M}} c(x)$$

Since $x_0 \in \Omega$ is the unique point of global maximum of $m(x)$ (see the assumption (A3)); hence by Lemma 4.2(b), we have $\theta(x_0;\beta,\nu) > m^*$ where $m(x_0) = m^*$. By Theorem 4.5, we observe that the principal eigenvalue $\tau_1 = \tau_1(\alpha)$ of (47) satisfies:

$$\lim_{\alpha\to\infty} \tau_1(\alpha) = \max_{x\in\mathbb{M}}[m(x) - \theta(x;\beta,\nu)] = m^* - \theta(x_0;\beta,\nu) < 0$$

for any given β/ν with $\beta/\nu \geq 1/\min_{\overline{\Omega}} m$. We should notice that the above inequality may be false for *some range of β/ν*. However, this inequality provides a clue to expect that $(0, \theta(x;\beta,\nu))$ is locally stable.

***Lemma* 4.6.** *(c.f.[6]) Suppose that (A3) holds and $m > 0$ in $\overline{\Omega}$. For any $\eta > 1/\min_{\overline{\Omega}} m$, if $\beta/\nu \in [1/\min_{\overline{\Omega}} m, \eta]$, then some constant $C_2 = C_2(\mu,\nu,m,\Omega,\eta) > 0$ exists such that $(0, \theta(x;\beta,\nu))$ is locally stable provided that $\alpha \geq C_2$.*

Remark. *C_2 depends on η which determines the range of β/ν; hence how large α should be depends on β/ν.*

Proof. Suppose the statement is false, then there exist some $\eta > 1/\min_{\overline{\Omega}} m$, sequences $\{\alpha_i, \beta_i\}_{i=1}^{\infty}$ with $\alpha_i \to \infty$ and $\beta_i/\nu \in [1/\min_{\overline{\Omega}} m]$ such that the eigenvalue problem

$$\begin{cases} \nabla \cdot (\mu \nabla \phi - \alpha_i \phi \nabla m) + \phi[m - \theta(\cdot; \beta_i, \nu)] = \tau \phi & \text{in } \Omega \\ B[\phi] = \mu \partial_n \phi - \alpha_i \phi \partial_n m = 0 & \text{on } \partial\Omega \end{cases}$$

has the principal eigenvalue $\tau_i \geq 0$ with the corresponding principal eigenfunction $\phi_i > 0$. Set $\phi_i \mapsto e^{-(\alpha_i/\mu)m}\phi_i$ to change the above eigenvalue problem into the equivalent form:

$$\begin{cases} \mu \Delta \phi_i + \alpha_i \nabla \phi_i \cdot \nabla m + \phi_i[m - \theta(\cdot; \beta_i, \nu)] = \tau_i \phi_i & \text{in } \Omega \\ B[\phi_i] = \partial_n \phi_i = 0 & \text{on } \partial\Omega \end{cases}$$

Passing to a subsequence if necessary, we let $\beta_i \to \beta$ for some $\beta/\nu \geq 1/\min_{\overline{\Omega}} m$. By the assumption (A3) and Lemma 4.2(b), we have $\theta(x_0; \beta, \nu) - m(x_0) > 0$ where $m(x_0) = m^*$. Set $\epsilon = \frac{1}{2}[\theta(x_0; \beta, \nu) - m(x_0)] > 0$, and let $\tau_i(\epsilon)$ be the principal eigenvalue of the eigenvalue problem:

$$\begin{cases} \mu \Delta \phi + \alpha_i \nabla \phi \cdot \nabla m + \phi[m - \theta(\cdot; \beta, \nu) + \epsilon] = \tau \phi & \text{in } \Omega \\ B[\phi] = \partial_n \phi = 0 & \text{on } \partial\Omega \end{cases}$$

Since β *is a fixed number*, we can apply Theorem 4.5 to obtain

$$\lim_{i \to \infty} \tau_i(\epsilon) = \max_{x \in \mathbb{M}} [m(x) - \theta(\cdot; \beta, \nu) + \epsilon] = m(x_0) - \theta(x_0; \beta, \nu) + \epsilon < 0$$

However, since $\theta(\cdot; \beta_i, \nu) \to \theta(\cdot; \beta, \nu)$ uniformly as $\beta_i \to \beta$ (see Lemma 3.2), we have $\theta(\cdot; \beta_i, \nu) > \theta(\cdot; \beta, \nu) - \epsilon$ in $\overline{\Omega}$ for sufficiently large i. By the variational characterization of principal eigenvalues (8), we have $\tau_i(\epsilon) \geq \tau_i$ for sufficiently large i; hence $\tau_i \geq 0$ implies $\tau_i(\epsilon) \geq 0$ for sufficiently large i, which is a contradiction. □

Local Stability of $(\theta(x; \alpha, \mu), 0)$

Let $\psi > 0$ be the principal eigenfunction with the corresponding principal eigenvalue σ_1, and we set $\psi \mapsto e^{-(\beta/\nu)m}\psi$ to change (38) into the equivalent form:

$$\begin{cases} \nu \nabla \cdot [e^{(\beta/\nu)m} \nabla (e^{-(\beta/\nu)m} \psi)] + \psi[m - \theta(\cdot; \alpha, \mu)] = \sigma_1 \psi & \text{in } \Omega \\ B[\psi] = \partial_n \psi = 0 & \text{on } \partial\Omega \end{cases}$$

Dividing the above equation by $e^{-(\beta/\nu)m}\psi$ and integrating over Ω, we obtain

$$\int_\Omega \frac{\nu\nabla\cdot[e^{(\beta/\nu)m}\nabla(e^{-(\beta/\nu)m}\psi)]}{e^{(\beta/\nu)m}\psi}dx + \int_\Omega e^{(\beta/\nu)m}[m-\theta(\cdot;\alpha,\mu)]dx = \sigma_1\int_\Omega e^{(\beta/\nu)m}dx$$

By the divergence theorem and the Neumann boundary condition, we have

$$\int_\Omega \frac{\nu\nabla\cdot[e^{(\beta/\nu)m}\nabla(e^{-(\beta/\nu)m}\psi)]}{e^{(\beta/\nu)m}\psi}dx = \int_\Omega \frac{\nu e^{(\beta/\nu)m}}{(e^{-(\beta/\nu)m}\psi)^2}\cdot|\nabla(e^{(\beta/\nu)m}\psi)|^2dx \geq 0$$

hence given $\eta > 0$ and if $\beta/\nu \in [0,\eta]$, we have

$$\begin{aligned}\sigma_1\int_\Omega e^{(\beta/\nu)m}dx &\geq \int_\Omega e^{(\beta/\nu)m}[m-\theta(\cdot;\alpha,\mu)]dx = \int_\Omega e^{(\beta/\nu)m}mdx - \int_\Omega e^{(\beta/\nu)m}\theta(\cdot;\alpha,\mu)dx \\ &\geq \int_\Omega e^{(\beta/\nu)m}mdx - e^{(\beta/\nu)m^*}\int_\Omega \theta(\cdot;\alpha,\mu)dx \\ &\geq \int_\Omega mdx - e^{\eta m^*}\int_\Omega \theta(\cdot;\alpha,\mu)dx\end{aligned}$$

where we have utilized Lemma 1.5(a) for the last inequality. Since $\int_\Omega mdx > 0$, we find that if we can show

$$\lim_{\alpha\to\infty}\int_\Omega \theta(x;\alpha,\mu)dx = 0$$

then $\sigma_1 > 0$ provided that α is sufficiently large, and thus $(\theta(x;\alpha,\mu),0)$ is unstable.

***Lemma* 4.7.** *(c.f.[4]) Suppose that (A2) holds, then*

$$\lim_{\alpha\to\infty}\int_\Omega \theta(x;\alpha,\mu)dx = 0$$

Proof. Multiplying the equation of $\theta_1 \equiv \theta(\cdot;\alpha,\mu)$

$$\begin{cases}\nabla\cdot(\mu\nabla\theta_1 - \alpha\theta_1\nabla m) + \theta_1(m-\theta_1) = 0 & \text{in } \Omega \\ B[\theta_1] = \mu\partial_n\theta_1 - \alpha\theta_1\partial_n m = 0 & \text{on } \partial\Omega\end{cases} \tag{49}$$

by $g \in S \equiv \{g \in C^2(\overline{\Omega}) : \partial_n g = 0 \text{ on } \partial\Omega\}$, integrating over Ω, and utilizing the boundary condition of g, we have

$$\mu\int_\Omega \theta_1\Delta g dx + \alpha\int_\Omega \theta_1\nabla m\cdot\nabla g dx + \int_\Omega \theta_1 g(m-\theta_1)dx = 0 \tag{50}$$

Integrating (49) over Ω and utilizing the boundary condition, we have

$$\int_\Omega \theta_1^2 dx = \int_\Omega m\theta_1 dx \leq \|m\|_{L^2(\Omega)}\|\theta_1\|_{L^2(\Omega)}$$

hence $\|\theta_1\|_{L^2(\Omega)}$ is uniformly bounded by $\|m\|_{L^2(\Omega)}$. Therefore, passing to a subsequence if necessary, we assume $\theta_1 \to \theta^*$ weakly in $L^2(\Omega)$ as $\alpha \to \infty$ and $\theta_1 \geq 0$ almost everywhere in Ω. Dividing (50) by α and letting $\alpha \to \infty$, then

$$\int_\Omega \theta^* \nabla m \cdot \nabla g dx = 0$$

holds for all $g \in S$. Since S is dense in $H^1(\Omega)$, we have $\int_\Omega \theta^* \nabla m \cdot \nabla g dx = 0$ for all $g \in H^1(\Omega)$. In particular, we put $g = m$ to derive $\int_\Omega \theta^* |\nabla m|^2 dx = 0$; hence $\theta^* |\nabla m|^2 = 0$ almost everywhere in Ω. Since the set of critical points of m has Lebesgue measure zero (see the assumption (A2)), we have $\theta^* = 0$ almost everywhere in Ω. Thus, $\theta_1 \to 0$ weakly in $L^2(\Omega)$ as $\alpha \to \infty$, which implies

$$\lim_{\alpha \to \infty} \int_\Omega \theta_1 \chi(\Omega) dx = \lim_{\alpha \to \infty} \int_\Omega \theta_1 dx = 0$$

where $\chi(\Omega)$ is the characteristic function of Ω. □

As a consequence, we have proved the following lemma:

