Mathematical Biology

Population dynamics with resource-dependent dispersal: single- and two-species models

De Tang[1] · Zhi-An Wang[2]

© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2022

Abstract

In this paper, we consider the population models with resource-dependent dispersal for single-species and two-species with competition. For the single-species model, it is well-known that the total population supported by the environment is always greater than the environmental carrying capacity if the dispersal is simply random diffusion. However, we find that the total population supported can be equal or smaller than the environmental carrying capacity when the dispersal depends on the resource distribution. This analytical finding not only well agrees with the yeast experiment observation of Zhang et al. (Ecol Lett 20(9):1118–1128, 2017), but also indicates that resource-dependent dispersal may produce different outcomes compared to the random dispersal. For the two-species competition model, when two competing species use the same dispersal strategy up to a multiplicative constant (i.e. their dispersal strategies are proportional) or both diffusion coefficients are large, we give a classification of global dynamics. We also show, along with numerical simulations, that if the dispersal strategies are resource-dependent, even one species has slower diffusion, coexistence is possible though competitive exclusion may occur under different conditions. This is distinct from the prominent result that with random dispersal the slower diffuser

✉ Zhi-An Wang
mawza@polyu.edu.hk

De Tang
tangd7@mail.sysu.edu.cn

[1] School of Mathematics (Zhuhai), Sun Yat-sen University, Zhuhai 519082, Guangdong, People's Republic of China

[2] Department of Applied Mathematics, The Hong Kong Polytechnic University, Hung Hom, Hong Kong S.A.R., People's Republic of China

always wipes out its fast competitor. Our analytical results, supported by the numerical simulations, show that the resource-dependent dispersal strategy has profound impact on the population dynamics and evolutionary processes.

Keywords Resource-dependent dispersal · Lotka–Volterra competition · Environmental heterogeneity · Coexistence steady state · Global stability

Mathematics Subject Classification 35K57 · 35K61 · 37C65 · 92D25

1 Introduction

Dispersal is a vital life-history strategy used for gene flow, resource competition, population dynamics, and the distribution of species (Clobert et al. 2001). It is one of the hardest parameters to estimate despite its importance and hence dispersal processes are often poorly understood (Duarte and Mali 2019). There are many approaches that have been adopted to model the dispersal process and its ecological effects. Among them are reaction-diffusion models which are widely used to describe dispersal in terms of diffusion. Let $u(x, t)$ represent a population density at location x at time t, where $(x, t) \in \Omega \times (0, \infty)$ and $\Omega \subset \mathbb{R}^N (N \geq 2)$ is a bounded domain with smooth boundary representing the species habitat. Then one of the prototypical models for a single species dispersing through a closed environment takes the following form

$$\begin{cases} u_t = \mu \Delta u + u(r(x) - u), & x \in \Omega, \ t > 0, \\ \nabla u \cdot n = 0, & x \in \partial\Omega, \ t > 0 \end{cases} \tag{1.1}$$

where the non-negative function $r(x)$ denotes the environmental resource available to the species, μ is the diffusion coefficient (dispersal rate) and n is the unit outer normal vector on the boundary $\partial\Omega$. The homogeneous Neumann (or zero-flux) boundary conditions means no individuals cross the habitat boundary. When $r(x)$ is a constant, the first equation of (1.1) is well-known as the Fisher-KPP equation originally proposed in Fisher (1917), Kolmogorov et al. (1937). It was shown in Cantrell and Cosner (2003) that if $r(x) \geq 0$ is a bounded measurable positive function, then for every $\mu > 0$ the problem (1.1) has a unique positive steady state, denoted by $u_{r,\mu}$, which is globally asymptotically stable, where $u_{r,\mu} = a$ if $r(x) = a > 0$ is a constant and $u_{r,\mu}$ is non-constant if $r(x)$ is so. It was further observed in Lou (2006) that if $r(x)$ is non-constant, then $u_{r,\mu}$ satisfies

$$\int_\Omega u_{r,\mu}(x)\mathrm{d}x = \mu \int_\Omega \frac{|\nabla u_{r,\mu}|^2}{u_{r,\mu}^2}\mathrm{d}x + \int_\Omega r(x)\mathrm{d}x > \int_\Omega r(x)\mathrm{d}x \tag{1.2}$$

for all $\mu > 0$. Usually $\int_\Omega r(x)\mathrm{d}x$ is defined as the environmental (or resource) carrying capacity. Then (1.2) says that with dispersal the total population is always greater than the environmental carrying capacity in a spatially heterogeneous environment. If there is no diffusion ($\mu = 0$), the equilibrium is just $r(x)$. Hence dispersal increases

population abundance in a single-species community. In a multi-species community, dispersal has even more profound ecological effects. Let us consider the following two-species Lotka–Volterra competition–diffusion system in a closed habitat $\Omega \subset \mathbb{R}^N (N \geq 2)$

$$\begin{cases} u_t = \mu_1 \Delta u + u(r(x) - b_1 u - c_1 v), & x \in \Omega, \ t > 0, \\ v_t = \mu_2 \Delta v + v(r(x) - b_2 u - c_2 v), & x \in \Omega, \ t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \ t > 0, \end{cases} \qquad (1.3)$$

where $u(x, t)$ and $v(x, t)$ denote the densities of two competing species with dispersal rates $\mu_1 > 0$ and $\mu_2 > 0$, respectively. The parameters $b_i, c_i \ (i = 1, 2)$ are all positive constants, and $r(x)$ is the environmental resource shared by two species.

When the resource is spatially homogeneous, namely $r(x)$ is a constant say $r(x) = a > 0$, (1.3) is called the classical Lotka–Volterra competition system, which has four equilibria $A = (u_A, 0)$, $B = (0, v_B)$, $C = (u_*, v_*)$, and $O = (0, 0)$, where

$$u_A = \frac{a}{b_1}, \quad v_B = \frac{a}{c_2}, \quad u_* = \frac{a(c_2 - c_1)}{b_1 c_2 - b_2 c_1}, \quad v_* = \frac{a(b_1 - b_2)}{b_1 c_2 - b_2 c_1}.$$

The global stability of the above equilibria crucially depends on the ecological reaction coefficients (e.g. see de Mottoni 1979). Set $b = b_1/b_2$, $c = c_1/c_2$. Then the positive coexistence equilibrium (u_*, v_*) is globally asymptotically stable if $c < 1 < b$ (weak competition) while competitive exclusion equilibrium $(u_A, 0)$ (resp. $(0, v_B)$) is globally asymptotically stable if $1 > \max\{b, c\}$ (resp. $1 < \min\{b, c\}$). If $b < 1 < c$ (strong competition), the coexistence steady state is unstable and the two exclusion steady states are locally stable where which species survives in competition depends on the initial data. When the resource is spatially heterogeneous (i.e. $r(x)$ is non-constant), the global dynamics of (1.3) may be quite different from the case of spatially homogeneous resource. The most prominent consequence resulting from (1.3) with non-constant $r(x)$ is the phenomenon "slower diffuser always prevails" (namely *the slower diffuser wipes out its fast competitor regardless of the initial value*), which was first observed in Dockery et al. (1998) for the case $b_1 = c_1 = b_2 = c_2 = 1$ (two species are ecologically identical except their dispersal rates) and was further extended in Lou (2006) to the case of weak competition. A complete classification of the global dynamics of (1.3) in the parameter regime $0 < bc \leq 1$ has been given in a series of essential works (He and Ni 2016a, b, 2017) and we omit the details here for brevity.

We underline that in the afore-mentioned typical one- and two-species population models, the species dispersal was described by random diffusion. However, due to biological complexity, dispersal of biological species may depend on many factors such as local population size, resource competition, habitat quality/size, inbreeding avoidance and so on (cf. Bowler and Benton 2005; Maag et al. 2018; Okubo and Levin 2001; Skellam 1973). In this scenario, density-dependent dispersal will be more appropriate. Among many ways modeling density-dependent dispersal (cf. Braverman and Makrujjaman 2016; Cosner 2014 and references therein), in this paper, we will explore the effects of resource-dependent dispersal on the population dynamics. In a

single-species community, we shall consider a variant of (1.1) with Fokker–Planck type diffusion as follows

$$
\begin{cases}
w_t = \mu \Delta(d(r)w) + w(r(x) - w), & x \in \Omega, \ t > 0, \\
\nabla(d(r)w) \cdot n = 0, & x \in \partial\Omega, \ t > 0, \\
w(x,0) = w_0(x) \gneq 0, & x \in \Omega,
\end{cases}
\tag{1.4}
$$

where the dispersal of the species depends on the resource distribution $r(x)$ via a dispersal rate function $d(r)$. We assume the resource function $r(x)$ satisfies

(H_0) $r(x) \in C^2(\overline{\Omega})$ and $r(x) \geq 0$ is not constant in Ω

and $d(r)$ satisfies

(H_1) $d(r) \in C^2([0,\infty))$, $d(r) > 0$ and $d'(r) \leq 0$ on $[0,\infty)$.

The model (1.4) can be regarded as a special case of models considered in Korobenko and Braverman (2009) and we refer to Potapov et al. (2014) for a mathematical derivation of such kind model with Fokker–Planck type diffusion (see also Cosner 2014). The assumption $d'(r) \leq 0$ describes the fact that the dispersal rate of species will be slower in the area with more abundant resources, which seems to be universal and appears widely in other biological processes such as preytaxis (Kareiva and Odell 1987), bacterial movement (Liu et al. 2021; Jin et al. 2020), starvation-driven diffusion (Cho and Kim 2013) and chemotaxis (Jin and Wang 2021; Keller and Segel 1971). It was shown in Korobenko and Braverman (2009) that the problem (1.4) admits a unique positive steady state $w_{\mu,d}(x)$ which is globally asymptotically stable and in particular, if $d(r)r = $ constant, then $w_{\mu,d}(x) = r(x)$ is the ideal free distribution (i.e., the species can perfectly match the environmental resource and hence optimize its fitness). However, the effect of resource-dependent dispersal on the population size, like whether the total population $\int_\Omega w_{\mu,d}(x)\mathrm{d}x$ increases or decreases, was not examined in Korobenko and Braverman (2009). The answer is clear when $d(r)r$ is constant as mentioned above, but remains obscure when $d(r)r$ is non-constant. This becomes the first goal of this paper and the main result obtained on (1.4) can be described as follows.

- If $d(r) = e^{-kr}$ or $d(r) = (1+r)^{-k}$ with $k > 0$, then the total population $\int_\Omega w_{\mu,d}(x)\mathrm{d}x$ may be greater than the environmental carrying capacity $m_0 := \int_\Omega r(x)\mathrm{d}x$ if k is small, while it may be smaller than m_0 if both k and μ are large (see Theorem 2.1).

When the resource-dependent dispersal rate $d(r)$ is a constant, the well-known results (cf. Lou 2006 or (1.2)) assert that the total population supported is always greater than the environmental carrying capacity. On the contrary, when $d(r)$ is non-constant, we show that there is $d(r)$ such that the total population supported can be equal or smaller than the environmental carrying capacity (see Theorem 2.1 and numerical simulations in Fig. 1). Our result adds a theoretical support to the yeast experiment observation in Zhang et al. (2017) that a consumer diffusing in a region with a heterogeneously distributed input of exploitable renewed limiting resources can have smaller total population abundance at equilibrium than a population diffusing in a space with the

same total amount of resources distributed homogeneously. This in turn implies that the resource-dependent dispersal may play a role in regulating the population size.

Next we turn to consider the following two-species competition–diffusion model with resource-dependent dispersal rates

$$
\begin{cases}
\partial_t u_1 = \mu_1 \Delta(d_1(r)u_1) + u_1(r(x) - u_1 - u_2), & x \in \Omega, t > 0, \\
\partial_t u_2 = \mu_2 \Delta(d_2(r)u_2) + u_2(r(x) - u_1 - u_2), & x \in \Omega, t > 0, \\
\nabla(d_1(r)u_1) \cdot n = \nabla(d_2(r)u_2) \cdot n = 0, & x \in \partial\Omega, t > 0, \\
u_1(x, 0) = u_{1,0}(x) \gneqq 0, u_2(x, 0) = u_{2,0}(x) \gneqq 0, & x \in \Omega,
\end{cases}
\tag{1.5}
$$

where $d_i(r)(i = 1, 2)$ satisfies

(H_2) $d_i(r) \in C^2([0, \infty))$, $d_i(r) > 0$ and $d_i'(r) \leq 0$ on $[0, \infty)$.

The main purpose of this paper is to explore how the resource-dependent dispersal affects the global (or local) dynamics of populations compared to the resource-independent dispersal (i.e. random diffusion) like the model (1.3). The resource-dependent dispersal rate functions $d_i(r)(i = 1, 2)$ will bring considerable difficulties to analysis and analyzing the model (1.5) directly is very inconvenient. In this paper, we shall develop an idea by changing the variables

$$
u = d_1(r)u_1 \quad \text{and} \quad v = d_2(r)u_2
\tag{1.6}
$$

and transforming (1.5) to equations for (u, v) as follows

$$
\begin{cases}
u_t = \mu_1 d_1(r)\Delta u + u(r(x) - \frac{u}{d_1(r)} - \frac{v}{d_2(r)}), & x \in \Omega, t > 0, \\
v_t = \mu_2 d_2(r)\Delta v + v(r(x) - \frac{u}{d_1(r)} - \frac{v}{d_2(r)}), & x \in \Omega, t > 0, \\
\nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, t > 0, \\
u(x, 0) = u_{1,0}(x)d_1(r(x)) \gneqq 0, & x \in \Omega, \\
v(x, 0) = u_{2,0}(x)d_2(r(x)) \gneqq 0, & x \in \Omega.
\end{cases}
\tag{1.7}
$$

The transformed system (1.7) generates a monotone dynamical system (cf. Zhou et al. 2021, Theorem 7) and the local qualitative properties of its steady states may determine the global dynamics by the well-known results for monotone dynamical systems. Hence we turn to study the steady state problem of (1.7), where the steady state solution, denoted by $(U, V)(x)$, satisfies

$$
\begin{cases}
\mu_1 d_1(r)\Delta U + U(r(x) - \frac{U}{d_1(r)} - \frac{V}{d_2(r)}) = 0, & x \in \Omega, \\
\mu_2 d_2(r)\Delta V + V(r(x) - \frac{U}{d_1(r)} - \frac{V}{d_2(r)}) = 0, & x \in \Omega, \\
\nabla U \cdot n = \nabla V \cdot n = 0, & x \in \partial\Omega.
\end{cases}
\tag{1.8}
$$

Since $d_i(r) > 0$ on $\overline{\Omega}$ for $i = 1, 2$, it follows from (1.6) that

$$
(u_1, u_2) = \left(\frac{u}{d_1(r)}, \frac{v}{d_2(r)}\right), \quad (U_1, U_2) = \left(\frac{U}{d_1(r)}, \frac{V}{d_2(r)}\right)
$$

where $(U_1, U_2)(x)$ denotes the steady state solution of (1.5). Therefore all qualitative behaviors of the solution to (1.5) can be recovered by the solution (u, v) of (1.7) through (1.6). Hereafter, our analysis will be focused on the transformed system (1.7) and (1.8) only. However, the numerical simulations will be directly performed to (1.5) for illustration when doing so. The main results of this paper on (1.7) or (1.8) are described as follows.

- If $d_1(r) = \vartheta d_2(r)$ for some constant $\vartheta > 0$, namely two competing species have the same resource-dependent dispersal strategies up to a positive multiplicative constant, then the semi-trivial (exclusion) steady state $(\theta_{\mu_1, d_1}, 0)$ (resp. $(0, \theta_{\mu_2, d_2})$) of system (1.7) is globally asymptotically stable for any $\vartheta \mu_1 < \mu_2$ (resp. $\vartheta \mu_1 > \mu_2$) provided that $d_2(r)r$ is not constant (see Theorem 3.1), where θ_{μ_i, d_i} is the unique positive solution of

$$\begin{cases} \mu_i d_i(r)\Delta\theta_{\mu_i, d_i} + \theta_{\mu_i, d_i}\left(r(x) - \frac{\theta_{\mu_i, d_i}}{d_i(r)}\right) = 0, & x \in \Omega, \\ \nabla\theta_{\mu_i, d_i} \cdot n = 0, & x \in \partial\Omega. \end{cases}$$

  If $d_2(r)r$ is constant, then system (1.7) has a global attractor consisting of a continuum of constant steady states, see Remark 3.1-(b).
- If $d_1(r) \neq Cd_2(r)$ for any constant $C > 0$, when μ_1 and μ_2 are large, both globally asymptotically stable semi-trivial and coexistence steady states are possible (see Theorem 3.2). In particular, we can construct some $d_i(r)$ such that the coexistence steady state exist if one species has slower diffusion than the other (see Proposition 3.2 and Remark 3.3), which implies the prominent phenomenon "slower diffuser prevails" may not occur for populations with resource-dependent dispersal.
- Consider specific dispersal strategies $d_i(r) = e^{-k_i r}$ or $d_i(r) = (1 + r)^{-k_i}$ with $k_i > 0$ for $i = 1, 2$ and $k_1 \neq k_2$ in $\Omega = [0, L]$. If the resource $r(x)$ is monotone in $[0, L]$, then we can find some parameter regimes in which semi-trivial or positive steady states are globally asymptotically stable (see Theorem 3.3). We also use numerical simulations to illustrate that the competitive outcomes could be generic despite of the dispersal strength in certain parameter regimes (see Remark 3.5 and Fig. 3).

Before concluding this section, we shall mention a few related works. In Braverman and Makrujjaman (2016), the authors have considered a general competition–diffusion model with resource-dependent dispersal and explore the effects of competition and different dispersal strategies. But their study was mainly focused on the case of weak competition or competitive exclusion. However, this paper primarily aims to study the effect of resource-dependent dispersal by assuming that two competing species are ecologically identical, namely $b_1 = b_2 = c_1 = c_2 = 1$ in (1.3). The result in Braverman and Makrujjaman (2016) regarding this case states that if $d_1(r)r$ is constant and $d_2(r)r$ is not constant, then the steady state $(r(x), 0)$ is globally asymptotically stable, namely the species u_1 attains the ideal free distribution. We remark it was previously shown in Cantrell et al. (2010), Gejji et al. (2012), Averill et al. (2012) that the ideal free distribution can be achieved in the competition–diffusion–advection model with constant diffusion if one species employs the logarithmic advective strategy and the

other does not. In the case $d_1(r) = \vartheta d_2(r)$ for some constant $\vartheta > 0$, the problem (1.8) falls into the model class considered in Guo et al. (2020). Here we obtain the same results as in Guo et al. (2020) with a different approach, see Theorem 3.1 and Remark 3.1-(a). Recently the global existence and stability of solutions to a special competition–diffusion model with dynamical resource and resource-dependent dispersal was studied in Wang and Xu (2021). The system (1.7) can be regarded as a competition system with inhomogeneous competition coefficients and inhomogeneous dispersal rates. In this case, we refer to Ni et al. (2020) for the global stability of inhomogeneous equilibrium solutions (if exist) under certain conditions.

