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

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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]:

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

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; \(\Omega\), the habitat, is a bounded smooth domain in \(\mathbb{R}^N\); \(d_1, d_2 > 0\) are the...
dispersal rates of $U$ and $V$, respectively; $\Delta = \sum_{i=1}^{N} \frac{\partial^2}{\partial x_i^2}$ is the usual Laplace operator; and $\partial_{\nu} = \nu \cdot \nabla$, where $\nu$ 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 $\int_{\Omega} g \geq 0$ and $g \neq 0$. We denote by $\theta_{d,g}$ the unique positive solution of:

\begin{equation}
(1.2) \quad d \Delta \theta + \theta(g(x) - \theta) = 0 \quad \text{in } \Omega, \quad \partial_{\nu} \theta = 0 \quad \text{on } \partial \Omega.
\end{equation}

(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 $0 < m(x) \neq \text{const}$ 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{equation}
(1.3) \quad \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}
\end{equation}

with

\begin{equation}
(1.4) \quad 0 < b, c < 1,
\end{equation}
where $b$ and $c$ represent interspecific competition coefficients, while both intra-
specific competition coefficients in (1.3) are normalized to 1. Again assuming that
$m(x) \in C^\alpha(\Omega)$ ($\alpha \in (0, 1)$), $m(x) > 0$ on $\bar{\Omega}$, and $m \neq \text{const}$, we define

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

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

(1.6) \[ \int_\Omega \theta_{d,m} > \int_\Omega m \text{ for all } d > 0. \]

This implies that

$$ E(m) > 1. $$

Furthermore, define

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

where

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

Then Lou’s results may be described as follows.

**Theorem B (27).** Assume that $0 < m(x) \neq \text{const}$ on $\bar{\Omega}$ and $m(x) \in C^\alpha(\bar{\Omega})$
($\alpha \in (0, 1)$) in (1.3). Then

$$ \Sigma_U \neq \emptyset \text{ if and only if } b > \frac{1}{E(m)}. $$

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 $0 < m(x) \neq \text{const}$ on $\bar{\Omega}$ and $m(x) \in C^\alpha(\bar{\Omega})$
($\alpha \in (0, 1)$) 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 $(d_1, d_2) \notin \Sigma_U$ and $d_1 \leq d_2$.

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 $\bar{c} > 0$ such
that for all $c < \bar{c}$ and $b \in (0, 1)$, $(\theta_{d_1,m}, 0)$ is globally asymptotically stable for
all $(d_1, d_2) \in \Sigma_U$ (i.e., global stability holds on the boundary of $\Sigma_U$ 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 $(d_1, d_2) \notin \Sigma_U$. 
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 $bc \leq 1$, 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 $\Sigma_U$ defined in (1.7), we define the following subsets of $Q$ for system (1.3):

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

(1.8) $$
\Sigma_- := \{(d_1, d_2) \in Q \mid \text{both } (\theta_{d_1,m}, 0) \text{ and } (0, \theta_{d_2,m}) \text{ are linearly unstable}\}.
$$

Furthermore, define

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

(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 $0 < m(x) \neq \text{const on } \Omega$ and $m(x) \in C^a(\Omega)$ ($a \in (0, 1)$). Then the following statements hold for (1.3):

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

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

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

(iv) If $1/E(m) < b < S(m)$, $1/E(m) < c < S(m)$, $bc \leq 1$, and $(b, c) \neq (1, 1)$, then $\Sigma_U$, $\Sigma_V$, $\Sigma_- \neq \emptyset$ and $Q = \Sigma_U \cup \Sigma_V \cup \Sigma_-$. 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;

(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 $\Sigma_- = \emptyset$, $\Sigma_U = \{(d_1, d_2) \mid d_2 > d_1\}$, 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 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:

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

(1.10)

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:

\[(M^+) \quad m_i(x) \in C^\alpha(\overline{\Omega}) \ (\alpha \in (0, 1)), \quad m_i > 0 \quad \text{on } \overline{\Omega}, \ i = 1, 2.\]

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 \(Q\), the first quadrant of the \(d_1d_2\)-plane, for system (1.10):

\[
\begin{align*}
\Sigma_U := \{(d_1, d_2) \in Q \mid (\theta_{d_1,m_1}, 0) \text{ is linearly stable}\}, \\
\Sigma_V := \{(d_1, d_2) \in Q \mid (0, \theta_{d_2,m_2}) \text{ is linearly stable}\}, \\
\Sigma_- := \{(d_1, d_2) \in Q \mid \text{both } (\theta_{d_1,m_1}, 0) \text{ and } (0, \theta_{d_2,m_2}) \\
\text{are linearly unstable}\},
\end{align*}
\]

(1.11)

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 \(Q\), we also need to consider those \((d_1, d_2) \in Q\) such that one (or both) of the two semifitial 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

\[
\begin{align*}
d \Delta \psi + h(x) \psi + \mu \psi &= 0 \quad \text{in } \Omega, \\
\partial_\nu \psi &= 0 \quad \text{on } \partial \Omega.
\end{align*}
\]

(1.12)

In particular, we call \(\mu_1(d, h)\) the first eigenvalue of (1.12).
Now we are ready to define the following subsets of $Q$ where at least one of the two semitrivial steady states is neutrally stable:

\[
\Sigma_{U,0} := \{(d_1, d_2) \in Q \mid \mu_1(d_2, m_2 - b\theta_{d_1, m_1}) = 0\},
\]

\[
\Sigma_{V,0} := \{(d_1, d_2) \in Q \mid \mu_1(d_1, m_1 - c\theta_{d_2, m_2}) = 0\},
\]

\[
\Pi := \Sigma_{U,0} \cap \Sigma_{V,0}.
\]

Define

\[
L_U := \frac{m_2}{m_1} \cdot \frac{1}{E(m_1)}, \quad S_U := \sup_{d_1 > 0} \sup_{\Omega} \frac{m_2}{\theta_{d_1, m_1}},
\]

\[
L_V := \frac{m_1}{m_2} \cdot \frac{1}{E(m_2)}, \quad S_V := \sup_{d_2 > 0} \sup_{\Omega} \frac{m_1}{\theta_{d_2, m_2}}
\]

and

\[
\Xi := \{(b, c) \mid b, c > 0 \text{ and } bc \leq 1\} \cup \{(b, c) \mid 0 < c \leq \frac{1}{S_U}\} \cup \{(b, c) \mid 0 < b \leq \frac{1}{S_V}\}.
\]

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

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

\[
Q = (\Sigma_U \cup \Sigma_{U,0} \setminus \Pi) \cup (\Sigma_V \cup \Sigma_{V,0} \setminus \Pi) \cup \Sigma_- \cup \Pi.
\]

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 \((M^7)\) holds, at least one of \(m_1\) and \(m_2\) is nonconstant, and \((b, c) \in \Xi\). Then

\[
0 < L_U L_V < 1, \quad L_U S_V > 1, \quad L_V S_U > 1,
\]

and the following hold for (1.10):

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

(ii) If \(c \geq S_V\) and \(b \leq 1/S_V\), then \(Q = \Sigma_V\); 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 \(Q = \Sigma_{-}\); 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 \(Q = \Sigma_{-} \cup \Sigma_{U,0}\) where \(\Sigma_{U,0}\) may be empty; if \(b < L_U\) and \(c = L_V\), then \(Q = \Sigma_{-} \cup \Sigma_{V,0}\) where \(\Sigma_{V,0}\) may be empty; if \(b = L_U\) and \(c = L_V\), then \(Q = \Sigma_{-} \cup \Sigma_{U,0} \cup \Sigma_{V,0}\), where \(\Sigma_{U,0} \cup \Sigma_{V,0}\) may be empty.

