SCIENCE CHINA
Mathematics

Special Topic on Mathematical Biology
• ARTICLES •

March 2020 Vol. 63 No. 3: 441–464
https://doi.org/10.1007/s11425-019-1623-2

Populations with individual variation in dispersal in heterogeneous environments: Dynamics and competition with simply diffusing populations

Robert Stephen Cantrell[1], Chris Cosner[1,*] & Xiao Yu[2]

[1]*Department of Mathematics, University of Miami, Coral Gables, FL* 33146*, USA;*
[2]*School of Mathematical Sciences, South China Normal University, Guangzhou* 510631*, China*

*Email: rsc@math.miami.edu, gcc@math.miami.edu, xymath*19*@m.scnu.edu.cn*

Received July 12, 2019; accepted December 7, 2019; published online January 3, 2020

Abstract We consider a model for a population in a heterogeneous environment, with logistic-type local population dynamics, under the assumption that individuals can switch between two different nonzero rates of diffusion. Such switching behavior has been observed in some natural systems. We study how environmental heterogeneity and the rates of switching and diffusion affect the persistence of the population. The reaction-diffusion systems in the models can be cooperative at some population densities and competitive at others. The results extend our previous work on similar models in homogeneous environments. We also consider competition between two populations that are ecologically identical, but where one population diffuses at a fixed rate and the other switches between two different diffusion rates. The motivation for that is to gain insight into when switching might be advantageous versus diffusing at a fixed rate. This is a variation on the classical results for ecologically identical competitors with differing fixed diffusion rates, where it is well known that "the slower diffuser wins".

Keywords reaction-diffusion, ecology and evolutionary biology, population dynamics, animal behavior, individual variation in dispersal, evolution of dispersal

MSC(2010) 92D40, 92D50, 35K40, 35K57

Citation: Cantrell R S, Cosner C, Yu X. Populations with individual variation in dispersal in heterogeneous environments: Dynamics and competition with simply diffusing population. Sci China Math, 2020, 63: 441–464, https://doi.org/10.1007/s11425-019-1623-2

1 Introduction

The problem of understanding how dispersal patterns affect population interactions and thus are subject to evolutionarily selection has generated much interest among mathematical biologists. Classical models for dispersal typically assume that any given type of organism will disperse according to a single pattern or strategy, which may or may not be conditional on environmental conditions. Various models of that type are discussed in [4, 8]. One specific line of inquiry that has generated significant interest is the problem of deciding which types of dispersal, if any, are advantageous. A well-known result in that direction is that in environments that vary in space but not in time, if populations that are ecologically

* Corresponding author

identical except for their dispersal pattern compete, and the populations diffuse at different rates, the slower diffuser wins [10, 18]. However, there is considerable evidence that many organisms can switch between different dispersal modes depending on whether they are searching for resources or exploiting them (see [13, 14, 32–35, 42]). Models that capture the idea of switching between movement modes are developed in [12, 36, 41]. In [6] we developed basic theory for a model where a population consists of two sub-populations that diffuse at different rates, individuals can switch between sub-populations, and where there is logistic-type self-limitation. Somewhat similar types of models have been proposed in a related but different context, where a population has sub-populations that have different dispersal rates and perhaps different population dynamics and each sub-population is subject to mutations that produce offspring that belong to other sub-populations. This idea was already discussed in [10]. It has been used to study how dispersal polymorphism can affect the spreading speed of biological invasions [11, 31]. Some very strong and interesting results on traveling waves, spreading speeds, and dynamics for Fisher-Kolmogorov-Petrovsky-Piskunov (KPP) models with switching or mutation are presented in [15–17]. Existence results for equilibria of some related systems on bounded domains are derived in [2, 20].

The models for populations where individuals can switch between two sub-populations that we considered in [6] and will use here turn out to potentially be cooperative systems at some densities and competitive ones at others. Roughly speaking, when switching rates are high, the models are asymptotically cooperative while if switching rates are low they are asymptotically competitive. The version of the model treated in [6] had constant coefficients. In the present paper we extend some of the results of [6] to cases where some coefficients can vary in space. We also consider a model for competition on a bounded domain between a population whose members can switch between two diffusion rates and an otherwise ecologically identical population whose members diffuse at a single intermediate rate. This is motivated by previous work from the viewpoint of [10] on the evolution of slow diffusion in systems where each competing population has a single fixed diffusion rate. See [19] for more recent results that give a more complete treatment of the case of two competing populations with fixed diffusion rates. We are primarily interested in extending results such as those in [10, 19] on how diffusion rates influence competitive interactions to the case where one of the competitors switches between two diffusion rates. We have chosen to follow their modeling assumptions and use no-flux boundary conditions, which are Neumann boundary conditions in our models. The reason for that choice is that with Dirichlet or Robin boundary conditions, increasing the diffusion rate causes a loss of population across the domain boundary as well as causing different movement patterns in the interior, so it is clear that faster diffusion will be a disadvantage. However, in the Neumann case, there is no boundary loss so it is very interesting that faster diffusion may still be a disadvantage. In [6] we considered both Neumann and Dirichlet boundary conditions in the case of a single population that could switch between two different diffusion rates. We found that many of the general abstract results about the models with Dirichlet conditions were similar to those for models with Neumann conditions, but there were some differences in more refined specific results, and in some cases Dirichlet conditions caused additional technical difficulties that limited what we could do (see [6] for details). It would be interesting to consider Dirichlet boundary conditions in the of models we study in this paper. That would present some challenges but based on the analysis in [6] it should be possible to make some progress. More generally we think that extending the theory for models with switching to cover a broader range of dispersal operators, boundary conditions, and population interactions is an interesting topic for future research.

It turns out that in our model the result of the competition between the populations with and without switching depends on the relative sizes of the diffusion coefficients and on the rates of switching between faster and slower diffusion by the population that uses two distinct movement modes. In studying competition between populations with and without switching, we assume that the system describing the switching competitor is asymptotically cooperative, so that the full system is eventually cooperative-cooperative-competitive. This type of system was considered in the case of ordinary differential equations in [37, 38]. It is monotone with respect to the ordering given by $(u_1, v_1, w_1) \geqslant (u_2, v_2, w_2) \Leftrightarrow u_1 \geqslant u_2, v_1 \geqslant v_2, w_1 \leqslant w_2$. The main methods we use are primarily monotone dynamical systems theory, positive operator theory (specifically the Krein-Rutman theorem), and estimates of principal eigenvalues.

2 Analysis of semi-trivial steady states

Consider the system

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1\Delta u - \alpha(x)u + \beta(x)v + u(m(x) - u - bv) & \text{in } (0,\infty)\times\Omega, \\ \dfrac{\partial v}{\partial t} = d_2\Delta v + \alpha(x)u - \beta(x)v + v(m(x) - cu - v) & \text{in } (0,\infty)\times\Omega, \\ \dfrac{\partial u}{\partial n} = \dfrac{\partial v}{\partial n} = 0 & \text{on } (0,\infty)\times\partial\Omega, \\ u(0,x) = \phi_1(x), \quad v(0,x) = \phi_2(x) & \text{in } \Omega, \end{cases} \tag{2.1}$$

where $\Omega \subset \mathbb{R}^N$ ($N \geqslant 1$) is a bounded domain with boundary $\partial\Omega$ of class $C^{2+\theta}$ ($0 < \theta \leqslant 1$), and $\frac{\partial}{\partial n}$ denotes the differentiation in the direction of outward normal n to $\partial\Omega$. In general, we suppose that $0 < d_1 \leqslant d_2$ and $\alpha, \beta, m \in C^{\nu}(\bar{\Omega})$ ($0 < \nu < 1$), $\alpha(x)$ and $\beta(x)$ are non-negative and both positive for some $x_0 \in \bar{\Omega}$. We also assume that $m(x)$ is positive for some $x_1 \in \bar{\Omega}$, but we consider some cases where $m(x)$ changes sign and others where $m(x)$ is positive. The system (2.1) describes the dispersal and population dynamics of a single species that is divided into two groups, for example individuals that are seeking resources and other individuals who have found resources and are exploiting them, and where individuals can switch between groups. The corresponding model with constant coefficients was studied in [6]. In this section we extend some of the ideas and results of [6] to cases with variable coefficients.

