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Calculus of Variations

Global dynamics of the Lotka–Volterra competition–diffusion system with equal amount of total resources, III

Xiaoqing He[1] · **Wei-Ming Ni**[1,2]

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Abstract In this paper—Part III of this series of three papers, we continue to investigate the joint effects of diffusion and spatial concentration on the global dynamics of the classical Lotka–Volterra competition–diffusion system. To further illustrate the general results obtained in Part I (He and Ni in Commun Pure Appl Math 69:981–1014, 2016. doi:10.1002/cpa.21596), we have focused on the case when the two competing species have identical competition abilities and the same amount of total resources. In contrast to Part II (He and Ni in Calc Var Partial Differ Equ 2016. doi:10.1007/s00526-016-0964-0), our results here show that in case both species have spatially heterogeneous distributions of resources, the outcome of the competition is independent of initial values but depends solely on the dispersal rates, which in turn depends on the distribution profiles of the resources—thereby extending the celebrated phenomenon "slower diffuser always prevails!" Furthermore, the species with a "sharper" spatial concentration in its distribution of resources seems to have the edge of competition advantage. Limiting behaviors of the globally asymptotically stable steady states are also obtained under various circumstances in terms of dispersal rates.

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✉ Xiaoqing He
xqhe@cpde.ecnu.edu.cn

Wei-Ming Ni
weiming.ni@gmail.com

1 Center for Partial Differential Equations, East China Normal University, Minhang 200241, Shanghai, People's Republic of China

2 School of Mathematics, University of Minnesota, Minneapolis, MN 55455, USA

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1 Introduction

In [8]—Part I of this series of three papers, complete global dynamics of a general heterogeneous Lotka–Volterra competition–diffusion model was obtained. To further illustrate the effects of spatial concentration on its global dynamics, we investigate two special cases of the Lotka–Volterra competition–diffusion model in Parts II [9] and III, where the two competing species are assumed to have identical competition abilities and the same amount of total resources. In particular, in Part II [9], we compared a spatially heterogeneous distribution of resources with its spatially homogeneous counterpart. Our results there showed that *the species with homogeneous distribution of resources never prevails!*

Comparing to Part II [9], this paper focuses on the case that both species have spatially heterogeneous distributions of resources. To be more precise, we consider the following system:

$$\begin{cases} U_t = d_1 \Delta U + U(m_1(x) - U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ V_t = d_2 \Delta V + V(m_2(x) - U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\ U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{in } \Omega, \end{cases} \tag{1.1}$$

where $U(x,t)$ and $V(x,t)$ denote the population densities of two competing species; Ω, the habitat, is a bounded smooth domain in $\mathbb{R}^N$; d_1 and d_2 are diffusion rates of the species U and V respectively and $\Delta = \sum_{i=1}^N \frac{\partial^2}{\partial x_i^2}$ is the usual Laplace operator. The no-flux boundary condition means that no individual crosses the boundary $\partial\Omega$ of the habitat, where ν is the unit outward normal on $\partial\Omega$ and $\partial_\nu = \nu \cdot \nabla$. We assume that the initial data U_0 and V_0 are non-negative and non-trivial. The functions $m_1(x)$ and $m_2(x)$ represent the carrying capacities or intrinsic growth rates of U and V respectively.

To begin our discussion on the global dynamics of (1.1), we first recall an interesting phenomenon when both species are assumed to have identical heterogeneous distribution of resources, namely, "the slower diffuser always prevails!" To state the result mathematically, let $g(x) \in C^\gamma(\bar{\Omega})(\gamma \in (0,1))$ with $\int_\Omega g \geqslant 0$ and $g \not\equiv 0$ and denote by $\theta_{d,g}$ the unique positive solution of:

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

[See, e.g. [3] for the proof of existence and uniqueness results of (1.2).]

Theorem 1.1 ([4]) *Suppose that $m_1(x) \equiv m_2(x) \equiv m(x)$ in (1.1), where $m(x) \in C^\gamma(\bar{\Omega})$ $(\gamma \in (0,1))$ is nonconstant, $m \geqslant 0$ on $\bar{\Omega}$. Then the semi-trivial steady state $(\theta_{d_1,m}, 0)$ of (1.1) is globally asymptotically stable when $d_1 < d_2$, i.e. every solution of (1.1) converges to $(\theta_{d_1,m}, 0)$ as $t \to \infty$, regardless of initial conditions.*

Theorem 1.1 implies that given two competing species with different dispersal rates but otherwise identical, the slower diffuser will always wipe out its faster competitor, regardless of the initial values.

It seems natural to ask what if the distributions of resources of two competing species are not identical but still have the same amount of total resources, i.e. m_1 and m_2 satisfy the following condition:

(M) *Both $m_1(x)$ and $m_2(x)$ are nonnegative, nonconstant functions in $C^\gamma(\bar{\Omega})$ $(\gamma \in (0,1))$, $m_1 \not\equiv m_2$, but $\overline{m_1} = \overline{m_2}$, where $\overline{m_i} := \frac{1}{|\Omega|}\int_\Omega m_i$, $i = 1, 2$.*

The goal of this paper is to understand the competition outcome under the hypothesis (**M**), which will be assumed throughout the rest of this paper. *Our results here give a quantitative description of the conclusion that the competition outcome is somewhat "comparable" to that of "slower diffuser always prevails" except that the co-existence now becomes a much stronger possibility in terms of dispersal rates.*

To state our results precisely, we introduce the following elliptic eigenvalue problem.

Definition 1.2 Given a positive constant d and a function $h \in L^\infty(\Omega)$, we define $\mu_1(d, h)$ to be the first eigenvalue of

$$\begin{cases} d\Delta\psi + h(x)\psi + \mu\psi = 0 & \text{in } \Omega, \\ \partial_\nu\psi = 0 & \text{on } \partial\Omega. \end{cases} \tag{1.3}$$

It is easy to see that (1.1) has two semi-trivial steady states $(\theta_{d_1,m_1}, 0)$ and $(0, \theta_{d_2,m_2})$. To characterize their linear stability properties, we introduce the following subsets in the first quadrant of the d_1d_2-plane for (1.1) as in [8]:

$$\begin{aligned}
\Sigma_U &:= \{(d_1, d_2) \in \mathcal{Q} \mid (\theta_{d_1,m_1}, 0) \text{ is linearly stable}\},\\
\Sigma_V &:= \{(d_1, d_2) \in \mathcal{Q} \mid (0, \theta_{d_2,m_2}) \text{ is linearly stable}\},\\
\Sigma_- &:= \{(d_1, d_2) \in \mathcal{Q} \mid \text{both } (\theta_{d_1,m_1}, 0) \text{ and } (0, \theta_{d_2,m_2}) \text{ are linearly unstable}\},\\
\Sigma_{U,0} &:= \{(d_1, d_2) \in \mathcal{Q} \mid \mu_1(d_2, m_2 - \theta_{d_1,m_1}) = 0\},\\
\Sigma_{V,0} &:= \{(d_1, d_2) \in \mathcal{Q} \mid \mu_1(d_1, m_1 - \theta_{d_2,m_2}) = 0\},\\
\Pi &:= \Sigma_{U,0} \cap \Sigma_{V,0},
\end{aligned} \tag{1.4}$$

where

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

For the precise definition of linear stability/instability of a steady state of (1.1) and their characterizations, see e.g., [8, Section 3].

The following result, as a first step in determining the global dynamics of (1.1), follows immediately from Theorem 3.4 in Part I [8] (with $b = c = 1$):

Theorem 1.3 ([8]) *Assume that* (**M**) *holds. Then we have the following mutually disjoint decomposition of* $\mathcal{Q}$*:*

$$\mathcal{Q} = (\Sigma_U \cup \Sigma_{U,0} \setminus \Pi) \cup (\Sigma_V \cup \Sigma_{V,0} \setminus \Pi) \cup \Sigma_- \cup \Pi \tag{1.5}$$

and

$$\Pi = \{(d_1, d_2) \in \mathcal{Q} \mid \theta_{d_1,m_1} \equiv \theta_{d_2,m_2}\}. \tag{1.6}$$

Hence, $\Pi \neq \emptyset$ *if and only if there exists* $(d_1, d_2) \in \mathcal{Q}$ *such that* $\theta_{d_1,m_1} \equiv \theta_{d_2,m_2}$*. Moreover, the following hold for* (1.1)*:*

(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* $(d_1, d_2) \in \Sigma_-$*,* (1.1) *has a unique coexistence steady state that is globally asymptotically stable.*
(iv) *For all* $(d_1, d_2) \in \Pi$*,* (1.1) *has a compact global attractor consisting of a continuum of steady states* $\{(\xi\theta_{d_1,m_1}, (1-\xi)\theta_{d_1,m_1}) \mid \xi \in [0, 1]\}$ *connecting the two semi-trivial steady states.*

As was mentioned in Part I [8], each of the four components in the decomposition of $\mathcal{Q}$ in the above general theorem could be empty. In our case, it turns out that the global dynamics of (1.1) can be further clarified as follows.

Theorem 1.4 *Assume that* (**M**) *holds, then* $\Sigma_U, \Sigma_V, \Sigma_- \neq \emptyset$ *and* $\mathcal{Q} = \overline{\Sigma_U} \cup \overline{\Sigma_V} \cup \Sigma_-$, *where* $\overline{\Sigma_U}$ *and* $\overline{\Sigma_V}$ *denote the closure of* Σ_U *and* Σ_V *in* $\mathcal{Q}$ *respectively. Moreover,* $(\theta_{d_1,m_1}, 0)$ *is globally asymptotically stable for all* $(d_1, d_2) \in \overline{\Sigma_U}$, $(0, \theta_{d_2,m_2})$ *is globally asymptotically stable for all* $(d_1, d_2) \in \overline{\Sigma_V}$ *and* (1.1) *has a unique coexistence steady state that is globally asymptotically stable for all* $(d_1, d_2) \in \Sigma_-$.

Our ultimate goal is to "visualize" those sets Σ_U, Σ_V and Σ_-. To achieve that we need to analyze geometric properties of the sets Σ_U, Σ_V and Σ_-. We first recall the following characterizations of Σ_U and Σ_V obtained in [6]:

Theorem 1.5 ([6]) *Assume that* (**M**) *holds. Then there exist two continuous functions* $d_2^*(d_1)$ *and* $d_1^*(d_2)$ *defined on* $\mathbb{R}^+$ *such that the following hold for system* (1.1)*:*

$$\Sigma_U = \{(d_1, d_2) \in \mathcal{Q} \mid d_2 > d_2^*(d_1)\} \tag{1.7}$$

and

$$\Sigma_V = \{(d_1, d_2) \in \mathcal{Q} \mid d_1 > d_1^*(d_2)\}, \tag{1.8}$$

Moreover,

$$\lim_{d_2 \to 0} d_1^*(d_2) = \lim_{d_2 \to \infty} d_1^*(d_2) = \infty, \quad \lim_{d_1 \to 0} d_2^*(d_1) = \lim_{d_1 \to \infty} d_2^*(d_1) = \infty. \tag{1.9}$$

Hence, to understand the effects of spatial concentrations of $m_1(x)$ and $m_2(x)$ on the global dynamics of (1.1) when d_1 and d_2 are large, it is necessary to analyze the asymptotic geometric properties of Σ_U, Σ_V and Σ_- as $d_1, d_2 \to \infty$ in terms of m_1 and m_2 in more details. For this purpose, we introduce the following notation as in [9]. Denote by ρ_m the unique solution of

$$\begin{cases} \Delta \rho_m + \overline{m}(m - \overline{m}) = 0 \text{ in } \Omega, \\ \partial_\nu \rho_m = 0 \text{ on } \partial\Omega, \quad \int_\Omega \rho_m = 0, \end{cases} \tag{1.10}$$

and set

$$C(m) := \frac{\int_\Omega |\nabla \rho_m|^2}{|\Omega| \overline{m}^2}. \tag{1.11}$$

We now characterize the asymptotic properties of the curves $d_2^*(d_1)$ and $d_1^*(d_2)$ as d_1 and d_2 go to infinity respectively as follows.