(iv) If \(L_U < b < S_U\) and \(c < L_V\), then \(\Sigma_{U,0} \cup \Sigma_{V,0} = \Sigma_{-} \neq \emptyset\). Moreover, \(\Sigma_{-} = \emptyset\) if and only if \(m_1 \equiv cm_2\) 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 \(\Sigma_{U,0} \cup \Sigma_{V,0} = \Sigma_{U,0} = \Pi = \emptyset\); 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 \(\Sigma_{V,0} \cup \Sigma_{U,0} = \Sigma_V = \emptyset\); if \(L_V < c < S_U\) 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 \((M^7)\) is relaxed. Note that the sets \(\Sigma_U\) and \(\Sigma_{U,0}\) are independent of \(c\) and the sets \(\Sigma_V\) and \(\Sigma_{V,0}\) are independent of \(b\). Denote by \(\overline{\Sigma_U}\) and \(\overline{\Sigma_V}\) the closure of \(\Sigma_U\) and \(\Sigma_V\) 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 \(m_i \neq \text{const}\) and \(m_i > 0\) on \(\Omega_i, i = 1, 2\). See Theorem [1.4].

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

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 \(m \neq s \theta_{d,m}\) for any \(s > 0\), it follows from the characterizations of \(\Sigma_{U,0}\) and \(\Sigma_{V,0}\) in Theorem [3.3] below that

\[
\Sigma_{U,0} = \partial \Sigma_U \quad \text{(i.e., } \Sigma_U \cup \Sigma_{U,0} = \Sigma_U),
\]

\[
\Sigma_{V,0} = \partial \Sigma_V \quad \text{(i.e., } \Sigma_V \cup \Sigma_{V,0} = \Sigma_V).
\]

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

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

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., \(L_V\)),

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

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 \(m \neq s \theta_{d,m}\) for any \(s > 0\), it follows from the characterizations of \(\Sigma_{U,0}\) and \(\Sigma_{V,0}\) in Theorem [3.3] below that

\[
\Sigma_{U,0} = \partial \Sigma_U \quad \text{(i.e., } \Sigma_U \cup \Sigma_{U,0} = \Sigma_U),
\]

\[
\Sigma_{V,0} = \partial \Sigma_V \quad \text{(i.e., } \Sigma_V \cup \Sigma_{V,0} = \Sigma_V).
\]

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

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

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., \(L_V\),

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

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 \(m \neq s \theta_{d,m}\) for any \(s > 0\), it follows from the characterizations of \(\Sigma_{U,0}\) and \(\Sigma_{V,0}\) in Theorem [3.3] below that

\[
\Sigma_{U,0} = \partial \Sigma_U \quad \text{(i.e., } \Sigma_U \cup \Sigma_{U,0} = \Sigma_U),
\]

\[
\Sigma_{V,0} = \partial \Sigma_V \quad \text{(i.e., } \Sigma_V \cup \Sigma_{V,0} = \Sigma_V).
\]

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

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

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 \( \Omega \), 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 \( \Sigma_U, \Sigma_{U,0}, \Sigma_V, \Sigma_{V,0}, \Sigma_{-}, \) and \( \Pi \) in the \( d_1d_2 \)-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:

\[
\text{(M)} \quad m_i(x) \in C^\alpha(\bar{\Omega}) \ (\alpha \in (0,1)), \quad \int_\Omega m_i \geq 0 \text{ and } m_i \neq 0 \ (i = 1, 2),
\]

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

\[
(U_1, V_1) \leq (U_2, V_2) \quad \text{if} \quad U_1 \leq U_2 \text{ and } V_1 \geq V_2 \text{ in } \Omega,
\]

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 \( U \geq 0 \) and \( V \geq 0 \) 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
\[
\begin{align*}
&d_1 \Delta \Phi + \Phi(m_1 - U - cV) - U(\Phi + c\Psi) + \lambda \Phi = 0 \quad \text{in } \Omega, \\
&d_2 \Delta \Psi + \Psi(m_2 - bU - V) - V(b \Phi + \Psi) + \lambda \Psi = 0 \quad \text{in } \Omega, \\
&\partial_v \Phi = \partial_v \Psi = 0 \quad \text{on } \partial \Omega.
\end{align*}
\]
When \((U, V)\) is a trivial or semitrivial steady state, we can characterize the sign of the principal eigenvalue \(\lambda_1\) 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., \(\lambda_1\) is simple and has the least real part among all eigenvalues of (2.1). Moreover, the corresponding eigenfunction \((\Phi_1, \Psi_1)\) of \(\lambda_1\) can be chosen to satisfy \(\Phi_1 > 0 > \Psi_1\) on \(\Omega\). We call a steady state \((U, V)\) of (1.10) linearly stable (resp., linearly unstable) if the principal eigenvalue \(\lambda_1\) 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 \(C(\Omega) \times C(\Omega)\) 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:
\[
\mu_1(d, h) = \inf_{\psi \in H_1(\Omega) \setminus \{0\}} \frac{\int_{\Omega} (d|\nabla \psi|^2 - h(x)\psi^2) dx}{\int_{\Omega} \psi^2}.
\]
To further characterize properties of \(\mu_1(d, h)\), we need to first introduce the following eigenvalue problem with indefinite weight:
\[
\begin{align*}
&\Delta \varphi + \lambda h(x) \varphi = 0 \quad \text{in } \Omega, \\
&\partial_v \varphi = 0 \quad \text{on } \partial \Omega,
\end{align*}
\]
where \(h \in L^\infty(\Omega)\) is nonconstant and could change sign in \(\Omega\). We say that \(\lambda\) 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
\begin{itemize}
  \item[(i)] \(\int_{\Omega} h = 0 \iff 0\) is the only principal eigenvalue,
  \item[(ii)] \(\int_{\Omega} h > 0 \iff \lambda_1(h) < 0\),
  \item[(iii)] \(\int_{\Omega} h < 0 \iff \lambda_1(h) > 0\),
  \item[(iv)] \(\lambda_1(h_1) > \lambda_1(h_2)\) if \(h_1 \leq h_2, h_1 \neq h_2\) a.e., and \(h_1, h_2\) both change sign.
\end{itemize}

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) \( \int_\Omega h > 0 \) and \( h \neq 0 \) \( \Rightarrow \mu_1(d, h) < 0 \) for all \( d > 0 \).

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

(iii) Assume that \( h \) is nonconstant. Then \( \mu_1(d, h) \) is strictly increasing and concave in \( d > 0 \). Moreover,

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

where \( \bar{h} \) is the average of \( h \).

(iv) \( \mu_1(d, h_1) < \mu_1(d, h_2) \) if \( h_1 \geq h_2 \) and \( h_1 \neq h_2 \). In particular \( \mu_1(d, h) > 0 \) if \( h \leq (\neq) 0 \).

The following lemma characterizes the linear stability of the trivial steady state \((0, 0)\) and the two semitrivial steady states \((d_1, m_1, 0)\) and \((0, d_2, m_2)\) 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 \( \theta_{d,j} \) as the unique positive solution of (1.2). We end this section with the following lemma, which summarizes some useful properties of \( \theta_{d,j} \).