The local existence of classical solutions follows from standard results (see for example the discussion and references in [4, Subsections 1.6.5 and 1.6.6]). The global existence follows if solutions are bounded by some finite $B(T)$ in $[L^{\infty}(\Omega)]^2$ on any finite time interval $(0,T)$ with $T > 0$. Let

$$\begin{aligned} g_1(x,u,v) &= (m(x) - \alpha(x) - u)u + (\beta(x) - bu)v, \\ g_2(x,u,v) &= (m(x) - \beta(x) - v)v + (\alpha(x) - cv)u. \end{aligned} \tag{2.2}$$

Clearly, there exist $M^+, N^+ > 0$ such that $g_1(x, M^+, v) < 0$ and $g_2(x,u,N^+) < 0$ for any $(x,u,v) \in \bar{\Omega} \times [0, M^+] \times [0, N^+]$. For such (x,u,v), we have $g_1(x,u,v) \geqslant u(m - \alpha - bN^+ - u) + \beta(x)v$, and $g_2(x,u,v) \geqslant v(m - \beta - cM^+ - v) + \alpha(x)u$. The comparison principle for a scalar parabolic equation applied to each of the equations in (2.1) implies that for any nonnegative and nontrivial initial data, the solution of the system (2.1) will stay positive for any $t > 0$. Indeed, we have the following result on the uniform boundedness of the solution.

Proposition 2.1. *There exist positive numbers B_1 and B_2, such that for any $M \geqslant B_1$ and $N \geqslant B_2$, the rectangular region $[0,M]\times[0,N]$ is invariant and attracting from above, i.e., $g_1(x,0,v) \geqslant 0$, $g_2(x,u,0) \geqslant 0$, $g_1(x,M,v) < 0$ and $g_2(x,u,N) < 0$, for any $(x,u,v) \in \bar{\Omega}\times[0,M]\times[0,N]$. Thus, any solution of (2.1) with nonnegative bounded initial data exists for all $t \geqslant 0$, and eventually lies in the rectangular region $[0,B_1]\times[0,B_2]$. Moreover, if there exist positive numbers A_1 and A_2 such that $g_1(x,A_1,v) > 0$ and $g_2(x,u,A_2) > 0$ for any $(x,u,v) \in \bar{\Omega}\times[A_1,B_1]\times[A_2,B_2]$, then any nontrivial solution of (2.1) with nonnegative bounded initial data eventually lies in the rectangular region $[A_1,B_1]\times[A_2,B_2]$.*

Proof. We only show the second part of the proof. Let

$$g_i^-(u_1,u_2) = \inf\{g_i(x,\theta_1,\theta_2), \theta_i = u_i, (x,\theta_j) \in \bar{\Omega}\times[u_j,B_j], j \neq i\}, \quad i = 1,2.$$

Then $g_i^-(u_1,u_2), i = 1,2$ is Lipschitz continuous in $[0,B_1]\times[0,B_2]$ and $g_i^-(u_1,u_2)$ is nondecreasing with u_j, $j \neq i, i = 1,2$. Thus, the ODE system $\frac{du_i}{dt} = g_i^-(u_1,u_2), i = 1,2$, is a cooperative system. By our assumption, we see that

$$g_1^-(A_1,v) \geqslant g_1^-(A_1,A_2) = \inf\{g_1(x,A_1,v),(x,v) \in \bar{\Omega}\times[A_2,B_2]\} > 0$$

for any $v \in [A_2,B_2]$ and $g_2^-(u,A_2) > 0$ for any $u \in [A_1,B_1]$. Thus (A_1,A_2) is a strict lower solution for the ODE system. Note that $g = (g_1,g_2)$ is subhomogeneous, in the sense that, for any $\gamma \in (0,1]$,

$g_i(x,\gamma u_1,\gamma u_2) \geqslant \gamma g_i(x,u_1,u_2)$, $(u_1,u_2)\in[0,B_1]\times[0,B_2], i=1,2$, and thus so is $g_i^-, i=1,2$. One can show that for any $\gamma\in(0,1]$, $[\gamma A_1,B_1]\times[\gamma A_2,B_2]$ is contracting from below for the ODE system. Indeed, $g_1^-(\gamma A_1,v)\geqslant g_1^-(\gamma A_1,\gamma A_2)\geqslant \gamma g_1^-(A_1,A_2)>0$ for any $v\in[\gamma A_2,B_2]$. Let $U(t,x,\phi)$ be a solution of the system (2.1) with $U(0,x,\phi)=(\phi_1,\phi_2)\in(0,B_1]\times(0,B_2]$. Then there exists $\gamma_0\in(0,1)$ such that $\phi_i\geqslant\gamma_0 A_i>0, i=1,2$. Let $U_-(t)$ be the solution of $U_t=G^-(U)=(g_1^-(u_1,u_2),g_2^-(u_1,u_2))$ with $U_-(0)=(\gamma_0A_1,\gamma_0A_2)$. It follows from [7, Theorem 1] that $U(t,x,\phi)\geqslant U_-(t)$ for any $t\geqslant0$. Indeed, $U^-(t)$ is nondecreasing in t and bounded from above and thus converges to some positive point. Since $\lim_{t\to\infty}U_-(t)\geqslant(A_1+\epsilon,A_2+\epsilon)$ for some small $\epsilon>0$, $U(t,x,\phi)$ will eventually lie in $[A_1,B_1]\times[A_2,B_2]$. □

Set $\underline{F}:=\min_{x\in\bar\Omega}F(x)$ and $\bar F:=\max_{x\in\bar\Omega}F(x)$. Based on the preceding observations, we obtain the following result.

Proposition 2.2. *The following statements are valid:*

(1) *Assume that $\underline{m}$, $\underline{\alpha}$, $\underline{\beta}>0$ and let $k=\min\{\underline{\alpha}/\bar\alpha,\underline{\beta}/\bar\beta\}\leqslant1$. If $k>\max\{1-\underline{m}/(b\bar m),1-\underline{m}/(c\bar m)\}$ and $(\bar\beta,\bar\alpha)\in S_1:=\{(x,y):\underline{m}+b(k-1)\bar m-y-x/b>0,\underline{m}+c(k-1)\bar m-x-y/c>0,x>0,y>0\}$, then any solution of the system* (2.1) *with positive bounded initial data eventually lies in $(\bar\beta/b,\bar m]\times(\bar\alpha/c,\bar m]$, where* (2.1) *is a competitive system.*

(2) *Let $k_1:=\max\{\bar\beta/\underline{\beta},\bar\alpha/\underline{\alpha}\}\geqslant1$. Assume that $k_1<1+k_0$, where k_0 is the larger root of $(bx-c)(cx-b)-1=0$. Then any solution of the system* (2.1) *with positive bounded initial data eventually lies in $(0,\underline{\beta}/b)\times(0,\underline{\alpha}/c)$, where* (2.1) *is a cooperative system, provided $(\underline{\beta}/b,\underline{\alpha}/c)\in S_2:=\{(x,y):\bar m-x+(b(k_1-1)-c)y<0,\bar m-y+(c(k_1-1)-b)x<0,x>0,y>0\}$.*

