The effects of diffusion and spatial variation in the Lotka-Volterra competition-diffusion system

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Abstract

It is well known that the interactions between diffusion and spatial heterogeneity could create very interesting phenomena. In this thesis, using the classical Lotka-Volterra competition system, we will illustrate the combined effects of dispersal and spatial variation on the outcome of the competition.

We first show that, with the total resources being fixed at exactly the same level, a heterogeneous distribution of resources is usually superior to its homogeneous counterpart in the presence of diffusion. Then we study the more general case when both species have heterogeneous carrying capacities, but still with the same amount of total resources. Limiting behaviors of co-existence steady states as the dispersal rates tend to 0 or ∞ are also obtained.

In the end, we investigate the much broader situations - including different strengths and distributions of the resources, and with different competition abilities. Stability properties of semi-trivial and co-existence steady states are characterized under various circumstances.

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Chapter 1

Introduction

Spatial characteristics of the environment play an important role in ecology and evolution. An interesting example illustrating the joint effects of diffusion and spatial heterogeneity is the "slower diffuser always prevails" phenomenon in [DHMP], where the authors considered the following Lotka-Volterra competition-diffusion model:

$$\begin{cases} U_t = d_1\Delta U + U(m(x) - U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ V_t = d_2\Delta V + V(m(x) - U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\ U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{in } \Omega. \end{cases} \tag{1.1}$$

Here $\Delta = \sum_{i=1}^N \frac{\partial^2}{\partial x_i^2}$ is the usual Laplace operator; $U(x,t)$ and $V(x,t)$ represent the population densities of two competing species which are therefore assumed to be non-negative, with corresponding migration rates d_1 and d_2; and Ω, the habitat, is a bounded smooth domain in $\mathbb{R}^N$. For simplicity, we assume that both U_0 and V_0 are non-negative and not identically zero. The function $m(x)$ represents their common local carrying capacity. We assume that $m(x)$ satisfies the following hypothesis:

(M1) $m(x) \in C^\gamma(\bar{\Omega})$ $(\gamma \in (0,1))$ is nonconstant, $m(x) \geq 0$ on $\bar{\Omega}$ and $\overline{m} := \frac{1}{|\Omega|}\int_\Omega m(x)\,dx > 0$.

If $m(x) \equiv \overline{m} := \frac{1}{|\Omega|}\int_\Omega m > 0$ on $\bar{\Omega}$ (i.e., the spatial distribution of the resources is homogeneous for both species), U and V always co-exist regardless of the diffusion rates d_1 and d_2. However, when spatial heterogeneity is incorporated into the nonlinearity (i.e., $m(x)$ *is nonconstant*), the situation changes drastically. It is shown by Dockery et al. [DHMP] that if $d_1 < d_2$, then *the slower diffuser U always wipes* *the faster competitor* V *out regardless of initial conditions*, i.e., $(\theta_{d_1,m}, 0)$ is globally asymptotically stable, where $\theta_{d,m}$ denotes the unique positive solution to

$$d\Delta\theta + \theta(m(x) - \theta) = 0 \text{ in } \Omega, \quad \partial_\nu \theta = 0 \text{ on } \partial\Omega. \tag{1.2}$$

(See, e.g., [CC] for the proof of existence and uniqueness results of (1.2).)

Such drastic change in dynamics of (1.1) has brought about tremendous interests from both mathematicians and ecologists. (See [L1, L2, LN] and the references therein.)

Note that $\theta_{d,m}$ enjoys the following important property very different from the case when m is constant on $\bar{\Omega}$:

$$\int_\Omega \theta_{d,m} > \int_\Omega m \tag{1.3}$$

for all $d > 0$, as observed by Lou in [L1]. Indeed, dividing the equation of $\theta_{d,m}$ in (1.2) by $\theta_{d,m}$ and integrating over Ω, we obtain that

$$\int_\Omega (m - \theta_{d,m}) = -d \int_\Omega \frac{|\nabla \theta_{d,m}|^2}{\theta_{d,m}^2} < 0, \tag{1.4}$$

since $\theta_{d,m} \not\equiv$ const, as $m \not\equiv$ const. This fact indicates that *for any dispersal rate the system* (1.2) *with spatially heterogeneous resources will always support a total population larger than the environment's total carrying capacity* - a curious fact indeed.

Motivated by this observation, we would like to pursue further to understand the impact of spatial heterogeneity in two competing species.

First, we consider the following 2×2 Lotka-Volterra competition system

$$\begin{cases} U_t = d_1 \Delta U + U(m(x) - U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ V_t = d_2 \Delta V + V(\overline{m} - U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\ U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{in } \Omega, \end{cases} \tag{1.5}$$

where $m(x)$ is a *non-negative nonconstant* function representing the local carrying capacity of U at x, which reflects *the heterogeneous distribution of resources for* U. For comparison purposes, we have assumed that V *has the same total resources as* U *but distributed uniformly in* Ω. In other words, we assume that species U and V

are *identical* in their competition abilities; however, the distribution of resources is *heterogeneous* for species U but *homogeneous* for V, while the two have *exactly the same* total resources.

Indeed, we will show that the species U usually will have some advantage over the species V during the competition; in particular, the semi-trivial steady state $(0, \overline{m})$ can never be stable, which implies that the species U will always survive!

Before we state our precise results, we introduce the following notation. For the two semi-trivial steady states $(\theta_{d_1,m}, 0)$ and $(0, \overline{m})$ of (1.5), the following three subsets of the first quadrant $\mathcal{Q} := \{(d_1, d_2) \mid d_1, d_2 > 0\}$ are of interest:

$$\begin{aligned}
\Sigma_U &:= \{(d_1, d_2) \in \mathcal{Q} \mid (\theta_{d_1,m}, 0) \text{ is linearly stable}\}, \\
\Sigma_V &:= \{(d_1, d_2) \in \mathcal{Q} \mid (0, \overline{m}) \text{ is linearly stable}\}, \\
\Sigma_- &:= \{(d_1, d_2) \in \mathcal{Q} \mid \text{both } (\theta_{d_1,m}, 0) \text{ and } (0, \overline{m}) \text{ are linearly unstable}\}.
\end{aligned} \tag{1.6}$$

(For the notion and characterization of linear stability and instability, see Chapter 2.1 below. Also note that, from the theory of monotone flow, for all (d_1, d_2) in Σ_-, U and V always co-exist!)

Theorem 1.1. *Assume that* (**M1**) *holds. Then the following hold for system* (1.5)*:*

(i) $\Sigma_V = \emptyset$.

(ii)
$$\Sigma_U = \{(d_1, d_2) \in \mathcal{Q} \mid d_2 > d_2^*(d_1)\}, \tag{1.7}$$
where $d_2^*(d_1)$ *is a continuous function of* d_1 *defined in* $\mathbb{R}^+$. *Moreover,*
$$\lim_{d_1 \to 0^+} d_2^* = \infty, \tag{1.8}$$
$$\lim_{d_1 \to \infty} d_2^* = 0. \tag{1.9}$$
Thus in particular, for all d_1, d_2 *small,* (1.5) *has a stable co-existence steady state.*

(iii) For every fixed $d_1 > 0$, $(\theta_{d_1,m}, 0)$ *is globally asymptotically stable for all* d_2 *sufficiently large.*

(iv) Let (U, V) *be any steady state of* (1.5). *Then for any* $\delta > 0$, *there exists a*

constant $C(\delta)$ such that for all $d_2 > \delta$, we have

$$\|V\|_{L^\infty(\Omega)} \le \frac{C(\delta)}{d_1}.$$

In particular, for all $d_2 > \delta$, we have

$$\lim_{d_1\to\infty} (U, V) = (\overline{m}, 0). \tag{1.10}$$

Although it is not yet known if for all $(d_1, d_2) \in \Sigma_U$, $(\theta_{d_1,m}, 0)$ is globally asymptotically stable, Theorem 1.1(iv) asserts that at least for d_1 large, the population density of species U dominates even if U does not wipe out V completely. For an illustration of the curve d_2^* and the region Σ_U, see Figures 1.1 and 1.2.

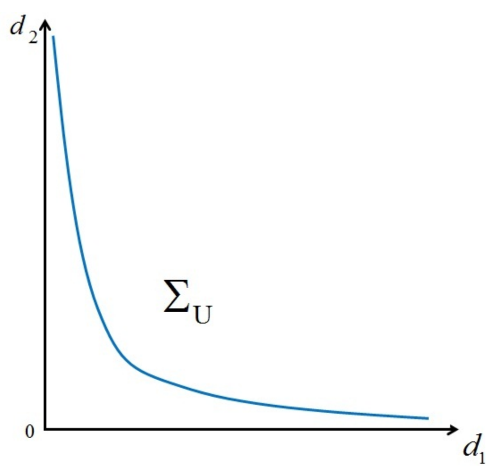

Figure 1.1: Possible shape of Σ_U, which lies above the curve d_2^*. $\Sigma_V = \emptyset$.

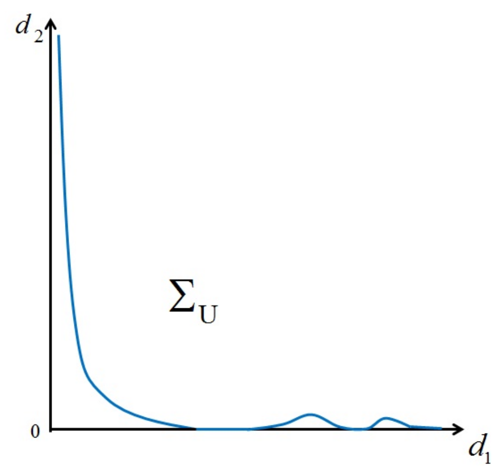

Figure 1.2: Another scenario of Σ_U, whose boundary touches, or coincides with part of, d_1-axis. $\Sigma_V = \emptyset$.

Theorem 1.1 shows that, given equal amount of total resources for species U and V, competition seems to favor heterogeneous distributions of resources. Next we want to study the case that the distributions of resources for U and V are both *heterogeneous*:

$$\begin{cases} U_t = d_1\Delta U + U(m_1(x) - U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ V_t = d_2\Delta V + V(m_2(x) - U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\ U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{in } \Omega, \end{cases} \tag{1.11}$$

where the functions $m_1(x)$ and $m_2(x)$ represent the (spatially inhomogeneous) carrying capacities or intrinsic growth rates of U and V respectively and satisfy the following condition:

(**M2**) $m_i(x) \in C^\gamma(\bar{\Omega})$ ($\gamma \in (0,1)$) is nonconstant, $m_i \geq 0$ on $\bar{\Omega}$, $i = 1, 2$, and $m_1 \not\equiv m_2$, but $\int_\Omega m_1 = \int_\Omega m_2$.

It turns out that the dynamics of (1.11) changes a lot under condition (**M2**) as now (1.11) can support many more stable co-existence steady states in terms of d_1 and d_2. To state our result precisely, similarly as before, we define the following three subsets of the first quadrant $\mathcal{Q} = \{(d_1, d_2) \mid d_1, d_2 > 0\}$ for system (1.11):

$$\begin{aligned} \widetilde{\Sigma}_U &:= \{(d_1, d_2) \in \mathcal{Q} \mid (\theta_{d_1,m_1}, 0) \text{ is linearly stable}\}, \\ \widetilde{\Sigma}_V &:= \{(d_1, d_2) \in \mathcal{Q} \mid (0, \theta_{d_2,m_2}) \text{ is linearly stable}\}, \\ \widetilde{\Sigma}_- &:= \{(d_1, d_2) \in \mathcal{Q} \mid \text{both } (\theta_{d_1,m_1}, 0) \text{ and } (0, \theta_{d_2,m_2}) \text{ are linearly unstable}\}. \end{aligned} \tag{1.12}$$

Theorem 1.2. *Assume that* (**M2**) *holds. Then the following hold for system* (1.11)*:*

(i)

$$\widetilde{\Sigma}_U = \{(d_1, d_2) \in \mathcal{Q} \mid d_2 > \widetilde{d}_2^*(d_1)\} \tag{1.13}$$

and

$$\widetilde{\Sigma}_V = \{(d_1, d_2) \in \mathcal{Q} \mid d_1 > \widetilde{d}_1^*(d_2)\}, \tag{1.14}$$

where $\widetilde{d}_2^*(d_1)$ (resp. $\widetilde{d}_1^*(d_2)$) is a continuous function of d_1 (resp. d_2) defined in $\mathbb{R}^+$. Moreover,

$$\lim_{d_2 \to 0^+} \widetilde{d}_1^* = \lim_{d_2 \to \infty} \widetilde{d}_1^* = \infty, \quad \lim_{d_1 \to 0^+} \widetilde{d}_2^* = \lim_{d_1 \to \infty} \widetilde{d}_2^* = \infty. \tag{1.15}$$

(ii) $\overline{\widetilde{\Sigma}_U} \cap \overline{\widetilde{\Sigma}_V} = \emptyset$.

(iii) For every fixed $d_1 > 0$, $(\theta_{d_1,m_1}, 0)$ is globally asymptotically stable for all d_2 sufficiently large. Symmetrically, for every fixed $d_2 > 0$, $(0, \theta_{d_2,m_2})$ is globally asymptotically stable for all d_1 sufficiently large.

It is easy to see from Theorem 1.2(i) and (ii) that $\widetilde{\Sigma}_-$ contains a small neighborhood of $(0,0)$ in $\mathcal{Q}$, and, there exists a sequence $(d_1, d_2) \in \widetilde{\Sigma}_-$ with $d_1, d_2 \to \infty$. Also we know from the theory of monotone flow that for all $(d_1, d_2) \in \widetilde{\Sigma}_-$, (1.11) has

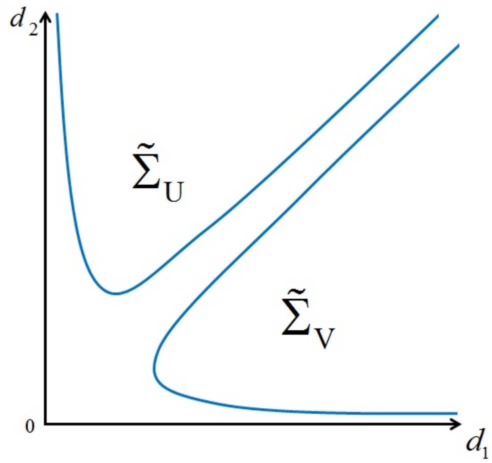

Figure 1.3: Possible shapes of $\widetilde{\Sigma}_U$ and $\widetilde{\Sigma}_V$ for (1.11). Both $\widetilde{d_2^*}$ and $\widetilde{d_1^*}$ are away from the d_1- and d_2-axis respectively.

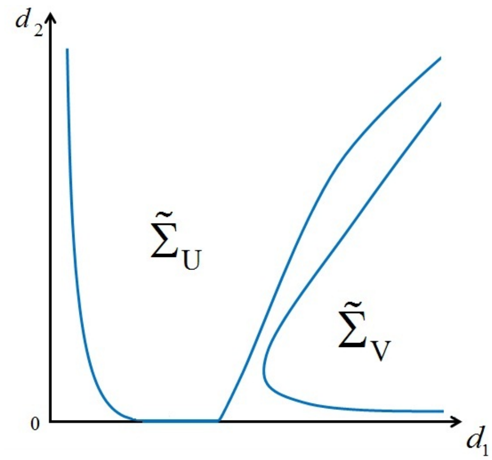

Figure 1.4: Another scenario of $\widetilde{\Sigma}_U$ and $\widetilde{\Sigma}_V$ for (1.11). The upper curve is $\widetilde{d_2^*}$ which could touch, or coincide with part of, the d_1-axis.

a stable co-existence steady state. Moreover, Theorem 1.2 (ii) implies that the two semi-trivial steady states can never be both stable. For an illustration of $\widetilde{d_2^*}$, $\widetilde{d_1^*}$, $\widetilde{\Sigma}_U$ and $\widetilde{\Sigma}_V$, see Figures 1.3 and 1.4.

Remark 1.3. Theorem 1.2 indicates that, given equal total amount of resources both of which distributed *heterogeneously*, the competition between U and V has certain "symmetries" and the two species are more comparable; consequently, the co-existence becomes a much stronger possibility. It seems natural to ask that, among the class of heterogeneous distributions, if there is a "most advantageous" distribution of resources for competition. We hope to return to this problem in the future.

As mentioned before, for all $(d_1, d_2) \in \Sigma_-$ (resp. $\widetilde{\Sigma}_-$), system (1.5) (resp. (1.11)) has a stable co-existence steady state. In Chapter 3.2, we will investigate various limiting behaviors of all steady states - co-existence as well as semi-trivial - as d_1 and d_2 approach 0^+ or ∞ in systems (1.5) and (1.11).

It turns out that when $m(x)$, $m_1(x)$, and $m_2(x)$ change sign, our analysis still applies and similar results hold. We will indicate the necessary modifications in Chapter 3.3.

In Chapter 4, we continue to study the combined effects of diffusion, spatial heterogeneity and general inter-specific competition coefficients but under much broader situations - including different strengths and distributions of the resources, and with different competition abilities:

$$\begin{cases} U_t = d_1 \Delta U + U(m_1(x) - U - c\,V) & \text{in } \Omega \times \mathbb{R}^+, \\ V_t = d_2 \Delta V + V(\beta m_2(x) - b\,U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\ U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{in } \Omega, \end{cases} \tag{1.16}$$

where the functions $m_1(x)$ and $\beta m_2(x)$ represent their (spatially inhomogeneous) carrying capacities or intrinsic growth rates respectively. For convenience, we have introduced a parameter $\beta > 0$, as a coefficient of m_2, which measures the relative strength of the carrying capacity or intrinsic growth rate for V versus that for U. The constants b and c are inter-specific competition coefficients, while we already have normalized both the intra-specific competition coefficients to be 1. Throughout this paper we shall assume that d_1, d_2, b and c are all positive constants, and impose the following condition on m_1 and m_2 unless otherwise explicitly stated:

(M) $m_i(x) \in C^\gamma(\bar{\Omega})$ ($\gamma \in (0,1)$) is nonconstant and $m_i(x) > 0$ on $\bar{\Omega}$, $i = 1, 2$.

For comparison purposes, we briefly recall the corresponding homogeneous Lotka-Volterra competition-diffusion system of (1.16) as follows:

$$\begin{cases} U_t = d_1 \Delta U + U(a_1 - U - c\,V) & \text{in } \Omega \times \mathbb{R}^+, \\ V_t = d_2 \Delta V + V(\beta a_2 - b\,U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\ U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{in } \Omega, \end{cases} \tag{1.17}$$

where a_1, a_2 are two positive constants. The following result is well-known (see e.g. [B, D]):

Theorem 1.4. *Assume that $a_1, a_2 > 0$, $b\,c \le 1$ and $\beta > 0$ is a parameter. Define*

$$\beta^U := b\,\frac{a_1}{a_2}, \quad \beta^V := \frac{1}{c}\,\frac{a_1}{a_2}. \tag{1.18}$$

Then the following statements hold for system (1.17):

(i) If $\beta \in (0, \beta^U)$, then for all d_1, $d_2 > 0$, $(a_1, 0)$ is globally asymptotically stable.

(ii) If $\beta \in (\beta^V, \infty)$, then for all $d_1,\ d_2 > 0$, $(0, \beta a_2)$ is globally asymptotically stable.

(iii) If $b\,c < 1$, then $\beta^U < \beta^V$; and, for any $\beta \in (\beta^U, \beta^V)$, (1.17) *has a globally asymptotically stable co-existence steady state $((a_1 - c\beta a_2)/(1-bc), (\beta a_2 - ba_1)/(1-bc))$ for any $d_1,\ d_2 > 0$. If $b\,c = 1$, then $\beta^U = \beta^V$; and, at $\beta = \beta^U$,* (1.17) *has a compact global attractor consisting of a continuum of steady states $\{(\xi a_1, (1-\xi)a_1/c) \,|\, \xi \in [0,1]\}$.*

When spatial heterogeneity comes into play in (1.16), the roles of β^U and β^V become more complicated. To state our first result, we define the following two numbers:

$$\beta_{**} := b\,\frac{\inf_{\bar\Omega} m_1}{\sup_{\bar\Omega} m_2}, \quad \beta^{**} := \frac{1}{c}\frac{\sup_{\bar\Omega} m_1}{\inf_{\bar\Omega} m_2}. \tag{1.19}$$

Theorem 1.5. *Assume that* (**M**) *holds and $b\,c \le 1$. Then the following statements hold for system* (1.16)*:*

(i) If $\beta \in (0,\ \beta_{**})$, then for all $d_1,\ d_2 > 0$, $(\theta_{d_1,m_1}, 0)$ is globally asymptotically stable.

(ii) If $\beta \in (\beta^{**}, \infty)$, then for all $d_1,\ d_2 > 0$, $(0, \theta_{d_2,\beta m_2})$ is globally asymptotically stable.

When $b = c = 1$, Theorem 1.5(i) says that whenever $\inf_{\bar\Omega} m_1 > \sup_{\bar\Omega} \beta m_2$, $(\theta_{d_1,m_1}, 0)$ is globally asymptotically stable. However, it seems interesting to note that *merely assuming that $m_1 - \beta m_2 > 0$ everywhere (pointwise) on $\bar\Omega$ is not enough to guarantee even the local linear stability of $(\theta_{d_1,m_1}, 0)$* as we shall see from Theorem 1.8 below. The reason is that in the range (β_{**}, β^{**}) where the strengths of the carrying capacities of the two competing species are "comparable", the roles of diffusion rates d_1 and d_2 become more important. Thus we shall first characterize the linear stability of the two semi-trivial steady states $(\theta_{d_1,m_1}, 0)$ and $(0, \theta_{d_2,\beta m_2})$ of (1.16) as β increases from 0 to ∞ for fixed $d_1, d_2 > 0$.

Theorem 1.6. *Assume that* (**M**) *holds. Then for any $d_1, d_2 > 0$, there exist two positive numbers $\beta^U_{d_1,d_2}, \beta^V_{d_1,d_2} \in (\beta_{**}, \beta^{**})$ such that the following hold for system* (1.16)*:*

(i) $(\theta_{d_1,m_1}, 0)$ is linearly stable if $\beta \in (0, \beta^U_{d_1,d_2})$, and is linearly unstable if $\beta \in (\beta^U_{d_1,d_2}, \infty)$.

(ii) $(0,\theta_{d_2,\beta m_2})$ *is linearly unstable if* $\beta \in (0,\beta^V_{d_1,d_2})$*, and is linearly stable if* $\beta \in (\beta^V_{d_1,d_2},\infty)$.

