Global Dynamics of the Lotka-Volterra Competition-Diffusion System: Diffusion and Spatial Heterogeneity I

XIAOQING HE
East China Normal University

WEI-MING NI
East China Normal University and University of Minnesota

Abstract

In the first part of this series of three papers, we investigate the combined effects of diffusion, spatial variation, and competition ability on the global dynamics of a classical Lotka-Volterra competition-diffusion system. We establish the main results that determine the global asymptotic stability of semitrivial as well as coexistence steady states. Hence a complete understanding of the change in dynamics is obtained immediately. Our results indicate/confirm that, when spatial heterogeneity is included in the model, "diffusion-driven exclusion" could take place when the diffusion rates and competition coefficients of both species are chosen appropriately. © 2015 Wiley Periodicals, Inc.

1 Introduction

It is well-known that interactions between (random) diffusion and spatial heterogeneity can create some very interesting, perhaps even surprising phenomena in population dynamics in mathematical ecology. Among them two seem particularly outstanding.

First, in 1998, Dockery, Hutson, Mischaikow, and Pernarowski [7] showed that, in a heterogeneous environment, given two competing species with different dispersal rates but otherwise identical, the slower one always wipes out its faster counterpart regardless of their initial values; that is, *the slower diffuser always prevails!* To be more precise, the following Lotka-Volterra competition system was considered in [7]:

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

where $U(x,t)$ and $V(x,t)$ represent the population densities of two competing species at location $x \in \Omega$ and at time $t > 0$, which are therefore assumed to be nonnegative; Ω, the habitat, is a bounded smooth domain in $\mathbb{R}^N$; $d_1, d_2 > 0$ are the

Communications on Pure and Applied Mathematics, 0001–0034 (PREPRINT)

dispersal rates of U and V, respectively; $\Delta = \sum_{i=1}^N \partial^2/\partial x_i^2$ is the usual Laplace operator; and $\partial_\nu = \nu \cdot \nabla$, where ν denotes the outward unit normal vector on $\partial\Omega$, is the normal derivative on the boundary. For simplicity, we will assume throughout this paper that the initial data U_0 and V_0 are nonnegative and nontrivial, i.e., not identically zero. The zero Neumann (no-flux) boundary condition is imposed on $\partial\Omega$ to ensure that no individual crosses the boundary of the habitat. The function $m(x)$ represents the local carrying capacity or intrinsic growth rate of the species U and V, which reflects the environmental influence on the species.

Let $g(x) \in C^\alpha(\bar{\Omega})(\alpha \in (0,1))$ with $\int_\Omega g \geqslant 0$ and $g \not\equiv 0$. We denote by $\theta_{d,g}$ the unique positive solution of:

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

(See, e.g., [6] for the proof of existence and uniqueness results of (1.2).) Then the following result is established in [7]:

THEOREM A ([7]). *Suppose that* $0 < m(x) \not\equiv \text{const}$ *on* $\bar{\Omega}$ *and* $m(x) \in C^\alpha(\bar{\Omega})$ $(\alpha \in (0,1))$. *Then the semitrivial steady state* $(\theta_{d_1,m}, 0)$ *of* (1.1) *is globally asymptotically stable when* $d_1 < d_2$; *i.e., every solution* (U, V) *of* (1.1) *converges to* $(\theta_{d_1,m}, 0)$ *as* $t \to \infty$ *regardless of initial values* (U_0, V_0).

This result is remarkable, as it is easy to see that, with a homogeneous intrinsic growth rate $m(x) \equiv \text{const}$, for any $d_1, d_2 > 0$, (1.1) has a compact global attractor consisting of a continuum of steady states $\{((1-s)m, sm) | s \in [0,1]\}$ connecting the two semitrivial steady states. Theorem A then shows that, *in contrast, when spatial inhomogeneity is present in* (1.1)*, the slower diffuser is superior to its faster competitor, regardless of the initial values.*

In an attempt to understand this phenomenon, in 2006, Lou [27] adopted the weak competition approach to study system (1.1) above. For the classical Lotka-Volterra system in a homogeneous environment, it has been known for decades that *two weakly competing species will always coexist regardless of their* (*random*) *dispersal rates or initial values.* It therefore came as a surprise when Lou proved in [27], among other things, that *in a spatially heterogeneous environment, certain weakly competing species with appropriate dispersal rates can no longer coexist, again, regardless of their initial values!* In other words, diffusion and spatial heterogeneity could effectively change the nature of weak competitions as we knew it—another remarkable fact!

To describe Lou's result [27] mathematically, consider the following system:

$$\begin{cases} U_t = d_1 \Delta U + U(m(x) - U - cV) & \text{in } \Omega \times \mathbb{R}^+, \\ V_t = d_2 \Delta V + V(m(x) - bU - V) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\ U(x,0) = U_0(x), \ \ V(x,0) = V_0(x) & \text{in } \Omega, \end{cases} \tag{1.3}$$

with

$$0 < b, c < 1, \tag{1.4}$$

where b and c represent interspecific competition coefficients, while both intraspecific competition coefficients in (1.3) are normalized to 1. Again assuming that $m(x) \in C^{\alpha}(\overline{\Omega})$ ($\alpha \in (0,1)$), $m(x) > 0$ on $\overline{\Omega}$, and $m \not\equiv$ const, we define

$$E(m) := \sup_{d>0} \frac{\int_\Omega \theta_{d,m}}{\int_\Omega m}. \tag{1.5}$$

Then as observed by Lou [27], $\theta_{d,m}$ enjoys the following important property very different from the case when m is constant on $\overline{\Omega}$:

$$\int_\Omega \theta_{d,m} > \int_\Omega m \quad \text{for all } d > 0. \tag{1.6}$$

This implies that

$$E(m) > 1.$$

Furthermore, define

$$\Sigma_U := \{(d_1, d_2) \in \mathcal{Q} \mid (\theta_{d_1,m}, 0) \text{ is linearly stable}\}, \tag{1.7}$$

where

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

Then Lou's results may be described as follows.

THEOREM B ([27]). *Assume that* $0 < m(x) \not\equiv \text{const}$ *on* $\overline{\Omega}$ *and* $m(x) \in C^{\alpha}(\overline{\Omega})$ ($\alpha \in (0,1)$) *in* (1.3). *Then*

$$\Sigma_U \neq \varnothing \quad \textit{if and only if} \quad b > \frac{1}{E(m)}.$$

Moreover, for every $b \in (1/E(m), 1)$*, there exists some* $c_* \in (0,1)$ *such that for all* $0 < c < c_*$ *and* $(d_1, d_2) \in \Sigma_U$*, the semitrivial steady state* $(\theta_{d_1,m}, 0)$ *of* (1.3) *is globally asymptotically stable.*

In addition, Lou [27] proposed the following conjecture regarding the global dynamics of (1.3):

CONJECTURE C. *Assume that* $0 < m(x) \not\equiv \text{const}$ *on* $\overline{\Omega}$ *and* $m(x) \in C^{\alpha}(\overline{\Omega})$ ($\alpha \in (0,1)$) *in* (1.3). *For all* $b \in (1/E(m), 1)$ *and* $c \in (0, 1]$,

(i) $(\theta_{d_1,m}, 0)$ *is globally asymptotically stable for all* $(d_1, d_2) \in \Sigma_U$;
(ii) *there exists a unique coexistence steady state that is globally asymptotically stable if* $(d_1, d_2) \notin \overline{\Sigma_U}$ *and* $d_1 \leqslant d_2$.

Recently Lam and Ni [25] established both parts of Conjecture C for c small (but independent of $b \in (0,1)$). In fact, they showed that there exists some $\overline{c} > 0$ such that for all $c < \overline{c}$ and $b \in (0,1)$, $(\theta_{d_1,m}, 0)$ is globally asymptotically stable for all $(d_1, d_2) \in \overline{\Sigma_U}$ (i.e., global stability holds on the boundary of Σ_U as well) and (1.3) has a unique coexistence steady state that is globally asymptotically stable for any $d_1 \leq d_2$ such that $(d_1, d_2) \notin \overline{\Sigma_U}$.

In this paper, we will first settle Lou's conjecture completely. Furthermore, our result will encompass both Lou's conjecture as well as "the slower diffuser always prevails" phenomenon and hopefully put them in perspective. In fact, complete global dynamics of (1.3) are obtained in Theorem 1.1 below. Our basic assumption on b and c includes the range $bc \leqslant 1$, which contains the weak competition case (1.4) as well as the case $b = c = 1$ for "the slower diffuser always prevails" phenomenon in (1.1).

To describe our results, in addition to the set Σ_U defined in (1.7), we define the following subsets of $\mathcal{Q}$ for system (1.3):

$$\begin{aligned} &\Sigma_V := \{(d_1, d_2) \in \mathcal{Q} \mid (0, \theta_{d_2,m}) \text{ is linearly stable}\}, \\ &\Sigma_- := \{(d_1, d_2) \in \mathcal{Q} \mid \text{both } (\theta_{d_1,m}, 0) \text{ and } (0, \theta_{d_2,m}) \\ &\qquad\qquad \text{are linearly unstable}\}. \end{aligned} \tag{1.8}$$

Furthermore, define

$$S(m) := \sup_{d>0} \sup_{\bar{\Omega}} \frac{m}{\theta_{d,m}}; \tag{1.9}$$

then

$$\frac{1}{E(m)} < 1 < S(m) < \infty,$$

where the second inequality follows from Lemma 2.5(ii) below.

We now state the following result concerning the global dynamics of (1.3).

THEOREM 1.1. *Assume that* $0 < m(x) \not\equiv \text{const}$ *on* $\bar{\Omega}$ *and* $m(x) \in C^{\alpha}(\bar{\Omega})$ $(\alpha \in (0,1))$. *Then the following statements hold for* (1.3)*:*

(i) *If* $b \geqslant S(m)$ *and* $c \leqslant 1/S(m)$, *then* $\mathcal{Q} = \Sigma_U$, *and for all* $d_1, d_2 > 0$, $(\theta_{d_1,m}, 0)$ *is globally asymptotically stable.*

(ii) *If* $c \geqslant S(m)$ *and* $b \leqslant 1/S(m)$, *then* $\mathcal{Q} = \Sigma_V$, *and for all* $d_1, d_2 > 0$, $(0, \theta_{d_2,m})$ *is globally asymptotically stable.*

(iii) *If* $b \leqslant 1/E(m)$ *and* $c \leqslant 1/E(m)$, *then* $\mathcal{Q} = \Sigma_-$, *and for all* $d_1, d_2 > 0$, (1.3) *has a unique coexistence steady state that is globally asymptotically stable.*

(iv) *If* $1/E(m) < b < S(m)$, $1/E(m) < c < S(m)$, $bc \leqslant 1$, *and* $(b, c) \neq (1, 1)$, *then* $\Sigma_U, \Sigma_V, \Sigma_- \neq \varnothing$ *and* $\mathcal{Q} = \overline{\Sigma_U} \cup \overline{\Sigma_V} \cup \Sigma_-$. *Moreover,*
  (a) *for all* $(d_1, d_2) \in \overline{\Sigma_U}$, $(\theta_{d_1,m}, 0)$ *is globally asymptotically stable*;
  (b) *for all* $(d_1, d_2) \in \overline{\Sigma_V}$, $(0, \theta_{d_2,m})$ *is globally asymptotically stable*;
  (c) *for all* $(d_1, d_2) \in \Sigma_-$, (1.3) *has a unique coexistence steady state that is globally asymptotically stable.*

(v) *If* $b = c = 1$, *then* $\Sigma_- = \varnothing$, $\Sigma_U = \{(d_1, d_2) \mid d_2 > d_1\}$, *and* $\Sigma_V = \{(d_1, d_2) \mid d_2 < d_1\}$. *Moreover,*
  (a) *for all* $(d_1, d_2) \in \Sigma_U$, $(\theta_{d_1,m}, 0)$ *is globally asymptotically stable*;
  (b) *for all* $(d_1, d_2) \in \Sigma_V$, $(0, \theta_{d_2,m})$ *is globally asymptotically stable*;

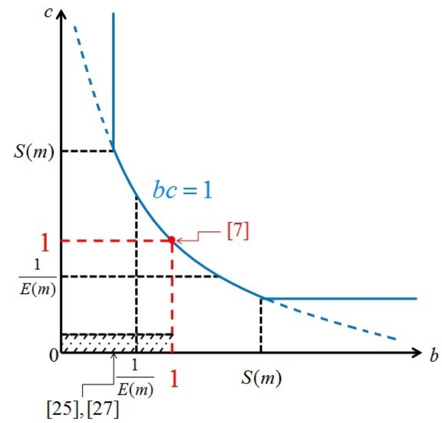

FIGURE 1.1. Global dynamics of (1.3) with $m > 0$ on $\overline{\Omega}$. See Theorem 1.1.

(c) *for all* $(d_1, d_2) \in \{(d_1, d_2) \mid d_2 = d_1\}$, (1.3) *has a compact global attractor consisting of a continuum of steady states*

$$\{((1-\xi)\theta_{d_1,m}, \xi\theta_{d_1,m}) \mid \xi \in [0,1]\}$$

connecting the two semitrivial steady states.

(vi) *If* $1/E(m) < b < S(m)$, $c \leqslant 1/E(m)$, *and* $bc \leqslant 1$, *then* $\Sigma_U, \Sigma_- \neq \varnothing$, $\Sigma_V = \varnothing$, *and* $\mathcal{Q} = \overline{\Sigma_U} \cup \Sigma_-$. *Moreover, for all* $(d_1, d_2) \in \overline{\Sigma_U}$, $(\theta_{d_1,m}, 0)$ *is globally asymptotically stable; and, for all* $(d_1, d_2) \in \Sigma_-$, (1.3) *has a unique coexistence steady state that is globally asymptotically stable.*

(vii) *If* $1/E(m) < c < S(m)$, $b \leqslant 1/E(m)$, *and* $bc \leqslant 1$, *then* $\Sigma_V, \Sigma_- \neq \varnothing$, $\Sigma_U = \varnothing$, *and* $\mathcal{Q} = \overline{\Sigma_V} \cup \Sigma_-$. *Moreover, for all* $(d_1, d_2) \in \overline{\Sigma_V}$, $(0, \theta_{d_1,m})$ *is globally asymptotically stable; and, for all* $(d_1, d_2) \in \Sigma_-$, (1.3) *has a unique coexistence steady state that is globally asymptotically stable.*

Figure 1.1 illustrates all the regions in the bc-plane considered in Theorem 1.1 where the corresponding global dynamics of (1.3) are described. Note that the figure is "symmetric" with respect to the line $b = c$. We also point out there the corresponding parts where previous results—Theorems A, B, and the results in [25]—apply.

It turns out that we can completely clarify global dynamics of a more general heterogeneous Lotka-Volterra competition-diffusion system than (1.3), and Theorem 1.1 above is just a special case of our main results. In fact, the proof becomes more transparent when we allow the species U and V to have *different* distributions of resources or intrinsic growth rates as follows:

$$(1.10)\qquad \begin{cases} U_t = d_1\Delta U + U(m_1(x) - U - cV) & \text{in } \Omega\times\mathbb{R}^+, \\ V_t = d_2\Delta V + V(m_2(x) - bU - V) & \text{in } \Omega\times\mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega\times\mathbb{R}^+, \\ U(x,0) = U_0(x),\ \ V(x,0) = V_0(x) & \text{in } \Omega, \end{cases}$$

where the functions $m_1(x)$ and $m_2(x)$ represent the carrying capacities or intrinsic growth rates, which reflect the environmental influence on the species U and V, respectively.