Proof. (1) Clearly, if $(\bar\beta,\bar\alpha)\in S_1$, then $g_1(x,\bar m,v)<(\bar\beta-b\bar m)v\leqslant0$ for any $v\in[0,\bar m]$ and $g_2(x,u,\bar m)<(\bar\alpha-c\bar m)u\leqslant0$ for any $u\in[0,\bar m]$. Moreover,

$$g_1\left(x,\frac{\bar\beta}{b},v\right)\geqslant\left(\underline{m}-\bar\alpha-\frac{\bar\beta}{b}\right)\frac{\bar\beta}{b}+(\underline{\beta}-\bar\beta)\bar m\geqslant\frac{\bar\beta}{b}\left[\underline{m}-\bar\alpha-\frac{\bar\beta}{b}+b(k-1)\bar m\right]>0$$

and

$$g_2\left(x,u,\frac{\bar\alpha}{c}\right)\geqslant\left(\underline{m}-\bar\beta-\frac{\bar\alpha}{c}\right)\frac{\bar\alpha}{c}+(\underline{\alpha}-\bar\alpha)\bar m\geqslant\frac{\bar\alpha}{c}\left[\underline{m}-\bar\beta-\frac{\bar\alpha}{c}+c(k-1)\bar m\right]>0$$

for any $(x,u,v)\in\bar\Omega\times[\frac{\bar\beta}{b},\bar m]\times[\frac{\bar\alpha}{c},\bar m]$. It follows immediately from Proposition 2.1 that the solution of the system (2.1) eventually lies in $(\frac{\bar\beta}{b},\bar m]\times(\frac{\bar\alpha}{c},\bar m]$.

(2) For S_2, if either $b(k_1-1)-c\leqslant0$ or $c(k_1-1)-b\leqslant0$, i.e., $k_1\leqslant1+\frac{c}{b}$ or $k_1\leqslant1+\frac{b}{c}$, then S_2 is nonempty. If $b(k_1-1)-c>0$ and $c(k_1-1)-c>0$, as long as $(b(k_1-1)-c)(c(k_1-1)-b)<1$, it is still nonempty. Clearly $k_0>\max\{\frac{b}{c},\frac{c}{b}\}$. Thus if $1\leqslant k_1<1+k_0$, S_2 is nonempty. Now for any $(\frac{\underline{\beta}}{b},\frac{\underline{\alpha}}{c})\in S_2$, we have

$$g_1\left(x,\frac{\underline{\beta}}{b},v\right)\leqslant\frac{\underline{\beta}}{b}\left[\bar m-\underline{\alpha}-\frac{\underline{\beta}}{b}+b(k-1)\frac{\underline{\alpha}}{c}\right]=\frac{\underline{\beta}}{b}\left[\bar m-\frac{\underline{\beta}}{b}+(b(k-1)-c)\frac{\underline{\alpha}}{c}\right]<0$$

and

$$g_2\left(x,u,\frac{\underline{\alpha}}{c}\right)\leqslant\frac{\underline{\alpha}}{c}\left[\bar m-\underline{\beta}-\frac{\underline{\alpha}}{c}+c(k-1)\frac{\underline{\beta}}{b}\right]=\frac{\underline{\alpha}}{c}\left[\bar m-\frac{\underline{\alpha}}{c}+(c(k-1)-b)\frac{\underline{\beta}}{b}\right]<0$$

holds for $(x,u,v)\in\bar\Omega\times[0,\frac{\underline{\beta}}{b}]\times[0,\frac{\underline{\alpha}}{c}]$. The result then follows. □

Throughout this paper, denote by $\lambda(d,e)$ the principal eigenvalue of

$$\lambda\phi=d\Delta\phi+e(x)\phi\quad\text{in}\ \ \Omega,\quad\frac{\partial\phi}{\partial n}=0\quad\text{on}\ \ \partial\Omega.$$

Here $e\in L^\infty(\Omega)$. We collect some useful information on $\lambda(d,e)$; refer to [3,4,19,21] and the references therein.

Proposition 2.3. (a) *$\lambda(d,e)$ depends smoothly on $d>0$, and depends continuously on $e\in L^\infty(\Omega)$.*

(b) *If $e_1,e_2\in L^\infty(\Omega)$ and $e_1(x)\geqslant e_2(x)$ in Ω, then $\lambda(d,e_1)\geqslant\lambda(d,e_2)$ with equality holding if and only if $e_1\equiv e_2$ a.e. in Ω.*

(c) *If e is non-constant, then $\lambda(d, e)$ is strictly decreasing in $d > 0$.*

(d) *Assume that e is non-constant and changes sign. Then*

(i) *if $\int_\Omega e \geqslant 0$, then $\lambda(d, e) > 0$;*

(ii) *if $\int_\Omega e < 0$, then there exists a unique $\mu^* > 0$ independent of d such that,* $\mathrm{sign}(1 - d\mu^*) = \mathrm{sign}(\lambda(d, e))$.

By the celebrated Krein-Rutman theorem, the eigenvalue problem

$$\begin{cases} \lambda\phi_1 = d_1\Delta\phi_1 - \alpha(x)\phi_1 + \beta(x)\phi_2 + m(x)\phi_1 & \text{in } \Omega, \\ \lambda\phi_2 = d_2\Delta\phi_2 + \alpha(x)\phi_1 - \beta(x)\phi_2 + m(x)\phi_2 & \text{in } \Omega, \\ \dfrac{\partial\phi_1}{\partial n} = \dfrac{\partial\phi_2}{\partial n} = 0 & \text{on } \partial\Omega \end{cases} \tag{2.3}$$

admits a principal eigenvalue λ_0 with a positive eigenfunction $\psi = (\psi_1, \psi_2)$ (see [1, 27, 30]). Clearly, if $m > 0$ on $\bar{\Omega}$, then $\lambda_0 > 0$; if $m < 0$ on $\bar{\Omega}$, then $\lambda_0 < 0$. An interesting question arises when m changes sign. In that case, what kind of sufficient conditions will guarantee that $\lambda_0 > 0$, so that 0 is linearly unstable? Next, we explore some sufficient conditions through some simple investigation.

Proposition 2.4. *Assume that m changes sign. Then the following statements are valid*:

(i) *If $\max\{\lambda(d_1, m - \alpha), \lambda(d_2, m - \beta)\} \geqslant 0$, then $\lambda_0 > 0$.*

(ii) *If $\int_\Omega m \geqslant \frac{\int_\Omega(\sqrt{\alpha}-\sqrt{\beta})^2}{2}$, then $\lambda_0 > 0$.*

Proof. Observe that $(\lambda_0 I - L_1)\phi = \beta\psi_2 \geqslant 0 \not\equiv 0$ in Ω has a unique positive solution ψ_1, where $L_1\phi := d_1\Delta\phi_1 + (m(x) - \alpha(x))\phi_1$ with the zero Neumann boundary condition. This yields that $\lambda_0 > s(L_1) = \lambda(d_1, m - \alpha)$. Similarly, we have $\lambda_0 > \lambda(d_2, m - \beta)$. Consequently, the statement (i) holds true.