Theorem 1.6 *Assume that* (**M**) *holds. Then there exist two constants* $B_1 := B_1(m_1, m_2)$ *and* $B_2 := B_2(m_1, m_2)$ *such that*

$$d_2^*(d_1) = \frac{C(m_2)}{C(m_1)} d_1 + B_1 + O\left(\frac{1}{d_1}\right), \quad \textit{for all} \quad d_1 > D^*, \tag{1.12}$$

$$d_1^*(d_2) = \frac{C(m_1)}{C(m_2)} d_2 + B_2 + O\left(\frac{1}{d_2}\right), \quad \textit{for all} \quad d_2 > D^*, \tag{1.13}$$

where $D^* = D^*(\Omega, m_1, m_2)$ *is a positive constant depending only on* Ω, m_1 *and* m_2. *Furthermore, as* $d_1, d_2 \to \infty$, Σ_- *approaches asymptotically a band in* $\mathcal{Q}$ *with slope* $C(m_2)/C(m_1)$ *and width*

$$\frac{C(m_1)}{\sqrt{C^2(m_1)+C^2(m_2)}}\left(B_1+\frac{C(m_2)}{C(m_1)}B_2\right)>0.$$

Since $\Sigma_- = \mathcal{Q}\setminus(\overline{\Sigma_U}\cup\overline{\Sigma_V})$ by Theorem 1.4, the line $d_2=\frac{C(m_2)}{C(m_1)}d_1$ lies in Σ_- for all d_1 large if both $B_1, B_2>0$. Although B_1 and B_2 are given explicitly by (3.10) and (3.11) respectively in Sect. 3 below, in general, it is difficult to determine the signs of B_1 and B_2 except in some special cases [e.g., Proposition 1.7(iii)]. To visualize the set Σ_-, we compute the slope $C(m_2)/C(m_1)$ for some special choices of the pair m_1 and m_2 in the following proposition.

Proposition 1.7 *Assume that* (**M**) *holds.*

(i) *If $(m_1-\overline{m_1})=\tau(m_2-\overline{m_2})$, where $\tau>0$ is a constant, then $C(m_2)/C(m_1)=1/\tau^2$.*
(ii) *Let $N=1$ and $\Omega=(0,1)$. If $m_1=1+\cos(k_1\pi x)$ and $m_2=1+\cos(k_2\pi x)$, where k_1 and k_2 are two positive integers, then $C(m_2)/C(m_1)=k_1^2/k_2^2$.*
(iii) *Suppose $\Omega=\mathcal{S}(\Omega)$ and $m_1(x)=m_2(\mathcal{S}x)$ for all $x\in\bar{\Omega}$ for some $\mathcal{S}\in SO(\mathbb{R}^N)$, the special orthogonal group in $\mathbb{R}^N$. Then $C(m_2)/C(m_1)=1$ and $B_1(m_1,m_2)$, $B_2(m_1,m_2)>0$, which implies that for all d_1 large, the line $d_2=d_1$ lies in Σ_-.*

To illustrate some implications of Proposition 1.7, we consider the following special case of system (1.1) where U and V have identical diffusion rate $d_1=d_2=d>0$:

$$\begin{cases} U_t=d\Delta U+U(m_1(x)-U-V) & \text{in } \Omega\times\mathbb{R}^+,\\ V_t=d\Delta V+V(m_2(x)-U-V) & \text{in } \Omega\times\mathbb{R}^+,\\ \partial_\nu U=\partial_\nu V=0 & \text{on } \partial\Omega\times\mathbb{R}^+,\\ U(x,0)=U_0(x),\quad V(x,0)=V_0(x) & \text{in } \Omega. \end{cases} \tag{1.14}$$

Then Proposition 1.7(i)(ii) together with Theorems 1.4–1.6 imply the following result:

Corollary 1.8 *Under the hypothesis* (**M**)*, the followings hold for system* (1.14)*:*

(i) *If $m_1(x)=1+\alpha g(x)$ and $m_2(x)=1+\beta g(x)$, where $\alpha>\beta>0$, $\overline{g}=0$ and $g\not\equiv 0$, then for all d sufficiently small,* (1.14) *has a unique coexistence steady state that is globally asymptotically stable, and for all d sufficiently large, $(\theta_{d,m_1},0)$ is globally asymptotically stable.*
(ii) *Let $\Omega=(0,1)$. If $m_1=1+\cos(k_1\pi x)$ and $m_2=1+\cos(k_2\pi x)$, where k_1,k_2 are two integers satisfying $0<k_1<k_2$, then for all d sufficiently small,* (1.14) *has a unique coexistence steady state that is globally asymptotically stable, and for all d sufficiently large, $(\theta_{d,m_1},0)$ is globally asymptotically stable.*

Corollary 1.8(i) indicates that the "sharper spatial concentration" in the distribution of resources the better; and Corollary 1.8(ii) indicates that the "lesser spatial oscillation" in the distribution of resources the better for the species' competition.

For more examples of calculating the explicit value of $C(\cdot)$, we refer to Theorems 4.1 and 4.2 in [9]. Roughly speaking, results there indicate that in the one-dimensional case (i.e., Ω is an interval), if m is sufficiently close to, in the distributional sense, a δ-function supported on one endpoint of the interval, then $C(m)$ tends to achieve a larger value. We intend to investigate properties of $C(m)$ in more details in the near future.

Next, we characterize asymptotic behaviors of the unique coexistence steady states of (1.1) in the region $(d_1,d_2)\in\Sigma_-=\mathcal{Q}\setminus(\overline{\Sigma_U}\cup\overline{\Sigma_V})$ as $d_1,d_2\to\infty$.

Theorem 1.9 *Assume that* (**M**) *holds. Let* $\{(d_{1,k}, d_{2,k})\}_{k=1}^{\infty}$ *be any sequence in* Σ_- *satisfying*

$$\begin{cases} d_{1,k} \to \infty, \\ d_{2,k} - \frac{C(m_2)}{C(m_1)} d_{1,k} \to B_1 - p\left(B_1 + \frac{C(m_2)}{C(m_1)} B_2\right), \quad \text{for some } p \in (0,1), \end{cases} \quad \text{as } k \to \infty, \tag{1.15}$$

then

$$(U_k, V_k) \to ((1-p)\overline{m_1}|\Omega|, p\overline{m_1}|\Omega|) \text{ in } C^2(\bar{\Omega}) \times C^2(\bar{\Omega}), \quad \text{as } k \to \infty,$$

where (U_k, V_k) *is the unique coexistence steady state of* (1.1) *with* $(d_1, d_2) = (d_{1,k}, d_{2,k})$.

Finally, to complement Theorem 1.9, we state the following results concerning limiting behaviors of the unique coexistence steady states of (1.1) with $(d_1, d_2) \in \Sigma_-$, which is a direct consequence of [6, Theorem 4.1] and Theorem 1.4.

Theorem 1.10 *Assume that* (**M**) *holds. Let* $(d_1, d_2) \in \Sigma_- = \mathcal{Q} \setminus (\overline{\Sigma_U} \cup \overline{\Sigma_V})$ *and* (U, V) *be the corresponding unique coexistence steady state of* (1.1), *then*

(i) $\lim\limits_{d_1 \to \infty} \lim\limits_{d_2 \to 0^+} (U, V) = (\inf\limits_{\Omega} m_2, m_2 - \inf\limits_{\Omega} m_2)$.
(ii) $\lim\limits_{d_2 \to \infty} \lim\limits_{d_1 \to 0^+} (U, V) = (m_1 - \inf\limits_{\Omega} m_1, \inf\limits_{\Omega} m_1)$.
(iii) $\lim\limits_{d_1, d_2 \to 0^+} (U, V) = (u_*, v_*)$ *uniformly on compact subsets of* $\bar{\Omega} \setminus \{x \in \bar{\Omega} \mid m_1(x) = m_2(x)\}$, *where*

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

and

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

We remark that the positivity condition $m_i(x) \geqslant 0$ on $\bar{\Omega}$ for $i = 1, 2$ in (**M**) can be relaxed to $\overline{m_1} = \overline{m_2} > 0$ and most of our results still hold. When $m_1(x)$ or $m_2(x)$ changes sign in Ω, we refer the readers to [6, Section 5] for the necessary modifications. For previous work on models similar to (1.1), we refer the reader to e.g., [2–4,6,7,10–17,20] and references therein.

The rest of this paper is organized as follows. In Sect. 2, we prove Theorem 1.4 and then establish some preliminaries which will be used in subsequent sections. In Sect. 3, we prove Theorem 1.6, Proposition 1.7 and Theorem 1.9. In Sect. 4, we illustrate the transition of the dynamics of (1.1) when the spatial distribution of resources for the species V deforms smoothly from a heterogeneous one to its average. By connecting the dynamics of the two systems studied in Part II [9] and Part III here, we hope to exhibit a clear understanding of the effects of spatial concentration on the global dynamics of (1.1).

2 Preliminaries and proof of Theorem 1.4

In this section, we first show that Theorem 1.4 is a direct consequence of Theorem 1.3 and the following result.

Proposition 2.1 *Assume that* (**M**) *holds. Then for* (1.1), *we have* $\Pi = \emptyset$, $\Sigma_U \cup \Sigma_{U,0} = \overline{\Sigma_U}$, $\Sigma_V \cup \Sigma_{V,0} = \overline{\Sigma_V}$ *and* $\Sigma_- = \mathcal{Q} \setminus (\overline{\Sigma_U} \cup \overline{\Sigma_V})$.

Proof By (1.6), to prove that $\Pi = \emptyset$, if suffices to show that the set

$$\{(d_1, d_2) \in \mathcal{Q} \mid \theta_{d_1,m_1} \equiv \theta_{d_2,m_2}\} = \emptyset.$$

Assume for contradiction that there exists some $(d_1^*, d_2^*) \in \mathcal{Q}$ such that $\theta_{d_1^*,m_1} \equiv \theta_{d_2^*,m_2}$, then dividing the equation for $\theta_{d_1^*,m_1}$ and $\theta_{d_2^*,m_2}$ by $d_1^*\theta_{d_1^*,m_1}$ and $d_2^*\theta_{d_2^*,m_2}$ respectively, we obtain that

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

Integrating the above identity over Ω and using condition (**M**), we obtain that

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

As first observed by Lou [15], dividing the equation for θ_{d_i,m_i} by θ_{d_i,m_i} itself and integrating over Ω, $i = 1, 2$, we obtain that

$$\int_\Omega \theta_{d_i,m_i} > \int_\Omega m_i, \quad \text{for all } d_i > 0, i = 1, 2. \tag{2.1}$$

Thus the above equality implies that $d_1^* = d_2^*$, which in turn implies that $m_1 \equiv m_2$, contradicting (**M**). This proves that $\Pi = \emptyset$.

To prove the second and third identities, by Theorem 3.3(iii) and (iv) in [8], it suffices to show that

$$m_1 \not\equiv \theta_{d_2,m_2} \text{ and } m_2 \not\equiv \theta_{d_1,m_1} \quad \text{for any } d_1, d_2 > 0, \tag{2.2}$$

which again follows from (2.1) directly.

The last identity follows from the mutually disjoint decomposition of $\mathcal{Q}$ in (1.5). □

Next we introduce the following eigenvalue problem with indefinite weight:

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

where $h \in L^\infty(\Omega)$ is nonconstant and could change sign in Ω. We say that λ is a *principal eigenvalue*, if (2.3) has a positive solution. (Notice that 0 is always a principal eigenvalue.) The following result is standard. For a proof, see e.g., [1,19].

Proposition 2.2 *The problem* (2.3) *has a nonzero principal eigenvalue* $\lambda_1 = \lambda_1(h)$ *if and only if* h *changes sign and* $\int_\Omega h \neq 0$. *More precisely, if* h *changes sign, then*

(i) $\int_\Omega h = 0 \Leftrightarrow 0$ *is the only principal eigenvalue.*
(ii) $\int_\Omega h > 0 \Leftrightarrow \lambda_1(h) < 0$.
(iii) $\int_\Omega h < 0 \Leftrightarrow \lambda_1(h) > 0$.
(iv) $\lambda_1(h_1) > \lambda_1(h_2)$ *if* $h_1 \leq h_2$, $h_1 \not\equiv h_2$ *a.e., and* h_1, h_2 *both change sign.*
(v) $\lambda_1(h)$ *is continuous in* h*; more precisely,* $\lambda_1(h_\ell) \to \lambda_1(h)$ *if* $h_\ell \to h$ *in* $L^\infty(\Omega)$.

Recall that we have defined $\theta_{d,g}$ as the unique positive solution of (1.2). The following lemma summarizes some useful properties of $\theta_{d,g}$ which will be used in subsequent sections.

Lemma 2.3 *Assume that* $g(x) \in C^\alpha(\bar{\Omega})$ $(\alpha \in (0, 1))$, $\int_\Omega g \geqslant 0$, *and* $g \not\equiv \text{const}$. *Then the following hold:*

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

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

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

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

The continuous dependence of $\theta_{d,g}$ on d can be proved by an application of Implicit Function Theorem. (See Proposition 3.6 in [3] and remarks there.) The proofs of limiting behaviors of $\theta_{d,g}$ as d goes to 0^+ and ∞ are standard, see e.g. [3,11]. The proofs of Lemma 2.3(ii) can be found in [14, Proposition 2.4] and [6, Lemma 2.3].

Finally, we recall the following asymptotically expansion of $\theta_{d,m}$ as $d \to \infty$ established in [9].