The rest of this paper is arranged as follows. In Sect. 2, we focus on the single-species model (1.4) and study the effect of resource-dependent dispersal on the population size. Then we study the effect of resource-dependent dispersals for the two-species model (1.5) by studying the transformed system (1.7) in Sect. 3. In Sect. 4, we summarize our results and discuss some open questions.

2 Single-species model

In this section, we study the global dynamics of the single species model (1.4) with resource-dependent dispersal, where $d(r)$ satisfies the assumption (H_1) with r fulfilling the assumption (H_0). The steady state solution of (1.4), denoted by $W(x)$, satisfies the following equations

$$\begin{cases} \mu \Delta (d(r)W) + W(r(x) - W) = 0, & x \in \Omega, \\ \nabla (d(r)W) \cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{2.1}$$

Below we shall investigate the existence and properties of solutions to (2.1) for the non-constant dispersal rate $d(r)$ and compare the results with those for the constant $d(r)$. In the sequel, we write the positive solution of (2.1) as $W_{\mu,d}$ to indicate the dependencies of solutions on μ and non-constant $d(r)$. When $d(r)$ is constant, we shall assume that $d(r) = 1$ without loss of generality and denote the solution by $W_{\mu,1}$. The following results on $W_{\mu,1}$ are well-known (cf. Lou 2006).

Proposition 2.1 *Let r satisfy the condition (H_0). Then the problem (1.4) with $d(r) = 1$ admits a unique positive steady state $W_{\mu,1}$ which is globally asymptotically stable and satisfies the following properties:*

(1) $\lim\limits_{\mu \to 0} W_{\mu,1} = r$ *and* $\lim\limits_{\mu \to \infty} W_{\mu,1} = \dfrac{1}{|\Omega|} \int_\Omega r dx$ *in* $L^\infty(\Omega)$.

(2) $\int_\Omega W_{\mu,1} dx > \int_\Omega r dx$ *for every* $\mu > 0$.

Next, we shall explore whether the problem (1.4) with non-constant dispersal rate $d(r)$ has similar/different results as/from those in Proposition 2.1 for the constant $d(r)$. The typical examples of decreasing function $d(r)$ satisfying the hypothesis (H_1) include $d(r) = e^{-kr}$ or $d(r) = (1 + r)^{-k}$ with a constant $k > 0$. We shall prove the following theorem.

Theorem 2.1 *Let $d(r)$ satisfy condition (H_1) with r fulfilling (H_0). Then the problem (1.4) admits a unique positive steady state $W_{\mu,d}$ which is globally asymptotically stable and satisfies*

(1) $\displaystyle\lim_{\mu\to 0} W_{\mu,d} = r$ *and* $\displaystyle\lim_{\mu\to\infty} W_{\mu,d} = \frac{\int_\Omega r d(r)^{-1} dx}{\int_\Omega d(r)^{-2} dx} d(r)^{-1}$ *in* $L^\infty(\Omega)$.

(2) If $d(r)r = c_0$ ($c_0 > 0$ is a constant), then $W_{\mu,d}(x) = r$ and $\displaystyle\int_\Omega W_{\mu,d} dx = \int_\Omega r dx$.

(3) Let $d(r) = e^{-kr}$ or $d(r) = (1+r)^{-k}$ with $k > 0$. Then for small $k > 0$ and any $\mu > 0$, it holds that

$$\int_\Omega W_{\mu,d} dx > \int_\Omega r dx.$$

While if $k > 0$ is sufficiently large, there exist $\mu > 0$ large enough such that

$$\int_\Omega W_{\mu,d} dx < \int_\Omega r dx.$$

Remark 2.1 We give two remarks to highlight some new findings in Theorem 2.1.

(a) Comparing the results between Proposition 2.1 and Theorem 2.1, we find that although solutions $W_{\mu,1}$ and $W_{\mu,d}$ share some similar properties, there exist significant differences. When $d(r)$ is constant, Proposition 2.1-(2) asserts that the total population of unique positive solution is always greater than the total carrying capacity. However Theorem 2.1-(2) says that if $d(r)$ is proportional to $\frac{1}{r}$, the total population is equal to the environmental carrying capacity. Furthermore Theorem 2.1-(3) asserts that there exist some decreasing dispersal rate function $d(r)$ such that the total population can even be smaller than the environmental carrying capacity, which is confirmed by numerical simulations shown in Fig. 1.

(b) In the yeasts experiment of Zhang et al. (2017), it was found that a consumer diffusing in a region with a heterogeneously distributed input of exploitable renewed limiting resources can have smaller total population abundance at equilibrium than a population diffusing in a space with the same total amount of resources distributed homogeneously. This is exactly supported by our results of Theorem 2.1-(3) since total population at equilibrium is the same as the total amount of resources in the case of homogeneously distributed resources (r is constant). This observation has been supported by the theoretical models in DeAngelis et al. (2016), He et al. (2019) where both intrinsic growth of the species and environmental carrying capacity are spatially heterogenous. Our analytical results here add another support to this important experimental finding using different mechanism (i.e. density-dependent dispersal).

Next we proceed to prove Theorem 2.1. Studying (2.1) directly appears to be inconvenient due to the resource-dependent dispersal rate. Hence we make a change of
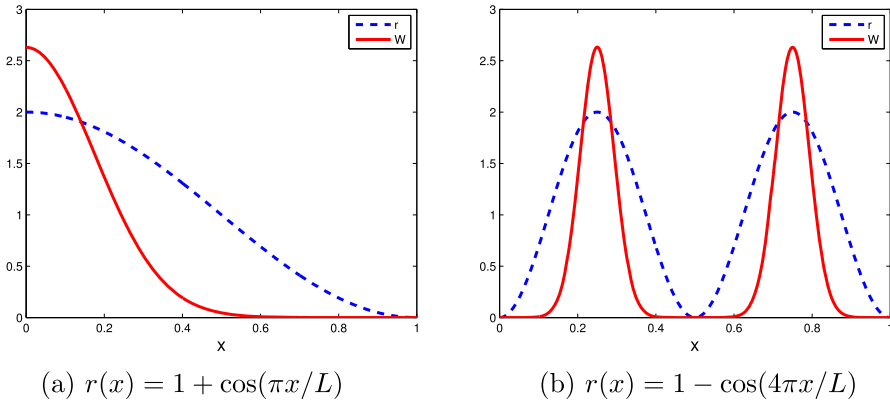
(a) $r(x) = 1 + \cos(\pi x/L)$　　　　　　(b) $r(x) = 1 - \cos(4\pi x/L)$

Fig. 1 Numerical simulations of spatial profile of solutions to (2.1) with $d(r) = (1+r)^{-k}$ in $[0, L]$, showing that the supported total population is less than the total carrying capacity of the resource r, where $r(x)$ is indicated in the figure and $L = 1, k = 10, \mu = 10^5$

variable: $W(x) = \frac{\theta(x)}{d(r)}$ and transform (2.1) to the Neumann problem for $\theta(x)$

$$
\begin{cases}
\mu d(r)\Delta\theta + \theta\left(r(x) - \frac{\theta}{d(r)}\right) = 0, & x \in \Omega, \\
\nabla\theta \cdot n = 0, & x \in \partial\Omega.
\end{cases}
\tag{2.2}
$$

In the following, we shall denote the positive solution of (2.2) by $\theta_{\mu,d}$ to indicate the dependencies of solutions on μ and d. Note that if $d(r)$ depends on k, then $\theta_{\mu,d}$ also depends on k. With $W_{\mu,d} = \frac{\theta_{\mu,d}}{d(r)}$, it suffices to investigate (2.2) for the steady state problem (2.1). To this end, we consider the following linear eigenvalue problem

$$
\begin{cases}
D(x)\Delta\phi + m(x)\phi = \lambda\phi, & x \in \Omega, \\
\nabla\phi \cdot n = 0, & x \in \partial\Omega,
\end{cases}
\tag{2.3}
$$

where $D(x)$ and $m(x)$ satisfy

$$
D(x) \in C(\bar{\Omega}; (0, \infty)), \; m(x) \in C(\bar{\Omega}; \mathbb{R}).
$$

Based on the celebrated Krein–Rutman Theorem (Krein and Rutman 1948), problem (2.3) admits a principal eigenvalue, denoted by $\lambda_1(D(x), m)$, which has a strictly positive eigenfunction $\phi_1(D(x), m)$ in Ω with $\|\phi_1(D(x), m)\|_{L^\infty(\Omega)} = 1$. Moreover, by the variational approach, $\lambda_1(D(x), m)$ can be represented as

$$
\lambda_1(D(x), m) = \sup_{0 \neq \phi \in H^1(\Omega)} \frac{\int_\Omega (-|\nabla\phi|^2 + \frac{m}{D(x)}\phi^2)\mathrm{d}x}{\int_\Omega \frac{\phi^2}{D(x)}\mathrm{d}x}.
\tag{2.4}
$$

If $D(x) \in C^1(\bar{\Omega}; (0, \infty))$, by the change of variable $\phi = \psi \sqrt{D(x)}$, one can characterize the principal eigenvalue by the following expression

$$\lambda_1(D(x), m) = \sup_{0 \neq \psi \in H^1(\Omega)} \frac{\int_\Omega \left(-|\nabla(\psi \sqrt{D(x)})|^2 + m\psi^2 \right) \mathrm{d}x}{\int_\Omega \psi^2 \mathrm{d}x}. \tag{2.5}$$

The existence and uniqueness of solutions of (2.2) is established in the following Lemma.

Lemma 2.1 *Let $d(r)$ satisfy assumption (H_1) with r fulfilling assumption (H_0). Then the problem (2.2) admits a unique positive solution $\theta_{\mu,d}$ which is globally asymptotically stable for the corresponding parabolic equations.*

Proof Since the nonlinear reaction term of problem (2.2) is of logistic type, it is well-known that the existence of a positive solution of (2.2) is determined by the linear instability of the zero solution. As we know that the zero solution is linearly stable (resp. linearly unstable) provided $\lambda_1(\mu d(r), r) < 0$ (resp. $\lambda_1(\mu d(r), r) > 0$). Furthermore, if problem (2.2) admits a positive solution, it must be unique and globally asymptotically stable (cf. Cantrell and Cosner 2003).

By the variational characterization (2.4), choosing 1 as a test function, one can deduce that

$$\lambda_1(\mu d(r), r) \geq \frac{\int_\Omega \frac{r}{d(r)} \mathrm{d}x}{\int_\Omega \frac{1}{d(r)} \mathrm{d}x} > 0,$$

where we have used the hypotheses (H_1) and (H_0). This fact suggests that the zero solution is linearly unstable, which completes the proof.   □

Next, we provide some *prior* estimates for the upper bound of the unique positive solution $\theta_{\mu,d}$ of problem (2.2).

Lemma 2.2 *If $d(r)$ satisfies (H_1) with r fulfilling (H_0), then the unique positive solution $\theta_{\mu,d}$ of problem (2.2) satisfies*

$$\theta_{\mu,d} \leq \max_{x \in \bar{\Omega}}(d(r)r), \quad on \ \bar{\Omega}.$$

Proof Let $x_0 \in \bar{\Omega}$ be such that $\theta_{\mu,d}(x_0) = \max_{x \in \bar{\Omega}} \theta_{\mu,d}$. Then by the Hopf boundary lemma, $x_0 \in \Omega$ and hence $\Delta\theta_{\mu,d}(x_0) \leq 0$, which combined with the first equation of (2.2) suggests that

$$\theta_{\mu,d}(x_0) = \max_{x \in \bar{\Omega}}(\theta_{\mu,d}) \leq d(r)r|_{x=x_0} \leq \max_{x \in \bar{\Omega}}(d(r)r),$$

which completes the proof.   □

Remark 2.2 If $d(r)r \equiv C$ (C is a positive constant), then $\theta_{\mu,d} \equiv C$; while if $d(r)r \not\equiv C$ for any positive constant number C, by the strong maximum principle, one can deduce that

$$\theta_{\mu,d} < \max_{x \in \bar{\Omega}}(d(r)r), \quad \text{on } \bar{\Omega}.$$

Then, we describe the limiting profile of the unique positive solution of problem (2.2) as $\mu \to 0$ (or ∞).

Lemma 2.3 *If $d(r)$ satisfies (H_1) with r fulfilling (H_0), then the unique positive solution $\theta_{\mu,d}$ of problem (2.2) satisfies*

$$\|\theta_{\mu,d} - rd(r)\|_{L^\infty(\Omega)} \to 0 \text{ as } \mu \to 0 \text{ and } \|\theta_{\mu,d} - c_r\|_{C^1(\Omega)} \to 0 \text{ as } \mu \to \infty,$$

where $c_r = \frac{\int_\Omega rd(r)^{-1}dx}{\int_\Omega d(r)^{-2}dx}$. Moreover, if $\nabla r \cdot n = 0$ on $\partial\Omega$, $\min_{x \in \bar{\Omega}} r > 0$ and $d(r) = e^{-kr}$ or $d(r) = (1+r)^{-k}$, then the unique positive solution $\theta_{\mu,d}$ of problem (2.2) satisfies

$$\|\theta_{\mu,d} - rd(r)\|_{L^\infty(\Omega)} \to 0 \text{ as } k \to \infty.$$

Proof By Lemma A.1 in Hutson et al. (2005), we have

$$\|\theta_{\mu,d} - rd(r)\|_{L^\infty(\Omega)} \to 0 \text{ as } \mu \to 0.$$

Following the approach in Lemma 2.2 of Tang and Zhou (2020), one can deduce

$$\|\theta_{\mu,d} - c_r\|_{C^1(\Omega)} \to 0 \text{ as } \mu \to \infty,$$

where $c_r = \frac{\int_\Omega rd(r)^{-1}dx}{\int_\Omega d(r)^{-2}dx}$.

Furthermore, if $\nabla r \cdot n = 0$ on $\partial\Omega$, we only consider the case $d(r) = e^{-kr}$, and the case $d(r) = (1+r)^{-k}$ can be treated in the same manner. let $U_k = \frac{\theta_{\mu,e^{-kr}}}{e^{-kr}}$ on $\bar{\Omega}$. Then, U_k satisfies

$$\begin{cases} \mu\Delta(e^{-kr}U_k) + U_k(r - U_k) = 0, & x \in \Omega, \\ \nabla U_k \cdot n = 0, & x \in \partial\Omega \end{cases}$$

where we have used the fact $\nabla r \cdot n = 0$ on $\partial\Omega$. The above equations can be rewritten as

$$\begin{cases} \mu e^{-kr}\Delta U_k - 2\mu k e^{-kr}\nabla r \cdot \nabla U_k + U_k(r_k - U_k) = 0, & x \in \Omega, \\ \nabla U_k \cdot n = 0, & x \in \partial\Omega \end{cases} \quad (2.6)$$

where $r_k = r + \mu k^2 e^{-kr}|\nabla r|^2 - \mu k e^{-kr}\Delta r$. For any $\epsilon > 0$, by assumption (H_0), $\min_{x \in \bar{\Omega}} r > 0$, and $\nabla r \cdot n = 0$ on $\partial\Omega$, we can directly verify that $\hat{U} = r + \epsilon$ and

$\check{U} = r - \min\left\{\epsilon, \frac{\min\limits_{x \in \bar{\Omega}} r}{2}\right\}$ are the super-solution and sub-solution of problem (2.6) for large k, respectively. Then by the method of super and sub solutions, one finds a constant $k^*(\epsilon) > 0$ such that

$$r - \min\left\{\epsilon, \frac{\min\limits_{x \in \bar{\Omega}} r}{2}\right\} \leq U_k \leq r + \epsilon, \quad k \geq k^*(\epsilon).$$

Noting that $\epsilon > 0$ is arbitrary, one obtains

$$r \leq \frac{\theta_{\mu,d}}{d(r)} \leq r, \quad \text{as } k \to \infty,$$

which completes the proof.   □

In the following we shall study whether the total population supported by the environment can exceed the environmental carrying capacity. Below we shall prove a general results that will be used later in several places. For the convenience of presentation, we shall assume $d(r) =: d(k; r)$ sometimes, where $d(k; r)$ satisfies

(H_3) $d(k; r)$ depends smoothly on $k \geq 0$ satisfying $\lim\limits_{k \to 0} d(k; r) = 1$.

The typical examples are $d(k; r) = e^{-kr}$ or $d(k; r) = (1 + r)^{-k}$ with $k > 0$. But note that the hypothesis (H_3) covers more general form of $d(k; r)$ where k is not necessarily the exact decay rate of $d(k; r)$, for instance $d(k; r) = e^{-\frac{k}{1+k}r}$ or $d(k; r) = 1 + \frac{k}{1+r}$.

We first prove some useful results for the principal eigenvalue $\lambda_1(\mu d(k; r), m)$ of problem (2.3), where $m(x) \in C(\bar{\Omega}; \mathbb{R})$.

Lemma 2.4 *Assume that $m(x) \in C(\bar{\Omega}; \mathbb{R})$ is non-constant, $d(r) = d(k; r)$ satisfies (H_1) with $d(k; r)$ fulfilling (H_3) and r satisfying (H_0). Then the following results for the principal eigenvalue $\lambda_1(\mu d(k; r), m)$ of problem (2.3) with corresponding eigenfunction $\phi_1(\mu d(k; r), m)$ hold.*

(i) $\lambda_1(\mu d(k; r), m)$ and $\phi_1(\mu d(k; r), m)$ depend smoothly on parameter $k \in [0, \infty)$ and on parameter $\mu \in (0, \infty)$, respectively.