Note that the components of the positive eigenfunction $\psi = (\psi_1, \psi_2)$ associated with λ_0 cannot both be constant. Otherwise, adding equations of (2.3) together, we obtain that $\lambda_0 = m(x)$, which is impossible. Now dividing equations of (2.3) by $\psi_i, i = 1, 2$ and integrating over Ω, respectively, we have

$$\begin{aligned} 2\lambda_0 &= d_1\int_\Omega\left|\frac{\nabla\psi_1}{\psi_1}\right|^2 + d_2\int_\Omega\left|\frac{\nabla\psi_2}{\psi_2}\right|^2 + 2\int_\Omega m - \int_\Omega\alpha - \int_\Omega\beta + \int_\Omega\left(\beta\frac{\psi_2}{\psi_1} + \alpha\frac{\psi_1}{\psi_2}\right) \\ &> 2\int_\Omega m - \int_\Omega\alpha - \int_\Omega\beta + 2\int_\Omega\sqrt{\alpha\beta} \geqslant 2\int_\Omega m - \int_\Omega(\sqrt{\alpha} - \sqrt{\beta})^2 \geqslant 0. \end{aligned}$$

This completes the proof. □

We can also examine our eigenvalue problem (2.3), by inserting a parameter μ multiplying m and considering how the principal eigenvalue depends on μ. Let $\lambda(\mu), \mu \in \mathbb{R}$ be the principal eigenvalue of

$$\begin{cases} \lambda\phi_1 = d_1\Delta\phi_1 - \alpha(x)\phi_1 + \beta(x)\phi_2 + \mu m(x)\phi_1 & \text{in } \Omega, \\ \lambda\phi_2 = d_2\Delta\phi_2 + \alpha(x)\phi_1 - \beta(x)\phi_2 + \mu m(x)\phi_2 & \text{in } \Omega, \\ \dfrac{\partial\phi_1}{\partial n} = \dfrac{\partial\phi_2}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{2.4}$$

It is easy to see that the principal eigenvalue $\lambda(0)$ of (2.4) is zero with a positive eigenfunction (Φ_1^*, Φ_2^*). The principal eigenvalue $\lambda(\mu)$ is always simple and isolated by [30, Theorem 4.1], so it is analytic in μ by results from [26, Chapter 7, Section 1 and Chapter 2, Section 1]. The operator on the right-hand side of (2.4) has a positive resolvent, so $\lambda(\mu)$ is convex in μ by results of [25]. Let $\tilde{\lambda}(\mu)$ and $\tilde{\phi} > 0$ be the principal eigenvalue and eigenfunction for

$$\lambda\phi_1 = d_1\Delta\phi - \alpha(x)\phi_1 + \mu m(x)\phi \quad \text{in } \Omega, \quad \frac{\partial\phi}{\partial n} = 0 \quad \text{on } \partial\Omega.$$

Since we assume that $m(x) > 0$ for some x, [21, Lemma 15.4] implies that $\tilde{\lambda}(\mu) \to \infty$ as $\mu \to \infty$. (The notation of [21] switches the roles of λ and μ we use in our notation and puts a minus sign on the eigenvalues corresponding to those we denote by λ.) Finally, if we multiply the first equation of (2.4) by $\tilde{\phi}$, integrate over Ω, then use Green's formula and the equation for ϕ we obtain

$$[\lambda(\mu)-\tilde{\lambda}(\mu)]\int_{\Omega}\phi_1\tilde{\phi}=\int_{\Omega}\beta\phi_2\tilde{\phi}>0,$$

so that $\lambda(\mu)>\tilde{\lambda}(\mu)$ and hence $\lambda(\mu)\to\infty$ as $\mu\to\infty$. Alternatively, we can show that $\lambda(\mu)$ and the normalized eigenfunctions associated with it are differentiable by methods similar to those used in the proof of Lemma 1.2 of [3]. (We show the details of a similar argument later in this paper, in the proof of Lemma 5.1.) We have the following observation.

Proposition 2.5. *Assume that m changes sign. Then the following statements are valid*:

(i) *If $\int_{\Omega}m(\Phi_1^*+\Phi_2^*)\geqslant 0$, then $\lambda_0>0$.*

(ii) *If $\int_{\Omega}m(\Phi_1^*+\Phi_2^*)<0$, then there exists a unique positive $\mu^0>0$ such that* $\mathrm{sign}(1-\mu^0)=\mathrm{sign}(\lambda_0)$.

Proof. If $\lambda'(0)>0$, it then easily follows from the convexity of $\lambda(\mu)$ that $\lambda(\mu)>\lambda(0)=0,\forall\,\mu>0$. If $\lambda'(0)=0$, since $\lambda(\mu)$ is analytic, convex and $\lambda(\infty)=\infty$, we have $\lambda'(\mu)>\lambda'(0)=0$ for $\mu>0$. Thus, $\lambda(\mu)>\lambda(0)=0$. If $\lambda'(0)<0$, then $\lambda(\mu)<0$ for $0<\mu\ll 1$. Note that $\lambda(\infty)=\infty$, we infer that there exists a $\mu^0>0$ such that $\lambda(\mu^0)=0$. Now the convexity and analyticity of $\lambda(\mu)$ yield that μ^0 has to be unique. Moreover, $\lambda(\mu)<0$ when $0<\mu<\mu^0$, and $\lambda(\mu)>0$ when $\mu>\mu^0$.

Next, we compute $\lambda'(0)$. Let $(\tilde{\Phi}_1(x,\mu),\tilde{\Phi}_2(x,\mu))$ be the positive eigenfunction associated with $\lambda(\mu)$. By arguments similar to those used in the proofs of Lemma 1.2 of [3] and Lemma 5.1 of the present paper, we can differentiate (2.4) with respect to μ at $\mu=0$. It then follows that

$$\begin{aligned}\lambda'(0)\Phi_1^*&=d_1\Delta\tilde{\Phi}_{1\mu}-\alpha(x)\tilde{\Phi}_{1\mu}+\beta(x)\tilde{\Phi}_{2\mu}+m(x)\Phi_1^*,\\ \lambda'(0)\Phi_2^*&=d_2\Delta\tilde{\Phi}_{2\mu}+\alpha(x)\tilde{\Phi}_{1\mu}-\beta(x)\tilde{\Phi}_{2\mu}+m(x)\Phi_2^*,\end{aligned}\tag{2.5}$$

where $\tilde{\Phi}_{i\mu}=\frac{\partial\tilde{\Phi}_i}{\partial\mu}(x,0)$, $i=1,2$. Adding the above equations together and integrating over Ω, we obtain that

$$\lambda'(0)=\frac{\int_{\Omega}m(\Phi_1^*+\Phi_2^*)}{\int_{\Omega}(\Phi_1^*+\Phi_2^*)}.$$

The proof is completed. □

Note that

$$\begin{aligned}&0=d_1\Delta\Phi_1^*-\alpha(x)\Phi_1^*+\beta(x)\Phi_2^*,\\ &0=d_2\Delta\Phi_2^*+\alpha(x)\Phi_1^*-\beta(x)\Phi_2^*,\\ &\frac{\partial\Phi_1^*}{\partial n}=\frac{\partial\Phi_2^*}{\partial n}=0\end{aligned}\tag{2.6}$$

implies $\Delta(d_1\Phi_1^*+d_2\Phi_2^*)=0$ in Ω, and $\frac{\partial(d_1\Phi_1^*+d_2\Phi_2^*)}{\partial n}=0$ on $\partial\Omega$. Therefore, $d_1\Phi_1^*+d_2\Phi_2^*=C>0$ for some constant C. Then substitute $\Phi_2^*=\frac{C}{d_2}-\frac{d_1}{d_2}\Phi_1^*$ into the first equation of (2.6) and integrate over Ω, it gives

$$0=-\int_{\Omega}\alpha\Phi_1^*+\int_{\Omega}\beta\left[\frac{C}{d_2}-\frac{d_1}{d_2}\Phi_1^*\right],$$

and hence, $C=\frac{\int_{\Omega}(d_2\alpha+d_1\beta)\Phi_1^*}{\int_{\Omega}\beta}$. It now follows that $\int_{\Omega}m(\Phi_1^*+\Phi_2^*)=[1-\frac{d_1}{d_2}]\int_{\Omega}\Phi_1^*m+\frac{C}{d_2}\int_{\Omega}m$. Therefore, $\mathrm{sign}(\lambda'(0))$ is the same as that of $[1-\frac{d_1}{d_2}]\int_{\Omega}\Phi_1^*m+\frac{C}{d_2}\int_{\Omega}m$.

Suppose that $\alpha(x)=k\beta(x)$ for some constant $k>0$. Then (Φ_1^*,Φ_2^*) is constant, in fact we can choose $(\Phi_1^*,\Phi_2^*)=c_0(1,k)$, and as a consequence, Proposition 2.5 gives the following result.