Proposition 2.4 *Assume that* (**M**) *holds. Then there exists a constant $D_m > 0$ depending only on m such that*

$$\theta_{d,m} = \overline{m} + \frac{\rho_m + C(m)}{d} + \frac{\gamma_m + K(m)}{d^2} + O\left(\frac{1}{d^3}\right) \quad \textit{for all} \quad d > D_m, \tag{2.4}$$

where ρ_m and $C(m)$ are defined in (1.10) *and* (1.11) *respectively, γ_m is the unique solution of*

$$\begin{cases} \Delta\gamma_m + (m - 2\overline{m})(\rho_m + C(m)) = 0 \text{ in } \Omega, \\ \partial_\nu \gamma_m = 0 \text{ on } \partial\Omega, \quad \int_\Omega \gamma_m = 0, \end{cases} \tag{2.5}$$

and

$$K(m) := \frac{1}{\overline{m}^2 |\Omega|} \int_\Omega (m - 3\overline{m}) \rho_m^2. \tag{2.6}$$

3 Proofs of the main results

In this section, we prove Theorem 1.6, Proposition 1.7 and Theorem 1.9. We first prove Theorem 1.6.

Proof of Theorem 1.6 We first prove (1.12). From the proof of Theorem 1.5(i) in [6], we know that

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

Note that $\lambda_1(h)$ is defined as the nonzero principal eigenvalue of (2.3). By Lemma 2.3 and (**M**), $m_2 - \theta_{d_1,m_1}$ changes sign for all d_1 large. Therefore to prove (1.12), it suffices to show that there exist two constants $D^* := D^*(\Omega, m_1, m_2) > 0$ and $B_1 := B_1(m_1, m_2)$ such that

$$\frac{1}{\lambda_1(m_2 - \theta_{d_1,m_1})} = \frac{C(m_2)}{C(m_1)} d_1 + B_1 + O\left(\frac{1}{d_1}\right) \quad \text{for all } d_1 > D^*. \tag{3.1}$$

For notational convenience, we denote

$$\lambda_1 := \lambda_1(m_2 - \theta_{d_1,m_1})$$

in the rest of this proof. First we claim that

$$d_1\lambda_1 - \frac{C(m_1)}{C(m_2)} = o(1) \quad \text{as } d_1 \to \infty. \tag{3.2}$$

Let $\varphi_1 > 0$ be the eigenfunction corresponding to λ_1 normalized such that

$$\|\varphi_1\|_{L^\infty(\Omega)} = \overline{m_2}.$$

By Lemma 2.3 and (**M**), $\int_\Omega (m_2 - \theta_{d_1,m_1}) \to 0$ as $d_1 \to \infty$. Therefore by Proposition 2.2(i) and (v), $\lambda_1 \to 0$ as $d_1 \to \infty$. Now letting $d_1 \to \infty$, by standard elliptic regularity estimates, we deduce that, passing to a subsequence of d_1 if necessary, φ_1 converges to $\hat{\varphi}_1$ in $W^{2,p}(\Omega) \cap C^{1,\alpha}(\bar{\Omega})$ for some constant $\hat{\varphi}_1 \geqslant 0$. Since $\|\varphi_1\|_{L^\infty(\Omega)} = \overline{m_2}$, we must have $\hat{\varphi}_1 = \overline{m_2}$. This implies that $\varphi_1 = \overline{m_2} + o(1)$ as $d_1 \to \infty$. Next rewrite

$$\varphi_1 = \overline{m_2} + \lambda_1 \rho_{m_2} + \frac{\omega}{d_1^2}.$$

By direct calculation, ω satisfies the following equation

$$\begin{cases} \Delta\omega + \lambda_1 \cdot (m_2 - \theta_{d_1,m_1})\omega + R = 0 & \text{in } \Omega, \\ \partial_\nu \omega = 0 \quad \text{on } \partial\Omega, \end{cases}$$

where

$$R := (\lambda_1 d_1)^2 \rho_{m_2}(m_2 - \theta_{d_1,m_1}) + \lambda_1 d_1^2 \overline{m_2}(\overline{m_2} - \theta_{d_1,m_1}). \tag{3.3}$$

Multiplying the equation for φ_1 by ω and the equation for ω by φ_1, integrating over Ω and subtracting the results, we obtain that

$$\int_\Omega R\varphi_1 = 0.$$

Dividing both sides of the above identity by $\lambda_1 d_1$, by (2.4), (3.3) and the fact that $\varphi_1 = \overline{m_2} + o(1)$ on $\bar{\Omega}$, we can further compute that as $d_1 \to \infty$,

$$\begin{aligned} 0 &= \lambda_1 d_1 \int_\Omega \rho_{m_2}(m_2 - \overline{m_2} + o(1))(\overline{m_2} + o(1)) - \int_\Omega \overline{m_2}(\rho_{m_1} + C(m_1) + o(1))(\overline{m_2} + o(1)) \\ &= \lambda_1 d_1 (\overline{m_2}^2 |\Omega| C(m_2) + o(1)) - \overline{m_2}^2 |\Omega| C(m_1) + o(1), \end{aligned} \tag{3.4}$$

where we used the identity

$$\int_\Omega \overline{m_i}(m_i - \overline{m_i})\rho_{m_i} = \int_\Omega |\nabla \rho_{m_i}|^2 = \overline{m_i}^2 |\Omega| C(m_i), \quad i = 1, 2, \tag{3.5}$$

obtained by multiplying the equation for ρ_{m_i} by ρ_{m_i} and integrating over Ω. Therefore (3.2) follows by letting $d_1 \to \infty$ in (3.4).

Define

$$\psi_1 := \frac{\overline{m_2}|\Omega|}{\|\varphi_1\|_{L^1(\Omega)}} \varphi_1,$$

i.e., $\psi_1 > 0$ is a renormalization of φ_1 such that $\|\psi_1\|_{L^1(\Omega)} = \overline{m_2}|\Omega|$. Rewrite

$$\psi_1 = \overline{m_2} + \lambda_1 \rho_{m_2} + \frac{\chi}{d_1^2}.$$

Since $\varphi_1 = \overline{m_2} + o(1)$ on $\bar{\Omega}$ and $\|\varphi_1\|_{L^1(\Omega)} = \overline{m_2}|\Omega| + o(1)$ as $d_1 \to \infty$,

$$\psi_1 = \frac{\overline{m_2}|\Omega|}{\overline{m_2}|\Omega| + o(1)}(\overline{m_2} + o(1)) = \overline{m_2} + o(1) \quad \text{as } d_1 \to \infty.$$

As $\psi_1 > 0$ on $\bar{\Omega}$, $\|\psi_1\|_{L^1(\Omega)} = \overline{m_2}|\Omega|$ and $\int_\Omega \rho_{m_2} = 0$, we have $\int_\Omega \chi = 0$. Hence χ satisfies the following equation:

$$\begin{cases} \Delta\chi + \lambda_1 \cdot (m_2 - \theta_{d_1,m_1})\chi + R = 0 & \text{in } \Omega, \\ \partial_\nu \chi = 0 \quad \text{on } \partial\Omega, \quad \int_\Omega \chi = 0. \end{cases}$$

Note that χ satisfies the same equation as ω.

Let us denote by $[\psi_1]^\perp$ the complement of ψ_1 in $L^2(\Omega)$. By Fredholm alternative, we can define the inverse of $\Delta + \lambda_1 \cdot (m_2 - \theta_{d_1,m_1})$ when restricted to $[\psi_1]^\perp$. Let us denote by $\mathcal{L}_{d_1}^{-1}$ its inverse. Then it is obvious that $\|\mathcal{L}_{d_1}^{-1}\|_{[\psi_1]^\perp}$ is bounded uniformly for all d_1 large. Decompose χ as

$$\chi = c\psi_1 + \mathcal{L}_{d_1}^{-1} R,$$

where c is a constant such that $\int_\Omega \chi = 0$. Since R converges and $\lim_{d_1\to\infty} \mathcal{L}_{d_1}^{-1}$ equals Δ^{-1} restricted to $\{f \in L^2(\Omega) \mid \overline{f} = 0\}$, we deduce that $c \to 0$, as $d_1 \to \infty$. Therefore $\|\chi\|_{L^\infty(\Omega)}$ is bounded uniformly for all d_1 large. Hence

$$\psi_1 = \overline{m_2} + \lambda_1 \rho_{m_2} + O\left(\frac{1}{d_1^2}\right) \quad \text{for all } d_1 > D^*(\Omega, m_1, m_2). \tag{3.6}$$

Similar as before, we can show that $\int_\Omega R\psi_1 = 0$. Dividing both sides of the identity $\int_\Omega R\psi_1 = 0$ by λ_1 and by (3.3), we have

$$0 = \lambda_1 d_1^2 \int_\Omega \rho_{m_2}(m_2 - \theta_{d_1,m_1})\psi_1 + d_1^2 \int_\Omega \overline{m_2}(\overline{m_2} - \theta_{d_1,m_1})\psi_1 =: I_1 + I_2. \tag{3.7}$$

By (**M**), (2.4), (3.2), (3.5) and (3.6), we can estimate I_1 and I_2 as follows:

$$\begin{aligned} I_1 &= \lambda_1 d_1^2 \int_\Omega \rho_{m_2} \left[m_2 - \overline{m_2} - \frac{1}{d_1}(\rho_{m_1} + C(m_1)) + O\left(\frac{1}{d_1^2}\right)\right] \left(\overline{m_2} + \lambda_1\rho_{m_2} + O\left(\frac{1}{d_1^2}\right)\right) \\ &= \lambda_1 d_1^2 \overline{m_2}^2 C(m_2)|\Omega| - \lambda_1 d_1 \overline{m_2} \int_\Omega \rho_{m_1}\rho_{m_2} + (\lambda_1 d_1)^2 \int_\Omega (m_2 - \overline{m_2})\rho_{m_2}^2 + O\left(\frac{1}{d_1}\right), \\ I_2 &= -d_1 \int_\Omega \overline{m_2} \left[(\rho_{m_1} + C(m_1)) + \frac{1}{d_1}(\gamma_{m_1} + K(m_1)) + O\left(\frac{1}{d_1^2}\right)\right] \left(\overline{m_2} + \lambda_1\rho_{m_2} + O\left(\frac{1}{d_1^2}\right)\right) \\ &= -d_1 \overline{m_2}^2 C(m_1)|\Omega| - \lambda_1 d_1 \overline{m_2} \int_\Omega \rho_{m_1}\rho_{m_2} - \overline{m_2}^2 K(m_1)|\Omega| + O\left(\frac{1}{d_1}\right), \end{aligned}$$

for all $d_1 > D^*(\Omega, m_1, m_2)$. Therefore by (2.6) and (3.7), we have

$$\begin{aligned} &d_1(\overline{m_2}^2 C(m_1)|\Omega| - \lambda_1 d_1 \overline{m_2}^2 C(m_2)|\Omega|) \\ &\quad = (\lambda_1 d_1)^2 \int_\Omega \overline{m_2}\rho_{m_2}^2 - 2\lambda_1 d_1 \overline{m_2} \int_\Omega \rho_{m_1}\rho_{m_2} + \int_\Omega \overline{m_2}\rho_{m_1}^2 \\ &\quad\quad + (\lambda_1 d_1)^2 \int_\Omega (m_2 - 2\overline{m_2})\rho_{m_2}^2 - \int_\Omega (m_1 - 2\overline{m_1})\rho_{m_1}^2 + O\left(\frac{1}{d_1}\right), \end{aligned} \tag{3.8}$$

for all $d_1 > D^*(\Omega, m_1, m_2)$. Dividing both sides of (3.8) by $\lambda_1 d_1 \overline{m_2}^2 |\Omega|$ and using (3.2), we have

$$\begin{aligned} & d_1 C(m_1) \left(\frac{1}{\lambda_1 d_1} - \frac{C(m_2)}{C(m_1)} \right) \\ & = \frac{1}{\overline{m_2}|\Omega|} \int_\Omega \left(\sqrt{\lambda_1 d_1} \rho_{m_2} - \frac{\rho_{m_1}}{\sqrt{\lambda_1 d_1}} \right)^2 \\ & \quad + \frac{1}{\overline{m_2}^2 |\Omega|} \left((\lambda_1 d_1) \int_\Omega (m_2 - 2\overline{m_2}) \rho_{m_2}^2 - \frac{1}{\lambda_1 d_1} \int_\Omega (m_1 - 2\overline{m_1}) \rho_{m_1}^2 \right) + O\left(\frac{1}{d_1}\right), \end{aligned} \tag{3.9}$$

for all $d_1 > D^*(\Omega, m_1, m_2)$. Therefore by (3.2),

$$\frac{1}{\lambda_1 d_1} - \frac{C(m_2)}{C(m_1)} = O\left(\frac{1}{d_1}\right),$$

i.e.,

$$\lambda_1 d_1 = \frac{C(m_1)}{C(m_2)} + O\left(\frac{1}{d_1}\right) \quad \text{for all } d_1 > D^*(\Omega, m_1, m_2).$$