If we further assume that $b\,c \le 1$*, then the following statements hold:*

(iii) If $b\,c < 1$ *or* $\theta_{d_1,m_1} \not\equiv c\,\theta_{d_2,sm_2}$ *for any* $s > 0$*, then* $\beta^U_{d_1,d_2} < \beta^V_{d_1,d_2}$*. In this case, for every* $\beta \in (\beta^U_{d_1,d_2},\beta^V_{d_1,d_2})$*, system* (1.16) *has a stable co-existence steady state.*

(iv) If $b\,c = 1$ *and* $\theta_{d_1,m_1} \equiv c\,\theta_{d_2,sm_2}$ *for some* $s > 0$*, then* $\beta^U_{d_1,d_2} = \beta^V_{d_1,d_2} = s$*. Conversely, if* $\beta^U_{d_1,d_2} = \beta^V_{d_1,d_2}$*, then* $b\,c = 1$ *and* $\theta_{d_1,m_1} \equiv c\,\theta_{d_2,\beta^V_{d_1,d_2}m_2}$.

The above theorem implies that for fixed d_1, d_2, the local linear stability of the two semi-trivial steady states of (1.16) still resembles that of the homogeneous system. However, as the two numbers $\beta^U_{d_1,d_2}$ and $\beta^V_{d_1,d_2}$ change when d_1 and d_2 vary, it seems natural to ask, for fixed b, c with $b\,c \le 1$, if we could find β such that (1.16) has a stable co-existence steady state for all $d_1, d_2 > 0$. The following theorem answers this question.

Theorem 1.7. *Assume that* (**M**) *holds. Set*

$$\underline{\beta} := \sup_{d_1,d_2>0} \beta^U_{d_1,d_2}, \quad \overline{\beta} := \inf_{d_1,d_2>0} \beta^V_{d_1,d_2}, \tag{1.20}$$

where $\beta^U_{d_1,d_2}, \beta^V_{d_1,d_2}$ *are given in Theorem* 1.6*, and*

$$\Lambda := \inf_{d_1>0} \frac{\overline{m_1}}{\overline{\theta_{d_1,m_1}}} \cdot \inf_{d_2>0} \frac{\overline{m_2}}{\overline{\theta_{d_2,m_2}}}. \tag{1.21}$$

Then we have

$$\underline{\beta} = b \sup_{d_1>0} \frac{\overline{\theta_{d_1,m_1}}}{\overline{m_2}}, \quad \overline{\beta} = \frac{1}{c} \inf_{d_2>0} \frac{\overline{m_1}}{\overline{\theta_{d_2,m_2}}}, \tag{1.22}$$

and the following statements hold:

(i) If $0 < b\,c < \Lambda$*, then* $\underline{\beta} < \overline{\beta}$*; moreover, for any* $\beta \in (\underline{\beta},\overline{\beta})$ *and* $d_1, d_2 > 0$*, both semi-trivial steady states* $(\theta_{d_1,m_1},0)$ *and* $(0,\theta_{d_2,\beta m_2})$ *of system* (1.16) *are linearly unstable, which implies that* (1.16) *has a stable co-existence steady state.*

(ii) If $\Lambda < b\,c \le 1$*, then* $\underline{\beta} > \overline{\beta}$*; moreover, for any* $\beta > 0$*, there exist* $d_1, d_2 > 0$ *such that one of the semi-trivial steady states* $(\theta_{d_1,m_1},0)$ *and* $(0,\theta_{d_2,\beta m_2})$ *of system* (1.16) *is linearly stable, and the other is linearly unstable.*

Comparing Theorem 1.7(ii) with Theorem 1.4(iii), we see that the range of β for which (1.16) has a globally stable co-existence steady state regardless of d_1 and d_2 can no longer be obtained for all b, c satisfying $b\,c \leq 1$ any more.

Our next theorem characterizes the range of β on which (4.4) *may* have a co-existence steady state for suitably chosen d_1 and d_2.

Theorem 1.8. *Assume that* (**M**) *holds. Define*

$$\beta_* := \inf_{d_1, d_2 > 0} \beta^U_{d_1,d_2}, \quad \beta^* := \sup_{d_1, d_2 > 0} \beta^V_{d_1,d_2}, \tag{1.23}$$

where $\beta^U_{d_1,d_2}, \beta^V_{d_1,d_2}$ *are given in Theorem* 1.6. *Then we have*

$$\beta_* = b \inf_{d_1 > 0} \inf_{\bar{\Omega}} \frac{\theta_{d_1,m_1}}{m_2}, \quad \beta^* = \frac{1}{c} \sup_{d_2 > 0} \sup_{\bar{\Omega}} \frac{m_1}{\theta_{d_2,m_2}}. \tag{1.24}$$

Assume further that $b\,c \leq 1$, *then for any* $\beta \in (\beta_*, \beta^*)$, *there exist some* $d_1, d_2 > 0$ *such that* (1.16) *has a stable co-existence steady state.*

Suppose that (**M**) holds, define

$$\tilde{\beta} := \inf_{\bar{\Omega}} \frac{m_1}{m_2}, \quad \hat{\beta} := \sup_{\bar{\Omega}} \frac{m_1}{m_2}.$$

When $b = c = 1$, we have $\beta_* \leq \tilde{\beta} < \hat{\beta} \leq \beta^*$. Thus the conclusion of Theorem 1.8 holds for all $\beta \in (\tilde{\beta}, \hat{\beta})$. The intuitive biological interpretation is that as long as *neither of the resources (or intrinsic growth rates) for the two competing species completely dominates the other, there will be suitable dispersal rates* d_1 *and* d_2 *for which* (1.16) *has a stable co-existence steady state.* We ought to mention that a similar result in this direction has been obtained by [HLMV].

Furthermore, it seems interesting to note that when $b = c = 1$ (that is, the two species have equal competition abilities), for those m_1 and m_2 satisfying $\beta_* < \tilde{\beta} < \hat{\beta} < \beta^*$, the above result implies that, even when the intrinsic growth rate of one species is strictly larger than that of the other *everywhere (pointwise)* on $\bar{\Omega}$, i.e. $\beta \in (\beta_*, \tilde{\beta}) \cup (\hat{\beta}, \beta^*)$, system (1.16) still has a stable co-existence steady state for suitably chosen d_1 and d_2.

This thesis is organized as follows. In Chapter 2, we establish some preliminaries concerning the notion of linear stability/instability of a given steady state of a general Lotka-Volterra competition-diffusion system and a criterion for determining such stability properties. In Chapter 3, we study stabilities properties of both semi-trivial steady states of (1.5) and (1.11). Limiting behaviors of co-existence steady states as the dispersal rates tend to 0 or ∞ are also obtained. In Chapter 4, we study the general case (1.16) and characterize the change of dynamics of (1.16), as β increases from 0 to ∞, near the two semi-trivial steady states $(\theta_{d_1,m_1}, 0)$ and $(0, \theta_{d_2,\beta m_2})$ of (1.16) for all $(d_1, d_2) \in \mathcal{Q}$.

Chapter 2

Preliminaries

2.1 Notion/Criterion of Stability of Steady States

In this chapter, we recall the notions of linear stability and instability of steady states of the following system:

$$\begin{cases} U_t = d_1\Delta U + U(m_1(x) - U - c\,V) & \text{in } \Omega \times \mathbb{R}^+, \\ V_t = d_2\Delta V + V(m_2(x) - b\,U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\ U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{in } \Omega \end{cases} \tag{2.1}$$

which includes (1.5), (1.11) and (1.16). We also allow $m_1(x)$ and $m_2(x)$ to change sign in this chapter so that results in this chapter can be applied to the sign-changing case in Chapter 3.3. Therefore, through out this chapter, we shall assume that $b, c > 0$ and $m_1(x)$ and $m_2(x)$ satisfy the following hypothesis:

(**H**) $m_i(x) \in C^\gamma(\bar{\Omega})$ $(\gamma \in (0,1))$, $\int_\Omega m_i \geq 0$, and if equality holds, then $m_i \not\equiv 0$, $i = 1, 2$.

As (2.1) generates a monotone dynamical system [He, Hi, HiS] preserving the order

$$(U_1, V_1) \preceq (U_2, V_2) \text{ if } U_1 \leq U_2 \text{ and } V_1 \geq V_2 \text{ in } \Omega,$$

it is well known that, to a large extent, the dynamics of (2.1) are determined by its steady states and their stability properties. To be precise, we first recall the notion of linear stability of a steady state. Linearizing the corresponding elliptic system of

(2.1) at a steady state (U, V), we have

$$\begin{cases} d_1\Delta\Psi_1 + \Psi_1(m_1 - 2\,U - c\,V) - \,U\Psi_2 + \lambda\Psi_1 = 0 & \text{in } \Omega, \\ d_2\Delta\Psi_2 + \Psi_2(m_2 - b\,U - 2\,V) - \,V\Psi_1 + \lambda\Psi_2 = 0 & \text{in } \Omega, \\ \partial_\nu\Psi_1 = \partial_\nu\Psi_2 = 0 & \text{on } \partial\Omega. \end{cases} \tag{2.2}$$

According to the Krein-Rutman Theorem [KR, S], (2.2) has a principal eigenvalue $\lambda_1 \in \mathbb{R}$, i.e. λ_1 is simple and has the least real part among all eigenvalues. If (U, V) is a trivial or semi-trivial steady state, then the sign of the principal eigenvalue can be determined according to Lemma 2.3 below. In the following, we call a steady state (U, V) of (2.1) *linearly stable* (resp. *linearly unstable*) if the principal eigenvalue λ_1 of (2.2) is positive (resp. negative). *It is well known that a steady state of* (2.1) *is linearly stable (resp. linearly unstable), then it is asymptotically stable (resp. unstable).* (See e.g. Theorem 7.6.2 in [S]. Here the notion of *stability* and *asymptotic stability* are defined in the standard dynamical system sense.)

To characterize the principal eigenvalue of (2.2), we need to introduce the following eigenvalue problem with indefinite weight

$$\begin{cases} \Delta\varphi + \lambda h(x)\varphi = 0 & \text{in } \Omega, \\ \partial_\nu\varphi = 0 & \text{on } \partial\Omega, \end{cases} \tag{2.3}$$

where $h \in L^\infty(\Omega)$ is nonconstant and h could change sign in Ω. We say that λ is a *principal eigenvalue* if (2.3) has a positive solution. (Notice that 0 is always a principal eigenvalue.) The following result is standard.

Proposition 2.1. *The problem* (2.3) *has a nonzero principal eigenvalue* $\lambda_1 = \lambda_1(h)$ *if and only if* h *changes sign and* $\int_\Omega h \neq 0$. *More precisely, if* h *changes sign, then*

(i) $\int_\Omega h = 0 \Leftrightarrow$ 0 *is the only principal eigenvalue.*

(ii) $\int_\Omega h > 0 \Leftrightarrow \lambda_1(h) < 0$.

(iii) $\int_\Omega h < 0 \Leftrightarrow \lambda_1(h) > 0$. *Moreover, for* $\int_\Omega h < 0$, $\lambda_1(h)$ *is given by the following variational characterization:*

$$\lambda_1(h) = \inf\left\{ \frac{\int_\Omega |\nabla\varphi|^2}{\int_\Omega h\,\varphi^2} \,\middle|\, \varphi \in H_1(\Omega) \text{ and } \int_\Omega h\,\varphi^2 > 0 \right\}. \tag{2.4}$$

(iv) $\lambda_1(h_1) > \lambda_1(h_2)$ *if* $h_1 \leq h_2$, $h_1 \not\equiv h_2$, *and* h_1, h_2 *both change sign.*

(v) $\lambda_1(h)$ *is continuous in* h*; more precisely,* $\lambda_1(h_\ell) \to \lambda_1(h)$ *if* $h_\ell \to h$ *in* $L^\infty(\Omega)$*.*

(vi) Suppose that h_ℓ *changes sign with* $\|h_\ell\|_{L^\infty(\Omega)} \le M$ *and* $\int_\Omega h_\ell < -C$ *for all* $\ell = 1, 2, \cdots$*, where* M, C *are two positive constants. If* $\int_\Omega h_\ell^+ \to 0$*, then* $\lambda_1(h_\ell) \to \infty$ *as* $\ell \to \infty$*.*

The proofs of (i)-(v) are standard [BL, SH], and we refer to [U] for a proof of (vi).

It turns out that the indefinite weight eigenvalue problem (2.3) is very much related to the following eigenvalue problem

$$\begin{cases} d\Delta\psi + h(x)\psi + \mu\psi = 0 & \text{in } \Omega, \\ \partial_\nu \psi = 0 & \text{on } \partial\Omega. \end{cases} \tag{2.5}$$

Denote $\mu_1(d, h)$ as the *first eigenvalue* of (2.5), then we have the following variational characterization

$$\mu_1(d, h) = \inf_{\psi \in H_1(\Omega)\setminus\{0\}} \frac{\int_\Omega \left(d|\nabla\psi|^2 - h(x)\psi^2\right) \, dx}{\int_\Omega \psi^2}. \tag{2.6}$$

The following proposition collects some important properties of $\mu_1(d, h)$ in connection with $\lambda_1(h)$. For a proof, see e.g. p. 95 in [CC] or p. 69 in [N].

Proposition 2.2. *The first eigenvalue* $\mu_1(d, h)$ *of* (2.5) *depends smoothly on* $d > 0$ *and continuously on* $h \in L^\infty(\Omega)$*. Moreover, it has the following properties:*

(i) $\int_\Omega h \ge 0$ *and* $h \not\equiv 0 \Rightarrow \mu_1(d, h) < 0$ *for all* $d > 0$*.*

(ii)

$$\int_\Omega h < 0 \text{ and } h \text{ changes sign in } \Omega \Rightarrow \begin{cases} \mu_1(d, h) < 0 & \text{for all } d < 1/\lambda_1(h), \\ \mu_1(d, h) = 0 & \text{if } d = 1/\lambda_1(h), \\ \mu_1(d, h) > 0 & \text{for all } d > 1/\lambda_1(h). \end{cases}$$

(iii) $\mu_1(d, h)$ *is strictly increasing and concave in* $d > 0$*. Furthermore,*

$$\lim_{d \to 0} \mu_1(d, h) = \min_{\overline{\Omega}}(-h) \quad \text{and} \quad \lim_{d \to \infty} \mu_1(d, h) = -\overline{h}$$

where $\overline{h}$ *is the average of* h*.*

(iv) $\mu_1(d, h_1) < \mu_1(d, h_2)$ *if* $h_1 \geq h_2$ *and* $h_1 \not\equiv h_2$. *In particular* $\mu_1(d, h) > 0$ *if* $h \leq (\not\equiv) 0$.

For linear stability of the trivial steady state $(0, 0)$ and the two semi-trivial steady states $(\theta_{d_1,m_1}, 0)$ and $(0, \theta_{d_2,m_2})$ of system (1.11), we have the following relatively simple criterion. The proof uses the same arguments as in that of Corollary 2.10 in [LN], and is therefore omitted here.

Lemma 2.3. *The linear stability of* $(\theta_{d_1,m_1}, 0)$, $(0, \theta_{d_2,m_2})$ *and* $(0, 0)$ *in system* (2.1) *are determined by the sign of* $\mu_1(d_2, m_2 - \theta_{d_1,m_1})$, $\mu_1(d_1, m_1 - \theta_{d_2,m_2})$ *and* $\min\{\mu_1(d_1, m_1), \mu_1(d_2, m_2)\}$ *respectively. In particular,* $(0, 0)$ *is always linearly unstable for any* $d_1, d_2 > 0$.

We are going to use the following lemma derived from the theory of monotone dynamical system repeatedly. (See, e.g., Proposition 9.1 and Theorem 9.2 in [He].)

Lemma 2.4. *For any* $d_1, d_2 > 0$, *assume that every co-existence steady state of* (2.1), *if exists, is asymptotically stable, then one of the following alternatives holds:*

(i) There exists a unique co-existence steady state of (2.1) *which is globally asymptotically stable.*

(ii) System (2.1) *has no co-existence steady state and either one of* $(\theta_{d_1,m_1}, 0)$, $(0, \theta_{d_2,m_2})$ *is globally asymptotically stable, while the other one is unstable.*

2.2 Properties of Steady State Solutions

Since in this chapter we allow the resources functions $m_1(x)$ and $m_2(x)$ to change sign, we will denote $\theta_{d,g}$ the unique positive solution of

$$d\Delta\theta + \theta(g(x) - \theta) = 0 \text{ in } \Omega, \quad \partial_\nu \theta = 0 \text{ on } \partial\Omega, \tag{2.7}$$

where $g(x)$ may change sign in Ω. (See, e.g. [CC] for the proof of existence and uniqueness results of (2.7).)

We now collect some useful properties of $\theta_{d,g}$ defined by (2.7) and co-existence steady state (U, V) of system (2.1). Note that for any co-existence steady state (U, V), by the Maximum Principle, $U, V > 0$ on $\bar{\Omega}$.

Lemma 2.5.

(i) Assume that $g \in C^\gamma(\bar\Omega)$ is nonconstant and $\int_\Omega g \geq 0$. Then the following hold:

(a) $d \mapsto \theta_{d,g}$ is continuous from $\mathbb{R}^+$ to $W^{2,p}(\Omega) \cap C^2(\bar\Omega)$. Moreover,

$$\theta_{d,g} \to \begin{cases} g^+ & \text{as } d \to 0^+, \\ \overline{g} & \text{as } d \to \infty, \end{cases}$$

uniformly on $\bar\Omega$, where $g^+(x) = \max\{g(x), 0\}$, and $\overline{g}$ is the average of g.

(b) $\|\theta_{d,g}\|_{L^\infty(\Omega)} < \|g\|_{L^\infty(\Omega)}$. In particular, we have $\sup_{\bar\Omega} \theta_{d,g} < \sup_{\bar\Omega} g$ and $\inf_{\bar\Omega} \theta_{d,g} > \inf_{\bar\Omega} g$.

(ii) Assume that ($\mathbf{H}$) holds and (U, V) is a co-existence steady state of (2.1), then $\|U\|_{L^\infty(\Omega)} < \|m_1\|_{L^\infty(\Omega)}$ and $\|V\|_{L^\infty(\Omega)} < \|m_2\|_{L^\infty(\Omega)}$.

Proof. In (i) (a), the continuous dependence of $\theta_{d,g}$ in d can be proved by an application of Implicit Function Theorem. (See Proposition 3.6 in [CC] and remarks there.) The proofs of limiting behaviors of $\theta_{d,g}$ as d goes to 0^+ or ∞ are standard, see e.g. [N].

Except for $\inf_{\bar\Omega} \theta_{d,g} > \inf_{\bar\Omega} g$, everything else in (i) (b) and (ii) can be proved by the same arguments in Proposition 2.4 in [LN]. *(Note that no assumption on the sign of m_1 and m_2 is needed for* (ii) *here.)* To see that $\inf_{\bar\Omega} \theta_{d,g} > \inf_{\bar\Omega} g$, if g is non-positive somewhere in Ω, then it is obviously true since $\theta_{d,g} > 0$ in $\bar\Omega$. So we assume $g > 0$ in $\bar\Omega$.

First, by standard arguments, we have that:

$$\Delta\theta_{d,g}(P) \geq 0 \text{ where } \theta_{d,g}(P) = \inf_{\bar\Omega} \theta_{d,g}.$$

Now evaluating the equation of $\theta_{d,g}$ at P obtained from the above claim, we get $\theta_{d,g} \geq \inf\limits_{\bar\Omega} \theta_{d,g} = \theta_{d,g}(P) \geq g(P) \geq \inf\limits_{\bar\Omega} g$. Let $w := \inf\limits_{\bar\Omega} g - \theta_{d,g}$. Then $w \leq 0$ satisfies

$$d\Delta w + w(\inf_{\bar\Omega} g - \theta_{d,g} - g) = (2\theta_{d,g} - \inf_{\bar\Omega} g)(g - \inf_{\bar\Omega} g) \geq 0 \text{ in } \Omega, \quad \partial_\nu w = 0 \text{ on } \partial\Omega.$$

Notice that $\inf_{\bar\Omega} g - \theta_{d,g} - g < 0$, so the Strong Maximum Principle (Theorem 9.6 of [GT]) applies. Since w is nonconstant, we see that w cannot attain a nonnegative maximum in Ω. It also cannot attain a non-negative maximum on $\partial\Omega$ (by Hopf Boundary Lemma). Hence $\inf_{\bar\Omega} g - \theta_{d,g} = w < 0$ in $\bar\Omega$. □

The following proposition will be used in the proof of Theorem 1.1.

Proposition 2.6. *Assume that m satisfies condition* (**M1**)*, and that $\overline{m} - \theta_{d,m}$ changes sign in Ω. Then*

$$\lim_{d\to\infty} \lambda_1(\overline{m} - \theta_{d,m}) = \infty. \tag{2.8}$$

Proof. By (1.3) and Proposition 2.1, $\lambda_1(\overline{m} - \theta_{d,m})$ is well defined and positive. For notational convenience, denote $\theta := \theta_{d,m}$, $\lambda_1 := \lambda_1(\overline{m} - \theta_{d,m})$ and $\|\cdot\|_\infty := \|\cdot\|_{L^\infty(\Omega)}$. Let $\varphi > 0$ be the eigenfunction corresponding to λ_1 whose normalization is to be specified later. Then φ satisfies

$$\Delta\varphi + \lambda_1 \cdot (\overline{m} - \theta)\varphi = 0 \text{ in } \Omega, \quad \partial_\nu \varphi = 0 \text{ on } \partial\Omega.$$

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

$$\begin{aligned}
0 &= \int_\Omega |\nabla\varphi|^2 + \lambda_1 \int_\Omega (\theta - \overline{m})\varphi^2 \\
&= \int_\Omega |\nabla\varphi|^2 + \lambda_1 \int_\Omega (\theta - \bar{\theta})(\varphi - \bar{\varphi})(\varphi + \bar{\varphi}) + \lambda_1 \int_\Omega (\bar{\theta} - \overline{m})\varphi^2 \\
&> \int_\Omega |\nabla\varphi|^2 - \frac{\lambda_1 \|\varphi + \bar{\varphi}\|_\infty}{2} \int_\Omega \left[(\theta - \bar{\theta})^2 + (\varphi - \bar{\varphi})^2\right] + \frac{\lambda_1 d\, \overline{\varphi^2}}{\|m\|_\infty^2} \int_\Omega |\nabla\theta|^2 \\
&> \left(1 - \frac{C\lambda_1 \|\varphi + \bar{\varphi}\|_\infty}{2}\right) \int_\Omega |\nabla\varphi|^2 + \lambda_1 \left(\frac{d\, \overline{\varphi^2}}{\|m\|_\infty^2} - \frac{C\|\varphi + \bar{\varphi}\|_\infty}{2}\right) \int_\Omega |\nabla\theta|^2,
\end{aligned}$$

where in the last two inequalities we have used (1.4), Lemma 2.5(i)(b), and the Poincaré inequality with the constant C only depending on Ω. Now suppose for contradiction that (2.8) is not true. Then there exists some $\lambda^* \in [0, \infty)$ such that passing to a subsequence of d if necessary, $\lambda_1 \to \lambda^*$. Since $\overline{m} - \theta \to 0$ uniformly on $\bar{\Omega}$ by Lemma 2.5(i)(a), standard elliptic regularity implies that φ must converge to some constant as $d \to \infty$. Now normalize φ such that for all $d > 0$,

$$\sup_\Omega \varphi = \begin{cases} \frac{1}{8C\lambda^*} & \text{if } \lambda^* > 0, \\ 1 & \text{if } \lambda^* = 0. \end{cases}$$

Then $\varphi \to \varphi^* \equiv \frac{1}{8C\lambda^*}$ if $\lambda^* > 0$, and $\varphi \to 1$ if $\lambda^* = 0$. Thus both terms in the last inequality above are strictly positive for all d large, which is a contradiction. This finishes the proof of the proposition. □

The following monotonicity property of $\theta_{d,g}$ is simple but fundamental.