The model (1.10) and its variants have attracted considerable interest in the past two decades; see, e.g., [5–7, 12, 13, 19, 22, 23, 25–28, 32] and references therein.

To describe our results on (1.10), for simplicity, throughout this section, we assume that m_1 and m_2 satisfy the following condition:

$$(\mathrm{M}^+)\qquad m_i(x) \in C^\alpha(\bar{\Omega})\ \ (\alpha\in(0,1)), \quad m_i > 0 \ \text{ on } \bar{\Omega}, i = 1,2.$$

In fact, the pointwise positivity assumption for the growth rates m_1 and m_2 may be relaxed by requiring that the average of m_1 and m_2 be nonnegative; see Section 3 and the condition (M) below.

We now define the following three subsets of $\mathcal{Q}$, the first quadrant of the d_1d_2-plane, for system (1.10):

$$(1.11)\qquad \begin{aligned} \Sigma_U &:= \{(d_1,d_2)\in\mathcal{Q} \mid (\theta_{d_1,m_1},0) \text{ is linearly stable}\}, \\ \Sigma_V &:= \{(d_1,d_2)\in\mathcal{Q} \mid (0,\theta_{d_2,m_2}) \text{ is linearly stable}\}, \\ \Sigma_- &:= \{(d_1,d_2)\in\mathcal{Q} \mid \text{both } (\theta_{d_1,m_1},0) \text{ and } (0,\theta_{d_2,m_2}) \\ &\qquad\qquad \text{are linearly unstable}\}, \end{aligned}$$

where for simplicity we have adopted the same notation for system (1.3). For the precise definition of linear stability/instability of a steady state of (1.10) and their characterizations, see Section 2 below.

To completely understand the global dynamics of (1.10) in $\mathcal{Q}$, we also need to consider those $(d_1,d_2)\in\mathcal{Q}$ such that one (or both) of the two semitrivial steady states is neither linearly stable nor linearly unstable (i.e., neutrally stable). For this purpose, we first introduce the following elliptic eigenvalue problem.

DEFINITION 1.2. Given a positive constant d and a function $h\in L^\infty(\Omega)$, we define $\mu_k(d,h)$ to be the k^{th} eigenvalue (counting multiplicities) of

$$(1.12)\qquad \begin{cases} d\Delta\psi + h(x)\psi + \mu\psi = 0 & \text{in } \Omega, \\ \partial_\nu\psi = 0 & \text{on } \partial\Omega. \end{cases}$$

In particular, we call $\mu_1(d,h)$ the *first eigenvalue* of (1.12).

Now we are ready to define the following subsets of $\mathcal{Q}$ where at least one of the two semitrivial steady states is neutrally stable:

$$\begin{aligned} \Sigma_{U,0} &:= \{(d_1, d_2) \in \mathcal{Q} \mid \mu_1(d_2, m_2 - b\theta_{d_1,m_1}) = 0\}, \\ \Sigma_{V,0} &:= \{(d_1, d_2) \in \mathcal{Q} \mid \mu_1(d_1, m_1 - c\theta_{d_2,m_2}) = 0\}, \\ \Pi \quad &:= \Sigma_{U,0} \cap \Sigma_{V,0}. \end{aligned} \tag{1.13}$$

Define

$$L_U := \frac{\overline{m_2}}{\overline{m_1}} \cdot \frac{1}{E(m_1)}, \qquad S_U := \sup_{d_1>0} \sup_{\bar{\Omega}} \frac{m_2}{\theta_{d_1,m_1}}, \tag{1.14}$$

$$L_V := \frac{\overline{m_1}}{\overline{m_2}} \cdot \frac{1}{E(m_2)}, \qquad S_V := \sup_{d_2>0} \sup_{\bar{\Omega}} \frac{m_1}{\theta_{d_2,m_2}} \tag{1.15}$$

and

(1.16)

$$\Xi := \{(b,c) | b, c > 0 \text{ and } bc \leqslant 1\} \cup \{(b,c) | 0 < c \leqslant \frac{1}{S_U}\} \cup \{(b,c) | 0 < b \leqslant \frac{1}{S_V}\}.$$

We now state our first basic result that characterizes the global dynamics of (1.10) in $\mathcal{Q}$.

THEOREM 1.3. *Assume that* $(\mathbf{M}^+)$ *holds and* $(b, c) \in \Xi$. *Then we have the following mutually disjoint decomposition of* $\mathcal{Q}$*:*

$$\mathcal{Q} = (\Sigma_U \cup \Sigma_{U,0} \setminus \Pi) \cup (\Sigma_V \cup \Sigma_{V,0} \setminus \Pi) \cup \Sigma_- \cup \Pi. \tag{1.17}$$

Moreover, the following statements hold for (1.10)*:*

(i) *For all* $(d_1, d_2) \in (\Sigma_U \cup \Sigma_{U,0} \setminus \Pi)$, $(\theta_{d_1,m_1}, 0)$ *is globally asymptotically stable.*
(ii) *For all* $(d_1, d_2) \in (\Sigma_V \cup \Sigma_{V,0} \setminus \Pi)$, $(0, \theta_{d_2,m_2})$ *is globally asymptotically stable.*
(iii) *For all* $(d_1, d_2) \in \Sigma_-$, (1.10) *has a unique coexistence steady state that is globally asymptotically stable.*
(iv) *For all* $(d_1, d_2) \in \Pi$, $\theta_{d_1,m_1} \equiv c\theta_{d_2,m_2}$ *and* (1.10) *has a compact global attractor consisting of a continuum of steady states*

$$\{(\xi\theta_{d_1,m_1}, (1-\xi)\theta_{d_1,m_1}/c) \mid \xi \in [0,1]\}$$

connecting the two semitrivial steady states.

We remark that Theorem 1.3 is a special case of Theorem 3.4 in Section 3, where the positivity assumption (M$^+$) is relaxed. The main ingredient of our proof for Theorem 1.3 or 3.4 is to show that every coexistence steady state of (1.10), if it exists, is linearly stable, except for the degenerate case that $(d_1, d_2) \in \Pi$. Therefore by monotone flow theory, if one of the two semitrivial steady states of (1.10) is linearly stable, then it is globally asymptotically stable; on the other hand, if both semitrivial steady states of (1.10) are linearly unstable, then there exists a coexistence steady state of (1.10) that must be unique and hence globally asymptotically stable. Finally, for $(d_1, d_2) \in \Pi$, where the linear stabilities of both semitrivial steady states are degenerate, (1.10) has a compact global attractor consisting of a continuum of steady states connecting the two semitrivial steady states. In other words, *whenever* $(b, c) \in \Xi$, *global dynamics of* (1.10) *are completely determined by its local dynamics around the two semitrivial steady states*. Note that it will be clear, from Theorems 3.3 and 3.5 below, that under suitable hypothesis each of the four components in the decomposition (1.17) could be empty.

Hence, for any fixed pair $(b, c) \in \Xi$, Theorem 1.3 characterizes all possible long-term dynamical behaviors of (1.10) for all $(d_1, d_2) \in \mathcal{Q}$. Our next goal is to further classify the global dynamics of (1.10), when at least one of m_1 and m_2 is nonconstant, in terms of b and c, and the exact location of $(d_1, d_2) \in \mathcal{Q}$.

THEOREM 1.4. *Assume that* (M^+) *holds, at least one of* m_1 *and* m_2 *is nonconstant, and* $(b, c) \in \Xi$. *Then*

$$0 < L_U L_V < 1, \quad L_U S_V > 1, \quad L_V S_U > 1, \tag{1.18}$$

and the following hold for (1.10):

(i) *If* $b \geqslant S_U$ *and* $c \leqslant 1/S_U$, *then* $\mathcal{Q} = \Sigma_U$; *i.e., for all* $d_1, d_2 > 0$, $(\theta_{d_1,m_1}, 0)$ *is globally asymptotically stable.*

(ii) *If* $c \geqslant S_V$ *and* $b \leqslant 1/S_V$, *then* $\mathcal{Q} = \Sigma_V$; *i.e., for all* $d_1, d_2 > 0$, $(0, \theta_{d_2,m_2})$ *is globally asymptotically stable.*

(iii) *If* $b < L_U$ *and* $c < L_V$, *then* $\mathcal{Q} = \Sigma_-$; *i.e., for all* $d_1, d_2 > 0$, (1.10) *has a unique coexistence steady state that is globally asymptotically stable; if* $b = L_U$ *and* $c < L_V$, *then* $\mathcal{Q} = \Sigma_- \cup \Sigma_{U,0}$ *where* $\Sigma_{U,0}$ *may be empty; if* $b < L_U$ *and* $c = L_V$, *then* $\mathcal{Q} = \Sigma_- \cup \Sigma_{V,0}$ *where* $\Sigma_{V,0}$ *may be empty; if* $b = L_U$ *and* $c = L_V$, *then* $\mathcal{Q} = \Sigma_- \cup \Sigma_{U,0} \cup \Sigma_{V,0}$, *where* $\Sigma_{U,0} \cup \Sigma_{V,0}$ *may be empty.*

(iv) *If* $L_U < b$ *and* $L_V < c$, *then* $\Sigma_U, \Sigma_{U,0}, \Sigma_V, \Sigma_{V,0} \neq \varnothing$. *Moreover,* $\Sigma_- = \varnothing$ *if and only if* $m_1 \equiv c m_2$ *and* $bc = 1$, *and in that case,* $\Sigma_{U,0} = \Sigma_{V,0} = \Pi = \{(d_1, d_2) \mid d_2 = d_1/c\}$, $\Sigma_U = \{(d_1, d_2) \mid d_2 > d_1/c\}$, *and* $\Sigma_V = \{(d_1, d_2) \mid d_2 < d_1/c\}$.

(v) *If* $L_U < b < S_U$ *and* $c < L_V$, *then* $\Sigma_U, \Sigma_{U,0}, \Sigma_- \neq \varnothing$ *and* $\Sigma_V = \Sigma_{V,0} = \Pi = \varnothing$; *if* $L_U < b < S_U$ *and* $c = L_V$, *then the same statement holds except for* $\Sigma_{V,0}$, *which may be nonempty.*

(vi) *If* $L_V < c < S_V$ *and* $b < L_U$, *then* $\Sigma_V, \Sigma_{V,0}, \Sigma_- \neq \varnothing$ *and* $\Sigma_U = \Sigma_{U,0} = \Pi = \varnothing$; *if* $L_V < c < S_V$ *and* $b = L_U$, *then the same statement holds except for* $\Sigma_{U,0}$, *which may be nonempty.*

Figure 1.2 illustrates all the regions in bc-plane considered in Theorem 1.4 where the corresponding global dynamics of (1.10) are described. We remark that Theorem 1.4 is a special case of Theorem 3.6 in Section 3, where the positivity condition (M^+) is relaxed. Note that the sets Σ_U and $\Sigma_{U,0}$ are independent of c and the sets Σ_V and $\Sigma_{V,0}$ are independent of b. Denote by $\overline{\Sigma_U}$ and $\overline{\Sigma_V}$ the closure of Σ_U and Σ_V in $\mathcal{Q}$, respectively; then $\partial\Sigma_U = \overline{\Sigma_U} \setminus \Sigma_U \subset \Sigma_{U,0}$ and

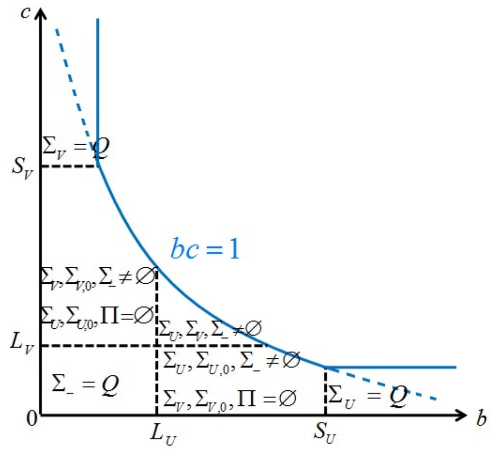

FIGURE 1.2. Global dynamics of (1.10) with $m_i \not\equiv$ const and $m_i > 0$ on $\bar{\Omega}$, $i = 1, 2$. See Theorem 1.4.

$\partial\Sigma_V = \overline{\Sigma_V} \setminus \Sigma_V \subset \Sigma_{V,0}$. In general, it may happen that $\partial\Sigma_U \subsetneq \Sigma_{U,0}$ and $\partial\Sigma_V \subsetneq \Sigma_{V,0}$. However, for those special cases of (1.10) that we will study in parts II and III of this series of papers, namely, [14] and [15], they are equal and moreover $\Pi = \varnothing$. For a detailed characterization of the sets Σ_U, $\Sigma_{U,0}$, Σ_V, $\Sigma_{V,0}$, Σ_-, and Π, see Theorems 3.3 and 3.5 below.

We now return to the special case of (1.10) where $m_1 \equiv m_2 \equiv m$, i.e., system (1.3), and show that Theorem 1.1 follows directly from Theorems 1.3 and 1.4 and from Theorems 3.3 and 3.5 in Section 3 below. Indeed, in this case,

$$L_U = L_V = 1/E(m) \quad \text{and} \quad S_U = S_V = S(m).$$

Moreover, since $m \not\equiv s\theta_{d,m}$ for any $s > 0$, it follows from the characterizations of $\Sigma_{U,0}$ and $\Sigma_{V,0}$ in Theorem 3.3 below that

$$\Sigma_{U,0} = \partial\Sigma_U \quad (\text{i.e., } \Sigma_U \cup \Sigma_{U,0} = \overline{\Sigma_U}),$$
$$\Sigma_{V,0} = \partial\Sigma_V \quad (\text{i.e., } \Sigma_V \cup \Sigma_{V,0} = \overline{\Sigma_V}).$$

In particular, if $b = L_U$, $\Sigma_{U,0} = \varnothing$, and if $c = L_V$, $\Sigma_{V,0} = \varnothing$. Finally, from the characterization of Π in Theorem 3.5(ii) below, we deduce that

$$\Pi = \begin{cases} \varnothing & \text{if } (b,c) \neq (1,1), \\ \{(d,d) \mid d > 0\} & \text{if } (b,c) = (1,1). \end{cases}$$

Consequently, Theorem 1.1 follows.

We see from Theorem 1.4 that in a spatially heterogeneous environment, the interactions of diffusion and spatial variation can effectively change the global dynamics of (1.10) so that "diffusion-driven exclusion" is possible only when the competition coefficient b (resp., c) lies above the threshold value L_U (resp., L_V), which is determined solely by m_1 and m_2. Therefore, we have the following observation:

REMARK 1.5. *For fixed* $0 < b, c < \infty$ *with* $bc \leq 1$, *Theorem* 1.4 *implies that, if the total amount of resources for species* U *and* V *are fixed, the larger* $E(m_1)$ (*resp.,* $E(m_2)$), *the more advantageous the species* U (*resp.,* V) *during the competition.*

Furthermore, Remark 1.5 reveals that the problem

$$\sup\{E(g) \mid g(x) > 0 \text{ in } \Omega\}$$

plays an important role in the dynamics of the two-species competition model. It is not clear whether $E(g)$ is bounded above for all g's that are nonnegative in Ω, or if it is bounded above, what the supremum is. In other words, we want to know how much more the total population could be supported by the same total resources if the resources were distributed in an "optimal" way, and what that optimal distribution would be. Species with resources distributed in such an optimal way, if it exists, would obtain more advantages during the competition in the two-species competition model (1.10). We hope to explore further in this direction in a future paper.