Proposition 2.6. *Assume that m changes sign and $\alpha(x)=k\beta(x)$ for some constant $k>0$. Then the following statements are valid*:

(i) *If $\int_{\Omega}m\geqslant 0$, then $\lambda_0>0$.*

(ii) *If $\int_{\Omega}m<0$, then there exists a unique positive $\mu^*>0$ such that* $\mathrm{sign}(1-\mu^*)=\mathrm{sign}(\lambda_0)$.

(This is analogous to the case of a single equation.) Clearly, by Propositions 2.3(d) and 2.4, if, for example, $\int_\Omega(m-\alpha)<0$ and $m-\alpha$ changes sign, when d_1 is small, $\lambda_0>0$. This suggests we could study the effects of diffusion rates on λ_0 in a more direct way.

Consider the eigenvalue problem with $d>0$ and $\mu>0$

$$L\Phi := d\mathcal{L}\Phi+\mu M(x)\Phi=\lambda\Phi \quad \text{in } \Omega, \quad \frac{\partial\Phi}{\partial n}=0 \quad \text{on } \partial\Omega, \tag{2.7}$$

where $\mathcal{L}\phi=\left(\begin{smallmatrix}\Delta & 0\\ 0 & d_0\Delta\end{smallmatrix}\right)\left(\begin{smallmatrix}\phi_1\\ \phi_2\end{smallmatrix}\right)$ with $\frac{\partial\phi_i}{\partial n}=0$, $i=1,2$, $d_0>0$ is given and

$$M(x)=\begin{pmatrix} m(x)-\alpha(x) & \beta(x)\\ \alpha(x) & m(x)-\beta(x)\end{pmatrix}.$$

We extend our notation to denote the principal eigenvalue of (2.7) as $\lambda(d,\mu M)$. Note that if $d_0=1$, the problem (2.7) can be reduced to the classical scalar eigenvalue problem $d\Delta\Phi+\mu m(x)\Phi=\lambda\Phi$, in other words, $\lambda(d,\mu M)=\lambda(d,\mu m)$. Below we only focus on $d_0>1$.

For each given $x\in\bar\Omega$, let $s(M(x))$ be the spectral bound of $M(x)$, which is the largest real eigenvalue due to the Perron-Frobenius theorem. Since $\lambda_1=m(x)$ and $\lambda_2=m(x)-\alpha(x)-\beta(x)$ are the two real eigenvalues of $M(x)$, it easily follows that $s(M(x))=m(x)$.

Proposition 2.7. *Assume that m changes sign and $\int_\Omega m<0$. Then when $d=1$, there exist finitely many values of $\mu>0$ such that $\lambda(1,\mu M)=0$.*

Proof. We first claim that when $d=1$, there exists $\mu_0(d_0)>0$, such that $\lambda(1,\mu)>0$ for any $\mu>\mu_0$. Note that $\lim_{d\to0}\lambda(d,M)=\max_{x\in\bar\Omega}s(M(x))=\max_{x\in\bar\Omega}m(x)>0$ (see, e.g., [9, 27]; related results on singularly perturbed competition systems are obtained in [29]). So there exists a small $\delta_0>0$ such that $\lambda(d,M)>0$ for $d\in(0,\delta_0)$. Now let $\mu_0=\frac{1}{\delta_0}>0$. It follows from $\lambda(1,\mu M)=\mu\lambda(\frac{1}{\mu},M)$ that $\lambda(1,\mu M)>0$ for any $\mu>\mu_0$.

Set $k_0=\frac{\int_\Omega\alpha}{\int_\Omega\beta}>0$. Let $f_1(\mu,\cdot)$ and $f_2(\mu,\cdot)$ be the eigenfunctions associated with $\lambda(1,\mu(m-\alpha+k_0\beta))$ and $\lambda(d_0,\mu(m-\beta+\frac{1}{k_0}\alpha))$, such that $f_1(0,\cdot)=1$ and $f_2(0,\cdot)=k_0$. Note that for any $D>0$, we have $\lambda(D,0)=0$. As in the derivation of (2.5) in the proof of Proposition 2.5, the eigenvalues $\lambda(1,\mu(m-\alpha+k_0\beta))$ and $\lambda(d_0,\mu(m-\beta+\frac{1}{k_0}\alpha))$ are differentiable with respect to μ. Differentiating with respect to μ, integrating over Ω, and letting $\mu\to0$, we obtain that

$$\frac{\partial\lambda(D,\mu(m-\alpha+k_0\beta))}{\partial\mu}(D,0)=\frac{\partial\lambda(D,\mu(m-\beta+\frac{1}{k_0}\alpha))}{\partial\mu}(D,0)=\frac{1}{|\Omega|}\int m:=A<0.$$

Our next goal is to show that if $\mu>0$ is sufficiently small, then there exists $\phi(\mu)=(\phi_1,\phi_2)$ such that $L\phi\ll0$. If such a ϕ exists, it will be a positive super solution of $L\phi=0$ with L as in (2.7), which then implies that $\lambda(1,\mu M)<0$. (This follows from the characterization of the strong maximum principle in [1, Theorem 13], which gives an extension of results of [30] to systems with general boundary conditions. The key results of [1, 30] are that for cooperative systems such as (2.7), three things are equivalent: the operator L has a strong maximum principle, the principal eigenvalue is negative, and there exists a strictly positive supersolution.)

Denote $\beta_{\max}=\max_{x\in\bar\Omega}\beta(x)$ and $\alpha_{\max}=\max_{x\in\bar\Omega}\alpha(x)$. For any sufficiently small $\epsilon>0$ satisfying $(A+\epsilon)(1-\epsilon)+(k_0+1)\beta_{\max}\epsilon<0$ and $(A+\epsilon)(k_0-\epsilon)+(\frac{1}{k_0}+1)\alpha_{\max}\epsilon<0$, there exists $\mu_0>0$, such that for any $0<\mu<\mu_0$, we have

$$\|f_1(\mu,\cdot)-1\|_\infty<\epsilon, \quad \|f_2(\mu,\cdot)-k_0\|_\infty<\epsilon$$

and

$$\left|\frac{\lambda(1,\mu(m-\alpha+k_0\beta))}{\mu}-A\right|<\epsilon, \quad \left|\frac{\lambda(d_0,\mu(m-\beta+\frac{1}{k_0}\beta))}{\mu}-A\right|<\epsilon.$$

Let $\phi(\mu)=(f_1(\mu),f_2(\mu))$. Then for $0<\mu<\mu_0$, we have

$$\Delta f_1+\mu(m-\alpha+k_0\beta)f_1+\mu(-k_0\beta f_1+\beta f_2)$$

$$
\begin{aligned}
&= \mu\bigg(\frac{\lambda(1,\mu(m-\alpha+k_0\beta))}{\mu}f_1 - k_0\beta f_1 + \beta f_2\bigg)\\
&< \mu[(A+\epsilon)(1-\epsilon) - k_0\beta(1-\epsilon) + \beta(k_0+\epsilon)]\\
&\leqslant \mu[(A+\epsilon)(1-\epsilon) + (k_0+1)\beta_{\max}\epsilon] < 0
\end{aligned}
$$

and

$$
\begin{aligned}
&d_0\Delta f_2 + \mu\bigg(m - \beta + \frac{1}{k_0}\alpha\bigg)f_2 + \mu\bigg(-\frac{\alpha}{k_0}f_2 + \alpha f_1\bigg)\\
&= \mu\bigg(\frac{\lambda(d_0,\mu(m-\beta+\frac{\alpha}{k_0}))}{\mu}f_2 - \frac{\alpha}{k_0}f_2 + \alpha f_1\bigg)\\
&< \mu\bigg[(A+\epsilon)(k_0-\epsilon) - \frac{\alpha}{k_0}(k_0-\epsilon) + \alpha(1+\epsilon)\bigg]\\
&\leqslant \mu\bigg[(A+\epsilon)(k_0-\epsilon) + \bigg(\frac{1}{k_0}+1\bigg)\alpha_{\max}\epsilon\bigg] < 0.
\end{aligned}
$$

So $L\phi \ll 0$, and hence, the characterization of the maximum principle in [1] implies that $\lambda(1,\mu M) < 0$ for any $0 < \mu < \mu_0$.