***Lemma* 4.8.** *(c.f.[6]) Suppose that (A1) and (A2) hold. For any $\eta > 0$, if $\beta/\nu \in [0, \eta]$, then some constant $C_3 = C_3(\eta) > 0$ exists such that $(\theta(x; \alpha, \mu), 0)$ is unstable provided that $\alpha \geq C_3$.*

Remark. *C_3 depends on η which determines the range of β/ν; hence how large α should be depends on β/ν.*

Advection-induced Coexistence

Combining with Lemma 1.5(b), Theorem 1.6, and Lemma 1.8, we can apply the following theorem from the theory of monotone dynamical systems:

***Theorem* 4.9.** *(c.f.[13], Theorem 4) The full system (35) has at least one locally stable equilibrium.*

Proof of Theorem 1.3(a)

Proof. By Lemma 4.3 and Lemma 4.8, both semi-trivial equilibria are unstable provided that $\alpha \geq \max\{C_1, C_3\}$. But Theorem 4.9 guarantees at least one locally stable equilibrium. Consequently, such equilibrium must be a positive equilibrium. □

Advection-induced Extinction

To determine the global stability, we need to rule out the possibility of positive equilibria.

***Lemma* 4.10.** *(c.f.[6]) Suppose that (A3) holds and $m > 0$ in $\overline{\Omega}$. For any $\eta > 1/\min_{\overline{\Omega}} m$, if $\beta/\nu \in [1/\min_{\overline{\Omega}} m, \eta]$, then some constant $C_4 = C_4(\mu, \nu, m, \Omega, \eta) > 0$ exists such that (35) has no positive equilibria provided that $\alpha \geq C_4$.*

Remark. *C_4 depends on η which determines the range of β/ν; hence how large α should be depends on β/ν.*

Proof. Suppose the statement is false, then there exist some $\eta > 1/\min_{\overline{\Omega}} m$, sequences $\{\alpha_i, \beta_i\}_{i=1}^{\infty}$ with $\alpha_i \to \infty$ and $\beta_i/\nu \in [1/\min_{\overline{\Omega}} m] \to \beta/\nu \in [1/\min_{\overline{\Omega}} m]$ such that the full system (35) has positive equilibria (U_i, V_i) with respect to (α_i, β_i). We set $W_i = e^{-(\alpha_i/\mu)m} U_i$ to obtain the equivalent form:

$$\begin{cases} \mu \nabla \cdot (e^{(\alpha_i/\mu)m} \nabla W_i) + e^{(\alpha_i/\mu)m} W_i (m - U_i - V_i) = 0 & \text{in } \Omega \\ B[W_i] = \partial_n W_i = 0 & \text{on } \partial\Omega \end{cases} \tag{51}$$

For any $0 < \epsilon < 1$, we let $\lambda_i(\epsilon)$ be the principal eigenvalue of the eigenvalue problem

$$\begin{cases} \mu \nabla \cdot (e^{(\alpha_i/\mu)m} \nabla \phi_i) + e^{(\alpha_i/\mu)m} \phi_i [m - (1-\epsilon)\theta(\cdot; \beta, \nu)] = \lambda_i(\epsilon) e^{(\alpha_i/\mu)m} \phi_i & \text{in } \Omega \\ B[\phi_i] = \partial_n \phi_i = 0 & \text{on } \partial\Omega \end{cases} \tag{52}$$

where $\phi_i > 0$ is the corresponding principal eigenfunction. Multiplying (51) by ϕ_i and (52) by W_i, subtracting, and integrating over Ω yield

$$\int_\Omega e^{(\alpha_i/\mu)m} W_i \phi_i [U_i + V_i - (1-\epsilon)\theta(\cdot; \beta, \nu)] dx = \lambda_i(\epsilon) \int_\Omega e^{(\alpha_i/\mu)m} W_i \phi_i dx$$

We observe that for fixed $0 < \epsilon < 1$, if $V_i - (1-\epsilon)\theta(\cdot;\beta,\nu) > 0$ in Ω for sufficiently large i, then $\lambda_i(\epsilon) > 0$ for sufficiently large i. Thus, from Theorem 4.5, we have

$$\lim_{i\to\infty} \lambda_i(\epsilon) = \max_{x\in\mathbb{M}}[m(x) - (1-\epsilon)\theta(x;\beta,\nu)] = m^* - (1-\epsilon)\theta(x_0;\beta,\nu) > 0$$

Letting $\epsilon \to 0$, we derive $m^* \geq \theta(x_0;\beta,\nu)$, which contradicts to Lemma 4.2(b).

To justify the observation, it suffices to show $V_i \to \theta(\cdot;\beta,\nu)$ uniformly in Ω as $i \to \infty$. Since V_i and $\theta \equiv \theta(\cdot;\beta,\nu)$ satisfy

$$\begin{cases} \nabla\cdot(\nu\nabla V_i - \beta V_i\nabla m) + V_i(m - U_i - V_i) = 0 & \text{in } \Omega \\ B[V_i] = \nu\partial_n V_i - \beta V_i \partial_n m = 0 & \text{on } \partial\Omega \end{cases}$$

$$\begin{cases} \nabla\cdot(\nu\nabla\theta - \beta\theta\nabla m) + \theta(m - \theta) = 0 & \text{in } \Omega \\ B[\theta] = \nu\partial_n\theta - \beta\theta\partial_n m = 0 & \text{on } \partial\Omega \end{cases}$$

respectively, we may expect that $U_i \to 0$ *in some norm* as $i \to \infty$. By the Comparison Principle, we know $U_i \leq \theta(\cdot;\alpha,\mu)$ for all i. Furthermore, Lemma 4.4, the inequality (46), and the Dominated Convergence Theorem imply $U_i \to 0$ in $L^p(\Omega)$ as $i \to \infty$ for all $p > 1$. By the *elliptic regularity* (see the proof of Lemma 3.5), we have $V_i \to \theta(\cdot;\beta,\nu)$ in $W^{2,p}(\Omega)$ as $i \to \infty$ for all $p > 1$; hence the Morray's inequality implies $W^{2,p}(\Omega) \hookrightarrow C^1(\Omega)$ for p sufficiently large, which proves the observation. □

Proof of Theorem 1.3(b)

Proof. For $\alpha \geq \max\{C_2, C_3, C_4\}$, $(0, \theta(x;\beta,\nu))$ is locally stable by Lemma 4.6, whereas $(\theta(x;\alpha,\mu), 0)$ is unstable by Lemma 4.8. Lemma 4.10 rules out the possibility of positive equilibria. Consequently, $(0,\theta(x;\beta,\nu))$ is globally asymptotically stable by Theorem 1.9. □

The Asymptotic Behavior of Principal Eigenvalues

We devote this subsection to proving Theorem 4.5 which characterizes the asymptotic behavior of principal eigenvalues $\lambda_1(\alpha)$ that satisfy: [9]

$$\begin{cases} -\Delta\phi - 2\alpha\nabla\phi\cdot\nabla m + \phi c = \lambda_1(\alpha)\phi & \text{in } \Omega \\ B[\phi] = \partial_n \phi = 0 & \text{on } \partial\Omega \end{cases} \tag{53}$$

where $m \in C^2(\overline{\Omega})$, $c \in C(\overline{\Omega})$, and $\phi > 0$ in $\overline{\Omega}$ is the eigenfunction normalized by $\displaystyle\int_\Omega e^{2\alpha m}\phi^2 dx = 1$. It is clear that Theorem 4.5 is equivalent to

$$\lim_{\alpha\to\infty} \lambda_1(\alpha) = \min_{x\in\mathbb{M}} c(x)$$

Setting $w = e^{\alpha m}\phi$, since $\{w^2(\cdot;\alpha)\}$ is weakly compact and $\displaystyle\int_\Omega w^2 dx = 1$, there exist a subsequence $\{\alpha_j\}_{j=1}^\infty$ with $\alpha_j \to \infty$ as $j \to \infty$ and a probability measure P such that

$$\lim_{j\to\infty} \int_\Omega w^2(x;\alpha_j)\eta(x)dx = \int_{\overline{\Omega}} \eta(x)dP, \text{ for all } \eta \in C(\overline{\Omega}) \tag{54}$$

The principal eiganvalues can be characterized by the variational characterization:

$$\lambda_1(\alpha) = \inf_{\int_\Omega e^{2\alpha m}\psi^2 dx = 1} \int_\Omega e^{2\alpha m}(|\nabla\psi|^2 + c\psi)dx = \inf_{\int_\Omega v^2 dx=1} \int_\Omega |\nabla v - \alpha v\nabla m|^2 + cv^2 dx \tag{55}$$

where $v = e^{\alpha m}\psi$. Since the limit of $\lambda_1(\alpha)$ is not a priori known, we define

$$\lambda^* = \limsup_{\alpha\to\infty} \lambda_1(\alpha), \;\; \lambda_* = \liminf_{\alpha\to\infty} \lambda_1(\alpha)$$

The following lemma provides an upper bound of λ^*.

***Lemma* 4.11.** *(c.f.[6]) Suppose that all critical points of m are non-degenerate. Let $\mathbb{M}$ be the set of points of local maximum of m, then*

$$\lambda^* \le \min_{x\in\mathbb{M}} c(x)$$

[9] Notational convenience is the only reason to consider (53) rather than (48).