The rest of this paper is organized as follows. In Section 2 we collect some preliminaries that will be used in the following sections. All the main results are established in Section 3. In particular, we give a detailed description of various sets Σ_U, $\Sigma_{U,0}$, Σ_V, $\Sigma_{V,0}$, Σ_-, and Π in the $d_1 d_2$-plane corresponding to different dynamical behaviors in terms of b and c. Finally, some concluding remarks and extensions are included in Section 4.

2 Preliminaries

In this section, we assume that in (1.10), m_1 and m_2 satisfy the following condition:

$$\text{(M)} \qquad m_i(x) \in C^\alpha(\bar{\Omega}) \ \ (\alpha \in (0,1)), \quad \int_\Omega m_i \geqslant 0 \text{ and } m_i \not\equiv 0 \ \ (i = 1, 2),$$

which includes (M^+) as a special case. We now establish some basic facts and preliminary results that will be needed in subsequent sections.

As system (1.10) generates a monotone dynamical system [16–18] that preserves the order

$$(U_1, V_1) \preccurlyeq (U_2, V_2) \quad \text{if} \quad U_1 \leqslant U_2 \text{ and } V_1 \geqslant V_2 \text{ in } \Omega,$$

the dynamics of (1.10) is determined to a large extent by its steady states and their stability properties. If a steady state (U, V) satisfying $U \geqslant 0$ and $V \geqslant 0$ is neither a trivial nor a semitrivial steady state, then by the maximum principle [9], we must have $U > 0$ and $V > 0$ on $\bar{\Omega}$. In this case, we call (U, V) a *coexistence steady state*.

We first review the definition of linear stability of a given steady state (U, V) of (1.10). Linearizing the steady state problem of (1.10) at (U, V), we have

$$
\begin{cases} d_1 \Delta \Phi + \Phi(m_1 - U - cV) - U(\Phi + c\Psi) + \lambda \Phi = 0 & \text{in } \Omega, \\ d_2 \Delta \Psi + \Psi(m_2 - bU - V) - V(b\Phi + \Psi) + \lambda \Psi = 0 & \text{in } \Omega, \\ \partial_\nu \Phi = \partial_\nu \Psi = 0 & \text{on } \partial\Omega. \end{cases} \tag{2.1}
$$

When (U, V) is a trivial or semitrivial steady state, we can characterize the sign of the principal eigenvalue λ_1 according to Lemma 2.3 below. On the other hand, if (U, V) is a coexistence steady state of (1.10), then by the Krein-Rutman theorem [24,33], (2.1) has a principal eigenvalue $\lambda_1 \in \mathbb{R}$; i.e., λ_1 is simple and has the least real part among all eigenvalues of (2.1). Moreover, the corresponding eigenfunction (Φ_1, Ψ_1) of λ_1 can be chosen to satisfy $\Phi_1 > 0 > \Psi_1$ on $\bar{\Omega}$. We call a steady state (U, V) of (1.10) *linearly stable* (resp., *linearly unstable*) if the principal eigenvalue λ_1 of (2.1) is positive (resp., negative). By theorem 7.6.2 in [33], *we know that if a steady state of* (1.10) *is linearly stable* (*resp., linearly unstable*)*, then it is asymptotically stable* (*resp., unstable*)*,* where the notion of *stability* and *asymptotic stability* are defined in the standard dynamical system sense with the $C(\bar{\Omega}) \times C(\bar{\Omega})$ topology.

Recall that we have defined the principal eigenvalue $\mu_1(d, h)$ for (1.12) in Definition 1.2. The following variational characterization of $\mu_1(d, h)$ is well known:

$$
\mu_1(d, h) = \inf_{\psi \in H_1(\Omega) \setminus \{0\}} \frac{\int_\Omega (d|\nabla \psi|^2 - h(x)\psi^2) dx}{\int_\Omega \psi^2}. \tag{2.2}
$$

To further characterize properties of $\mu_1(d, h)$, we need to first 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 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. For a proof, see e.g., [1,31].

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) $\int_\Omega h < 0 \Leftrightarrow \lambda_1(h) > 0$*,*
(iv) $\lambda_1(h_1) > \lambda_1(h_2)$ *if* $h_1 \le h_2$, $h_1 \not\equiv h_2$ *a.e., and* h_1, h_2 *both change sign.*

We now state the following proposition, which collects some important properties of $\mu_1(d, h)$. For a proof, see, e.g., [6, p. 95] or [29, p. 69].

PROPOSITION 2.2. *The first eigenvalue* $\mu_1(d,h)$ *of* (1.12) *depends smoothly on* $d > 0$ *and continuously on* $h \in L^\infty(\Omega)$. *Moreover, it has the following properties*:

(i) $\int_\Omega h \geq 0$ *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) *Assume that* h *is nonconstant. Then* $\mu_1(d,h)$ *is strictly increasing and concave in* $d > 0$. *Moreover,*

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

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* $h \leq (\not\equiv) 0$.

The following lemma characterizes the linear stability of the trivial steady state $(0,0)$ and the two semitrivial steady states $(\theta_{d_1,m_1},0)$ and $(0,\theta_{d_2,m_2})$ of (1.10). The proof follows essentially from the same arguments as in that of corollary 2.10 in [25] and therefore is 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* (1.10) *is determined by the sign of* $\mu_1(d_2, m_2 - b\theta_{d_1,m_1})$, $\mu_1(d_1, m_1 - c\theta_{d_2,m_2})$, *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 will also use the following lemma derived from the theory of monotone dynamical systems. (See, e.g., proposition 9.1 and theorem 9.2 in [16].)

LEMMA 2.4. *For any* $d_1, d_2 > 0$, *assume that every coexistence steady state of* (1.10), *if it exists, is asymptotically stable; then one of the following alternatives holds:*

(i) *There exists a unique coexistence steady state of* (1.10) *that is globally asymptotically stable.*

(ii) *System* (1.10) *has no coexistence steady state and either one of* $(\theta_{d_1,m_1},0)$ *or* $(0,\theta_{d_2,m_2})$ *is globally asymptotically stable, while the other one is unstable.*

Recall that we have defined $\theta_{d,g}$ as the unique positive solution of (1.2). We end this section with the following lemma, which summarizes some useful properties of $\theta_{d,g}$.

LEMMA 2.5. *Assume that* $g(x) \in C^\alpha(\overline{\Omega})$ $(\alpha \in (0,1))$, $\int_\Omega g \geqslant 0$, *and* $g \not\equiv$ const. *Then the following hold*:

(i) $d \mapsto \theta_{d,g}$ *is continuous from* $\mathbb{R}^+$ *to* $C^{2,\alpha}(\overline{\Omega})$. *Moreover,*

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

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

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

The continuous dependence of $\theta_{d,g}$ on d can be proved by an application of the implicit function theorem. (See proposition 3.6 in [6] and remarks there.) The proofs of limiting behaviors of $\theta_{d,g}$ as d goes to 0^+ and ∞ are standard; see, e.g., [29]. The proofs of Lemma 2.5(ii) can be found in [25, prop. 2.4] and [12, lemma 2.3].

3 Main Results and Proofs

In this section, we state and prove our main results concerning the global dynamics of (1.10) under condition (M), which includes condition (M$^+$) as a special case. Hence Theorems 1.3 and 1.4 in Section 1 are actually special cases of Theorems 3.4 and 3.6, respectively, in this section.

First of all, we trivially extend definitions of the sets Σ_U, $\Sigma_{U,0}$, Σ_V, $\Sigma_{V,0}$, Σ_-, and Π defined in (1.11) and (1.13) to m_1 and m_2 satisfying condition (M) for system (1.10). We also extend definitions of L_U, S_U, L_V and S_V in (1.14) and (1.15) to m_1 and m_2 satisfying condition (M) as follows:

$$L_U := \inf_{d_1>0} \frac{\overline{m_2}}{\overline{\theta_{d_1,m_1}}} \in [0,\infty), \qquad S_U := \sup_{d_1>0} \sup_{\overline{\Omega}} \frac{m_2}{\theta_{d_1,m_1}} \in (0,\infty], \tag{3.1}$$

$$L_V := \inf_{d_2>0} \frac{\overline{m_1}}{\overline{\theta_{d_2,m_2}}} \in [0,\infty), \qquad S_V := \sup_{d_2>0} \sup_{\overline{\Omega}} \frac{m_1}{\theta_{d_2,m_2}} \in (0,\infty]. \tag{3.2}$$

Then the definition of Ξ in (1.16) is extended accordingly with S_U and S_V defined as above. Note that in case $S_U = \infty$, the subset $\{(b,c)|0 < c \leqslant 1/S_U\}$ of Ξ is empty and in case $S_V = \infty$, the subset $\{(b,c)|0 < b \leqslant 1/S_V\}$ of Ξ is empty. Hence

$$\text{if } S_U = \infty \text{ and } S_V = \infty, \text{ then } \Xi = \Xi_1, \tag{3.3}$$

where

$$\Xi_1 := \{(b,c) \mid b,c > 0 \text{ and } bc \leqslant 1\}. \tag{3.4}$$

Note that if both m_1 and m_2 are constant, then

$$L_U = S_U = \frac{\overline{m_2}}{\overline{m_1}}, \qquad L_V = S_V = \frac{\overline{m_1}}{\overline{m_2}},$$

$$\Xi = \{(b,c) \mid 0 < c \leqslant \overline{m_1}/\overline{m_2}\} \cup \{(b,c) \mid 0 < b \leqslant \overline{m_2}/\overline{m_1}\},$$

and system (1.10) reduces to the classical homogeneous Lotka-Volterra competition system. In this case, its dynamics has been studied extensively. See, e.g., [2,11,34] and references therein. It turns out that the two ratios $\overline{m_2}/\overline{m_1}$ and $\overline{m_1}/\overline{m_2}$ play an important role in determining the asymptotic behavior of solutions of (1.10) when both m_1 and m_2 are constant.

THEOREM 3.1. *Assume that* (M) *holds,* $m_i \equiv \text{const}$ $(i = 1, 2)$ *and* $(b, c) \in \Xi$. *Then the following statements hold for system* (1.10)*:*

(i) *If* $b \geqslant m_2/m_1$, $c \leqslant m_1/m_2$, *and* $(b, c) \neq (m_2/m_1, m_1/m_2)$, *then for all* $d_1, d_2 > 0$, $(m_1, 0)$ *is globally asymptotically stable.*
(ii) *If* $c \geqslant m_1/m_2$, $b \leqslant m_2/m_1$, *and* $(b, c) \neq (m_2/m_1, m_1/m_2)$, *then for all* $d_1, d_2 > 0$, $(0, m_2)$ *is globally asymptotically stable.*
(iii) *If* $b < m_2/m_1$ *and* $c < m_1/m_2$, *then for all* $d_1, d_2 > 0$, (1.10) *has a globally asymptotically stable coexistence steady state* $((m_1 - cm_2)/(1 - bc), (m_2 - bm_1)/(1 - bc))$.
(iv) *If* $b = m_2/m_1 = 1/c$, *then* (1.10) *has a compact global attractor consisting of a continuum of steady states* $\{(\xi m_1, (1 - \xi)m_1/c) \mid \xi \in [0, 1]\}$.

Theorem 3.1 seems well known, but it also seems difficult to find a convenient reference with a complete proof in the literature. For a proof of Theorem 3.1(iii), see [2]. Some of the results in Theorem 3.1(i)–(iii) are also proved in [34] under restricted initial conditions. In [10, 20], a Lyapunov functional method is used to study global dynamics of the corresponding kinetic system of (1.10) (i.e., without diffusion terms) and its variants. The extension of this method to Lotka-Volterra systems with diffusion including (1.10) is discussed in [11, 21], which can be applied to prove Theorem 3.1(i)–(iii). For Theorem 3.1(iv), we cannot find a proof in the literature. However, it does follow from (the proof of) Theorem 3.4(iv) below. First, it is easy to check that the set of steady states of (1.10) is

$$\{(0, 0)\} \cup \{(\xi m_1, (1 - \xi)m_1/c) \mid \xi \in [0, 1]\},$$

with $(0, 0)$ being a repeller. Hence it follows directly from [18, theorem 3] that the compact continuum of steady states $\{(\xi m_1, (1 - \xi)m_1/c) \mid \xi \in [0, 1]\}$ is a global attractor.

Therefore, for the homogeneous Lotka-Volterra competition-diffusion system, the global dynamics is determined only by the strengths of the two species' competition abilities regardless of their diffusion rates. As is well known, this is no longer the case when the environment is spatially inhomogeneous. In particular, if m_1 and m_2 satisfy condition (M^+) and at least one of m_1 and m_2 is nonconstant, then

$$0 < L_U \leqslant \frac{\overline{m_2}}{\overline{m_1}} < S_U < \infty \quad \text{and} \quad 0 < L_V \leqslant \frac{\overline{m_1}}{\overline{m_2}} < S_V < \infty,$$

where the first equality holds if and only if $m_1 \equiv \text{const}$ and the second equality holds if and only if $m_2 \equiv \text{const}$. Therefore the threshold value $\overline{m_2}/\overline{m_1}$ (resp., $\overline{m_1}/\overline{m_2}$) when both m_1 and m_2 are constant in Theorem 3.1 now splits into two numbers L_U and S_U (resp., L_V and S_V), with the lower values L_U and L_V each deviating by a factor $1/E(m_1)$ and $1/E(m_2)$, respectively. The following lemma characterizes the relative positions of the points (L_U, L_V), (L_U, S_V), and (L_V, S_U) with respect to the curve $bc = 1$ in the first quadrant of bc-plane.

LEMMA 3.2. *Assume that* (M) *holds and that at least one of* m_1 *and* m_2 *is nonconstant. Let* L_U*,* S_U*,* L_V*, and* S_V *be defined in* (3.1) *and* (3.2)*. Then the following hold:*

(i) $L_U L_V < 1$*;*
(ii) *if* $L_U > 0$ *and* $S_V < \infty$*, then* $L_U S_V > 1$*;*
(iii) *if* $L_V > 0$ *and* $S_U < \infty$*, then* $L_V S_U > 1$.