Lemma 2.7. *Assume that $g_i(x) \in C^\gamma(\bar{\Omega})(\gamma \in (0,1))$ is nonconstant and $\int_\Omega g_i \geq 0$ for $i = 1,2$. If $g_1 \leq (\not\equiv) g_2$, then $\theta_{d,g_1} < \theta_{d,g_2}$ on $\bar{\Omega}$ for any $d > 0$. In particular if $g_1(x) \geq (\not\equiv) 0$ on $\bar{\Omega}$, then θ_{d,sg_1} is strictly increasing in $s > 0$ for all $x \in \bar{\Omega}$.*

Proof. From the equation satisfied by θ_{d,g_1}, we have:

$$d\Delta\theta_{d,g_1} + \theta_{d,g_1}(g_2 - \theta_{d,g_1}) = (g_2 - g_1)\theta_{d,g_1} \geq 0.$$

Thus θ_{d,g_1} is a lower solution to

$$d\Delta\theta + \theta(g_2(x) - \theta) = 0 \text{ in } \Omega, \quad \partial_\nu\theta = 0 \text{ on } \partial\Omega.$$

Since any large constant is an upper solution to the above equation, by uniqueness of θ_{d,g_2} and the Maximum Principle, we must have $\theta_{d,g_1} < \theta_{d,g_2}$. □

2.3 Monotonicity of Two Eigenvalue Problems

The following two propositions will be used in Chapter 4.

Proposition 2.8. *Suppose that $m, p \in L^\infty(\Omega)$, $\int_\Omega m(x) \geq 0$, $p(x) > 0$ on $\bar{\Omega}$ and $m/p \not\equiv \mathrm{const}$ on $\bar{\Omega}$. Then $\lambda_1(m(x) - sp(x)) > 0$ if and only if $s \in (\underline{s}, \overline{s})$, where*

$$\underline{s} = \frac{\overline{m}}{\overline{p}} \geq 0, \quad \overline{s} = \sup_{\{m>0\}} \frac{m(x)}{p(x)}.$$

Moreover, $\lambda_1(m(x) - sp(x))$ is continuous and strictly increasing in $s \in (\underline{s}, \overline{s})$ with

$$\lambda_1(m(x) - sp(x)) = \begin{cases} \infty & \text{as } s \nearrow \overline{s}, \\ 0 & \text{as } s \searrow \underline{s}. \end{cases}$$

Proof. It is easy to verify that $\lambda_1(m(x) - sp(x)) > 0$ if and only if $s \in (\underline{s}, \overline{s})$ by Proposition 2.1. Now suppose $\underline{s} < s_1 < s_2 < \overline{s}$, then $m(x) - s_1 p(x) > m(x) - s_2 p(x)$ since $p(x) > 0$ on $\bar{\Omega}$. Thus by Proposition 2.1(iv), $\lambda_1(m(x) - s_1 p(x)) < \lambda_1(m(x) - s_2 p(x))$. This proves that $\lambda_1(m(x) - sp(x))$ is strictly increasing in s. The fact that $\lambda_1(s) \to \infty$ as $s \nearrow \overline{s}$ follows from Proposition 2.1(vi). Finally, the assertion that $\lambda_1(m(x) - \underline{s}p(x)) = 0$ and the continuity of $\lambda_1(s)$ in s follow from Proposition 2.1(i) and (v). □

Proposition 2.9. *Suppose that* $m, p \in L^\infty(\Omega)$, $\int_\Omega m(x) \geq 0$, $p(x) > 0$ *on* $\bar{\Omega}$ *and* $m/p \not\equiv \mathrm{const}$ *on* $\bar{\Omega}$. *Then* $\lambda_1(tm(x) - p(x)) > 0$ *if and only if* $t \in (\underline{t}, \bar{t})$, *where*

$$\underline{t} = \inf_{\{m>0\}} \frac{p(x)}{m(x)} > 0, \quad \bar{t} = \frac{\overline{p}}{\overline{m}} \leq \infty.$$

Moreover, $\lambda_1(tm(x) - p(x))$ *is continuous and strictly decreasing in* $t \in (\underline{t}, \bar{t})$ *with*

$$\lambda_1(tm(x) - p(x)) = \begin{cases} 0 & \text{as } s \nearrow \bar{t}, \\ \infty & \text{as } s \searrow \underline{t}. \end{cases}$$

Proof. It is easy to verify that $\lambda_1(tm(x) - p(x)) > 0$ if and only if $t \in (\underline{t}, \bar{t})$ by Proposition 2.1. Now suppose that $\varphi > 0$ is an eigenfunction corresponding to $\lambda := \lambda_1(tm(x) - p(x))$, where $t \in (\underline{t}, \bar{t})$. Then φ satisfies the following equation:

$$\Delta\varphi + \lambda \cdot (tm(x) - p(x))\varphi = 0 \text{ in } \Omega, \quad \partial_\nu \varphi = 0 \text{ on } \partial\Omega.$$

Since $t > \underline{t} > 0$, we can rewrite the above equation as follows:

$$\Delta\varphi + \lambda t \cdot (m(x) - \frac{p(x)}{t})\varphi = 0 \text{ in } \Omega, \quad \partial_\nu \varphi = 0 \text{ on } \partial\Omega.$$

This implies that

$$t\lambda_1(tm(x) - p(x)) = \lambda_1(m(x) - \tfrac{p(x)}{t}).$$

Therefore all other properties of $\lambda_1(tm(x) - p(x))$ follow from Proposition 2.8. This finishes the proof of the proposition. $\square$

Chapter 3

Homogeneity vs. Heterogeneity

3.1 Stability Properties of Semi-trivial Steady States

In this section, we prove Theorems 1.1 and 1.2. We first prove Theorem 1.2.

Proof of Theorem 1.2. First, we prove (i). By Lemma 2.3,

$$\widetilde{\Sigma}_U = \{(d_1, d_2) \mid \mu_1(d_2, m_2 - \theta_{d_1,m_1}) > 0\}, \quad \widetilde{\Sigma}_V = \{(d_1, d_2) \mid \mu_1(d_1, m_1 - \theta_{d_2,m_2}) > 0\}.$$

By (1.3) and (**M2**), both $\int_\Omega (m_2 - \theta_{d_1,m_1}) < 0$ and $\int_\Omega (m_1 - \theta_{d_2,m_2}) < 0$ for all $d_1, d_2 > 0$. If for some $d_1 > 0$, $m_2 - \theta_{d_1,m_1}$ changes sign in Ω, then by Proposition 2.1(iii) and Proposition 2.2(ii), $\lambda_1(m_2 - \theta_{d_1,m_1}) > 0$ and

$$\mu_1(d_2, m_2 - \theta_{d_1,m_1}) > 0 \Leftrightarrow d_2 > \frac{1}{\lambda_1(m_2 - \theta_{d_1,m_1})}.$$

On the other hand, if d_1 satisfies that $m_2 - \theta_{d_1,m_1} \le 0$ on $\bar{\Omega}$, then $\mu_1(d_2, m_2 - \theta_{d_1,m_1}) > 0$ for all $d_2 > 0$ by Proposition 2.2(iv). Now defining

$$\widetilde{d_2^*}(d_1) := \begin{cases} 0 & \text{if } m_2 - \theta_{d_1,m_1} \le 0 \quad \text{on } \bar{\Omega}, \\ \dfrac{1}{\lambda_1(m_2 - \theta_{d_1,m_1})} & \text{otherwise,} \end{cases} \tag{3.1}$$

and by similar arguments, letting

$$\widetilde{d_1^*}(d_2) := \begin{cases} 0 & \text{if } m_1 - \theta_{d_2,m_2} \leq 0 \text{ on } \bar{\Omega}, \\ \dfrac{1}{\lambda_1(m_1 - \theta_{d_2,m_2})} & \text{otherwise,} \end{cases} \tag{3.2}$$

we obtain (1.13) and (1.14). Since $m_1 \geq 0$, by Lemma 2.5(i)(a),

$$m_2 - \theta_{d_1,m_1} \to \begin{cases} m_2 - m_1 & \text{as } d_1 \to 0^+, \\ m_2 - \overline{m_1} & \text{as } d_1 \to \infty, \end{cases}$$

uniformly on $\bar{\Omega}$. By (**M2**), $m_2 - \theta_{d_1,m_1}$ must change sign in Ω for all d_1 small and large, and $\int_\Omega (m_2 - \theta_{d_1,m_1}) \to 0$ as d_1 approaches 0^+ or ∞. Thus (1.15) follows from Proposition 2.1 (i) and (v). It only remains to show that $\widetilde{d_2^*}(d_1)$ and $\widetilde{d_1^*}(d_2)$ defined by (3.1) and (3.2) respectively are continuous in $\mathbb{R}^+$. Set

$$\begin{aligned} I_1 &:= \{d_1 > 0 \mid m_2 - \theta_{d_1,m_1} \text{ changes sign in } \Omega\}, \\ I_2 &:= \{d_1 > 0 \mid m_2 - \theta_{d_1,m_1} \leq (\not\equiv) 0 \text{ in } \bar{\Omega}\}. \end{aligned}$$

Then

$$\mathbb{R}^+ = I_1 \cup I_2.$$

Moreover, I_1 equals the union of at most countably many open intervals, and by previous arguments there exists some $\varepsilon > 0$ such that

$$I_1 \supset (0, \varepsilon) \cup (\varepsilon^{-1}, \infty).$$

Now, for given $d_1 \in \partial I_2$, it suffices to show that when d_1' approaches d_1 from the interior of I_1, $\lambda_1(m_2 - \theta_{d_1',m_1}) \to \infty$, i.e. $\widetilde{d_2^*}(d_1') \to 0$. But this follows immediately from Proposition 2.1 (vi). The proofs for the continuity of $\widetilde{d_1^*}(d_2)$ and limits of $\widetilde{d_1^*}(d_2)$ in (1.15) are similar. This completes the proof of (i).

Next we prove (ii). Multiplying the equation of $\theta_{d,m}$ in (2.7) by $\theta_{d,m}$ and integrating over Ω, we obtain that

$$d \int_\Omega |\nabla \theta_{d,m}|^2 = \int_\Omega \theta_{d,m}^2 (g - \theta_{d,m}). \tag{3.3}$$

Choosing θ_{d_1,m_1} as a test function in the variational characterization for $\mu_1(d_1, m_1 -$

$\theta_{d_2,m_2})$, by (2.6) and (3.3), we obtain that

$$\begin{aligned}\mu_1(d_1, m_1 - \theta_{d_2,m_2}) &\le \frac{d_1 \int_\Omega |\nabla \theta_{d_1,m_1}|^2 + \int_\Omega (\theta_{d_2,m_2} - m_1)\theta_{d_1,m_1}^2}{\int_\Omega \theta_{d_1,m_1}^2} \\ &= \frac{\int_\Omega (\theta_{d_2,m_2} - \theta_{d_1,m_1})\theta_{d_1,m_1}^2}{\int_\Omega \theta_{d_1,m_1}^2}.\end{aligned} \tag{3.4}$$

Similarly, choosing θ_{d_2,m_2} as a test function in the variational characterization for $\mu_1(d_2, m_2 - \theta_{d_1,m_1})$, we obtain that

$$\begin{aligned}\mu_1(d_2, m_2 - \theta_{d_1,m_1}) &\le \frac{d_2 \int_\Omega |\nabla \theta_{d_2,m_2}|^2 + \int_\Omega (\theta_{d_1,m_1} - m_2)\theta_{d_2,m_2}^2}{\int_\Omega \theta_{d_2,m_2}^2} \\ &= \frac{\int_\Omega (\theta_{d_1,m_1} - \theta_{d_2,m_2})\theta_{d_2,m_2}^2}{\int_\Omega \theta_{d_2,m_2}^2}.\end{aligned} \tag{3.5}$$

Combining (3.4) and (3.5) together, we have

$$\begin{aligned}&\mu_1(d_2, m_2 - \theta_{d_1,m_1}) \int_\Omega \theta_{d_2,m_2}^2 + \mu_1(d_1, m_1 - \theta_{d_2,m_2}) \int_\Omega \theta_{d_1,m_1}^2 \\ &\le - \int_\Omega (\theta_{d_2,m_2} - \theta_{d_1,m_1})^2 (\theta_{d_2,m_2} + \theta_{d_1,m_1}) \le 0,\end{aligned} \tag{3.6}$$

where both equalities hold if and only if $\theta_{d_2,m_2} \equiv \theta_{d_1,m_1}$. Thus it is impossible that both $\mu_1(d_2, m_2 - \theta_{d_1,m_1}) > 0$ and $\mu_1(d_1, m_1 - \theta_{d_2,m_2}) > 0$. Therefore by Lemma 2.3

$$\widetilde{\Sigma}_U \cap \widetilde{\Sigma}_V = \emptyset. \tag{3.7}$$

By (1.15), (3.1) and (3.2), we have

$$\begin{aligned}\partial \widetilde{\Sigma}_U = &\{(d_1, d_2) \mid m_2 - \theta_{d_1,m_1} \text{ changes sign in } \Omega \text{ and } d_2 = 1/\lambda_1(m_2 - \theta_{d_1,m_1})\} \\ &\cup \{(d_1, 0) \mid m_2 - \theta_{d_1,m_1} \le 0 \text{ on } \bar{\Omega}\},\end{aligned} \tag{3.8}$$

and

$$\begin{aligned}\partial \widetilde{\Sigma}_V = &\{(d_1, d_2) \mid m_1 - \theta_{d_2,m_2} \text{ changes sign in } \Omega \text{ and } d_1 = 1/\lambda_1(m_1 - \theta_{d_2,m_2})\} \\ &\cup \{(0, d_2) \mid m_1 - \theta_{d_2,m_2} \le 0 \text{ on } \bar{\Omega}\},\end{aligned} \tag{3.9}$$

as it is obvious that $\partial \widetilde{\Sigma}_U$ does not touch d_2-axis, and $\partial \widetilde{\Sigma}_V$ does not touch d_1-axis.

Now, suppose for contradiction that (ii) is not true. Then there exists $(d_1, d_2) \in \partial\widetilde{\Sigma}_U \cap \partial\widetilde{\Sigma}_V$. In view of (1.15), (3.8) and (3.9), $(d_1, d_2) \in \mathcal{Q}$ and satisfies that $d_2 = 1/\lambda_1(m_2 - \theta_{d_1,m_1})$ and $d_1 = 1/\lambda_1(m_1 - \theta_{d_2,m_2})$, i.e., $\mu_1(d_2, m_2 - \theta_{d_1,m_1}) = \mu_1(d_1, m_1 - \theta_{d_2,m_2}) = 0$. By (3.6), we must have $\theta_{d_2,m_2} \equiv \theta_{d_1,m_1}$, i.e.,

$$\frac{m_1 - \theta_{d_1,m_1}}{d_1} \equiv \frac{m_2 - \theta_{d_2,m_2}}{d_2}.$$

Integrating the above identity over Ω, we obtain that

$$(d_1 - d_2)\int_\Omega m_1 = (d_1 - d_2)\int_\Omega \theta_{d_1,m_1}.$$

Thus $d_1 = d_2$ by (1.3), which in turn implies that $m_1 \equiv m_2$, contradicting (**M2**). This finishes the proof of (ii).

Now we come to prove (iii). To show that $(\theta_{d_1,m_1}, 0)$ is globally asymptotically stable for all d_2 large, it suffices to show that (1.11) has no co-existence steady state for all d_2 large. Then by Lemma 2.4 (ii), $(\theta_{d_1,m_1}, 0)$ must be globally asymptotically stable. Suppose this is not true. Then there exists some $d_1 > 0$ such that (1.11) has a co-existence steady state $(U_{d_1,d_2}, V_{d_1,d_2})$ along a sequence of d_2 tending to ∞. By Lemma 2.5 (ii), both U_{d_1,d_2} and V_{d_1,d_2} are uniformly bounded on $\bar{\Omega}$ independent of d_1 and d_2. By passing to a subsequence of d_2 if necessary, we may assume that

$$\lim_{d_2\to\infty}(U_{d_1,d_2}, V_{d_1,d_2}) = (U_{d_1,\infty}, V_{d_1,\infty}).$$

Dividing the equation of V_{d_1,d_2} by d_2 and letting $d_2 \to \infty$, we conclude that the limiting function $V_{d_1,\infty}$ satisfies that

$$\Delta V_{d_1,\infty} = 0 \text{ in } \Omega, \qquad \partial_\nu V_{d_1,\infty} = 0 \text{ on } \partial\Omega.$$

Thus by the Maximum Principle, $V_{d_1,\infty} \equiv \xi$ for some constant $\xi \geq 0$. Setting

$$W_{d_1,d_2} := V_{d_1,d_2}/\|V_{d_1,d_2}\|_{L^\infty(\Omega)},$$

then W_{d_1,d_2} satisfies

$$\Delta W_{d_1,d_2} + W_{d_1,d_2}\left(\frac{m_2 - U_{d_1,d_2} - V_{d_1,d_2}}{d_2}\right) = 0 \text{ in } \ \Omega, \quad \partial_\nu W_{d_1,d_2} = 0 \text{ on } \partial\Omega.$$

By similar arguments as before, W_{d_1,d_2} converges to some non-negative constant $W_{d_1,\infty}$ as $d_2 \to \infty$. Since $\|W_{d_1,d_2}\|_{L^\infty(\Omega)} = 1$, $W_{d_1,\infty} \equiv 1$.

Integrating the equation of V_{d_1,d_2} and then dividing by $\|V_{d_1,d_2}\|_{L^\infty(\Omega)}$, we have

$$\int_\Omega W_{d_1,d_2}(m_2 - U_{d_1,d_2} - V_{d_1,d_2}) = 0.$$

Letting $d_2 \to \infty$, we obtain that

$$\int_\Omega (m_2 - U_{d_1,\infty} - \xi) = 0. \tag{3.10}$$

Thus $\int_\Omega (m_1 - \xi) = \int_\Omega (m_2 - \xi) \geq 0$. By Proposition 2.5 (a) in [LN] or Lemma 2.4 in [HLMV],

$$U_{d_1,\infty} = \theta_{d_1,m_1-\xi}.$$

However, since $\overline{m_1} = \overline{m_2}$ and $\overline{\theta_{d_1,m_1-\xi}} > \overline{m_1} - \xi$ for any $d_1 > 0$, we obtain a contradiction to (3.10).

Using similar arguments, we can show that $(0, \theta_{d_2,m_2})$ is globally asymptotically stable for all d_1 large. □

Remark 3.1. Note that with mild modifications, it is not hard to show that (3.7) holds for (2.1) with m_1, m_2 satisfying condition (**H**) and $b, c > 0$ satisfying $b\,c \leq 1$. (See Section 5.) It is also possible to discuss the extension of Theorem 1.2 (ii) to (2.1). However, we will leave it to the interested readers to pursue in this direction.

Proof of Theorem 1.1. The two semi-trivial steady states for (1.5) are $(\theta_{d_1,m}, 0)$ and $(0, \overline{m})$. For the linear instability of $(0, \overline{m})$, since $\int_\Omega (m - \overline{m}) = 0$ and $m - \overline{m} \not\equiv 0$, by Proposition 2.2 (i), $\mu_1(d_1, m - \overline{m}) < 0$ for all $d_1 > 0$. Thus $(0, \overline{m})$ is linearly unstable for all $d_1, d_2 > 0$ by Lemma 2.3. This implies that $\Sigma_V = \emptyset$, which proves (i).

For (ii), we proceed as follows. By Lemma 2.3,

$$\Sigma_U = \{(d_1, d_2) \in \mathcal{Q} \mid \mu_1(d_2, \overline{m} - \theta_{d_1,m}) > 0\}.$$

By (1.3), $\int_\Omega (\overline{m} - \theta_{d_1,m}) < 0$ for all $d_1 > 0$. If for some $d_1 > 0$, $\overline{m} - \theta_{d_1,m}$ changes sign in Ω, then by Proposition 2.1 (iii) and Proposition 2.2 (ii), $\lambda_1(\overline{m} - \theta_{d_1,m}) > 0$ and $\mu_1(d_2, \overline{m} - \theta_{d_1,m}) > 0$ if and only if $d_2 > \frac{1}{\lambda_1(\overline{m} - \theta_{d_1,m})}$. On the other hand, if $\overline{m} - \theta_{d_1,m} \leq 0$ on $\bar{\Omega}$ for some $d_1 > 0$, then $\mu_1(d_2, \overline{m} - \theta_{d_1,m}) > 0$ for all $d_2 > 0$ by

Proposition 2.2 (iv). Now defining

$$d_2^*(d_1) := \begin{cases} 0 & \text{if } \overline{m} - \theta_{d_1,m} \le 0 \quad \text{on } \bar{\Omega}, \\ \dfrac{1}{\lambda_1(\overline{m} - \theta_{d_1,m})} & \text{otherwise,} \end{cases} \tag{3.11}$$

we thus obtain (1.7). By Lemma 2.5 (i) (a), as $d_1 \to 0^+$,

$$(\overline{m} - \theta_{d_1,m}) \to (\overline{m} - m)$$

uniformly on $\bar{\Omega}$. Thus $\overline{m} - \theta_{d_1,m}$ must change sign in Ω for all d_1 small, and $\int_\Omega (\overline{m} - \theta_{d_1,m}) \to 0$ as d_1 approaches 0^+. So (1.8) follows from Proposition 2.1 (i) and (v).