**Lemma 2.5.** Assume that \( g(x) \in C^\alpha(\bar{\Omega}) \ (\alpha \in (0, 1)), \int_\Omega g \geq 0, \) and \( g \neq \text{const.} \). Then the following hold:
(i) $d \mapsto \theta_{d,g}$ is continuous from $\mathbb{R}^+ \to C^2(\overline{\Omega})$. 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 $\infty$ 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 $\Sigma_U$, $\Sigma_{U,0}$, $\Sigma_V$, $\Sigma_{V,0}$, $\Sigma_-$, and $\Pi$ 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:

\begin{align*}
(3.1) & \quad L_U := \inf_{d_1>0} \frac{m_2}{\theta_{d_1,m_1}} \in [0, \infty), \quad S_U := \sup_{d_1>0} \frac{m_2}{\theta_{d_1,m_1}} \in (0, \infty], \\
(3.2) & \quad L_V := \inf_{d_2>0} \frac{m_1}{\theta_{d_2,m_2}} \in [0, \infty), \quad S_V := \sup_{d_2>0} \frac{m_1}{\theta_{d_2,m_2}} \in (0, \infty].
\end{align*}

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

\begin{align*}
(3.3) & \quad \text{if } S_U = \infty \text{ and } S_V = \infty, \text{ then } \Xi = \Xi_1,
\end{align*}

where

\begin{align*}
(3.4) & \quad \Xi_1 := \{(b,c) \mid b, c > 0 \text{ and } bc \leq 1\}.
\end{align*}

Note that if both $m_1$ and $m_2$ are constant, then

\begin{align*}
L_U &= S_U = \frac{m_2}{m_1}, \quad L_V = S_V = \frac{m_1}{m_2}, \\
\Xi &= \{(b,c) \mid 0 < c \leq \frac{1}{m_2/m_1}\} \cup \{(b,c) \mid 0 < b \leq \frac{1}{m_2/m_1}\},
\end{align*}

respectively.
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 $m_2/m_1$ and $m_1/m_2$ 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 $(b, c) \in \mathcal{Z}$. Then the following statements hold for system (1.10):

(i) If $b \geq m_2/m_1$, $c \leq m_1/m_2$, 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 $c \geq m_1/m_2$, $b \leq m_2/m_1$, 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

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

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 $\frac{m_2}{m_1}$ (resp., $\frac{m_1}{m_2}$) 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 \(\text{(M)}\) 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,

$$L_U S_V = \inf_{d_1 > 0} \frac{m_2}{\theta_{d_1, m_1}} \cdot \sup_{d_2 > 0} \frac{m_1}{\theta_{d_2, m_2}}$$

$$= \frac{m_2}{\sup_{d_1 > 0} \theta_{d_1, m_1} \sup_{d_2 > 0} \theta_{d_2, m_2}} \geq \frac{m_2}{\sup_{d_1 > 0} \theta_{d_1, m_1} \sup_{d_2 > 0} \theta_{d_2, m_2}} \cdot \frac{m_1}{m_2} = \frac{\sup_\Omega m_1}{\sup_{d_1 > 0} \theta_{d_1, m_1}} \geq 1.$$ 

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 $\Omega$, which implies that the first inequality is strict. This finishes the proof of (ii). \(\square\)

To state our results concerning the global dynamics of (1.10) when at least one of $m_1$ and $m_2$ is nonconstant and $(b, c) \in \mathbb{Z}$, we first describe in the following how the sets $\Sigma_U$ and $\Sigma_{U,0}$ (resp., $\Sigma_V$ and $\Sigma_{V,0}$) change in the $d_1d_2$-plane when we vary $b$ (resp., $c$). To characterize the set $\Sigma_U$ in terms of $b > 0$, we define for each $b > 0$,

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

where

$$I_b^0 := \left\{ d_1 > 0 \mid m_2 - b \theta_{d_1, m_1} \leq (\neq) 0 \text{ on } \Omega \right\},$$

$$I_b^1 := \left\{ d_1 \in I_b \mid \sup_\Omega (m_2 - b \theta_{d_1, m_1}) > 0 \right\}.$$ 

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 $\Sigma_V$ in terms of $c > 0$, we define for
each $c > 0$,

\begin{equation}
I_c := \left\{ d_2 > 0 \mid \int_\Omega (m_1 - c) \theta_{d_2, m_2} < 0 \right\} = I_c^0 \cup I_c^1,
\end{equation}

where

\begin{equation}
\begin{aligned}
I_c^0 & := \{ d_2 > 0 \mid m_1 - c \theta_{d_2, m_2} \leq (\neq) 0 \text{ on } \Omega \}, \\
I_c^1 & := \{ d_2 \in I_c \mid \sup_{\Omega} (m_1 - c) \theta_{d_2, m_2} > 0 \}.
\end{aligned}
\end{equation}

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 $\Sigma_U$, we have the following characterization:

\begin{equation}
\Sigma_U = \begin{cases}
\emptyset & \text{if } 0 < b \leq L_U, \\
\{(d_1, d_2) \mid d_1 \in I_b, d_2 > \hat{d}_2^*(d_1) \} \subseteq \mathcal{Q} & \text{if } L_U < b < S_U, \\
\mathcal{Q} & \text{if } b \geq S_U,
\end{cases}
\end{equation}

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:

\begin{equation}
\hat{d}_2^*(d_1) := \begin{cases}
0 & \text{if } d_1 \in I_b^0, \\
\frac{1}{x_1(m_2 - b \theta_{d_1, m_1})} & \text{if } d_1 \in I_b^1.
\end{cases}
\end{equation}

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

(ii) For $\Sigma_V$, we have the following characterization:

\begin{equation}
\Sigma_V = \begin{cases}
\emptyset & \text{if } 0 < c \leq L_V, \\
\{(d_1, d_2) \mid d_2 \in I_c, d_1 > \hat{d}_1^*(d_2) \} \subseteq \mathcal{Q} & \text{if } L_V < c < S_V, \\
\mathcal{Q} & \text{if } c \geq S_V.
\end{cases}
\end{equation}

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:

\begin{equation}
\hat{d}_1^*(d_2) := \begin{cases}
0 & \text{if } d_2 \in I_c^0, \\
\frac{1}{x_1(m_1 - c \theta_{d_2, m_2})} & \text{if } d_2 \in I_c^1.
\end{cases}
\end{equation}

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


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

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

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:

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

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 $b \leq 0$ (resp., $c \leq 0$), and in case $S_U = \infty$ (resp., $S_V = \infty$), we simply do not need the statements involving $b \geq \infty$ (resp., $c \geq \infty$).

**Proof.** If both $m_1$ and $m_2$ are constant, then the theorem follows directly from Theorem [5.1]. 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 $b \leq 0$ (resp., $c \leq 0$) below should be skipped; Similarly, if $S_U = \infty$ (resp., $S_V = \infty$), all arguments involving the case $b \geq \infty$ (resp., $c \geq \infty$) 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 $\int_{\bar{\Omega}} (m_2 - b \theta_{d_1,m_1}) \geq 0$. 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 $b \leq L_U$, then by definition of $L_U$ in (3.1), $\int_{\Omega} (m_2 - b \theta_{d_1,m_1}) > 0$ for all $d_1 > 0$. Hence $I_b = \emptyset$ and $\Sigma_U = \emptyset$. It is easy to check that if $I_b$ is the union of finitely many open intervals and thus is open in $\mathbb{R}^+$. By continuity of $\theta_{d_1,m_1}$ in $d_1$, $I_{b_0}$ is closed and $I_{b_0}$ is open in $\mathbb{R}^+$. Moreover,

$$I_b \neq \emptyset \quad \text{if and only if} \quad L_U < b < S_U.$$

Indeed, if $d'_1 \in I_b \neq \emptyset$, then $L_U < b$ and $(m_2 - b \theta_{d_1',m_1})(x_0) > 0$ for some $x_0 \in \bar{\Omega}$. 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

\[
(m_2 - b\theta_{d''_1,m_1})(y_0) > 0 \quad \text{and} \quad \int_{\overline{\Omega}} (m_2 - b\theta_{d''_1,m_1}) < 0,
\]

i.e., \( d''_1 \in I_b^1 \neq \emptyset \). This finishes the proof of (3.15).