An alternative approach: Let $S_\mu(t)$ be the solution semigroup for $U_t = \mathcal{L}U + \mu M(x)U$ on $X := C(\bar{\Omega},\mathbb{R}^2)$. For every $\mu > 0$, $S_\mu(t)$ is compact and strongly positive for $t > 0$, in view of the Krein-Rutman theorem (see [21, Theorem 7.2] and [39, Theorem 7.6.1]), it follows that the spectral radius $r(S_\mu(t)) = \mathrm{e}^{\lambda(1,\mu M)t}$ for any $t > 0$. Clearly, for any given $0 < \mu < \mu_0$, $1\cdot\phi - S_\mu(t)\phi := h > 0$ in X for $t > 0$.

Now [21, Theorem 7.3] implies $1 > r(S_\mu(t)) = \mathrm{e}^{\lambda(1,\mu M)t}$ for every $t > 0$, and hence, $\lambda(1,\mu M) < 0$.

As a consequence, we see that equation $\lambda(1,\mu M) = 0$ admits at least one positive root. Indeed, the roots of $\lambda(1,\mu M) = 0$ are isolated due to the fact that λ is analytic in $\mu \in (0,\infty)$ (see, e.g., [30, Theorem 4.1] and [26]). Thus, there are a finite number of values of $\mu \in (0,\mu_0)$ such that $\lambda(1,\mu M) = 0$. (We cannot give conditions that guarantee there is a unique value of μ, as in the scalar case, because the key lemma derived for that purpose in [22] is not available for systems.) □

Lemma 2.8. *Assume that m changes sign. Let $d_0 = \frac{d_2}{d_1}$ be fixed and $d = d_1$ vary.*

(a) *If $\int_\Omega m < 0$, then there exists $0 < C_1 \leqslant C_2$ dependent on d_0 and M such that,*

(i) *if $d < C_1$, then $\lambda_0 > 0$;*

(ii) *if $d > C_2$, then $\lambda_0 < 0$;*

(iii) *there are a finite number of $d \in [C_1, C_2]$, such that $\lambda_0 = 0$.*

(b) *If $\int_\Omega m > 0$, then $\lambda_0 > 0$ provided d is either large or small.*

Proof. Statement (a) is a direct consequence of Proposition 2.7. The proof of Statement (b) is similar to that in Proposition 2.7. Indeed, we can construct $\psi(\mu) \gg 0$ such that $L\psi \gg 0$ when μ is sufficiently small. Moreover, $(-\psi) - S_\mu(t)(-\psi) =: h_1 > 0$ in X. Then [21, Theorem 7.3] again implies $1 < r(S_\mu(t)) = \mathrm{e}^{\lambda(1,\mu M)t}$, i.e., $\lambda(1,\mu M) > 0$ for μ sufficiently small. □

Because we are unable to show that there is a unique root of $\lambda(1,\mu M) = 0$ in Proposition 2.7, a sharper result for Statement (b) is not available that for arbitrary $d > 0$, $\lambda_0 > 0$. However when $d_1 = d_2$, the result is analogous to a scalar equation, and λ_0 depends continuously on d_1 and d_2. Therefore, a perturbation argument implies the following result.

Lemma 2.9. *Assume that m changes sign. Let $d = d_1$ be fixed and $d_0 = \frac{d_2}{d_1}$ vary.*

(a) *If $\int_\Omega m < 0$ and μ^* is defined in Proposition 2.3, then there exists a small $\delta(d_1) > 0$, such that for any $d_0 \in (1, 1+\delta)$,*

(i) *if $d_1 > \frac{1}{\mu^*}$, then $\lambda_0 < 0$;*

(ii) *if $d_1 < \frac{1}{\mu^*}$, then $\lambda_0 > 0$.*

(b) *If $\int_\Omega m \geqslant 0$, there exists a small $\delta(d_1) > 0$, such that for any $d_0 \in (1, 1+\delta)$, $\lambda_0 > 0$.*

Proof. (a) (i) When $d_0 = 1$, there exists $\mu^* > 0$ such that $\lambda_0 = \lambda(d_1, \mu m) < 0$ if and only if $d_1 > \frac{1}{\mu^*}$. Now for any given $d_1 > \frac{1}{\mu^*}$ and $d_0 = 1$, we have $\lambda_0 < 0$. Since λ_0 depends continuously on $d_0 > 0$, there exists some $\delta(d_1) > 0$, such that $\lambda_0 < 0$ for any $d_0 \in (1, 1 + \delta)$. Similarly, we can verify other cases. □

Now we have the following practical persistence result in terms of λ_0. Let $X_1 = C(\bar{\Omega}, \mathbb{R}^2)$ and $X_1^+ = C(\bar{\Omega}, \mathbb{R}^2_+)$.

Theorem 2.10. *Let $u(t, x, \phi)$ be the solution of (2.1) with $u(0, \cdot, \phi) = \phi \in X_1^+$.*

(i) *If $\lambda_0 \leqslant 0$, then 0 is globally attractive for any $\phi \in X_1^+$.*

(ii) *If $\lambda_0 > 0$, then the system (2.1) admits at least one positive steady state (U^*, V^*), and there exists an $\eta > 0$ such that for any $\phi \in X_1^+ \setminus \{0\}$, we have*

$$\liminf_{t\to\infty} u_i(t, x, \phi) \geqslant \eta, \quad \forall\, i = 1, 2.$$

Proof. (i) It is easy to see that for any $t > 0$,

$$\begin{aligned} \frac{\partial u_1}{\partial t} &\leqslant d_1 \Delta u_1 - \alpha(x) u_1 + \beta(x) u_2 + m(x) u_1, \\ \frac{\partial u_2}{\partial t} &\leqslant d_2 \Delta u_2 + \alpha(x) u_1 - \beta(x) u_2 + m(x) u_2. \end{aligned}$$

Therefore, for any $\phi \in X_1^+$, there exists a number $p > 0$, such that $\phi \leqslant p\psi$ where ψ is the positive eigenfunction associated with λ_0, and hence, the comparison principle (for the linearized system of (2.1)) implies $u(t, \cdot, \phi) \leqslant p e^{\lambda_0 t} \psi$ for any $t \geqslant 0$. If $\lambda_0 < 0$, let $t \to \infty$. Then the statement (i) follows for that case.

Suppose that $\lambda_0 = 0$. It follows from the Krein-Rutman theorem that the adjoint of the operator on the right-hand side of (2.3) has a principal eigenvalue equal to $\lambda_0 = 0$ with a positive eigenfunction. Let $\psi^* = (\psi_1^*, \psi_2^*)$ be a positive eigenfunction for the adjoint problem for (2.3). If we multiply the first equation in (2.1) by ψ_1^* and the second by ψ_2^* and then integrate over Ω and add the resulting equations, all the terms arising from the linear part of the right-hand side of (2.1) drop out and we obtain

$$\frac{d}{dt} \int_\Omega (\psi_1^* u + \psi_2^* v) = -\int_\Omega [\psi_1^* u(u + bv) + \psi_2^* v(cu + v)]. \tag{2.8}$$

Since ψ_1^* and ψ_2^* are positive and continuous on $\bar{\Omega}$, they are bounded above and below by positive constants so that $[\psi_1^* u(u + bv) + \psi_2^* v(cu + v)] \geqslant c_0 (\psi_1^* u + \psi_2^* v)^2$ for some positive constant c_0. It then follows from (2.8) and the Cauchy-Schwartz inequality that

$$\frac{d}{dt} \int_\Omega (\psi_1^* u + \psi_2^* v) \leqslant -c_0 \int_\Omega (\psi_1^* u + \psi_2^* v)^2 \leqslant -\frac{c_0}{|\Omega|} \left[\int_\Omega (\psi_1^* u + \psi_2^* v) \right]^2$$

so that

$$\int_\Omega (\psi_1^* u + \psi_2^* v) \to 0 \quad \text{as} \quad t \to \infty. \tag{2.9}$$