To prove (1.9), we set

$$\begin{aligned} J_1 &:= \{d_1 > 0 \mid \overline{m} - \theta_{d_1,m} \text{ changes sign in } \Omega\}, \\ J_2 &:= \{d_1 > 0 \mid \overline{m} - \theta_{d_1,m} \le (\not\equiv) 0 \text{ in } \bar{\Omega}\}. \end{aligned}$$

Given any sequence $\{d_{1,k}\}$ such that $d_{1,k} \to \infty$ as $k \to \infty$, by passing to a subsequence of k, it suffices to consider the following two cases:

(i) $d_{1,k} \in J_1$ for all k.

(ii) $d_{1,k} \in J_2$ for all k.

For case (i), our conclusion follows from Proposition 2.6. For case (ii), the conclusion follows from (3.11).

It only remains to show that d_2^* is continuous in $\mathbb{R}^+$. We know that $\mathbb{R}^+ = J_1 \cup J_2$, and J_1 equals union of at most countably many open intervals. Now, for given $d_1 \in \partial J_2$, it suffices to show that when d_1' approaches d_1 from the interior of J_1, $\lambda_1(\overline{m} - \theta_{d_1',m}) \to \infty$, i.e. $d_2^*(d_1') \to 0$. This follows immediately from Proposition 2.1 (vi). This completes the proof of (ii).

The proof of (iii) uses similar arguments as in that of Theorem 1.2 (iii) above, and is therefore omitted here.

Finally, we prove (iv). First we show that for all $d_2 > \delta$, any steady state solution (U, V) of (1.5) satisfies that $\|V\|_{L^\infty(\Omega)} < C(\delta)\|V\|_{L^1(\Omega)}$, where $C(\delta)$ denotes a positive constant which only depends on δ but may vary from place to place. If $V = 0$, then the claim is obviously true. So now we assume that (U, V) is a co-existence steady state. Since both U and V are uniformly bounded in Ω by Lemma 2.5 (ii), the claim follows from standard L^1 elliptic regularity estimates.

Next, multiplying the equation of V by V and integrating over Ω, we arrive at

$$\begin{aligned}
0 &= d_2 \int_\Omega |\nabla V|^2 - \int_\Omega (\overline{m} - U - V)V^2 \\
&= d_2 \int_\Omega |\nabla V|^2 - \int_\Omega (\bar{U} - U + \bar{V} - V)(V - \bar{V})(V + \bar{V}) - \int_\Omega (\overline{m} - \bar{U} - \bar{V})V^2 \\
&> d_2 \int_\Omega |\nabla V|^2 + \int_\Omega \frac{(V - \bar{V})^2(V + \bar{V})}{2} - \frac{\|V + \bar{V}\|_\infty}{2} \int_\Omega (U - \bar{U})^2 + \frac{d_1 \overline{V^2}}{\|m\|_\infty^2} \int_\Omega |\nabla U|^2 \\
&> d_2 \int_\Omega |\nabla V|^2 + \int_\Omega \frac{(V - \bar{V})^2(V + \bar{V})}{2} + \left(\frac{d_1 \bar{V}^2}{\|m\|_\infty^2} - 2C(\delta)\bar{V} \right) \int_\Omega |\nabla U|^2,
\end{aligned}$$

where we have used Hölder's inequality, Poincaré inequality, and the identity

$$\int_\Omega (\overline{m} - \bar{U} - \bar{V}) = -d_1 \int_\Omega \frac{|\nabla U|^2}{U^2}$$

obtained by dividing the equation of U by U and integrating over Ω.

Thus

$$\|V\|_{L^\infty(\Omega)} < C(\delta)\bar{V} < \frac{C(\delta)}{d_1}.$$

Since $U = \theta_{d_1, m-V}$, our conclusion (1.10) follows from Proposition 2.5 (b) in [LN]. □

3.2 Limiting Behaviors of Steady States

In this section, we mainly investigate, when d_1 and d_2 approach 0^+ or ∞, the limiting behaviors of co-existence steady states of (1.5) and (1.11).

Theorem 3.2. *Assume that* (**M1**) *holds. Let* (U, V) *be any co-existence steady state of* (1.5)*, if exists, then*

(i) $\lim\limits_{d_1 \to \infty} \lim\limits_{d_2 \to 0^+} (U, V) = (\overline{m}, 0)$.

(ii) $\lim\limits_{d_2 \to \infty} \lim\limits_{d_1 \to 0^+} (U, V) = (m - \inf\limits_\Omega m, \inf\limits_\Omega m)$.

(iii) $\lim\limits_{d_1, d_2 \to 0^+} (U, V) = (u_*, v_*)$ *uniformly on compact subsets of* $\bar{\Omega} \setminus \{x \in \bar{\Omega} \mid m(x) = \overline{m}\}$*, where*

$$u_*(x) = \begin{cases} m(x) & \text{if } m(x) > \overline{m}, \\ 0 & \text{if } m(x) < \overline{m}, \end{cases}$$

and

$$v_*(x) = \begin{cases} 0 & \text{if } m(x) > \overline{m}, \\ \overline{m} & \text{if } m(x) < \overline{m}. \end{cases}$$

Theorem 3.3. *Assume that* (**M2**) *holds. Let* (U, V) *be any co-existence steady state of* (1.11)*, if exists, then*

(i) $\lim_{d_1\to\infty} \lim_{d_2\to 0^+} (U, V) = (\inf_\Omega m_2, m_2 - \inf_\Omega m_2)$.

(ii) $\lim_{d_2\to\infty} \lim_{d_1\to 0^+} (U, V) = (m_1 - \inf_\Omega m_1, \inf_\Omega m_1)$.

(iii) $\lim_{d_1,d_2\to 0^+} (U, V) = (\widetilde{u}_*, \widetilde{v}_*)$ *uniformly on compact subsets of* $\bar{\Omega} \setminus \{x \in \bar{\Omega} \mid m_1(x) = m_2(x)\}$*, where*

$$\widetilde{u}_*(x) = \begin{cases} m_1(x) & \text{if } m_1(x) > m_2(x), \\ 0 & \text{if } m_1(x) < m_2(x), \end{cases}$$

and

$$\widetilde{v}_*(x) = \begin{cases} 0 & \text{if } m_1(x) > m_2(x), \\ m_2(x) & \text{if } m_1(x) < m_2(x). \end{cases}$$

The proof of Theorem 3.2 uses similar arguments as in that of Theorem 3.3. Thus we will only prove the latter.

Proof of Theorem 3.3. We will prove (ii) here, as the proof of (i) is similar. Without loss of generality, we may assume that $(d_1, d_2) \in \widetilde{\Sigma}_-$ and $(U_{d_1,d_2}, V_{d_1,d_2})$ is any co-existence steady state solution to (1.11). Passing to a subsequence of d_1 if necessary, we may assume

$$\lim_{d_1\to 0^+} (U_{d_1,d_2}, V_{d_1,d_2}) := (U_{0,d_2}, V_{0,d_2}). \tag{3.12}$$

First we show that,

$$\|V_{0,d_2}\|_{L^\infty(\Omega)} > \inf_\Omega m_1. \tag{3.13}$$

Indeed, suppose that $\|V_{0,d_2}\|_{L^\infty(\Omega)} \le \inf_\Omega m_1$. Since $U_{0,d_2} = (m_1 - V_{0,d_2})^+$ by Proposition 2.5(a) in [LN] or Lemma 2.4 in [HLMV], we have

$$U_{0,d_2} = m_1 - V_{0,d_2}.$$

Thus as $d_1 \to 0^+$,

$$m_2 - U_{d_1,d_2} - V_{d_1,d_2} \to (m_2 - m_1) \text{ uniformly on } \bar{\Omega}.$$

However, since $\overline{m_1} = \overline{m_2}$ and $m_1 \not\equiv m_2$, by Proposition 2.1(v) and (i),

$$d_2^{-1} = \lambda_1(m_2 - U_{d_1,d_2} - V_{d_1,d_2}) \to \lambda_1(m_2 - m_1) = 0,$$

which is contradiction.

By (3.12), for each $d_2 > 0$, there exists some $\hat{d}_1 := d_1(d_2) > 0$ small and a co-existence steady state $(U_{\hat{d}_1,d_2}, V_{\hat{d}_1,d_2})$ of (1.11) with $(d_1, d_2) = (\hat{d}_1, d_2)$ satisfies that

$$\|U_{\hat{d}_1,d_2} - U_{0,d_2}\|_{L^\infty(\Omega)} + \|V_{\hat{d}_1,d_2} - V_{0,d_2}\|_{L^\infty(\Omega)} < \frac{1}{d_2}.$$

Thus letting $d_2 \to \infty$, we have

$$\lim_{d_2\to\infty} (U_{0,d_2}, V_{0,d_2}) = \lim_{d_2\to\infty} (U_{\hat{d}_1,d_2}, V_{\hat{d}_1,d_2}). \tag{3.14}$$

To finish the proof, it suffices to show that any co-existence steady state solution $(U_{d_1,d_2}, V_{d_1,d_2})$ of (1.11) must satisfy that

$$\lim_{d_1\to 0^+, d_2\to\infty} (U_{d_1,d_2}, V_{d_1,d_2}) = (m_1 - \xi, \xi) \tag{3.15}$$

for some $\xi \in [0, \inf_{\Omega} m_1]$. Then from (3.13) and (3.14), (ii) follows.

We now prove (3.15). By similar arguments as in the proof of (3.10) in Theorem 1.2(iii), passing to a subsequence of d_1 and d_2 if necessary, we have

$$\lim_{d_1\to 0^+, d_2\to\infty} (U_{d_1,d_2}, V_{d_1,d_2}) = (U_{0,\infty}, V_{0,\infty}),$$

where $V_{0,\infty} \equiv \xi$ for some constant $\xi \geq 0$ and $U_{0,\infty} = (m_1 - \xi)^+$ and

$$\int_\Omega (m_2 - (m_1 - \xi)^+ - \xi) = 0.$$

Since $\overline{m_1} = \overline{m_2}$, we must have $\xi \leq \inf_{\Omega} m_1$.

The proof of (iii) uses the same arguments as in that of Theorem 4.1 in [HLMV]. For completeness reason, we include a proof in the Appendix. $\square$

3.3 Cases of Sign-changing Intrinsic Growth Rates

In this section, we relax the condition (**M1**) for (1.5) and (**M2**) for (1.11) to allow the intrinsic growth rates to change sign in Ω. We will only indicate the necessary modifications from those in previous sections.

Assume that $m(x)$ satisfies the following condition for (1.5):

(M1′) $m(x) \in C^\gamma(\bar{\Omega})$ $(\gamma \in (0,1))$ is nonconstant and $\overline{m} > 0$.

Note that we do not require $m \geq 0$ in Ω any more. The main issue is that when $d_1 \to 0^+$, by Lemma 2.5 (i)(a), $\theta_{d_1,m} \to m^+$ which differs from m itself when m changes sign in Ω. Similar situation happens when we allow m_i $(i = 1,2)$ to change sign for (1.11) and corresponding modifications will be made clear later in this section.

Theorem 3.4. *Assume that* (**M1′**) *holds. Let* Σ_U, Σ_V *and* Σ_- *be defined as in* (1.6). *Then all statements in Theorem* 1.1 *hold except* (1.8) *which should be replaced by*

$$\lim_{d_1 \to 0^+} d_2^* \to \begin{cases} \infty & \text{if } m \geq 0 \text{ on } \Omega, \\ \dfrac{1}{\lambda_1(\overline{m} - m^+)} & \text{if } m \text{ changes sign on } \Omega. \end{cases} \tag{3.16}$$

Proof. Indeed, suppose that $m(x_0) < 0$ for some $x_0 \in \Omega$. Then by Lemma 2.5 (i)(a), as $d_1 \to 0^+$,

$$\overline{m} - \theta_{d_1,m} \to \overline{m} - m^+$$

uniformly on $\bar{\Omega}$. Since $\overline{m} - m^+ \leq \overline{m} - m$, $\int_\Omega (\overline{m} - m^+) < 0$ and $\overline{m} - m^+$ changes sign, by Proposition 2.1,

$$\lim_{d_1 \to 0^+} d_2^* = \frac{1}{\lambda_1(\overline{m} - m^+)} \in (0, \infty). \qquad \square$$

For illustration of the curve d_2^* and geometric shape of Σ_U for (1.5) when m changes sign in Ω, see Figures 3.1 and 3.2.

Theorem 3.5. *Assume that* (**M1′**) *holds, then all statements in Theorem* 3.2 *hold except for Theorem* 3.2*(ii) which should be complemented by the following: Suppose that* m *changes sign in* Ω*, then for all* d_1 *small and* d_2 *large,* $(\theta_{d_1,m}, 0)$ *is globally asymptotically stable.*

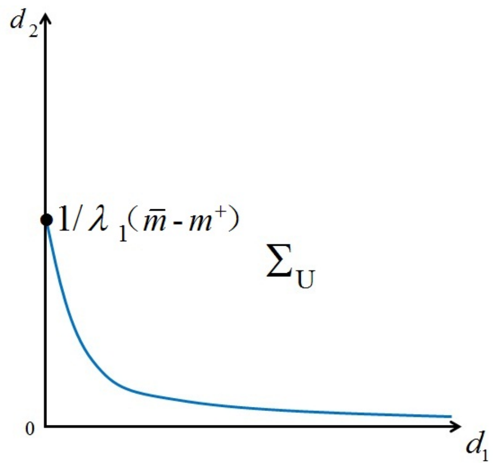

Figure 3.1: m changes sign and satisfies (**M1′**). Possible shape of Σ_U which lies above the curve d_2^*. $\Sigma_V = \emptyset$.

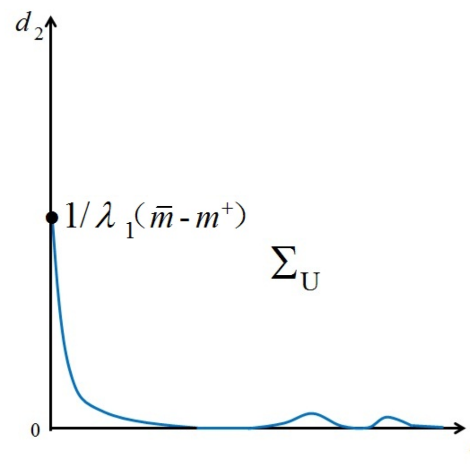

Figure 3.2: m changes sign and satisfies (**M1′**). The boundary of Σ_U could touch, or coincide with part of, d_1-axis. $\Sigma_V = \emptyset$.

The proof uses similar arguments as in that of Theorem 3.7(ii) below and is therefore omitted here.

Similarly, condition (**M2**) in Theorem 1.2 can be relaxed to the following:

(**M2′**) $m_i(x) \in C^\gamma(\bar{\Omega})$ ($\gamma \in (0,1)$) is nonconstant, $i = 1, 2$. $m_1 \not\equiv m_2$ and $\int_\Omega m_1 = \int_\Omega m_2 > 0$.

In this case, (1.15) does not necessarily hold any more.

Theorem 3.6. *Assume that* (**M2′**) *holds. Let* $\widetilde{\Sigma}_U$, $\widetilde{\Sigma}_V$ *and* $\widetilde{\Sigma}_-$ *be defined as in* (1.12). *Then all statements in Theorem* 1.2 *hold except*

(i) (1.15) *in Theorem* 1.2 *(i) should be modified as follows:*

(a) If m_1 changes sign in Ω, then

$$\lim_{d_1 \to 0^+} \widetilde{d}_2^* \in [0, \infty), \quad \lim_{d_1 \to \infty} \widetilde{d}_2^* = \infty, \tag{3.17}$$

(b) If m_2 changes sign in Ω, then

$$\lim_{d_2 \to 0^+} \widetilde{d}_1^* \in [0, \infty), \quad \lim_{d_2 \to \infty} \widetilde{d}_1^* = \infty. \tag{3.18}$$

(ii) Moreover, if m_1 or m_2 changes sign, then Theorem 1.2 *(ii) should be replaced by a weaker version* (3.7). *(See Remark* 3.1.*)*

Proof. Here we only show (3.17). The proof of the second half of (3.17) is the same as before. For the first half, suppose that $m_1(y_0) < 0$ for some $y_0 \in \Omega$. Then by Lemma 2.5 (i) (a), as $d_1 \to 0^+$,

$$m_2 - \theta_{d_1,m_1} \to m_2 - m_1^+$$

uniformly on $\bar{\Omega}$. Since $m_2 - m_1^+ < m_2 - m_1$ at y_0, $\int_\Omega (m_2 - m_1^+) < 0$. If $m_2 - m_1^+$ changes sign in Ω, then for all d_1 small, $\lambda_1(m_2 - \theta_{d_1,m_1})$ exists and $d_2^*(d_1) \to 1/\lambda_1(m_2 - m_1^+) \in (0, \infty)$ by Proposition 2.1. If $m_2 - m_1^+ \leq 0$ in Ω, then by Proposition 2.1 (vi), either $\lambda_1(m_2 - \theta_{d_1,m_1})$ exists for d_1 small and

$$\lambda_1(m_2 - \theta_{d_1,m_1}) \to \infty, \text{ as } d_1 \to 0^+,$$

or $d_2^*(d_1) = 0$ for d_1 small. □

Theorem 3.7. *Assume that* ($\mathbf{M2'}$) *holds.*

(i) Suppose that m_2 changes sign in Ω, then for all d_1 large and d_2 small, $(0, \theta_{d_2,m_2})$ is globally asymptotically stable.

(ii) Suppose that m_1 changes sign in Ω, then for all d_1 small and d_2 large, $(\theta_{d_1,m_1}, 0)$ is globally asymptotically stable.

(iii) Let (U, V) be any co-existence steady state of (1.11), then $\lim_{d_1,d_2 \to 0^+} (U, V) = (\widetilde{u}_*, \widetilde{v}_*)$ uniformly on compact subsets of $\bar{\Omega} \setminus \{x \in \bar{\Omega} \mid m_1(x) = m_2(x)$ and $m_1(x) > 0\}$, where

$$\widetilde{u}_*(x) = \begin{cases} m_1(x) & \text{if } m_1(x) > m_2(x) \text{ and } m_1(x) > 0, \\ 0 & \text{if } m_1(x) \leq 0 \text{ or } m_2(x) > m_1(x) > 0, \end{cases}$$

and

$$\widetilde{v}_*(x) = \begin{cases} 0 & \text{if } m_2(x) \leq 0 \text{ or } m_1(x) > m_2(x) > 0, \\ m_2(x) & \text{if } m_2(x) > m_1(x) \text{ and } m_2(x) > 0. \end{cases}$$

Proof. We will prove (ii) here, as the proof of (i) is similar. To show that $(\theta_{d_1,m_1}, 0)$ is globally asymptotically stable for all d_1 small and d_2 large, it suffices to show that (1.11) has no co-existence steady state in view of Lemma 2.4 (ii). Suppose this is not true. Then (1.11) has a co-existence steady state $(U_{d_1,d_2}, V_{d_1,d_2})$ along a sequence (d_1, d_2) with $d_1 \to 0^+$ and $d_2 \to \infty$. By Lemma 2.5 (ii) (which holds true for general

m_1, m_2 with exactly the same proof), both U_{d_1,d_2} and V_{d_1,d_2} are uniformly bounded on $\bar{\Omega}$ independent of d_1 and d_2. By passing to a subsequence of d_1 and d_2 if necessary, and using similar arguments as in the proof of (3.10) in Theorem 1.2 (iii), we obtain

$$\lim_{d_1 \to 0^+, d_2 \to \infty} (U_{d_1,d_2}, V_{d_1,d_2}) = (U_{0,\infty}, V_{0,\infty})$$

where $V_{0,\infty} \equiv \xi$ for some constant $\xi \geq 0$, $U_{0,\infty} = (m_1 - \xi)^+$ and

$$\int_\Omega (m_2 - (m_1 - \xi)^+ - \xi) = 0. \tag{3.19}$$

However, since $\overline{m_1} = \overline{m_2}$ and m_1 changes sign in Ω, (3.19) can not hold for any $\xi \geq 0$. Thus we get a contradiction.

Again, the proof of (iii) uses the same arguments as in that of Theorem 4.1 in [HLMV] and is included in the Appendix. (Note that compared to Theorem 3.3(iii) only the definition of $(\widetilde{u}_*, \widetilde{v}_*)$ is modified accordingly.) $\square$

Chapter 4

Dynamics of general Lotka-Volterra Competition-diffusion Systems

4.1 Backgrounds & Proof of Theorem 1.5

In Chapter 3, we have discussed the dynamics of (2.1) when $b = c = 1$ with various choices of m_1 and m_2 satisfying $\overline{m_1} = \overline{m_2}$, where $\overline{m_i} := \frac{1}{|\Omega|}\int_\Omega m_i$ denotes the average of m_i. In this chapter we shall incorporate different competition abilities (i.e. b, c different from 1) into our study. Through out this chapter, we will assume that m_1 and m_2 satisfies the following condition

(M) $m_i(x) \in C^\gamma(\bar{\Omega})$ $(\gamma \in (0,1))$ is nonconstant and $m_i(x) > 0$ on $\bar{\Omega}$, $i = 1, 2$,

as defined in Chapter 1.

First, we recall some related results concerning the weak competition case. The following result, due to Hutson, Lou and Mischaikow [HLM], and Lou [L1], addresses the global dynamics of (2.1) when d_1 and d_2 are both large or both small.

Theorem 4.1. *Assume that* $(\mathbf{M})$ *holds,* $0 < b < \inf_{\bar{\Omega}} \frac{m_2}{m_1}$ *and* $0 < c < \inf_{\bar{\Omega}} \frac{m_1}{m_2}$*.*

(i) For all d_1, d_2 *sufficiently small,* (2.1) *has a unique steady state* $(\tilde{U}, \tilde{V})$ *which is globally asymptotically stable and* $(\tilde{U}, \tilde{V}) \to \left(\frac{m_1 - cm_2}{1-bc}, \frac{m_2 - bm_1}{1-bc}\right)$ *as* $d_1, d_2 \to 0$*.*

(ii) For all d_1, d_2 *sufficiently large,* (2.1) *has a unique steady state* $(\hat{U}, \hat{V})$ *which is globally asymptotically stable and* $(\hat{U}, \hat{V}) \to \left(\frac{\overline{m_1} - c\overline{m_2}}{1-bc}, \frac{\overline{m_2} - b\overline{m_1}}{1-bc}\right)$ *as* $d_1, d_2 \to \infty$*.*

For a proof of Theorem 4.1(i), see [HLM]. Theorem 4.1(ii) is due to Lou [L1]. See [N, Sec. 4.4] for a proof. Note that if $m_1 \equiv m_2$, then the above theorem holds for all $b, c \in (0,1)$. Loosely speaking, when the inter-specific competition is weak, for small d_1, d_2, the dynamics of (2.1) behaves rather similarly to that of (2.1) with $d_1 = d_2 = 0$; while as d_1, d_2 are both large, the dynamics is similar to that of the spatially averaged ODE. In other words, for d_1, d_2 both small or both large, co-existence is the only possibility, and the situation is similar to the homogeneous case.