We now claim that \( I_b \) admits the following decomposition:

\[
\begin{aligned}
I_b &= \emptyset \quad \text{if } b \leq L_U, \\
I_b &= I_b^0 \cup I_b^1 \subset \mathbb{R}^+ \quad \text{if } L_U < b < S_U, \\
I_b &= I_b^0 = \mathbb{R}^+ \quad \text{if } b \geq S_U.
\end{aligned}
\]

(3.16)

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

\[
m_2 - b\theta_{d_1,m_1} \leq 0 \quad \text{in } \Omega \quad \text{for all } d_1 > 0 \text{ and } b \geq S_U.
\]

Hence to show that \( I_b = I_b^0 = \mathbb{R}^+ \), it suffices to show that \( m_2 - b\theta_{d_1,m_1} \neq 0 \) for any \( d_1 > 0 \) and \( b \geq S_U \). This is obviously true if \( b > S_U \). If \( m_1 \equiv \text{const} \), then \( m_2 \equiv \text{const} \) by our assumption and \( \theta_{d_1,m_1} \equiv 1 \equiv \text{const} \) for all \( d_1 > 0 \); if \( m_2 \equiv \text{const} \), then \( m_1 \equiv \text{const} \) by our assumption and \( \theta_{d_1,m_1} \neq \text{const} \) for any \( d_1 > 0 \). Hence it suffices to prove that \( m_2 - b\theta_{d_1,m_1} \neq 0 \) 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

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

Hence \( \theta_{d_1',m_1} - \theta_{d_1',m_1} \leq (\neq)0 \) on \( \overline{\Omega} \) for all \( d_1 \neq d_1' \). However, this is impossible since \( \theta_{d_1',m_1} \) 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),

\[
(3.17)
\]

\[
\begin{aligned}
&b \geq S_U \Rightarrow \mu_1(d_2,m_2 - b\theta_{d_1,m_1}) > 0 \\
&\text{for all } (d_1,d_2) \in Q, \quad \text{i.e., } \Sigma_U = Q.
\end{aligned}
\]

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 \( d_2 > 0 = \hat{d}_2^*(d_1) \) 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 \( d_2 > 1/\lambda_1(m_2 - b\theta_{d_1,m_1}) = \hat{d}_2^*(d_1) \) by Proposition 2.2(ii). Hence \((d_1,d_2) \in \Sigma_U \) if and only if \( d_1 \in I_b \) and \( d_2 > \hat{d}_2^*(d_1) \). This finishes the proof of (3.10). Now it follows from (3.10) and (3.15) that when \( b \in (L_U,S_U), \Sigma_U \subset Q \) and furthermore, by Proposition 2.1(iv), \( \Sigma_U \) 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 \( b \leq L_U \), then \( \int_{\Omega} (m_2 - b \theta_{d_1,m_1}) \geq 0 \) for all \( d_1 > 0 \). Hence by Proposition 2.2(i), \( \mu_1(d_2,m_2 - b \theta_{d_1,m_1}) \leq 0 \) for all \((d_1,d_2) \in \mathbb{Q}\) and \( \mu_1(d_2,m_2 - b \theta_{d_1,m_1}) = 0 \) (i.e., \((d_1,d_2) \in \Sigma_{U,d}\)) 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 \( \Sigma_{U,0} = \emptyset \). 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 \( m_1 \neq \text{const} \) and such \( d_1^* \) exists, then the equation satisfied by \( \theta_{d_1^*,m_1} \) implies that

\[
d_1^* = \frac{-\theta_{d_1^*,m_1}(m_1 - \theta_{d_1^*,m_1})}{\Delta \theta_{d_1^*,m_1}} = \frac{-m_2(L_U m_1 - m_2)}{L_U \Delta m_2},
\]

which is obviously unique; if \( m_1 \equiv \text{const} \), then \( m_2 \neq \text{const} \) 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 \( \Sigma_{U,0} = \emptyset \). If \( b \geq S_U \), then it follows from (3.17) that \( \Sigma_{U,0} = \emptyset \). 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(ii), when \( L_U < b < S_U \), \( \partial \Sigma \neq \emptyset \). Thus \( \partial \Sigma \not\subset \Sigma_{U,0} \).

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 \( m_2 - b \theta_{d_1',m_1} \neq 0 \), 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 \( \Omega \). 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.

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

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

\[
\mathbb{Q} = (\Sigma_U \cup \Sigma_{U,0} \setminus \Pi) \cup (\Sigma_V \cup \Sigma_{V,0} \setminus \Pi) \cup \Sigma - \cup \Pi.
\]

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 \((b, c) \in \Xi,\) where \(\Xi\) 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 \(\Omega,\) we obtain that

\[
(3.19) \quad d \int_{\Omega} |\nabla \theta_{d,g}|^2 = \int_{\Omega} \theta_{d,g}^2 (g - \theta_{d,g}).
\]

Choosing \(\theta_{d_1,m_1}\) 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

\[
(3.20) \quad \mu_1(d_1, m_1 - c\theta_{d_2,m_2}) \leq \frac{d_1 \int_{\Omega} |\nabla \theta_{d_1,m_1}|^2 + \int_{\Omega} (c\theta_{d_2,m_2} - m_1)\theta_{d_1,m_1}^2}{\int_{\Omega} \theta_{d_1,m_1}^2}.
\]

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

\[
(3.21) \quad \mu_1(d_2, m_2 - b\theta_{d_1,m_1}) \leq \frac{d_2 \int_{\Omega} |\nabla \theta_{d_2,m_2}|^2 + \int_{\Omega} (b\theta_{d_1,m_1} - m_2)\theta_{d_2,m_2}^2}{\int_{\Omega} \theta_{d_2,m_2}^2}.
\]
Since \((b,c) \in \mathcal{Z}\), i.e., \(bc \leq 1\), combining (3.20) and (3.21) together, we have

\[
\mu_1(d_1, m_1 - c\theta_{d_2, m_2}) \int_{\Omega} \theta^2_{d_1, m_1} + c^3 \mu_1(d_2, m_2 - b \theta_{d_1, m_1}) \int_{\Omega} \theta^2_{d_2, m_2} \\
\leq \int_{\Omega} (c \theta_{d_2, m_2} - \theta_{d_1, m_1}) \theta^2_{d_1, m_1} + \int_{\Omega} (bc \theta_{d_1, m_1} - c \theta_{d_2, m_2}) c^2 \theta^2_{d_2, m_2} \\
\leq - \int_{\Omega} (c \theta_{d_2, m_2} - \theta_{d_1, m_1})^2 (c \theta_{d_2, m_2} + \theta_{d_1, m_1}) \leq 0,
\]

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

\[
(\Sigma_U \cup \Sigma_{U,0} \setminus \Pi) \cap (\Sigma_V \cup \Sigma_{V,0} \setminus \Pi) = \emptyset.
\]

This proves the mutually disjoint decomposition of \(Q\) 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

\[
\Pi \subset \{(d_1, d_2) \mid \theta_{d_1, m_1} \equiv c \theta_{d_2, m_2}\}.
\]