Plugging them back to the right hand side of (3.9), we obtain that

$$d_1 \left(\frac{1}{\lambda_1 d_1} - \frac{C(m_2)}{C(m_1)} \right) = B_1(m_1, m_2) + O\left(\frac{1}{d_1}\right),$$

for all $d_1 > D^*(\Omega, m_1, m_2)$, where

$$\begin{aligned} B_1(m_1, m_2) := & \frac{1}{\overline{m_2}|\Omega|} \int_\Omega \left(\frac{\rho_{m_2}}{\sqrt{C(m_2)}} - \frac{\sqrt{C(m_2)}}{C(m_1)} \rho_{m_1} \right)^2 \\ & + \frac{1}{\overline{m_2}^2 |\Omega|} \left(\frac{1}{C(m_2)} \int_\Omega (m_2 - 2\overline{m_2}) \rho_{m_2}^2 - \frac{C(m_2)}{C^2(m_1)} \int_\Omega (m_1 - 2\overline{m_1}) \rho_{m_1}^2 \right). \end{aligned} \tag{3.10}$$

This finishes the proof of (3.1). (1.13) follows by similar arguments as in the proof of (1.12) with $B_2 := B_2(m_1, m_2)$ defined by

$$\begin{aligned} B_2(m_1, m_2) := & \frac{1}{\overline{m_2}|\Omega|} \int_\Omega \left(\frac{\rho_{m_1}}{\sqrt{C(m_1)}} - \frac{\sqrt{C(m_1)}}{C(m_2)} \rho_{m_2} \right)^2 \\ & + \frac{1}{\overline{m_2}^2 |\Omega|} \left(\frac{1}{C(m_1)} \int_\Omega (m_1 - 2\overline{m_1}) \rho_{m_1}^2 - \frac{C(m_1)}{C^2(m_2)} \int_\Omega (m_2 - 2\overline{m_2}) \rho_{m_2}^2 \right). \end{aligned} \tag{3.11}$$

Hence

$$B_1 + \frac{C(m_2)}{C(m_1)} B_2 = \frac{2}{\overline{m_2}|\Omega|} \int_\Omega \left(\frac{\rho_{m_2}}{\sqrt{C(m_2)}} - \frac{\sqrt{C(m_2)}}{C(m_1)} \rho_{m_1} \right)^2. \tag{3.12}$$

It is obvious that $B_1 + \frac{C(m_2)}{C(m_1)} B_2 = 0$ if and only of

$$\rho_{m_1} \equiv \frac{C(m_1)}{C(m_2)} \rho_{m_2}.$$

By (1.10), (1.11) and (**M**), this implies that

$$(m_1 - \overline{m_1}) \equiv \frac{C(m_1)}{C(m_2)}(m_2 - \overline{m_2}) \quad \text{and} \quad \frac{C^2(m_1)}{C^2(m_2)} = \frac{C(m_1)}{C(m_2)}.$$

Hence $C(m_1) = C(m_2)$ and $m_1 \equiv m_2$, which is a contradiction to (**M**). Therefore the distance between the two parallel lines $d_2 = \frac{C(m_2)}{C(m_1)} d_1 + B_1$ and $d_1 = \frac{C(m_1)}{C(m_2)} d_2 + B_2$ is

$$\begin{aligned} &\frac{C(m_1)}{\sqrt{C^2(m_1) + C^2(m_2)}} \left(B_1 + \frac{C(m_2)}{C(m_1)} B_2 \right) \\ &\quad = \frac{2}{\overline{m_2}|\Omega|\sqrt{C^2(m_1) + C^2(m_2)}} \int_\Omega \left(\sqrt{\frac{C(m_1)}{C(m_2)}} \rho_{m_2} - \sqrt{\frac{C(m_2)}{C(m_1)}} \rho_{m_1} \right)^2 > 0 \end{aligned}$$

with the first line lying above the second one. Since $\Sigma_- = \mathcal{Q} \setminus (\overline{\Sigma_U} \cup \overline{\Sigma_V})$, the last statement of the theorem follows. □

Proof of Proposition 1.7 (i) follows from (1.11) and the fact that $\rho_{m_1} = \tau \rho_{m_2}$. For (ii), it is easy to check that

$$\rho_{m_1} = \frac{1}{k_1^2} \cos(k_1 \pi x), \qquad \rho_{m_2} = \frac{1}{k_2^2} \cos(k_2 \pi x).$$

Therefore by (1.11) and direct computation, we obtain (ii). Finally we show (iii). It is obvious that $C(m_1) = C(m_2)$, since $\rho_{m_1}(x) = \rho_{m_2}(\mathcal{S}x)$. Then $B_i(m_1, m_2) > 0, i = 1, 2$, follow from (3.10) and (3.11). Therefore by Theorem 1.6, $d_2 = d_1$ lies in Σ_- for all d_1 large. □

To prove Theorem 1.9, we need some *uniform estimates* related to the coexistence steady state solution (U, V) of (1.1) *in terms of* d_1 *and* d_2 when $(d_1, d_2) \in \Sigma_-$. Therefore, from now on we make it a *standing convention* that the estimate in the O-notation is uniform in all other variables which do not appear explicitly. We will also denote C^* a sufficiently large positive number which depends only on m_1 and m_2 and may change from place to place in the rest of this paper.

First we establish the following fundamental but important estimates.

Lemma 3.1 *Assume that* (**M**) *holds. Let* (U, V) *be the unique coexistence steady state of* (1.1) *with* $(d_1, d_2) \in \Sigma_-$ *and* $d_1, d_2 > C^*$, *then the following hold:*

$$\frac{\int_\Omega |\nabla U|^2}{\overline{U}^2} = O\left(\frac{1}{d_1^2}\right) \text{ uniformly in } d_2, \quad \text{for all } d_1 > C^* \tag{3.13}$$

and

$$\frac{\int_\Omega |\nabla V|^2}{\overline{V}^2} = O\left(\frac{1}{d_2^2}\right) \text{ uniformly in } d_1, \quad \text{for all } d_2 > C^*. \tag{3.14}$$

Let z *be the unique solution to*

$$\Delta z + \overline{U} - U = 0 \text{ in } \Omega, \quad \partial_\nu z = 0 \text{ on } \partial\Omega, \quad \int_\Omega z = 0, \tag{3.15}$$

and r *be the unique solution to*

$$\Delta r + \overline{V} - V = 0 \text{ in } \Omega, \quad \partial_\nu r = 0 \text{ on } \partial\Omega, \quad \int_\Omega r = 0. \tag{3.16}$$

Then we have the following estimates:

$$\int_\Omega |\nabla z|^2 = O\left(\frac{\overline{U}^2}{d_1^2}\right) \quad \textit{and} \quad \int_\Omega z^2 = O\left(\frac{\overline{U}^2}{d_1^2}\right) \textit{ uniformly in } d_2, \textit{ for all } d_1 > C^*, \tag{3.17}$$

$$\int_\Omega |\nabla r|^2 = O\left(\frac{\overline{V}^2}{d_2^2}\right) \quad \textit{and} \quad \int_\Omega r^2 = O\left(\frac{\overline{V}^2}{d_2^2}\right) \textit{ uniformly in } d_1, \textit{ for all } d_2 > C^*, \tag{3.18}$$

$$C(m_i - U) = C(m_i) + O\left(\frac{\overline{U}}{d_1}\right) \quad \textit{uniformly in } d_2, \quad \textit{for all } d_1 > C^*, i = 1, 2, \tag{3.19}$$

$$C(m_i - V) = C(m_i) + O\left(\frac{\overline{V}}{d_2}\right) \quad \textit{uniformly in } d_1, \quad \textit{for all } d_2 > C^*, i = 1, 2. \tag{3.20}$$

Proof First we prove (3.13). Multiplying the equation for U by $U - \overline{U}$ and integrating over Ω, we obtain that

$$\begin{aligned} d_1 \int_\Omega |\nabla U|^2 &= \int_\Omega (U - \overline{U}) U (m_1 - U - V) \\ &\leqslant \left(\int_\Omega (U - \overline{U})^2\right)^{1/2} \left(\int_\Omega U^2 (m_1 - U - V)^2\right)^{1/2} \\ &\leqslant C_\Omega \left(\int_\Omega |\nabla U|^2\right)^{1/2} \left(\int_\Omega U^2 (m_1 - U - V)^2\right)^{1/2}, \end{aligned} \tag{3.21}$$

where we have used Hölder's inequality and Poincaré's inequality with the constant C_Ω only depending on Ω. By the Maximum Principle, both $\|U\|_{L^\infty(\Omega)}$ and $\|V\|_{L^\infty(\Omega)}$ are uniformly bounded in d_1 and d_2. Hence, by standard L^1 elliptic regularity estimates, we have

$$\|U\|_{L^\infty(\Omega)} = O(\|U\|_{L^1(\Omega)}) = O(\overline{U}) \text{ uniformly in } d_2, \text{ for all } d_1 > C^*.$$

Therefore, by (3.21), we have

$$d_1 \left(\int_\Omega |\nabla U|^2\right)^{1/2} \leqslant C_\Omega \|U\|_{L^\infty(\Omega)} \left(\int_\Omega (m_1 - U - V)^2\right)^{1/2} = O(\overline{U})$$

uniformly in d_2, for all $d_1 > C^*$. This implies (3.13). The proof of (3.14) is similar to that of (3.13) and is thus omitted.

Multiplying the equation for z by z and integrating over Ω, we obtain that

$$\begin{aligned} \int_\Omega |\nabla z|^2 &= \int_\Omega (\overline{U} - U) z \leqslant c(\delta) \int_\Omega (\overline{U} - U)^2 + \delta \int_\Omega z^2 \\ &\leqslant c(\delta) C_\Omega^2 \int_\Omega |\nabla U|^2 + \delta C_\Omega^2 \int_\Omega |\nabla z|^2, \end{aligned}$$

where we used Young's inequality and Poincaré's inequality. Thus the first estimate in (3.17) follows from (3.13) and the above estimate by choosing $\delta > 0$ small such that $\delta C_\Omega^2 < 1/2$. The second estimate in (3.17) follows from Poincaré's inequality.

The proof of (3.18) is similar to that of (3.17) and is thus omitted.

By (1.10), (3.15) and (3.16), it is easy to see that

$$\rho_{m_i-U}=\overline{m_i-U}\left(\frac{\rho_{m_i}}{\overline{m_1}}+z\right),\qquad \rho_{m_i-V}=\overline{m_i-V}\left(\frac{\rho_{m_i}}{\overline{m_1}}+r\right),\qquad i=1,2. \tag{3.22}$$

Therefore by (1.11),

$$C(m_i-U)=C(m_i)-\frac{2}{\overline{m_1}|\Omega|}\int_\Omega \rho_{m_i}(U-\overline{U})+\int_\Omega |\nabla z|^2,\quad i=1,2, \tag{3.23}$$

$$C(m_i-V)=C(m_i)-\frac{2}{\overline{m_1}|\Omega|}\int_\Omega \rho_{m_i}(V-\overline{V})+\int_\Omega |\nabla r|^2,\quad i=1,2. \tag{3.24}$$

By Hölder's inequality and Poincaré's inequality,

$$\begin{aligned}\int_\Omega \rho_{m_i}(U-\overline{U}) &\leqslant \left(\int_\Omega \rho_{m_i}^2\right)^{1/2}\left(\int_\Omega (U-\overline{U})^2\right)^{1/2}\\ &\leqslant C_\Omega\left(\int_\Omega \rho_{m_i}^2\right)^{1/2}\left(\int_\Omega |\nabla U|^2\right)^{1/2}.\end{aligned}$$

Thus (3.19) follows from (3.13) and (3.17). By similarly arguments, we can prove (3.20). □

In the next proposition, we will derive expansions of U and V in a similar fashion as we did in Proposition 2.4. However, as U and V depend on both d_1 and d_2 and we need uniform estimates in all other variables which do not appear explicitly in the $O-$notation, we will be very careful when calculating those estimates.

Proposition 3.2 *Assume that* (**M**) *holds. Let* (U,V) *be the unique coexistence steady state of* (1.1) *with* $(d_1,d_2)\in\Sigma_-$, *then the following holds:*

$$\overline{m_1}<\overline{U}+\overline{V}<\overline{m_1}+\min\left\{O\left(\frac{1}{d_1}\right),O\left(\frac{1}{d_2}\right)\right\},\quad \textit{for all}\quad d_1,d_2>C^*. \tag{3.25}$$

Moreover, let $\xi,\eta>0$ *be any two fixed constants, then the following hold:*

(i) *There exist a constant* $C_1^*(\xi)$ *which depends only on* ξ, Ω, m_1, *and* m_2 *and may change from place to place, and a constant* $D_1^*(\xi)$ *which depends only on* ξ, Ω, m_1, *and* m_2 *such that if* $\overline{U}\geqslant\xi\overline{m_1}$, *then*

$$U=\overline{m_1-V}+\frac{\rho_{m_1-V}+C(m_1-V)}{d_1}+\frac{\gamma_{m_1-V}+K(m_1-V)}{d_1^2}+O\left(\frac{C_1^*(\xi)}{d_1^3}\right), \tag{3.26}$$

$$d_2=\frac{C(m_2-V)}{C(m_1-V)}d_1+B_1(m_1-V,m_2-V)+O\left(\frac{C_1^*(\xi)}{d_1}\right) \tag{3.27}$$

uniformly in $d_2>C^*$, *for all* $d_1>D_1^*(\xi)$.