PROOF. Since at least one of m_1 and m_2 is nonconstant, (i) follows from (1.6) (which obviously also holds for sign-changing m's). We now prove (ii). The proof of (iii) follows from similar arguments as in that of (ii) and is thus omitted. If $L_U > 0$ and $S_V < \infty$, by (3.1), (3.2), and Lemma 2.5,

$$\begin{aligned} L_U S_V &= \inf_{d_1>0} \frac{\overline{m_2}}{\overline{\theta_{d_1,m_1}}} \cdot \sup_{d_2>0} \sup_{\bar{\Omega}} \frac{m_1}{\theta_{d_2,m_2}} \\ &\geqslant \frac{\overline{m_2}}{\sup\limits_{d_1>0} \overline{\theta_{d_1,m_1}}} \cdot \lim_{d_2\to\infty} \sup_{\bar{\Omega}} \frac{m_1}{\theta_{d_2,m_2}} \\ &= \frac{\overline{m_2}}{\sup\limits_{d_1>0} \overline{\theta_{d_1,m_1}}} \cdot \sup_{\bar{\Omega}} \frac{m_1}{\overline{m_2}} = \frac{\sup_{\bar{\Omega}} m_1}{\sup\limits_{d_1>0} \overline{\theta_{d_1,m_1}}} \geqslant 1. \end{aligned}$$

Here, if m_1 is nonconstant, the last inequality is strict by Lemma 2.5 and (1.6); if m_2 is nonconstant, it follows from $S_V < \infty$ and Lemma 2.5 that $m_2 > 0$ on $\bar{\Omega}$, which implies that the first inequality is strict. This finishes the proof of (ii). □

To state our results concerning the global dynamics of (1.10) when at least one of m_1 and m_2 is nonconstant and $(b, c) \in \Xi$, we first describe in the following how the sets Σ_U and $\Sigma_{U,0}$ (resp., Σ_V and $\Sigma_{V,0}$) change in the $d_1 d_2$-plane when we vary b (resp., c). To characterize the set Σ_U in terms of $b > 0$, we define for each $b > 0$,

$$I_b := \left\{ d_1 > 0 \;\middle|\; \int_\Omega (m_2 - b\theta_{d_1,m_1}) < 0 \right\} = I_b^0 \cup I_b^1, \tag{3.5}$$

where

$$\begin{aligned} I_b^0 &:= \{d_1 > 0 \mid m_2 - b\theta_{d_1,m_1} \le (\not\equiv) 0 \text{ on } \bar{\Omega}\}, \\ I_b^1 &:= \{d_1 \in I_b \mid \sup_{\bar{\Omega}}(m_2 - b\theta_{d_1,m_1}) > 0\}. \end{aligned} \tag{3.6}$$

Note that I_b is the union of finitely many open intervals, I_b^0 is closed, and I_b^1 is open in $\mathbb{R}^+$. Similarly, to characterize the set Σ_V in terms of $c > 0$, we define for each $c > 0$,

$$I_c := \left\{ d_2 > 0 \;\middle|\; \int_\Omega (m_1 - c\theta_{d_2,m_2}) < 0 \right\} = I_c^0 \cup I_c^1, \tag{3.7}$$

where

$$\begin{aligned} I_c^0 &:= \{d_2 > 0 \mid m_1 - c\theta_{d_2,m_2} \leq (\not\equiv) 0 \text{ on } \overline{\Omega}\}, \\ I_c^1 &:= \{d_2 \in I_c \mid \sup_{\overline{\Omega}}(m_1 - c\theta_{d_2,m_2}) > 0\}. \end{aligned} \tag{3.8}$$

Note that I_c is the union of finitely many open intervals, I_c^0 is closed, and I_c^1 is open in $\mathbb{R}^+$.

Now we are ready to state the following result:

THEOREM 3.3. *Assume that* (M) *holds. Let L_U, S_U, L_V, and S_V be defined as in* (3.1) *and* (3.2). *Then the following hold for* (1.10):

(i) *For Σ_U, we have the following characterization*:

$$\Sigma_U = \begin{cases} \varnothing & \text{if } 0 < b \leqslant L_U, \\ \{(d_1, d_2) \mid d_1 \in I_b, d_2 > \hat{d}_2^*(d_1)\} \subsetneq \mathcal{Q} & \text{if } L_U < b < S_U, \\ \mathcal{Q} & \text{if } b \geqslant S_U, \end{cases} \tag{3.9}$$

where I_b, I_b^0, and I_b^1 are defined in (3.5) *and* (3.6) *and $\hat{d}_2^*(d_1)$ is defined in I_b as follows*:

$$\hat{d}_2^*(d_1) := \begin{cases} 0 & \text{if } d_1 \in I_b^0, \\ \frac{1}{\lambda_1(m_2 - b\theta_{d_1,m_1})} > 0, & \text{if } d_1 \in I_b^1. \end{cases} \tag{3.10}$$

Hence $\Sigma_U \neq \varnothing$ if and only if $b > L_U$ and Σ_U is strictly monotonically increasing in $b \in (L_U, S_U)$.

(ii) *For Σ_V, we have the following characterization*:

$$\Sigma_V = \begin{cases} \varnothing & \text{if } 0 < c \leqslant L_V, \\ \{(d_1, d_2) \mid d_2 \in I_c, d_1 > \hat{d}_1^*(d_2)\} \subsetneq \mathcal{Q} & \text{if } L_V < c < S_V, \\ \mathcal{Q} & \text{if } c \geqslant S_V, \end{cases} \tag{3.11}$$

where I_c, I_c^0, and I_c^1 are defined in (3.7) *and* (3.8) *and $\hat{d}_1^*(d_2)$ is defined in I_c as follows*:

$$\hat{d}_1^*(d_2) := \begin{cases} 0, & \text{if } d_2 \in I_c^0, \\ \frac{1}{\lambda_1(m_1 - c\theta_{d_2,m_2})} > 0, & \text{if } d_2 \in I_c^1. \end{cases} \tag{3.12}$$

Hence $\Sigma_V \neq \varnothing$ if and only if $c > L_V$ and Σ_V is strictly monotonically increasing in $c \in (L_V, S_V)$.

(iii) *For $\Sigma_{U,0}$, we have the following characterization*:

$$\Sigma_{U,0} = \begin{cases} \varnothing & \text{if } 0 < b < L_U \text{ or } b \geqslant S_U, \\ \{(d_1, d_2) \mid m_2 \equiv L_U \theta_{d_1,m_1}\} & \text{if } b = L_U, \\ \partial\Sigma_U \cup \{(d_1, d_2) \mid m_2 \equiv b\theta_{d_1,m_1}\} & \text{if } L_U < b < S_U, \end{cases} \tag{3.13}$$

where for any $s > 0$, the set $\{(d_1, d_2) \mid m_2 \equiv s\,\theta_{d_1,m_1}\}$ is either empty or equal to a single straight vertical line segment $\{(d_1^*, d_2) \mid d_2 > 0\}$ where d_1^* is the unique d_1 with the property that $m_2 \equiv s\,\theta_{d_1,m_1}$.

(iv) *For $\Sigma_{V,0}$, we have the following characterization*:

$$\Sigma_{V,0} = \begin{cases} \varnothing & \text{if } 0 < c < L_V \text{ or } c \geqslant S_V, \\ \{(d_1, d_2) \mid m_1 \equiv L_V \theta_{d_2,m_2}\} & \text{if } c = L_V, \\ \partial\Sigma_V \cup \{(d_1, d_2) \mid m_1 \equiv c\theta_{d_2,m_2}\} & \text{if } L_V < c < S_V, \end{cases} \tag{3.14}$$

where for each $s > 0$, the set $\{(d_1, d_2) \mid m_1 \equiv s\theta_{d_2,m_2}\}$ is either empty or equal to a single straight horizontal line segment $\{(d_1, d_2^*) \mid d_1 > 0\}$ where d_2^* is the unique d_2 with the property that $m_1 \equiv s\theta_{d_2,m_2}$.

In all statements above, in case $L_U = 0$ (resp., $L_V = 0$), we simply do not need the statements involving $b \leqslant 0$ (resp., $c \leqslant 0$), and in case $S_U = \infty$ (resp., $S_V = \infty$), we simply do not need the statements involving $b \geqslant \infty$ (resp., $c \geqslant \infty$).

PROOF. If both m_1 and m_2 are constant, then the theorem follows directly from Theorem 3.1. Consequently, we only need to prove the theorem assuming that at least one of m_1 and m_2 is nonconstant.

We start the proof with the comment that if $L_U = 0$ (resp., $L_V = 0$), all arguments involving the case $b \leqslant 0$ (resp., $c \leqslant 0$) below should be skipped; Similarly, if $S_U = \infty$ (resp., $S_V = \infty$), all arguments involving the case $b \geqslant \infty$ (resp., $c \geqslant \infty$) below should be skipped.

First, we prove Theorem 3.3(i). By Lemma 2.3,

$$\Sigma_U = \{(d_1, d_2) \mid \mu_1(d_2, m_2 - b\theta_{d_1,m_1}) > 0\}.$$

Suppose that $d_1 \notin I_b$, where I_b is defined in (3.5); then $\int_\Omega (m_2 - b\theta_{d_1,m_1}) \geq 0$. By Proposition 2.2(i), $\mu_1(d_2, m_2 - b\theta_{d_1,m_1}) \leq 0$ for all d_2, i.e., $(d_1, d_2) \notin \Sigma_U$ for all $d_2 > 0$. Hence $(d_1, d_2) \in \Sigma_U$ implies that $d_1 \in I_b$. We now characterize the set I_b for all $b > 0$ in detail. If $b \leqslant L_U$, then by definition of L_U in (3.1), $\int_\Omega (m_2 - b\theta_{d_1,m_1}) \geqslant 0$ for all $d_1 > 0$. Hence $I_b = \varnothing$ and $\Sigma_U = \varnothing$. It is easy to check that I_b is the union of finitely many open intervals and thus is open in $\mathbb{R}^+$. By continuity of θ_{d_1,m_1} in d_1, I_b^0 is closed and I_b^1 is open in $\mathbb{R}^+$. Moreover,

$$I_b^1 \neq \varnothing \quad \text{if and only if} \quad L_U < b < S_U. \tag{3.15}$$

Indeed, if $d_1' \in I_b^1 \neq \varnothing$, then $L_U < b$ and $(m_2 - b\theta_{d_1',m_1})(x_0) > 0$ for some $x_0 \in \overline{\Omega}$. Hence

$$b < \frac{m_2(x_0)}{\theta_{d_1',m_1}(x_0)} < S_U.$$

On the other hand, if $L_U < b < S_U$, then there exists some $d_1'' > 0$ and $y_0 \in \overline{\Omega}$ such that

$$(m_2 - b\theta_{d_1'',m_1})(y_0) > 0 \quad \text{and} \quad \int_\Omega (m_2 - b\theta_{d_1'',m_1}) < 0,$$

i.e., $d_1'' \in I_b^1 \neq \varnothing$. This finishes the proof of (3.15).

We now claim that I_b admits the following decomposition:

$$\begin{cases} I_b = \varnothing & \text{if } b \leqslant L_U, \\ I_b = I_b^0 \cup I_b^1 \subset \mathbb{R}^+ & \text{if } L_U < b < S_U, \\ I_b = I_b^0 = \mathbb{R}^+ & \text{if } b \geqslant S_U. \end{cases} \tag{3.16}$$

To finish the proof of (3.16), it suffices to show that if $S_U < \infty$ and $b \geqslant S_U$, then $I_b = I_b^0 = \mathbb{R}^+$. By the definition of S_U in (3.1), we deduce that

$$m_2 - b\theta_{d_1,m_1} \leqslant 0 \text{ in } \Omega \text{ for all } d_1 > 0 \text{ and } b \geqslant S_U.$$

Hence to show that $I_b = I_b^0 = \mathbb{R}^+$, it suffices to show that $m_2 - b\theta_{d_1,m_1} \not\equiv 0$ for any $d_1 > 0$ and $b \geqslant S_U$. This is obviously true if $b > S_U$. If $m_1 \equiv$ const, then $m_2 \not\equiv$ const by our assumption and $\theta_{d_1,m_1} \equiv m_1 \equiv$ const for all $d_1 > 0$; if $m_2 \equiv$ const, then $m_1 \not\equiv$ const by our assumption and $\theta_{d_1,m_1} \not\equiv$ const for any $d_1 > 0$. Hence it suffices to prove that $m_2 - b\theta_{d_1,m_1} \not\equiv 0$ for any $d_1 > 0$ for the case that $b = S_U$ and both m_1 and m_2 are nonconstant. Assume for contradiction that $m_2 - S_U\,\theta_{d_1',m_1} \equiv 0$ for some $d_1' > 0$. Then the definition of S_U in (3.1) implies that

$$\frac{m_2}{\theta_{d_1',m_1}} \equiv \text{const} \quad \text{and} \quad \frac{m_2}{\theta_{d_1',m_1}} \geqslant \sup_{\overline{\Omega}} \frac{m_2}{\theta_{d_1,m_1}} \text{ for all } d_1 > 0.$$

Hence $\theta_{d_1',m_1} - \theta_{d_1,m_1} \leqslant (\not\equiv) 0$ on $\overline{\Omega}$ for all $d_1 \neq d_1'$. However, this is impossible since $\overline{\theta_{d_1,m_1}}$ cannot attain its global minimum at some finite d_1' by Lemma 2.5 and (1.6). This finishes the proofs of (3.16). Hence by (3.16) and Proposition 2.2(iv),

$$\begin{gathered} b \geqslant S_U \Rightarrow \mu_1(d_2, m_2 - b\theta_{d_1,m_1}) > 0 \\ \text{for all } (d_1, d_2) \in \mathcal{Q}, \text{ i.e., } \Sigma_U = \mathcal{Q}. \end{gathered} \tag{3.17}$$

Now assume that $L_U < b < S_U$ and $d_1 \in I_b = I_b^0 \cup I_b^1$. If $d_1 \in I_b^0$, $\mu_1(d_2, m_2 - b\theta_{d_1,m_1}) > 0$ for all $d_2 > 0 = \widehat{d}_2^*(d_1)$ by Proposition 2.2(iv); If $d_1 \in I_b^1$, then $\mu_1(d_2, m_2 - b\theta_{d_1,m_1}) > 0$ for all $d_2 > 1/\lambda_1(m_2 - b\theta_{d_1,m_1}) = \widehat{d}_2^*(d_1)$ by Proposition 2.2(ii). Hence $(d_1, d_2) \in \Sigma_U$ if and only if $d_1 \in I_b$ and $d_2 > \widehat{d}_2^*(d_1)$. This finishes the proof of (3.10). Now it follows from (3.10) and (3.15) that when $b \in (L_U, S_U)$, $\Sigma_U \subsetneq \mathcal{Q}$ and furthermore, by Proposition 2.1(iv), Σ_U is strictly monotonically increasing in $b \in (L_U, S_U)$. This finishes the proof of Theorem 3.3(i).

The proof of Theorem 3.3(ii) is similar to that of Theorem 3.3(i) and is thus omitted.

We now prove Theorem 3.3(iii). If $b \leqslant L_U$, then $\int_\Omega (m_2 - b\theta_{d_1,m_1}) \geqslant 0$ for all $d_1 > 0$. Hence by Proposition 2.2(i), $\mu_1(d_2, m_2 - b\theta_{d_1,m_1}) \leqslant 0$ for all $(d_1, d_2) \in \mathcal{Q}$ and $\mu_1(d_2, m_2 - b\theta_{d_1,m_1}) = 0$ (i.e., $(d_1, d_2) \in \Sigma_{U,0}$) if and only if $b = L_U$ and $m_2 \equiv L_U\, \theta_{d_1,m_1}$. This implies that if $b < L_U$, then $\Sigma_{U,0} = \varnothing$. Thus it remains to show for the case $b = L_U$ that, if there exists some $d_1^* > 0$ such that $m_2 \equiv L_U\, \theta_{d_1^*,m_1}$, then it is unique. Indeed, if $m_1 \not\equiv$ const and such d_1^* exists, then the equation satisfied by $\theta_{d_1^*,m_1}$ implies that

$$d_1^* \equiv -\frac{\theta_{d_1^*,m_1}(m_1 - \theta_{d_1^*,m_1})}{\Delta\theta_{d_1^*,m_1}} \equiv -\frac{m_2(L_U m_1 - m_2)}{L_U \Delta m_2},$$

which is obviously unique; if $m_1 \equiv$ const, then $m_2 \not\equiv$ const by our assumption and $\theta_{d_1,m_1} \equiv m_1$ for all $d_1 > 0$, which implies that such d_1^* does not exist and $\Sigma_{U,0} = \varnothing$. If $b \geqslant S_U$, then it follows from (3.17) that $\Sigma_{U,0} = \varnothing$. Hence to finish the proof of Theorem 3.3(iii), it only remains to prove the case $L_U < b < S_U$. By Theorem 3.3(i), when $L_U < b < S_U$, $\varnothing \neq \Sigma_U \subsetneq \mathcal{Q}$. Thus $\varnothing \neq \partial\Sigma_U \subset \Sigma_{U,0}$. Now assume that $(d_1', d_2') \in \Sigma_{U,0} \setminus \partial\Sigma_U$. We claim that $m_2 - b\theta_{d_1',m_1} \equiv 0$. Indeed, if $m_2 - b\theta_{d_1',m_1} \not\equiv 0$, then it follows from $\mu_1(d_1', m_2 - b\theta_{d_1',m_1}) = 0$ and Proposition 2.2(i)(iv) that $\int_\Omega (m_2 - b\theta_{d_1',m_1}) < 0$ and $m_2 - b\theta_{d_1',m_1}$ changes sign in Ω. Then by Propositions 2.1(iii) and 2.2(ii), $1/d_2' = \lambda_1(m_2 - b\theta_{d_1',m_1})$. Hence Proposition 2.2(ii) implies that, for all $d_2 > d_2'$, $\mu_1(d_2, m_2 - b\theta_{d_1',m_1}) > 0$, i.e., $(d_1', d_2) \in \Sigma_U$. This implies that $(d_1', d_2') \in \partial\Sigma_U$, which is a contradiction to $(d_1', d_2') \in \Sigma_{U,0} \setminus \partial\Sigma_U$. Hence $m_2 - b\theta_{d_1',m_1} \equiv 0$. By similar arguments as in the case $b = L_U$ above, we can show that such d_1' with the property that $m_2 \equiv b\theta_{d_1',m_1}$, if it exists, must be unique. This finishes the proof of Theorem 3.3(iii).