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 \(\theta_{d_2, m_2}\) being its corresponding eigenfunction and \(\mu_1(d_1, m_1 - c \theta_{d_2, m_2}) = 0\) with \(\theta_{d_1, m_1}\) being its corresponding eigenfunction. This together with (3.24) implies that

\[
\Pi = \{(d_1, d_2) \mid \theta_{d_1, m_1} \equiv c \theta_{d_2, m_2}\}.
\]

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

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

To see the claim, we first assume that (S) is true. By (3.18) and (3.23), for any \((d_1, d_2) \in Q \setminus \Pi\), 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) \((d_1, d_2) \in \Sigma_\perp\); 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

(3.26) \[ \mu_1(d_2^*, m_2 - b\theta_{d_1^*, m_1}) = 0, \quad \mu_1(d_1^*, m_1 - c\theta_{d_2^*, m_2}) < 0. \]

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

(3.27) \[
\begin{align*}
&d_1^* \Delta U^* + U^*(m_1(x) - U^* - c V^*) = 0 \quad \text{in } \Omega, \\
&d_2^* \Delta V^* + V^*(m_2(x) - b U^* - V^*) = 0 \quad \text{in } \Omega, \\
&\partial_v U^* = \partial_v V^* = 0 \quad \text{on } \partial \Omega.
\end{align*}
\]

Define

(3.28) \[ F : (\hat{b}, \hat{c}, U, V) \mapsto \left( \begin{array}{c}
    d_1^* \Delta U + U(m_1(x) - U - \hat{c} V) \\
    d_2^* \Delta V + V(m_2(x) - \hat{b} U - V)
\end{array} \right), \]

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

\[ X := \{ \phi \in H^1(\Omega) \mid \partial_v \phi = 0 \text{ on } \partial \Omega \}. \]

(Note that here $b$ and $c$ are any two fixed numbers that have been chosen satisfying $(b, c) \in \Xi_1$, i.e., $bc \leq 1$, while $\hat{b}$ and $\hat{c}$ 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.,

\[ \frac{\partial F(\hat{b}, \hat{c}, U, V)}{\partial (U, V)} \bigg|_{(\hat{b}, \hat{c}, U, V) = (b, c, U^*, V^*)} \]

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

(3.29) \[ b' > b, \quad 0 < c' < c, \quad \text{and} \quad b'c' \leq 1. \]

However, let us consider the following system:

(3.30) \[
\begin{align*}
&U_t = d_1^* \Delta U + U(m_1(x) - U - c' V) \quad \text{in } \Omega \times \mathbb{R}^+, \\
&V_t = d_2^* \Delta V + V(m_2(x) - b' U - V) \quad \text{in } \Omega \times \mathbb{R}^+, \\
&\partial_v U = \partial_v V = 0 \quad \text{on } \partial \Omega \times \mathbb{R}^+.
\end{align*}
\]

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, \((\theta_1, m_1, 0)\) is linearly stable and \((0, \theta_2, m_2)\) 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 \((\theta_1, m_1, 0)\) 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 \(\Omega\). Let \(\lambda_1\) be the principal eigenvalue of the linearized elliptic system at \((U, V)\) and \((\hat{\Phi}_1, \hat{\Psi}_1)\) be the corresponding eigenfunction satisfying \(\Phi_1 > 0 > \Psi_1\) on \(\Omega\) and normalized such that \(\|\Phi_1\|_{L^2(\Omega)}^2 + \|\Psi_1\|_{L^2(\Omega)}^2 = 1\). By direct calculation, using the equation satisfied by \(U\) and \(\hat{\Phi}_1\), we obtain that

\[
d_1 \nabla \cdot \left(U^2 \nabla \frac{\Phi_1}{U}\right) = U^2(\Phi_1 + c\Psi_1) - \lambda_1 U \Phi_1.
\]

Multiplying both sides by \(\Phi_1^2 / U^2\) and integrating over \(\Omega\), 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

\[
-\lambda_1 \int_\Omega \left(\frac{\Phi_1^3}{U} - c^3 \frac{\Psi_1^3}{V}\right) = -2d_1 \int_\Omega U \Phi_1 \left|\nabla \frac{\Phi_1}{U}\right|^2 + 2d_2 c^3 \int_\Omega V \Psi_1 \left|\nabla \frac{\Psi_1}{V}\right|^2
\]

\[
\leq - \int_\Omega \Phi_1^2(\Phi_1 + c\Psi_1) + \int_\Omega c^2 \Psi_1^2(b \Phi_1 + c\Psi_1)
\]

\[
(3.31)
\]

\[
\leq -2d_1 \int_\Omega U \Phi_1 \left|\nabla \frac{\Phi_1}{U}\right|^2 + 2d_2 c^3 \int_\Omega V \Psi_1 \left|\nabla \frac{\Phi_1}{U}\right|^2
\]

\[
- \int_\Omega (\Phi_1 - c\Psi_1)(\Phi_1 + c\Psi_1)^2 \leq 0,
\]

where we used the fact that \(bc \leq 1\) and \(\Phi_1 > 0 > \Psi_1\) on \(\Omega\). \((3.31)\) 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

\[
(3.32) \quad bc = 1, \quad \Phi_1 / U \equiv \text{const}, \quad \Psi_1 / V \equiv \text{const}, \quad \text{and} \quad \Phi_1 \equiv -c\Psi_1.
\]
By (3.32), \(U \equiv \eta V\) for some \(\eta > 0\), i.e., \((U, V)\) satisfies the following system:

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

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,

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

Hence (3.32) implies that

\[
(3.33) \quad bc = 1 \quad \text{and} \quad \theta_{d_1,m_1} = c\theta_{d_2,m_2};
\]

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 \(U/V \equiv \text{const}\). Let \(\lambda_1\) be the principal eigenvalue of the linearized elliptic system at \((U, V)\) and \((\Phi_1, \Psi_1)\) be the corresponding eigenfunction satisfying \(\Phi_1 > 0 > \Psi_1\) on \(\Omega\) and normalized such that \(\|\Phi_1\|_{L^2(\Omega)}^2 + \|\Psi_1\|_{L^2(\Omega)}^2 = 1\). 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

\[
(3.34) \quad b' > b, \quad 0 < c' < c, \quad \text{and} \quad b'c' \leq 1.
\]

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., \(U/V \equiv \text{const}\). 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

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

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 \(3.4.iv\).

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 \((b, c) \in \{(b, c) \mid b \geq S_U \text{ and } c \leq 1/S_U\} \setminus \Xi_1\);

(b) if \(S_V < \infty\), then \((0, \theta_{d_2,m_2})\) is globally asymptotically stable for all \((b, c) \in \{(b, c) \mid c \geq S_V \text{ and } b \leq 1/S_V\} \setminus \Xi_1\).