(ii) *There exist a constant* $C_2^*(\eta)$ *which depends only on* η, Ω, m_1, *and* m_2 *and may change from place to place, and a constant* $D_2^*(\eta)$ *which depends only on* η, Ω, m_1, *and* m_2 *such that if* $\overline{V}\geqslant\eta\overline{m_1}$, *then*

$$V=\overline{m_2-U}+\frac{\rho_{m_2-U}+C(m_2-U)}{d_2}+\frac{\gamma_{m_2-U}+K(m_2-U)}{d_2^2}+O\left(\frac{C_2^*(\eta)}{d_2^3}\right), \tag{3.28}$$

$$d_1=\frac{C(m_1-U)}{C(m_2-U)}d_2+B_2(m_1-U,m_2-U)+O\left(\frac{C_2^*(\eta)}{d_2}\right) \tag{3.29}$$

uniformly in $d_1 > C^*$, *for all* $d_2 > D_2^*(\eta)$.

Proof Note that by the Maximum Principle and Harnack inequality [5], any coexistence steady state (U, V) of (1.1) satisfies that $U, V > 0$ on $\bar{\Omega}$. Dividing the equation for U (resp. V) by U (resp. V) and integrating over Ω, we obtain by (**M**) that

$$|\Omega|(\overline{U} + \overline{V} - \overline{m_1}) = d_1 \int_\Omega \frac{|\nabla U|^2}{U^2} = d_2 \int_\Omega \frac{|\nabla V|^2}{V^2}.$$

Since both $U, V \not\equiv$ const, the first inequality in (3.25) is proved. Integrating the equation for U over Ω, we have

$$\begin{aligned}
0 &= \int_\Omega U(U + V - m_1) \\
&= \int_\Omega U(\overline{U} + \overline{V} - \overline{m_1}) + \int_\Omega (U - \overline{U})U - \int_\Omega (m_1 - V - \overline{m_1 - V})U \\
&= |\Omega|\overline{U}(\overline{U} + \overline{V} - \overline{m_1}) + \int_\Omega (U - \overline{U})^2 - \int_\Omega (m_1 - V - \overline{m_1 - V})(U - \overline{U}).
\end{aligned}$$

Hence, by Hölder's inequality and Poincaré's inequality,

$$\begin{aligned}
|\Omega|(\overline{U} + \overline{V} - \overline{m_1}) &= -\int_\Omega \frac{(U - \overline{U})^2}{\overline{U}} + \frac{1}{\overline{U}} \int_\Omega (m_1 - V - \overline{m_1 - V})(U - \overline{U}) \\
&\leqslant \frac{1}{\overline{U}} \left(\int_\Omega (m_1 - V - \overline{m_1 - V})^2 \right)^{1/2} \left(\int_\Omega (U - \overline{U})^2 \right)^{1/2} \\
&\leqslant C_\Omega \left(\int_\Omega (m_1 - V - \overline{m_1 - V})^2 \right)^{1/2} \frac{\left(\int_\Omega |\nabla U|^2\right)^{1/2}}{\overline{U}} \\
&= O\left(\frac{1}{d_1}\right)
\end{aligned}$$

uniformly in d_2, for all $d_1 > C^*$, where we used (3.13) in the last identity. Similarly, we can show that

$$|\Omega|(\overline{U} + \overline{V} - \overline{m_2}) = O\left(\frac{1}{d_2}\right) \text{ uniformly in } d_1, \quad \text{for all } d_2 > C^*.$$

Therefore, we obtain the second inequality in (3.25) since $\overline{m_1} = \overline{m_2}$.

Now we proceed to prove (i). Define

$$\begin{aligned}
U^\pm := \overline{m_1 - V} &+ \frac{\rho_{m_1 - V} + C(m_1 - V)}{d_1} \\
&+ \frac{\gamma_{m_1 - V} + K(m_1 - V)}{d_1^2} + \frac{Q_3 + C_3}{d_1^3} + \frac{Q_4}{d_1^4} \pm \left(\frac{1}{d_1^3} + \frac{\rho_{m_1 - V}}{\overline{m_1 - V} d_1^4} \right),
\end{aligned}$$

where Q_3 is the unique solution to

$$\begin{cases}
\Delta Q_3 + (m_1 - V - 2\overline{m_1 - V})(\gamma_{m_1 - V} + K(m_1 - V)) - (\rho_{m_1 - V} + C(m_1 - V))^2 = 0 \text{ in } \Omega, \\
\partial_\nu Q_3 = 0 \text{ on } \partial\Omega, \quad \int_\Omega Q_3 = 0,
\end{cases}$$

Q_4 is the unique solution to

$$\begin{cases} \Delta Q_4 + (m_1 - V - 2\overline{m_1 - V})(Q_3 + C_3) \\ -2(\rho_{m_1-V} + C(m_1 - V))(\gamma_{m_1-V} + K(m_1 - V)) = 0 \text{ in } \Omega, \\ \partial_\nu Q_4 = 0 \text{ on } \partial\Omega, \quad \int_\Omega Q_4 = 0, \end{cases} \tag{3.30}$$

and C_3 is the unique number such that (3.30) has a solution. By (3.16), $\|r\|_{L^\infty(\Omega)}$ is uniformly bounded for all $d_1, d_2 > C^*$, which implies that by (3.22), $\|\rho_{m_1-V}\|_{L^\infty(\Omega)}$ is uniformly bounded for all $d_1, d_2 > C^*$. By (2.6) and (3.22),

$$\begin{aligned} K(m_1 - V) &= \frac{1}{\overline{m_1 - V}^2|\Omega|}\int_\Omega (m_1 - V - 3\overline{m_1 - V})\rho_{m_1-V}^2 \\ &= \frac{1}{\overline{m_1}^2|\Omega|}\int_\Omega (m_1 - V - 3\overline{m_1 - V})(\rho_{m_1}^2 + 2\overline{m_1}\rho_{m_1} r + \overline{m_1}^2 r^2). \end{aligned}$$

Therefore, by (3.18) and (3.20), $C(m_1 - V)$ and $|K(m_1 - V)|$ are uniformly bounded for all $d_1, d_2 > C^*$. Similarly, we can show that $\|\gamma_{m_1-V}\|_{L^\infty(\Omega)}$ and $\|Q_3\|_{L^\infty(\Omega)}$ are also uniformly bounded for all $d_1, d_2 > C^*$. Next we estimate $|C_3|$ and $\|Q_4\|_{L^\infty(\Omega)}$. Integrating the equation for Q_4 in (3.30) over Ω, we obtain that

$$\begin{aligned} \overline{m_1 - V}C_3|\Omega| = \int_\Omega &[(m_1 - V - 2\overline{m_1 - V})Q_3 - 2(\rho_{m_1-V} \\ &+ C(m_1 - V))(\gamma_{m_1-V} + K(m_1 - V))]. \end{aligned}$$

Since $\overline{U} \geqslant \xi\overline{m_1}$, by (3.25), there exists some $D_1^*(\xi) > 0$ such that $\overline{m_1 - V} > \xi\overline{m_1}/2$ for all $d_1 > D_1^*(\xi)$. Therefore $|C_3|$ and hence $\|Q_4\|_{L^\infty(\Omega)}$ are uniformly bounded by a constant $C_1^*(\xi)$ which depends only on ξ, Ω, m_1 and m_2, for all $d_1 > D_1^*(\xi)$ and $d_2 > C^*$ such that $\overline{U} \geqslant \xi\overline{m_1}$. Consequently, by similar calculations as in the proof of Proposition 2.4, we can show that

$$d_1\Delta U^\pm + U^\pm(m_1 - U^\pm - V) = \mp\frac{\overline{m_1 - V}}{d_1^3} + O\left(\frac{C_1^*(\xi)}{d_1^4}\right)$$

uniformly in $d_2 > C^*$, for all $d_1 > D_1^*(\xi)$. As $\overline{m_1 - V} > \xi\overline{m_1}/2$ for all $d_1 > D_1^*(\xi)$, by choosing $D_1^*(\xi)$ even larger if necessary, we see that $U^\pm$ is a pair of upper and lower solutions to

$$d_1\Delta U + U(m_1 - U - V) = 0 \text{ in } \Omega, \quad \partial_\nu U = 0 \text{ on } \partial\Omega$$

for all $d_1 > D_1^*(\xi)$ and $d_2 > C^*$ satisfying $0 < U^- < U^+$. By the upper/lower solution method [18] and uniqueness of U, we must have $U^- \leqslant U \leqslant U^+$ for all $d_1 > D_1^*(\xi)$ and $d_2 > C^*$. This finishes the proof of (3.26). The proof of (3.28) is similar to that of (3.26) and is thus omitted.

The proof of (3.27) follows from similar ideas as in the proof of Theorem 1.6. However, we need to show that the estimate in (3.27) is uniform in $d_2 > C^*$. The equation for V implies that

$$d_2 = \frac{1}{\lambda_1(m_2 - U - V)}.$$

For fixed $\xi > 0$, we claim that if $\overline{U} \geqslant \xi\overline{m_1}$, then

$$d_1\lambda_1(m_2 - U - V) - \frac{C(m_1 - V)}{C(m_2 - V)} = o(1) \text{ uniformly in } d_2 > C^*, \quad \text{as } d_1 \to \infty. \tag{3.31}$$

For notational convenience, we denote

$$\lambda_1^* := \lambda_1(m_2 - U - V)$$

in the rest of this proof. Let $\phi_1 > 0$ be the eigenfunction corresponding to λ_1^* normalized such that

$$\|\phi_1\|_{L^\infty(\Omega)} = \overline{m_2 - V}.$$

By (3.25), $\int_\Omega (m_2 - U - V) = o(1)$ uniformly in d_2 as $d_1 \to \infty$. Therefore by Proposition 2.2(i) and (v), $\lambda_1^* = o(1)$ uniformly in d_2 as $d_1 \to \infty$. (This forces $d_2 \to \infty$ as $d_2 = 1/\lambda_1^*$.) Moreover, since $\overline{U} \geqslant \xi\overline{m_1}$, passing to a subsequence of d_1 if necessary, we deduce that $\overline{V}$ converges to some constant $\widehat{V} \in [0, (1-\xi)\overline{m_1}]$ as $d_1 \to \infty$ by (3.25). Therefore, by standard elliptic regularity estimates, we deduce that, passing to a subsequence of d_1 again if necessary, ϕ_1 converges to some constant $\widehat{\phi_1} \in [\xi\overline{m_1}, \overline{m_1}]$ in $W^{2,p}(\Omega) \cap C^{1,\alpha}(\bar{\Omega})$. Since $\|\phi_1\|_{L^\infty(\Omega)} = \overline{m_2 - V}$, this implies that $\phi_1 = \overline{m_2} - \widehat{V} + o(1) = \overline{m_2 - V} + o(1)$ uniformly in $d_2 > C^*$ as $d_1 \to \infty$. Next rewrite

$$\phi_1 = \overline{m_2 - V} + \lambda_1^* \rho_{m_2 - V} + \frac{\vartheta}{d_1^2}.$$

By direct calculation, ϑ satisfies the following equation

$$\begin{cases} \Delta\vartheta + \lambda_1^* \cdot (m_2 - U - V)\vartheta + H = 0 & \text{in } \Omega, \\ \partial_\nu \vartheta = 0 & \text{on } \partial\Omega, \end{cases}$$

where

$$H := (\lambda_1^* d_1)^2 \rho_{m_2 - V}(m_2 - V - U) + \lambda_1^* d_1^2 \overline{m_2 - V}(\overline{m_2 - V} - U). \tag{3.32}$$

Multiplying the equation for ϕ_1 by ϑ and the equation for ϑ by ϕ_1, integrating over Ω and subtracting, we obtain that

$$\int_\Omega H\phi_1 = 0.$$

Dividing both sides of the above identity by $\lambda_1^* d_1$, by (3.26), (3.32) and the fact that $\phi_1 = \overline{m_2 - V} + o(1)$, we can further compute that as $d_1 \to \infty$,

$$\begin{aligned} 0 &= \lambda_1^* d_1 \int_\Omega \rho_{m_2 - V}(m_2 - V - \overline{m_2 - V} + o(1))(\overline{m_2 - V} + o(1)) \\ &\quad - \int_\Omega \overline{m_2 - V}(\rho_{m_1 - V} + C(m_1 - V) + o(1))(\overline{m_2 - V} + o(1)) \\ &= \lambda_1^* d_1 (\overline{m_2 - V}^2 |\Omega| C(m_2 - V) + o(1)) - \overline{m_2 - V}^2 |\Omega| C(m_1 - V) + o(1) \end{aligned} \tag{3.33}$$

uniformly in $d_2 > C^*$, where we used the identity

$$\int_\Omega \overline{m_i - V}(m_i - V - \overline{m_i - V})\rho_{m_i - V} = \int_\Omega |\nabla \rho_{m_i - V}|^2 = \overline{m_i - V}^2 |\Omega| C(m_i - V), \quad i = 1, 2, \tag{3.34}$$

obtained by multiplying the equation for $\rho_{m_i - V}$ by $\rho_{m_i - V}$ and integrating over Ω. By (3.25), $\overline{m_2 - V} > \xi\overline{m_1}/2$ for all d_1 large. By (3.20) and the fact that $d_2 \to \infty$ as $d_1 \to \infty$, we have

$$C(m_i - V) > C(m_i)/2, \quad i = 1, 2, \quad \text{for all } d_1 \text{ large}.$$

Therefore (3.31) follows by letting $d_1 \to \infty$ in (3.33).