If $(0, 0)$ is not globally attractive, then for some solution (u, v) of (2.1) there must exist a constant $\epsilon > 0$ and a sequence $\{t_n\}$ with $t_n \to \infty$ as $n \to \infty$ such that $\|(u(t_n), v(t_n)\|_{X_1} > \epsilon$. All solutions of (2.1) in X_1^+ are bounded by Proposition 2.1. Standard results on the parabolic regularity and Sobolev embedding then imply that forward orbits are precompact in X_1, so there must be a subsequence of $\{(u(t_n), v(t_n))\}$ that converges in X_1. By re-indexing we can denote this subsequence as $(u(t_n), v(t_n))$, and then $(u(t_n), v(t_n)) \to (u^*, v^*)$ for some (u^*, v^*) as $n \to \infty$, with $\|(u(t_n), v(t_n))\|_{X_1} \geqslant \epsilon$ so that $(u^*, v^*) \neq (0, 0)$. For all sufficiently large n we must have $u(t_n) \geqslant u^*/2$ and $v(t_n) \geqslant v^*/2$ so that

$$\int_\Omega (\psi_1^* u(t_n) + \psi_2^* v(t_n)) \geqslant \frac{1}{2} \int_\Omega (\psi_1^* u* + \psi_2^* v*) > 0.$$

Since $t_n \to \infty$ as $n \to \infty$, this contradicts (2.9). To avoid a contradiction we must have $(0, 0)$ globally attractive.

(ii) Since $\lambda_0 > 0$, there exists small $\epsilon > 0$ such that the perturbed eigenvalue problem

$$\begin{cases} \lambda\phi_1 = d_1\Delta\phi_1 - \alpha(x)\phi_1 + \beta(x)\phi_2 + (m(x) - 2\epsilon)\phi_1 & \text{in } \Omega, \\ \lambda\phi_2 = d_2\Delta\phi_2 + \alpha(x)\phi_1 - \beta(x)\phi_2 + (m(x) - 2\epsilon)\phi_2 & \text{in } \Omega, \\ \dfrac{\partial\phi_1}{\partial n} = \dfrac{\partial\phi_2}{\partial n} = 0 & \text{on } \partial\Omega \end{cases} \tag{2.10}$$

admits a positive principal eigenvalue λ_0^ϵ with a positive eigenfunction ψ^ϵ.

Let $\mathbb{W} := \{\phi \in X_1^+ : \phi \not\equiv 0\}$ and $\partial\mathbb{W} := \{\phi \in X_1^+ : \phi \equiv 0\}$. Note that for any $\phi \in \mathbb{W}$, we have the solution $u(t,\cdot,\phi) \gg 0$ for any $t > 0$. We now prove the zero is a uniform weak repeller for $\mathbb{W}$ in the sense that there exists $\delta_0 > 0$ such that $\limsup_{t\to\infty} \|u(t,\cdot,\phi)\|_{X_1} \geqslant \delta_0$ for all $\phi \in \mathbb{W}$. Suppose, by contradiction, that $\limsup_{t\to\infty} \|u(t,\cdot,\phi_0)\|_{X_1} < \epsilon$ for some $\phi_0 \in \mathbb{W}$. Then there exists $t_1 > 0$ such that $u_1(t,\cdot,\phi_0) < \epsilon$ and $u_2(t,\cdot,\phi_0) < \epsilon$ for any $t \geqslant t_1$ satisfying

$$\begin{aligned} \frac{\partial u}{\partial t} &\geqslant d_1\Delta u - \alpha(x)u + \beta(x)v + u(m(x) - 2\epsilon), \\ \frac{\partial v}{\partial t} &\geqslant d_2\Delta v + \alpha(x)u - \beta(x)v + v(m(x) - 2\epsilon). \end{aligned}$$

Since $u(t_1,\cdot,\phi_0)$ is positive, there exists an $a > 0$ such that $u(t_1,\cdot,\phi_0) \geqslant a\phi^\epsilon$. Then the comparison principle implies that $u(t,\cdot,\phi_0) \geqslant a\mathrm{e}^{\lambda^\epsilon(t-t_1)}\psi^\epsilon$ for any $t \geqslant t_1$. It then follows that $u(t,\cdot,\phi_0)$ is unbounded, which is impossible.

The above argument shows that $W^s(\{0\}) \cap \mathbb{W} = \emptyset$ and $\{0\}$ is isolated in X_1^+, where $W^s(\{0\})$ is the stable set of $\{0\}$. Define $p(\phi) = \min_{1\leqslant i\leqslant 2}\{\min_{x\in\bar\Omega} \phi_i(x)\}$. It is easy to see that p is a generalized distance function for the semiflow: $Q_t : X_1^+ \to X_1^+$. The dissipativity and precompactness of forward orbits for (2.1) imply that the semi-dynamical system $Q_t(\phi) := u(t,\cdot,\phi)$ admits a compact global attractor on $\mathbb{W}$, and hence, it contains an equilibrium $(U^*, V^*) \in \mathbb{W}$. Moreover, it follows from [40, Theorem 3] that there exists an $\eta > 0$ such that $\min\{p(\psi) : \psi \in \omega(\phi)\} > \eta$ for any $\phi \in \mathbb{W}$. Therefore, for any $\phi \in \mathbb{W}$, we have

$$\liminf_{t\to\infty} u_i(t,x,\phi) \geqslant \eta, \quad \forall\, i = 1, 2.$$

This completes the proof. □

3 The system with small switching rates and positive $m(x)$

Throughout this section, we assume conditions in Proposition 2.2(1) hold and $bc \leqslant 1$. Roughly speaking, as long as positive β and α are very small, the requirements in Proposition 2.2(1) would be valid. We consider the submodel

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1\Delta u - \alpha u + \beta v + u(m(x) - u - bv) & \text{in } (0,\infty)\times\Omega, \\ \dfrac{\partial v}{\partial t} = d_2\Delta v + \alpha u - \beta v + v(m(x) - cu - v) & \text{in } (0,\infty)\times\Omega, \\ \dfrac{\partial u}{\partial n} = \dfrac{\partial v}{\partial n} = 0 & \text{on } (0,\infty)\times\partial\Omega, \\ u(0,x) = \phi_1(x), \quad v(0,x) = \phi_2(x) & \text{in } \Omega. \end{cases} \tag{3.1}$$

When $\alpha = \beta \equiv 0$, this is the model studied in [19]. Since $(0,0)$ is unstable due to the fact $m > 0$ on $\bar\Omega$, the existence of the positive steady state follows immediately from Theorem 2.10. By Proposition 2.2, we can show that every solution with positive initial data will eventually lie in the region $(\frac{\bar\beta}{b}, \bar m) \times (\frac{\bar\alpha}{c}, \bar m)$, where the system will be a competitive system. Thus we can apply ideas based on the theory of positive operators and monotone semi-dynamical systems with respect to the competitive ordering.