The proof of Theorem 3.3(iv) is similar to that of Theorem 3.3(iii) and is thus omitted. $\square$

Now we are ready to state the following result that characterizes the global dynamics of (1.10) under condition (M) for all $(b, c) \in \Xi$. Note that Theorem 1.3 is a special case of the following result.

THEOREM 3.4. *Assume that* (M) *holds and that* $(b, c) \in \Xi$. *Then we have the following mutually disjoint decomposition of* $\mathcal{Q}$:

$$\mathcal{Q} = (\Sigma_U \cup \Sigma_{U,0} \setminus \Pi) \cup (\Sigma_V \cup \Sigma_{V,0} \setminus \Pi) \cup \Sigma_- \cup \Pi. \tag{3.18}$$

Moreover, the following hold for (1.10):

(i) *For all* $(d_1, d_2) \in (\Sigma_U \cup \Sigma_{U,0} \setminus \Pi)$, $(\theta_{d_1,m_1}, 0)$ *is globally asymptotically stable.*
(ii) *For all* $(d_1, d_2) \in (\Sigma_V \cup \Sigma_{V,0} \setminus \Pi)$, $(0, \theta_{d_2,m_2})$ *is globally asymptotically stable.*

(iii) *For all* $(d_1, d_2) \in \Sigma_-$, (1.10) *has a unique coexistence steady state that is globally asymptotically stable.*

(iv) *For all* $(d_1, d_2) \in \Pi$, $\theta_{d_1,m_1} \equiv c\theta_{d_2,m_2}$ *and* (1.10) *has a compact global attractor consisting of a continuum of steady states*

$$\{(\xi\theta_{d_1,m_1}, (1-\xi)\theta_{d_1,m_1}/c) \mid \xi \in [0,1]\}$$

connecting the two semitrivial steady states.

PROOF. We first prove Theorem 3.4 assuming that $(b, c) \in \Xi_1$, where Ξ_1 is defined in (3.4).

By Lemma 2.3,

$$\Sigma_U = \{(d_1, d_2) \mid \mu_1(d_2, m_2 - b\theta_{d_1,m_1}) > 0\},$$
$$\Sigma_V = \{(d_1, d_2) \mid \mu_1(d_1, m_1 - c\theta_{d_2,m_2}) > 0\}.$$

Multiplying the equation of $\theta_{d,g}$ in (1.2) by $\theta_{d,g}$ and integrating over Ω, we obtain that

$$d\int_\Omega |\nabla\theta_{d,g}|^2 = \int_\Omega \theta_{d,g}^2(g - \theta_{d,g}). \tag{3.19}$$

Choosing θ_{d_1,m_1} as a test function in the variational characterization for $\mu_1(d_1, m_1 - c\theta_{d_2,m_2})$, by (2.2) and (3.19), we obtain that

$$\begin{aligned}\mu_1(d_1, m_1 - c\theta_{d_2,m_2}) &\le \frac{d_1 \int_\Omega |\nabla\theta_{d_1,m_1}|^2 + \int_\Omega (c\theta_{d_2,m_2} - m_1)\theta_{d_1,m_1}^2}{\int_\Omega \theta_{d_1,m_1}^2} \\ &= \frac{\int_\Omega (c\theta_{d_2,m_2} - \theta_{d_1,m_1})\theta_{d_1,m_1}^2}{\int_\Omega \theta_{d_1,m_1}^2}.\end{aligned} \tag{3.20}$$

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

$$\begin{aligned}\mu_1(d_2, m_2 - b\theta_{d_1,m_1}) &\le \frac{d_2 \int_\Omega |\nabla\theta_{d_2,m_2}|^2 + \int_\Omega (b\theta_{d_1,m_1} - m_2)\theta_{d_2,m_2}^2}{\int_\Omega \theta_{d_2,m_2}^2} \\ &= \frac{\int_\Omega (b\theta_{d_1,m_1} - \theta_{d_2,m_2})\theta_{d_2,m_2}^2}{\int_\Omega \theta_{d_2,m_2}^2}.\end{aligned} \tag{3.21}$$

Since $(b,c) \in \Xi_1$, i.e., $bc \leqslant 1$, combining (3.20) and (3.21) together, we have

$$
\begin{aligned}
&\mu_1(d_1, m_1 - c\theta_{d_2,m_2}) \int_\Omega \theta^2_{d_1,m_1} + c^3\mu_1(d_2, m_2 - b\theta_{d_1,m_1}) \int_\Omega \theta^2_{d_2,m_2} \\
&\leqslant \int_\Omega (c\theta_{d_2,m_2} - \theta_{d_1,m_1})\theta^2_{d_1,m_1} + \int_\Omega (bc\theta_{d_1,m_1} - c\theta_{d_2,m_2})c^2\theta^2_{d_2,m_2} \\
&\leqslant -\int_\Omega (c\theta_{d_2,m_2} - \theta_{d_1,m_1})^2 (c\theta_{d_2,m_2} + \theta_{d_1,m_1}) \le 0,
\end{aligned} \tag{3.22}
$$

where the last two inequalities are actually equalities if and only if $\theta_{d_1,m_1} \equiv c\theta_{d_2,m_2}$ and $bc = 1$. Therefore (1.13) and (3.22) imply that

$$
(\Sigma_U \cup \Sigma_{U,0} \setminus \Pi) \cap (\Sigma_V \cup \Sigma_{V,0} \setminus \Pi) = \varnothing. \tag{3.23}
$$

This proves the mutually disjoint decomposition of $\mathcal{Q}$ in (3.18). Moreover, when $\mu_1(d_2, m_2 - b\theta_{d_1,m_1}) = \mu_1(d_1, m_1 - c\theta_{d_2,m_2}) = 0$, i.e., $(d_1, d_2) \in \Pi$, it forces the last two inequalities in (3.22) to become equalities. Hence

$$
\Pi \subset \{(d_1, d_2) \mid \theta_{d_1,m_1} \equiv c\theta_{d_2,m_2} \text{ and } bc = 1\}. \tag{3.24}
$$

On the other hand, assuming that $\theta_{d_1,m_1} \equiv c\theta_{d_2,m_2}$ and $bc = 1$, then it is easy to verify that $\mu_1(d_2, m_2 - b\theta_{d_1,m_1}) = 0$ with θ_{d_2,m_2} being its corresponding eigenfunction and $\mu_1(d_1, m_1 - c\theta_{d_2,m_2}) = 0$ with θ_{d_1,m_1} being its corresponding eigenfunction. This together with (3.24) implies that

$$
\Pi = \{(d_1, d_2) \mid \theta_{d_1,m_1} \equiv c\theta_{d_2,m_2} \text{ and } bc = 1\}. \tag{3.25}
$$

We claim that to prove Theorem 3.4(i)–(iii), it suffices to show the following:

(S) For all $(d_1, d_2) \in \mathcal{Q} \setminus \Pi$, every coexistence steady state of (1.10), if it exists, is linearly stable.

To see the claim, we first assume that (S) is true. By (3.18) and (3.23), for any $(d_1, d_2) \in \mathcal{Q} \setminus \Pi$, there are the following five possibilities:

(i) $(d_1, d_2) \in \Sigma_U$; i.e., $(\theta_{d_1,m_1}, 0)$ is linearly stable and $(0, \theta_{d_2,m_2})$ is linearly unstable.
(ii) $(d_1, d_2) \in \Sigma_V$; i.e., $(\theta_{d_1,m_1}, 0)$ is linearly unstable and $(0, \theta_{d_2,m_2})$ is linearly stable.
(iii) $(d_1, d_2) \in \Sigma_-$; i.e., both $(\theta_{d_1,m_1}, 0)$ and $(0, \theta_{d_2,m_2})$ are linearly unstable.
(iv) $(d_1, d_2) \in \Sigma_{U,0} \setminus \Pi$; i.e., $(0, \theta_{d_2,m_2})$ is linearly unstable and the first eigenvalue of the linearized system around $(\theta_{d_1,m_1}, 0)$ is 0.
(v) $(d_1, d_2) \in \Sigma_{V,0} \setminus \Pi$; i.e., $(\theta_{d_1,m_1}, 0)$ is linearly unstable and the first eigenvalue of the linearized system around $(0, \theta_{d_2,m_2})$ is 0.

By Lemma 2.4, we have the following conclusion: $(\theta_{d_1,m_1}, 0)$ is globally asymptotically stable in case (i), $(0, \theta_{d_2,m_2})$ is globally asymptotically stable in case (ii), and in case (iii) there exists a unique coexistence steady state that is globally asymptotically stable. Next we claim that one can rule out the possibility of coexistence in cases (iv) and (v); hence $(\theta_{d_1,m_1},0)$ is in fact globally asymptotically stable in case (iv) and $(0,\theta_{d_2,m_2})$ is in fact globally asymptotically stable in case (v) by Lemma 2.4. Assume for contradiction that in case (iv), there exists a coexistence steady state (U^*,V^*) of (1.10) with $(d_1,d_2)=(d_1^*,d_2^*)$ for some point $(d_1^*,d_2^*)\in(\Sigma_{U,0}\setminus\Pi)$; then

$$\mu_1(d_2^*,m_2-b\theta_{d_1^*,m_1})=0,\qquad \mu_1(d_1^*,m_1-c\theta_{d_2^*,m_2})<0, \tag{3.26}$$

and (U^*,V^*) satisfies the following system:

$$\begin{cases} d_1^*\Delta U^*+U^*(m_1(x)-U^*-c\,V^*)=0 & \text{in }\Omega,\\ d_2^*\Delta V^*+V^*(m_2(x)-b\,U^*-V^*)=0 & \text{in }\Omega,\\ \partial_\nu U^*=\partial_\nu V^*=0 & \text{on }\partial\Omega. \end{cases} \tag{3.27}$$

Define

$$F:(\tilde b,\tilde c,U,V)\mapsto \begin{pmatrix} d_1^*\Delta U+U(m_1(x)-U-\tilde c\,V)\\ d_2^*\Delta V+V(m_2(x)-\tilde b\,U-V)\end{pmatrix}, \tag{3.28}$$

where $(\tilde b,\tilde c,U,V)\in(0,\infty)\times(0,\infty)\times X\times X$ and

$$X:=\{\phi\in H^1(\Omega)\mid \partial_\nu\phi=0\text{ on }\partial\Omega\}.$$

(Note that here b and c are any two fixed numbers that have been chosen satisfying $(b,c)\in\Xi_1$, i.e., $bc\leqslant 1$, while $\tilde b$ and $\tilde c$ denote the first two parameters or variables of the map F.) Since all eigenvalues of the linearized system of F at (b,c,U^*,V^*) are positive by (S), i.e.,

$$\left.\frac{\partial F(\tilde b,\tilde c,U,V)}{\partial(U,V)}\right|_{(\tilde b,\tilde c,U,V)=(b,c,U^*,V^*)} \text{ is invertible,}$$

and $F(b,c,U^*,V^*)=0$, by the implicit function theorem for every pair of $(\tilde b,\,\tilde c)$ in a neighborhood of (b,c), $F(\tilde b,\tilde c,U,V)=0$ has a solution close to (U^*,V^*). In particular, this is true for some (b',c') satisfying that

$$b'>b,\quad 0<c'<c,\quad\text{and}\quad b'c'\leqslant 1. \tag{3.29}$$

However, let us consider the following system:

$$\begin{cases} U_t=d_1^*\Delta U+U(m_1(x)-U-c'\,V) & \text{in }\Omega\times\mathbb{R}^+,\\ V_t=d_2^*\Delta V+V(m_2(x)-b'\,U-V) & \text{in }\Omega\times\mathbb{R}^+,\\ \partial_\nu U=\partial_\nu V=0 & \text{on }\partial\Omega\times\mathbb{R}^+. \end{cases} \tag{3.30}$$

Note that the two semitrivial steady states of (3.30) are again $(\theta_{d_1^*,m_1},0)$ and $(0,\theta_{d_2^*,m_2})$. Hence by (3.26), our choices of b' and c' in (3.29), and Proposition 2.2(iv), we must have

$$\mu_1(d_2^*,m_2-b'\theta_{d_1^*,m_1})>0\quad\text{and}\quad \mu_1(d_1^*,m_1-c'\theta_{d_2^*,m_2})<0.$$

In other words, $(\theta_{d_1^*,m_1},0)$ is linearly stable and $(0,\theta_{d_2^*,m_2})$ is linearly unstable for system (3.30). Hence applying our conclusion for case (i) in the above argument to system (3.30) at the point (d_1^*,d_2^*), we deduce that $(\theta_{d_1^*,m_1},0)$ is globally asymptotically stable, which is a contradiction since we have shown that $F(b',c',U,V)=0$ has a solution close to (U^*,V^*). This finishes the proof of case (iv). For case (v), the arguments are similar to those for case (iv) and are thus omitted.