Define

$$\widetilde{\phi}_1 := \frac{\overline{m_2 - V}|\Omega|}{\|\phi_1\|_{L^1(\Omega)}}\phi_1,$$

i.e., $\widetilde{\phi}_1 > 0$ is a renormalization of ϕ_1 such that $\|\widetilde{\phi}_1\|_{L^1(\Omega)} = \overline{m_2 - V}|\Omega|$. Rewrite

$$\widetilde{\phi}_1 = \overline{m_2 - V} + \lambda_1^* \rho_{m_2-V} + \frac{\zeta}{d_1^2}.$$

Since $\phi_1 = \overline{m_2 - V} + o(1)$ on $\bar{\Omega}$ and $\|\phi_1\|_{L^1(\Omega)} = \overline{m_2 - V}|\Omega| + o(1)$ uniformly in $d_2 > C^*$ as $d_1 \to \infty$,

$$\widetilde{\phi}_1 = \frac{\overline{m_2 - V}|\Omega|}{\|\phi_1\|_{L^1(\Omega)}}\phi_1 = \overline{m_2 - V} + o(1) \text{ uniformly in } d_2 > C^*, \quad \text{as } d_1 \to \infty.$$

As $\widetilde{\phi}_1 > 0$ on $\bar{\Omega}$, $\|\widetilde{\phi}_1\|_{L^1(\Omega)} = \overline{m_2 - V}|\Omega|$ and $\int_\Omega \rho_{m_2-V} = 0$, we have $\int_\Omega \zeta = 0$. Hence ζ satisfies the following equation

$$\begin{cases} \Delta\zeta + \lambda_1^* \cdot (m_2 - U - V)\zeta + H = 0 & \text{in } \Omega, \\ \partial_\nu \zeta = 0 \quad \text{on } \partial\Omega, \quad \int_\Omega \zeta = 0. \end{cases}$$

Note that ζ satisfies the same equation as ϑ.

Let us denote by $[\widetilde{\phi}_1]^\perp$ the complement of $\widetilde{\phi}_1$ in $L^2(\Omega)$. By Fredholm alternative, we can define the inverse of $\Delta + \lambda_1^* \cdot (m_2 - U - V)$ when restricted to $[\widetilde{\phi}_1]^\perp$. Let us denote by $\mathcal{K}_{d_1,d_2}^{-1}$ its inverse. Since $\lambda_1^* = o(1)$ uniformly in d_2 as $d_1 \to \infty$, it is obvious that $\|\mathcal{K}_{d_1,d_2}^{-1}\|_{[\widetilde{\phi}_1]^\perp}$ is bounded uniformly in d_2 for all $d_1 > D_1^*(\xi)$. Decompose ζ as

$$\zeta = \tilde{c}\widetilde{\phi}_1 + \mathcal{K}_{d_1,d_2}^{-1} H,$$

where $\tilde{c}$ is the unique constant such that $\int_\Omega \zeta = 0$. Since H converges by (3.26), (3.31) and (3.32), and $\mathcal{K}_{d_1,d_2}^{-1}$ converges to Δ^{-1} restricted to $\{f \in L^2(\Omega) \,|\, \overline{f} = 0\}$ as $d_1 \to \infty$, we deduce that $\tilde{c} \to 0$, as $d_1 \to \infty$. Therefore choosing $D_1^*(\xi)$ even larger if necessary, we obtain that $\|\zeta\|_{L^\infty(\Omega)}$ is uniformly bounded in $d_2 > C^*$ for all $d_1 > D_1^*(\xi)$. Hence

$$\widetilde{\phi}_1 = \overline{m_2 - V} + \lambda_1^* \rho_{m_2-V} + O\left(\frac{C_1^*(\xi)}{d_1^2}\right) \text{ uniformly in } d_2, \quad \text{for all } d_1 > D_1^*(\xi). \tag{3.35}$$

Similar as before, we can show that $\int_\Omega H\widetilde{\phi}_1 = 0$. Dividing both sides of the identity $\int_\Omega H\widetilde{\phi}_1 = 0$ by λ_1^* and by (3.32), we have

$$0 = \lambda_1^* d_1^2 \int_\Omega \rho_{m_2-V}(m_2 - V - U)\widetilde{\phi}_1 + d_1^2 \int_\Omega \overline{m_2 - V}(\overline{m_2 - V} - U)\widetilde{\phi}_1 =: J_1 + J_2. \tag{3.36}$$

By (**M**), (3.26), (3.31), (3.34) and (3.35), we can estimate J_1 and J_2 as follows:

$$\begin{aligned} J_1 &= \lambda_1^* d_1^2 \int_\Omega \rho_{m_2-V} \left[m_2 - V - \overline{m_2 - V} - \frac{1}{d_1}(\rho_{m_1-V} + C(m_1 - V)) + O\left(\frac{C_1^*(\xi)}{d_1^2}\right)\right] \\ &\quad \times \left(\overline{m_2 - V} + \lambda_1^* \rho_{m_2-V} + O\left(\frac{C_1^*(\xi)}{d_1^2}\right)\right) \\ &= \lambda_1^* d_1^2 \overline{m_2 - V}^2 C(m_2 - V)|\Omega| - \lambda_1^* d_1 \overline{m_2 - V} \int_\Omega \rho_{m_1-V}\rho_{m_2-V} \\ &\quad + (\lambda_1^* d_1)^2 \int_\Omega (m_2 - V - \overline{m_2 - V})\rho_{m_2-V}^2 + O\left(\frac{C_1^*(\xi)}{d_1}\right), \end{aligned}$$

and

$$\begin{aligned} J_2 &= -d_1 \int_\Omega \overline{m_2 - V} \left[(\rho_{m_1-V} + C(m_1 - V)) + \frac{1}{d_1}(\gamma_{m_1-V} + K(m_1 - V)) + O\left(\frac{C_1^*(\xi)}{d_1^2}\right)\right] \\ &\quad \times \left(\overline{m_2 - V} + \lambda_1^* \rho_{m_2-V} + O\left(\frac{C_1^*(\xi)}{d_1^2}\right)\right) \\ &= -d_1 \overline{m_2 - V}^2 C(m_1 - V)|\Omega| - \lambda_1^* d_1 \overline{m_2 - V} \int_\Omega \rho_{m_1-V}\rho_{m_2-V} \\ &\quad - \overline{m_2 - V}^2 K(m_1 - V)|\Omega| + O\left(\frac{C_1^*(\xi)}{d_1}\right) \end{aligned}$$

uniformly in $d_2 > C^*$, for all $d_1 > D_1^*(\xi)$. Therefore by (2.6) and (3.36), we have

$$\begin{aligned} & d_1(\overline{m_2 - V}^2 C(m_1 - V)|\Omega| - \lambda_1^* d_1 \overline{m_2 - V}^2 C(m_2 - V)|\Omega|) \\ &= (\lambda_1^* d_1)^2 \int_\Omega \overline{m_2 - V}\rho_{m_2-V}^2 - 2\lambda_1^* d_1 \overline{m_2 - V} \int_\Omega \rho_{m_1-V}\rho_{m_2-V} + \int_\Omega \overline{m_2 - V}\rho_{m_1-V}^2 \\ &\quad + (\lambda_1^* d_1)^2 \int_\Omega (m_2 - V - 2\overline{m_2 - V})\rho_{m_2-V}^2 - \int_\Omega (m_1 - V - 2\overline{m_1 - V})\rho_{m_1-V}^2 \\ &\quad + O\left(\frac{C_1^*(\xi)}{d_1}\right) \end{aligned}$$

uniformly in $d_2 > C^*$, for all $d_1 > D_1^*(\xi)$. By (3.20), (3.31) and the fact that $d_2 = 1/\lambda_1^* \to \infty$ as $d_1 \to \infty$, $\lambda_1^* d_1$ is bounded from below by some positive constant C^* depending only on $C(m_1)$ and $C(m_2)$ uniformly in $d_2 > C^*$ for all $d_1 > D_1^*(\xi)$. Therefore dividing both sides of the above identity by $\lambda_1^* d_1 \overline{m_2 - V}^2|\Omega|$, we obtain that

$$\begin{aligned} & d_1 C(m_1 - V)\left(\frac{1}{\lambda_1^* d_1} - \frac{C(m_2 - V)}{C(m_1 - V)}\right) \\ &= \frac{1}{\overline{m_2 - V}|\Omega|} \int_\Omega \left(\sqrt{\lambda_1^* d_1}\rho_{m_2-V} - \frac{\rho_{m_1-V}}{\sqrt{\lambda_1^* d_1}}\right)^2 + O\left(\frac{C_1^*(\xi)}{d_1}\right) \\ &\quad + \frac{1}{\overline{m_2 - V}^2|\Omega|}\left(\lambda_1^* d_1 \int_\Omega (m_2 - V - 2\overline{m_2 - V})\rho_{m_2-V}^2 \right. \\ &\quad \left. - \frac{1}{\lambda_1^* d_1} \int_\Omega (m_1 - V - 2\overline{m_1 - V})\rho_{m_1-V}^2 \right) \end{aligned} \tag{3.37}$$

uniformly in $d_2 > C^*$, for all $d_1 > D_1^*(\xi)$. Therefore by (3.20) and (3.31),

$$\frac{1}{\lambda_1^* d_1} - \frac{C(m_2 - V)}{C(m_1 - V)} = O\left(\frac{C_1^*(\xi)}{d_1}\right)$$

i.e.,

$$\lambda_1^* d_1 = \frac{C(m_1 - V)}{C(m_2 - V)} + O\left(\frac{C_1^*(\xi)}{d_1}\right)$$

uniformly in $d_2 > C^*$, for all $d_1 > D_1(\xi)$. Plugging them back to the right hand side of (3.37), we obtain that

$$d_1\left(\frac{1}{\lambda_1^* d_1} - \frac{C(m_2 - V)}{C(m_1 - V)}\right) = B_1(m_1 - V, m_2 - V) + O\left(\frac{C_1^*(\xi)}{d_1}\right)$$

uniformly in $d_2 > C^*$, for all $d_1 > D_1(\xi)$, where $B_1(\cdot, \cdot)$ is defined by (3.10). This finishes the proof of (3.27).

The proof of (3.29) is similar to that of (3.27) and is thus omitted. □

To prove Theorem 1.9, we need to study properties of coexistence steady states of (1.1) in the following two regions:

$$\mathcal{E}_{1,\delta} := \Sigma_- \cap \left\{(d_1, d_2) \in \mathcal{Q} \,|\, d_2 > \frac{C(m_2)}{C(m_1)} d_1 + B_1 - \delta\left(B_1 + \frac{C(m_2)}{C(m_1)} B_2\right)\right\}, \tag{3.38}$$

$$\mathcal{E}_{2,\delta} := \Sigma_- \cap \left\{(d_1, d_2) \in \mathcal{Q} \,|\, d_1 > \frac{C(m_1)}{C(m_2)} d_2 + B_2 - \delta\left(B_2 + \frac{C(m_1)}{C(m_2)} B_1\right)\right\}, \tag{3.39}$$

where $\delta \in (0, 1)$, $B_1 = B_1(m_1, m_2)$ and $B_2 = B_2(m_1, m_2)$ are defined by (3.10) and (3.11) respectively.