For intermediate d_1, d_2, the situation is, however, drastically different. In particular, Lou [L1] studied the case when $m_1 \equiv m_2 \equiv: m$, i.e.,

$$\begin{cases} U_t = d_1 \Delta U + U(m(x) - U - cV) & \text{in } \Omega \times \mathbb{R}^+, \\ V_t = d_2 \Delta V + V(m(x) - bU - V) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\ U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{in } \Omega. \end{cases} \tag{4.1}$$

Lou proved in [L1] that given any nonconstant positive function $m(x)$, there exist $b, c \in (0,1)$ and $d_1, d_2 > 0$ such that one of the semi-trivial steady states of (4.1) is the global attractor. In other words, the joint action of spatial heterogeneity and diffusion could drive one of the species to extinction, even in the weak competition case. This marks a dramatic departure from its homogeneous counterpart. A complete characterization of changes of dynamics of (4.1) is obtained by Lam and Ni in [LN] recently for $d_1 \leq d_2$ and c small, as b increases from 0 to 1. To describe their precise results, we first define

$$\Sigma_U^m := \{(d_1, d_2) \in \mathcal{Q} \,|\, (\theta_{d_1,m}, 0) \text{ is linearly stable in (4.1)}\}, \tag{4.2}$$

where $\mathcal{Q} := \mathbb{R}^+ \times \mathbb{R}^+$ and $\mathbb{R}^+ := (0, \infty)$.

Theorem 4.2 ([LN]). *Suppose that $m(x) \in C^\gamma(\bar{\Omega})$ $(\gamma \in (0,1))$ is nonconstant and $m(x) > 0$ on $\bar{\Omega}$. Then there exists $\bar{c} > 0$ such that for all $c \in (0, \bar{c})$ and for all $b \in [0,1]$, the following hold for system (4.1):*

(i) *$(\theta_{d_1,m}, 0)$ is globally asymptotically stable for all $(d_1, d_2) \in \overline{\Sigma_U^m}$.*

(ii) *For any $d_1 \leq d_2$ such that $(d_1, d_2) \notin \overline{\Sigma_U^m}$, (4.1) has a unique co-existence steady state which is globally asymptotically stable.*

For a detailed characterizations of the sets Σ_U^m and $\overline{\Sigma_U^m}$, see [LN]. In particular, it is proved in [L1, LN] that Σ_U^m is nonempty if and only if

$$b > b_* := \inf_{d_1>0} \frac{\overline{m}}{\overline{\theta_{d_1,m}}}. \tag{4.3}$$

The purpose of this chapter is to investigate the dynamics of system (2.1) for general m_1 and m_2 satisfying condition ($\mathbf{M}$). It seems convenient to introduce a parameter $\beta > 0$, as a coefficient of m_2, which measures the relative strength of the carrying capacity or intrinsic growth rate for V versus that for U; i.e., we rewrite (2.1) as follows:

$$\begin{cases} U_t = d_1 \Delta U + U(m_1(x) - U - c\,V) & \text{in } \Omega \times \mathbb{R}^+, \\ V_t = d_2 \Delta V + V(\beta m_2(x) - b\,U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\ U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{in } \Omega. \end{cases} \tag{4.4}$$

When both m_1 and m_2 are constants, (4.4) reduces to (1.17) and the global dynamics is completely determined in Theorem 1.4. When spatial heterogeneity comes into play in (4.4), the roles of β^U and β^V in Theorem 1.4 become more complicated. As we shall in Chapter 4.3, β^U (resp. β^V) splits into three numbers β_{**}, β_* and $\underline{\beta}$ (resp. β^{**}, β^* and $\overline{\beta}$) which are defined by (1.19), (1.23) and (1.20) respectively. Our goal is to characterize dynamics of (4.4) for fixed $b, c > 0$ satisfying $bc \leqslant 1$ when β is restricted on certain ranges and finish the proof of Theorems 1.5-1.8.

In the end of this section, we prove Theorem 1.5.

Proof of Theorem 1.5. It suffices to show (i), as the proof of (ii) is similar. For (i), first we claim that $(\theta_{d_1,m_1}, 0)$ is linearly stable. By Lemma 2.3, it suffices to show that $\mu_1(d_2, \beta m_2 - b\,\theta_{d_1,m_1}) > 0$. By Lemma 2.5(i)(b), $\beta m_2 - b\,\theta_{d_1,m_1} \leq \beta \sup_{\bar\Omega} m_2 - b \inf_{\bar\Omega} m_1 < 0$ since $\beta < \beta_{**}$. Thus $\mu_1(d_2, \beta m_2 - b\,\theta_{d_1,m_1}) > 0$ by Proposition 2.2(iv). Similarly, we can show that $(0, \theta_{d_2,\beta m_2})$ is linearly unstable for all $\beta < \beta_{**}$.

Next we show that there is no co-existence steady state of system (4.4) for all $\beta \in (0, \beta_{**})$. Then by Lemma 2.4, $(\theta_{d_1,m_1}, 0)$ must be globally asymptotically stable. Assume for contradiction that (U, V) is a co-existence steady state of (4.4), i.e. U, $V > 0$ in $\bar\Omega$. From standard arguments it follows that

$$\Delta U(P) \geq 0 \quad \text{and} \quad \Delta V(Q) \leq 0,$$

where $U(P) = \inf_{\bar\Omega} U$ and $V(Q) = \sup_{\bar\Omega} V$.

Now to finish the proof, we evaluate the equation of U at P. Since $\Delta U(P) \geq 0$, $m_1(P) - U(P) - c\,V(P) \leq 0$. Thus $U(P) \geq m_1(P) - c\,V(P)$. Similarly, evaluating the equation of V at Q, we obtain that $\beta m_2(Q) - b\,U(Q) - V(Q) \geq 0$. Thus

$$\begin{aligned} V(Q) &\leq \beta m_2(Q) - b\,U(Q) \leq \beta m_2(Q) - b\,U(P) \leq \beta m_2(Q) - b\,(m_1(P) - c\,V(P)) \\ &= b\,c\,V(P) - (b\,m_1(P) - \beta m_2(Q)) \leq b\,c\,V(P) - \delta, \end{aligned}$$

where $\delta = b\,\inf_{\bar\Omega} m_1 - \beta \sup_{\bar\Omega} m_2 > 0$ since $\beta < \beta_{**}$. Thus we arrive at a contradiction as $b\,c \leq 1$, $\delta > 0$ and $V(Q)$ is the global maximum of V on $\bar\Omega$. Thus the theorem is proved. □

4.2 Stability Properties of Semi-trivial Steady States

In this section, we characterize the change of linear stability of the two semi-trivial steady states $(\theta_{d_1,m_1}, 0)$ and $(0, \theta_{d_2,\beta m_2})$ of (4.4) as β increases from 0 to ∞.

Proposition 4.3. (I) *Assume that $m_i(x) \in C^\gamma(\bar\Omega)$ ($\gamma \in (0,1)$) is nonconstant and $\int_\Omega m_i \geq 0$ for $i = 1, 2$. Then for any $d_1, d_2 > 0$, there exists a unique number $\beta^U_{d_1,d_2} > 0$ such that*

$$\mu_1(d_2, \beta^U_{d_1,d_2} m_2 - b\,\theta_{d_1,m_1}) = 0. \tag{4.5}$$

Moreover, the following statements hold:

(i) For system (4.4), $(\theta_{d_1,m_1}, 0)$ is linearly stable if $\beta \in (0, \beta^U_{d_1,d_2})$ and linearly unstable if $\beta \in (\beta^U_{d_1,d_2}, \infty)$.

(ii) $\beta^U_{d_1,d_2}$ is strictly increasing in d_2 if $\frac{\theta_{d_1,m_1}}{m_2} \not\equiv \mathrm{const}$.

(iii) $\beta^U_{d_1,d_2} = b\frac{\theta_{d_1,m_1}}{m_2}$ for all $d_2 > 0$ if $\frac{\theta_{d_1,m_1}}{m_2} \equiv \mathrm{const}$ on $\bar\Omega$.

(II) *If in addition we assume that m_1 and m_2 satisfy* (**M**), *then all four limits of $\beta^U_{d_1,d_2}$, as d_1 or d_2 approaches 0 or ∞, exist:*

$$\begin{aligned} \beta^U_{d_1,0} &:= \lim_{d_2\to 0} \beta^U_{d_1,d_2}, \quad \beta^U_{d_1,\infty} := \lim_{d_2\to\infty} \beta^U_{d_1,d_2}, \\ \beta^U_{0,d_2} &:= \lim_{d_1\to 0} \beta^U_{d_1,d_2}, \quad \beta^U_{\infty,d_2} := \lim_{d_1\to\infty} \beta^U_{d_1,d_2}. \end{aligned}$$

Moreover, we have

(i) $\beta^U_{d_1,0} = b \inf_{\bar\Omega} \frac{\theta_{d_1,m_1}}{m_2}$.

(ii) $\beta^U_{d_1,\infty} = b \frac{\overline{\theta_{d_1,m_1}}}{\overline{m_2}}$.

(iii) $\mu_1(d_2, \beta^U_{0,d_2} m_2 - b\, m_1) = 0$*; or equivalently*

$$\begin{cases} \beta^U_{0,d_2} = b\, r & \textit{if } m_1 \equiv r m_2 \textit{ for some } r > 0, \\ \lambda_1(\beta^U_{0,d_2} m_2 - b\, m_1) = d_2^{-1} & \textit{otherwise.} \end{cases}$$

(iv) $\mu_1(d_2, \beta^U_{\infty,d_2} m_2 - b\, \overline{m_1}) = 0$*; or equivalently,* $\lambda_1(\beta^U_{\infty,d_2} m_2 - b\, \overline{m_1}) = d_2^{-1}$.

Note that the condition in Part (I) of the above proposition is more general than (**M**). In fact, it will be clear from the proof below that under the same general hypothesis as in Part (I), we still have Part (II)(ii) and Part (II)(i) should be replaced by: (II)(i)′ $\beta^U_{d_1,0} = b \inf_{\{m_2>0\}} \frac{\theta_{d_1,m_1}}{m_2}$.

Proof of Proposition 4.3. To prove Part (I) of the proposition, we assume that $m_i(x) \not\equiv$ const, $\int_\Omega m_i \geq 0$ for $i = 1, 2$.

To show Part (I)(i), by Lemma 2.3, it suffices to show that there exists a unique $\beta^U_{d_1,d_2} > 0$ such that

$$\begin{cases} \mu_1(d_2, \beta m_2 - b\, \theta_{d_1,m_1}) > 0 & \text{if } \beta \in (0, \beta^U_{d_1,d_2}), \\ \mu_1(d_2, \beta m_2 - b\, \theta_{d_1,m_1}) = 0 & \text{if } \beta = \beta^U_{d_1,d_2}, \\ \mu_1(d_2, \beta m_2 - b\, \theta_{d_1,m_1}) < 0 & \text{if } \beta \in (\beta^U_{d_1,d_2}, \infty). \end{cases} \tag{4.6}$$

If $\frac{\theta_{d_1,m_1}}{m_2} \equiv$ const (this implies that $m_2 > 0$ on $\bar\Omega$), we define $\beta^U_{d_1,d_2} = b \frac{\theta_{d_1,m_1}}{m_2}$. Then (4.6) follows from Proposition 2.2(i) and (iv). Therefore Part (I)(iii) is proved. Moreover, Parts (II)(i) and (II)(ii) above also obviously hold in this case.

So now we assume that $\frac{\theta_{d_1,m_1}}{m_2} \not\equiv$ const. Consider $\lambda_1(s m_2 - b\, \theta_{d_1,m_1})$ as a function in s. Then by Proposition 2.9, there exists a unique $\beta^U_{d_1,d_2} > 0$ such that $\lambda_1(\beta^U_{d_1,d_2} m_2 - b\, \theta_{d_1,m_1}) = d_2^{-1}$. Thus (4.5) holds by Proposition 2.2(ii). Since $\lambda_1(s m_2 - b\, \theta_{d_1,m_1})$ is strictly decreasing in s by Proposition 2.9, $\beta^U_{d_1,d_2}$ is strictly increasing in d_2. Therefore Part (I)(ii) holds. Parts (II)(i)′ and (II)(ii) also follow from Proposition 2.9. Note that

(i) if $\beta \leq b \inf_{\{m>0\}} \frac{\theta_{d_1,m_1}}{m_2}$, $\beta m_2 - b\, \theta_{d_1,m_1} \leq (\not\equiv)\, 0$;

(ii) if $\beta \in (b \inf_{\{m>0\}} \frac{\theta_{d_1,m_1}}{m_2}, \beta^U_{d_1,d_2})$, $\lambda_1(\beta m_2 - b\,\theta_{d_1,m_1}) > d_2^{-1}$;

(iii) if $\beta \in (\beta^U_{d_1,d_2}, b\frac{\overline{\theta_{d_1,m_1}}}{\overline{m_2}})$, $\lambda_1(\beta m_2 - b\,\theta_{d_1,m_1}) < d_2^{-1}$;

(iv) if $\beta \geq b\frac{\overline{\theta_{d_1,m_1}}}{\overline{m_2}}$, $\int_\Omega(\beta m_2 - b\,\theta_{d_1,m_1}) \geq (\not\equiv) 0$.

(If $\int_\Omega m_2 = 0$, then case (iii) above holds for all $\beta \in (\beta^U_{d_1,d_2}, \infty)$ and we do not need case (iv).) Thus (4.6) follows from Proposition 2.2. This finishes the proof of Part (I).

Now it only remains to prove Parts (II)(iii) and (II)(iv) under condition (**M**). From the proof of Theorem 1.5, it is easy to see that $\beta^U_{d_1,d_2} \in (\beta_{**}, \beta^{**})$ for all $d_1, d_2 > 0$. When $d_1 \to 0$, $\theta_{d_1,m_1} \to m_1$ by Lemma 2.5(i)(a). Passing to a subsequence of d_1 if necessary, we may assume $\beta^U_{d_1,d_2} \to \beta^U_{0,d_2}$ as $d_1 \to 0$. By (4.5) and the continuity of $\mu_1(d_2, \cdot)$, we have

$$\mu_1(d_2, \beta^U_{0,d_2} m_2 - b m_1) = 0.$$

If $m_1 = r m_2$ for some $r > 0$, since $m_2 > 0$ on $\bar{\Omega}$, we must have $\beta^U_{0,d_2} = b\,r$ by Proposition 2.2(i) and (iv). If m_1 is not a constant multiple of m_2, then $\beta^U_{0,d_2} m_2 - b m_1$ must change sign thus satisfies that $\lambda_1(\beta^U_{0,d_2} m_2 - b m_1) = d_2^{-1}$. Since β^U_{0,d_2} is uniquely determined in both cases and is independent of the subsequence chosen, it must be the limit of $\beta^U_{d_1,d_2}$ as $d_1 \to 0$. When $d_1 \to \infty$, $\theta_{d_1,m_1} \to \overline{m_1}$ by Lemma 2.5(i)(a) and by similar arguments, Part (II)(iv) holds. □

Proposition 4.4. *Assume that* (**M**) *holds.*

(I) *For any $d_1, d_2 > 0$, there exists a unique number $\beta^V_{d_1,d_2} > 0$ such that*

$$\mu_1(d_1, m_1 - c\,\theta_{d_2, \beta^V_{d_1,d_2} m_2}) = 0. \tag{4.7}$$

Moreover, the following statements hold:

(i) For system (4.4), $(0, \theta_{d_2,\beta m_2})$ is linearly unstable if $\beta \in (0, \beta^V_{d_1,d_2})$ and linearly stable if $\beta \in (\beta^V_{d_1,d_2}, \infty)$.

(ii) $\beta^V_{d_1,d_2}$ is strictly decreasing in d_1 if $m_1 \not\equiv c\,\theta_{d_2,sm_2}$ for any $s > 0$.

(iii) If there exists some $s > 0$ such that $m_1 \equiv c\,\theta_{d_2,sm_2}$, then $\beta^V_{d_1,d_2} = s$ for all $d_1 > 0$.

(II) *All four limits of* $\beta^V_{d_1,d_2}$ *as* d_1 *or* d_2 *approaches* 0 *or* ∞ *exist:*

$$\beta^V_{d_1,0} := \lim_{d_2\to 0}\beta^V_{d_1,d_2}, \quad \beta^V_{d_1,\infty} := \lim_{d_2\to\infty}\beta^V_{d_1,d_2},$$
$$\beta^V_{0,d_2} := \lim_{d_1\to 0}\beta^V_{d_1,d_2}, \quad \beta^V_{\infty,d_2} := \lim_{d_1\to\infty}\beta^V_{d_1,d_2}.$$

Moreover, we have

(i) $\beta^V_{0,d_2} = \inf\{s \,|\, c\,\theta_{d_2,sm_2} \geq m_1 \text{ in } \Omega\}$.

(ii) $\beta^V_{\infty,d_2} = \inf\{s \,|\, \overline{c\,\theta_{d_2,sm_2}} \geq \overline{m_1}\}$.

(iii) $\mu_1(d_1, m_1 - c\,\beta^V_{d_1,0}m_2) = 0$*; or equivalently*

$$\begin{cases} \beta^V_{d_1,0} = r/c & \text{if } m_1 \equiv rm_2 \text{ for some } r>0,\\ \lambda_1(m_1 - c\beta^V_{d_1,0}m_2) = d_1^{-1} & \text{otherwise.}\end{cases}$$

(iv) $\mu_1(d_1, m_1 - c\,\beta^V_{d_1,\infty}\overline{m_2}) = 0$*; or equivalently,* $\lambda_1(m_1 - c\,\beta^V_{d_1,\infty}\overline{m_2}) = d_1^{-1}$.

Proof. For any $d_1, d_2 > 0$ fixed, it follows from Lemma 2.7 and Proposition 2.2(i) and (iv) that $\mu_1(d_1, m_1 - c\,\theta_{d_2,\beta m_2}) < 0$ for all β small and $\mu_1(d_1, m_1 - c\,\theta_{d_2,\beta m_2}) > 0$ for all β large. Moreover, since $m_1 - c\,\theta_{d_2,\beta m_2}$ is continuous and strictly decreasing in β by Lemma 2.7, $\mu_1(d_1, m_1 - c\,\theta_{d_2,\beta m_2})$ is continuous and strictly increasing in β by Proposition 2.2. Therefore, there exists a unique number $\beta^V_{d_1,d_2} > 0$ such that (4.7) holds and hence Part (I)(i) follows from the strict monotonicity of $\mu_1(d_1, m_1 - c\,\theta_{d_2,\beta m_2})$ in β and Lemma 2.3.

If there exists some $s > 0$, which must be unique by Lemma 2.7, such that $m_1 \equiv c\,\theta_{d_2,sm_2}$, then $\mu_1(d_1, m_1 - c\,\theta_{d_2,sm_2}) = 0$. Thus the uniqueness of $\beta^V_{d_1,d_2}$ implies that $\beta^V_{d_1,d_2} = s$ for all $d_1 > 0$. Thus $\beta^V_{0,d_2} = \beta^V_{\infty,d_2} = s$ and in this case we have obtained Parts (I)(iii), (II)(i) and (ii).

If $m_1 \not\equiv c\,\theta_{d_2,sm_2}$ for any $s > 0$, then $m_1 - c\,\theta_{d_2,\beta^V_{d_1,d_2}m_2}$ must change sign. By Proposition 2.1(iii) and 2.2(ii), (4.7) implies that

$$\lambda_1(m_1 - c\,\theta_{d_2,\beta^V_{d_1,d_2}m_2}) = d_1^{-1}.$$

Set

$$s_1 := \inf\{s \,|\, c\,\overline{\theta_{d_2,sm_2}} \geq \overline{m_1}\} \quad \text{and} \quad s_2 := \inf\{s \,|\, c\,\theta_{d_2,sm_2} - m_1 \geq 0 \text{ in } \Omega\}.$$

By Lemma 2.7, both s_1 and s_2 are well-defined and $0 < s_1 < s_2$. By similar arguments as in the proof of Proposition 2.8, $\lambda_1(m_1 - c\,\theta_{d_2,sm_2}) > 0$ if and only if $s \in (s_1, s_2)$. Moreover, $\lambda_1(m_1 - c\,\theta_{d_2,sm_2})$ is strictly increasing in $s \in (s_1, s_2)$. Thus $\beta^V_{d_1,d_2}$ is strictly decreasing in d_1, which implies Part I(ii). Moreover,

$$\lambda_1(m_1 - c\,\theta_{d_2,sm_2}) \to 0 \text{ as } s \to s_1, \quad \lambda_1(m_1 - c\,\theta_{d_2,sm_2}) \to \infty \text{ as } s \to s_2.$$

Therefore, Part (II)(i) and (ii) for the case $m_1 \not\equiv c\,\theta_{d_2,sm_2}$ for any $s > 0$ follow.

By Theorem 1.5, $\beta^V_{d_1,d_2} \in (\beta_{**}, \beta^{**})$ for all $d_1, d_2 > 0$. When $d_2 \to 0$, passing to a subsequence if necessary, we may assume that $\beta^V_{d_1,d_2} \to \beta^V_{d_1,0}$ and $\theta_{d_2,\beta^V_{d_1,d_2} m_2} \to \beta^V_{d_1,0} m_2$ by Lemma 2.5(i)(a). By (4.7) and the continuity of $\mu_1(d_1, \cdot)$, we have

$$\mu_1(d_1, m_1 - c\,\beta^V_{d_1,0} m_2) = 0.$$

If $m_1 \equiv r m_2$ for some $r > 0$, since $m_2 > 0$ on $\bar{\Omega}$, we must have $\beta^V_{d_1,0} = r\,c$ by Proposition 2.2(i) and (iv). If m_1 is not a constant multiple of m_2, then $m_1 - c\,\beta^V_{d_1,0} m_2$ must change sign and satisfy that $\lambda_1(m_1 - c\,\beta^V_{d_1,0} m_2) = d_1^{-1}$. Since $\beta^V_{d_1,0}$ is uniquely determined in both cases and is therefore independent of the subsequence chosen, it must be the limit of $\beta^V_{d_1,d_2}$ as $d_2 \to 0$. Thus Part II(iii) holds. Similarly, when $d_2 \to \infty$, passing to a subsequence if necessary, we have $\beta^V_{d_1,d_2} \to \beta^V_{d_1,\infty}$ and $\theta_{d_2,\beta^V_{d_1,d_2} m_2} \to \beta^V_{d_1,\infty} \overline{m_2}$ by Lemma 2.5(i)(a). Thus $\beta^V_{d_1,d_2} \to \beta^V_{d_1,\infty}$ and Part II(iv) holds, which completes our proof. $\square$

4.3 Proofs of Theorems 1.6-1.8

Now we are ready to prove Theorem 1.6.