Proof. Let $x \in \mathbb{M}$, since $m \in C^2(\overline{\Omega})$ and all critical points are non-degenerate, there exists some sequence $\{\beta_i\}_{i=1}^{\infty}$ with $\beta_i \to 0$ as $i \to \infty$ such that

$$m(x) > \max_{\partial B(x,\beta_i)\cap\overline{\Omega}} m$$

for all i. For each β_i, define r_i and d_i with $0 < d_i < r_i < \beta_i$ such that

$$\min_{\bar{B}(x,d_i)\cap\overline{\Omega}} m \equiv m_i > M_i \equiv \max_{B(x,\beta_i)\setminus B(x,r_i)\cap\overline{\Omega}} m$$

Define

$$u_i(x) = \begin{cases} 1 & \text{if } x \in B(x, r_i) \\ \dfrac{\beta_i - |x|}{\beta_i - r_i} & \text{if } x \in B(x,\beta_i) \setminus B(x, r_i) \\ 0 & \text{if } x \in \mathbb{R}^l \setminus B(x,\beta_i) \end{cases}$$

then the principal eigenvalues satisfy

$$\lambda_1(\alpha) \le \frac{\int_\Omega e^{2\alpha m} c u_i^2 + e^{2\alpha m}|\nabla u_i|^2 dx}{\int_\Omega e^{2\alpha m} u_i^2 dx} \le \max_{\bar{B}(x,\beta_i)} c + \frac{e^{2\alpha M_i}\beta_i^l}{|\beta_i - r_i|^2 d_i^l e^{2\alpha m_i}}$$

Letting $\alpha \to \infty$ first, and then $i \to \infty$, we derive $\lambda^* \le c(x)$ for all $x \in \mathbb{M}$. □

The proof in Lemma 4.11 explains the reason why we focus on the set $\mathbb{M}$. To show that $\lambda_* = \lambda^*$, we select a subsequence $\{\alpha_j\}_{j=1}^{\infty}$ with $\alpha_j \to \infty$ as $j \to \infty$ such that $\lim_{j\to\infty} \lambda_1(\alpha_j) = \lambda_*$. From (55), we obtain

$$\lambda_* \ge \lim_{j\to\infty} \int_\Omega c(x) w^2(x;\alpha_j) dx = \int_{\overline{\Omega}} c(x) dP \tag{56}$$

The main observation is that if the support of P is contained M, then combining with Lemma 4.11, we can derive

$$\int_{\overline{\Omega}} c(x) dP \ge \min_{x\in\mathbb{M}} c(x) \int_{\overline{\Omega}} dP = \min_{x\in\mathbb{M}} c(x) \ge \lambda^* \tag{57}$$

Thus, $\lim_{\alpha\to\infty} \lambda_1(\alpha) = \min_{x\in\mathbb{M}} c(x)$***, and Theorem 4.5 follows from (56) and (57)***.

How can we measure the support of P? According to the main observation, it is natural to classify points in $\overline{\Omega} \setminus \mathbb{M}$ firstly:

1. *Non-critical interior points*:

$\Omega_1 \equiv \{x \in \Omega : |\nabla m(x)| > 0\}$

2. *Non-degenerate critical interior points which are not points of local maxima*:

$\Omega_2 \equiv \{x \in \Omega : \nabla m(x) = 0,\ \exists e \in \mathbb{S}^{l-1} \ni (e \cdot \nabla)^2 m(x) > 0\}$

where $\mathbb{S}^{l-1}$ is the unit sphere in $\mathbb{R}^l$ and the term $(e \cdot \nabla)^2 m(x) > 0$ means that $D^2 m(x)$ is positive-definite along the direction e.

To classify the boundary points, we define the operator $\nabla_{\partial\Omega} \equiv \nabla - n\partial_n$ which is the gradient restricted to $\partial\Omega$, and the *boundary critical points* x are defined as $x \in \partial\Omega$ satisfying $\nabla_{\partial\Omega} m(x) = 0$. We note that the condition $\nabla_{\partial\Omega} m(x) = 0$ is equivalent to $|\nabla m(x)| = |\partial_n m(x)|$. The *boundary Hessian* of m, denoted by $D^2_{\partial\Omega} m$, is defined as follows: Let $x \in \partial\Omega$, we make a rotation such that $n(x) = -e_l \equiv (0, ..., 0, -1)$. Locally $\partial\Omega$ can be written as a graph $x_l = f(x')$ where $x = (x', x_l)$ and $f_{x_i}(x') = 0$ for $i = 1, ..., l-1$, then $m(x) = m(x', f(x'))$ and

$$\nabla_{\partial\Omega} m(x) = \nabla m(x) - n\partial_n m(x) = (m_{x_1}(x), ..., m_{x_{l-1}}(x), 0)$$
$$D^2_{\partial\Omega} m(x) \equiv [m_{x_i x_j}(x) + m_{x_l}(x) f_{x_i x_j}(x')]_{(l-1)\times(l-1)}$$

Non-degenerate boundary critical points $x \in \partial\Omega$ can be classified as follows:

Points of boundary local minima:

$\{x : |\nabla m(x)| = -\partial_n m(x) > 0 \wedge D^2_{\partial\Omega} m(x) > 0\} \cup \{x : |\nabla m(x)| = 0 \wedge D^2 m(x) > 0\}$

Points of boundary local maxima:

$\{x : |\nabla m(x)| = \partial_n m(x) > 0 \wedge D^2_{\partial\Omega} m(x) < 0\} \cup \{x : |\nabla m(x)| = 0 \wedge D^2 m(x) < 0\}$

Boundary saddle points:

$\{x : |\nabla m(x)| = -\partial_n m(x) > 0 \wedge \exists e \in \mathbb{S}^{l-1}, e \perp n(x) \ni (e \cdot \nabla)^2 m(x) < 0\}$

$\{x : |\nabla m(x)| = \partial_n m(x) > 0 \wedge \exists e \in \mathbb{S}^{l-1}, e \perp n(x) \ni (e \cdot \nabla)^2 m(x) > 0\}$

$\{x : |\nabla m(x)| = 0 \wedge \exists e_1, e_2 \in \mathbb{S}^{l-1}, (e_1 \cdot \nabla)^2 m(x) > 0 > (e_2 \cdot \nabla)^2 m(x)\}$

We continue classifying points in $\overline{\Omega} \setminus \mathbb{M}$:

3. *Non-critical boundary points*:

$\Omega_3 \equiv \{x \in \partial\Omega : |\nabla m(x)| > |\partial_n m(x)| \vee |\nabla m(x)| < |\partial_n m(x)|\}$

4. *Non-degenerate boundary critical points which are not points of local maxima*:

$\Omega_4 \equiv \{x \in \partial\Omega : |\nabla m(x)| = \partial_n m(x) > 0 \wedge \exists e \in \mathbb{S}^{l-1}, e \perp n(x) \ni (e \cdot \nabla)^2 m(x) > 0\}$

$\Omega_5 \equiv \{x \in \partial\Omega : |\nabla m(x)| = -\partial_n m(x) > 0\}$

$\Omega_6 \equiv \{x \in \partial\Omega : |\nabla m(x)| = 0 \wedge \exists e \in \mathbb{S}^{l-1} \ni (e \cdot \nabla)^2 m(x) > 0\}$

A direct observation shows that

$$\overline{\Omega} \setminus \mathbb{M} \subset \bigcup_{i=1}^{6} \Omega_i$$

As a result, the support of P ***is contained in*** $\mathbb{M}$ ***if we can show*** $P(\Omega_i) = 0$ ***for*** $i = 1, ..., 6$. How can we compute $P(\Omega_i)$? A surprising guideline follows from the simple inequality:

$$c^* - c_* \geq \int_\Omega |\nabla w(x;\alpha) - \alpha w(x;\alpha)\nabla m(x)|^2 dx \tag{58}$$

where $c_* = \min_{\overline{\Omega}} c$ and $c^* = \max_{\overline{\Omega}} c$ because (55) implies $c^* \geq \lambda_1(\alpha)$ by taking $v = e^{\alpha m}/\|e^{\alpha m}\|_{L^2(\overline{\Omega})}$ and thus the inequality

$$\begin{aligned} &c^* - \int_\Omega |\nabla w(x;\alpha) - \alpha w(x;\alpha)\nabla m(x)|^2 dx \\ &\geq \lambda_1(\alpha) - \int_\Omega |\nabla w(x;\alpha) - \alpha w(x;\alpha)\nabla m(x)|^2 dx = \int_\Omega c(x) w^2(x;\alpha) dx \geq c_* \end{aligned}$$

holds for all $\alpha \in \mathbb{R}$.

***Lemma* 4.12.** *(c.f.[5])* $P(\Omega_1) = 0$ *and* $P(\Omega_2) = 0$.

Proof. Fix $\tilde{x} \in \Omega_1$, there exist $K > 0$ and $R > 0$ such that $|\nabla m| > K$ in $B(\tilde{x}, 2R) \subset \Omega$. Let ρ be a smooth cut-off function satisfying

$$\rho = 1 \text{ in } B(0,1), \quad \rho = 0 \text{ in } \mathbb{R}^l \setminus B(0,2), \quad 0 \leq \rho \leq 1, \quad |\nabla \rho| \leq 2 \text{ in } B(0,2)$$

Setting $\xi(x) = \rho(\frac{x - \tilde{x}}{R})$, then

$$\xi = 1 \text{ in } B(\tilde{x}, R), \quad \xi = 0 \text{ in } \mathbb{R}^l \setminus B(\tilde{x}, 2R), \quad 0 \leq \xi \leq 1, \quad |\nabla \xi| \leq \frac{2}{R} \text{ in } B(\tilde{x}, 2R)$$

From (54), we have

$$P(B(\tilde{x}, R)) = \lim_{\alpha_j \to \infty} \int_{B(\tilde{x},R)} w^2(x;\alpha_j) dx \leq \lim_{\alpha \to \infty} \int_\Omega \xi^2(x) w^2(x;\alpha) dx$$

hence if we can show $\lim_{\alpha\to\infty} \int_\Omega \xi^2(x) w^2(x;\alpha) dx = 0$, then $P(B(\tilde{x}, R)) = 0$, and thus $P(\Omega_1) = 0$.