(ii) The derivatives of $\lambda_1(\mu d(k; r), m)$ with respect to k and μ are, respectively, given by

$$\frac{\partial \lambda_1(\mu d(k; r), m)}{\partial k} = \frac{\mu \int_\Omega \frac{\phi_1}{d(k;r)} \cdot \frac{\partial d(k;r)}{\partial k} \Delta \phi_1 dx}{\int_\Omega \frac{\phi_1^2}{d(k;r)} dx}, \tag{2.7}$$

and

$$\frac{\partial \lambda_1(\mu d(k; r), m)}{\partial \mu} = \frac{\int_\Omega \phi_1 \Delta \phi_1 dx}{\int_\Omega \frac{\phi_1^2}{d(k;r)} dx} = -\frac{\int_\Omega |\nabla \phi_1|^2 dx}{\int_\Omega \frac{\phi_1^2}{d(k;r)} dx}, \tag{2.8}$$

where $\phi_1 = \phi_1(\mu d(k;r), m)$. *Moreover,* $\lambda_1(\mu d(k;r), m)$ *is strictly decreasing with respect to parameter* $\mu \in (0, \infty)$ *such that*

$$\lim_{\mu \to 0} \lambda_1(\mu d(k;r), m) = \max_{x \in \bar{\Omega}} m(x), \quad \lim_{\mu \to \infty} \lambda_1(\mu d(k;r), m) = \frac{\int_\Omega \frac{m}{d(k;r)} dx}{\int_\Omega \frac{1}{d(k;r)} dx},$$

and

$$\lim_{k \to 0} \lambda_1(\mu d(k;r), r) = \lambda_1(\mu, r).$$

Furthermore, if $d(k;r) = e^{-kr}$ *or* $d(k;r) = (1+r)^{-k}$, *and* $\sup_{x \in \Omega^m} r(x) > 0$, *then*

$$\lim_{k \to \infty} \lambda_1(\mu d(k;r), m) = \max_{x \in \bar{\Omega}} m(x),$$

where $\Omega^m = \{x \in \bar{\Omega} | m(x) = \max_{x \in \bar{\Omega}} m(x)\}$.

Proof The proof of assertion (i) is standard and we refer to [Cantrell and Cosner (2003), p. 163] for details. For assertion (ii), we prove (2.7) only and (2.8) can be shown similarly. For simplicity, we abbreviate $(\lambda_1(\mu d(k;r), m), \phi_1(\mu d(k;r), m))$ as (λ_1, ϕ_1). Recall that (λ_1, ϕ_1) satisfies

$$\begin{cases} \mu d(k;r)\Delta\phi_1 + m\phi_1 = \lambda_1\phi_1, & x \in \Omega, \\ \nabla\phi_1 \cdot n = 0, & x \in \partial\Omega. \end{cases} \quad (2.9)$$

Differentiating (2.9) with respect to k, we get

$$\begin{cases} \mu d(k;r)\Delta\phi_1' + \mu \frac{\partial d(k;r)}{\partial k}\Delta\phi_1 + m\phi_1' = \lambda_1\phi_1' + \lambda_1'\phi_1, & x \in \Omega, \\ \nabla\phi_1' \cdot n = 0, & x \in \partial\Omega \end{cases} \quad (2.10)$$

where we use $'$ to denote $\frac{\partial}{\partial k}$. Multiplying the first equation of (2.9) by $\frac{\phi_1'}{d(k;r)}$, and then integrating the resulting equation on Ω, one obtains

$$\int_\Omega \left(\mu\phi_1'\Delta\phi_1 + \frac{m\phi_1\phi_1'}{d(k;r)} \right) dx = \lambda_1 \int_\Omega \frac{\phi_1\phi_1'}{d(k;r)} dx.$$

Similarly, multiplying the first equation of (2.10) by $\frac{\phi_1}{d(k;r)}$, and integrating the resulting equation on Ω, we get

$$\int_\Omega \left(\mu\phi_1\Delta\phi_1' + \mu \frac{\phi_1}{d(k;r)} \cdot \frac{\partial d(k;r)}{\partial k}\Delta\phi_1 + \frac{m\phi_1\phi_1'}{d(k;r)} \right) dx = \lambda_1 \int_\Omega \frac{\phi_1\phi_1'}{d(k;r)} dx + \lambda_1' \int_\Omega \frac{\phi_1^2}{d(k;r)} dx.$$

Subtracting the above two equations and applying the integration by parts immediately give (2.7). Next, we will show that ϕ_1 is not constant in Ω. Indeed, if ϕ_1 is constant in

Ω, then $m = \lambda_1$ is constant in Ω by (2.9), which contradicts our assumption that m is non-constant. Therefore, it follows that

$$\frac{\partial \lambda_1(\mu d(k;r), m)}{\partial \mu} = -\frac{\int_\Omega |\nabla \phi_1|^2 dx}{\int_\Omega \frac{\phi_1^2}{d(k;r)} dx} < 0,$$

which entails that the principal eigenvalue λ_1 is strictly decreasing with respect to parameter $\mu \in (0, \infty)$. Multiplying the first equation of (2.9) with $\frac{1}{d(k;r)}$, and then integrating the resulting equation on Ω, one obtains

$$\lambda_1 \int_\Omega \frac{\phi_1}{d(k;r)} dx = \int_\Omega \frac{m \phi_1}{d(k;r)} dx. \tag{2.11}$$

To proceed, we Claim that $\phi_1 \to 1$ in $C^1(\bar\Omega)$ as $\mu \to \infty$. Indeed from the variational characterization (2.4), it follows that

$$\lambda_1(\mu d(k;r), m) = \sup_{0 \neq \phi \in H^1(\Omega)} \frac{\int_\Omega (-\mu |\nabla \phi|^2 + \frac{m\phi^2}{d(k;r)}) dx}{\int_\Omega \frac{\phi^2}{d(k;r)} dx}$$

$$\leq \sup_{0 \neq \phi \in H^1(\Omega)} \frac{\int_\Omega \frac{m\phi^2}{d(k;r)} dx}{\int_\Omega \frac{\phi^2}{d(k;r)} dx}$$

$$\leq \max_{x \in \bar\Omega} m(x), \tag{2.12}$$

and

$$\lambda_1(\mu d(k;r), m) = \sup_{0 \neq \phi \in H^1(\Omega)} \frac{\int_\Omega (-\mu |\nabla \phi|^2 + \frac{m\phi^2}{d(k;r)}) dx}{\int_\Omega \frac{\phi^2}{d(k;r)} dx} \geq \frac{\int_\Omega \frac{m}{d(k;r)} dx}{\int_\Omega \frac{1}{d(k;r)} dx}. \tag{2.13}$$

Based on the facts that $\|\phi_1(\mu d(k;r), m)\|_{L^\infty(\Omega)} = 1$ for any $\mu > 0$, (2.12), (2.13), $m(x) \in C(\bar\Omega; \mathbb{R})$, (H_1) and L^p estimates, one can derive that $\|\phi_1(\mu d(k;r), m)\|_{W^{2,p}(\Omega)}$ is bounded uniformly for any $p \geq 1$ as $\mu \to \infty$ (cf. Gilbarg and Trudinger 2001). From the Sobolev imbedding theorem, one can deduce from (2.3) along with $D(x) = \mu d(r)$ that $\phi_1(\mu d(k;r), m)$ converges to some function ϕ^* in $C^1(\bar\Omega)$ as $\mu \to \infty$, where $\phi^* \geq 0$ in Ω satisfies (in the weak sense)

$$\begin{cases} \Delta \phi^* = 0, & x \in \Omega, \\ \nabla \phi^* \cdot n = 0, & x \in \partial\Omega, \end{cases}$$

and $\|\phi^*\|_{L^\infty(\Omega)} = 1$. Hence the claim holds, which combined with (2.11) implies

$$\lim_{\mu \to \infty} \lambda_1(\mu d(k;r), m) = \frac{\int_\Omega \frac{m}{d(k;r)} dx}{\int_\Omega \frac{1}{d(k;r)} dx}.$$

Next, we estimate the principal eigenvalue $\lambda_1(\mu d(k;r), m)$ as $\mu \to 0$. Since $m(x) \in C(\bar{\Omega}; \mathbb{R})$, for any $\epsilon > 0$, there exists some $\phi_\epsilon \in H^1(\Omega)$ such that

$$\text{supp}(\phi_\epsilon) \subseteq \{x \in \Omega | m(x) \geq \max_{x \in \bar{\Omega}} m(x) - \epsilon\} \quad \text{and} \quad \int_\Omega \frac{\phi_\epsilon^2}{d(k;r)} dx = 1,$$

where $\text{supp}(\phi_\epsilon) = \overline{\{x \in \Omega | \phi_\epsilon(x) > 0\}}$. Taking ϕ_ϵ as a test function, by the variational characterization (2.4), we have

$$\begin{aligned}
\lambda_1(\mu d(k;r), m) &= \sup_{0 \neq \phi \in H^1(\Omega)} \frac{\int_\Omega (-\mu |\nabla \phi|^2 + \frac{m\phi^2}{d(k;r)}) dx}{\int_\Omega \frac{\phi^2}{d(k;r)} dx} \\
&\geq \frac{\int_\Omega (-\mu |\nabla \phi_\epsilon|^2 + \frac{m\phi_\epsilon^2}{d(k;r)}) dx}{\int_\Omega \frac{\phi_\epsilon^2}{d(k;r)} dx} \\
&\geq \max_{x \in \bar{\Omega}} m(x) - \epsilon - \mu \int_\Omega |\nabla \phi_\epsilon|^2 dx.
\end{aligned} \tag{2.14}$$

Combining (2.12), (2.14) and noticing that ϵ is arbitrarily small, one finds

$$\lim_{\mu \to 0} \lambda_1(\mu d(k;r), m) = \max_{x \in \bar{\Omega}} m(x).$$

From assertion (i) and (H_3), one arrives at

$$\lim_{k \to 0} \lambda_1(\mu d(k;r), r) = \lambda_1(\mu, r).$$

Finally, we calculate $\lim_{k \to \infty} \lambda_1(\mu e^{-kr}, m)$ and $\lim_{k \to \infty} \lambda_1(\mu(1+r)^{-k}, m)$ can be obtained similarly. We note that (2.12) always holds. Since $\sup_{x \in \Omega^m} r(x) > 0$, for any $\epsilon_1 > 0$, we can choose $\phi_{\epsilon_1} \in H^1(\Omega)$ such that

$$m(x) \geq \max_{x \in \bar{\Omega}} m(x) - \epsilon_1 \quad \text{and} \quad r(x) > 0, \quad \text{for } x \in \text{supp}(\phi_{\epsilon_1}).$$

By the variational characterization (2.4), taking ϕ_{ϵ_1} as a test function, we find that

$$\begin{aligned}
\lim_{k \to \infty} \lambda_1(\mu e^{-kr}, m) &= \lim_{k \to \infty} \sup_{0 \neq \phi \in H^1(\Omega)} \frac{\int_\Omega (-\mu |\nabla \phi|^2 + m\phi^2 e^{kr}) dx}{\int_\Omega \phi^2 e^{kr} dx} \\
&\geq \lim_{k \to \infty} \frac{\int_{\text{supp}(\phi_{\epsilon_1})} (-\mu |\nabla \phi_{\epsilon_1}|^2 + m\phi_{\epsilon_1}^2 e^{kr}) dx}{\int_{\text{supp}(\phi_{\epsilon_1})} \phi_{\epsilon_1}^2 e^{kr} dx} \\
&\geq \max_{x \in \bar{\Omega}} m(x) - \epsilon_1,
\end{aligned} \tag{2.15}$$

which, with the help of (2.12) and the arbitrariness of ϵ_1, implies that

$$\lim_{k\to\infty} \lambda_1(\mu e^{-kr}, m) = \max_{x\in\bar\Omega} m(x).$$

$\square$

Applying the implicit function theorem, one can obtain the following result [for example, see Theorem 3.5 and Proposition 3.6 in Cantrell and Cosner (2003)].

Proposition 2.2 *If $d(r) = d(k; r)$ satisfies (H_1) with $d(k; r)$ fulfilling (H_3) and r satisfying (H_0), then the unique positive solution $\theta_{\mu,d}$ of problem (2.2) depends smoothly on μ in $(0, \infty)$ and smoothly on k in $[0, \infty)$, respectively. Moreover, $\theta_{\mu,d}$ depends continuously on r.*

Lemma 2.5 *If $d(r) = d(k; r)$ satisfies (H_1) with $d(k; r)$ fulfilling (H_3) and r fulfilling (H_0), then the followings results hold.*

(i) *If $d(r)r \equiv c_0$(where c_0 is a positive constant), then $\theta_{\mu,d} = c_0$.*

(ii) *If $d(r)r$ is not constant in Ω, then $\int_\Omega \frac{\theta_{\mu,d}}{d(r)}dx > \int_\Omega r dx$ as k is small enough. If $d(k; r) = e^{-kr}$ or $d(k; r) = (1+r)^{-k}$, then for any $\epsilon > 0$, there exists $k_\epsilon > 0$ such that for any $k \geq k_\epsilon$, we have*

$$\left| \int_\Omega \frac{\theta_{\mu,d}}{d(r)}dx - r_{max}|\Omega^r| \right| < \epsilon$$

as $\mu \to \infty$, where $r_{max} = \max\limits_{x\in\bar\Omega} r(x)$ and $\Omega^r = \{x \in \Omega | r(x) = r_{max}\}$.

Proof If $d(r)r \equiv c_0$, one can verify that $\theta_{\mu,d} = c_0$ by the uniqueness of solutions, yielding the assertion (i) holds. Next we prove the assertion (ii). If $d(r)r$ is not constant in Ω, then it is direct to show that

$$\int_\Omega \theta_{\mu,1}dx = \int_\Omega r dx + \mu \int_\Omega \frac{|\nabla\theta_{\mu,1}|^2}{\theta_{\mu,1}^2}dx > \int_\Omega r dx, \qquad (2.16)$$

due to the fact that $\theta_{\mu,1}$ is not constant in Ω by the assumption that r is not constant in Ω. From the Proposition 2.2, and (H_3), it follows that

$$\lim_{k\to 0} \frac{\theta_{\mu,d}}{d(r)} = \theta_{\mu,1},$$

which along with (2.16) yields the first part of assertion (ii).

For the second part of assertion (ii), we only consider the case $d(k; r) = e^{-kr}$ while $d(k; r) = (1+r)^{-k}$ can be treated similarly. By Lemma 2.3, if $d(r) = e^{-kr}$, one obtains

$$\lim_{\mu\to\infty} \theta_{\mu,d} = \frac{\int_\Omega r e^{kr}dx}{\int_\Omega e^{2kr}dx},$$

which suggests that

$$\lim_{\mu \to \infty} \int_{\Omega} \frac{\theta_{\mu,d}}{d(r)} \mathrm{d}x = \frac{\int_{\Omega} e^{kr} \mathrm{d}x \cdot \int_{\Omega} r e^{kr} \mathrm{d}x}{\int_{\Omega} e^{2kr} \mathrm{d}x}.$$

To complete the proof of assertion (ii), we are left to show $\lim_{k \to \infty} \frac{\int_{\Omega} e^{kr} \mathrm{d}x \cdot \int_{\Omega} r e^{kr} \mathrm{d}x}{\int_{\Omega} e^{2kr} \mathrm{d}x}$
$= r_{\max} |\Omega^r|$. For any $\epsilon > 0$, define

$$\Omega_{\epsilon} = \{x \in \Omega | r(x) \geq r_{\max} - \epsilon\}.$$

Since $r \in C(\bar{\Omega})$, one has $|\Omega_{\epsilon}| > 0$. Obviously,

$$\int_{\Omega} e^{kr} \cdot \int_{\Omega} r e^{kr} = \int_{\Omega_{\epsilon}} e^{kr} \cdot \int_{\Omega_{\epsilon}} r e^{kr} + \int_{\Omega_{\epsilon}^c} e^{kr} \cdot \int_{\Omega_{\epsilon}^c} r e^{kr} + \int_{\Omega_{\epsilon}} e^{kr} \cdot \int_{\Omega_{\epsilon}^c} r e^{kr}$$
$$+ \int_{\Omega_{\epsilon}^c} e^{kr} \cdot \int_{\Omega_{\epsilon}} r e^{kr}$$
$$=: A_1 + A_2 + A_3 + A_4.$$

We only show that $\lim_{k \to \infty} \frac{A_3}{\int_{\Omega} e^{2kr}} = 0$ and $\lim_{k \to \infty} \frac{A_i}{\int_{\Omega} e^{2kr}} = 0 (i = 2, 4)$ can be proved similarly. Indeed,

$$0 \leq \lim_{k \to \infty} \frac{A_3}{\int_{\Omega} e^{2kr}} \leq \lim_{k \to \infty} \frac{A_3}{\int_{\Omega_{\frac{\epsilon}{3}}} e^{2kr}} \leq \lim_{k \to \infty} \frac{r_{\max} |\Omega|^2 e^{2kr_{\max} - k\epsilon}}{|\Omega_{\frac{\epsilon}{3}}| e^{2kr_{\max} - \frac{2k\epsilon}{3}}} = 0.$$

It is straightforward to check that

$$0 \leq \lim_{k \to \infty} \frac{\int_{\Omega_{\epsilon}^c} e^{2kr} \mathrm{d}x}{\int_{\Omega_{\epsilon}} e^{kr} \mathrm{d}x \cdot \int_{\Omega_{\epsilon}} r e^{kr} \mathrm{d}x} \leq \lim_{k \to \infty} \frac{|\Omega| e^{2k(r_{\max} - \epsilon)}}{|\Omega_{\frac{\epsilon}{2}}|^2 (r_{\max} - \frac{\epsilon}{2}) e^{2k(r_{\max} - \frac{\epsilon}{2})}} = 0.$$

Since $\epsilon > 0$ is arbitrary and noting that $\Omega_0 = \Omega^r$, from the above results, we have

$$\lim_{k \to \infty} \frac{\int_{\Omega} e^{kr} \mathrm{d}x \cdot \int_{\Omega} r e^{kr} \mathrm{d}x}{\int_{\Omega} e^{2kr} \mathrm{d}x} = \lim_{k \to \infty} \frac{\int_{\Omega_{\epsilon}} e^{kr} \mathrm{d}x \cdot \int_{\Omega_{\epsilon}} r e^{kr} \mathrm{d}x}{\int_{\Omega} e^{2kr} \mathrm{d}x}$$
$$= \lim_{k \to \infty} \frac{\int_{\Omega_{\epsilon}} e^{kr} \mathrm{d}x \cdot \int_{\Omega_{\epsilon}} r e^{kr} \mathrm{d}x}{\int_{\Omega_{\epsilon}} e^{2kr} \mathrm{d}x + \int_{\Omega_{\epsilon}^c} e^{2kr} \mathrm{d}x}$$
$$= \lim_{k \to \infty} \frac{\int_{\Omega_{\epsilon}} e^{kr} \mathrm{d}x \cdot \int_{\Omega_{\epsilon}} r e^{kr} \mathrm{d}x}{\int_{\Omega_{\epsilon}} e^{2kr} \mathrm{d}x}$$
$$= r_{\max} |\Omega^r|.$$