Theorem 3.3 *Assume that* (**M**) *holds. Let* (U, V) *be the unique coexistence steady state of* (1.1) *with* $(d_1, d_2) \in \Sigma_-$. *Then the following hold:*

(i) *If* $(d_1, d_2) \in \mathcal{E}_{1,\delta} \cap \mathcal{Q}_D$, *where* $\delta \in (0, 1)$, *then* $\liminf_{D\to\infty} \overline{U} \geqslant (1 - \delta)\overline{m_1}$.
(ii) *If* $(d_1, d_2) \in \mathcal{E}_{2,\delta} \cap \mathcal{Q}_D$, *where* $\delta \in (0, 1)$, *then* $\liminf_{D\to\infty} \overline{V} \geqslant (1 - \delta)\overline{m_1}$.

Proof We will only prove (i), as (ii) follows similarly. Without loss of generality, we may assume that for any $\delta \in (0, 1)$, there exists a sequence $(d_{1,k}, d_{2,k}) \in \mathcal{E}_{1,\delta} \cap \{(d_1, d_2) \,|\, d_1 > k\}$ such that (1.1) with $(d_1, d_2) = (d_{1,k}, d_{2,k})$ has a coexistence steady steady state (U_k, V_k) satisfying $\overline{V_k} \geqslant \delta\overline{m_1}$. Otherwise, (i) follows directly from (3.25). Passing to a subsequence of k, we have the following two cases to discuss:

(a) $\overline{U_k} < \xi(\delta)\overline{m_1}$ for all k;
(b) $\overline{U_k} \geqslant \xi(\delta)\overline{m_1}$ for all k.

Here $\xi(\delta) > 0$ is a constant which depends only on δ and is to be determined later. For simplicity, we suppress the subscript k in the rest of this proof whenever it does not cause any confusion. For Case (a), since $\overline{V} \geqslant \delta\overline{m_1}$ for all k, choosing $D(\delta)$ large such that

$$\frac{C(m_2)}{C(m_1)} D(\delta) + B_1 - \delta\left(B_1 + \frac{C(m_2)}{C(m_1)} B_2\right) > D_2^*(\delta).$$

By (3.19), we have

$$|C(m_i - U) - C(m_i)| = O\left(\frac{\xi(\delta)}{d_1}\right)$$

uniformly in d_2, for all $D > D(\delta)$ and $(d_1, d_2) \in \mathcal{E}_{1,\delta} \cap \mathcal{Q}_D$. By (3.11), (3.17), (3.19) and (3.22),

$$\begin{aligned}B_2(m_1 - U, m_2 - U) = &\frac{\overline{m_1 - U}}{\overline{m_1}^2|\Omega|} \int_\Omega \left(\frac{\rho_{m_1}}{\sqrt{C(m_1)}} - \frac{\sqrt{C(m_1)}}{C(m_2)}\rho_{m_2} \right)^2 \\ &+ \frac{1}{\overline{m_2}^2|\Omega|} \left(\frac{1}{C(m_1)} \int_\Omega (m_1 - 2\overline{m_1})\rho_{m_1}^2 - \frac{C(m_1)}{C^2(m_2)} \int_\Omega (m_2 - 2\overline{m_2})\rho_{m_2}^2 \right) \\ &+ O(\xi(\delta)) + O\left(\frac{\xi(\delta)}{d_1}\right)\end{aligned}$$

uniformly in d_2, for all $D > D(\delta)$ and $(d_1, d_2) \in \mathcal{E}_{1,\delta} \cap \mathcal{Q}_D$. Therefore,

$$\begin{aligned}d_1 &= \frac{C(m_1 - U)}{C(m_2 - U)} d_2 + B_2(m_1 - U, m_2 - U) + O\left(\frac{C_2^*(\delta)}{d_2}\right) \\ &\geqslant \frac{C(m_1 - U)}{C(m_2 - U)} \left(\frac{C(m_2)}{C(m_1)} d_1 + B_1(m_1, m_2) - \delta(B_1(m_1, m_2) + \frac{C(m_2)}{C(m_1)} B_2(m_1, m_2)) \right) \\ &\quad + B_2(m_1 - U, m_2 - U) + O(\frac{C_2^*(\delta))}{d_2}) \\ &= d_1 + \frac{\overline{m_1 - U} + \overline{m_1} - 2\delta\overline{m_1}}{\overline{m_1}^2|\Omega|} \int_\Omega \left(\frac{\rho_{m_1}}{\sqrt{C(m_1)}} - \frac{\sqrt{C(m_1)}}{C(m_2)}\rho_{m_2} \right)^2 + O(\xi(\delta)) \\ &\quad + O(\frac{\xi(\delta)}{d_1}) + O\left(\frac{C_2^*(\delta)}{d_2}\right),\end{aligned}$$

uniformly for all $D > D(\delta)$ and $(d_1, d_2) \in \mathcal{E}_{1,\delta} \cap \mathcal{Q}_D$. Since $\overline{U} < \xi(\delta)\overline{m_1}$ and $\delta \in (0, 1)$, we have

$$\begin{aligned}&\frac{\overline{m_1 - U} + \overline{m_1} - 2\delta\overline{m_1}}{\overline{m_1}^2|\Omega|} \int_\Omega \left(\frac{\rho_{m_1}}{\sqrt{C(m_1)}} - \frac{\sqrt{C(m_1)}}{C(m_2)}\rho_{m_2} \right)^2 + O(\xi(\delta)) \\ &> \frac{2(1 - \delta) - \xi(\delta)}{\overline{m_1}|\Omega|} \int_\Omega \left(\frac{\rho_{m_1}}{\sqrt{C(m_1)}} - \frac{\sqrt{C(m_1)}}{C(m_2)}\rho_{m_2} \right)^2 + O(\xi(\delta)) \\ &> \frac{(1 - \delta)}{\overline{m_1}|\Omega|} \int_\Omega \left(\frac{\rho_{m_1}}{\sqrt{C(m_1)}} - \frac{\sqrt{C(m_1)}}{C(m_2)}\rho_{m_2} \right)^2\end{aligned}$$

for all $D > D(\delta)$ and $(d_1, d_2) \in \mathcal{E}_{1,\delta} \cap \{(d_1, d_2) \,|\, d_1 > D\}$, where in the last inequality above, we have chosen $\xi(\delta) > 0$ sufficiently small such that

$$\begin{aligned}&\frac{-\xi(\delta)}{\overline{m_1}|\Omega|} \int_\Omega \left(\frac{\rho_{m_1}}{\sqrt{C(m_1)}} - \frac{\sqrt{C(m_1)}}{C(m_2)}\rho_{m_2} \right)^2 + O(\xi(\delta)) \\ &\quad > -\frac{(1 - \delta)}{\overline{m_1}|\Omega|} \int_\Omega \left(\frac{\rho_{m_1}}{\sqrt{C(m_1)}} - \frac{\sqrt{C(m_1)}}{C(m_2)}\rho_{m_2} \right)^2.\end{aligned}$$

Thus a contradiction is in order for all D sufficiently large.

Therefore only Case (b) is possible, i.e., $\overline{V} \geqslant \delta\overline{m_1}$ and $\overline{U} \geqslant \xi(\delta)\overline{m_1}$ for some $\xi(\delta) > 0$ for all k. By similar arguments as in the proof of Case (a) in (i), choosing $D(\delta)$ such that $D(\delta) > D_1^*(\xi(\delta))$ and

$$\frac{C(m_2)}{C(m_1)} D(\delta) + B_1 - \delta\left(B_1 + \frac{C(m_2)}{C(m_1)} B_2\right) > D_2^*(\delta).$$

Then by Proposition 3.2, (3.26)–(3.29) hold for all $D > D(\delta)$ and $(d_1, d_2) \in \mathcal{E}_{1,\delta} \cap \mathcal{Q}_D$. Therefore, by (3.17), (3.22) and (3.23), we obtain that

$$C(m_i - U) = C(m_i) - \frac{1}{d_1}\frac{2\overline{m_1 - V}}{\overline{m_1}^2|\Omega|}\int_\Omega \rho_{m_i}\rho_{m_1} + O\left(\frac{C_1^*(\xi(\delta))}{d_1^2}\right)$$

and

$$\begin{aligned} B_2(m_1 - U, m_2 - U) = {} & \frac{\overline{m_1 - U}}{\overline{m_1}^2|\Omega|}\int_\Omega \left(\frac{\rho_{m_1}}{\sqrt{C(m_1)}} - \frac{\sqrt{C(m_1)}}{C(m_2)}\rho_{m_2}\right)^2 \\ & + \frac{1}{\overline{m_2}^2|\Omega|}\left(\frac{1}{C(m_1)}\int_\Omega (m_1 - 2\overline{m_1})\rho_{m_1}^2 - \frac{C(m_1)}{C^2(m_2)}\int_\Omega (m_2 - 2\overline{m_2})\rho_{m_2}^2\right) \\ & + \frac{\overline{m_1 - V}}{\overline{m_1}^2|\Omega|}\left(\frac{1}{C(m_1)}\int_\Omega \rho_{m_1}^2 - \frac{C(m_1)}{C^2(m_2)}\int_\Omega \rho_{m_2}^2\right) + O\left(\frac{C_1^*(\xi(\delta))}{d_1}\right) \end{aligned}$$

uniformly in d_2, for all $D > D(\delta)$ and $(d_1, d_2) \in \mathcal{E}_{1,\delta} \cap \mathcal{Q}_D$. Therefore by (3.29), we obtain that

$$\begin{aligned} d_1 \geqslant {} & d_1 + \frac{\overline{m_1 - U} + \overline{m_1} - \overline{m_1 - V} - 2\delta\overline{m_1}}{\overline{m_1}^2|\Omega|}\int_\Omega \left(\frac{\rho_{m_1}}{\sqrt{C(m_1)}} - \frac{\sqrt{C(m_1)}}{C(m_2)}\rho_{m_2}\right)^2 \\ & + O\left(\frac{C_1^*(\xi(\delta))}{d_1} + \frac{C_2^*(\delta)}{d_2}\right), \end{aligned}$$

for all $D > D(\delta)$ and $(d_1, d_2) \in \mathcal{E}_{1,\delta} \cap \{(d_1, d_2) \mid d_1 > D\}$. Taking limit-sup on both sides as $k \to \infty$, we obtain that:

$$0 \geqslant \overline{m_1} - \liminf_{k\to\infty} \overline{U} + \limsup_{k\to\infty} \overline{V} - 2\delta\overline{m_1}.$$

Since $\overline{V} \geqslant \delta\overline{m_1}$ for all k, we must have

$$\liminf_{k\to\infty} \overline{U} \geqslant (1 - \delta)\overline{m_1}.$$

This finishes the proof of (i) and hence the theorem. □

Now we are ready to prove Theorem 1.9.

Proof of Theorem 1.9 By Theorem 3.3(i) and (ii), it is easy to see that

$$\overline{U_k} > \frac{1 - p}{4\overline{m_1}}, \quad \overline{V_k} > \frac{p}{4\overline{m_1}} \quad \text{for all } k \text{ large.} \tag{3.40}$$

Choose $K \in \mathbb{N}^+$ such that for all $k > K$,

$$d_{1,k} > D_1^*((1 - p)/4)$$

and

$$\frac{C(m_2)}{C(m_1)}d_{2,k} + B_1 - p(B_1 + \frac{C(m_2)}{C(m_1)}B_2) > D_2^*(p/4).$$

Then by Proposition 3.2, (3.26)-(3.29) hold for all $k > K$. For simplicity, we suppress the subscript k in the rest of this proof whenever it does not cause any confusion. By similar estimates of $C(m_i - U) - C(m_i)$ and $B_2(m_1 - U, m_2 - U)$ in Case (b) in the proof of Theorem 3.3(i), we obtain that

$$\begin{aligned} d_1 &= \frac{C(m_1-U)}{C(m_2-U)} d_2 + B_2(m_1-U, m_2-U) + O(\frac{C_2^*(p)}{d_2}) \\ &= \frac{C(m_1-U)}{C(m_2-U)} \left(\frac{C(m_2)}{C(m_1)} d_1 + B_1 - p\left(B_1 + \frac{C(m_2)}{C(m_1)} B_2 \right) + o(1) \right) \\ &\quad + B_2(m_1-U, m_2-U) + O\left(\frac{C_2^*(p)}{d_2} \right) \\ &= d_1 + \frac{\overline{m_1 - U} + \overline{m_1} - \overline{m_1 - V} - 2p\overline{m_1}}{\overline{m_1}^2 |\Omega|} \int_\Omega \left(\frac{\rho_{m_1}}{\sqrt{C(m_1)}} - \frac{\sqrt{C(m_1)}}{C(m_2)} \rho_{m_2} \right)^2 \\ &\quad + o(1) + O\left(\frac{C_1^*(p)}{d_1} + \frac{C_2^*(p)}{d_2} \right), \end{aligned}$$

for all $k > K$. Therefore letting $k \to \infty$, we obtain that

$$\lim_{k\to\infty} \overline{V} - \lim_{k\to\infty} \overline{U} + \overline{m_1} - 2p\overline{m_1} = 0, \tag{3.41}$$

which together with (3.26) and (3.28) implies that

$$(\overline{U}, \overline{V}) \to ((1-p)\overline{m_1}|\Omega|, p\overline{m_1}|\Omega|) \quad \text{as } k \to \infty. \tag{3.42}$$

By standard elliptic regularity estimates, we deduce that passing to a subsequence of k if necessary,

$$(U, V) \to (\widehat{U}, \widehat{V}) \text{ in } C^2(\bar{\Omega}) \times C^2(\bar{\Omega}) \quad \text{as } k \to \infty,$$

for some constants $\widehat{U}, \widehat{V} \geqslant 0$. This together with (3.42) finishes the proof of the theorem. □

Note that by Theorem 3.3(i) and (ii), it is easy to see that in Theorem 1.9, the convergence is uniform in p on any compact subset of $(0, 1)$.