From (58), a careful calculation gives

$$\begin{aligned}
c^* - c_* &\geq \int_\Omega \xi^2(x)|\nabla w(x;\alpha) - \alpha w(x;\alpha)\nabla m(x)|^2 dx \\
&= \int_\Omega \xi^2(|\nabla w|^2 + \alpha^2 w^2|\nabla m|^2) - \alpha\xi^2\nabla(w^2)\cdot\nabla m dx \\
&= \int_\Omega \xi^2|\nabla w|^2 + \xi^2 w^2(\alpha^2|\nabla m|^2 + \alpha\Delta m) + 2\alpha w^2\xi\nabla\xi\cdot\nabla m dx \\
&\geq \int_\Omega \xi^2 w^2(\frac{1}{2}\alpha^2|\nabla m|^2 + \alpha\Delta m) - 2w^2|\nabla\xi|^2 dx \\
&\geq \int_\Omega \xi^2 w^2(\frac{1}{2}\alpha^2|\nabla m|^2 + \alpha\Delta m)dx - \frac{8}{R^2}
\end{aligned}$$

where the second equality follows from integration by parts, and the second inequality follows from

$$\xi^2\alpha^2|\nabla m|^2 + 2\alpha\xi\nabla\xi\cdot\nabla m \geq \frac{1}{2}\xi^2\alpha^2|\nabla m|^2 - 2\alpha|\xi\nabla\xi\cdot\nabla m| \geq -2|\nabla\xi|^2$$

Since $|\nabla m| > K$ in $B(\tilde{x}, 2R)$, some constant $C > 0$ exists such that $\frac{1}{2}|\nabla m| + \frac{\Delta m}{\alpha} > C$ in $B(\tilde{x}, 2R)$ for sufficiently large α. Thus, for sufficiently large α, we obtain

$$\frac{c^* - c_* + \frac{8}{R}}{\alpha^2} = \int_\Omega (\frac{1}{2}|\nabla m|^2 + \frac{\Delta m}{\alpha})\xi^2 w^2 dx \geq C\int_\Omega \xi^2 w^2 dx$$

That is, $\lim_{\alpha\to\infty}\int_\Omega \xi^2(x)w^2(x;\alpha)dx = 0$.

The proof of $P(\Omega_2) = 0$ is almost similar. Fix $\tilde{x} \in \Omega_2$ and let $(e\cdot\nabla)^2 m(\tilde{x}) > 0$ for some $e \in \mathbb{S}^{l-1}$. By rotation, we assume $e = e_1 = (1, 0, ..., 0)$, then there exist $K > 0$ and $R > 0$ such that $(e\cdot\nabla)^2 m = m_{x_1x_1} > K$ in $B(\tilde{x}, 2R) \subset \Omega$. Let $\xi(x) = \rho(\frac{x-\tilde{x}}{R})$, then a similar calculation gives

$$\begin{aligned}
c^* - c_* &\geq \int_\Omega \xi^2(x)|\nabla w(x;\alpha) - \alpha w(x;\alpha)\nabla m(x)|^2 dx \geq \int_\Omega \xi^2|w_{x_1} - \alpha w m_{x_1}|^2 dx \\
&= \int_\Omega \xi^2 w_{x_1}^2 + \xi^2 w^2(\alpha^2 m_{x_1}^2 + \alpha m_{x_1x_1}) + 2\alpha w^2\xi\xi_{x_1}m_{x_1} dx \\
&\geq \int_\Omega \alpha\xi^2 w^2 m_{x_1x_1} - 2w^2\xi_{x_1}^2 dx \\
&\geq \alpha K\int_\Omega \xi^2 w^2 dx - \frac{8}{R^2}
\end{aligned}$$

hence $\int_\Omega \xi^2 w^2 dx \leq \frac{1}{\alpha K}(c^* - c_* + \frac{8}{R^2})$, and we can conclude

$$P(B(\tilde{x}, R)) = \lim_{\alpha_j\to\infty}\int_{B(\tilde{x},R)} w^2(x;\alpha_j)dx \leq \lim_{\alpha\to\infty}\int_\Omega \xi^2(x)w^2(x;\alpha)dx = 0$$

That is, $P(B(\tilde{x}, R)) = 0$, and thus $P(\Omega_2) = 0$. $\square$

***Lemma* 4.13.** *(c.f.[5])* $P(\Omega_3) = 0$ *and* $P(\Omega_4) = 0$.

Proof. The main idea is to *flatten the boundary* via some change of variables. Let $\tilde{x} \in \Omega_3$. By translation and rotation, we can assume $\tilde{x} = 0$, $n(0) = -e_l$, and $\nabla m(0) = Ke_1 + [-\partial_n m(0)]e_l$ where $K = \frac{1}{2}\sqrt{||\nabla m(0)|^2 - |\partial_n m(0)|^2|} > 0$.

We flatten $\partial\Omega$ near $\tilde{x} = 0$ as follows: locally $\partial\Omega$ can be written as a graph $x_l = f(x')$ where $x = (x', x_l)$, $f(0') = 0$, and $f_{x_i}(0') = 0$ for $i = 1, ..., l-1$. $\partial\Omega$ is flattened by

$$y = Y(x) \equiv (x', x_l - f(x')) \Leftrightarrow x = X(y) \equiv (y', y_l + f(y'))$$

Since $D_y X(0)$ is the identity matrix, there exists $R > 0$ such that

$$\|D_y X(y)\| \leq 2, \ |detD_y X(y)| \geq \frac{1}{2}, \text{ and } m_{y_1}(X(y)) > K$$

in $B^+(0, 2R) = Y(\Omega \cap B(0, 2R)) = \{y \in B(0, 2R) : y_l > 0\}$. Let $\xi(y) = \rho(\frac{y}{R})$, then a careful calculation gives

$$\begin{aligned}
c^* - c_* &\geq \int_\Omega \xi^2(Y(x))|\nabla w(x;\alpha) - \alpha w(x;\alpha)\nabla m(x)|^2 dx = \int_\Omega \xi^2 w^2 |\nabla_x (lnw - \alpha m)|^2 dx \\
&\geq \frac{1}{4}\int_{B^+(0,2R)} \xi^2 w^2 |\nabla_y (lnw - \alpha m)|^2 |det(D_y X(y))| dy \\
&\geq \frac{1}{8}\int_{B^+(0,2R)} \xi^2 |w_{y_1} - \alpha w m_{y_1}|^2 dy \\
&\geq \frac{1}{8}\int_{B^+(0,2R)} \xi^2 w_{y_1}^2 + \xi^2 w^2(\alpha^2 m_{y_1}^2 + \alpha m_{y_1 y_1}) + 2\alpha w^2 \xi \xi_{y_1} m_{y_1} dy \\
&\geq \frac{1}{8}\int_{B^+(0,2R)} \xi^2 w^2 (\frac{1}{2}\alpha^2 m_{y_1}^2 + \alpha m_{y_1 y_1}) - 2w^2 |\nabla \xi|^2 dy \\
&\geq \frac{1}{8}\int_{B^+(0,2R)} \xi^2 w^2 (\frac{1}{2}\alpha^2 m_{y_1}^2 + \alpha m_{y_1 y_1}) dy - \frac{1}{R^2}
\end{aligned}$$

Since $m_{y_1}(X(y)) > K$ in $B^+(0, 2R)$, some constant $C > 0$ exists such that $\frac{1}{2}\alpha^2 m_{y_1}^2 + \frac{m_{y_1 y_1}}{\alpha} > C$ in $B^+(0, 2R)$ for sufficiently large α. Thus, for sufficiently large α, we obtain

$$\frac{c^* - c_* + \frac{1}{R}}{\alpha^2} = \int_\Omega (\frac{1}{2} m_{y_1 y_1}^2 + \frac{m_{y_1 y_1}}{\alpha}) \xi^2 w^2 dy \geq C \int_\Omega \xi^2 w^2 dy$$

which implies

$$P(B(0,R)\cap\overline{\Omega}) = \lim_{\alpha_j\to\infty}\int_{B(0,R)\cap\overline{\Omega}} w^2(x;\alpha_j)dx \le \lim_{\alpha\to\infty}\int_{B^+(0,2R)} \xi^2(x)w^2(x;\alpha)dy = 0.$$

The case of the proof of $P(\Omega_4) = 0$ is almost the same since the differences are $K = 0$ and $m_{y_1y_1} > 0$ by choosing $e = e_1$ in the case of Ω_4. □

***Lemma* 4.14.** *(c.f.[5])* $P(\Omega_5) = 0$.

Proof. Fix $\tilde{x} \in \Omega_5$, there exist $K > 0$ and $R > 0$ such that $|\nabla m| > K$ and $\partial_n m < 0$ in $B(\tilde{x}, 2R) \cap \overline{\Omega}$. Setting $\xi(x) = \rho(\frac{x-\tilde{x}}{R})$, then a similar calculation gives

$$\begin{aligned}
c^* - c_* &\ge \int_\Omega \xi^2(x)|\nabla w(x;\alpha) - \alpha w(x;\alpha)\nabla m(x)|^2 dx \\
&= \int_\Omega \xi^2(|\nabla w|^2 + \alpha^2 w^2|\nabla m|^2) - \alpha\xi^2\nabla(w^2)\cdot\nabla m dx \\
&= -\alpha\int_{\partial\Omega}\xi^2 w^2\partial_n m ds + \int_\Omega \xi^2|\nabla w|^2 + \xi^2 w^2(\alpha^2|\nabla m|^2 + \alpha\Delta m) + 2\alpha w^2\xi\nabla\xi\cdot\nabla m dx \\
&\ge \int_\Omega \xi^2|\nabla w|^2 + \xi^2 w^2(\alpha^2|\nabla m|^2 + \alpha\Delta m) + 2\alpha w^2\xi\nabla\xi\cdot\nabla m dx
\end{aligned}$$

where the last inequality follows from $\partial_n m < 0$. The remaining proof is the same as the proof in Lemma 4.12. □