We proceed to prove the last equality above. If $|\Omega^r| = 0$, for any $\delta > 0$, then

$$0 \leq \lim_{k \to \infty} \frac{\int_{\Omega_\epsilon} e^{kr}\,\mathrm{d}x \cdot \int_{\Omega_\epsilon} re^{kr}\,\mathrm{d}x}{\int_{\Omega_\epsilon} e^{2kr}\,\mathrm{d}x} \leq \lim_{k \to \infty} \frac{|\Omega_\epsilon|^{\frac{1}{2}}\|r\|_{L^2(\Omega_\epsilon)}\int_{\Omega_\epsilon} e^{2kr}\,\mathrm{d}x}{\int_{\Omega_\epsilon} e^{2kr}\,\mathrm{d}x}$$

$$\leq |\Omega_\epsilon|^{\frac{1}{2}}\|r\|_{L^2(\Omega)} \leq \delta,$$

due to the fact that $\epsilon > 0$ is arbitrary, $|\Omega_\epsilon| \to |\Omega^r|$ as $\epsilon \to 0$, and $|\Omega^r| = 0$. Therefore,

$$\lim_{k \to \infty} \frac{\int_\Omega e^{kr}\,\mathrm{d}x \cdot \int_\Omega re^{kr}\,\mathrm{d}x}{\int_\Omega e^{2kr}\,\mathrm{d}x} = 0 = r_{\max}|\Omega^r|.$$

If $|\Omega^r| > 0$, similarly, for $\varepsilon > 0$ arbitrarily small, one can conclude that

$$\lim_{k \to \infty} \frac{\int_\Omega e^{kr}\,\mathrm{d}x \cdot \int_\Omega re^{kr}\,\mathrm{d}x}{\int_\Omega e^{2kr}\,\mathrm{d}x}$$

$$= \lim_{k \to \infty} \frac{\int_{\Omega_\epsilon} e^{kr}\,\mathrm{d}x \cdot \int_{\Omega_\epsilon} re^{kr}\,\mathrm{d}x}{\int_{\Omega_\epsilon} e^{2kr}\,\mathrm{d}x}$$

$$= \lim_{k \to \infty} \frac{\left(\int_{\Omega_\epsilon \setminus \Omega^r} e^{kr}\,\mathrm{d}x + \int_{\Omega^r} e^{kr}\,\mathrm{d}x\right) \cdot \left(\int_{\Omega_\epsilon \setminus \Omega^r} re^{kr}\,\mathrm{d}x + \int_{\Omega^r} re^{kr}\,\mathrm{d}x\right)}{\int_{\Omega_\epsilon \setminus \Omega^r} e^{2kr}\,\mathrm{d}x + \int_{\Omega^r} e^{2kr}\,\mathrm{d}x}$$

$$= \lim_{k \to \infty} \frac{\left(\int_{\Omega_\epsilon \setminus \Omega^r} e^{k(r-r_{\max})}\,\mathrm{d}x + |\Omega^r|\right) \cdot \left(\int_{\Omega_\epsilon \setminus \Omega^r} re^{k(r-r_{\max})}\,\mathrm{d}x + r_{\max}|\Omega^r|\right)}{\int_{\Omega_\epsilon \setminus \Omega^r} e^{2k(r-r_{\max})}\,\mathrm{d}x + |\Omega^r|}$$

$$= r_{\max}|\Omega^r|.$$

Therefore, the proof is completed. $\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\square$

Now we are in a position to prove Theorem 2.1.

Proof of Theorem 2.1. With the transformation $W(x) = \frac{\theta_{\mu,d}}{d(r)}$, the existence of unique positive steady state $W_{\mu,d}$ of (1.4) and its global stability follows from Lemma 2.1 directly. The assertions of Theorem 2.1-(1) are given by Lemma 2.3, while the results of Theorem 2.1-(2) are consequences of Lemma 2.5-(i). The first part of Theorem 2.1-(3) results from the first part of Lemma 2.5-(ii) directly. We shall use the second of Lemma 2.5-(ii) to prove the second part of Theorem 2.1-(3). Indeed since r is non-constant, it can be easily shown that

$$\int_\Omega r(x)\,\mathrm{d}x > r_{\max}|\Omega^r|.$$

Define a constant $\omega = \int_\Omega r(x)\,dx - r_{\max}|\Omega^r| > 0$ and take $\varepsilon = \omega$. Then it follows from the results of Lemma 2.5-(ii) that

$$\int_\Omega W_{\mu,d}\,\mathrm{d}x = \int_\Omega \frac{\theta_{\mu,d}}{d(r)}\mathrm{d}x < r_{\max}|\Omega^r| + \varepsilon = \int_\Omega r(x)\,dx$$

which completes the proof.

3 Two species competitive model

In this section, we investigate the global dynamics of two species Lotka–Volterra competition model (1.7) with resource-dependent dispersals. It is known that the system (1.7) generates a monotone dynamical system and the local qualitative properties of its steady states may determine the global dynamics (cf. Hess 1991; Smith 1995). In particular, we have the following results (cf. Zhou et al. 2021, Theorem 7).

Proposition 3.1 *With the hypotheses* (H_2) *and* (H_0), *the following results hold.*

   (i) *If a steady state of system* (1.7) *is linearly stable (resp. linearly unstable), then it is locally asymptotically stable (resp. unstable);*
  (ii) *If system* (1.7) *admits two semi-trivial steady states* $(U, 0)$ *and* $(0, V)$, *and does not admit any coexistence steady state, then one of the semi-trivial steady states is globally asymptotically stable and the other one is unstable;*
 (iii) *If system* (1.7) *admits two linearly unstable(resp. stable) semi-trivial steady states, then it admits at least one locally asymptotically stable(resp. unstable) coexistence steady state;*
 (iv) *If every coexistence steady state of system* (1.7) *is linearly stable, then either there are no coexistence steady states and one of the two semi-trivial steady state is globally asymptotically stable while the other one is unstable, or there is a unique coexistence steady state which is globally asymptotically stable.*

We recall that $W_{\mu_i,d_i} = \frac{\theta_{\mu_i,d_i}}{d_i(r)}$ and $\theta_{\mu_i,d_i}(i = 1, 2)$ satisfies (see (2.2))

$$\begin{cases} \mu_i d_i(r)\Delta\theta_{\mu_i,d_i} + \theta_{\mu_i,d_i}\left(r(x) - \frac{\theta_{\mu_i,d_i}}{d_i(r)}\right) = 0, & x \in \Omega, \\ \nabla\theta_{\mu_i,d_i} \cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{3.1}$$

Note that the existence of unique positive solution of (3.1) has been established in Lemma 2.1. By similar argument as in Lam and Ni (2012, Lemma 2.9), one can show that the sign of $\lambda_1(\mu_2 d_2(r), r - W_{\mu_1,d_1})$ and $\lambda_1(\mu_1 d_1(r), r - W_{\mu_2,d_2})$ determine the linear stability of $(\theta_{\mu_1,d_1}, 0)$ and $(0, \theta_{\mu_2,d_2})$, respectively. More precisely, if $\lambda_1(\mu_2 d_2(r), r - W_{\mu_1,d_1}) > 0$ (resp. $\lambda_1(\mu_2 d_2(r), r - W_{\mu_1,d_1}) < 0$), then $(\theta_{\mu_1,d_1}, 0)$ is linearly unstable (resp. linearly stable). In particular if $\lambda_1(\mu_2 d_2(r), r - W_{\mu_1,d_1}) = 0$, $(\theta_{\mu_1,d_1}, 0)$ is said to be neutrally stable. The linear stability of $(0, \theta_{\mu_2,d_2})$ can be characterized in a similar way. We proceed with several different cases.

3.1 Same dispersal strategies

In this subsection, we shall show that if two competing species have the same dispersal strategies up to a multiplicative constant, then phenomenon "slower diffuser prevails" will occur, as described in the following Theorem.

Theorem 3.1 *If $d_1(r)$ and $d_2(r)$ satisfy (H_2) with r fulfilling (H_0). If $d_1(r) = \vartheta d_2(r)$ for some constant $\vartheta > 0$ and $d_2(r)r$ is not constant in Ω, then the semi-trivial steady state $(\theta_{\mu_1,d_1}, 0)$ (resp. $(0, \theta_{\mu_2,d_2})$ of system (1.7) is globally asymptotically stable for any $\vartheta\mu_1 < \mu_2$ (resp. $\vartheta\mu_1 > \mu_2$).*

Proof First notice that if $d_1(r) = \vartheta d_2(r) := \vartheta d(r)$ for some constant $\vartheta > 0$, then it follows from (1.8) that

$$\begin{cases} \mu_1\vartheta d(r)\Delta U + U\left(r(x) - \frac{U}{\vartheta d(r)} - \frac{V}{d(r)}\right) = 0, & x \in \Omega, \\ \mu_2 d(r)\Delta V + V\left(r(x) - \frac{U}{\vartheta d(r)} - \frac{V}{d(r)}\right) = 0, & x \in \Omega, \\ \nabla U \cdot n = \nabla V \cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{3.2}$$

Let $\tilde{U} = \frac{U}{\vartheta}$. Then $\tilde{U}$ and V satisfy

$$\begin{cases} \tilde{\mu}_1 d(r)\Delta\tilde{U} + \tilde{U}\left(r(x) - \frac{\tilde{U}}{d(r)} - \frac{V}{d(r)}\right) = 0, & x \in \Omega, \\ \mu_2 d(r)\Delta V + V\left(r(x) - \frac{\tilde{U}}{d(r)} - \frac{V}{d(r)}\right) = 0, & x \in \Omega, \\ \nabla U \cdot n = \nabla V \cdot n = 0, & x \in \partial\Omega, \end{cases} \tag{3.3}$$

with $\tilde{\mu}_1 = \vartheta\mu_1$.

If $d(r)$ is constant, it is well-known that "slower diffuser prevails", see Hastings (1983). If $d(r)$ is not constant in Ω, we first establish two claims.

Claim 1: system (1.7) doesn't admit any positive steady state. If not, we assume that system (1.7) admits a positive steady state (U, V) which satisfies (3.2). Therefore, $(\tilde{U}, V)$ satisfies (3.3). Consider an auxiliary linear eigenvalue problem

$$\begin{cases} \mu d(r)\Delta\phi + m\phi = \tau\phi, & x \in \Omega, \\ \nabla\phi \cdot n = 0, & x \in \partial\Omega, \end{cases} \tag{3.4}$$

where $m = r(x) - \frac{\tilde{U}}{d(r)} - \frac{V}{d(r)}$ in Ω. Denote the principal eigen-pair of problem (3.4) by (τ_μ, ϕ_μ) where ϕ_μ satisfies that $\phi_\mu > 0$ on $\overline{\Omega}$ and $\|\phi_\mu\|_{L^\infty(\Omega)} = 1$. Recalling assertion (ii) of Lemma 2.4, one finds that

$$\frac{\partial\tau_\mu}{\partial\mu} = -\frac{\int_\Omega |\nabla\phi_\mu|^2 dx}{\int_\Omega \frac{\phi_\mu^2}{d(r)}dx} \leq 0.$$

Next, we will show that $\frac{\partial\tau_\mu}{\partial\mu} < 0$. If $\frac{\partial\tau_\mu}{\partial\mu} = 0$, then $\phi_\mu \equiv 1$ due to $\phi_\mu > 0$ and $\|\phi_\mu\|_{L^\infty(\Omega)} = 1$. Substituting $\phi_\mu \equiv 1$ into problem (3.4), one obtains

$$m \equiv \tau_\mu. \tag{3.5}$$

Multiplying the first equation of system (3.3) by $\frac{1}{d(r)}$ and integrating the resulting equation on Ω, one can deduce that $\int_\Omega \frac{\tilde{U}m}{d(r)}dx = 0$, which along with (3.5) and $\tilde{U} > 0$

in Ω implies that $m \equiv 0$. This together with equations in (3.3) yields some positive constants $C_1 > 0$ and $C_2 > 0$ such that $\tilde{U} \equiv C_1$ and $V \equiv C_2$, which suggests that $d(r)r \equiv C_1 + C_2$ due to $m \equiv 0$. This contradicts the assumption that $rd(r)$ is not constant in Ω. Therefore, we have

$$\frac{\partial \tau_\mu}{\partial \mu} < 0. \tag{3.6}$$

However, by (3.3), one finds $\tau_{\tilde{\mu}_1} = \tau_{\mu_2} = 0$, which contradicts (3.6) due to $\tilde{\mu}_1 < \mu_2$. So, Claim 1 is proved.

Claim 2: $(\theta_{\mu_1,d_1}, 0)$ is linearly stable and $(0, \theta_{\mu_2,d_2})$ is linearly unstable. It suffices to show that

$$\lambda_1(\mu_2 d(r), r - W_{\tilde{\mu}_1,d}) < 0 \text{ and } \lambda_1(\tilde{\mu}_1 d(r), r - W_{\mu_2,d}) > 0. \tag{3.7}$$

Employing the above arguments as in Claim 1, one can deduce that

$$\frac{\partial \lambda_1(\mu d(r), r - W_{\tilde{\mu}_1,d})}{\partial \mu} < 0 \text{ and } \frac{\partial \lambda_1(\mu d(r), r - W_{\mu_2,d})}{\partial \mu} < 0. \tag{3.8}$$

Recall that (3.1), which combined with the Krein–Rutman Theorem Krein and Rutman (1948), implies

$$\lambda_1(\tilde{\mu}_1 d(r), r - W_{\tilde{\mu}_1,d}) = \lambda_1(\mu_2 d(r), r - W_{\mu_2,d}) = 0,$$

which along with (3.8) and $\tilde{\mu}_1 < \mu_2$ yields (3.7). Thus, Claim 2 is proved.

Finally, combining Claim 1, Claim 2 and Proposition 3.1 (ii), one obtains that $(\theta_{\mu_1,d_1}, 0)$ is globally asymptotically stable, which completes the proof. $\qquad\square$

Remark 3.1 We give several remarks on the result.

(a) Theorem 3.1 indicates that "slower diffuser prevails", which is consistent with the well-known result in Hastings (1983). Therefore, our results generalize the results of Hastings (1983) to the competition system with resource-dependent dispersal. We also remark the results of Theorem 3.1 are also consequences of general results in Guo et al. (2020, Theorem 1.2 (i)–(ii)). Here we use a different approach (mainly in Claim 1) to obtain the same results.

(b) If $d_i(r)r \equiv c_i$ for $i = 1, 2$, where c_1 and c_2 are positive constants, then it is straightforward to show that system (1.7) admits a continuum of steady states given by

$$\mathcal{S} = \left\{ (U, V) = (\eta_1, \eta_2) \mid \eta_1, \eta_2 \geq 0 \text{ and } \frac{\eta_1}{c_1} + \frac{\eta_2}{c_2} = 1 \right\}.$$

Then by the result of Guo et al. (2020, Theorem 1.2 (iv)), this continuum of steady states indeed comprises a global attractor.

3.2 Different dispersal strategies with large diffusion coefficients

In this subsection, we shall investigate possible (global) dynamics of system (1.7) as $\mu_1 \to 0, \infty$ and/or $\mu_2 \to 0, \infty$. We first characterize the limiting profile of the coexistence steady state (if it exists) of system (1.7).

Lemma 3.1 *Let $d_i(r)$ satisfy (H_2) $(i = 1, 2)$ for $i = 1, 2$ with r fulfilling (H_0). Then we have the following results.*

(i) If system (1.7) admits a coexistence steady state denoted by (U_{μ_i}, V_{μ_i}) as $\mu_i \to 0$, then there exists some constant $C \geq 0$ where "=" holds if $\min_{x \in \bar{\Omega}} r(x) = 0$ such that

$$(U_{\mu_i}, V_{\mu_i}) \to \begin{cases} ((r - \frac{C}{d_2(r)})d_1(r), C), & \text{if } i = 1, \\ (C, (r - \frac{C}{d_1(r)})d_2(r)), & \text{if } i = 2, \end{cases} \quad \text{as } \mu_i \to 0,$$

where $C \leq \min_{x \in \bar{\Omega}}(rd_2(r))$ if $i = 1$ and $C \leq \min_{x \in \bar{\Omega}}(rd_1(r))$ if $i = 2$.