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 \(1/S_U \leq d < 1/S_U\), \((d_{1}^{*},d_{2}^{*})\) of \((1.10)\) 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 \((b^{*},c^{*}) \in \{(b, c) \mid b \geq S_U \text{ and } c \leq 1/S_U\} \setminus \Xi_1\) such that \((1.10)\) with \((d_{1},d_{2}) = (d_{1}^{*},d_{2}^{*})\) has a coexistence steady state \((U^{*},V^{*})\). We now consider the following system:

\[
\begin{aligned}
U_t &= d_{1}^{*} \Delta U + U(m_1(x) - U - c^{*} V) \quad \text{in } \Omega \times \mathbb{R}^{+}, \\
V_t &= d_{2}^{*} \Delta V + V(m_2(x) - S_U U - V) \quad \text{in } \Omega \times \mathbb{R}^{+}, \\
\partial_{\nu} U &= \partial_{\nu} V = 0 \quad \text{on } \partial \Omega \times \mathbb{R}^{+}, \\
U(x,0) &= U_0(x), \quad V(x,0) = V_0(x) \quad \text{in } \Omega. 
\end{aligned}
\]

Since \(c^{*} \leq 1/S_U\), \((S_U,c^{*}) \in \Xi_1\), 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

\((U^{*},V^{*})\) is an upper solution to \((3.35)\) and \((\varepsilon \psi_1, \theta_{d_{2}^{*},m_2})\) is a lower solution to \((3.35)\) for all \(\varepsilon\) sufficiently small, where \(\psi_1 > 0\) is the principal eigenfunction of \(\mu_1^{*} := \mu_1(d_{1}^{*},m_1 - c^{*} \theta_{d_{2}^{*},m_2})\) normalized such that \(\max_{\Omega} \psi_1 = 1\), and

\[
\begin{aligned}
d_{1}^{*} \Delta \psi_1 + (m_1 - c^{*} \theta_{d_{2}^{*},m_2}) \psi_1 + \mu_1^{*} \psi_1 &= 0 \quad \text{in } \Omega, \\
\partial_{\nu} \psi_1 &= 0 \quad \text{on } \partial \Omega. 
\end{aligned}
\]

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

\[
\begin{aligned}
d_{1}^{*} \Delta U^{*} + U^{*}(m_1 - U^{*} - c^{*} V^{*}) &= 0 \quad \text{in } \Omega, \\
d_{2}^{*} \Delta V^{*} + V^{*}(m_2 - S_U U^{*} - V^{*}) &= (b^{*} - S_U)U^{*}V^{*} > 0 \quad \text{in } \Omega. 
\end{aligned}
\]

\(^{1}\) Note that we do not need the condition in \([18, \text{ theorem 3}]\) 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 \([18, \text{ theorem 3}]\), 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 \( e^* \leq 1/S_U < L_V \) by Lemma 3.2(iii), Theorem 3.3(ii) and (iv) implies that \( \Sigma_V = \Sigma_{V,0} = \emptyset \) for system (3.35), i.e., \( \mu^*_1 < 0 \). Hence by (3.36), \( (\epsilon \varphi_1, \theta_{d_2^*,m_2}) \) satisfies that
\[
\begin{align*}
d_1^* \Delta(\epsilon \varphi_1) + \epsilon \varphi_1 (m_1 - \epsilon \varphi_1 - c^* \theta_{d_2^*,m_2}) & = \epsilon \varphi_1 (-\mu^*_1 - \epsilon \varphi_1) > 0 \quad \text{in } \Omega, \\
d_2^* \Delta \theta_{d_2^*,m_2} + \theta_{d_2^*,m_2} (m_2 - S_U \epsilon \varphi_1 - \theta_{d_2^*,m_2}) & = -\epsilon S_U \epsilon \varphi_1 \theta_{d_2^*,m_2} < 0 \quad \text{in } \Omega,
\end{align*}
\]
for all \( \epsilon \) sufficiently small. This finishes the proof of claim (S).

Since \( U^* \geq \epsilon \varphi_1 \) and \( V^* \leq \theta_{d_2^*,m_2} \), and they all satisfy the zero-flux boundary condition, by the upper-solution and lower-solution method \cite{30}, we see that (3.35) has a positive solution, which is a contradiction since we have shown that the semitrivial steady state \((\theta_{d_2^*,m_1}, 0)\) 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 \( \Sigma_- \) and \( \Pi \) change when we vary \( b \) and \( c \) for all \((b, c) \in \Sigma\), 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 \( (b, c) \in \Sigma \). Then the following hold for (1.10):

(i) For \( \Sigma_- \) we have the following characterization:

\[
\Sigma_- = \begin{cases} 
\emptyset & \text{if } b \geq S_U \text{ or } c \geq S_V, \\
\emptyset & \text{if } b < L_U \text{ and } c < L_V, \\
\emptyset \setminus \Sigma_{U,0} & \text{if } b = L_U \text{ and } c < L_V, \\
\emptyset \setminus \Sigma_{V,0} & \text{if } b < L_U \text{ and } c = L_V, \\
\emptyset \setminus (\Sigma_{U,0} \cup \Sigma_{V,0}) & \text{if } b = L_U \text{ and } c = L_V, \\
\emptyset \setminus (\Sigma_U \cup \Sigma_{U,0} \cup \Sigma_{V,0}) & \text{if } L_U < b < S_U \text{ and } c \leq L_V, \\
\emptyset \setminus (\Sigma_U \cup \Sigma_{U,0} \cup \Sigma_{V,0}) & \text{if } b \leq L_U \text{ and } L_V < c < S_U, \\
\emptyset \setminus (\Sigma_U \cup \Sigma_{U,0} \cup \Sigma_{V,0}) & \text{if } L_U < b < S_U \text{ and } L_V < c < S_V,
\end{cases}
\]

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

(ii) For \( \Pi \), 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, \( \Pi \neq \emptyset \) 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 \( b \leq 0 \) (resp., \( c \leq 0 \)), and in case \( S_U = \infty \) (resp., \( S_V = \infty \)), we simply do not need the statements involving \( b \geq \infty \) (resp., \( c \geq \infty \)).

Except for that \( \Sigma_- = \emptyset \) 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
We now claim that \( bc < 3.3 \) and \( 3.5 \) (excluding the last statement in Theorem 3.5(i)). \( b, c \) refers to Theorem 1.4(i)–(vi), respectively.

For case (i), since \( c < S \), therefore by Proposition 2.2(ii), then as \( m_1 < 2 \), \( c \) is linearly unstable. Since \( c < S \), there exists some \( d_1 \) large such that \((m_1 - c \theta_{d_1,m_2}) < 0 \) for all \( d_1 \) large, i.e., \((\theta_{d_1,m_2}, 0) \) is linearly unstable. Since \( c < S \), there exists some \( d_2 \) large such that \((m_2 - b \theta_{d_1,m_1}) > 0 \) for all \( d_1 \) large. 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., \((\theta_{d_1,m_2}, 0) \) is linearly unstable. Since \( c < S \), there exists some \( d_3 \) large such that \((m_3 - c \theta_{d_1,m_2}(x_0)) > 0 \) for some \( x_0 \in \Omega \). If \( \int_{\Omega}(m_1 - c \theta_{d_1,m_2}) \) is large, then \( \mu_1(d_1, m_1 - c \theta_{d_1,m_2}) < 0 \) for all \( d_1 > 0 \) by Proposition 2.2(i); if \( \int_{\Omega}(m_1 - c \theta_{d_1,m_2}) < 0 \), then as \( m_1 - c \theta_{d_1,m_2} \) changes signs in \( \Omega \), \( \mu_1(d_1, m_1 - c \theta_{d_1,m_2}) < 0 \) for all \( d_1 \) sufficiently large by Proposition 2.2(ii). Therefore, \((d_1, d_1') \in \Sigma_- \) for all \( d_1 \) large, i.e., \( \Sigma_- \) is not empty. This finishes the proof for case (i).

For case (ii), \( \mu_2 < b m_2 \) implies that \( c \) is linearly unstable. As \( L_V < c < S \), 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 \( \Sigma_- = \emptyset \) if and only if \( m_1 \equiv cm_2 \) and \( bc = 1 \).