***Lemma* 4.15.** *(c.f.[5])* $P(\Omega_6) = 0$.

Proof. The difficulty of our proof comes from the condtions $|\nabla m(x)| = 0$ and *arbitrary* direction e. The way to deal with such situation is to *flatten* $\partial\Omega$ *and change the Hessian of* m *into a diagonal matrix via some change of variables.*

Let $\tilde{x}$ be a non-degenerate boundary critical point, $a_1, ..., a_{l-1}$ be the eigenvalues of $D^2_{\partial\Omega}m(\tilde{x})$ and $a_1, ..., a_{l-1}, a_l$ be of $D^2m(\tilde{x})$. By rotation, we assume $n(\tilde{x}) = -e_l$ and $[D^2_{\partial\Omega}m(\tilde{x})]_{ij} = a_i\delta_{ij}$ for $i, j = 1, ..., l-1$. Let $y = Y(x)$ be a change of variables that flattens $\partial\Omega \cap B(\tilde{x}, 4R)$ where $R > 0$ is sufficiently small, then $Y(\tilde{x}) = 0$, $D_xY(\tilde{x})$ is the identity matrix, and $Y(\partial\Omega \cap B(\tilde{x}, 4R)) \subset \{y : y_l = 0\}$. Let $x = X(y)$ be the inverse of $y = Y(x)$, then the conditions that $\nabla m(\tilde{x}) = 0$ and $D_xY(\tilde{x})$ is the identity matrix imply

$$m(X(y)) = m(\tilde{x}) + \frac{1}{2}\sum_{i=1}^{l-1}(a_i y_i^2 + 2a_{il}y_i y_l) + \frac{1}{2}a_{ll}y_l^2 + O(|y|^3)$$

$$= \frac{1}{2}\sum_{i=1}^{l-1} a_i(y_i + \frac{a_{il}}{a_i}y_l)^2 + \frac{1}{2}y_l^2(a_{ll} - \sum_{i=1}^{l-1}\frac{a_{il}^2}{a_i}) + O(|y|^3)$$

Thus, there exists a change of variables $z = Z(y)$ defined by

$$z_i = y_i + \frac{a_{il}y_l}{a_i} + O(|y|^2) \text{ for } i = 1, ..., l-1 \text{ and } z_l = y_l[1 + O(y)]$$

such that

$$m(X(y)) = m(\tilde{x}) + \frac{1}{2}\sum_{i=1}^{l} a_i z_i^2$$

That is, the Hessian of m is a diagonal matrix with variables z. We note that the definition of z_l implies $Z \circ Y(\partial\Omega \cap B(0, 4R)) \subset \{z : z_l = 0\}$.

The above discussion holds for all points of Ω_6. Let $\tilde{x} \in \Omega_6$, then there exists $a_i > 0$ for some $i \in \{1, ..., l\}$. Setting $B^+ = B^+(0, 2R) = \{z \in B(0, 2R) : z_l > 0\}$ and $\xi(z) = \rho(\frac{z}{R})$, a careful calculation gives

$$\begin{aligned}
&c^* - c_* \\
&\geq \int_\Omega \xi^2|\nabla_x w - \alpha w\nabla_x m(x)|^2 dx = \int_\Omega \xi^2 w^2|\nabla_x(lnw - \alpha m)|^2 dx \\
&\geq \int_{B^+} \xi^2 w^2|\nabla_z(lnw - \alpha m)D_x Z|^2|det(D_z X)|dz \\
&\geq C\int_{B^+} \xi^2 w^2|\nabla_z(lnw - \alpha m)|^2 dz = C\int_{B^+} \xi^2|\nabla_z w - \alpha w\nabla_z m)|^2 dz \\
&\geq \int_{B^+} \xi^2|w_{z_i} - \alpha w m_{z_i})|^2 dz \\
&= -C\alpha\int_{\partial B^+} \xi^2 w^2\partial_n m ds + C\int_{B^+} \xi^2 w_{z_i}^2 + \xi^2 w^2(\alpha^2 m_{z_i}^2 + \alpha m_{z_i z_i}) + 2\alpha w^2\xi\xi_{z_i}m_{z_i}dz \\
&= C\int_{B^+} \xi^2 w_{z_i}^2 + \xi^2 w^2(\alpha^2 m_{z_i}^2 + \alpha m_{z_i z_i}) + 2\alpha w^2\xi\xi_{z_i}m_{z_i}dz \\
&\geq C\int_{B^+} \alpha\xi^2 w^2 m_{z_i z_i} - 2w^2\xi_{z_i}^2 dz \\
&\geq Ca_i\alpha\int_{B^+(0,R)} \xi^2 w^2 dz - C\frac{4}{R^2}\int_{B^+} w^2 dz
\end{aligned}$$

where $0 < C < |D_x Z|^2|detD_z X|$ in B^+ and the fourth equation follows from

$$\int_{\partial B^+} \xi^2 w^2\partial_n m ds = 0$$

because e_l is a normal vector of $\{z : z_l = 0\}$ and $m_{z_l} = 0$ on $\{z : z_l = 0\}$ in case $i = l$. Let $R' > 0$ satisfy $B(\tilde{x}, R') \cap \overline{\Omega} \subset X(Z^{-1}(B^+(0, R))$, then

$$P(B(\tilde{x}, R') \cap \overline{\Omega}) = \lim_{\alpha_j \to \infty} \int_{B^+(\tilde{x}, R') \cap \overline{\Omega}} w^2(x; \alpha_j) dx \leq \lim_{\alpha \to \infty} \int_{B^+(0,R)} \xi^2(z) w^2(z; \alpha) dz = 0.$$

□

Proof of Theorem 4.5

Proof. It suffices to show that (56) and (57) hold. (56) follows from (55). (57) follows from Lemma 4.12, 4.13, 4.14, and 4.15. □

5 Discussions

Conclusions: a Bifurcation Diagram

To organize our main results, we focus on the case $N = 2$, and establish a *bifurcation diagram* with α as the bifurcation parameter.

Case: $\beta/\nu \in [0, 1/\max_{\overline{\Omega}} m]$.

We fix Ω, m, μ, ν, and consider the case $\mu < \nu$. Let $\theta_1 \equiv (\theta(\cdot;\alpha,\mu), 0)$ and $\theta_2 \equiv (0;\theta(\cdot,\beta,\nu))$. When $\alpha = 0$ and $\beta/\nu = 0$, then θ_1 is globally asymptotically stable (or the slower-diffusing species wins), whereas θ_2 is globally asymptotically stable (or the faster-diffusing species wins) if the diffusion rates are similar, $\beta/\nu > 0$ is small, and the shape of the environment is convex (see Theorem 1.1(b) and Theorem 1.2). By some *perturbation argument*, the results still hold in the range $0 \le \alpha < \epsilon_1$ for some $\epsilon_1 > 0$ sufficiently small.

When $\alpha \ge \max\{C_1, C_3\}$ where C_1 and C_3 come from Lemma 4.3 and Lemma 4.8 respectively, then coexistence is a stable state.

In fact, all we have dealed with are the *limiting cases*: the advective tendency α is sufficiently small or large. The reason is that the limiting behaviors of the positive steady-state and the principal eigenvalues are easier to control (see Lemma 4.7 and Theorem 4.5). In the *intermediate cases* $\epsilon_1 \le \alpha \le \max\{C_1, C_3\}$, the stable states, even the dynamics of the full system are unknown. As a consequence, the following table organizes our main results:

Parameter Range	Stable States	Related Theorems	Remarkable Conditions
$0 \le \alpha < \epsilon_1$, $\mu < \nu$	θ_1	Theorem 1.1(b), 1.2	$\beta/\nu = 0$
	θ_2	Theorem 1.2	$\mu \approx \nu$, $\beta/\nu > 0$ small
			Ω is convex
$\epsilon_1 \le \alpha < \max\{C_1, C_3\}$	unknown		
$\alpha \ge \max\{C_1, C_3\}$	coexistence	Theorem 1.3(a)	(A2)

Remark. *The case* $\mu > \nu$ *is almost analogous. In the singular case* $\mu = \nu$, *if* $\alpha = \beta = 0$, *then a continuum of positive equilibria of the form* $\{(\kappa\theta(x;0,\mu),(1-\kappa)\theta(x;0,\mu)) : 0 \le \kappa \le 1\}$ *is globally asymptotically stable. If* $\alpha > 0$ *is small and* $\beta = 0$, *then* θ_1 *is still globally asymptotically stable. (see Theorem 3.4).*

Case: $\beta/\nu \in [1/\min_{\overline{\Omega}} m, \infty)$**.**

We fix Ω, m, μ, and ν. When $0 \le \alpha \le \mu/\max_{\overline{\Omega}} m$ and $\beta \ge \max\{C_1, C_3\}$, then coexistence is a stable state (see Theorem 1.3(a)).[10] When $\alpha \ge \tilde{C} \equiv \max\{C_2, C_3, C_4\}$ where C_2, C_3, and C_4 come from Lemma 4.3, Lemma 4.6, and Lemma 4.8 respectively, then θ_2 is globally asymptotically stable (or the species with less advective tendency wins) provided that (A3) holds and $m > 0$ in $\overline{\Omega}$ (see Theorem 1.3(b)). In the *intermediate cases* $\mu/\max_{\overline{\Omega}} m < \alpha < \tilde{C}$, the stable states, even the dynamics of the full system are unknown. As a consequence, the following table organizes our main results:

Parameter Range	Stable States	Related Theorems	Remarkable Conditions
$0 \le \alpha \le \mu/\max_{\overline{\Omega}} m$	coexistence	Theorem 1.3(a)	$\beta \ge \max\{C_1, C_3\}$
$\mu/\max_{\overline{\Omega}} m < \alpha < \tilde{C}$	unknown		
$\alpha \ge \tilde{C}$	θ_2	Theorem 1.3(b)	(A3), $m > 0$ in $\overline{\Omega}$

Further Problems

The following are some interesting problems which may be worth further researching:

1. Problems concerning the bifurcation diagram

To completely establish the bifurcation diagram, a challenging task is to control the behaviors of the positive steady-state and the principal eigenvalues when α lies in intermediate ranges. Another problem arises when $\beta/\nu \in (1/\max_{\overline{\Omega}} m, 1/\min_{\overline{\Omega}} m)$, a challenging task is to construct some useful estimates alike to Lemma 4.2 and Lemma 4.4.