(ii) If system (1.7) admits a coexistence steady state denoted by (U_{μ_i}, V_{μ_i}) as $\mu_i \to \infty$, then

$$(U_{\mu_1}, V_{\mu_1}) \to (0, \theta_{\mu_2, d_2}) \text{ or } (U_\perp, V_\infty) \text{ in } C^1(\Omega) \text{ as } \mu_1 \to \infty,$$

and

$$(U_{\mu_2}, V_{\mu_2}) \to (\theta_{\mu_1, d_1}, 0) \text{ or } (U_\infty, V_\perp) \text{ in } C^1(\Omega) \text{ as } \mu_2 \to \infty,$$

where $U_\perp = \frac{\int_\Omega (r - V_\infty d_2^{-1}(r))d_1^{-1}(r)dx}{\int_\Omega d_1^{-2}(r)dx}$, $V_\perp = \frac{\int_\Omega (r - U_\infty d_1^{-1}(r))d_2^{-1}(r)dx}{\int_\Omega d_2^{-2}(r)dx}$ and (U_∞, V_∞) satisfies

$$\begin{cases} \mu_1 d_1(r)\Delta U_\infty + U_\infty(r - \frac{U_\infty}{d_1(r)} - \frac{V_\perp}{d_2(r)}) = 0, & x \in \Omega, \\ \mu_2 d_2(r)\Delta V_\infty + V_\infty(r - \frac{U_\perp}{d_1(r)} - \frac{V_\infty}{d_2(r)}) = 0, & x \in \Omega, \\ \nabla U_\infty \cdot n = \nabla V_\infty \cdot n = 0, & x \in \partial\Omega. \end{cases}$$

Proof We only prove the case $\mu_2 \to 0$ in (i) and $\mu_2 \to \infty$ in (ii), while the proofs for cases $\mu_1 \to 0$ and $\mu_1 \to \infty$ are the same. We first prove (i) for $\mu_2 \to 0$. Recall that (U_{μ_2}, V_{μ_2}) satisfies

$$\begin{cases} \mu_1 d_1(r)\Delta U_{\mu_2} + U_{\mu_2}(r(x) - \frac{U_{\mu_2}}{d_1(r)} - \frac{V_{\mu_2}}{d_2(r)}) = 0, & x \in \Omega, \\ \mu_2 d_2(r)\Delta V_{\mu_2} + V_{\mu_2}(r(x) - \frac{U_{\mu_2}}{d_1(r)} - \frac{V_{\mu_2}}{d_2(r)}) = 0, & x \in \Omega, \quad (3.9) \\ \nabla U_{\mu_2} \cdot n = \nabla V_{\mu_2} \cdot n = 0, & x \in \partial\Omega. \end{cases}$$

The maximum and comparison principles directly yield that

$$\|U_{\mu_2}\|_{L^\infty(\Omega)} \leq \|rd_1(r)\|_{L^\infty(\Omega)} \text{ and } \|V_{\mu_2}\|_{L^\infty(\Omega)} \leq \|rd_2(r)\|_{L^\infty(\Omega)}.$$

From the elliptic regularity Agmon et al. ([1959](#), [1964](#)), it follows that $\|U_{\mu_2}\|_{W^{2,p}(\Omega)}$ and $\|V_{\mu_2}\|_{L^p(\Omega)}$ are uniformly bounded as $\mu_2 \to 0$ for any $1 \le p < \infty$. By the Sobolev imbedding theorem, one can deduce that U_{μ_2}(resp. V_{μ_2}), passing to a subsequence if necessary, converges to some nonnegative function U_0(resp. V_0) in $C^1(\Omega)$(resp. weakly in $L^p(\Omega)$) as $\mu_2 \to 0$. Following the approach as that in the proof of Lam and Ni ([2012](#), Proposition 2.5), one can derive that $V_{\mu_2} \to (r - \frac{U_0}{d_1(r)})^+ d_2(r)$ in $L^\infty(\Omega)$ as $\mu_2 \to 0$, where

$$\left(r - \frac{U_0}{d_1(r)}\right)^+ = \max\left\{0, r - \frac{U_0}{d_1(r)}\right\}.$$

Then, U_0 satisfies (in the weak sense)

$$\begin{cases} \mu_1 d_1(r)\Delta U_0 + U_0\left(r(x) - \frac{U_0}{d_1(r)} - (r - \frac{U_0}{d_1(r)})^+\right) = 0, & x \in \Omega, \\ \nabla U_0 \cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{3.10}$$

We proceed to show that

$$r(x) - \frac{U_0}{d_1(r)} \ge 0 \text{ in } \Omega. \tag{3.11}$$

By the argument of contradiction, we assume that $r(x) - \frac{U_0}{d_1(r)} < 0$ in some open subset Ω^* of Ω. Multiplying the first equation of (3.10) by $\frac{1}{d_1(r)}$ and integrating the resulting equation on Ω, one obtains

$$\int_\Omega \frac{U_0}{d_1(r)}\left[r(x) - \frac{U_0}{d_1(r)} - \left(r - \frac{U_0}{d_1(r)}\right)^+\right]\mathrm{d}x = 0,$$

which combined with the fact $U_0 \ge 0$ yields that $U_0(x) = 0$ in Ω^*. This together with the maximum principle implies that $U_0 \equiv 0$ in Ω, which further indicates that $r(x) - \frac{U_0}{d_1(r)} \ge 0$ in Ω, due to $r \ge 0$ in Ω. This contradict our assumption and hence we have (3.11). Therefore

$$r(x) - \frac{U_0}{d_1(r)} - \left(r - \frac{U_0}{d_1(r)}\right)^+ \equiv 0 \text{ in } \Omega.$$

So, U_0 satisfies

$$\Delta U_0 = 0 \text{ in } \Omega \text{ and } \nabla U_0 \cdot n = 0 \text{ on } \partial\Omega,$$

which along with $U_0 \ge 0$ in Ω and (3.11) suggests that $U_0 \equiv C$ for some $C \in [0, \min_{x \in \bar\Omega}(r d_1(r))]$ and hence $V_{\mu_2} \to (r - \frac{C}{d_1(r)})d_2(r)$ in $L^\infty(\Omega)$ as $\mu_2 \to 0$. These facts together with the definitions of (U_{μ_2}, V_{μ_2}) give that

$$(U_{\mu_2}, V_{\mu_2}) \to \left(C, (r - \frac{C}{d_1(r)})d_2(r)\right) \text{ in } L^\infty(\Omega) \text{ as } \mu_2 \to 0.$$

Next, we prove (ii) with $\mu_2 \to \infty$. Similar to the above analysis, without loss of generality, one can deduce from (3.9) that (U_{μ_2}, V_{μ_2}) converges to some nonnegative function (U_∞, V_∞) in $C^1(\Omega)$ as $\mu_2 \to \infty$, which satisfies

$$V_{\mu_2} \to C_0 \geq 0 \text{ in } C^1(\Omega) \text{ as } \mu_2 \to \infty$$

and

$$\begin{cases} \mu_1 d_1(r)\Delta U_\infty + U_\infty\left(r - \frac{U_\infty}{d_1(r)} - \frac{C}{d_2(r)}\right) = 0, & x \in \Omega, \\ \nabla U_\infty \cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{3.12}$$

We proceed to consider two separate cases: $C_0 = 0$ and $C_0 > 0$.

For the case $C_0 = 0$, one directly obtains from (3.12) and Lemma 2.1 that $(U_{\mu_2}, V_{\mu_2}) \to (\theta_{\mu_1, d_1}, 0)$ in $C^1(\Omega)$ as $\mu_2 \to \infty$.

For the case $C_0 > 0$, multiplying the second equation of (3.9) by $\frac{1}{d_2(r)}$ and integrating the resulting equation on Ω, one finds $\int_\Omega \frac{V_{\mu_2}}{d_2(r)}\left(r(x) - \frac{U_{\mu_2}}{d_1(r)} - \frac{V_{\mu_2}}{d_2(r)}\right)dx = 0$, which along with the fact $(U_{\mu_2}, V_{\mu_2}) \to (U_\infty, C_0)$ in $C^1(\Omega)$ as $\mu_2 \to \infty$ suggests that

$$C_0 = \frac{\int_\Omega (r - U_\infty d_1^{-1}(r))d_2^{-1}(r)dx}{\int_\Omega d_2^{-2}(r)dx}.$$

This completes the proof.   □

Next, we investigate the global dynamics of system (1.7) as $\mu_1, \mu_2 \to \infty$. To this end, we define several quantities as follows

$$\delta_1 := \int_\Omega r d_2(r)^{-1}dx \int_\Omega d_1(r)^{-2}dx - \int_\Omega r d_1(r)^{-1}dx \int_\Omega [d_1(r)d_2(r)]^{-1}dx,$$

$$\delta_2 := \int_\Omega r d_1(r)^{-1}dx \int_\Omega d_2(r)^{-2}dx - \int_\Omega r d_2(r)^{-1}dx \int_\Omega [d_1(r)d_2(r)]^{-1}dx, \tag{3.13}$$

$$c_0 = \int_\Omega d_1(r)^{-2}dx \int_\Omega d_2(r)^{-2}dx - \left(\int_\Omega [d_1(r)d_2(r)]^{-1}dx\right)^2.$$

We note that $c_0 \geq 0$ by Hölder's inequality and in particular $c_0 > 0$ if $d_1(r)$ and $d_2(r)$ are not proportional. Then we can show the following results.

Theorem 3.2 *Let δ_1, δ_2 and c_0 be defined in (3.13). If $d_i(r)(i = 1, 2)$ satisfies (H_2) with r fulfilling (H_0), and $d_1(r) \not\equiv C d_2(r)$ for any constant $C > 0$, then the following results hold.*

(i) *(Competitive exclusion) If $\delta_1 < 0 < \delta_2$ (resp. $\delta_2 < 0 < \delta_1$), then the system (1.7) has a globally asymptotically stable steady state $(\theta_{\mu_1, d_1}, 0)$ (resp. $(0, \theta_{\mu_2, d_2})$) for large μ_1, μ_2.*

(ii) *(Coexistence) If $\delta_1, \delta_2 > 0$, then the system* (1.7) *admits a globally asymptotically stable coexistence steady state* (U_*, V_*) *for large* μ_1, μ_2. *Furthermore, the coexistence steady state* (U_*, V_*) *converges to* $(\frac{\delta_1}{c_0}, \frac{\delta_2}{c_0})$ *in* $C^1(\Omega)$ *as* $\mu_1, \mu_2 \to \infty$.

Proof We only prove the case $\delta_1 < 0 < \delta_2$ in (i) and the proof for the case $\delta_2 < 0 < \delta_1$ is similar. We first show two claims.

Claim A: *system* (1.7) *doesn't admit any positive steady state for large* μ_1 *and* μ_2. Arguing by contradiction, we assume that there exist sequences $\{\mu_{i,1}\}_{i \geq 1}$ and $\{\mu_{i,2}\}_{i \geq 1}$ satisfying $\mu_{i,1}, \mu_{i,2} \to \infty$ as $i \to \infty$ such that system (1.7) admits a positive steady state denoted by (U_i, V_i). Then, (U_i, V_i) satisfies

$$
\begin{cases}
\mu_{i,1}d_1(r)\Delta U_i + U_i\big(r(x) - \frac{U_i}{d_1(r)} - \frac{V_i}{d_2(r)}\big) = 0, & x \in \Omega, \\
\mu_{i,2}d_2(r)\Delta V_i + V_i\big(r(x) - \frac{U_i}{d_1(r)} - \frac{V_i}{d_2(r)}\big) = 0, & x \in \Omega, \\
\nabla U_i \cdot n = \nabla V_i \cdot n = 0, & x \in \partial\Omega.
\end{cases}
\tag{3.14}
$$

Applying the comparison principle, for any $i \geq 1$, one can show that

$$
\|U_i\|_{L^\infty(\Omega)} \leq \|rd_1(r)\|_{L^\infty(\Omega)} \text{ and } \|V_i\|_{L^\infty(\Omega)} \leq \|rd_2(r)\|_{L^\infty(\Omega)}.
\tag{3.15}
$$

From the elliptic regularity (cf. Gilbarg and Trudinger 2001), it follows that $\|U_i\|_{W^{2,p}(\Omega)}$ and $\|V_i\|_{W^{2,p}(\Omega)}$ are uniformly bounded in i for any $1 \leq p < \infty$. By the Sobolev imbedding theorem, one can deduce from (3.14) that (U_i, V_i), passing to a subsequence if necessary, converges to some nonnegative function (U_∞, V_∞) in $C^1(\Omega)$ as $i \to \infty$, where (U_∞, V_∞) satisfies (in the weak sense)

$$
\begin{cases}
\Delta U_\infty = \Delta V_\infty = 0, & x \in \Omega, \\
\nabla U_\infty \cdot n = \nabla V_\infty \cdot n = 0, & x \in \partial\Omega.
\end{cases}
$$

Therefore, there exist some constants $C_1, C_2 \geq 0$ such that $(U_\infty, V_\infty) = (C_1, C_2)$. Then, there are four possible cases to consider:

(1) $C_1 = C_2 = 0$; (2) $C_1 > C_2 = 0$; (3) $C_2 > C_1 = 0$; (4) $C_1, C_2 > 0$.

For case (1): $C_1 = C_2 = 0$. Multiplying the first equation of (3.14) by $\frac{1}{d_1(r)}$ and integrating the resulting equation on Ω, one has

$$
\int_\Omega \frac{U_i}{d_1(r)}\Big(r - \frac{U_i}{d_1(r)} - \frac{V_i}{d_2(r)}\Big)dx = 0,
$$

which contradicts the facts that $U_i > 0$, $r \gneqq 0$, $d_i(r) > 0 (i = 1, 2)$, and $(U_i, V_i) \to (0, 0)$ in $C^1(\Omega)$ as $i \to \infty$.

For case (2): $C_1 > C_2 = 0$. By Lemma 2.3, one further obtains $C_1 = \frac{\int_\Omega rd_1^{-1}(r)dx}{\int_\Omega d_1^{-2}(r)dx}$. Setting $\hat{V}_i = \frac{V_i}{\|V_i\|_{L^\infty(\Omega)}}$, similar to the above analysis in the proof of Lemma 3.1, one

can conclude that

$$(U_i, \hat{V}_i) \to \left(\frac{\int_\Omega r d_1^{-1}(r)\mathrm{d}x}{\int_\Omega d_1^{-2}(r)\mathrm{d}x}, 1 \right) \text{ in } C^1(\Omega) \text{ as } i \to \infty. \tag{3.16}$$

Multiplying the second equation of (3.14) by $d_2(r)$ and integrating the resulting equation on Ω yield that

$$\int_\Omega \frac{\hat{V}_i}{d_2(r)} \left(r - \frac{U_i}{d_1(r)} - \frac{\hat{V}_i \|V_i\|_{L^\infty(\Omega)}}{d_2(r)} \right) \mathrm{d}x = 0,$$

which together with (3.16) implies that $\delta_1 = 0$, contradicting the fact $\delta_1 < 0$.

Case (3) can be treated similarly. We omits the details.

For case (4): $C_1, C_2 > 0$, similar to the arguments as in the proof of Lemma 3.1, one can deduce that

$$C_1 = \frac{\delta_2}{c_0}, \ C_2 = \frac{\delta_1}{c_0} \text{ with } c_0 = \int_\Omega \frac{1}{d_1^2(r)}\mathrm{d}x \int_\Omega \frac{1}{d_2^2(r)}\mathrm{d}x - \left(\int_\Omega \frac{1}{d_1(r)d_2(r)}\mathrm{d}x \right)^2 \tag{3.17}$$

which contradicts $\delta_1 < 0$ and $\int_\Omega \frac{1}{d_1^2(r)}\mathrm{d}x \int_\Omega \frac{1}{d_2^2(r)}\mathrm{d}x > (\int_\Omega \frac{1}{d_1(r)d_2(r)}\mathrm{d}x)^2$ due to the assumption that $d_1(r) \not\equiv Cd_2(r)$ for any $C > 0$. Thus Claim A is proved.

Claim B: *the semi-trivial steady state $(\theta_{\mu_1,d_1}, 0)$ is linearly stable and $(0, \theta_{\mu_2,d_2})$ is linearly unstable for large μ_1, μ_2.* By Lemmas 2.3 and 2.4 (ii), one can derive that

$$\lim_{\mu_1,\mu_2\to\infty} \lambda_1(\mu_2 d_2(r), r - W_{\mu_1,d_1}) = \frac{\int_\Omega (r - \frac{c_{r_1}}{d_1(r)})d_2^{-1}(r)\mathrm{d}x}{\int_\Omega d_2^{-1}(r)\mathrm{d}x} = \frac{\delta_1}{\int_\Omega d_1^{-2}(r)\mathrm{d}x \int_\Omega d_2^{-1}(r)\mathrm{d}x}$$

and

$$\lim_{\mu_1,\mu_2\to\infty} \lambda_1(\mu_1 d_1(r), r - W_{\mu_2,d_2}) = \frac{\int_\Omega (r - \frac{c_{r_2}}{d_2(r)})d_1^{-1}(r)\mathrm{d}x}{\int_\Omega d_1^{-1}(r)\mathrm{d}x} = \frac{\delta_2}{\int_\Omega d_2^{-2}(r)\mathrm{d}x \int_\Omega d_1^{-1}(r)\mathrm{d}x}$$

where $c_{r_i} = \frac{\int_\Omega r d_i^{-1}(r)\mathrm{d}x}{\int_\Omega d_i^{-2}(r)\mathrm{d}x}$ $(i = 1, 2)$. These facts together with $\delta_1 < 0 < \delta_2$ imply that Claim B holds. Then, combining Claim A, Claim B, and Proposition 3.1 (ii), we prove assertion (i).

For assertion (ii): $\delta_1, \delta_2 > 0$, similar to the analysis in the proof of Claim B above, one can deduce that $(\theta_{\mu_1,d_1}, 0)$ and $(0, \theta_{\mu_2,d_2})$ are linearly unstable for large μ_1, μ_2, which upon the application of Proposition 3.1-(iii) entails that system (1.7) admits a locally asymptotically stable coexistence steady state (U_*, V_*) for large μ_1, μ_2. Furthermore, by the arguments in the proof of Lemma 3.1, one can derive that, as $\mu_1, \mu_2 \to \infty$,

The coexistence steady state of system (1.7)(if it exits) converges to (C_1, C_2) in $C^1(\Omega)$, (3.18)

where C_1 and C_2 are given in (3.17). Finally, we show that the coexistence steady state (U_*, V_*) is globally asymptotically stable for large μ_1, μ_2.

Claim C: *every coexistence steady state of system* (1.7) *is not neutrally stable for large* μ_1, μ_2. Suppose the claim is false, and we assume that, as $\mu_1, \mu_2 \to \infty$, system (1.7) admits a coexistence steady state $(U_{\mu_1,\mu_2}, V_{\mu_1,\mu_2})$, which is neutrally stable. Linearizing system (1.8) at $(U, V) = (U_{\mu_1,\mu_2}, V_{\mu_1,\mu_2})$, one has

$$
\begin{cases}
\mu_1 d_1(r)\Delta\phi_1 + \phi_1\big(r(x) - \frac{U_{\mu_1,\mu_2}}{d_1(r)} - \frac{V_{\mu_1,\mu_2}}{d_2(r)}\big) - \frac{U_{\mu_1,\mu_2}\phi_1}{d_1(r)} - \frac{U_{\mu_1,\mu_2}\psi_1}{d_2(r)} = 0, & x \in \Omega, \\
\mu_2 d_2(r)\Delta\psi_1 + \psi_1\big(r(x) - \frac{U_{\mu_1,\mu_2}}{d_1(r)} - \frac{V_{\mu_1,\mu_2}}{d_2(r)}\big) - \frac{V_{\mu_1,\mu_2}\psi_1}{d_2(r)} - \frac{V_{\mu_1,\mu_2}\phi_1}{d_1(r)} = 0, & x \in \Omega, \\
\nabla\phi_1 \cdot n = \nabla\psi_1 \cdot n = 0, & x \in \partial\Omega,
\end{cases}
\tag{3.19}
$$

where (ϕ_1, ψ_1) is the corresponding principal eigenfunction satisfying $\|\phi_1\|_{L^2(\Omega)}^2 + \|\psi_1\|_{L^2(\Omega)}^2 = 1$ and $\phi_1 > 0 > \psi_1$ on $\bar{\Omega}$. Similar to (3.15), for any $\mu_1, \mu_2 > 0$, one obtains

$$
\|U_{\mu_1,\mu_2}\|_{L^\infty(\Omega)} \le \|r d_1(r)\|_{L^\infty(\Omega)} \quad\text{and}\quad \|V_{\mu_1,\mu_2}\|_{L^\infty(\Omega)} \le \|r d_2(r)\|_{L^\infty(\Omega)}.
$$

Employing similar arguments as those in Claim A, one can deduce that

$$
(\phi_1, \psi_1) \to (\hat{c}_1, \hat{c}_2) \text{ in } H^1(\Omega) \text{ as } \mu_1, \mu_2 \to \infty \text{ and hence } (\hat{c}_1^2 + \hat{c}_2^2)|\Omega| = 1.
\tag{3.20}
$$

It is clear that $\hat{c}_1 \ge 0 \ge \hat{c}_2$ since $\phi_1 > 0 > \psi_1$ on $\bar{\Omega}$. Next we will show that

$$
\hat{c}_1 > 0 > \hat{c}_2.
\tag{3.21}
$$

Then it suffices to show that $\hat{c}_1 \ne 0$ and $\hat{c}_2 \ne 0$. Since the proof is similar, we only prove $\hat{c}_1 \ne 0$. Using the argument of contradiction, we assume $\hat{c}_1 = 0$, which combined with (3.20) gives that $\hat{c}_2 = |\Omega|^{-\frac{1}{2}} > 0$. Multiplying the second equations of system (3.19) by $\frac{1}{d_2(r)}$, integrating the resulting equation in Ω, and sending $\mu_1, \mu_2 \to \infty$, one concludes that

$$
\int_\Omega \frac{C_2}{d_2^2(r)} dx = 0,
$$

where we have used (3.18), (3.20) and $\hat{c}_2 > \hat{c}_1 = 0$. This is impossible due to the fact that $C_2 > 0$. Therefore, (3.21) holds. We next multiply the first and second equations of system (3.19) by $\frac{1}{d_1(r)}$ and $\frac{1}{d_2(r)}$, respectively, integrate the resulting equations in Ω with a substraction. Then sending $\mu_1, \mu_2 \to \infty$, one obtains from (3.18) and (3.20)

$$
\int_\Omega \Big(\frac{\hat{c}_1}{d_1^2(r)} + \frac{\hat{c}_2}{d_1(r)d_2(r)}\Big)dx = \int_\Omega \Big(\frac{\hat{c}_1}{d_1(r)d_2(r)} + \frac{\hat{c}_2}{d_2^2(r)}\Big)dx = 0,
$$

which along with (3.21) gives that

$$\int_\Omega \frac{1}{d_1^2(r)}dx \int_\Omega \frac{1}{d_2^2(r)}dx - \left(\int_\Omega \frac{1}{d_1(r)d_2(r)}dx\right)^2 = 0.$$

This is impossible due to the assumption that $d_1(r) \not\equiv Cd_2(r)$ for any $C > 0$. Thus, Claim C holds. From (3.18), Claim C and the fact that system (1.7) admits a locally asymptotically stable coexistence steady state for large μ_1, μ_2, it follows that every coexistence steady state of system (1.7) is linearly stable for large μ_1, μ_2. Then, Proposition 3.1 (iv) proves that assertion (ii) holds, which completes the proof. □

Remark 3.2 We add several remarks for the results in Theorem 3.2.