Proof of Theorem 1.6. Parts (i) and (ii) are direct consequences of Propositions 4.3(I)(i) and 4.4(I)(i) respectively. Thus it only remains to prove Parts (iii) and (iv).

Choosing θ_{d_1,m_1} as a test function for $\mu_1(d_1, m_1 - c\,\theta_{d_2,\beta^V_{d_1,d_2} m_2})$, by (4.7) and (2.6), we obtain that

$$\begin{aligned}
0 &= \mu_1(d_1, m_1 - c\,\theta_{_{d_2,\beta^V_{d_1,d_2}m_2}}) \\
&\le \frac{d_1 \int_\Omega |\nabla\theta_{d_1,m_1}|^2 + \int_\Omega (c\,\theta_{_{d_2,\beta^V_{d_1,d_2}m_2}} - m_1)\theta^2_{d_1,m_1}}{\int_\Omega \theta^2_{d_1,m_1}} \\
&= \frac{\int_\Omega (c\,\theta_{_{d_2,\beta^V_{d_1,d_2}m_2}} - \theta_{d_1,m_1})\theta^2_{d_1,m_1}}{\int_\Omega \theta^2_{d_1,m_1}},
\end{aligned}$$

where we have used the following identity obtained by multiplying the equation of θ_{d_1,m_1} by itself and integrating over Ω:

$$d_1 \int_\Omega |\nabla\theta_{d_1,m_1}|^2 = \int_\Omega \theta^2_{d_1,m_1}(m_1 - \theta_{d_1,m_1}). \tag{4.8}$$

Thus

$$A := \int_\Omega (c\,\theta_{_{d_2,\beta^V_{d_1,d_2}m_2}} - \theta_{d_1,m_1})\theta^2_{d_1,m_1} \ge 0. \tag{4.9}$$

Similarly, choosing $\theta_{_{d_2,\beta^V_{d_1,d_2}m_2}}$ as a test function for $\mu_1(d_2, \beta^U_{d_1,d_2}m_2 - b\,\theta_{d_1,m_1})$, by (4.5) and (2.6), we obtain

$$\begin{aligned}
0 &= \mu_1(d_2, \beta^U_{d_1,d_2}m_2 - b\,\theta_{d_1,m_1}) \\
&\le \frac{d_2 \int_\Omega |\nabla\theta_{_{d_2,\beta^V_{d_1,d_2}m_2}}|^2 + \int_\Omega (b\,\theta_{d_1,m_1} - \beta^U_{d_1,d_2}m_2)\theta^2_{_{d_2,\beta^V_{d_1,d_2}m_2}}}{\int_\Omega \theta^2_{_{d_2,\beta^V_{d_1,d_2}m_2}}} \\
&= \frac{(\beta^V_{d_1,d_2} - \beta^U_{d_1,d_2}) \int_\Omega m_2\theta^2_{d_2,\beta^V_{d_1,d_2}m_2} + \int_\Omega \theta^2_{d_2,\beta^V_{d_1,d_2}m_2}(b\,\theta_{d_1,m_1} - \theta_{_{d_2,\beta^V_{d_1,d_2}m_2}})}{\int_\Omega \theta^2_{_{d_2,\beta^V_{d_1,d_2}m_2}}},
\end{aligned}$$

where we have used a similar identity to (4.8) for $\theta_{_{d_2,\beta^V_{d_1,d_2}m_2}}$. Thus

$$(\beta^V_{d_1,d_2} - \beta^U_{d_1,d_2}) \int_\Omega m_2\theta^2_{d_2,\beta^V_{d_1,d_2}m_2} \ge \int_\Omega \theta^2_{d_2,\beta^V_{d_1,d_2}m_2}(\theta_{_{d_2,\beta^V_{d_1,d_2}m_2}} - b\,\theta_{d_1,m_1}) =: B. \tag{4.10}$$

Since $b\,c \le 1$,

$$c^3 B - A \ge \int_\Omega (c\,\theta_{_{d_2,\beta^V_{d_1,d_2}m_2}} - \theta_{d_1,m_1})^2 (c\,\theta_{_{d_2,\beta^V_{d_1,d_2}m_2}} + \theta_{d_1,m_1}) \ge 0,$$

i.e., $B \ge A/c^3 \ge 0$, where both equalities hold if and only if $b\,c = 1$ and $c\,\theta_{_{d_2,\beta^V_{d_1,d_2}m_2}} =$

θ_{d_1,m_1}. Thus by (4.9) and (4.10), we obtain that $\beta^V_{d_1,d_2} \geq \beta^U_{d_1,d_2}$, where equality holds only if $b\,c = 1$ and $\theta_{d_1,m_1} \equiv c\,\theta_{d_2,\beta^V_{d_1,d_2}m_2}$ on $\bar{\Omega}$. In particular, if $b\,c < 1$ or $\theta_{d_1,m_1} \not\equiv c\,\theta_{d_2,sm_2}$ for any $s > 0$, then $\beta^U_{d_1,d_2} < \beta^V_{d_1,d_2}$. In this case, the theory of monotone flow implies that there exists a stable co-existence steady state of system (4.4) for all $\beta \in (\beta^U_{d_1,d_2}, \beta^V_{d_1,d_2})$ and this finishes the proof of Part (iii).

On the other hand, suppose that $b\,c = 1$ and there exists some $s > 0$ such that $\theta_{d_1,m_1} \equiv c\,\theta_{d_2,sm_2}$. The equation of θ_{d_2,sm_2} and $\theta_{d_1,m_1} \equiv c\,\theta_{d_2,sm_2}$ imply that $\beta^U_{d_1,d_2} = s$ by (4.5). Since $\theta_{d_1,m_1} \equiv c\,\theta_{d_2,sm_2}$, the equation of θ_{d_1,m_1} implies that $\beta^V_{d_1,d_2} = s$ by (4.7). Thus $\beta^U_{d_1,d_2} = \beta^V_{d_1,d_2} = s$ and Part (iv) is established. $\square$

The next theorem says that after taking limit on d_1 or d_2, the order between $\beta^U_{d_1,d_2}$ and $\beta^V_{d_1,d_2}$ in Theorem 1.6 is preserved.

Theorem 4.5. *Assume that* (**M**) *holds and that* $b\,c \leq 1$. *Then*

(i) $\beta^U_{d_1,\infty} < \beta^V_{d_1,\infty}$.

(ii) $\beta^U_{\infty,d_2} < \beta^V_{\infty,d_2}$.

(iii) *(a) If* $b\,c < 1$ *or* $\theta_{d_1,m_1} \not\equiv c\,\tilde{s}m_2$ *for any* $\tilde{s} > 0$*, then* $\beta^U_{d_1,0} < \beta^V_{d_1,0}$.

(b) If $b\,c = 1$ *and* $\theta_{d_1,m_1} \equiv c\,\tilde{s}m_2$ *for some* $\tilde{s} > 0$*, then* $\beta^U_{d_1,0} = \beta^V_{d_1,0} = \tilde{s}$*. Conversely, if* $\beta^U_{d_1,0} = \beta^V_{d_1,0}$*, then* $b\,c = 1$ *and* $\theta_{d_1,m_1} \equiv c\,\beta^V_{d_1,0}m_2$.

(iv) *(a) If* $b\,c < 1$ *or* $m_1 \not\equiv c\,\theta_{d_2,\hat{s}m_2}$ *for any* $\hat{s} > 0$*, then* $\beta^U_{0,d_2} < \beta^V_{0,d_2}$.

(b) If $b\,c = 1$ *and* $m_1 \equiv c\,\theta_{d_2,\hat{s}m_2}$ *for some* $\hat{s} > 0$*, then* $\beta^U_{0,d_2} = \beta^V_{0,d_2} = \hat{s}$*. Conversely, if* $\beta^U_{0,d_2} = \beta^V_{0,d_2}$*, then* $b\,c = 1$ *and* $m_1 \equiv c\,\theta_{d_2,\beta^V_{0,d_2}m_2}$.

Proof. First we prove that $\beta^U_{d_1,\infty} < \beta^V_{d_1,\infty}$. By Propositions 4.3(II)(ii) and 4.4(II)(iv), $\beta^U_{d_1,\infty} = b\frac{\overline{\theta_{d_1,m_1}}}{\overline{m_2}}$ and $\beta^V_{d_1,\infty}$ satisfies that $\lambda_1(m_1 - c\,\beta^V_{d_1,\infty}\overline{m_2}) = d_1^{-1}$. By Proposition 2.8, $\lambda_1(m_1 - c\,s\,\overline{m_2}) > 0$ if and only if $s \in (\frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}, \frac{1}{c}\frac{\sup_{\bar{\Omega}} m_1}{\overline{m_2}})$. If $\beta^U_{d_1,\infty} \leq \frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}$, then as $\beta^V_{d_1,\infty} \in (\frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}, \frac{1}{c}\frac{\sup_{\bar{\Omega}} m_1}{\overline{m_2}})$, we obtain $\beta^U_{d_1,\infty} < \beta^V_{d_1,\infty}$. Otherwise, since $b\,c \leq 1$, $\overline{\theta_{d_1,m_1}} < \sup_{\bar{\Omega}} \theta_{d_1,m_1} < \sup_{\bar{\Omega}} m_1$ by Lemma 2.5(i)(b), it follows that $\beta^U_{d_1,\infty} < \frac{\sup_{\bar{\Omega}} m_1}{c\overline{m_2}}$. Thus $\beta^U_{d_1,\infty} \in (\frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}, \frac{1}{c}\frac{\sup_{\bar{\Omega}} m_1}{\overline{m_2}})$. Denote $\lambda_\infty := \lambda_1(m_1 - c\,\beta^U_{d_1,\infty}\overline{m_2})$. Equivalently, by Proposition 2.2(ii), we have

$$\mu_1(\lambda_\infty^{-1}, m_1 - c\,\beta^U_{d_1,\infty}\overline{m_2}) = 0.$$

Since $\lambda_1(m_1 - c\,s\,\overline{m_2})$ is strictly increasing for all $s \in (\frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}, \frac{1}{c}\frac{\sup_{\bar{\Omega}} m_1}{\overline{m_2}})$ by Proposition 2.8, to prove $\beta^U_{d_1,\infty} < \beta^V_{d_1,\infty}$, it suffices to show that $\lambda_\infty < d_1^{-1}$. Choosing θ_{d_1,m_1} as a test function, by (2.6) and (4.8), we have

$$\begin{aligned}
0 &= \mu_1(\lambda_\infty^{-1}, m_1 - c\,\beta^U_{d_1,\infty}\overline{m_2}) \\
&\le \frac{\lambda_\infty^{-1}\int_\Omega |\nabla\theta_{d_1,m_1}|^2 + \int_\Omega (bc\,\overline{\theta_{d_1,m_1}} - m_1)\theta^2_{d_1,m_1}}{\int_\Omega \theta^2_{d_1,m_1}} \\
&= \frac{\int_\Omega (bc\,\overline{\theta_{d_1,m_1}} - m_1)\theta^2_{d_1,m_1} - (d_1\lambda_\infty)^{-1}\int_\Omega \theta^2_{d_1,m_1}(\theta_{d_1,m_1} - m_1)}{\int_\Omega \theta^2_{d_1,m_1}}.
\end{aligned}$$

Since $b\,c \le 1$, we have

$$\begin{aligned}
&\int_\Omega \theta^2_{d_1,m_1}(\theta_{d_1,m_1} - m_1) - \int_\Omega \theta^2_{d_1,m_1}(b\,c\,\overline{\theta_{d_1,m_1}} - m_1) \\
=&\int_\Omega \theta^2_{d_1,m_1}(\theta_{d_1,m_1} - bc\,\overline{\theta_{d_1,m_1}}) \\
\ge&\int_\Omega \theta^2_{d_1,m_1}(\theta_{d_1,m_1} - \overline{\theta_{d_1,m_1}}) \\
=&\int_\Omega (\theta_{d_1,m_1} + \overline{\theta_{d_1,m_1}})(\theta_{d_1,m_1} - \overline{\theta_{d_1,m_1}})(\theta_{d_1,m_1} - \overline{\theta_{d_1,m_1}}) \\
=&\int_\Omega (\theta_{d_1,m_1} + \overline{\theta_{d_1,m_1}})(\theta_{d_1,m_1} - \overline{\theta_{d_1,m_1}})^2 \\
>&0,
\end{aligned} \tag{4.11}$$

which implies that $\lambda_\infty < d_1^{-1}$. This finishes the proof of (i).

Next we show that $\beta^U_{\infty,d_2} < \beta^V_{\infty,d_2}$. By Proposition 4.3(II)(iv), β^U_{∞,d_2} satisfies that $\mu_1(d_2, \beta^U_{\infty,d_2}m_2 - b\,\overline{m_1}) = 0$. Choosing $\theta_{d_2,\beta^V_{\infty,d_2}m_2}$ as a test function, by (2.6), we obtain

$$\begin{aligned}
0 &= \mu_1(d_2, \beta^U_{\infty,d_2}m_2 - b\,\overline{m_1}) \\
&\le \frac{d_2\int_\Omega |\nabla\theta_{d_2,\beta^V_{\infty,d_2}m_2}|^2 + \int_\Omega (b\,\overline{m_1} - \beta^U_{\infty,d_2}m_2)\theta^2_{d_2,\beta^V_{\infty,d_2}m_2}}{\int_\Omega \theta^2_{d_2,\beta^V_{\infty,d_2}m_2}} \\
&= \frac{(\beta^V_{\infty,d_2} - \beta^U_{\infty,d_2})\int_\Omega m_2\theta^2_{d_2,\beta^V_{\infty,d_2}m_2} - \int_\Omega \theta^2_{d_2,\beta^V_{\infty,d_2}m_2}(\theta_{d_2,\beta^V_{\infty,d_2}m_2} - b\,\overline{m_1})}{\int_\Omega \theta^2_{d_2,\beta^V_{\infty,d_2}m_2}},
\end{aligned}$$

where we have used a similar identity to (4.8) for $\theta_{d_2,\beta^V_{\infty,d_2}m_2}$. By Proposition 4.4(II)(ii),

$\beta^V_{\infty,d_2} = \inf\{s \,|\, \overline{c\,\theta_{d_2,sm_2}} \geq \overline{m_1}\}$. Thus $\overline{c\,\theta_{d_2,\beta^V_{\infty,d_2}m_2}} = \overline{m_1}$. Similar to (4.11), we can show that

$$\int_\Omega \theta^2_{d_2,\beta^V_{\infty,d_2}m_2}(\theta_{d_2,\beta^V_{\infty,d_2}m_2} - b\overline{m_1}) = \int_\Omega \theta^2_{d_2,\beta^V_{\infty,d_2}m_2}(\theta_{d_2,\beta^V_{\infty,d_2}m_2} - bc\,\overline{\theta_{d_2,\beta^V_{\infty,d_2}m_2}}) > 0.$$

Thus $\beta^U_{\infty,d_2} < \beta^V_{\infty,d_2}$. This finishes the proof of (ii).

Now we are ready to prove (iii). We divide the proof into three steps.

First, suppose that $m_1 \equiv rm_2$ for some $r > 0$. Then it is easy to check that $b\,\theta_{d_1,m_1} \not\equiv \tilde{s}m_2$ for any $\tilde{s} > 0$. So we need to show that $\beta^U_{d_1,0} < \beta^V_{d_1,0}$. Indeed, by Proposition 4.4(II)(iii), $\beta^V_{d_1,0} = r/c$ which is obviously larger than $\beta^U_{d_1,0} = b\inf\limits_{\bar\Omega}\frac{\theta_{d_1,m_1}}{m_2}$ by Lemma 2.5(i)(b).

Next, suppose that m_1 is not a constant multiple of m_2. Then by Proposition 4.4(II)(iii), $\beta^V_{d_1,0}$ satisfies that $\lambda_1(m_1 - c\,\beta^V_{d_1,0}m_2) = d_1^{-1}$. Consider $\lambda_1(m_1 - c\,s\,m_2)$ as a function of s. By Proposition 2.8, $\lambda_1(m_1 - c\,s\,m_2) > 0$ if and only if $s \in (\frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}, \sup_{\bar\Omega}\frac{m_1}{cm_2})$. If $\beta^U_{d_1,0} \leq \frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}$, then as $\beta^V_{d_1,0} \in (\frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}, \sup_{\bar\Omega}\frac{m_1}{cm_2})$, we obtain that $\beta^U_{d_1,0} < \beta^V_{d_1,0}$. Otherwise, we must have $\beta^U_{d_1,0} \in (\frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}, \sup_{\bar\Omega}\frac{m_1}{cm_2})$. Indeed, let $P \in \bar\Omega$ such that $m_1(P) = \max_{\bar\Omega} m_1 > 0$. By Lemma 2.5(i)(b), $\theta_{d_1,m_1}(P) < m_1(P)$. Thus by Proposition 4.3(II)(i), $\beta^U_{d_1,0} \leq b\frac{\theta_{d_1,m_1}(P)}{m_2(P)} < b\frac{m_1(P)}{m_2(P)} \leq \sup_{\bar\Omega}\frac{m_1}{cm_2}$. Denote $\lambda_0 := \lambda_1(m_1 - c\,\beta^U_{d_1,0}m_2)$. Equivalently, by Proposition 2.2(ii), we have

$$\mu_1(\lambda_0^{-1}, m_1 - c\,\beta^U_{d_1,0}m_2) = 0.$$

Choosing θ_{d_1,m_1} as a test function, by (2.6) and (4.8), we have

$$\begin{aligned}
0 &= \mu_1(\lambda_0^{-1}, m_1 - c\,\beta^U_{d_1,0}m_2)\\
&\leq \frac{\lambda_0^{-1}\int_\Omega |\nabla\theta_{d_1,m_1}|^2 + \int_\Omega (c\,\beta^U_{d_1,0}m_2 - m_1)\theta^2_{d_1,m_1}}{\int_\Omega \theta^2_{d_1,m_1}}\\
&= \frac{\int_\Omega (c\,\beta^U_{d_1,0}m_2 - m_1)\theta^2_{d_1,m_1} - (d_1\lambda_0)^{-1}\int_\Omega \theta^2_{d_1,m_1}(\theta_{d_1,m_1} - m_1)}{\int_\Omega \theta^2_{d_1,m_1}}.
\end{aligned}$$

Since $\beta^U_{d_1,0} = b\inf\limits_{\bar\Omega} \frac{\theta_{d_1,m_1}}{m_2}$ by Proposition 4.3 (II)(i), we obtain

$$
\begin{aligned}
&\int_\Omega \theta^2_{d_1,m_1}(\theta_{d_1,m_1} - m_1) - \int_\Omega \theta^2_{d_1,m_1}(c\,\beta^U_{d_1,0}m_2 - m_1)\\
=&\int_\Omega \theta^2_{d_1,m_1}(\theta_{d_1,m_1} - b\,c\,m_2 \cdot \inf_{\bar\Omega} \frac{\theta_{d_1,m_1}}{m_2})\\
\geq& 0,
\end{aligned}
$$

where the last equality holds only if $b\,c = 1$ and $\theta_{d_1,m_1}/m_2 \equiv$ const on $\bar\Omega$. Thus $\lambda_0 \leq d_1^{-1}$. Since $\lambda_1(m_1 - c\,s\,m_2)$ is strictly increasing in $s \in (\frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}, \sup_{\bar\Omega}\frac{m_1}{cm_2})$, we must have $\beta^U_{d_1,0} \leq \beta^V_{d_1,0}$, where equality holds only if $\lambda_0 = d_1^{-1}$, i.e. $b\,c = 1$, $\theta_{d_1,m_1} \equiv \tilde s m_2$ on $\bar\Omega$ for some $\tilde s > 0$. Thus if $b\,c < 1$ or $\theta_{d_1,m_1} \not\equiv \tilde s m_2$ for any $\tilde s > 0$, we obtain that $\beta^U_{d_1,0} < \beta^V_{d_1,0}$, which finishes the proof of (iii)(a).

Now, assume that $b\,c = 1$ and that there exists $\tilde s > 0$ such that $\theta_{d_1,m_1} = c\,\tilde s m_2$. Since $\mu_1(d_1, m_1 - \theta_{d_1,m_1}) = \mu_1(d_1, m_1 - c\,\beta^V_{d_1,0}m_2) = 0$ by the equation of θ_{d_1,m_1} and Proposition 4.4(II)(iii), $\beta^V_{d_1,0} = \tilde s$. By Proposition 4.3(II)(i), $\beta^U_{d_1,0} = b\inf\limits_{\bar\Omega}\frac{\theta_{d_1,m_1}}{m_2} = bc\,\tilde s = \beta^V_{d_1,0}$. This finishes the proof of Part (iii).

Finally we come to Part (iv). Again we divide the proof into three steps.

First suppose that $m_1 \equiv rm_2$ for some $r > 0$. Then it is easy to check that $b\,m_1 \not\equiv \theta_{d_2,\hat s m_2}$ for any $\hat s > 0$. So we need to show that $\beta^U_{0,d_2} < \beta^V_{0,d_2}$. Indeed, by Proposition 4.3(II)(iii), $\beta^U_{0,d_2} = b\,r$. Thus $c\beta^U_{0,d_2}m_2 = b\,c\,m_1 \leq m_1$. Therefore by Lemma 2.5(i)(b), $\sup_{\bar\Omega} c\,\theta_{d_2,\beta^U_{0,d_2}m_2} < \sup_{\bar\Omega} c\beta^U_{0,d_2}m_2 \leq \sup_{\bar\Omega} m_1$. Thus by Proposition 4.4(II)(i), $\beta^U_{0,d_2} < \beta^V_{0,d_2}$.