Therefore, it suffices to prove (S) and Theorem 3.4(iv). Indeed, let (U,V) be any coexistence steady state of (1.10); then $U,V>0$ on $\bar\Omega$. Let λ_1 be the principal eigenvalue of the linearized elliptic system at (U,V) and (Φ_1,Ψ_1) be the corresponding eigenfunction satisfying $\Phi_1>0>\Psi_1$ on $\bar\Omega$ and normalized such that $\|\Phi_1\|^2_{L^2(\Omega)}+\|\Psi_1\|^2_{L^2(\Omega)}=1$. By direct calculation, using the equation satisfied by U and Φ_1, we obtain that

$$d_1\nabla\cdot\left(U^2\nabla\frac{\Phi_1}{U}\right)=U^2(\Phi_1+c\Psi_1)-\lambda_1U\Phi_1.$$

Multiplying both sides by Φ_1^2/U^2 and integrating over Ω, we have

$$-2d_1\int_\Omega U\Phi_1\left|\nabla\frac{\Phi_1}{U}\right|^2=\int_\Omega\Phi_1^2(\Phi_1+c\Psi_1)-\lambda_1\int_\Omega\frac{\Phi_1^3}{U}.$$

Similarly, we can derive the following identity:

$$-2d_2\int_\Omega V\Psi_1\left|\nabla\frac{\Psi_1}{V}\right|^2=\int_\Omega\Psi_1^2(b\,\Phi_1+\Psi_1)-\lambda_1\int_\Omega\frac{\Psi_1^3}{V}.$$

Combining the above two identities together, we obtain that

$$\begin{aligned}-\lambda_1\int_\Omega\left(\frac{\Phi_1^3}{U}-c^3\frac{\Psi_1^3}{V}\right)&=-2d_1\int_\Omega U\Phi_1\left|\nabla\frac{\Phi_1}{U}\right|^2+2d_2c^3\int_\Omega V\Psi_1\left|\nabla\frac{\Psi_1}{V}\right|^2\\&\quad-\int_\Omega\Phi_1^2(\Phi_1+c\Psi_1)+\int_\Omega c^2\Psi_1^2(bc\,\Phi_1+c\Psi_1)\\&\leqslant-2d_1\int_\Omega U\Phi_1\left|\nabla\frac{\Phi_1}{U}\right|^2+2d_2c^3\int_\Omega V\Psi_1\left|\nabla\frac{\Phi_1}{V}\right|^2\\&\quad-\int_\Omega(\Phi_1-c\Psi_1)(\Phi_1+c\Psi_1)^2\leqslant 0,\end{aligned}\tag{3.31}$$

where we used the fact that $bc\leqslant 1$ and $\Phi_1>0>\Psi_1$ on $\bar\Omega$. (3.31) implies that $\lambda_1\geq 0$ and that $\lambda_1=0$ (i.e., the last two inequalities in (3.31) become equalities) if and only if

$$bc=1,\quad \Phi_1/U\equiv\text{const},\quad \Psi_1/V\equiv\text{const},\quad\text{and}\quad \Phi_1\equiv -c\Psi_1.\tag{3.32}$$

By (3.32), $U \equiv \eta V$ for some $\eta > 0$, i.e., (U, V) satisfies the following system:

$$\begin{cases} d_1 \Delta U + U(m_1(x) - (1 + c/\eta)U) = 0 & \text{in } \Omega, \\ d_2 \Delta V + V(m_2(x) - (b\eta + 1)V) = 0 & \text{in } \Omega, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega. \end{cases}$$

By uniqueness of positive solution to (1.2), this implies that

$$(1 + c/\eta)U \equiv \theta_{d_1,m_1} \quad \text{and} \quad (b\eta + 1)V \equiv \theta_{d_2,m_2}.$$

Therefore,

$$\frac{\theta_{d_1,m_1}}{\theta_{d_2,m_2}} \equiv \frac{1 + c/\eta}{b\eta + 1} \cdot \frac{U}{V} \equiv \frac{1}{b} = c.$$

Hence (3.32) implies that

$$bc = 1 \quad \text{and} \quad \theta_{d_1,m_1} \equiv c\theta_{d_2,m_2}; \tag{3.33}$$

i.e., $(d_1, d_2) \in \Pi$. This finishes the proof of claim (S) and hence that of Theorem 3.4(i)–(iii).

It only remains to prove Theorem 3.4(iv). Let $(d_1, d_2) \in \Pi$ and (U, V) be a corresponding coexistence steady state of (1.10). We claim that $U/V \equiv$ const. Let λ_1 be the principal eigenvalue of the linearized elliptic system at (U, V) and (Φ_1, Ψ_1) be the corresponding eigenfunction satisfying $\Phi_1 > 0 > \Psi_1$ on $\overline{\Omega}$ and normalized such that $\|\Phi_1\|^2_{L^2(\Omega)} + \|\Psi_1\|^2_{L^2(\Omega)} = 1$. Then to prove the claim, it suffices to show that (3.32) holds. Assume that (3.32) is not true for contradiction, then (3.31) in the proof of (S) implies that $\lambda_1 > 0$. By similar arguments used for case (iv) during the proofs of Theorem 3.4(i)–(iii) above, we may perturb system (1.10) by replacing (b, c) by (b', c'), which is sufficiently close to (b, c) and satisfies that

$$b' > b, \quad 0 < c' < c, \quad \text{and} \quad b'c' \leqslant 1.$$

Then by the implicit function theorem, this new perturbed system again has a coexistence steady state that is close to (U, V). However, now for the new system at (d_1, d_2), the semitrivial steady state $(\theta_{d_1,m_1}, 0)$ is linearly stable and the other one $(0, \theta_{d_2,m_2})$ is linearly unstable. Therefore by Theorem 3.4(i), $(\theta_{d_1,m_1}, 0)$ is globally asymptotically stable for the new system, which is a contradiction to the existence of the coexistence steady state that is close to (U, V). Hence (3.32) must hold, i.e., $U/V \equiv$ const. This immediately implies that $(U, V) = (\xi\theta_{d_1,m_1}, (1 - \xi)\theta_{d_1,m_1}/c)$ for some $\xi \in (0, 1)$.

Consequently, we conclude that for any $(d_1, d_2) \in \Pi$, the set of equilibria of (1.10) is

$$\{(0, 0)\} \cup \{(\xi\theta_{d_1,m_1}, (1 - \xi)\theta_{d_1,m_1}/c) \mid \xi \in [0, 1]\}, \tag{3.34}$$

with $(0, 0)$ being a repeller by Lemma 2.3. Now by exactly the same arguments in the second part of the proof of theorem 3 in [18], it follows that every solution of (1.10) converges to a single equilibrium $(\xi\theta_{d_1,m_1}, (1-\xi)\theta_{d_1,m_1}/c)$ for some $\xi \in [0,1]$. This finishes the proof of Theorem 3.4(iv).[1]

Therefore by (3.3), we have finished the proof of Theorem 3.4 if $S_U = \infty$ and $S_V = \infty$. In view of Theorem 3.3(i) and (ii), it only remains to show that

(a) if $S_U < \infty$, then $(\theta_{d_1,m_1}, 0)$ is globally asymptotically stable for all $(b,c) \in \{(b,c) \mid b \geqslant S_U \text{ and } c \leqslant 1/S_U\} \setminus \Xi_1$;
(b) if $S_V < \infty$, then $(0, \theta_{d_2,m_2})$ is globally asymptotically stable for all $(b,c) \in \{(b,c) \mid c \geqslant S_V \text{ and } b \leqslant 1/S_V\} \setminus \Xi_1$.

We now prove case (a). The proof of case (b) is similar and thus omitted. To prove case (a), it suffices to show that for any $(b,c) \in \{(b,c) \mid b \geqslant S_U \text{ and } c \leqslant 1/S_U\} \setminus \Xi_1$, (1.10) has no coexistence steady state for any $(d_1,d_2) \in \mathcal{Q}$. Then case (a) follows from Theorem 3.3(i) and Lemma 2.4. Assume for contradiction that there exists some $(b^*,c^*) \in \{(b,c) \mid b \geqslant S_U \text{ and } c \leqslant 1/S_U\} \setminus \Xi_1$ such that (1.10) with $(d_1,d_2) = (d_1^*, d_2^*) \in \mathcal{Q}$ has a coexistence steady state (U^*, V^*). We now consider the following system:

$$
\begin{cases}
U_t = d_1^* \Delta U + U(m_1(x) - U - c^* V) & \text{in } \Omega \times \mathbb{R}^+, \\
V_t = d_2^* \Delta V + V(m_2(x) - S_U U - V) & \text{in } \Omega \times \mathbb{R}^+, \\
\partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\
U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{in } \Omega.
\end{cases}
\tag{3.35}
$$

Since $c^* \leqslant 1/S_U$, $c^* S_U \leqslant 1$, i.e., $(S_U, c^*) \in \Xi_1$, which implies that the semitrivial steady state $(\theta_{d_1^*,m_1}, 0)$ of (3.35) is globally asymptotically stable by the previous argument and Theorem 3.3(i). On the other hand, we claim that

(S′) (U^*, V^*) is an upper solution to (3.35) and $(\varepsilon\varphi_1, \theta_{d_2^*,m_2})$ is a lower solution to (3.35) for all ε sufficiently small, where $\varphi_1 > 0$ is the principal eigenfunction of $\mu_1^* := \mu_1(d_1^*, m_1 - c^*\theta_{d_2^*,m_2})$ normalized such that $\max_\Omega \varphi_1 = 1$, and

$$
d_1^* \Delta\varphi_1 + (m_1 - c^*\theta_{d_2^*,m_2})\varphi_1 + \mu_1^*\varphi_1 = 0 \ \text{ in } \Omega, \quad \partial_\nu\varphi_1 = 0 \ \text{ on } \partial\Omega. \tag{3.36}
$$

We now prove claim (S′). It is easy to check that (U^*, V^*) is an upper solution to (3.35), as it satisfies that

$$
\begin{aligned}
& d_1^* \Delta U^* + U^*(m_1 - U^* - c^* V^*) = 0 && \text{in } \Omega, \\
& d_2^* \Delta V^* + V^*(m_2 - S_U U^* - V^*) = (b^* - S_U) U^* V^* > 0 && \text{in } \Omega.
\end{aligned}
$$

[1] Note that we do not need the condition in [18, theorem 3] that the reaction terms in (1.10) are analytic, which was used to construct the analytic continuum of steady state solutions in alternative (i). In our case, since we have already explicitly found the set of all equilibria of (1.10) (e.g, (3.34)), which obviously satisfies alternative (i) in [18, theorem 3], all we need here is to apply their proof for the conclusion that the compact continuum of steady state solutions is a global attractor.

Since $c^* \leqslant 1/S_U < L_V$ by Lemma 3.2(iii), Theorem 3.3(ii) and (iv) implies that $\Sigma_V = \Sigma_{V,0} = \varnothing$ for system (3.35), i.e., $\mu_1^* < 0$. Hence by (3.36), $(\varepsilon\varphi_1, \theta_{d_2^*,m_2})$ satisfies that

$$\begin{aligned} d_1^*\Delta(\varepsilon\varphi_1) + \varepsilon\varphi_1(m_1 - \varepsilon\varphi_1 - c^*\theta_{d_2^*,m_2}) &= \varepsilon\varphi_1(-\mu_1^* - \varepsilon\varphi_1) > 0 \quad \text{in } \Omega, \\ d_2^*\Delta\theta_{d_2^*,m_2} + \theta_{d_2^*,m_2}(m_2 - S_U\varepsilon\varphi_1 - \theta_{d_2^*,m_2}) &= -\varepsilon S_U\varphi_1\theta_{d_2^*,m_2} < 0 \quad \text{in } \Omega, \end{aligned}$$

for all ε sufficiently small. This finishes the proof of claim (S$'$).

Since $U^* \geqslant \varepsilon\varphi_1$ and $V^* \leqslant \theta_{d_2^*,m_2}$, and they all satisfy the zero-flux boundary condition, by the upper-solution and lower-solution method [30], we see that (3.35) has a positive solution, which is a contradiction since we have shown that the semitrivial steady state $(\theta_{d_1^*,m_1}, 0)$ of (3.35) is globally asymptotically stable. This finishes the proof of case (a) and hence Theorem 3.4. □

Next we characterize how the sets Σ_- and Π change when we vary b and c for all $(b,c) \in \Xi$, as a complement to Theorem 3.3.

THEOREM 3.5. *Assume that* (M) *holds and that at least one of m_1 and m_2 is nonconstant. Let L_U, S_U, L_V, and S_V be defined as in* (3.1) *and* (3.2) *and* $(b,c) \in \Xi$. *Then the following hold for* (1.10):

(i) *For Σ_- we have the following characterization*:

$$\Sigma_- = \begin{cases} \varnothing & \text{if } b \geqslant S_U \text{ or } c \geqslant S_V, \\ \mathcal{Q} & \text{if } b < L_U \text{ and } c < L_V, \\ \mathcal{Q} \setminus \Sigma_{U,0} & \text{if } b = L_U \text{ and } c < L_V, \\ \mathcal{Q} \setminus \Sigma_{V,0} & \text{if } b < L_U \text{ and } c = L_V, \\ \mathcal{Q} \setminus (\Sigma_{U,0} \cup \Sigma_{V,0}) & \text{if } b = L_U \text{ and } c = L_V, \\ \mathcal{Q} \setminus (\Sigma_U \cup \Sigma_{U,0} \cup \Sigma_{V,0}) & \text{if } L_U < b < S_U \text{ and } c \leqslant L_V, \\ \mathcal{Q} \setminus (\Sigma_V \cup \Sigma_{V,0} \cup \Sigma_{U,0}) & \text{if } b \leqslant L_U \text{ and } L_V < c < S_U, \\ \mathcal{Q} \setminus (\Sigma_U \cup \Sigma_{U,0} \cup \Sigma_V \cup \Sigma_{V,0}) & \text{if } L_U < b < S_U \text{ and } L_V < c < S_V, \end{cases} \tag{3.37}$$

and $\Sigma_- = \varnothing$ if and only if the first case holds or $m_1 \equiv cm_2$ and $bc = 1$ in the last case.

(ii) *For Π, we have the following characterization*:

$$\Pi = \{(d_1,d_2) \in \mathcal{Q} \mid \theta_{d_1,m_1} \equiv c\theta_{d_2,m_2} \text{ and } bc = 1\}.$$

Hence, $\Pi \neq \varnothing$ if and only if there exists $(d_1,d_2) \in \mathcal{Q}$ such that $\theta_{d_1,m_1} \equiv c\theta_{d_2,m_2}$ and $bc = 1$.

In all statements above, in case $L_U = 0$ (resp., $L_V = 0$), we simply do not need the statements involving $b \leqslant 0$ (resp., $c \leqslant 0$), and in case $S_U = \infty$ (resp., $S_V = \infty$), we simply do not need the statements involving $b \geqslant \infty$ (resp., $c \geqslant \infty$).

Except for that $\Sigma_- = \varnothing$ if $m_1 \equiv cm_2$ and $bc = 1$ in the last statement of Theorem 3.5(i), which follows from Theorem 3.6 below, everything else in Theorem

3.5(i) follows from Lemma 3.2, Theorem 3.3, and the mutually disjoint decomposition of $\mathcal{Q}$ in (3.18). Theorem 3.5(ii) follows from the proof of Theorem 3.4. (See e.g., (3.25).)

At the end of this section, we state and prove the following result under the general condition (M). Note that Theorem 1.4 is a consequence of Lemma 3.2 and this result.

THEOREM 3.6. *Assume that* (M) *holds and that at least one of m_1 and m_2 is nonconstant. Let L_U, S_U, L_V, and S_V be defined as in* (3.1) *and* (3.2) *and* $(b, c) \in \Xi$. *Then Theorem* 1.4(i)–(vi) *holds, where in case* $L_U = 0$ (*resp.,* $L_V = 0$)*, we simply do not need the statements involving* $b \leqslant 0$ (*resp.,* $c \leqslant 0$)*, and in case* $S_U = \infty$ (*resp.,* $S_V = \infty$)*, we simply do not need the statements involving* $b \geqslant \infty$ (*resp.,* $c \geqslant \infty$).

PROOF. We start the proof with the comment that Theorem 3.6(i)–(vi) below refers to Theorem 1.4(i)–(vi), respectively.

It is easy to check that Theorem 3.6(i)–(iii) and (v)–(vi) follow from Theorems 3.3 and 3.5(excluding the last statement in Theorem 3.5(i)).