(a) Under the conditions of Theorem 3.2, one can deduce that $\delta_1, \delta_2 < 0$ can not occur by the argument of contradiction. For readers' convenience, we sketch the proof in the following two steps. Step 1, following the approaches as in the proof of Claim A for Theorem 3.2, one can deduce that system (1.7) doesn't admit any positive steady state as $\mu_1, \mu_2 \to \infty$; Step 2, with similar arguments as in the proof of Claim B for Theorem 3.2, one can derive that $(\theta_{\mu_1,d_1}, 0)$ and $(0, \theta_{\mu_2,d_2})$ are linearly stable as $\mu_1, \mu_2 \to \infty$, which together with Proposition 3.1-(iii) implies that system (1.7) admits an unstable coexistence steady state as $\mu_1, \mu_2 \to \infty$. Then, the results in step 1 and step 2 yield a contradiction, which confirms our claimed result.

(b) The following examples show that all situations (i) and (ii) of Theorem 3.2 may occur.

   (i) If $d_1(r) = e^{-kr}$ and $d_2(r) = 1$, then $\delta_1 < 0 < \delta_2$ provided k is small enough. Conversely if $d_1(r) = 1$ and $d_2(r) = e^{-kr}$, then $\delta_2 < 0 < \delta_1$ provided k is small enough;

   (ii) If $d_1(r) = e^{-kr}$ and $d_2(r) = \frac{1}{2}r_{\max}$, then $\delta_1, \delta_2 > 0$ provided k is large enough.

(c) If $d_1(r)r$ is constant and $d_2(r)r$ is not constant, it was shown in [Braverman and Makrujjaman (2016), Theorem 1] that $(r, 0)$ is globally asymptotically stable for system (1.5), namely the species u_1 wipes out the species u_2 and achieves the ideal free distribution. In this case $\delta_1 = 0$ and $\delta_2 > 0$. But for general $d_i(r)$ with $\delta_i = 0$, $i \in \{1, 2\}$, we are unable to determine the global dynamics.

(d) The numerical simulations of steady state profile (U_1, U_2) of (1.5) with $d_1(r) = e^{-kr}$ and $d_2(r) = 1$ are plotted in Fig. 2 with large $\mu_i > 0 (i = 1, 2)$ and small k in (a) and large k in (b), where we see the results of Theorem 3.2 are perfectly verified by our numerical results. One open question left in Theorem 3.2 is the global dynamics when μ_1 and/or μ_2 are not large. For this scenario, we also perform numerical simulations for moderate values of $\mu_i(i = 1, 2)$: $\mu_1 = \mu_2 = 1$ and small values $\mu_i(i = 1, 2)$: $\mu_1 = \mu_2 = 0.1$, we surprisingly find the steady profile (U_1, U_2) of (1.5) will remain the same as those for large $\mu_i(i = 1, 2)$ and fixed value of k. Hence we do not show the numerical simulations here for small or moderate values of $\mu_i(i = 1, 2)$. This indicates that the criteria used in Theorem 3.2 determining the global stability of competitive exclusion and coexistence steady
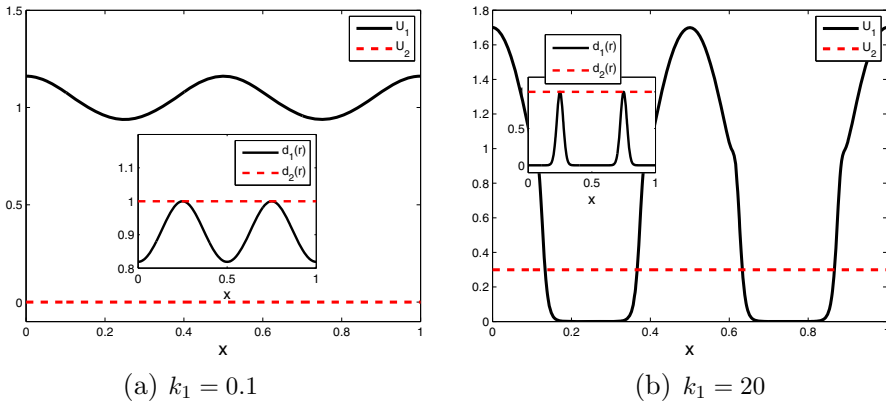
Fig. 2 Numerical simulations of stead state profile of the competition system (1.5) with $d_1(r) = e^{-k_1 r}$ and $d_2(r) = 1$ in $[0, 1]$ with resource $r(x) = 1 + \cos(4\pi x)$, where $k_1 = 0.1$ in (**a**) and $k_1 = 20$ in (**b**), where $\mu_1 = \mu_2 = 10$

states through the sign of $\delta_i(i = 1, 2)$ possibly hold for any $\mu_i > 0 (i = 1, 2)$. However we are unable to prove this and have to leave it out for the future.

The results of Theorem 3.2-(ii) provide a strategy to reach a coexistence steady state for competing species, which requires both μ_1 and μ_2 are large. We refer to a result in Cantrell et al. (2019) where the coexistence steady state in a competition–diffusion–advection model with inhomogeneous diffusion rates can also be achieved when the advection along the resource gradient is large. The following proposition will offer another possible mechanism for coexistence by requiring μ_2 be large only but $d_2(r)$ is close to a constant.

Proposition 3.2 (Coexistence) *If* $d_2(r) \equiv 1$, $d_1(r)$ *satisfies* (H_2) *with* r *fulfilling* (H_0) *such that* $\int_\Omega W_{\mu_1, d_1} dx < \int_\Omega r dx$ *where* $W_{\mu_1, d_1} = \frac{\theta_{\mu_1, d_1(r)}}{d_1(r)}$, *then system* (1.7) *admits a locally asymptotically stable coexistence steady state* (U_{μ_2}, V_{μ_2}) *for large* μ_2. *Furthermore, the coexistence steady state* (U_{μ_2}, V_{μ_2}) *converges to* (U_*, V_*) *in* $C^1(\Omega)$ *as* $\mu_2 \to \infty$, *where* (U_*, V_*) *satisfies*

$$\begin{cases} \mu_1 d_1(r) \Delta U_* + U_* \left(r - \frac{U_*}{d_1(r)} - V_* \right) = 0, & x \in \Omega, \\ \nabla U_* \cdot n = 0, & x \in \partial\Omega, \end{cases} \tag{3.22}$$

and

$$V_* = \frac{\int_\Omega \left(r - \frac{U_*}{d_1(r)} \right) dx}{|\Omega|} > 0. \tag{3.23}$$

Proof By the assumption $\int_\Omega W_{\mu_1, d_1} dx < \int_\Omega r dx$ and Lemma 2.4 (ii), one can deduce that

$$\lim_{\mu_2 \to \infty} \lambda_1(\mu_2, r - W_{\mu_1, d_1}) = \frac{1}{|\Omega|} \int_\Omega (r - W_{\mu_1, d_1}) dx > 0, \tag{3.24}$$

which suggests that $(\theta_{\mu_1,d_1(r)}, 0)$ is linearly unstable. Since $\lambda_1(D(x), m)$ continuously depends on m and $\theta_{\mu_2,1} \to \bar{r}$ with $\bar{r} = \frac{1}{|\Omega|}\int_\Omega r(x)dx$ as $\mu_2 \to \infty$ (see Lemma 2.3), then it follows that

$$\lim_{\mu_2 \to \infty} \lambda_1(d_1(r), r - \theta_{\mu_2,1}) = \lambda_1(d_1(r), r - \bar{r}).$$

By the variational characterization (2.4), choosing 1 as a test function, one obtains

$$\lambda_1(d_1(r), r - \bar{r}) = \sup_{0 \neq \phi \in H^1(\Omega)} \frac{\int_\Omega(-|\nabla\phi|^2 + \frac{(r-\bar{r})\phi^2}{d_1(r)})dx}{\int_\Omega \frac{\phi^2}{d_1(r)}dx} \geq \frac{\int_\Omega \frac{r-\bar{r}}{d_1(r)}dx}{\int_\Omega \frac{1}{d_1(r)}dx}.$$

We proceed to show that

$$\int_\Omega \frac{r - \bar{r}}{d_1(r)}dx > 0. \tag{3.25}$$

Since $\int_\Omega W_{\mu_1,d_1}dx < \int_\Omega rdx$, it is easy to show that $d_1(r)$ is not constant in Ω, which together with (H_2) and the assumption that r is not constant in Ω implies

$$\begin{aligned}
\int_\Omega \frac{r-\bar{r}}{d_1(r)}dx &= \int_{r\geq\bar{r}} \frac{r-\bar{r}}{d_1(r)}dx + \int_{r<\bar{r}} \frac{r-\bar{r}}{d_1(r)}dx \\
&> \int_{r\geq\bar{r}} \frac{r-\bar{r}}{d_1(\bar{r})}dx + \int_{r<\bar{r}} \frac{r-\bar{r}}{d_1(\bar{r})}dx \\
&= 0.
\end{aligned}$$

So, (3.25) holds and consequently we have

$$\lim_{\mu_2 \to \infty} \lambda_1(d_1(r), r - \theta_{\mu_2,1}) = \lambda_1(d_1(r), r - \bar{r}) > 0, \tag{3.26}$$

which indicates that $(0, \theta_{\mu_2,1})$ is linearly unstable.

From (3.24), (3.26) and Proposition 3.1 (iii), it follows that the system (1.7) admits a locally asymptotically stable coexistence steady state for large μ_2. Finally, since $(\theta_{\mu_1,d_1(r)}, 0)$ and $(0, \theta_{\mu_2,1})$ are linearly unstable, by the arguments in the proof of Lemma 3.1, one can derive that the coexistence steady state (U_{μ_2}, V_{μ_2}) converges to (U_*, V_*) in $C^1(\Omega)$ as $\mu_2 \to \infty$, where (U_*, V_*) satisfies (3.22) and (3.23). $\qquad\square$

Remark 3.3 By Lemma 2.5, one can find some $d_1(r)$ such that $\int_\Omega W_{\mu_1,d_1}dx < \int_\Omega rdx$. Moreover, if $d_1(r)$ satisfies the condition in Proposition 3.2 and $d_2(r)$ is constant, then system (1.7) admits a locally asymptotically stable coexistence steady state for large μ_2 even $\mu_1 d_1(r) < \mu_2 d_2(r)$. This implies that the "slower diffuser prevails" phenomenon may not happen if the resource-dependent dispersal strategy is employed. Instead the competing species with resource-dependent dispersal rates may coexist even if they have different diffusion strength (i.e. $\mu_1 d_1(r) \neq \mu_2 d_2(r)$ in Ω). Therefore the resource-dependent dispersal does provide a strategy for competing species to coexist.

Remark 3.4 Proposition 3.2 raises an interesting question: whether the problem (3.22)–(3.23) admit a unique positive solution? If so, then one can further derive that, under the conditions of Proposition 3.2, system (1.7) admits a globally asymptotically stable coexistence steady state for large μ_2.

3.3 Case studies for any $\mu_i > 0$

Theorem 3.2 gives conditions for the global stability of competitive exclusion steady states and the existence of coexistence steady states for large diffusion rates $\mu_i (i = 1, 2)$ when $d_1(r)$ and $d_2(r)$ are not proportional. Whether similar results hold true for diffusion rates that are not large remain unknown. In this section, we shall attempt this question by considering two types of specialized resource-dependent diffusion rate function $d_i(r) = e^{-k_i r}$ and $d_i(r) = (1 + r)^{-k_i}$ for $i = 1, 2$ and monotone resource $r(x)$ in an interval $\Omega = (0, L)$.

The main results for $d_i(r) = e^{-k_i r} (i = 1, 2)$ are the following.

Theorem 3.3 Let $d_i(r) = e^{-k_i r} (i = 1, 2)$ and k_r be such that $4k_r r_{\max} e^{k_r r_{\max}} = 1$. If $r_x > 0$ or $r_x < 0$ on $[0, L]$, $0 \le k_2 < k_1 \le k_r$ and $\mu_1 > 0$, then we have the following results.

(i) *(Competitive exclusion) If $\mu_2 \in [\mu_1 e^{(k_2-k_1)r_{\min}}, \infty)$, then $(\theta_{\mu_1, d_1}, 0)$ is globally asymptotically stable ;*
(ii) *(Coexistence) There exists some $\mu_2 \in \left(0, \mu_1 e^{(k_2-k_1)r_{\min}}\right)$ such that system (1.7) admits a positive steady state.*

Remark 3.5 Noticing that $\mu_2 \in [\mu_1 e^{(k_2-k_1)r_{\min}}, \infty)$ means that $\mu_1 e^{-k_1 r} < \mu_2 e^{-k_2 r}$ for all $x \in (0, L)$, Theorem 3.3-(i) basically asserts that the slower diffuser prevails in the competition, same as the classical competition model with resource-independent dispersals. This is verified by the numerical simulation shown in Fig. 3a. The result of Theorem 3.3-(ii) seems not as decisive as that of Theorem 3.3-(i). It turns out from numerical simulations that the dynamics of (1.7) are much more complex when $\mu_2 \in \left(0, \mu_1 e^{(k_2-k_1)r_{\min}}\right)$ as shown in Fig. 3b–d where we see that when μ_2 increases from 0 to $\mu_1 e^{(k_2-k_1)r_{\min}}$, the winner of the competition changes from U_1 to U_2. In particular coexistence appears in the period of transition even for $\mu_1 e^{-k_1 r} > \mu_2 e^{-k_2 r}$ as shown in Fig. 3c, which not only verifies the result of Theorem 3.3-(ii) but also implies that slower diffuser does not necessarily wipe out its faster competitor. Therefore the dynamics for $\mu_2 \in \left(0, \mu_1 e^{(k_2-k_1)r_{\min}}\right)$ is expected to be complicated and how to sharpen this interval so that more decisive conclusions can be drawn becomes an interesting open question.