**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 \( b, c \in \mathbb{R} \), by Lemma 3.2(ii) and (iii), \( L_U < b < S_U, \ L_V < c < S_V \), and \( bc \leq 1 \). By Theorem 3.3(i) and (ii), both \( \Sigma_U, \Sigma_V \neq \emptyset \) and thus \( \Sigma_U, \Sigma_V \neq \emptyset \). We now claim that

\[
\Sigma_- = \emptyset \quad \text{if and only if} \quad m_1 \equiv cm_2 \quad \text{and} \quad bc = 1.
\]

First we show that

\[
\Sigma_- \neq \emptyset \quad \text{if} \quad b \mu_1 \neq \mu_2 \quad \text{or} \quad c \mu_2 \neq \mu_1 \quad \text{or} \quad bc < 1.
\]

We now prove (3.39) assuming that \( b \mu_1 \neq \mu_2 \). The proof of (3.39) for the case \( c \mu_2 \neq \mu_1 \) is similar and is thus omitted. It suffices to consider the following two cases:

(i) \( L_U < b < S_U \) and \( b \mu_1 < \mu_2 \), and
(ii) \( L_U < b < S_U \) and \( \mu_2 < b \mu_1 \).

For case (i), since \( \mu_2 > b \mu_1 \geq 0 \), \( b > L_U > 0 \). 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 \( c < S \), there exists some \( d_3 \) large such that \((m_3 - c \theta_{d_1,m_2}(x_0)) > 0 \) for some \( x_0 \in \Omega \). If \( \int_{\Omega}(m_1 - c \theta_{d_1,m_2}) \) is large, then \( \mu_1(d_1, m_1 - c \theta_{d_1,m_2}) < 0 \) for all \( d_1 > 0 \) by Proposition 2.2(i); if \( \int_{\Omega}(m_1 - c \theta_{d_1,m_2}) < 0 \), then as \( m_1 - c \theta_{d_1,m_2} \) changes signs in \( \Omega \), \( \mu_1(d_1, m_1 - c \theta_{d_1,m_2}) < 0 \) for all \( d_1 \) sufficiently large by Proposition 2.2(ii). Therefore, \((d_1, d_1') \in \Sigma_- \) for all \( d_1 \) large, i.e., \( \Sigma_- \) is not empty. This finishes the proof for case (i).

For case (ii), \( \mu_2 < b \mu_1 \) implies that \( c \mu_2 < \mu_1 \) since \( bc \leq 1 \). As \( L_V < c < S \), 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 \( \Sigma_\pm \neq \emptyset \) 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 \( \Omega \). By Theorem 3.3(iii)-(iv), this implies that \( \Sigma_{U,0} = \partial \Sigma_U \) and \( \Sigma_{V,0} = \partial \Sigma_V \). Assume that \( \Sigma_- = \emptyset \) for contradiction; then by the mutually disjoint decomposition of \( \Omega \) in (3.18) and the fact that both \( \Sigma_U \) and \( \Sigma_V \) are nonempty and open in \( \Omega \), we must have \( \partial \Sigma_U = \partial \Sigma_V \). Hence \( \Pi \supset \partial \Sigma_U \neq \emptyset \), 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

(3.40)
\[
\text{if } bc = 1, b\overline{m}_1 = \overline{m}_2, \text{ and } c\overline{m}_2 = \overline{m}_1, \text{ then } \Sigma_- \neq \emptyset
\]

if and only if \( m_1 = cm_2 \).

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

\( \overline{U} := U, \overline{V} := cV, \)

(3.41)
\[
\tilde{d}_1 := d_1, \quad \tilde{d}_2 := cd_2, \quad \tilde{m}_1 := m_1, \quad \text{and} \quad \tilde{m}_2 := cm_2.
\]

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

(3.42)
\[
\begin{aligned}
\tilde{d}_1 \Delta \overline{U} + \overline{U} (\tilde{m}_1 - \overline{U} - \overline{V}) & \quad \text{in } \Omega \times \mathbb{R}^+, \\
c \tilde{d}_2 \Delta \overline{V} + \overline{V} (\tilde{m}_2 - \overline{U} - \overline{V}) & \quad \text{in } \Omega \times \mathbb{R}^+, \\
\partial_v \overline{U} = \partial_v \overline{V} & \quad \text{on } \partial \Omega \times \mathbb{R}^+,
\end{aligned}
\]

with \( \int_{\Omega} \tilde{m}_1 = \int_{\Omega} \tilde{m}_2 \). 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 \((\theta_{\tilde{d}_1,\tilde{m}_1}, 0)\) and \((0, \theta_{\tilde{d}_2,\tilde{m}_2})\) of system (3.42) are determined by the sign of \(\min\{\mu_1(\tilde{d}_1, \tilde{m}_1), \mu_1(\tilde{d}_2, \tilde{m}_2), \mu_1(\tilde{d}_2, \tilde{m}_2 - \theta_{\tilde{d}_1,\tilde{m}_1})\}, \mu_1(\tilde{d}_1, \tilde{m}_1 - \theta_{\tilde{d}_2,\tilde{m}_2}), \) and \(\mu_1(\tilde{d}_1, \tilde{m}_1 - \theta_{\tilde{d}_2,\tilde{m}_2})\), respectively. In particular, \((0,0)\) is always linearly unstable for any \(\tilde{d}_1, \tilde{d}_2 > 0\). Now for a given coexistence steady state \((\overline{U}, \overline{V})\) of (3.42), linearizing the steady state problem of (3.42) at \((\overline{U}, \overline{V})\), we have

(3.43)
\[
\begin{aligned}
\tilde{d}_1 \Delta \Phi + \Phi (\tilde{m}_1 - \overline{U} - \overline{V}) - \overline{U} (\Phi + \Psi) + \lambda \Phi &= 0 \quad \text{in } \Omega, \\
\tilde{d}_2 \Delta \Psi + \Psi (\tilde{m}_2 - \overline{U} - \overline{V}) - \overline{V} (\Phi + \Psi) + c \lambda \Psi &= 0 \quad \text{in } \Omega, \\
\partial_v \Phi = \partial_v \Psi &= 0 \quad \text{on } \partial \Omega.
\end{aligned}
\]

Thus
\[
\Phi = \Phi, \quad \Psi = c \Psi, \quad \text{and } \lambda = \lambda.
\]
where \((U, V)\) is the coexistence steady state of \((1.10)\) corresponding to \((\bar{U}, \bar{V})\) defined via \((3.41)\), and \(\lambda\) and \((\Phi, \Psi)\) 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 \((3.42)\):

\[
\tilde{\Sigma}_U := \{(\tilde{d}_1, \tilde{d}_2) \in Q \mid (\theta_{\bar{d}_1, \bar{m}_1}, 0) \text{ is linearly stable}\},
\]

\[
\tilde{\Sigma}_V := \{(\tilde{d}_1, \tilde{d}_2) \in Q \mid (0, \theta_{\bar{d}_2, \bar{m}_2}) \text{ is linearly stable}\},
\]

\[
\tilde{\Sigma}_- := \{(\tilde{d}_1, \tilde{d}_2) \in Q \mid \text{both } (\theta_{\bar{d}_1, \bar{m}_1}, 0) \text{ and } (0, \theta_{\bar{d}_2, \bar{m}_2}) \text{ are linearly unstable}\},
\]

\[
\tilde{\Sigma}_{U,0} := \{(\tilde{d}_1, \tilde{d}_2) \in Q \mid \mu_1(\tilde{d}_2, \bar{m}_2 - \bar{m}_1) = 0\},
\]

\[
\tilde{\Sigma}_{V,0} := \{(\tilde{d}_1, \tilde{d}_2) \in Q \mid \mu_1(\tilde{d}_1, \bar{m}_1 - \bar{m}_2) = 0\},
\]

\[
\tilde{\Pi} := \tilde{\Sigma}_{U,0} \cap \tilde{\Sigma}_{V,0}.
\]