[10] Here, α and β, μ and ν are switched mutually in order to apply Theorem 1.3(a).

2. Problems concerning the assumptions on the intrinsic growth rate m

We see that (A1) is not removable (see Lemma 1.5 and Theorem 1.6) and (A2) is not too biologically restrictive. The problem is that (A3) is not realistic. It is very challenging to weakend (A3) since if there are many points of local maxima of m, Theorem 4.5 may provide no useful information (see Lemma 4.2, the proof of Lemma 4.6 and 4.10).

3. Problems concerning the suitable modifications on the full system

We assume that the species move toward along the resource gradient ∇m, but neglect other crucial effects such as population densities. A more realistic term is $\nabla(m - g(u, v))$ rather than ∇m, then the first problem is to choose some suitable $g(u, v)$. For mathematical analysis, sometimes we need to guarantee the *"2 in 1" structure*, that is, two equations with the same parameters can be added into one equation (see the proof of Lemma 3.5 and ref.[7], Lemma 5.4). A suitable choice is $g(u, v) = \kappa(u + v)$ for some constant $\kappa > 0$. To study the modified full system is a challenging task. Indeed, our main results may provide some useful information for the modified full system since our full system (2) is an approximation if κ is sufficiently small.

Appendix: a Manual for Maximum Principles

This appendix is contributed to be a collection of (parabolic) maximum principles for *weakly-coupled parabolic linear systems* [11]. The main ideas to prove such maximum principles can be found in [16], Chapter 3, Section 8.

Let $\Omega \subset \mathbb{R}^l$ be a bounded domain with smooth boundary $\partial\Omega$. For given $T > 0$, let $u(x,t) = (u_1(x,t), u_2(x,t), ..., u_N(x,t))$ be continuous in $\overline{\Omega} \times [0,T]$, and $D_x u$, $D_x^2 u$, and u_t are continuous in $\Omega \times (0,T]$. Suppose that for each $k = 1, 2, ..., N$, $u_k(x,t)$ satisfies the *differential inequality*:

$$\frac{\partial u_k}{\partial t} \leq \sum_{i,j=1}^{l} a_{ij}^{(k)}(x,t) \frac{\partial^2 u_k}{\partial x_i \partial x_j} + \sum_{j=1}^{l} b_j^{(k)}(x,t) \frac{\partial u_k}{\partial x_j} + \sum_{j=1}^{N} c_j^{(k)}(x,t) u_j \text{ in } \Omega \times (0,T]$$

where $[a_{ij}^{(k)}(x,t)]_{l\times l}$ is non-negative definite and uniformly elliptic in $\Omega \times (0,T)$, $a_{ij}^{(k)}(x,t)$, $b_j^{(k)}(x,t)$, and $c_j^{(k)}(x,t)$ lie in $L^\infty(\overline{\Omega} \times [0,T])$. Suppose $c_j^{(k)} \geq 0$ in $\Omega \times (0,T]$ for $k \neq j$, then the following maximum principles hold.

The Parabolic Strong Maximum Principle

If $\max_j \max_{\overline{\Omega}\times[0,T]} u_j(x,t) = u_k(x_0,t_0)$ for some $(x_0,t_0) \in \Omega \times (0,T]$, then $u_k(x,t) = u_k(x_0,t_0)$ in $\Omega \times (0,t_0)$.

The Parabolic Hopf Boundary Lemma

If $\max_j \max_{\overline{\Omega}\times[0,T]} u_j(x,t) = u_k(x_0,t_0) \geq 0$ for some $(x_0,t_0) \in (\overline{\Omega}\times\{0\}) \cup (\partial\Omega\times(0,T))$, and (x_0,t_0) satisfies the interior sphere condition in $\Omega \times (0,T)$, then either u_k restricted in some neighborhood in $\Omega \times (0,t_0)$ is a constant function or $\partial_n u_k(x_0,t_0) > 0$.

The Parabolic Comparison Principle

Let $D \subset \mathbb{R}^N$ be a nonempty closed convex set, and $f : \overline{\Omega} \times D \to \mathbb{R}^N$ given by $f = f(x,u)$ is C^1 and *cooperative* in u. Let $\overline{u}$ and $\underline{u}$ be continuous in $\overline{\Omega} \times [0,T]$, and $D_x\overline{u}$, $D_x\underline{u}$, $D_x^2\overline{u}$, $D_x^2\underline{u}$, $\overline{u}_t$, and $\underline{u}_t$ are continuous in $\Omega \times (0,T]$. Suppose that for each $k = 1, 2, ...N$, the following differential conditions hold:

$$\begin{cases} \dfrac{\partial \underline{u_k}}{\partial t} \leq \displaystyle\sum_{i,j=1}^{l} a_{ij}^{(k)}(x,t) \frac{\partial^2 \underline{u_k}}{\partial x_i \partial x_j} + \sum_{j=1}^{l} b_j^{(k)}(x,t) \frac{\partial \underline{u_k}}{\partial x_j} + f_k(x,\underline{u}) & \text{in } \Omega \times (0,T) \\ B[\underline{u_k}] = \partial_n \underline{u_k} \leq 0 & \text{on } \partial\Omega \times (0,T) \end{cases}$$

[11] A parabolic linear system is weakly-coupled if it is coupled only in the reaction terms.

$$\begin{cases} \dfrac{\partial \overline{u_k}}{\partial t} \geq \displaystyle\sum_{i,j=1}^{l} a_{ij}^{(k)}(x,t)\frac{\partial^2 \overline{u_k}}{\partial x_i \partial x_j} + \sum_{j=1}^{l} b_j^{(k)}(x,t)\frac{\partial \overline{u_k}}{\partial x_j} + f_k(x,\overline{u}) & \text{in } \Omega \times (0,T) \\ B[\overline{u_k}] = \partial_n \overline{u_k} \geq 0 & \text{on } \partial\Omega \times (0,T) \end{cases}$$

If $\underline{u_k}(x,0) \leq \overline{u_k}(x,0)$ in $\overline{\Omega}$ for all k, then $\underline{u_k}(x,t) \leq \overline{u_k}(x,t)$ in $\overline{\Omega} \times [0,T]$ for all k.

Some Remarks

1. A direct consequence from the maximum principles is the uniqueness of the classical solution of the weakly-coupled parabolic linear system:

$$\begin{cases} \dfrac{\partial u_k}{\partial t} = \displaystyle\sum_{i,j=1}^{l} a_{ij}^{(k)}(x,t)\frac{\partial^2 u_k}{\partial x_i \partial x_j} + \sum_{j=1}^{l} b_j^{(k)}(x,t)\frac{\partial u_k}{\partial x_j} + \sum_{j=1}^{N} c_j^{(k)}(x,t)u_j & \text{in } \Omega \times (0,T) \\ B[u_k] = \partial_n u_k = 0 & \text{on } \partial\Omega \times (0,T) \end{cases}$$

For *any* given $T > 0$, the maximum principles are applicable whenever the solution of the above linear system for the domain $\Omega \times (0,\infty)$ is *restricted* on $\Omega \times (0,T)$; thus by the *uniqueness*, the maximum principles hold for the domain $\Omega \times (0,\infty)$.

2. In the full system (2):

$$[a_{ij}^{(k)}(x,t)]_{l\times l} = d_k \mathbb{I}_l$$

$$b_j^{(k)}(x,t) = -\alpha_k m_{x_j}(x)$$

$$c_j^{(k)}(x,t) = \begin{cases} [m(x) - \displaystyle\sum_{i=1}^{N} u_i(x,t) - \alpha_k \Delta m(x)] & \text{if } j = k \\ 0 & \text{if } j \neq k \end{cases}$$

$$D = K^+ = \{u \in C^{2+\delta}(\overline{\Omega}) : u \geq 0\}$$

$$f_k(x,u) = f_k(x,u_1,...,u_N) = u_k(x,t)[m(x) - \sum_{i=1}^{N} u_i(x,t)]$$

Hence, except that f_k may not be cooperative, all the required conditions are obviously satisfied.

3. If $N = 1$, then $f_k(x,u)$ is cooperative in u *vacuously by definition*; hence The Parabolic Comparison Principle is applicable.