We remark that the upper bound k_r defined in Theorem 3.3 is not optimal, which is a technical assumption. To prove Theorem 3.3, we first establish some technical lemmas. For any coexistence steady state (U, V) (if it exists) of system (1.7), it satisfies

$$\begin{cases} \mu_1 e^{-k_1 r} U_{xx} + U(r(x) - Ue^{k_1 r} - Ve^{k_2 r}) = 0, & x \in (0, L), \\ \mu_2 e^{-k_2 r} V_{xx} + V(r(x) - Ue^{k_1 r} - Ve^{k_2 r}) = 0, & x \in (0, L), \quad (3.27) \\ U_x = V_x = 0, & x = 0, L. \end{cases}$$
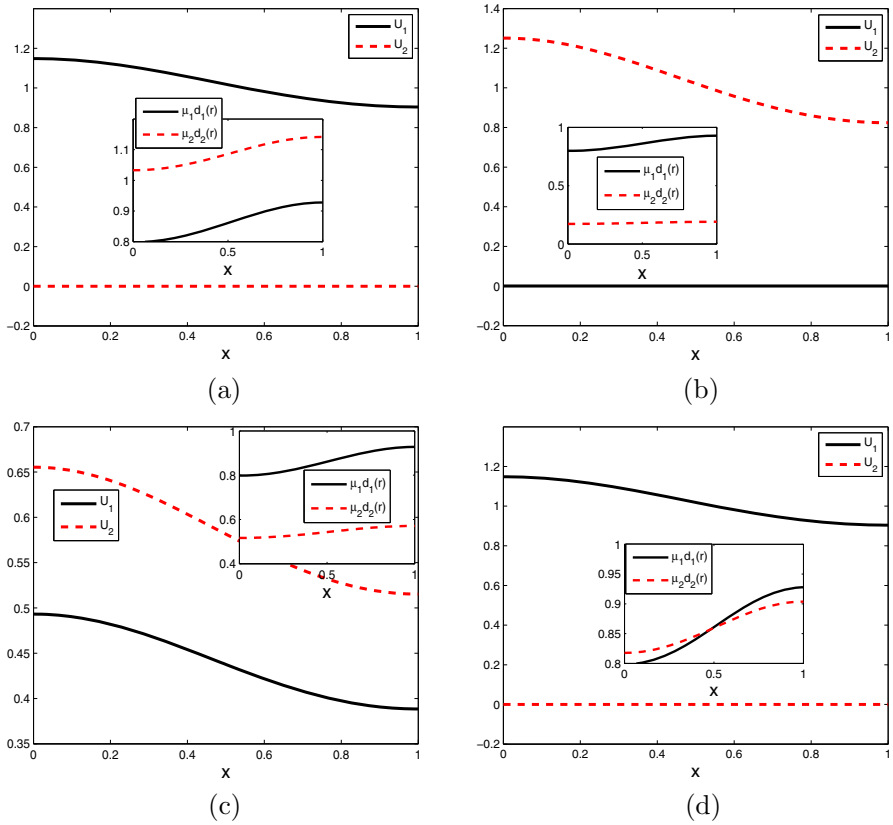
Fig. 3 Numerical simulations of steady state profile of the competition system (1.5) with $d_i(r) = e^{-k_i r}$ in $[0, 1]$ with monotone decreasing resource $r(x) = 1 + 0.5 \cos(\pi x)$, where $k_1 = 0.15$, $k_2 = 0.1$. The profile of steady state solution (U_1, V_1) are plotted in **a** for $\mu_2 = 1.2$, **b** for $\mu_2 = 0.2$, **c** for $\mu_2 = 0.6$ and **d** for $\mu_2 = 0.95$, where $\mu_1 = 1$, $k_r = 0.2039$ and $e^{(k_2 - k_1)r_{\min}} = 0.9753$

Let

$$T = \frac{U_x}{U} \quad \text{and} \quad S = \frac{V_x}{V} \qquad \text{for } x \in [0, L]. \tag{3.28}$$

A direct computation produces

$$\begin{cases} \mu_1 T_{xx} + 2\mu_1 T T_x + A r_x e^{k_1 r} - T U e^{2k_1 r} - S V e^{(k_1 + k_2)r} = 0, \ x \in (0, L), \\ \mu_2 S_{xx} + 2\mu_2 S S_x + B r_x e^{k_2 r} - S V e^{2k_2 r} - T U e^{(k_1 + k_2)r} = 0, \ x \in (0, L), \\ T(0) = T(L) = S(0) = S(L) = 0, \end{cases} \tag{3.29}$$

where

$$A = 1 + k_1 r - 2k_1 U e^{k_1 r} - (k_1 + k_2) V e^{k_2 r} \quad \text{and} \quad B = 1 + k_2 r - 2k_2 V e^{k_2 r} - (k_1 + k_2) U e^{k_1 r}.$$

The following results can be proved in a similar way as in Lou and Zhou (2015, Lemma 3.5).

Lemma 3.2 *Let T and S be defined in (3.28). For any interval (x_1, x_2) on $[0, L]$, if $0 \leq k_1, k_2 \leq k_r$, then the following results hold.*

(i) If $r_x < 0$ on $[0, L]$, then T(resp. S) can not achieve a positive local maximum in (x_1, x_2) with $S \geq 0$(resp. $T \geq 0$) in (x_1, x_2)

(ii) If $r_x > 0$ on $[0, L]$, then T(resp. S) can not achieve a negative local minimum in (x_1, x_2) with $S \leq 0$(resp. $T \leq 0$) in (x_1, x_2).

Proof Inspired by Lou and Zhou (2015, Lemma 3.5), it suffices to show that $A, B > 0$ on $[0, L]$. For any coexistence steady state (U, V) of system (1.7), by Corollary 9 of Zhou et al. (2021), one obtains that

$$U \leq \theta_{\mu_1, d_1} \quad \text{and} \quad V \leq \theta_{\mu_2, d_2} \quad \text{on } [0, L]. \tag{3.30}$$

By Lemma 2.2, one has

$$U \leq \max_{x \in \bar{\Omega}}(re^{-k_1 r}) < r_{\max} \quad \text{and} \quad V \leq \max_{x \in \bar{\Omega}}(re^{-k_2 r}) < r_{\max} \quad \text{on } [0, L]. \tag{3.31}$$

From (3.30), (3.31), and $r \geq 0$ on $[0, L]$, it follows that

$$A, B > 0 \quad \text{on } [0, L], \quad \text{for } k_1, k_2 \leq k_r, \tag{3.32}$$

where k_r satisfies $4k_r r_{\max} e^{k_r r_{\max}} = 1$. This completes the proof. $\square$

Similar to Zhou (2016, Lemma 3.29), one can derive the following result.

Lemma 3.3 *If (U, V) is a coexistence steady state of system (3.27), then for any $0 \leq y_1 \leq y_2 \leq L$, we have*

$$\int_{y_1}^{y_2} UVS\left\{T\left(1 - \frac{\mu_2}{\mu_1}e^{(k_1-k_2)r}\right) - \frac{\mu_2}{\mu_1}(k_1 - k_2)r_x e^{(k_1-k_2)r}\right\}dx$$
$$= TUV|_{y_1}^{y_2} - \frac{\mu_2}{\mu_1}SUVe^{(k_1-k_2)r}\Big|_{y_1}^{y_2}, \tag{3.33}$$

and

$$\int_{y_1}^{y_2} UVT\left\{S\left(1 - \frac{\mu_1}{\mu_2}e^{(k_2-k_1)r}\right) - \frac{\mu_1}{\mu_2}(k_2 - k_1)r_x e^{(k_2-k_1)r}\right\}dx$$
$$= SUV|_{y_1}^{y_2} - \frac{\mu_1}{\mu_2}TUVe^{(k_2-k_1)r}\Big|_{y_1}^{y_2}. \tag{3.34}$$

Moreover, if $k_1 > k_2$ and $\mu_1 \leq \mu_2 e^{(k_1-k_2)r_{\min}}$, the following results hold.

(i) If $r_x > 0$ on $[0, L]$, then there do not exist T and S satisfying $T(y)$, $S(y) \geq 0$ on $[y_1, y_2]$, $S(y_1) \geq S(y_2) = 0$, and $T(y_2) \geq T(y_1) = 0$ such that any of the following conditions hold:

(1) $T \not\equiv 0$ on $[y_1, y_2]$; (2) $S \not\equiv 0$ on $[y_1, y_2]$; (3) $T(y_2) > 0$; (4) $S(y_1) > 0$.

(ii) If $r_x < 0$ on $[0, L]$, then there do not exist T and S satisfying $T(y)$, $S(y) \leq 0$ on $[y_1, y_2]$, $S(y_2) \leq S(y_1) = 0$, and $T(y_1) \leq T(y_2) = 0$ such that any of the following conditions hold:

(1) $T \not\equiv 0$ on $[y_1, y_2]$; (2) $S \not\equiv 0$ on $[y_1, y_2]$; (3) $T(y_1) < 0$; (4) $S(y_2) < 0$.

Proof Multiplying the first equation and the second equation of system (3.27) by $e^{k_1 r} V$ and $e^{k_1 r} U$, respectively, integrating the resulting equations in (y_1, y_2) and making a substraction, one obtains

$$\mu_1 \int_{y_1}^{y_2} V U_{xx} dx = \mu_2 \int_{y_1}^{y_2} U e^{(k_1 - k_2) r} V_{xx} dx.$$

Then the integration by part yields

$$\mu_1 V U_x |_{y_1}^{y_2} - \mu_2 U e^{(k_1 - k_2) r} V_x |_{y_1}^{y_2} = \int_{y_1}^{y_2} \{\mu_1 U_x V_x - \mu_2 [U e^{(k_1 - k_2) r}]_x V_x\} dx,$$

which combined with (3.28) gives (3.33). The same argument will yield (3.34). Assertions (i) and (ii) follow directly from (3.33) and (3.34), which completes the proof. □

Now, we are ready to establish the non-existence of coexistence steady state for the system (3.27).

Lemma 3.4 *Assume $0 \leq k_2 < k_1 \leq k_r$ and $\mu_2 \geq \mu_1 e^{(k_2 - k_1) r_{\min}}$. If $r_x > 0$ or $r_x < 0$ on $[0, L]$, then system (3.27) does not admit any coexistence steady state.*

Proof We first consider the case $r_x > 0$ on $[0, L]$. By contradiction, we suppose that the system (3.27) has a coexistence steady state (U, V). To get a contradiction, we prove four claims first.

Claim 1: U_{xx} and V_{xx} have the same sign on $[0, L]$. This result follows directly from (3.27) and U, $V > 0$ on $[0, L]$.

Claim 2: there exists $\varrho > 0$ such that $T(x) > 0$ and $S(x) > 0$ in $(0, \varrho)$. It suffices to show that $T_x(0) > 0$ and $S_x(0) > 0$ as $T(0) = S(0) = 0$. We shall show $T_x(0) > 0$ only since the proof of $S_x(0) > 0$ is the same.

Suppose that $T_x(0) > 0$ is false. Then either $T_x(0) < 0$ or $T_x(0) = 0$.

If $T_x(0) < 0$, then there exists $\varrho_1 > 0$ such that $T(x) < 0$ in $(0, \varrho_1)$ as $T(0) = 0$. Moreover, by the definition of T and $U_x(0) = 0$, one finds that

$$T_x(0) = \frac{U_{xx}(0) U(0) - U_x^2(0)}{U^2(0)} = \frac{U_{xx}(0)}{U(0)} < 0, \tag{3.35}$$

which implies $U_{xx}(0) < 0$ and hence $V_{xx}(0) < 0$ by Claim 1. From $V_{xx}(0) < 0$, $V_x(0) = 0$ and the definition of S, it follows that $S_x(0) < 0$. This along with $S(0) = 0$ implies that there exists $\varrho_2 > 0$ such that $S(x) < 0$ in $(0, \varrho_2)$. These facts combined with $T(L) = S(L) = 0$ yields that there exist $x_1 \in [\varrho_1, L]$ and $x_2 \in [\varrho_2, L]$ such that

$$T(x) < 0 \text{ in } (0, x_1) \text{ and } T(x_1) = T(0) = 0 \tag{3.36}$$

and

$$S(x) < 0 \text{ in } (0, x_2) \text{ and } S(x_2) = S(0) = 0. \tag{3.37}$$

Without loss of generality, we assume that $x_1 \le x_2$. Then (3.36) implies that T achieves a negative local minimum at $x_3 \in (0, x_1)$. Moreover, $S(x_3) < 0$ due to $x_3 < x_1 \le x_2$ and (3.37). This is impossible by Lemma 3.2 (ii).

If $T_x(0) = 0$, then $U_{xx}(0) = 0$ by (3.35). Therefore, $V_{xx}(0) = 0$ by Claim 1, which suggests that $S_x(0) = 0$. Then, estimating the first and second equation of system (3.29) at $x = 0$, by $T(0) = S(0) = T_x(0) = S_x(0) = 0$, $r_x(0) > 0$ and $A, B > 0$ due to (3.32), one obtains $T_{xx}(0) < 0$ and $S_{xx}(0) < 0$. Combining the facts that $S(0) = T(0) = T_x(0) = S_x(0) = 0$, $T_{xx}(0) < 0$, $S_{xx}(0) < 0$, and $T(L) = S(L) = 0$, one can easily see that there exist $x_1, x_2 \in (0, L]$ such that (3.36) and (3.37) are satisfied. Hence a contradiction arises. Thus Claim 2 is proved. Similarly, one can derive the following result in Claim 3 below.

Claim 3: *there exists $\varrho^* \in (0, L)$ such that $T(x) > 0$ and $S(x) > 0$ in $(L - \varrho^*, L)$.*
We proceed to prove the following result.

Claim 4: S must change sign in $(0, L)$. Suppose that the claim is not true. Then it follows from Claim 2 or Claim 3 that

$$S \gneqq 0, \quad \text{in } (0, L). \tag{3.38}$$

Letting $(y_1, y_2) = (0, L)$ in (3.33), we have

$$\int_0^L UVS\left\{ T\left(1 - \frac{\mu_2}{\mu_1} e^{(k_1 - k_2)r}\right) - \frac{\mu_2}{\mu_1}(k_1 - k_2)r_x e^{(k_1 - k_2)r} \right\} \mathrm{d}x = 0.$$

With the assistance of this, $k_1 > k_2$, $\mu_2 \ge \mu_1 e^{(k_2 - k_1)r_{\min}}$, $U, V > 0$ on $[0, L]$, $r_x > 0$ on $[0, L]$, $r \gneqq 0$ in $(0, L)$, (3.38), and Claim 2, we can deduce that

$$T \text{ must change sign in } (0, L). \tag{3.39}$$

By Claim 2, Claim 3, and (3.39), there exists $x_4 \in (0, L)$ such that

$$T(x) > 0 \text{ in } (x_4, L) \text{ and } T(x_4) = 0. \tag{3.40}$$

Then, (3.38), (3.40), $T(L) = S(L) = 0$, Claim 3 and Lemma 3.3 (i) yield a contradiction with choosing $(y_1, y_2) = (x_4, L)$. Therefore, Claim 4 is proved.

According to Claim 2, Claim 3, and Claim 4, we see that S must have a negative local minimum in $(0, L)$. Define

$$x^* = \inf\{x \in [0, L] : S(x) < 0, S_x(x) = 0 \text{ and } S_{xx}(x) \geq 0\}.$$

Obviously, $x^* \in (0, L)$ and $S(x^*) \leq 0$. We will get a contradiction for each of the two cases, $S(x^*) < 0$ and $S(x^*) = 0$.

Case a: $S(x^*) < 0$.

Claim a.1: There exists $x_5 \in (0, x^*)$ such that $S(x_5) = 0$, $S_x(x) \leq 0$ on $[x_5, x^*]$, and $S(x) \geq 0$ on $[0, x_5]$.

By Claim 2, and $S(x^*) < 0$, we know that S has a zero in $(0, x^*)$. Denote

$$x_5 = \sup\{x \in (0, x^*) : \quad S(x) = 0\}.$$

Clearly, $S(x_5) = 0$ and $S(x) < 0$ for $x \in (x_5, x^*]$. By the definition of x^*, we see that $S(x) \geq 0$ on $[0, x_5]$ otherwise there is a negative local minimum in $(0, x_5)$ (contradicting the definition of x^*). Moreover, $S_x(x) \leq 0$ on $[x_5, x^*]$. If this is not true, then there exists $\hat{x} \in (x_5, x^*)$ such that $S_x(\hat{x}) > 0$. As $S(x) < 0$ for $x \in (x_5, \hat{x})$, there exists $\tilde{x} \in [x_5, \hat{x})$ such that $S_x(\tilde{x}) < 0$. Then there exists a negative local minimum of S in $(\tilde{x}, \hat{x})$, a contradiction to the definition of x^*. This proves Claim a.1.

Claim a.2: $T(x_5) < 0$.

Suppose by contradiction that $T(x_5) \geq 0$. If $T \geq 0$ in $(0, x_5)$, then by Claim a.1, Claim 2, and Lemma 3.3 (i) with $(y_1, y_2) = (0, x_5)$, one can derive a contradiction. So, there exists some point x_5^* in $(0, x_5)$ such that $T(x_5^*) < 0$. Then, we shall consider two cases:

$$(1) \ T(x_5) > 0, \quad (2) \ T(x_5) = 0.$$

If $T(x_5) > 0$, then there exits some $x_5^{**} \in (x_5^*, x_5)$ such that

$$T(x_5^{**}) = 0, \quad \text{and} \quad T(x) > 0 \text{ in } (x_5^{**}, x_5). \tag{3.41}$$

Combining Claim a.1, (3.41) and Lemma 3.3 (i) with $(y_1, y_2) = (x_5^{**}, x_5)$, one can derive a contradiction.

Next, we consider case 2: $T(x_5) = 0$. By Claim a.1, one obtains $V_{xx}(x_5) \leq 0$. If $V_{xx}(x_5) = 0$, then $S_x(x_5) = 0$, which together with the facts that $T(x_5) = S(x_5) = 0$, $r_x > 0$ on $[0, L]$, $B > 0$ on $[0, L]$ due to $k_1, k_2 < k_r$, and the second equation of system (3.29), implies $S_{xx}(x_5) < 0$. Then, by $S(x_5) = S_x(x_5) = 0$ and $S_{xx}(x_5) < 0$, one obtains that there exists some $\delta > 0$ such that

$$S(x) < 0 \text{ in } (x_5 - \delta, x_5 + \delta)\backslash\{x_5\},$$

which contradicts Claim a.1. Therefore, $V_{xx}(x_5) < 0$, which indicates that $U_{xx}(x_5) < 0$ due to Claim 1. This further yields that

$$T_x(x_5) < 0,$$

which suggests that there exits some $x_5^{**} \in (x_5^*, x_5)$ such that (3.41) holds. Then, one can also obtain a contradiction by Lemma 3.3 (i) with $(y_1, y_2) = (x_5^{**}, x_5)$. Therefore, Claim a.2 holds.

Claim a.3: There exists $x_6 \in (x_5, x^*)$ *such that* $T(x_6) = 0$ *and* $T(x) < 0$ *in* (x_5, x_6). It follows from the definition of x^* and the second equation in (3.29) that $T(x^*) > 0$. This along with Claim a.2 immediately confirms Claim a.3.

Recall from Claim a.1 that $S(x_5) = 0$ and $S_x(x_5) \le 0$. So, one gets $V_x(x_5) = 0$ and $V_{xx}(x_5) \le 0$. As V satisfies (3.27), evaluating it at $x = x_5$ produces

$$r(x_5) - U(x_5)e^{k_1 r(x_5)} - V(x_5)e^{k_2 r(x_5)} \ge 0. \tag{3.42}$$

Let $g(x) = r(x) - U(x)e^{k_1 r(x)} - V(x)e^{k_2 r(x)}$ on $[0, L]$. Then

$$g_x(x) = r_x(1 - k_1 U e^{k_1 r} - k_2 V e^{k_2 r}) - T U e^{k_1 r} - S V e^{k_2 r}.$$

With the facts that $r_x(x) > 0$ on $[0, L]$, $T(x) < 0$ and $S(x) < 0$ in (x_5, x_6), $0 < U, V < r_{\max}$ on $[0, L]$ by (3.31), and $k_1, k_2 < k_r$, one obtains that $g_x(x) > 0$ in (x_5, x_6), which along with (3.42) implies that $g(x_6) > 0$. Then, estimating the first equation of system (3.27), one finds $U_{xx}(x_6) < 0$, which further yields that

$$T_x(x_6) < 0. \tag{3.43}$$

However, by Claim a.3, we have

$$T_x(x_6) \ge 0,$$

which contradicts (3.43). This proves that $S(x^*) < 0$ can not occur.

Case b: $S(x^*) = 0$.