Then by the one-to-one correspondence between \(\tilde{K}\) 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 \(Q\):

\[
Q = (\tilde{\Sigma}_U \cup \tilde{\Sigma}_{U,0} \setminus \tilde{\Pi}) \cup (\tilde{\Sigma}_V \cup \tilde{\Sigma}_{V,0} \setminus \tilde{\Pi}) \cup \tilde{\Sigma}_- \cup \tilde{\Pi}
\]

and

\[
\tilde{\Pi} = \{(\tilde{d}_1, \tilde{d}_2) \in Q \mid \theta_{\bar{d}_1, \bar{m}_1} = \theta_{\bar{d}_2, \bar{m}_2}\}.
\]

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

\[
\tilde{\Sigma}_- = \emptyset \text{ if and only if } \bar{m}_1 = \bar{m}_2.
\]

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

\[
(3.48) \quad \partial \tilde{\Sigma}_U = \tilde{\Sigma}_{U,0} \quad \text{and} \quad \partial \tilde{\Sigma}_V = \tilde{\Sigma}_{V,0}.
\]

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

\[
\partial \tilde{\Sigma}_U = \partial \tilde{\Sigma}_V = \tilde{\Pi}.
\]

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

\[
\theta_{\tilde{d}_1, \bar{m}_1} = \theta_{\tilde{d}_2, \bar{m}_2}.
\]

Hence by \((1.2)\),

\[
\frac{\bar{m}_1 - \theta_{\tilde{d}_1, \bar{m}_1}}{\tilde{d}_1} = \frac{\bar{m}_2 - \theta_{\tilde{d}_2, \bar{m}_2}}{\tilde{d}_2}.
\]

Integrating the above identity over \(\Omega\), we obtain that

\[
(3.49) \quad \frac{\bar{m}_1 - \theta_{\tilde{d}_1, \bar{m}_1}}{\tilde{d}_1} \int_{\Omega} \bar{m}_1 = \frac{\bar{m}_2 - \theta_{\tilde{d}_2, \bar{m}_2}}{\tilde{d}_2} \int_{\Omega} \theta_{\tilde{d}_1, \bar{m}_1}.
\]
Thus by (1.6), \( \bar{d}_1 = \bar{d}_2 \), which in turn implies that \( \bar{m}_1 = \bar{m}_2 \). Therefore we finish the proof of (3.47) and hence (3.38). Moreover, when \( \bar{m}_1 = \bar{m}_2 \), \( \Sigma_U = \{(\bar{d}_1, \bar{d}_2) | \bar{d}_2 > \bar{d}_1 \}, \Sigma_V = \{(\bar{d}_1, \bar{d}_2) | \bar{d}_2 < \bar{d}_1 \}, \) and \( \partial \Sigma_U = \partial \Sigma_V = \bar{\Pi} = \{(\bar{d}_1, \bar{d}_2) | \bar{d}_2 = \bar{d}_1 \} \). This implies that when \( m_1 = cm_2 \) and \( bc = 1 \), \( \Sigma_U = \{(d_1, d_2) | d_2 > d_1/c \}, \Sigma_V = \{(d_1, d_2) | d_2 < d_1/c \}, \) and \( \Sigma_{U,0} = \Sigma_{V,0} = \Pi = \{(d_1, d_2) | d_2 = d_1/c \} \). This completes the proof of Theorem 3.6(iv). □

4 Concluding Remarks and Further Extensions

For the general \( 2 \times 2 \) Lotka-Volterra competition-diffusion system (1.10), under the very mild condition (M), we have completely classified, for all \((b, c) \in \mathcal{E}\), 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:

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

(4.1)

where \( d_i(x) \in C^{1,\alpha}(\bar{\Omega}) \) and \( d_i(x) \geq d_0 > 0 \) 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 \( \int_\Omega g \geq 0 \) and \( g \not\equiv 0 \). Consider the following elliptic problem:

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

By similar arguments as in the proofs of existence and uniqueness results for (1.2) in [7], 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 \( \mu_1(d(x), q(x)) \) be the principal eigenvalue of the following eigenvalue problem:

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

where \( d(x) \in C^1,\alpha(\Omega) \) with \( d(x) > d_0 > 0 \). Then \( \mu_1(d(x), q(x)) \) admits the following variational characterization:

\[
\mu_1(d(x), q(x)) = \inf_{\psi \in H_1(\Omega) \setminus \{0\}} \frac{\int_\Omega (d(x)| \nabla \psi |^2 - q(x) \psi^2) dx}{\int_\Omega \psi^2}.
\]

Similar to the arguments used in Section 2, we can show that the linear stability of \( (\Theta_{d_1}^1, 0) \) is determined by the sign of \( \mu_1(d_2(x), m_2 - b \Theta_{d_1,m_1}) \). In other words, \( (\Theta_{d_1,m_1}, 0) \) is linearly stable (resp., unstable) if the principal eigenvalue \( \mu_1(d_2(x), m_2 - b \Theta_{d_1,m_1}) > 0 \) (resp., \( \mu_1(d_2(x), m_2 - b \Theta_{d_1,m_1}) < 0 \)).

The linear stability of \( (0, \Theta_{d_2,m_2}) \) can be determined accordingly by the sign of \( \mu_1(d_1(x), m_1 - c \Theta_{d_2,m_2}) \). 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 \( bc \leq 1 \). Then

\[
\mu_1(d_1(x), m_1 - c \Theta_{d_2,m_2}) \int_\Omega \Theta_{d_1,m_1}^2 + c^2 \mu_1(d_2(x), m_2 - b \Theta_{d_1,m_1}) \int_\Omega \Theta_{d_2,m_2}^2 \leq 0,
\]

where equality holds if and only if

\[
b c = 1 \quad \text{and} \quad \Theta_{d_1,m_1} = c \Theta_{d_2,m_2}.
\]

Moreover, the following hold for (4.1):

1. If \( \mu_1(d_2(x), m_2 - b \Theta_{d_1,m_1}) \geq 0 \) and \( \mu_1(d_1(x), m_1 - c \Theta_{d_2,m_2}) < 0 \), then \( (\Theta_{d_1,m_1}, 0) \) is globally asymptotically stable.
2. If \( \mu_1(d_2(x), m_2 - b \Theta_{d_1,m_1}) < 0 \) and \( \mu_1(d_1(x), m_1 - c \Theta_{d_2,m_2}) \geq 0 \), then \( (0, \Theta_{d_2,m_2}) \) is globally asymptotically stable.
3. If \( \mu_1(d_2(x), m_2 - b \Theta_{d_1,m_1}) < 0 \) and \( \mu_1(d_1(x), m_1 - c \Theta_{d_2,m_2}) < 0 \), then there exists a unique coexistence steady state that is globally asymptotically stable.
4. If \( \mu_1(d_2(x), m_2 - b \Theta_{d_1,m_1}) = \mu_1(d_1(x), m_1 - c \Theta_{d_2,m_2}) = 0 \), then (4.1) 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 \( m_i \equiv \text{const} \quad (i = 1, 2) \), 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 \(\Omega\) 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.

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