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後記：研究歷程

見山是山、見山不是山、見山又是山。

一、 前言

本論文的研究歷程分爲三個階段：探索、研讀和撰寫。**探索階段**開始於碩一上 2009 年 1 月，夏俊雄老師要求寒假期間精讀參考文獻〔7〕(簡稱文獻〔7〕)，結束於碩二上 2010 年 2 月寒假結束，約歷時一年。接著，**研讀階段**開始於 2010 年 2 月，當時已備齊所有必須回顧的文獻〔1〕～〔7〕，之後陸續精讀，5 月讀完文獻〔6〕而結束。**撰寫階段**開始於 2010 年 4 月，初稿完成於 5 月，完稿則於 7 月完成，約歷時三個月。

二、 探索階段

我很幸運，發表於 2008 年的文獻〔7〕是一篇既新穎又極具啓發性的好文章。前兩節翔實闡釋了本文主要方程組（見論文式子（2），簡稱主方程組）的生態學意義、建構方法以及四個已知結果：由文獻〔1〕而來的 Theorem 2.1、文獻〔3〕〔4〕而來的 Theorem 2.2 和文獻〔6〕而來的 Theorem 2.3 與 2.4。事實上，**將上述四個結果的論證過程寫清楚是本論文的主要目的。**

文獻〔7〕在第四節給出局部穩定性（local stability）的判準以及主特徵值（principal eigenvalues）所滿足的積分方程，第五節給出排除共存（coexistence）的數學條件，第六節引進單調動力系統理論（the theory of monotone dynamical systems）來決定全域穩定性（global stability）。讀者可以發現：

局部穩定性 － 排除共存狀態 － 全域穩定性

這樣的思考及論證過程不只是文獻〔1〕〔3〕〔6〕〔7〕，也是本論文的共同特色。另外，文獻〔7〕主要使用的數學工具只有散度定理（divergence theorem）以及二階橢圓偏微分方程的基本知識，這些工具在研究所微分方程課程中都能學到。質言之，**因為主方程組具有豐富的生態學意義，對於碩士研究生而言，先備知識門檻適中，又可以練習不少數學工具，所以引起我進一步研究的興趣。**

碩一上的寒假，很感謝林紹雄老師撥空開設反應擴散方程（reaction-diffusion equations）的研討會。每週四上午三小時由老師講授基本知識：包含最大值原則（maximum principles）、半群理論（semi-group theory）、特徵值問題和中央流型理論（center manifold theory），這些知識奠定本論文研究的基礎；下午三小時由學生講解相關主題，我負責講解 Lotka-Volterra 模型[1]。那兩次講解雖然生澀，經常需要老師提示，但從反應擴散方程的一般性觀點探討 Lotka-Volterra 模型的存

1. 跟主方程不同之處是：內蘊生長率（intrinsic growth rate）是常數，而反應矩陣（interaction matrix）爲耗散（dissipative）形式。

在性與穩定性問題，對我而言是一個極爲寶貴的經驗。

讀完文獻〔7〕後，我已從引用文獻中按圖索驥找出所有相關文獻。然而，由於碩二時我花許多時間在學習林紹雄老師開設的偏微分方程課程上，直到 2010 年 2 月寒假結束時，我才下定決心研讀所有相關文獻。

三、 研讀階段

我研讀的文獻依序是：〔5〕〔1〕〔3〕〔4〕〔2〕〔6〕。

文獻〔5〕的前四節重構爲本論文第四節第三小節。先讀文獻〔5〕是因爲一開始我很好奇如何控制主特徵值的漸近行爲（asymptotic behaviors）。相較於文獻〔7〕，文獻〔5〕展示頗多細膩的估計，值得研讀。

文獻〔1〕重構爲本論文第二節，亦即 Type A 的主要結果。讀完文獻〔5〕之後，我認爲依照「發表年代」研讀較能掌握脈絡，因此從文獻〔1〕讀起。我從文獻〔1〕學習如何處理各種特徵值問題（eigenvalue problem）。令我困惑許久的是文獻〔1〕沒附證明的 Lemma 2.2，它涉及半均衡解（semi-trivial equilibrium）的存在性，至關緊要。我依照引用文獻找到出處[2]，但出處提供的證明不能適用於 Type B 與 Type C 等一般情形，幸運的是 2010 年 5 月找到了文獻〔8〕既精簡又具有一般性的證明（見論文 Theorem 1.6）。另外，請讀者注意，有兩種假設可適用文獻〔1〕的結果：內蘊生長率在某點爲正值且擴散速率（diffusion rate）夠小，或內蘊生長率的平均值爲正。唯有文獻〔1〕採取前者，其他文獻及本論文則採取後者。在超過兩種競爭物種的全域穩定性方面，不同於單調動力系統理論，文獻〔1〕採取 Morse 分解，但必須預設 Conjecture 1 爲真才能加以證明。然而，因爲無法確證 Conjecture 1，本論文也就沒有回顧 Morse 分解法及其相關結果。

文獻〔3〕重構成本論文第三節前半部分，亦即 Type B 中局部穩定性的結果（見論文 Theorem 3.4）。我從文獻〔3〕學習到擾動分析（perturbation analysis）方法，以及如何嚴謹地檢驗隱函數定理（implicit function theorem）的條件（見論文 Lemma 3.2），另一方面，在思維與論證方法上，文獻〔3〕可視爲文獻〔7〕的原型，從中我再一次學習如何透過已知參數來表示主特徵值的正負號，關鍵是從線性化後的相關方程組中推導出有用的積分方程。

文獻〔4〕重構成本論文第三節後半部分，亦即 Type B 中全域穩定性的結果（見論文 Lemma 3.4）。文獻〔4〕的內容十分豐富，事實上文獻〔6〕的許多結果是文獻〔4〕結果的一般化，雖然本論文只回顧 Lemma 3.4，但建議在閱讀文獻〔6〕前先研讀文獻〔4〕。我從文獻〔4〕學習到如何應用橢圓正則性（elliptic regularity）來控制參數趨近於 0 時，主方程組及其均衡解的行爲。其中，我深刻體會到主方程組的特殊結構所扮演的角色及其在推廣上可能無法克服的侷限。

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2. R. S. Cantrell, C. Cosner, and V. Hutson: Ecological models, permanence, and spatial heterogeneity. Rocky Mountain Journal of Mathematics. Vol.26, Number 1, 1-35. (1996)

文獻〔2〕的主要結果之一是假若環境形狀非凸（convex），則可以建構本論文 Theorem 1.2 的反例，因此產生一個十分有趣且值得討論的現象：環境幾何形狀的差異會影響競爭物種的演化結果。然而，讀完文獻〔2〕後，我認爲完整回顧該反例的建構過程要花費許多篇幅，而且**我逐漸確知論文的主軸是建立主方程組之長期演化結果的分歧圖**（bifurcation diagram），因此仔細衡量後，我決定只簡要提及（見論文第二節最後的 Remark）[3]。

文獻〔6〕重構成本論文第四節，亦即 Type C 的主要結果。由於 Type C 是主方程組在兩種競爭物種上最具一般性的情形，又兩個競爭物種所代表的方程在參數方面具有對稱性，所以數學上要先固定某一方程的參數區間，然後調整另一方程的特定參數，例如有向傾向（advective tendency），來考察競爭物種長期演化結果的變化，及決定是否有分歧現象。據此，相較於文獻〔1〕〔3〕〔4〕，文獻〔6〕面臨頗爲不同的問題，也需要更進一步的分析工具。首先，我從文獻〔6〕中學習到如何透過最大值原則找到適當的參數區間（見論文 Lemma 4.1 和 4.2）。然後，進行主特徵值比較時終於了解文獻〔5〕研究主特徵值之漸近行爲的原因（見論文 Lemma 4.6 和 4.10），以及主方程組必須配備不具生態一般性之（A3）假設的原因，而這個假設也構成推廣本論文 Theorem 1.3 最難克服的阻礙。

四、 撰寫階段

讀完必須回顧的文獻〔1〕～〔7〕後，2010 年 4 月我開始撰寫論文[4]。**我從一開始就定位本論文為一篇豐富、完整且具有「故事性」的回顧**。

爲了讓「故事」有好的開始，我在第一章簡要提及 Lotka-Volterra 模型的歷史[5]、利用常見的通量法（flux method）推導出主方程組，然後仔細說明（C1）～（C4）等數學限制（constraints）可能的生態學意義。在描述主要結果時，特別強調（A1）～（A3）等關於內蘊生長率之假設（assumptions）與定理之間的關係，以及每個定理可能的生態學意義與相關現象的詮釋。

值得說明的是第一章第二小節〈Frequently-applied Theorems and the Main Scheme〉的誕生是本論文結構的變革。區分出三種 Type 後，我發覺它們有共同的基本問題及需要的常用定理[6]（見論文 Theorem 1.6、1.7 和 1.9）。如果按照每個 Type 依序寫下來，那同樣型式的定理要證明三次。由於 Type C 最具一般性，所以我決定在第一章就提供 Type C 的主方程組所需要的常用定理。然而，過程

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3. 由於文獻〔3〕的第三節以及文獻〔4〕第二節第二小節重新回顧了文獻〔2〕，所以在 Remark 中我提供較晚發表的文章來源，若要完整了解建構過程，建議研讀文獻〔2〕。
4. 撰寫論文時，我花了不少時間學習 LaTex 與 TeXworks。許多朋友建議使用 LyX，因爲可以「邊打邊看」，但我已經學會 LyX，且 LaTex 是所有相關書寫軟體的始祖，所以我選擇使用 LaTex。
5. 由於 Lotka-Volterra 模型具有八十年歷史，數學上可分爲常微分方程組或偏微分方程組，類型上可分爲合作（cooperative）、競爭（competitive）或掠捕（prey-predator），設定上擴散速率、有向傾向、內蘊生長率和反應矩陣可以與時間或空間有關，因此對於一篇碩士論文而言，要完整回顧幾乎是不可能的任務。
6. 三個共通的基本問題是：半均衡解的存在性、局部穩定性的判準以及全域穩定性的判準。