4 Transition of the dynamics from heterogeneity to homogeneity

In this section, to put the results in Parts II [9] and III in perspective, we illustrate how the global dynamics of (1.1) evolves as the heterogeneous function m_2 gradually deforms to a constant while its average remains fixed during the deformation. For this purpose, we consider the following system

$$\begin{cases} U_t = d_1 \Delta U + U(m_1(x) - U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ V_t = d_2 \Delta V + V(m_{2,s}(x) - U - V) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \\ U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{in } \Omega, \end{cases} \tag{4.1}$$

where m_1 and m_2 satisfy condition (**M**) and

$$m_{2,s} := \overline{m_2} + s(m_2 - \overline{m_2}), \quad s \in [0, 1]. \tag{4.2}$$

When $s = 0$, system (4.1) reduces to the one studied in Part II [9]. We now roughly describe how the global dynamics of (4.1) evolves when $s \to 0$. For simplicity, we focus on the following case:

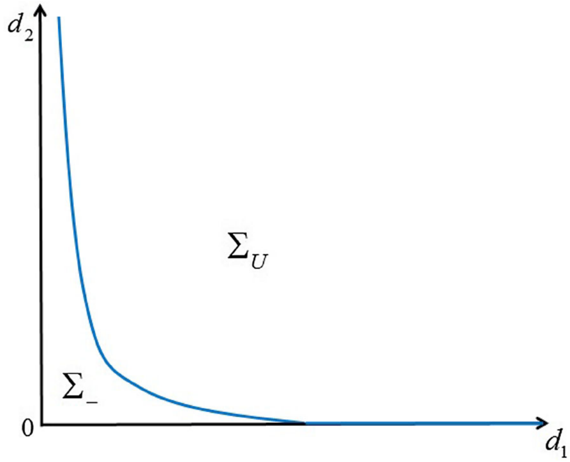

Fig. 1 Global dynamics of system (4.1) with $s = 0$ under condition (**A**)

(**A**) $\inf_{\Omega} \rho_{m_1} + C(m_1) > 0$.

The case $\inf_{\Omega} \rho_{m_1} + C(m_1) \leqslant 0$ is slightly different and we will leave it to the interested readers.

Note that now the sets Σ_U, Σ_V and Σ_- for system (4.1) depend continuously and implicitly on the parameter s. It is easy to see that

$$\frac{C(m_{2,s})}{C(m_1)} = s^2 \frac{C(m_2)}{C(m_1)}.$$

By (2.4) and (4.2), there exists a constant $D_{m_1} > 0$ depending on m_1 such that:

$$m_{2,s} - \theta_{d_1,m_1} = s(m_2 - \overline{m_2}) - \frac{\rho_{m_1} + C(m_1)}{d_1} + O\left(\frac{1}{d_1^2}\right) \tag{4.3}$$

for all $0 \leqslant s \leqslant 1$ and $d_1 > D_{m_1}$. Therefore, for each s sufficiently small, there exists a finite interval

$$(D_1^*(s), D_1^{**}(s)) \subset (D_{m_1}, \infty)$$

such that

$$m_{2,s} - \theta_{d_1,m_1} < 0 \text{ in } \Omega \text{ for all } d_1 \in (D_1^*(s), D_1^{**}(s)).$$

Therefore, $\mu_1(d_2, m_{2,s} - \theta_{d_1,m_1}) > \mu_1(d_2, 0) = 0$ for all $d_2 > 0$ by [8, Proposition 3.1]. Consequently, by Theorem 1.3, $(d_1, d_2) \in \Sigma_U$ and $(\theta_{d_1,m_1}, 0)$ is globally asymptotically stable for all $d_1 \in (D_1^*(s), D_1^{**}(s))$ and $d_2 > 0$. In other words,

$$\{(d_1, d_2) \mid d_1 \in (D_1^*(s), D_1^{**}(s)), d_2 > 0\} \subset \Sigma_U.$$

Moreover, by (**A**) we can choose $D_1^*(s)$ and $D_1^{**}(s)$ such that

$$D_1^{**}(s) = O(1/s) \quad \text{and} \quad D_1^*(s) \approx D_{m_1} \quad \text{for all } s \text{ small.}$$

Therefore,

$$\liminf_{s\to 0} D_1^{**}(s) = \infty \text{ and } \limsup_{s\to 0} D_1^*(s) =: D_{sup} > 0 \text{ is finite,}$$

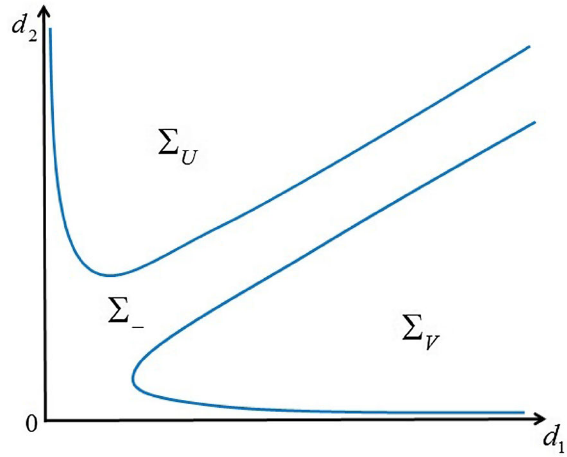

Fig. 2 Global dynamics of system (4.1) with $s > 0$

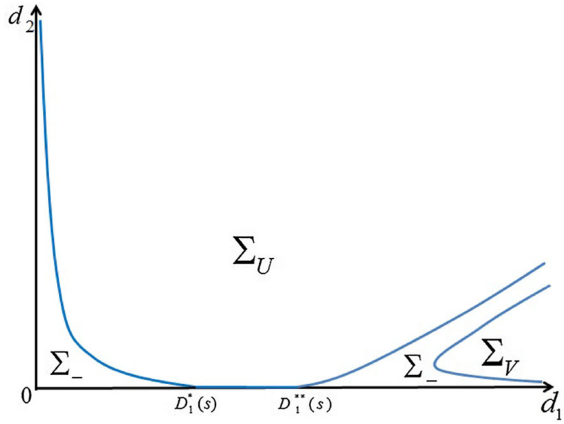

Fig. 3 Illustration of global dynamics of (4.1) for s small under the condition (**A**). As $s \to 0$, $D_1^{**}(s) \to \infty$, $\Sigma_V \to \emptyset$ and $\Sigma_U \cap \mathcal{Q}_D \to \mathcal{Q}_D$ for all D large, i.e. Fig. 2 deforms via Fig. 3 to 1

which implies that for all $D > 2D_{sup}$,

$$\Sigma_U \cap \mathcal{Q}_D \to \mathcal{Q}_D \quad \text{as } s \to 0.$$

This forces

$$\Sigma_V \cap \mathcal{Q}_D \to \emptyset \text{ and } \Sigma_- \cap \mathcal{Q}_D \to \emptyset \text{ as } s \to 0. \tag{4.4}$$

On the other hand, by Lemma 2.3,

$$\theta_{d_2,m_{2,s}} \to \overline{m_1} \text{ uniformly in } d_2 > 0 \text{ as } s \to 0.$$

Hence by Proposition 2.2, $\lambda_1(m_1 - \theta_{d_2,m_{2,s}}) \to 0$ uniformly in $d_2 > 0$ as $s \to 0$, which implies that

$$d_1^*(d_2) \to \infty \text{ uniformly in } d_2 > 0 \text{ as } s \to 0,$$

by the proof of Theorem 1.3 in [6]. Therefore $\Sigma_V \cap \{(d_1, d_2) \mid 0 < d_1 \leqslant 2D_{sup}, d_2 > 0\} = \emptyset$ for all s sufficiently small. This together with (4.4) imply that $\Sigma_V \to \emptyset$ as $s \to 0$.

Figures 1 and 2 illustrate schematically the dynamics of (4.1) with $s = 0$ and 1 respectively. The latter deforms through Fig. 3 gradually to the former, while Fig. 3 illustrates schematically the dynamics of (4.1) when s is sufficiently small.

References

1. Brown, K.J., Lin, S.S.: On the existence of positive eigenfunctions for an eigenvalue problem with indefinite weight function. J. Math. Anal. Appl. **75**, 112–120 (1980)
2. Cantrell, R.S., Cosner, C.: On the effects of spatial heterogeneity on the persistence of interacting species. J. Math. Biol. **37**, 103–145 (1998)
3. Cantrell, R.S., Cosner, C.: Spatial Ecology via Reaction–Diffusion Equations, Series in Mathematical and Computational Biology. Wiley, Chichester (2003)
4. Dockery, J., Hutson, V., Mischaikow, K., Pernarowski, M.: The evolution of slow dispersal rates: a reaction–diffusion model. J. Math. Biol. **37**, 61–83 (1998)
5. Gilbarg, D., Trudinger, N.S.: Elliptic Partial Differential Equations of Second Order, Grundlehren der Mathematicschen Wissenschaften, vol. 224. Springer, Berlin (1983)
6. He, X., Ni, W.-M.: The effects of diffusion and spatial variation in Lotka–Volterra competition–diffusion system, I: heterogeneity vs. homogeneity. J. Differ. Equ. **254**, 528–546 (2013)
7. He, X., Ni, W.-M.: The effects of diffusion and spatial variation in Lotka–Volterra competition–diffusion system, II: the general case. J. Differ. Equ. **254**, 4088–4108 (2013)
8. He, X., Ni, W.-M.: Global dynamics of the Lotka–Volterra competition–diffusion system: diffusion and spatial heterogeneity, I. Commun. Pure Appl. Math. **69**, 981–1014 (2016). doi:10.1002/cpa.21596
9. He, X., Ni, W.-M.: Global dynamics of the Lotka–Volterra competition–diffusion system with equal amount of total resources, II. Calc. Var. Partial Differ. Equ. (2016). doi:10.1007/s00526-016-0964-0
10. Holmes, E.E., Lewis, M.A., Banks, J.E., Veit, R.R.: Partial differential equations in ecology: spatial interactions and population dynamics. Ecology **75**, 17–29 (1994)
11. Hutson, V., López-Gómez, J., Mischaikow, K., Vickers, G.: Limit behavior for a competing species problem with diffusion. In: Dynamical Systems and Applications, World Scientific Series in Applicable Analysis, vol. 4, World Scientific Publishing, River Edge, pp. 343–358 (1995)
12. Hutson, V., Lou, Y., Mischaikow, K.: Spatial heterogeneity of resources versus Lotka–Volterra dynamics. J. Differ. Equ. **185**, 97–136 (2002)
13. Hutson, V., Lou, Y., Mischaikow, K.: Convergence in competition models with small diffusion coefficients. J. Differ. Equ. **211**, 135–161 (2005)
14. Lam, K.-Y., Ni, W.-M.: Uniqueness and complete dynamics in the heterogeneous competition–diffusion systems. SIAM J. Appl. Math. **72**, 1695–1712 (2012)
15. Lou, Y.: On the effects of migration and spatial heterogeneity on single and multiple species. J. Differ. Equ. **223**, 400–426 (2006)
16. Lou, Y.: Some challenging mathematical problems in evolution of dispersal and population dynamics. In: Tutorials in Mathematical Biosciences IV, Lecture Notes in Mathematics 1922, pp. 171–205, Springer, Berlin (2008)
17. Ni, W.-M.: The mathematics of diffusion. In: CBMS-NSF Regional Conference Series in Applied Mathematics, vol. 82, SIAM, Philadelphia (2011)
18. Sattinger, D.H.: Monotone methods in nonlinear elliptic and parabolic boundary value problems. Indiana Univ. Math. J. **21**, 979–1000 (1972)
19. Senn, S., Hess, P.: On positive solutions of a linear elliptic eigenvalue problem with Neumann boundary conditions. Math. Ann. **258**, 459–470 (1982)
20. Shigesada, N., Kawasaki, K.: Biological Invasions: Theory and Practice, Oxford Series in Ecology and Evolution. Oxford University Press, Oxford (1997)