Therefore it only remains to prove Theorem 3.6(iv). Since $L_U < b$, $L_V < c$, and $(b, c) \in \Xi$, by Lemma 3.2(ii) and (iii), $L_U < b < S_U$, $L_V < c < S_V$, and $bc \le 1$. By Theorem 3.3(i) and (ii), both $\Sigma_U, \Sigma_V \neq \varnothing$ and thus $\Sigma_{U,0}, \Sigma_{V,0} \neq \varnothing$. We now claim that

$$\Sigma_- = \varnothing \quad \text{if and only if} \quad m_1 \equiv cm_2 \text{ and } bc = 1. \tag{3.38}$$

First we show that

$$\Sigma_- \neq \varnothing \text{ if } b\overline{m_1} \neq \overline{m_2} \text{ or } c\overline{m_2} \neq \overline{m_1} \text{ or } bc < 1. \tag{3.39}$$

We now prove (3.39) assuming that $b\overline{m_1} \neq \overline{m_2}$. The proof of (3.39) for the case $c\overline{m_2} \neq \overline{m_1}$ is similar and is thus omitted. It suffices to consider the following two cases:

(i) $L_U < b < S_U$ and $b\overline{m_1} < \overline{m_2}$, and
(ii) $L_U < b < S_U$ and $\overline{m_2} < b\overline{m_1}$.

For case (i), since $\overline{m_2} > b\overline{m_1} \geqslant 0$, $b > L_U > 0$. Therefore by Lemma 2.5, $\int_\Omega (m_2 - b\theta_{d_1,m_1}) > 0$ for all d_1 large. The latter implies that $\mu_1(d_2, m_2 - b\theta_{d_1,m_1}) < 0$ for all d_1 large and $d_2 > 0$ by Proposition 2.2(i); i.e., $(\theta_{d_1,m_1}, 0)$ is linearly unstable. Since $c < S_V$, there exists some $d_2' > 0$ such that $(m_1 - c\theta_{d_2',m_2})(x_0) > 0$ for some $x_0 \in \overline{\Omega}$. If $\int_\Omega (m_1 - c\theta_{d_2',m_2}) \geqslant 0$, then $\mu_1(d_1, m_1 - c\theta_{d_2',m_2}) < 0$ for all $d_1 > 0$ by Proposition 2.2(i); if $\int_\Omega (m_1 - c\theta_{d_2',m_2}) < 0$, then as $m_1 - c\theta_{d_2',m_2}$ changes signs in Ω, $\mu_1(d_1, m_1 - c\theta_{d_2',m_2}) < 0$ for all d_1 sufficiently large by Proposition 2.2(ii). Therefore, $(d_1, d_2') \in \Sigma_-$ for all d_1 large, i.e., $\Sigma_- \neq \varnothing$. This finishes the proof for case (i).

For case(ii), $\overline{m_2} < b\overline{m_1}$ implies that $c\overline{m_2} < \overline{m_1}$ since $bc \le 1$. As $L_V < c < S_V$, by alternative symmetry, the proof for case (ii) is similar to that for case (i) and is thus omitted. To finish the proof of (3.39), it only remains to show that $\Sigma_- \neq \varnothing$ if $bc < 1$, $b\overline{m_1} = \overline{m_2}$ and $c\overline{m_2} = \overline{m_1}$. We now assume that $bc < 1$ and $\overline{m_1} = \overline{m_2} = 0$. Then both m_1 and m_2 change sign in Ω. By Theorem 3.3(iii)–(iv), this implies that $\Sigma_{U,0} = \partial\Sigma_U$ and $\Sigma_{V,0} = \partial\Sigma_V$. Assume that $\Sigma_- = \varnothing$ for contradiction; then by the mutually disjoint decomposition of $\mathcal{Q}$ in (3.18) and the fact that both Σ_U and Σ_V are nonempty and open in $\mathcal{Q}$, we must have $\partial\Sigma_U = \partial\Sigma_V$. Hence $\Pi \supset \partial\Sigma_U \neq \varnothing$, which is a contradiction to (3.25) since $bc < 1$. This finishes the proof of (3.39).

Hence to finish the proof of (3.38), it suffices to show that

$$\text{if } bc = 1,\ b\overline{m_1} = \overline{m_2}, \text{ and } c\overline{m_2} = \overline{m_1}, \text{ then } \Sigma_- \neq \varnothing \text{ if and only if } m_1 \equiv cm_2. \tag{3.40}$$

We now prove (3.40). Assuming that $bc = 1$, $b\overline{m_1} = \overline{m_2}$, and $c\overline{m_2} = \overline{m_1}$, let $(U(x,t), V(x,t))$ be the solution to (1.10). Denote

$$\begin{gathered} \widetilde{U} := U, \quad \widetilde{V} := cV, \\ \widetilde{d}_1 := d_1, \quad \widetilde{d}_2 := c\,d_2, \quad \widetilde{m}_1 := m_1, \quad \text{and} \quad \widetilde{m}_2 := cm_2. \end{gathered} \tag{3.41}$$

Then $(\widetilde{U}, \widetilde{V})$ satisfies the following system:

$$\begin{cases} \widetilde{U}_t = \widetilde{d}_1 \Delta \widetilde{U} + \widetilde{U}(\widetilde{m}_1 - \widetilde{U} - \widetilde{V}) & \text{in } \Omega \times \mathbb{R}^+, \\ c\,\widetilde{V}_t = \widetilde{d}_2 \Delta \widetilde{V} + \widetilde{V}(\widetilde{m}_2 - \widetilde{U} - \widetilde{V}) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu \widetilde{U} = \partial_\nu \widetilde{V} = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \end{cases} \tag{3.42}$$

with $\int_\Omega \widetilde{m}_1 = \int_\Omega \widetilde{m}_2$. It is easy to verify that there is a one-to-one correspondence between steady state solutions of (3.42) and steady state solutions of (1.10) via the transformation (3.41). Moreover, their linear stability properties are also preserved during the transformation.

To see this, first by similar arguments used for the proof of Lemma 2.3, it is easy to check that the linear stability of the trivial steady state $(0,0)$ and the two semitrivial steady states $(\theta_{\widetilde{d}_1,\widetilde{m}_1}, 0)$ and $(0, \theta_{\widetilde{d}_2,\widetilde{m}_2})$ of system (3.42) are determined by the sign of $\min\{\mu_1(\widetilde{d}_1, \widetilde{m}_1), \mu_1(\widetilde{d}_2, \widetilde{m}_2)\}$, $\mu_1(\widetilde{d}_2, \widetilde{m}_2 - \theta_{\widetilde{d}_1,\widetilde{m}_1})$, and $\mu_1(\widetilde{d}_1, \widetilde{m}_1 - \theta_{\widetilde{d}_2,\widetilde{m}_2})$, respectively. In particular, $(0,0)$ is always linearly unstable for any $\widetilde{d}_1, \widetilde{d}_2 > 0$. Now for a given coexistence steady state $(\widetilde{U}, \widetilde{V})$ of (3.42), linearizing the steady state problem of (3.42) at $(\widetilde{U}, \widetilde{V})$, we have

$$\begin{cases} \widetilde{d}_1 \Delta \widetilde{\Phi} + \widetilde{\Phi}(\widetilde{m}_1 - \widetilde{U} - \widetilde{V}) - \widetilde{U}(\widetilde{\Phi} + \widetilde{\Psi}) + \widetilde{\lambda}\widetilde{\Phi} = 0 & \text{in } \Omega, \\ \widetilde{d}_2 \Delta \widetilde{\Psi} + \widetilde{\Psi}(\widetilde{m}_2 - \widetilde{U} - \widetilde{V}) - \widetilde{V}(\widetilde{\Phi} + \widetilde{\Psi}) + c\,\widetilde{\lambda}\widetilde{\Psi} = 0 & \text{in } \Omega, \\ \partial_\nu \widetilde{\Phi} = \partial_\nu \widetilde{\Psi} = 0 & \text{on } \partial\Omega. \end{cases} \tag{3.43}$$

Thus

$$\widetilde{\Phi} = \Phi, \quad \widetilde{\Psi} = c\Psi, \quad \text{and} \quad \widetilde{\lambda} = \lambda,$$

where (U,V) is the coexistence steady state of (1.10) corresponding to $(\widetilde{U},\widetilde{V})$ defined via (3.41), and λ and (Φ,Ψ) are the eigenvalue and corresponding eigenfunction of (2.1) when we linearize the steady state problem of (1.10) at (U,V). We now define the following sets for system (3.42):

$$
\begin{aligned}
\widetilde{\Sigma}_U &:= \{(\tilde{d}_1,\tilde{d}_2)\in \mathcal{Q} \mid (\theta_{\tilde{d}_1,\tilde{m}_1},0) \text{ is linearly stable}\},\\
\widetilde{\Sigma}_V &:= \{(\tilde{d}_1,\tilde{d}_2)\in \mathcal{Q} \mid (0,\theta_{\tilde{d}_2,\tilde{m}_2}) \text{ is linearly stable}\},\\
\widetilde{\Sigma}_- &:= \{(\tilde{d}_1,\tilde{d}_2)\in \mathcal{Q} \mid \text{both } (\theta_{\tilde{d}_1,\tilde{m}_1},0) \text{ and } (0,\theta_{\tilde{d}_2,\tilde{m}_2}) \text{ are linearly unstable}\},\\
\widetilde{\Sigma}_{U,0} &:= \{(\tilde{d}_1,\tilde{d}_2)\in \mathcal{Q} \mid \mu_1(\tilde{d}_2,\tilde{m}_2-\theta_{\tilde{d}_1,\tilde{m}_1})=0\},\\
\widetilde{\Sigma}_{V,0} &:= \{(\tilde{d}_1,\tilde{d}_2)\in \mathcal{Q} \mid \mu_1(\tilde{d}_1,\tilde{m}_1-\theta_{\tilde{d}_2,\tilde{m}_2})=0\},\\
\widetilde{\Pi} &:= \widetilde{\Sigma}_{U,0}\cap\widetilde{\Sigma}_{V,0}.
\end{aligned}
\tag{3.44}
$$

Then by the one-to-one correspondence between $\widetilde{K}$ for (3.42) and K for (1.10) via the transformation (3.41), where $K\in\{\Sigma_U,\Sigma_{U,0},\Sigma_V,\Sigma_{V,0},\Sigma_-,\Pi\}$, and similar arguments used in the proof of Theorem 3.4, we obtain the following mutually disjoint decomposition of $\mathcal{Q}$:

$$
\mathcal{Q} = (\widetilde{\Sigma}_U\cup\widetilde{\Sigma}_{U,0}\setminus\widetilde{\Pi})\cup(\widetilde{\Sigma}_V\cup\widetilde{\Sigma}_{V,0}\setminus\widetilde{\Pi})\cup\widetilde{\Sigma}_-\cup\widetilde{\Pi}
\tag{3.45}
$$

and

$$
\widetilde{\Pi} = \{(\tilde{d}_1,\tilde{d}_2)\in\mathcal{Q} \mid \theta_{\tilde{d}_1,\tilde{m}_1}\equiv\theta_{\tilde{d}_2,\tilde{m}_2}\}.
\tag{3.46}
$$

Hence to prove (3.40), it suffices to show that

$$
\widetilde{\Sigma}_- = \varnothing \quad \text{if and only if} \quad \tilde{m}_1\equiv\tilde{m}_2.
\tag{3.47}
$$

If $\tilde{m}_1\equiv\tilde{m}_2$, then by Theorem A, $\widetilde{\Sigma}_-=\varnothing$. Now assume that $\widetilde{\Sigma}_-=\varnothing$; then by theorems 1.1 and 5.1 in [12], both $\tilde{m}_1$ and $\tilde{m}_2$ are nonconstant. This together with (1.6), Theorem 3.3(iii)–(iv), and the fact that $\int_\Omega\tilde{m}_1=\int_\Omega\tilde{m}_2$ imply that

$$
\partial\widetilde{\Sigma}_U=\widetilde{\Sigma}_{U,0} \quad\text{and}\quad \partial\widetilde{\Sigma}_V=\widetilde{\Sigma}_{V,0}.
\tag{3.48}
$$

Since $\widetilde{\Sigma}_U,\widetilde{\Sigma}_V\neq\varnothing$ and both $\widetilde{\Sigma}_U$ and $\widetilde{\Sigma}_V$ are relatively open in $\mathcal{Q}$, by (3.45) and (3.48), $\widetilde{\Sigma}_-=\varnothing$ implies that

$$
\partial\widetilde{\Sigma}_U=\partial\widetilde{\Sigma}_V=\widetilde{\Pi}.
$$

Let $(\tilde{d}_1,\tilde{d}_2)\in\widetilde{\Pi}=\mathcal{Q}\setminus(\widetilde{\Sigma}_U\cup\widetilde{\Sigma}_V)$; then by (3.46),

$$
\theta_{\tilde{d}_1,\tilde{m}_1}\equiv\theta_{\tilde{d}_2,\tilde{m}_2}.
$$

Hence by (1.2),

$$
\frac{\tilde{m}_1-\theta_{\tilde{d}_1,\tilde{m}_1}}{\tilde{d}_1}\equiv\frac{\tilde{m}_2-\theta_{\tilde{d}_2,\tilde{m}_2}}{\tilde{d}_2}.
$$

Integrating the above identity over Ω, we obtain that

$$
(\tilde{d}_1-\tilde{d}_2)\int_\Omega\tilde{m}_1=(\tilde{d}_1-\tilde{d}_2)\int_\Omega\theta_{\tilde{d}_1,\tilde{m}_1}.
\tag{3.49}
$$

Thus by (1.6), $\tilde{d}_1 = \tilde{d}_2$, which in turn implies that $\tilde{m}_1 \equiv \tilde{m}_2$. Therefore we finish the proof of (3.47) and hence (3.38). Moreover, when $\tilde{m}_1 \equiv \tilde{m}_2$, $\tilde{\Sigma}_U = \{(\tilde{d}_1, \tilde{d}_2) \mid \tilde{d}_2 > \tilde{d}_1\}$, $\tilde{\Sigma}_V = \{(\tilde{d}_1, \tilde{d}_2) \mid \tilde{d}_2 < \tilde{d}_1\}$, and $\partial\tilde{\Sigma}_U = \partial\tilde{\Sigma}_V = \tilde{\Pi} = \{(\tilde{d}_1, \tilde{d}_2) \mid \tilde{d}_2 = \tilde{d}_1\}$. This implies that when $m_1 \equiv cm_2$ and $bc = 1$, $\Sigma_U = \{(d_1, d_2) \mid d_2 > d_1/c\}$, $\Sigma_V = \{(d_1, d_2) \mid d_2 < d_1/c\}$, and $\Sigma_{U,0} = \Sigma_{V,0} = \Pi = \{(d_1, d_2) \mid d_2 = d_1/c\}$. This completes the proof of Theorem 3.6(iv). □

4 Concluding Remarks and Further Extensions

For the general 2×2 Lotka-Volterra competition-diffusion system (1.10), under the very mild condition (M), we have completely classified, for all $(b, c) \in \Xi$, its global dynamics in terms of the diffusion rates (d_1, d_2). As a special case, when the two species are competing for exactly the same resources with exactly the same growth rates, we have established Lou's conjecture, which asserts that, competition-exclusion becomes possible, even for weak competition, for appropriate diffusion rates if and only if at least one of the species' competition ability exceeds a threshold value. Furthermore, our result in this special case—Theorem 1.1—connects Lou's conjecture with the well-known phenomenon "the slower diffuser always prevails!" and hopefully has put them in perspective.