並不輕鬆。Theorem 1.6 的證明並不簡單。Theorem 1.7 的證明雖然直接，但預設了「線性化判準」（linearity criterion）[7]，我花了不少時間檢驗文獻〔15〕中該判準得以適用的條件。Theorem 1.9 處理均衡解的漸近行爲，需要大量單調動力系統的知識，所以我只檢驗文獻〔14〕適用 Theorem B 所需的條件[8]，而該定理幫助我萃取出決定全域穩定性的主要綱領（main scheme）。

我該如何「說故事」呢？這個問題不但涉及論文的行文風格，也關係到篇章結構的認知。眾所周知，大部分的數學文章都遵照**「邏輯脈絡」**將內容組織爲「定義 － 引理 － 定理」的結構，優點是節省篇幅，缺點是讀完後仍會覺得許多內容是「天外飛來一筆」。**「探索脈絡」**則強調探索與發現的過程，要求作者從思索問題的過程中「脈絡化」乍看抽象的定義與引理，因此結構通常是「問題 － 定理 － 定義 － 引理」，優點是讀完後對於內容不會產生「疏離感」，缺點則是作者要花費更多心思與篇幅。**既然本論文的定位是回顧，我當然不能照本宣科，於是我選擇「探索脈絡」，盡量嘗試「重建」文獻原作者們探索的過程[9]。**

要說出哪些「故事」呢？這個問題涉及讀者知識背景的預設。我的標準是：**如果是研究所微分方程必修課的內容，則我提供來源但不予以證明[10]；除此之外，我都努力在完全理解的前提下提供證明[11]**。

Type A 是 Type B 和 C 的原型，主要處理特徵值問題，使用的數學方法十分標準。不過，我起初寫得頗爲複雜，原因是我對於主方程組的本質與相關的數學方法還不是很熟悉，於是在撰寫其他 Type 的內容時一直回頭加以簡化[12]。另外，讀者或許注意到：爲何 Type A 第二小節名稱爲「插曲」（interlude）？原因是該小節內容與主要結果（見論文 Theorem 1.1）無關。那爲何加以回顧？當然，一個原因是該小節處理一個非常特別的問題：擾動後半均衡解是否仍落在生物合理區域（biological feasible region）？但最重要的理由是「友情」，是爲了紀念我的朋友硯仁當初用圖論方法在五分鐘內就證明 Lemma 2.5 給我的震撼與感動。

Type B 也處理特徵值問題，但我花了不少時間檢驗適用隱函數定理的條件和研讀文獻〔10〕第六章關於橢圓正則性的內容。當然，令人最感興趣的是環境

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7. 亦即考慮主方程組針對均衡解線性化後的特徵值問題，其主特徵值的正負號能決定均衡解的局部穩定性。
8. 要完整地回顧 Theorem B，至少需要十頁篇幅，而這將偏離本論文的主軸。
9. 我認爲本論文第四節最符合「探索脈絡」的要求，參見論文 Lemma 4.1、4.2、4.7 和 4.8 的論證過程。
10. 主要是橢圓型的最大值原則、基本的特徵值問題、Sobolev 不等式和橢圓正則性等研究所偏微分方程式相關課程都會學習到的內容。更具體的標準是文獻〔9〕〔10〕的內容。
11. 遵照這個標準的結果是本論文篇幅爲 62 頁，大約是一般數學研究所碩士論文的二到三倍。不過本論文回顧了主方程組十一年來（從 1998 年發表的文獻〔1〕到 2008 年發表的文獻〔7〕）的重要發展，必須回顧的文章篇幅超過兩百頁，又我相信本論文每個論證與定理都環環相扣，所以應該無法在不影響主要內容的前提下大幅減少篇幅。
12. 第二節原本有十頁，後來刪減爲七頁。簡化的當下會心疼時間精力付諸流水，但隨即感覺簡化後邏輯與結構上的清爽。

的幾何形狀與長期演化結果的關係（見論文 Lemma 3.3），我盡量在數學方面重建探索的過程，不過直到如今還是想不到生態學上的詮釋。另外，直到寫完 Lemma 3.5 後，才決定不回顧文獻〔2〕的結果。

撰寫 Type C 時，首先面臨的挑戰是如何說清楚 Theorem 1.3 中參數區間的由來。爲了符合「探索脈絡」的要求，我發覺從判定主特徵值正負號的問題出發，過程中適當地引入最大值定理（見論文 Lemma 4.1）能加以充分說明。接著，我發現主特徵值之漸近行爲的分析（見論文 Theorem 4.5）可以解釋提出 Lemma 4.6 和 4.10 等結果的原因，因此下一個挑戰是重建 Theorem 4.5 的探索過程。雖然 Theorem 4.5 使用的數學方法十分標準，但需要極細膩的觀察與分析，所以花了將近八頁的篇幅。另外，我也仔細檢驗了適用文獻〔13〕Theorem 4 的條件。

第五節的結論是研讀文獻〔6〕〔7〕後改寫而成。事實上，文獻〔6〕提供了比本論文更加完備的分歧圖，不過該分歧圖的基礎是文獻〔6〕中未附證明且尚未發表的 Theorem 5，我思索後，覺得在期限內無法證明，所以決定只就本論文的主要結果建立初步的分歧圖。在〈Further Problems〉的討論中，除了第二點外，都可以在文獻〔7〕找到更加完善的討論。

寫完 Type C 的主要結果後，我還有兩個煩惱許久而未解決的基本問題：

（1） 主方程組之解的存在性與有界性（見第一節第五頁的討論）。文獻〔15〕Corollary 4.1 確證了存在性，而拋物型最大值原則保證了有界性[13]。

（2） 如何嚴謹地適用最大值原則。爲此，我決定在附錄（appendix）提供拋物型最大值原則的敘述與相關注意事項[14]。

約莫 6 月底，論文本體幾乎完成。中間經歷 6 月 10 日的論文口試，我製作了 27 張投影片在半小時內介紹本論文第一章[15]，感謝夏俊雄老師、J. Bona 教授、陳虹秋教授跟林紹雄老師給我許多啓發與建議，讓我的論文更加完善[16]。

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13. 因爲有界性，亦即物種在有限時間內其密度不會達到無限大，是生態上很自然的結果，在數學上則與本論文 Theorem 1.6 有關，所以我花了好幾天思索證明。某天下午我想累了，在床上看書，突然就得到證明的線索，只需要一行就能說明。這樣戲劇性的結果是一個非常難忘的經驗。
14. 最大值原則分爲橢圓型跟拋物型。橢圓型最大值原則參照文獻〔9〕〔10〕即可，但有時候應用上需要一些調整，郭一鴻在這方面給我不少提示（見論文 Lemma 4.1）。拋物型最大值原則可參照文獻〔16〕，但我主要參照林紹雄老師的講義〈Lectures on Reaction-Diffusion Systems〉。由於該講義尚未出版，林老師也說主要的證明思維來自文獻〔16〕，因此本論文參考文獻只列出文獻〔16〕。
15. 歡迎讀者索取投影片，請來信聯絡：R97221006@ntu.edu.tw 或 ntutiws@hotmail.com。
16. 我在當時的論文和投影片中都沒有說明參數之間是否相關（見論文 Theorem 1.3），四位口試委員都提點出這個至關緊要的問題。另外，Bona 教授提醒我數值模擬在微分方程研究中的重要性。

五、 心路歷程

我曾在 5 月 12 日提交初稿兩天後，寫出醞釀已久的心情，其中一段是：

> 從前一陣子到現在，我都有個「心理障礙」：不知如何定位自己的「論文」。加引號是因為我做的是「回顧」，是「研究」的前置階段，還不算是「做研究」。我知道，我很希望自己能做研究，因為在數學這個領域，能夠想出專屬於自己的定理，或雖然是別人的定理，但有自己獨創的證明，都是人生中很特殊，印象很深刻的經驗。

雖然我深知在發展成熟的微分方程領域，要做「新問題」或只是證明「新定理」都真的很不容易，但如果沒有「創新」成份，又怎麼能稱爲論文？說得更直接，就是「回顧」與「抄襲」有何不同[17]？不過：

> 回想當初剛接觸這個研究主題，閱讀相關文獻，有多少定理是「硬啃硬證」，有多少定理是原作者說 standard、obvious 或 trivial，而我約莫一年後才真的弄清楚，才發現那些所謂 standard、obvious 和 trivial 的定理，可能是好幾頁的證明，甚至是一篇文章的主要結果。

所以，我認爲如果能理解所有內容，釐清或論證那些不 standard、obvious 或 trivial 的內容，並重建它們的「探索脈絡」，然後組織貫串爲一個故事，這樣應該就不是抄襲，而是一篇回顧。然而，我仍然煩惱這樣的回顧會有什麼知識上的「貢獻」，直到：

> 那天陳其誠老師關心我的論文進度，我有點慚愧地說在做 survey。他看著我說：很好阿！好好組合，可以造福學弟妹。對阿，我怎麼沒想到能有這個貢獻？

雖然讀者可遇不可求，但陳老師這句話讓我豁然開朗，因爲至少「造福了我自己」。回想整個研究歷程，不但讓我學習到有用的數學方法，也深刻體會「讀數學」與「做數學」的本質差異，更重要的，讓我更認識自己。

記得七年前，我第一次走在椰林大道上，要趕去共同教室上憲法課，那時的我絕對想不到七年後，我仍然選擇數學之路，還寫了一篇十分煩惱自己的論文。進入研究所之前總覺得人生很簡單，不外乎 all or nothing，如今，卻在該離開的時候才開始思索。

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17. 據我所知，可能因爲當代數學研究的本質，大部分碩士論文都屬於回顧，或所謂的「讀書報告」。能研究「新問題」或提供「新結果」的主題通常與圖論、組合學、計算數學或統計學有關，這些領域的特色是還有許多適合碩士階段研究的問題，且不需太長的養成教育就可以開始研究。當然，就算是發展成熟的學科，也有碩士論文研究「新問題」或提供「新結果」，但關鍵或許在於如何判斷以及如何評價「創新」。