Second, suppose that m_1 is not a constant multiple of m_2, then by Proposition 4.3(II)(iii), β^U_{0,d_2} is the unique positive number satisfying that $\mu_1(d_2, \beta^U_{0,d_2}m_2 - bm_1) = 0$. Choosing $\theta_{d_2,\beta^V_{0,d_2}m_2}$ as a test function for $\mu_1(d_2, \beta^U_{0,d_2}m_2 - b\,m_1)$, by (2.6), we obtain

$$
\begin{aligned}
0 &= \mu_1(d_2, \beta^U_{0,d_2}m_2 - b\,m_1)\\
&\leq \frac{d_2\int_\Omega |\nabla\theta_{d_2,\beta^V_{0,d_2}m_2}|^2 + \int_\Omega (b\,m_1 - \beta^U_{0,d_2}m_2)\theta^2_{d_2,\beta^V_{0,d_2}m_2}}{\int_\Omega \theta_{d_2,\beta^V_{0,d_2}m_2}}\\
&= \frac{(\beta^V_{0,d_2} - \beta^U_{0,d_2})\int_\Omega m_2\theta^2_{d_2,\beta^V_{0,d_2}m_2} + \int_\Omega \theta^2_{d_2,\beta^V_{0,d_2}m_2}(b\,m_1 - \theta_{d_2,\beta^V_{0,d_2}m_2})}{\int_\Omega \theta^2_{d_2,\beta^V_{0,d_2}m_2}},
\end{aligned}
$$

where we have used an identity similar to (4.8) for $\theta_{d_2,\beta^V_{0,d_2}m_2}$. By Proposition 4.4(II)(i), $c\,\theta_{d_2,\beta^V_{0,d_2}m_2} \geq m_1$ in Ω. Thus using $b\,c \leq 1$, we deduce that

$$\begin{aligned}
&(\beta^V_{0,d_2} - \beta^U_{0,d_2}) \int_\Omega m_2 \theta^2_{d_2,\beta^V_{0,d_2}m_2} \\
\geq &\int_\Omega \theta^2_{d_2,\beta^V_{0,d_2}m_2} (\theta_{d_2,\beta^V_{0,d_2}m_2} - b\,m_1) \\
\geq &\int_\Omega \theta^2_{d_2,\beta^V_{0,d_2}m_2} (\theta_{d_2,\beta^V_{0,d_2}m_2} - b\,c\,\theta_{d_2,\beta^V_{0,d_2}m_2}) \\
\geq &0,
\end{aligned} \tag{4.12}$$

where the last inequality follows by similar arguments to (4.11). Since the last two equalities in (4.12) hold if and only if $m_1 \equiv c\,\theta_{d_2,\beta^V_{0,d_2}m_2}$ on $\bar{\Omega}$ and $b\,c = 1$ respectively, this finishes the proof of (iv)(a).

Finally, assume that $b\,c = 1$ and that there exists $\hat{s} > 0$ such that $m_1 = c\,\theta_{d_2,\hat{s}m_2}$, i.e., $bm_1 = \theta_{d_2,\hat{s}m_2}$. By Proposition 4.3(II)(iii) and the equation of $\theta_{d_2,\hat{s}m_2}$, we have $\mu_1(d_2, \beta^U_{0,d_2}m_2 - bm_1) = \mu_1(d_2, \hat{s}m_2 - \theta_{d_2,\hat{s}m_2}) = 0$. Therefore by Proposition 2.2(iv), $\beta^U_{0,d_2} = \hat{s}$. By Proposition 4.4(II)(i) and monotonicity of $\theta_{d_2,sm}$ in s by Lemma 2.7, we also have $\beta^V_{0,d_2} = \hat{s}$. This finishes our proof of Part (iv). $\square$

Now we are ready to prove Theorem 1.7.

Proof of Theorem 1.7. First we establish (1.22). By Proposition 4.3, $\beta^U_{d_1,d_2}$ is increasing in d_2. Thus

$$\sup_{d_2>0} \beta^U_{d_1,d_2} = \beta^U_{d_1,\infty} = b\overline{\frac{\theta_{d_1,m_1}}{m_2}},$$

and the first identity in (1.22) is now obvious. By Proposition 4.4, $\beta^V_{d_1,d_2}$ is decreasing in d_1. Thus

$$\inf_{d_1>0} \beta^V_{d_1,d_2} = \beta^V_{\infty,d_2} = \inf\{s \,|\, \overline{c\,\theta_{d_2,sm_2}} \geq \overline{m_1}\}.$$

Hence

$$\overline{\beta} = \inf_{d_1>0} \inf_{d_2>0} \beta^V_{d_1,d_2} = \inf_{d_2>0} \inf\{s \,|\, \overline{c\,\theta_{d_2,sm_2}} \geq \overline{m_1}\},$$

and to prove the second identity in (1.22), we only need to show that

$$\inf_{d_2>0} \frac{1}{c} \frac{\overline{m_1}}{\overline{\theta_{d_2,m_2}}} = \inf_{d_2>0} \inf\{s \,|\, \overline{c\,\theta_{d_2,sm_2}} \geq \overline{m_1}\}.$$

First, we show that $\inf_{d_2>0} \inf\{s \,|\, \overline{c\,\theta_{d_2,sm_2}} \geq \overline{m_1}\} \geq \inf_{d_2>0} \frac{1}{c} \frac{\overline{m_1}}{\overline{\overline{\theta_{d_2,m_2}}}}$. Multiplying the equation of $\theta_{d,m}$ by c^2, we obtain that $c\,\theta_{d,m} = \theta_{cd,cm}$. For any $t > \inf_{d_2>0} \inf\{s \,|\, \overline{c\,\theta_{d_2,sm_2}} \geq \overline{m_1}\}$, there exists some $\tilde{d}_2 > 0$ such that $\overline{c\,\theta_{\tilde{d}_2,tm_2}} > \overline{m_1}$. Since $c\,\theta_{\tilde{d}_2,tm_2} = ct\,\theta_{\tilde{d}_2/t,m_2}$, we obtain that $\overline{ct\,\theta_{\tilde{d}_2/t,m_2}} > \overline{m_1}$, i.e.,

$$t > \frac{1}{c} \frac{\overline{m_1}}{\overline{\overline{\theta_{\tilde{d}_2/t,m_2}}}} \geq \inf_{d_2>0} \frac{1}{c} \frac{\overline{m_1}}{\overline{\overline{\theta_{d_2,m_2}}}}.$$

Since this is true for all $t > \inf_{d_2>0} \inf\{s \,|\, \overline{c\,\theta_{d_2,sm_2}} \geq \overline{m_1}\}$, we obtain that

$$\inf_{d_2>0} \inf\{s \,|\, \overline{c\,\theta_{d_2,sm_2}} \geq \overline{m_1}\} \geq \inf_{d_2>0} \frac{1}{c} \frac{\overline{m_1}}{\overline{\overline{\theta_{d_2,m_2}}}}.$$

Next we show the reversed inequality. Suppose that $t > \inf_{d_2>0} \frac{1}{c} \frac{\overline{m_1}}{\overline{\overline{\theta_{d_2,m_2}}}}$, then there exists some $d_2' > 0$ such that $t > \frac{1}{c} \frac{\overline{m_1}}{\overline{\overline{\theta_{d_2',m_2}}}}$, i.e. $\overline{c\,\theta_{td_2',tm_2}} > \overline{m_1}$. Thus

$$t > \inf\{s \,|\, \overline{c\,\theta_{td_2',sm_2}} \geq \overline{m_1}\} \geq \inf_{d_2>0} \inf\{s \,|\, \overline{c\,\theta_{d_2,sm_2}} \geq \overline{m_1}\}.$$

Since this is true for all $t > \inf_{d_2>0} \frac{1}{c} \frac{\overline{m_1}}{\overline{\overline{\theta_{d_2,m_2}}}}$, we obtain that

$$\inf_{d_2>0} \frac{1}{c} \frac{\overline{m_1}}{\overline{\overline{\theta_{d_2,m_2}}}} \geq \inf_{d_2>0} \inf\{s \,|\, \overline{c\,\theta_{d_2,sm_2}} \geq \overline{m_1}\}.$$

This finishes the proof of the second identity in (1.22).

Next we proceed to prove Part (i). Since $0 < b\,c < \Lambda$, by (1.22), we have $\underline{\beta} < \overline{\beta}$. Thus

$$\bigcap_{d_1,d_2>0} (\beta^U_{d_1,d_2}, \beta^V_{d_1,d_2}) = (\underline{\beta}, \overline{\beta}),$$

and (i) follows from Theorem 1.6(iii).

Finally, we come to Part (ii) for $\Lambda < b\,c \leq 1$. Since $b\,c > \Lambda$, again by (1.22) we conclude that $\underline{\beta} > \overline{\beta}$. Suppose, for contradiction, that there exists some $\beta_0 > 0$ such that for any $d_1, d_2 > 0$, either both semi-trivial steady states $(\theta_{d_1,m_1}, 0)$ and $(0, \theta_{d_2,\beta_0 m_2})$ of system (4.4) are linearly stable or both are linearly unstable. By Theorem 1.6, we must have $\beta_0 \in [\beta^U_{d_1,d_2}, \beta^V_{d_1,d_2}]$ for all $d_1, d_2 > 0$. (Note that in case $\beta^U_{d_1,d_2} = \beta^V_{d_1,d_2}$ takes place for some d_1, d_2, the interval $[\beta^U_{d_1,d_2}, \beta^V_{d_1,d_2}]$ simply means the singleton $\{\beta^U_{d_1,d_2}\}$.) Thus it must hold that $\beta_0 \in \bigcap_{d_1,d_2>0} [\beta^U_{d_1,d_2}, \beta^V_{d_1,d_2}]$. From the definition of $\underline{\beta}$ and $\overline{\beta}$ in (1.20), it follows that $\underline{\beta} \le \beta_0 \le \overline{\beta}$. Thus we get a contradiction and (ii) is established. $\square$

Theorem 1.8 is a direct consequence of the following result.

Theorem 4.6. *Assume that* (**M**) *holds, then we have* (1.24)*. Moreover, the following statements hold for* (4.4)*:*

(i) If $bc < 1$ or $m_1/m_2 \not\equiv \text{const}$, then for any $\beta \in (\beta_*, \beta^*)$, there exist some $d_1, d_2 > 0$ such that both semi-trivial steady states $(\theta_{d_1,m_1}, 0)$ and $(0, \theta_{d_2,\beta m_2})$ of (4.4) *are linearly unstable, and that* (4.4) *has a stable co-existence steady state; if $bc = 1$ and $m_1 \equiv rm_2$ for some constant $r > 0$, then same conclusion holds for $\beta \in (\beta_*, r/c) \cup (r/c, \beta^*)$.*

(ii) If $bc = 1$, $m_1 \equiv rm_2$ for some constant $r > 0$, and $\beta = r/c$, then

(a) $d_2 > cd_1 \Rightarrow (\theta_{d_1,m_1}, 0)$ is globally asymptotically stable.

(b) $d_2 = cd_1 \Rightarrow$ system (4.4) *has a compact global attractor consisting of a continuum of steady states $\{(\xi\theta_{d_1,m_1}, (1-\xi)\theta_{d_1,m_1}/c) \mid \xi \in [0,1]\}$.*

(c) $d_2 < cd_1 \Rightarrow (0, \theta_{d_2,\beta m_2})$ is globally asymptotically stable.

Proof. First we prove (1.24) in Theorem 1.8. By Proposition 4.3, $\beta^U_{d_1,d_2}$ is increasing in d_2. Thus $\inf\limits_{d_2>0} \beta^U_{d_1,d_2} = \beta^U_{d_1,0} = b \inf\limits_{\bar\Omega} \frac{\theta_{d_1,m_1}}{m_2}$ and the first identity in (1.24) holds.

By Proposition 4.4, $\beta^V_{d_1,d_2}$ is decreasing in d_1. Thus

$$\sup_{d_1>0} \beta^V_{d_1,d_2} = \beta^V_{0,d_2} = \inf\{s \mid c\,\theta_{d_2,sm_2} - m_1 \ge 0 \text{ in } \Omega\}.$$

Hence

$$\beta^* = \sup_{d_1,d_2>0} \beta^V_{d_1,d_2} = \sup_{d_2>0} \beta^V_{0,d_2} = \sup_{d_2>0} \inf\{s \mid c\,\theta_{d_2,sm_2} - m_1 \ge 0 \text{ in } \Omega\}. \tag{4.13}$$

Therefore to prove the second identity in (1.24), we only need to show that

$$\frac{1}{c} \sup_{d_2>0} \sup_{\bar\Omega} \frac{m_1}{\theta_{d_2,m_2}} = \sup_{d_2>0} \beta^V_{0,d_2}.$$

First, we show that $\frac{1}{c} \sup\limits_{d_2>0} \sup\limits_{\bar\Omega} \frac{m_1}{\theta_{d_2,m_2}} \le \sup\limits_{d_2>0} \beta^V_{0,d_2}$. For any $0 < t < \frac{1}{c} \sup\limits_{d_2>0} \sup\limits_{\bar\Omega} \frac{m_1}{\theta_{d_2,m_2}}$, there exists some $\tilde d_2 > 0$ such that $t < \sup_{\bar\Omega} \frac{m_1}{c\theta_{\tilde d_2,m_2}}$, i.e. there exists some $x \in \bar\Omega$, such that

$$(m_1 - ct\theta_{\tilde{d}_2,m_2})(x) = (m_1 - c\,\theta_{t\tilde{d}_2,tm_2})(x) > 0.$$

Thus by Proposition 4.4(II)(i) and monotonicity of $\theta_{t\tilde{d}_2,sm_2}$ in s,

$$t < \beta^V_{0,t\tilde{d}_2} \leq \sup_{d_2>0} \beta^V_{0,d_2}.$$

Since this is true for all $0 < t < \frac{1}{c} \sup\limits_{d_2>0} \sup\limits_{\bar{\Omega}} \frac{m_1}{\theta_{d_2,m_2}}$, we obtain that

$$\frac{1}{c} \sup_{d_2>0} \sup_{\bar{\Omega}} \frac{m_1}{\theta_{d_2,m_2}} \leq \sup_{d_2>0} \beta^V_{0,d_2}.$$

Now we show the reversed inequality. Suppose that $0 < t < \sup\limits_{d_2>0} \beta^V_{0,d_2}$, then there exists some $d_2' > 0$ such that $t < \beta^V_{0,d_2'}$. Then by Proposition 4.4(II)(i), there exists some $y \in \bar{\Omega}$, such that

$$(m_1 - c\,\theta_{d_2',tm_2})(y) = (m_1 - c\,t\theta_{d_2'/t,m_2})(y) > 0.$$

Thus $t < \sup\limits_{\bar{\Omega}} \frac{m_1}{c\,\theta_{d_2'/t,m_2}} \leq \frac{1}{c} \sup\limits_{d_2>0} \sup\limits_{\bar{\Omega}} \frac{m_1}{\theta_{d_2,m_2}}$. Since this is true for all $0 < t < \sup\limits_{d_2>0} \beta^V_{0,d_2}$, we conclude that

$$\sup_{d_2>0} \beta^V_{0,d_2} \leq \frac{1}{c} \sup_{d_2>0} \sup_{\bar{\Omega}} \frac{m_1}{\theta_{d_2,m_2}}.$$

This finishes the proof of the second identity in (1.24).

To finish the proof of the theorem, we first show that for all $\beta \in (\beta_*, \frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}) \bigcup (b\frac{\overline{m_1}}{\overline{m_2}}, \beta^*)$, there exist some $d_1, d_2 > 0$ such that both semi-trivial steady states $(\theta_{d_1,m_1}, 0)$ and $(0, \theta_{d_2,\beta m_2})$ of (4.4) are linearly unstable.

To this end, we begin with $\beta \in (\beta_*, \frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}})$. Since $\beta > \beta_*$, by (1.24) and Proposition 4.3(II)(i), there exists some $d_1^* > 0$, such that $\beta > \beta^U_{d_1^*,0}$. On the other hand, by Propositions 2.8 and 4.4(II)(iii), $\beta^V_{d_1^*,0} \geq \frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}} > \beta$, where the first equality holds if and only if $m_1 \equiv rm_2$ for some $r > 0$. Thus $\beta \in (\beta^U_{d_1^*,0}, \beta^V_{d_1^*,0})$. This implies that $\beta \in (\beta^U_{d_1^*,d_2}, \beta^V_{d_1^*,d_2})$ for all d_2 sufficiently small. Consequently system (4.4) has a stable co-existence steady state by Theorem 1.6(iii). Note that if $m_1/m_2 \not\equiv$ const, then the conclusion actually holds for $\beta \in (\beta_*, \frac{1}{c}\frac{\overline{m_1}}{\overline{m_2}}]$.

Next we assume that $\beta \in (b\frac{\overline{m_1}}{\overline{m_2}}, \beta^*)$. Since $\beta < \beta^*$, by (4.13), there exists some $d_2^* > 0$ such that $\beta < \beta^V_{0,d_2^*}$. On the other hand by Propositions 2.9 and 4.3(II)(iii), $\beta^U_{0,d_2^*} \leq b\frac{\overline{m_1}}{\overline{m_2}}$, where equality holds if and only if $m_1 \equiv rm_2$ for some $r > 0$. Thus

$\beta \in (\beta^U_{0,d_2^*}, \beta^V_{0,d_2^*})$. This implies that $\beta \in (\beta^U_{d_1,d_2^*}, \beta^V_{d_1,d_2^*})$ for all d_1 sufficiently small. Consequently system (4.4) has a stable co-existence steady state again by Theorem 1.6(iii). Note that if $m_1/m_2 \not\equiv$ const, then the conclusion actually holds for $\beta \in [b\overline{\frac{m_1}{m_2}}, \beta^*)$.

Thus if $b\,c < 1$ or $m_1/m_2 \not\equiv$ const, then for all $\beta \in (\beta_*, \beta^*)$, there exist $d_1, d_2 > 0$ such that $\beta \in (\beta^U_{d_1,d_2}, \beta^V_{d_1,d_2})$, i.e., both semi-trivial steady states $(\theta_{d_1,m_1}, 0)$ and $(0, \theta_{d_2,\beta m_2})$ of (4.4) are linearly unstable. If $b\,c = 1$ and $m_1 \equiv r m_2$ for some $r > 0$, then the conclusion holds for all $\beta \in (\beta_*, r/c) \cup (r/c, \beta^*)$. Thus we finish the proof of Theorem 4.6(i) by Theorem 1.6(iii).

Now suppose that $b\,c = 1$, $\beta = r/c$ and (U, V) is a steady state solution to (4.4). Multiplying the equation of V by c^2 and denoting $\tilde{d}_2 := c d_2$, $\tilde{V} := c\,V$, $(U, \tilde{V})$ satisfies the system

$$\begin{cases} d_1 \Delta U + U(m_1(x) - U - \tilde{V}) = 0 & \text{in } \Omega, \\ \tilde{d}_2 \Delta \tilde{V} + \tilde{V}(m_1(x) - U - \tilde{V}) = 0 & \text{in } \Omega, \\ \partial_\nu U = \partial_\nu \tilde{V} = 0 & \text{on } \partial\Omega. \end{cases}$$

Then Parts (a) and (c) of Theorem 4.6(ii) follow from Theorem 1.1, and Part (b) can be easily proved by simple standard arguments. □

4.4 Summary

Finally, as a consequence of Theorems 1.5-1.8 and Theorem 4.6 in Section 4.3, we can characterize the change of dynamics of (4.4), as β increases from 0 to ∞, near the two semi-trivial steady states $(\theta_{d_1,m_1}, 0)$ and $(0, \theta_{d_2,\beta m_2})$ for all $(d_1, d_2) \in \mathcal{Q}$. Thus we define the following three subsets of $\mathcal{Q}$ for system (4.4):

$$\begin{aligned} &\Sigma_{U,\beta} := \{(d_1, d_2) \in \mathcal{Q} \mid (\theta_{d_1,m_1}, 0) \text{ is linearly stable}\}, \\ &\Sigma_{V,\beta} := \{(d_1, d_2) \in \mathcal{Q} \mid (0, \theta_{d_2,\beta m_2}) \text{ is linearly stable}\}, \\ &\Sigma_{-,\beta} := \{(d_1, d_2) \in \mathcal{Q} \mid \text{both } (\theta_{d_1,m_1}, 0) \text{ and } (0, \theta_{d_2,\beta m_2}) \text{ are linearly unstable}\}. \end{aligned} \tag{4.14}$$

We will show how the three sets $\Sigma_{U,\beta}$, $\Sigma_{V,\beta}$ and $\Sigma_{-,\beta}$ vary for $b\,c \le 1$ and general m_1, m_2 satisfying condition (**M**) as follows.

Theorem 4.7. *Assume that* (**M**) *holds.*

(i) If $0 < b\,c < \Lambda$*, then the following hold for system* (4.4)*:*

(a) If $\beta \in (0, \beta_{**})$, $\Sigma_{U,\beta} = \mathcal{Q}$. Moreover, $(\theta_{d_1,m_1}, 0)$ is globally asymptotically stable for all $d_1, d_2 > 0$.

(b) If $\beta \in (\beta_{**}, \beta_*)$, $\Sigma_{U,\beta} = \mathcal{Q}$.

(c) If $\beta \in (\beta_*, \underline{\beta})$, $\Sigma_{U,\beta} \neq \emptyset$, $\Sigma_{-,\beta} \neq \emptyset$ and $\Sigma_{V,\beta} = \emptyset$.

(d) If $\beta \in (\underline{\beta}, \overline{\beta})$, $\Sigma_{-,\beta} = \mathcal{Q}$.

(e) If $\beta \in (\overline{\beta}, \beta^*)$, $\Sigma_{U,\beta} = \emptyset$, $\Sigma_{-,\beta} \neq \emptyset$ and $\Sigma_{V,\beta} \neq \emptyset$.

(f) If $\beta \in (\beta^*, \beta^{**})$, $\Sigma_{V,\beta} = \mathcal{Q}$.

(g) If $\beta \in (\beta^{**}, \infty)$, $\Sigma_{V,\beta} = \mathcal{Q}$. Moreover, $(0, \theta_{d_2,\beta m_2})$ is globally asymptotically stable for all $d_1, d_2 > 0$.

(ii) If $\Lambda < b\,c \leq 1$, cases (i) (a), (b), (f) and (g) above still hold. When $\beta \in (\beta_*, \beta^*)$, if we further assume that $m_1/m_2 \not\equiv \text{const}$, then the following hold for system (4.4):

(a) If $\beta \in (\beta_*, \overline{\beta})$, $\Sigma_{U,\beta} \neq \emptyset$, $\Sigma_{-,\beta} \neq \emptyset$ and $\Sigma_{V,\beta} = \emptyset$.

(b) If $\beta \in (\overline{\beta}, \underline{\beta})$, none of the three sets $\Sigma_{U,\beta}$, $\Sigma_{-,\beta}$ and $\Sigma_{V,\beta}$ is empty.

(c) If $\beta \in (\underline{\beta}, \beta^*)$, $\Sigma_{U,\beta} = \emptyset$, $\Sigma_{-,\beta} \neq \emptyset$ and $\Sigma_{V,\beta} \neq \emptyset$.