First, with similar arguments as those in the proof of Claim a.1, one can obtain

$$S(x) \ge 0 \ \text{ for } x \in (0, x^*). \tag{3.44}$$

Next, it follows from the definition of x^* that $S_x(x^*) = 0$ and $S_{xx}(x^*) \ge 0$. We claim that $S_{xx}(x^*) > 0$ cannot occur. Otherwise, if $S_{xx}(x^*) > 0$, then there exists $\varrho_4 > 0$ small enough such that

$$S(x) > 0 \ \text{ for } x \in (x^* - \varrho_4, x^* + \varrho_4) \backslash \{x^*\}.$$

This contradicts the definition of x^*. Thus $S_x(x^*) = S_{xx}(x^*) = 0$. Finally, evaluating the second equation of (3.29) at $x = x^*$, one easily sees

$$T(x^*) = \frac{r_x(x^*)B(x^*)}{U(x^*)e^{k_1 r(x^*)}} > 0,$$

where $B(x^*) > 0$ due to $k_1, k_2 < k_r$. This along with $T(0) = 0$ implies that there exists some $x_7 \in [0, x^*)$ such that

$$T(x_7) = 0, \quad \text{and} \quad T(x) > 0 \text{ in } (x_7, x^*). \tag{3.45}$$

Then the combination of $S(x^*) = 0$, (3.44) and (3.45) yields the results contradicting Lemma 3.3 (i) with $(y_1, y_2) = (x_7^*, x^*)$. So, $S(x^*) = 0$ can not happen, which shows that system (3.27) does not admit any coexistence steady state when $r_x > 0$ on $[0, L]$.

On the other hand, if $r_x < 0$ on $[0, L]$, by the argument of contradiction, we assume system (3.27) admits a coexistence steady state (U, V). Let $\tilde{U}(x) = U(L-x)$, $\tilde{V}(x) = V(L-x)$, and $\tilde{r}(x) = r(L-x)$. Then, $(\tilde{U}, \tilde{V})$ and $\tilde{r}$ satisfy

$$\begin{cases} \mu_1 e^{-k_1\tilde{r}} \tilde{U}_{xx} + \tilde{U}(\tilde{r}(x) - \tilde{U}e^{k_1\tilde{r}} - \tilde{V}e^{k_2\tilde{r}}) = 0, & x \in (0, L), \\ \mu_2 e^{-k_2\tilde{r}} \tilde{V}_{xx} + \tilde{V}(\tilde{r}(x) - \tilde{U}e^{k_1\tilde{r}} - \tilde{V}e^{k_2\tilde{r}}) = 0, & x \in (0, L), \\ \tilde{U}_x = \tilde{V}_x = 0, & x = 0, L, \end{cases}$$

where $\tilde{r}_x = -r_x > 0$ on $[0, L]$. This contradicts the first part of the Theorem, and hence completes the proof. □

Now we are ready to prove Theorem 3.3.

Proof of Theorem 3.3 We first prove assertion (i). Given all the parameters except μ_1, it suffices to show that $(\theta_{\mu_1,d_1}, 0)$ is globally asymptotically stable for $\mu_1 \in (0, \mu_2 e^{(k_1-k_2)r_{\min}}]$. From Lemma 2.4 (ii), it follows that

$$\lim_{\mu_1 \to 0} \lambda_1(\mu_1 d_1(r), r - W_{\mu_2,d_2}) = \max_{x \in \overline{\Omega}}(r - W_{\mu_2,d_2}).$$

Multiplying the equation (3.1) with $i = 2$ by $\frac{1}{d_2(r)}$ and integrating the resulting equation on Ω, one obtains

$$\int_{\Omega} W_{\mu_2,d_2}(r - W_{\mu_2,d_2})\mathrm{d}x = 0. \tag{3.46}$$

Since re^{-k_2r} is not constant in Ω, similar to the analysis in the Claim 1 in the proof of Theorem 3.1, one can derive that

$$r - W_{\mu_2,d_2} \not\equiv 0,$$

which along with (3.46) implies

$$\max_{x \in \overline{\Omega}}(r - W_{\mu_2,d_2}) > 0.$$

This further yields that

$$\lim_{\mu_1 \to 0} \lambda_1(\mu_1 d_1(r), r - W_{\mu_2,d_2}) = \max_{x \in \overline{\Omega}}(r - W_{\mu_2,d_2}) > 0,$$

which means that $(0, \theta_{\mu_2, d_2})$ is linearly unstable when μ_1 is small enough. This thanks to Lemma 3.4, and Proposition 3.1 (ii), shows that $(\theta_{\mu_1, d_1}, 0)$ is globally asymptotically stable when μ_1 is small enough. Following the approaches as those in the proof of Lou et al. (2019, Theorem 1.3) or Tang and Chen (2021, Theorem 1.3), one can prove that $(\theta_{\mu_1, d_1}, 0)$ is globally asymptotically stable for $\mu_1 \in \left(0, \mu_2 e^{(k_1 - k_2) r_{\min}}\right]$.

Next, we prove the assertion (ii) by the argument of contradiction. Given all the parameters except μ_2, we assume that system (1.7) doesn't admit any positive steady state for any $\mu_2 \in \left(0, \mu_1 e^{(k_2 - k_1) r_{\min}}\right)$. Similarly, one can prove that $(0, \theta_{\mu_2, d_2})$ is globally asymptotically stable when μ_2 is small enough. On the other hand, from assertion (i), it follows that $(\theta_{\mu_1, d_1}, 0)$ is globally asymptotically stable when $\mu_2 = \mu_1 e^{(k_2 - k_1) r_{\min}}$. Following the approaches as those in the proof of Zhou (2016, Theorem 1.1), one can derive a contradiction. This completes the proof. □

By the same arguments as for the case $d_i(r) = e^{-k_i r}$ $(i = 1, 2)$, we can show the following results for $d_i(r) = (1 + r)^{-k_i}$ $(i = 1, 2)$.

Theorem 3.4 *Assume $d_i(r) = (1 + r)^{-k_i}$ $(i = 1, 2)$. Let $\tilde{k}_r$ be such that $4\tilde{k}_r r_{max}(1 + r_{max})^{\tilde{k}_r} = 1$. If $r_x > 0$ or $r_x < 0$ on $[0, L]$, $0 \le k_2 < k_1 \le \tilde{k}_r$ and $\mu_1 > 0$, then we have the following results.*

(i) *(Competitive exclusion) If $\mu_2 \in [\mu_1 e^{(k_2 - k_1) r_{\min}}, \infty)$, then $(\theta_{\mu_1, d_1}, 0)$ is globally asymptotically stable;*

(ii) *(Coexistence) There exists some $\mu_2 \in \left(0, \mu_1 e^{(k_2 - k_1) r_{\min}}\right)$ such that system (1.7) admits a positive steady state.*

4 Summary and discussion

This paper investigates the effects of resource-dependent dispersal on the evolutionary dynamics by studying the single and two-species population models. In a single-species community, we can construct some resource-dependent dispersal strategies such that the total population supported may be smaller than the environmental carrying capacity (see the second part of Theorem 2.1-(3)), which is in contrast to the case of random dispersal with which the total population supported is always larger than its carrying capacity (Lou 2006), despite that some resource-dependent dispersal strategies may still enjoy the same properties as the random dispersal (see the first part of Theorem 2.1-(3)). In particular, if the dispersal strategy function $d(r)$ is $\frac{1}{r}$ up to a multiplicative constant, the idea free distribution will be achieved (see Theorem 2.1-(2) or Korobenko and Braverman 2009). However for resource-dependent dispersal strategies other than those constructed in Theorem 2.1-(3), how to determine the total population size supported remains unknown. This amounts to ask the following question:

(1) How does the total population $\int_\Omega W_{\mu, d}(x) dx$ change with respect to the diffusion coefficient μ for a given dispersal strategy $d(r)$?

Though the assertions in Theorem 2.1-(3) have partially addressed the above question, a full picture is still missing in this paper and deserves further studies in the future.

For the two-species competition model (1.5) where two competing species are ecologically identical, the resource-dependent dispersal strategies have more complicated and profound effects on the population dynamics. First if two competing species employ the same dispersal strategies in the sense that $d_1(r) = \vartheta d_2(r)$ for some constant $\vartheta > 0$, then the species with slower diffusion will win the competition if $d_2(r)r$ is not constant (see Theorem 3.1). While if $d_2(r)r$ is constant, there is a global attractor consisting of a continuum of steady states (see Remark 3.1-(b)). If two competing species employ different dispersal strategies (i.e. $d_1(r) \neq Cd_2(r)$ for any $C > 0$), the global dynamics is much harder to quantify. In this case, we resort to two quantities δ_1 and δ_2 associated with $r, d_1(r), d_2(r)$ as defined in (3.13). Noticing that the case $\delta_1 < 0, \delta_2 < 0$ is impossible (see Remark 3.2-(a)), we can classify the global dynamics for large diffusion coefficients μ_1, μ_2 (see Theorem 3.2) as follows: the two competing species are mutually excluded if $\delta_1 \delta_2 < 0$ and coexist if $\delta_1 > 0, \delta_2 > 0$. This classification seems to hold when $\mu_i (i = 1, 2)$ is not large (see Remark 3.2-(d)), but it is not justified in this paper. Hence the second interesting open question would be

(2) What is the global dynamics of (1.5) if μ_1 or μ_2 is not large when $d_1(r) \neq Cd_2(r)$ for any $C > 0$? Does the criterion in Theorem 3.2 still hold ?

When $\delta_1 = 0$ or $\delta_2 = 0$, the neutral stability will arise and further analysis/effrots are needed to draw a more decisive conclusion (see Remark 3.2-(c)), but we do not pursue this direction in the paper and leave it for future. The classical two-species competition–diffusion system (1.3) with random dispersal leads to a celebrated result: slower diffuser always prevails. Our third result is to investigate whether the two-species competition model (1.5) with resource-dependent dispersal will yield similar behaviors. It turns out there is not an affirmative answer to this question. When μ_1 and μ_2 are large, we construct a dispersal strategy in Proposition 3.2 to show that the coexistence exists if one species has slower diffusion than the other (see Remark 3.3). When μ_1 and μ_2 are not large, our results shown in Theorem 3.3 alongside Remark 3.5 and numerical simulations indicate the phenomenon "slower diffuser prevails" may occur (see Theorem 3.3-(i) and Fig. 3a or b) but may not occur either (see Theorem 3.3-(ii) and Fig. 3c) depending on the specific dispersal strategies. On the other hand, competitive exclusion may also happen without requiring slower diffusion as numerical shown in Fig. 3d. Our results imply the prominent phenomenon "slower diffuser always prevails" may occur under some simple biological circumstances, and does not necessarily happen in more complicated situations where the population dynamics are much harder to classify. For the competition model with resource-dependent dispersal, it seems hopeful to classify the dynamics to some extend for given dispersal strategies. Among other things, the following question is worthwhile to explore

(3) In the case stated in Theorem 3.3-(ii), are there some threshold values in $(0, \mu_1 e^{(k_2-k_1)r_{\min}})$ for μ_2 which can classify the coexistence and exclusion steady states ?

Interesting open questions arising from the current work are not limited to those mentioned above. Nevertheless, we hope these questions can stimulate further works to gain a more complete picture for the effects of resource-dependent dispersal on population dynamics.

References

Agmon S, Douglis A, Nirenberg L (1959) Estimates near the boundary for solutions of elliptic partial differential equations satisfying general boundary conditions. I. Commun Pure Appl Math 12:623–727

Agmon S, Douglis A, Nirenberg L (1964) Estimates near the boundary for solutions of elliptic partial differential equations satisfying general boundary conditions. II. Commun Pure Appl Math 17:35–92

Averill I, Lou Y, Munther D (2012) On several conjectures from evolution of dispersal. J Biol Dyn 6:117–130

Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev Camb Philos Soc 80(2):205–225

Braverman E, Makrujjaman Md (2016) Lotka systems with directed dispersal dynamics: competition and influence of diffusion strategies. Math Biosci 279:1–12

Cantrell RS, Cosner C (2003) Spatial ecology via reaction-diffusion equations. Wiley, Chichester

Cantrell RS, Cosner C, Lewis MA, Lou Y (2019) Evolution of dispersal in spatial population models with multiple timescales. J Math Biol 80:3–37

Cantrell RS, Cosner C, Lou Y (2010) Evolution of dispersal and ideal free distribution. Math Biosci Eng 7(1):17–36

Cho E, Kim Y-J (2013) Starvation driven diffusion as a survival strategy of biological organisms. Bull Math Biol 75(5):845–870

Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) (2001) Dispersal. Oxford University Press, Oxford

Cosner C (2014) Reaction–diffusion–advection models for the effects and evolution of dispersal. Discrete Contin Dyn Syst 34(5):1701–1745

de Mottoni P (1979) Qualitative analysis for some quasi-linear parabolic systems. Inst Math Polich Acad Sci Zam 190:11–70

DeAngelis DL, Ni W-M, Zhang B (2016) Dispersal and spatial heterogeneity: single species. J Math Biol 72:239–254

Dockery J, Hutson V, Mischaikow K, Pernarowski M (1998) The evolution of slow dispersal rates: a reaction diffusion model. J Math Biol 37(1):61–83

Duarte A, Mali I (2019) Modeling dispersal processes for ecological systems. Encyclopedia of ecology, 2nd edn, vol 2, pp 154–163

Fisher RA (1917) The wave of advance of advantageous genes. Ann Eugen 7:355–369

Gejji R, Lou Y, Munther D, Peyton J (2012) Evolutionary convergence to idea free dispersal strategies and coexistence. Bull Math Biol 74:257–299

Gilbarg D, Trudinger NS (2001) Elliptic partial differential equations of second order. Springer, Berlin

Guo Q, He X, Ni W-M (2020) Global dynamics of a general Lotka–Volterra competition–diffusion system in heterogeneous environments. Discrete Contin Dyn Syst 40(11):6547–6573

Hastings A (1983) Can spatial variation alone lead to selection for dispersal? Theor Popul Biol 24:244–251

He X, Lam K-Y, Lou Y, Ni W-M (2019) Dynamics of a consumer-resource reaction–diffusion model. J Math Biol 78:1605–1636

He X, Ni W-M (2016) Global dynamics of the Lotka–Volterra competition-diffusion system with equal amount of total resources II. Cal Var Partial Differ Equ 55(2):25, 20

He X, Ni W-M (2016) Global dynamics of the Lotka–Volterra competition-diffusion system: diffusion and spatial heterogeneity I. Commun Pure Appl Math 69(5):981–1014

He X, Ni W-M (2017) Global dynamics of the Lotka–Volterra competition-diffusion system with equal amount of total resources III. Cal Var Partial Differ Equ 56(5):132, 26

Hess P (1991) Periodic-parabolic boundary value problems and positivity. Longman Scientific & Technical, Harlow

Hutson V, Lou Y, Mischaikow K (2005) Convergence in competition models with small diffusion coefficients. J Differ Equ 211(1):135–161

Jin HY, Shi S, Wang Z-A (2020) Boundedness and asymptotics of a reaction–diffusion system with density-dependent motility. J Differ Equ 269:6758–6793

Jin HY, Wang Z-A (2021) The Keller–Segel system with logistic growth and signal-dependent motility. Disc Contin Dyn Syst B 26(6):3023–3041

Kareiva P, Odell GT (1987) Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. Am. Nat. 130(2):233–270

Keller EF, Segel LA (1971) Models for chemtoaxis. J Theor Biol 30:225–234

Kolmogorov AN, Petrovskii IG, Piskunov NS (1937) A study of the diffusion equation with increase in the amount of substance, and its application to a biological problem. Bull Moscow Univ Math Mech 1:1–26

Korobenko L, Braverman E (2009) A logistic model with a carrying capacity driven diffusion. Can Appl Math Q 17:85–100

Krein MG, Rutman MA (1948) Linear operators leaving invariant a cone in a Banach space. Uspekhi Mat Nauk (NS) 3(1):3–95

Lam K-Y, Ni N-W (2012) Uniqueness and complete dynamics in heterogeneous competition–diffusion systems. SIAM J Appl Math 72(6):1695–1712

Liu CL, Fu XF, Liu LL, Ren XJ, Chau CKL, Li SH, Xiang L, Zheng HL, Chen GH, Tang LH, Lenz P, Gui XD, Huang W, Hwa T, Huang JD (2021) Sequential establishment of stripe patterns in an expanding cell population. Science 334:238–241

Lou Y (2006) On the effects of migration and spatial heterogeneity on single and multiple species. J Differ Equ 223(2):400–426

Lou Y, Zhao X-Q, Zhou P (2019) Global dynamics of a Lotka–Volterra competition–diffusion–advection system in heterogeneous environments. J Math Pures Appl 121(9):47–82

Lou Y, Zhou P (2015) Evolution of dispersal in advective homogeneous environment: the effect of boundary conditions. J Differ Equ 259(1):141–171

Maag N, Cozzi G, Clutton-Brock T, Ozgul A (2018) Density-dependent dispersal strategies in a cooperative breeder. Ecology 99:1932–1941

Ni W, Shi J, Wang M (2020) Global stability of nonhomogeneous equilibrium solution for the diffusive Lotka–Volterra competition model. Calc Var Partial Differ Equ 4:132, 28

Okubo A, Levin SA (2001) Diffusion and ecological problems: modern perspectives. Springer, New York

Potapov A, Schlägel UE, Lewis MA (2014) Evolutionarily stable diffusive dispersal. Discrete Contin Dyn Syst Ser B 19:3319–3340

Skellam JG (1973) The formulation and interpretation of mathematical models of diffusionary processes in population biology. Academic Press, New York

Smith H (1995) Monotone dynamical systems: an introduction to the theory of competitive and cooperative systems. American Mathematical Society, Providence

Tang D, Chen Y (2021) Global dynamics of a Lotka–Volterra competition-diffusion system in advective heterogeneous environments. SIAM J Appl Dyn Syst 20(3):1232–1252

Tang D, Zhou P (2020) On a Lotka–Volterra competition–diffusion–advection system: homogeneity vs heterogeneity. J Differ Equ 268(4):1570–1599

Wang Z-A, Xu J (2021) On the Lotka–Volterra competition system with dynamical resources and density-dependent diffusion. J Math Biol 82(1–2):7, 37

Zhang B, Kula A, Mack KML, Zhai L, Ryce AL, Ni W-M, DeAngelis DL, Van Dyken JD (2017) Carrying capacity in a heterogeneous environment with habitat connectivity. Ecol Lett 20(9):1118–1128

Zhou P (2016) On a Lotka–Volterra competition system: diffusion vs advection. Calc Var Partial Differ Equ 55:137, 29

Zhou P, Tang D, Xiao D-M (2021) On Lotka–Volterra competitive parabolic systems: exclusion, coexistence and bistability. J Differ Equ 282:596–625