Our main results for general resources/growth rates, namely, Theorems 1.3 and 1.4, or rather, Theorems 3.3 through 3.6, seem to indicate that, as far as the distribution of resources is concerned, the more "heterogeneous" (measured by the quantity $E(m)$) the better!

In fact, our method applies to an even more general competition system in which the diffusion rates are allowed to be spatially dependent. More precisely, we consider the following system:

$$(4.1)\qquad \begin{cases} U_t = \nabla\cdot(d_1(x)\nabla U) + U(m_1(x) - U - c\,V) & \text{in } \Omega\times\mathbb{R}^+,\\ V_t = \nabla\cdot(d_2(x)\nabla V) + V(m_2(x) - b\,U - V) & \text{in } \Omega\times\mathbb{R}^+,\\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega\times\mathbb{R}^+,\\ U(x,0) = U_0(x),\quad V(x,0) = V_0(x) & \text{in } \Omega, \end{cases}$$

where $d_i(x) \in C^{1,\alpha}(\bar{\Omega})$ and $d_i(x) \geqslant d_0 > 0$ for $i = 1, 2$.

For population models in which the species' diffusion rates are spatially dependent, see [6,8] and references therein for more discussions. Let $g(x) \in C^{\alpha}(\bar{\Omega})(\alpha \in (0,1))$ with $\int_\Omega g \geqslant 0$ and $g \not\equiv 0$. Consider the following elliptic problem:

$$(4.2)\qquad \nabla\cdot(d(x)\nabla\Theta) + \Theta(g(x) - \Theta) = 0 \text{ in } \Omega,\quad \partial_\nu\Theta = 0 \text{ on } \partial\Omega.$$

By similar arguments as in the proofs of existence and uniqueness results for (1.2) in [6], we can show that (4.2) has a unique positive solution, which we denote by $\Theta_{d,m}$. (See also [8] for a study of (4.2) for the case $\int_\Omega g > 0$.) Moreover, $\Theta_{d,m}$ is globally asymptotically stable. Hence system (4.1) has two semitrivial steady states $(\Theta_{d_1,m_1}, 0)$ and $(\Theta_{d_2,m_2}, 0)$.

Let $\tilde{\mu}_1(d(x), q(x))$ be the principal eigenvalue of the following eigenvalue problem:

$$\nabla \cdot (d(x)\nabla\phi) + q(x)\phi + \mu\phi = 0 \ \text{ in } \Omega, \quad \partial_\nu \phi = 0 \ \text{ on } \partial\Omega. \tag{4.3}$$

where $d(x) \in C^{1,\alpha}(\bar{\Omega})$ with $d(x) > d_0 > 0$. Then $\tilde{\mu}_1(d(x), q(x))$ admits the following variational characterization:

$$\tilde{\mu}_1(d(x), q(x)) = \inf_{\psi \in H_1(\Omega)\setminus\{0\}} \frac{\int_\Omega (d(x)|\nabla\psi|^2 - q(x)\psi^2)dx}{\int_\Omega \psi^2}. \tag{4.4}$$

Similar to the arguments used in Section 2, we can show that the linear stability of $(\Theta_{d_1,m_1}, 0)$ is determined by the sign of $\tilde{\mu}_1(d_2(x), m_2 - b\,\Theta_{d_1,m_1})$. In other words, $(\Theta_{d_1,m_1}, 0)$ is linearly stable (resp., unstable) if the principal eigenvalue $\tilde{\mu}_1(d_2(x), m_2 - b\,\Theta_{d_1,m_1}) > 0$ (resp., $\tilde{\mu}_1(d_2(x), m_2 - b\,\Theta_{d_1,m_1}) < 0$). The linear stability of $(0, \Theta_{d_2,m_2})$ can be determined accordingly by the sign of $\tilde{\mu}_1(d_1(x), m_1 - c\,\Theta_{d_2,m_2})$. By similar arguments as in the proof of Theorem 3.4, we can show that the global dynamics of (4.1) can be characterized as follows:

THEOREM 4.1. *Assume that* (M) *holds and* $bc \leqslant 1$. *Then*

$$\tilde{\mu}_1(d_1(x), m_1 - c\,\Theta_{d_2,m_2}) \int_\Omega \Theta^2_{d_1,m_1} + c^3 \tilde{\mu}_1(d_2(x), m_2 - b\,\Theta_{d_1,m_1}) \int_\Omega \Theta^2_{d_2,m_2} \leqslant 0, \tag{4.5}$$

where equality holds if and only if

$$bc = 1 \quad \text{and} \quad \Theta_{d_1,m_1} \equiv c\Theta_{d_2,m_2}. \tag{4.6}$$

Moreover, the following hold for (4.1):

(i) *If* $\tilde{\mu}_1(d_2(x), m_2 - b\Theta_{d_1,m_1}) \geqslant 0$ *and* $\tilde{\mu}_1(d_1(x), m_1 - c\Theta_{d_2,m_2}) < 0$, *then* $(\Theta_{d_1,m_1}, 0)$ *is globally asymptotically stable.*

(ii) *If* $\tilde{\mu}_1(d_2(x), m_2 - b\Theta_{d_1,m_1}) < 0$ *and* $\tilde{\mu}_1(d_1(x), m_1 - c\Theta_{d_2,m_2}) \geqslant 0$, *then* $(0, \Theta_{d_2,m_2})$ *is globally asymptotically stable.*

(iii) *If* $\tilde{\mu}_1(d_2(x), m_2 - b\Theta_{d_1,m_1}) < 0$ *and* $\tilde{\mu}_1(d_1(x), m_1 - c\Theta_{d_2,m_2}) < 0$, *then there exists a unique coexistence steady state that is globally asymptotically stable.*

(iv) *If* $\tilde{\mu}_1(d_2(x), m_2 - b\Theta_{d_1,m_1}) = \tilde{\mu}_1(d_1(x), m_1 - c\Theta_{d_2,m_2}) = 0$, *then* (1.10) *has a compact global attractor consisting of a continuum of steady states* $\{(\xi\Theta_{d_1,m_1}, (1-\xi)\Theta_{d_1,m_1}/c) \mid \xi \in [0,1]\}$ *connecting the two semitrivial steady states.*

In particular, if $m_i \equiv \text{const}$ $(i = 1, 2)$, then Theorem 4.1 reduces to Theorem 3.1; i.e., the global dynamics of (4.1) does not depend on the diffusion rates $d_1(x)$ and $d_2(x)$. Therefore, it is interesting although not entirely surprising that, even for system (4.1) where spatial dependence of diffusion is incorporated into the model, still, “diffusion-driven exclusion” is possible only when spatial heterogeneity is present in the distributions of resources or the intrinsic growth rates.

We point out that, with mild modifications, our method in this paper also applies to the case when the Neumann boundary condition in (4.1) is replaced by the following boundary condition:

$$U + \beta(x)\partial_\nu U = V + \beta(x)\partial_\nu V = 0 \quad \text{on } \partial\Omega \times \mathbb{R}^+,$$

where $\beta(x) \in C^\alpha(\partial\Omega)$ ($\alpha \in (0,1)$) and $\beta(x) \geq 0$ on $\partial\Omega$. Note that when $\beta(x) \equiv 0$, it reduces to the Dirichlet boundary condition, which represents the case that the environment surrounding the habitat Ω is lethal.

Finally, we remark that many of the results in this paper also generalize to the case when competition coefficients depend on spatial variables. We will report our progress in this direction in a forthcoming paper.

Acknowledgment. Research supported in part by the National Science Foundation and the Natural Science Foundation of China, the “111” Project, and the Recruitment Program of Global Experts in China. Part of the work was done while the first author was at the National Center for Theoretical Sciences, National Tsing-Hua University in Taiwan. The authors are grateful to the two reviewers for their suggestions, which have improved the exposition of the paper.

Bibliography

[1] Brown, K. J.; Lin, S. S. On the existence of positive eigenfunctions for an eigenvalue problem with indefinite weight function. *J. Math. Anal. Appl.* **75** (1980), no. 1, 112–120. doi:10.1016/0022-247X(80)90309-1

[2] Brown, P. N. Decay to uniform states in ecological interactions. *SIAM J. Appl. Math.* **38** (1980), no. 1, 22–37. doi:10.1137/0138002

[3] Cantrell, R. S.; Cosner, C. Diffusive logistic equations with indefinite weights: population models in disrupted environments. *Proc. Roy. Soc. Edinburgh Sect. A* **112** (1989), no. 3-4, 293–318. doi:10.1017/S030821050001876X

[4] Cantrell, R. S.; Cosner, C. Diffusive logistic equations with indefinite weights: population models in disrupted environments. II. *SIAM J. Math. Anal.* **22** (1991), no. 4, 1043–1064. doi:10.1137/0522068

[5] Cantrell, R. S.; Cosner, C. On the effects of spatial heterogeneity on the persistence of interacting species. *J. Math. Biol.* **37** (1998), no. 2, 103–145. doi:10.1007/s002850050122

[6] Cantrell, R. S.; Cosner, C. *Spatial ecology via reaction-diffusion equations.* Wiley Series in Mathematical and Computational Biology. Wiley, Chichester, 2003. doi:10.1002/0470871296

[7] Dockery, J.; Hutson, V.; Mischaikow, K.; Pernarowski, M. The evolution of slow dispersal rates: a reaction diffusion model. *J. Math. Biol.* **37** (1998), no. 1, 61–83. doi:10.1007/s002850050120

[8] Flores, G.; Mischaikow, K. Selection of slow diffusion in a reaction diffusion model: limiting cases. *Rocky Mountain J. Math.* **34** (2004), no. 4, 1299–1324. doi:10.1216/rmjm/1181069801

[9] Gilbarg, D.; Trudinger, N. S. *Elliptic partial differential equations of second order.* Second edition. Grundlehren der mathematischen Wissenschaften, 224. Springer, Berlin, 1983. doi:10.1007/978-3-642-61798-0

[10] Goh, B. S. Global stability in many-species systems. *The American Naturalist* **111** (1977), 135–143.

[11] Hastings, A. Global stability in Lotka-Volterra systems with diffusion. *J. Math. Biol.* **6** (1978), no. 2, 163–168. doi:10.1007/BF02450786
[12] He, X.; Ni, W.-M. The effects of diffusion and spatial variation in Lotka-Volterra competition-diffusion system I: Heterogeneity vs. homogeneity. *J. Differential Equations* **254** (2013), no. 2, 528–546. doi:10.1016/j.jde.2012.08.032
[13] He, X.; Ni, W.-M. The effects of diffusion and spatial variation in Lotka-Volterra competition-diffusion system II: The general case. *J. Differential Equations* **254** (2013), no. 10, 4088–4108. doi:10.1016/j.jde.2013.02.009
[14] He, X.; Ni, W.-M. Global dynamics of the Lotka-Volterra competition-diffusion system with equal amount of total resources, II. Preprint.
[15] He, X.; Ni, W.-M. Global dynamics of the Lotka-Volterra competition-diffusion system with equal amount of total resources, III. Preprint.
[16] Hess, P. *Periodic-parabolic boundary value problems and positivity.* Pitman Research Notes in Mathematics Series, 247. Longman, Harlow, UK; Wiley, New York, 1991.
[17] Hirsch, M. W. Stability and convergence in strongly monotone dynamical systems. *J. Reine Angew. Math.* **383** (1988), 1–53. doi:10.1515/crll.1988.383.1
[18] Hirsch, M. W.; Smith, H. L. Asymptotically stable equilibria for monotone semiflows. *Discrete Contin. Dyn. Syst.* **14** (2006), no. 3, 385–398.
[19] Holmes, E. E.; Lewis, M. A.; Banks, J. E.; Veit, R. R. Partial differential equations in ecology: spatial interactions and population dynamics. *Ecology* **75** (1994), 17–29.
[20] Hsu, S. B. Limiting behavior for competing species. *SIAM J. Appl. Math.* **34** (1978), no. 4, 760–763. doi:10.1137/0134064
[21] Hsu, S.-B. A survey of constructing Lyapunov functions for mathematical models in population biology. *Taiwanese J. Math.* **9** (2005), no. 2, 151–173.
[22] Hutson, V.; Lou, Y.; Mischaikow, K. Spatial heterogeneity of resources versus Lotka-Volterra dynamics. *J. Differential Equations* **185** (2002), no. 1, 97–136. doi:10.1006/jdeq.2001.4157
[23] Hutson, V.; Lou, Y.; Mischaikow, K. Convergence in competition models with small diffusion coefficients. *J. Differential Equations* **211** (2005), no. 1, 135–161. doi:10.1016/j.jde.2004.06.003
[24] Kreĭn, M. G.; Rutman, M. A. Linear operators leaving invariant a cone in a Banach space. *Uspehi Matem. Nauk (N. S.)* **3** (1948), no. 1(23), 3–95.
[25] Lam, K.-Y.; Ni, W.-M. Uniqueness and complete dynamics in heterogeneous competition-diffusion systems. *SIAM J. Appl. Math.* **72** (2012), no. 6, 1695–1712. doi:10.1137/120869481
[26] Li, F.; Wang, L.; Wang, Y. On the effects of migration and inter-specific competitions in steady state of some Lotka-Volterra model. *Discrete Contin. Dyn. Syst. Ser. B 15* (2011), no. 3, 669–686. doi:10.3934/dcdsb.2011.15.669
[27] Lou, Y. On the effects of migration and spatial heterogeneity on single and multiple species. *J. Differential Equations* **223** (2006), no. 2, 400–426. doi:10.1016/j.jde.2005.05.010
[28] Lou, Y. Some challenging mathematical problems in evolution of dispersal and population dynamics. *Tutorials in mathematical biosciences. IV*, 171–205. Lecture Notes in Mathematics, 1922. Springer, Berlin, 2008. doi:10.1007/978-3-540-74331-6_5
[29] Ni, W.-M. *The mathematics of diffusion.* CBMS-NSF Regional Conference Series in Applied Mathematics, 82. Society for Industrial and Applied Mathematics (SIAM), Philadelphia, 2011. doi:10.1137/1.9781611971972
[30] Pao, C. V. *Nonlinear parabolic and elliptic equations*. Plenum Press, New York, 1992.
[31] Senn, S.; Hess, P. On positive solutions of a linear elliptic eigenvalue problem with Neumann boundary conditions. *Math. Ann.* **258** (1981/82), no. 4, 459–470. doi:10.1007/BF01453979
[32] Shigesada, N.; Kawasaki, K. *Biological invasions: theory and practice.* Oxford Series in Ecology and Evolution. Oxford University Press, Oxford–New York–Tokyo, 1997.

[33] Smith H. *Monotone dynamical systems: an introduction to the theory of competitive and cooperative systems*. Mathematical Surveys and Monographs, 41. American Mathematical Society, Providence, R.I., 1995.

[34] Zhou, L.; Pao, C. V. Asymptotic behavior of a competition-diffusion system in population dynamics. *Nonlinear Anal.* **6** (1982), no. 11, 1163–1184. doi:10.1016/0362-546X(82)90028-1

XIAOQING HE
Center for Partial Differential Equations
East China Normal University
200241 Minhang, Shanghai
CHINA
E-mail: xqhe@cpde.ecnu.edu.cn

WEI-MING NI
Center for Partial Differential Equations
East China Normal University
200241 Minhang, Shanghai
CHINA
and
School of Mathematics
University of Minnesota
Minneapolis, MN 55455
USA
E-mail: weiming.ni@gmail.com

Received June 2014.