Theorem 4.7 is almost obvious now from all previous results in this section. Therefore we only make some comments here. Parts (i)(a) and (i)(g) follow from Theorem 1.5. Parts (i)(b) and (i)(f) follow from the definition of β_*, β^* in (1.23), Theorem 1.6(i)(ii) and the fact that $\beta^U_{d_1,d_2} \leq \beta^V_{d_1,d_2}$ for all $d_1, d_2 > 0$. By the definition of $\underline{\beta}$ and $\overline{\beta}$ in (1.20), $(\theta_{d_1,m_1}, 0)$ is linearly unstable for all $d_1, d_2 > 0$ if and only if $\beta > \underline{\beta}$ and $(0, \theta_{d_2,\beta m_2})$ is linearly unstable for all $d_1, d_2 > 0$ if and only if $\beta < \overline{\beta}$. Also by Theorem 4.6(i), $\Sigma_{-,\beta} \neq \emptyset$ for all $\beta \in (\beta_*, \beta^*)$ and $b\,c < 1$. Combining these facts with Theorem 1.7, we obtain Theorem 4.7.

Theorem 4.7 indicates that for general m_1, m_2, b and c, the three sets $\Sigma_{U,\beta}$, $\Sigma_{V,\beta}$ and $\Sigma_{-,\beta}$ of (4.4) can evolve in a very complicated fashion when β increases from 0 to ∞. In particular, $\Sigma_{U,\beta}$ (resp. $\Sigma_{V,\beta}$) can be empty or disconnected, or its boundary can even contain a portion of the d_1-axis (resp. d_2-axis).

Much less is known about the global dynamics of system (4.4) for $\beta \in (\beta_{**}, \beta^{**})$, except for some partial results, e.g. Theorem 4.1 when d_1, d_2 are both large or both small, and Theorem 4.2 when c is sufficiently small. We hope to return to the global dynamics of (4.4) for $\beta \in (\beta_{**}, \beta^{**})$ in the future.

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Appendix

The proofs of Theorem 3.2(iii), Theorem 3.3(iii), Theorem 3.5 and Theorem 3.7(iii) use essentially the same arguments as in the proof of Theorem 4.1 in [HLMV]. Note that the extra assumptions $d_1 = d_2$ and that $m_1^+ - m_2^+$ changes sign in Ω in [HLMV] are *not* needed in the proof. Since it seems hard to locate the original proof in [HLMV], we include a proof to Theorem 5.4(iii) here.

The following three lemmas are useful in the proof of Theorem 5.4(iii).

Lemma A.1.

(i) Suppose that there exists $x_0 \in \bar{\Omega}$ such that $(m_2^+ - m_1^+)(x_0) > 0$, then the sequences $(\hat{u}_n, \check{v}_n)$ defined by $\hat{u}_1 := \theta_{d_1,m_1}$ and

$$\check{v}_n := \theta_{d_2,m_2-\hat{u}_n}, \quad \hat{u}_{n+1} := \theta_{d_1,m_1-\check{v}_n}, \quad n \geqslant 1, \tag{A-1}$$

are well-defined for all d_1, d_2 sufficiently small. Moreover, for any co-existence steady state (U, V) of (1.11), the following hold:

$$U \leqslant \hat{u}_{n+1} \leqslant \hat{u}_n, \quad V \geqslant \check{v}_{n+1} \geqslant \check{v}_n, \quad n \geqslant 1. \tag{A-2}$$

(ii) Suppose that there exists $y_0 \in \bar{\Omega}$ such that $(m_1^+ - m_2^+)(y_0) > 0$, then the sequences $(\check{u}_n, \hat{v}_n)$ defined by $\hat{v}_1 := \theta_{d_2,m_2}$ and

$$\check{u}_n := \theta_{d_1,m_1-\hat{v}_n}, \quad \hat{v}_{n+1} := \theta_{d_2,m_2-\check{u}_n} \quad n \geqslant 1, \tag{A-3}$$

are well-defined for all d_1, d_2 sufficiently small. Moreover,

$$U \geqslant \check{u}_{n+1} \geqslant \check{u}_n, \quad V \leqslant \hat{v}_{n+1} \leqslant \hat{v}_n, \quad n \geqslant 1. \tag{A-4}$$

Proof. It is enough to prove (i) as the proof of (ii) follows similarly.

The proof is by induction. First we show that $\theta_{d_2,m_2-\hat{u}_1} =: \check{v}_1$ indeed exists. Since $\hat{u}_1 = \theta_{d_1,m_1} \to m_1^+$ as $d_1 \to 0$ by Lemma 2.5(i)(a), there exists $x_0' \in \bar{\Omega}$ such that $(m_2 - \hat{u}_1)(x_0') > 0$ for all d_1 small by our assumption. Consequently by [CC], for all d_1, d_2 sufficiently small, $\theta_{d_2,m_2-\hat{u}_1}$ exists. Since $m_1 - V < m_1$, by Lemma 2.7, $U = \theta_{d_1,m_1-V} < \theta_{d_1,m_1} = \hat{u}_1$. Hence $m_2 - \hat{u}_1 < m_2 - U$. Again by Lemma 2.7, we can show that $\check{v}_1 = \theta_{d_2,m_2-\hat{u}_1} < \theta_{d_2,m_2-U} = V$. Now, going back to the equation of U, since

$$m_1 - V \leqslant m_1 - \check{v}_1 \leqslant m_1.$$

By definition of $\hat{u}_n$ and Lemma 2.7,

$$U \leqslant \hat{u}_2 \leqslant \hat{u}_1.$$

Going back to the equation of V, the above inequalities imply that

$$m_2 - U \geqslant m_2 - \hat{u}_2 \geqslant m_2 - \hat{u}_1.$$

Then it is obvious that $\theta_{d_2,m_2-\hat{u}_2} =: \check{v}_2$ exists and satisfies that

$$V \geqslant \check{v}_2 \geqslant \check{v}_1,$$

by Lemma 2.7. This completes the proof of (A-2) for $n = 1$. Now suppose that (A-2) is true for some $n \geqslant 1$. It suffices to show that

$$U \leqslant \hat{u}_{n+2} \leqslant \hat{u}_{n+1}, \quad V \geqslant \check{v}_{n+2} \geqslant \check{v}_{n+1}.$$

From $V \geqslant \check{v}_{n+1} \geqslant \check{v}_n$, we find that $m_1 - V \leqslant m_1 - \check{v}_{n+1} \leqslant m_1 - \check{v}_n$ and hence,

$$U \leqslant \theta_{d_1,m_1-\check{v}_{n+1}} := \hat{u}_{n+2} \leqslant \hat{u}_{n+1}.$$

Similarly, from the above inequalities, we find that $m_2 - U \geqslant m_2 - \hat{u}_{n+2} \geqslant m_2 - \hat{u}_{n+1}$ and hence, $\theta_{d_2,m_2-\hat{u}_{n+2}}$ exists and

$$V \geqslant \theta_{d_2,m_2-\hat{u}_{n+2}} := \check{v}_{n+2} \geqslant \check{v}_{n+1}.$$

This completes the proof. □

Lemma A.2. For all $n \geqslant 1$, each of the following limits is well defined in $C(\bar{\Omega})$:

$$\widehat{U}_n = \lim_{d_1,d_2\to 0^+} \hat{u}_n, \quad \check{V}_n = \lim_{d_1,d_2\to 0^+} \check{v}_n, \quad \check{U}_n = \lim_{d_1,d_2\to 0^+} \check{u}_n, \quad \widehat{V}_n = \lim_{d_1,d_2\to 0^+} \hat{v}_n,$$

where $\hat{u}_n$, $\check{v}_n$, $\check{u}_n$ and $\hat{v}_n$ are defined in Lemma A.1. Moreover, the following relations hold

$$\begin{aligned}
\widehat{U}_1 = m_1^+, \quad & \widehat{U}_{n+1} = (m_1 - (m_2 - \widehat{U}_n)^+)^+, \quad (n \geqslant 1),\\
\check{V}_1 = (m_2 - m_1^+)^+, \quad & \check{V}_{n+1} = (m_2 - (m_1 - \check{V}_n)^+)^+, \quad (n \geqslant 1),\\
\widehat{V}_1 = m_2^+, \quad & \widehat{V}_{n+1} = (m_2 - (m_1 - \widehat{V}_n)^+)^+, \quad (n \geqslant 1),\\
\check{U}_1 = (m_1 - m_2^+)^+, \quad & \check{U}_{n+1} = (m_1 - (m_2 - \check{U}_n)^+)^+, \quad (n \geqslant 1).
\end{aligned} \tag{A-5}$$

Proof. By Lemma 2.3,

$$\lim_{d_1,d_2\to 0^+} \widehat{U}_1 = \lim_{d_1\to 0^+} \theta_{d_1,m_1} = m_1^+,$$

in $C(\bar{\Omega})$. Suppose that $\widehat{U}_k := \lim_{d_1,d_2\to 0^+} \hat{u}_k$ in $C(\bar{\Omega})$ for all $1 \leqslant k \leqslant n$. Then since

$$\widehat{u}_{n+1} = \theta_{d_1,m_1-\theta_{d_2,m_2-\widehat{u}_n}},$$

we can pass to the limit as $d_1, d_2 \to 0^+$ and Lemma 2.3 gives $\widehat{U}_{n+1} = (m_1 - (m_2 - \widehat{U}_n)^+)^+$. The remaining relations in (A-5) follow similarly. This completes the proof of the lemma. $\square$

The above lemma allows us to get explicit formulae for each of the sequences $\widehat{U}_n, \check{V}_n, \check{U}_n$ and $\widehat{V}_n$. The following Lemma makes these precise.

Lemma A.3. Suppose that there exists $x_0 \in \bar{\Omega}$ such that $(m_2^+ - m_1^+)(x_0) > 0$, then the following holds:

$$\widehat{U}_{n+1} = \begin{cases} 0, & \text{if } m_1(x) \leqslant 0,\\ m_1(x), & \text{if } m_1(x) \geqslant m_2(x), m_1(x) > 0,\\ (n+1)m_1(x) - nm_2(x), & \text{if } 0 < m_1(x) < m_2(x) < \frac{n+1}{n} m_1(x),\\ 0, & \text{if } m_2(x) \geqslant \frac{n+1}{n} m_1(x) > 0, \end{cases} \tag{A-6}$$

and

$$
\check{V}_{n+1} = \begin{cases} m_2^+(x), & \text{if } m_1(x) \leqslant 0, \\ m_2(x), & \text{if } \frac{n}{n+1} m_2(x) \geqslant m_1(x) > 0, \\ (n+1)(m_2(x) - m_1(x)), & \text{if } 0 < \frac{n}{n+1} m_2(x) < m_1(x) \leqslant m_2(x), \\ 0, & \text{if } m_1(x) > m_2(x), m_1(x) > 0, \end{cases} \tag{A-7}
$$

for $n \geqslant 1$. By symmetry, Suppose that there exists $y_0 \in \bar{\Omega}$ such that $(m_1^+ - m_2^+)(y_0) > 0$, we can write down similar formulas for $\widehat{V}_n$ and $\check{V}_n$.

Proof. The proof is by induction. From (A-5) we readily get that for $n \geqslant 0$

$$
\widehat{U}_{n+2} = \begin{cases} 0, & \text{if } m_1(x) \leqslant 0, \\ m_1(x), & \text{if } \widehat{U}_{n+1} \geqslant m_2(x), m_1(x) > 0, \\ m_1(x) - m_2(x) + \widehat{U}_{n+1}(x), & \text{if } \widehat{U}_{n+1}(x) < m_2(x) < m_1(x) + \widehat{U}_{n+1}(x), \\ 0, & \text{if } m_1(x) > 0, m_1(x) + \widehat{U}_{n+1}(x) \leqslant m_2(x). \end{cases} \tag{A-8}
$$

Since $\widehat{U}_1 = m_1^+$, we find from (A-8) that

$$
\widehat{U}_2 = \begin{cases} 0, & \text{if } m_1(x) \leqslant 0, \\ m_1(x), & \text{if } m_1(x) \geqslant m_2(x), m_1(x) > 0, \\ 2m_1(x) - m_2(x), & \text{if } 0 < m_1(x) < m_2(x) < 2m_1(x), \\ 0, & \text{if } m_2(x) \geqslant 2m_1(x) > 0. \end{cases}
$$

Thus (A-6) is true for $n = 1$. Now suppose that (A-6) is true for some $n \geqslant 1$. If $m_1(x) \leqslant 0$, then it follows from (A-8) that $\widehat{U}_{n+2} = 0$. Suppose that $m_1(x) > 0$ and that $m_1(x) \geqslant m_2(x)$. Then by the induction assumption $\widehat{U}_{n+1} = m_1(x)$, and hence (A-8) implies that $\widehat{U}_{n+2} = m_1(x)$. So thus far the result is correct.

Suppose that $0 < m_1(x) < m_2(x) < \frac{n+2}{n+1} m_1(x)$. Then $0 < m_1(x) < m_2(x) < \frac{n+1}{n} m_1(x)$ and so $\widehat{U}_{n+1}(x) = (n+1)m_1(x) - nm_2(x)$. Moreover,

$$
(n+1)m_1(x) - nm_2(x) \leqslant m_2(x) < m_1(x) + (n+1)m_1(x) - nm_2(x),
$$

and so $\widehat{U}_{n+1}(x) \leqslant m_2(x) < m_1(x) + \widehat{U}_{n+1}(x)$. Hence it follows from (A-8) that

$$\widehat{U}_{n+2}(x) = m_1(x) - m_2(x) + \widehat{U}_{n+1}(x) = (n+2)m_1(x) - (n+1)m_2(x).$$

Finally assume that $m_2(x) \geqslant \frac{n+2}{n+1} m_1(x)$. If $m_2(x) \geqslant \frac{n+1}{n} m_1(x)$, then $\widehat{U}_{n+1}(x) = 0$ and since $m_2(x) \geqslant m_1(x)$ we get from (A-8) that $\widehat{U}_{n+2}(x) = 0$. If $\frac{n+2}{n+1} m_1(x) \leqslant m_2(x) < \frac{n+1}{n} m_1(x)$, then

$$\widehat{U}_{n+1}(x) = (n+1)m_1(x) - nm_2(x),$$

and hence

$$m_1(x) + \widehat{U}_{n+1}(x) = (n+2)m_1(x) - nm_2(x) \leqslant m_2(x).$$

Therefore, also in this case $\widehat{U}_{n+2}(x) = 0$. This completes the proof of (A-6).

Next we prove (A-7). Again from (A-5) we readily get that for $n \geqslant 0$

$$\check{V}_{n+2} = \begin{cases} m_2^+(x), & \text{if } m_1(x) \leqslant 0, \\ m_2^+(x), & \text{if } 0 < m_1(x) \leqslant \check{V}_{n+1}(x), \\ m_2(x) - m_1(x) + \check{V}_{n+1}(x), & \text{if } \check{V}_{n+1}(x) < m_1(x) \leqslant m_2(x) + \check{V}_{n+1}(x), \\ 0, & \text{if } m_2(x) + \check{V}_{n+1}(x) < m_1(x), m_1(x) > 0. \end{cases} \tag{A-9}$$

Since $\widehat{V}_1 = (m_2 - m_1^+)^+$, i.e.,

$$\check{V}_1 = \begin{cases} m_2^+(x), & \text{if } m_1(x) \leqslant 0, \\ m_2(x) - m_1(x), & \text{if } 0 < m_1(x) \leqslant m_2(x), \\ 0, & \text{if } m_2(x) < m_1(x), m_1(x) > 0, \end{cases}$$

we find from (A-9) that

$$\check{V}_2 = \begin{cases} m_2^+(x), & \text{if } m_1(x) \leqslant 0, \\ m_2(x), & \text{if } 0 < m_1(x) \leqslant \frac{1}{2} m_2(x), \\ 2(m_2(x) - m_1(x)) & \text{if } 0 < \frac{1}{2} m_2(x) < m_1(x) \leqslant m_2(x), \\ 0, & \text{if } m_2(x) < m_1(x), m_1(x) > 0. \end{cases}$$

Thus (A-7) is true for $n = 1$. Now suppose that (A-7) is true for some $n \geqslant 1$. If $m_1(x) \leqslant 0$, then it follows from (A-9) that $\check{V}_{n+2} = m_2^+(x)$. Suppose that $m_1(x) > 0$ and that $m_1(x) > m_2(x)$. Then by the induction assumption $\check{V}_{n+1} = 0$, and hence (A-9) implies that $\check{V}_{n+2} = 0$. So thus far the result is correct.

Suppose that $\frac{n+1}{n+2} m_2(x) \geqslant m_1(x) > 0$. If $\frac{n}{n+1} m_2(x) \geqslant m_1(x)$, then $\check{V}_{n+1}(x) = m_2(x)$. And so $\check{V}_{n+1}(x) > m_1(x) > 0$. Hence it follows from (A-9) that

$$\check{V}_{n+2}(x) = m_2(x).$$

If $\frac{n+1}{n+2} m_2(x) \geqslant m_1(x) > \frac{n}{n+1} m_2(x)$, then

$$\check{V}_{n+1}(x) = (n+1)(m_2(x) - m_1(x)),$$

and hence

$$m_1(x) \leqslant \check{V}_{n+1}(x).$$

Therefore, also in this case it follows from (A-9) that

$$\check{V}_{n+2}(x) = m_2(x).$$

Finally assume that $0 < \frac{n+1}{n+2} m_2(x) < m_1(x) \leqslant m_2(x)$. Then $0 < \frac{n}{n+1} m_2(x) < m_1(x) \leqslant m_2(x)$ and so $\check{V}_{n+1}(x) = (n+1)(m_2(x) - m_1(x))$. Therefore $\check{V}_{n+1}(x) < m_1(x) \leqslant m_2(x) + \check{V}_{n+1}(x)$ and hence we get from (A-8) that

$$\check{V}_{n+2}(x) = m_2(x) - m_1(x) + \check{V}_{n+1}(x) = (n+2)(m_2(x) - m_1(x)).$$

This completes the proof of (A-7). $\square$

We are now ready to complete the proof of Theorem 5.3(iii).

Proof of Theorem 5.3(iii). First we prove the case that there exist $x_0, y_0 \in \bar{\Omega}$ such that $(m_2^+ - m_1^+)(x_0) > 0$ and $(m_2^+ - m_1^+)(y_0) < 0$.

By Lemmas A.1 and A.2, any co-existence steady state (U, V) of (1.11) satisfies that

$$\check{u}_n \leqslant U \leqslant \hat{u}_n, \quad \check{v}_n \leqslant V \leqslant \hat{v}_n,$$

for all $n \geqslant 1$, where $(\check{u}_n, \hat{v}_n)$ and $(\hat{u}_n, \check{v}_n)$ are defined as in Lemmas A.1. Passing to the limit as $d_1, d_2 \to 0^+$, we obtain

$$\breve{U}_n \leqslant \liminf_{d_1,d_2\to 0^+} U \leqslant \limsup_{d_1,d_2\to 0^+} U \leqslant \widehat{U}_n, \quad \breve{V}_n \leqslant \liminf_{d_1,d_2\to 0^+} V \leqslant \limsup_{d_1,d_2\to 0^+} V \leqslant \widehat{V}_n, \tag{A-10}$$

where $\breve{U}_n$, $\widehat{U}_n$, $\breve{V}_n$ and $\widehat{V}_n$ are defined as in Lemma A.3. On the other hand, it follows easily from Lemma A.3 that

$$\lim_{n\to\infty} \breve{U}_n(x) = \lim_{n\to\infty} \widehat{U}_n(x) = \begin{cases} 0 & \text{if } m_1(x) \leqslant 0 \text{ or } m_2(x) > m_1(x) > 0, \\ m_1(x) & \text{if } m_1(x) > m_2(x), m_1(x) > 0, \end{cases} \tag{A-11}$$

and that

$$\lim_{n\to\infty} \breve{V}_n(x) = \lim_{n\to\infty} \widehat{V}_n(x) = \begin{cases} 0 & \text{if } m_2(x) \leqslant 0 \text{ or } m_1(x) > m_2(x) > 0, \\ m_2(x) & \text{if } m_2(x) > m_1(x), m_2(x) > 0. \end{cases} \tag{A-12}$$

Thus on any compact subset of $\Omega \setminus \{m_1(x) = m_2(x) > 0\}$, we obtain the uniform convergence of (U, V) to $(\widetilde{u}_*, \widetilde{v}_*)$.

Next we show the case that $m_1^+ - m_2^+$ does not change sign in Ω. Without loss of generality, we may assume that $m_2^+ - m_1^+ \geqslant 0$ in Ω. If $m_2^+ - m_1^+ \equiv 0$ in Ω, then

$$\bar{\Omega} \setminus \{x \in \bar{\Omega} \mid m_1(x) = m_2(x) > 0\} = \{m_2 \leqslant 0\} = \{m_1 \leqslant 0\}.$$

It is easy to see that any co-existence steady state (U, V) of (1.11) satisfies that $U < \theta_{d_1,m_1}$ and $V < \theta_{d_2,m_2}$. Therefore Theorem 5.4(iii) is a consequence of Lemma 2.5(i)(a). Thus we now assume that there exists some $x_0 \in \bar{\Omega}$ such that $(m_2^+ - m_1^+)(x_0) > 0$, which implies that

$$\{m_1 > 0\} \subsetneq \{m_2 > 0\}.$$

By Lemma A.1(i), we can define the sequence $(\hat{u}_n, \check{v}_n)$ for all d_1, d_2 sufficiently small. Moreover, since $V < \theta_{d_2,m_2}$, by Lemma 2.5(i)(a),

$$\breve{V}_n \leqslant \liminf_{d_1,d_2\to 0^+} V \leqslant \limsup_{d_1,d_2\to 0^+} V \leqslant m_2^+,$$

where $\check{V}_n$ is defined as in Lemma A.2. By Lemma A.3,

$$\lim_{n\to\infty} \check{V}_n(x) = \begin{cases} 0 & \text{if } m_2(x) \leqslant 0 \text{ or } m_1(x) > m_2(x) > 0, \\ m_2(x) & \text{if } m_2(x) > m_1(x), m_2(x) > 0. \end{cases} \tag{A-13}$$

Since $m_2^+ - m_1^+ \geqslant 0$, (A-13) implies that $V \to \widetilde{v}_*$ on any compact subset of $\Omega \setminus \{m_1(x) = m_2(x) > 0\}$, where $\widetilde{v}_*$ is defined in Theorem 3.7(iii). Since $U \to (m_1 - \widetilde{v}_*)^+$ and $\{m_1 > 0\} \subsetneq \{m_2 > 0\}$, we obtain that $U \to \widetilde{u}_* = 0$ on any compact subset of $\Omega \setminus \{m_1(x) = m_2(x) > 0\}$.

This completes the proof of Theorem 3.7(iii). $\square$