Proposition 3.1. *If a positive steady state (U, V) of (3.1) exists, it must be asymptotically stable.*

Proof. The essential idea is motivated by [19]. Linearizing the steady state problem of (3.1) at (U,V), we have

$$\begin{cases} \lambda\Phi_1 = d_1\Delta\Phi_1 + (m(x) - 2U - bV - \alpha)\Phi_1 + (\beta - bU)\Phi_2 & \text{in } \Omega, \\ \lambda\Phi_2 = d_2\Delta\Phi_2 + (\alpha - cV)\Phi_1 + (m(x) - cU - 2V - \beta)\Phi_2 & \text{in } \Omega, \\ \dfrac{\partial\Phi_1}{\partial n} = \dfrac{\partial\Phi_2}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{3.2}$$

By the Krein-Rutman theorem and the fact that $U(\cdot) > \frac{\bar{\beta}}{b}$ and $V(\cdot) > \frac{\bar{\alpha}}{c}$, the eigenvalue problem admits a principal eigenvalue λ_1, with the corresponding eigenfunction satisfying $\Phi_1^* > 0 > \Phi_2^*$ on $\bar{\Omega}$. By a straightforward calculation, using the equations satisfied by U and Φ_1^* (multiply U-equation by Φ_1^* and Φ_1^*-equation by U, and then do the subtraction) and the identity

$$(\Delta U)\Phi_1^* - U(\Delta\Phi_1^*) = \nabla\cdot[(\nabla U)\Phi_1^* - (\nabla\Phi_1^*)U],$$

we obtain that

$$-\lambda_1\Phi_1^*U = -d_1\nabla\cdot\left(U^2\nabla\frac{\Phi_1^*}{U}\right) + U^2(\Phi_1^* + b\Phi_2^*) + \beta(V\Phi_1^* - U\Phi_2^*). \tag{3.3}$$

Similarly, we have

$$-\lambda_1\Phi_2^*V = -d_2\nabla\cdot\left(V^2\nabla\frac{\Phi_2^*}{V}\right) + V^2(c\Phi_1^* + \Phi_2^*) + \alpha(U\Phi_2^* - V\Phi_1^*).$$

Multiplying both sides of (3.3) by $\frac{\Phi_1^{*2}}{U^2}$ and integrating over Ω, we see that

$$-\lambda_1\int_\Omega\frac{\Phi_1^{*3}}{U} = 2d_1\int_\Omega U\Phi_1^*\left|\nabla\frac{\Phi_1^*}{U}\right|^2 + \int_\Omega\Phi_1^{*2}(\Phi_1^* + b\Phi_2^*) + \int_\Omega\beta(V\Phi_1^* - U\Phi_2^*)\frac{\Phi_1^{*2}}{U^2}. \tag{3.4}$$

Likewise, we get

$$-\lambda_1\int_\Omega\frac{\Phi_2^{*3}}{V} = 2d_2\int_\Omega V\Phi_2^*\left|\nabla\frac{\Phi_2^*}{V}\right|^2 + \int_\Omega\Phi_2^{*2}(c\Phi_1^* + \Phi_2^*) + \int_\Omega\alpha(U\Phi_2^* - V\Phi_1^*)\frac{\Phi_2^{*2}}{V^2}. \tag{3.5}$$

Subtract (3.5) from the product of c^3 and (3.4). Then together with the fact that $bc \leqslant 1$ and $\Phi_2^* < 0$, we obtain

$$\begin{aligned} -\lambda_1\left(c^3\int_\Omega\frac{\Phi_1^{*3}}{U} - \int_\Omega\frac{\Phi_2^{*3}}{V}\right) \geqslant{}& 2c^3d_1\int_\Omega U\Phi_1^*\left|\nabla\frac{\Phi_1^*}{U}\right|^2 - 2d_2\int_\Omega V\Phi_2^*\left|\nabla\frac{\Phi_2^*}{V}\right|^2 \\ &+ \int_\Omega(c\Phi_1^* + \Phi_2^*)^2(c\Phi_1^* - \Phi_2^*) \\ &+ \int_\Omega(V\Phi_1^* - U\Phi_2^*)\left(c^3\beta\frac{\Phi_1^{*2}}{U^2} + \alpha\frac{\Phi_2^{*2}}{V^2}\right). \end{aligned} \tag{3.6}$$

It follows immediately from $\Phi_2^* < 0$ and $V\Phi_1^* - U\Phi_2^* > 0$ that the right-hand side of (3.6) is greater than zero, and hence, $\lambda_1 < 0$. Now it follows immediately from [39, Theorem 7.6.2] that linearly stable ($\lambda_1 < 0$) implies asymptotically stable. □

The following result is a direct consequence of Theorem 2.10, Proposition 3.1 and monotone dynamical systems approach (see, e.g., [21, Theorem 9.2]).

Theorem 3.2. *If the conditions of Proposition* 2.2(1) *are satisfied and* $bc \leqslant 1$*, then the system* (3.1) *admits a unique positive steady state* (U^*, V^*)*, which is globally asymptotically stable in* $X_1^+ \setminus \{0\}$*.*

4 The cooperative-cooperative-competition system

In this section, we consider one species having two different kinds of movements that competes with another ecologically identical species having only one movement mode. Now consider the system

$$\begin{cases}\dfrac{\partial u}{\partial t}=d_1\Delta u-\alpha u+\beta v+u(m(x)-u-v-w) & \text{in } (0,\infty)\times\Omega,\\ \dfrac{\partial v}{\partial t}=d_2\Delta v+\alpha u-\beta v+v(m(x)-u-v-w) & \text{in } (0,\infty)\times\Omega,\\ \dfrac{\partial w}{\partial t}=d_3\Delta w+w(m(x)-u-v-w) & \text{in } (0,\infty)\times\Omega,\\ \dfrac{\partial u}{\partial n}=\dfrac{\partial v}{\partial n}=\dfrac{\partial w}{\partial n}=0 & \text{on } (0,\infty)\times\partial\Omega,\\ u(0,x)=\phi_1(x),\quad v(0,x)=\phi_2(x),\quad w(0,x)=\phi_3(x) & \text{in } \Omega.\end{cases}\tag{4.1}$$

Here, $d_1<d_2$, d_3, α and β are positive numbers. Throughout this section, we impose the following assumption.

(H) m is non-constant, $\int_\Omega m\geqslant 0$ and $0<\max_{\bar\Omega}m(x)<\alpha+\beta$.

By (H) and Proposition 2.2, one can show that the subsystem

$$\begin{cases}\dfrac{\partial u}{\partial t}=d_1\Delta u-\alpha u+\beta v+u(m(x)-u-v) & \text{in } (0,\infty)\times\Omega,\\ \dfrac{\partial v}{\partial t}=d_2\Delta v+\alpha u-\beta v+v(m(x)-u-v) & \text{in } (0,\infty)\times\Omega,\\ \dfrac{\partial u}{\partial n}=\dfrac{\partial v}{\partial n}=0 & \text{on } (0,\infty)\times\partial\Omega,\\ u(0,x)=\phi_1(x),\quad v(0,x)=\phi_2(x) & \text{in } \Omega\end{cases}\tag{4.2}$$

is cooperative, irreducible and sub-homogeneous in a contracting rectangular region $[0,\beta]\times[0,\alpha]$ which attracts all positive trajectories. The approach of monotone dynamical systems, along with Proposition 2.6, implies the system (4.2) admits a globally attractively positive steady state (u^*,v^*) (see [6] for related results in the constant coefficient case).

Because the dynamics of the first two components move the system (4.2) into a region where they satisfy a cooperative system, we can treat the model (4.1) as a monotone system with respect to the ordering $(u_1,v_1,w_1)\geqslant(u_2,v_2,w_2)\Leftrightarrow u_1\geqslant u_2, v_1\geqslant v_2, w_1\leqslant w_2$. Systems of ordinary differential equations with this type of order structure are treated in [37] (see also the discussion of alternate cones in [38]). The ideas extend directly to reaction-diffusion systems via the maximum principle.

Also, the classic result on logistic-type reaction-diffusion equations shows that

$$\begin{cases}\dfrac{\partial w}{\partial t}=d_3\Delta w+w(m(x)-w) & \text{in } (0,\infty)\times\Omega,\\ \dfrac{\partial w}{\partial n}=0 & \text{on } (0,\infty)\times\partial\Omega,\\ w(0,x)=\phi(x) & \text{in } \Omega\end{cases}\tag{4.3}$$

admits a globally attractively positive steady state $w^*(\cdot)$.

The following observation is based on the strong maximum principle.

Proposition 4.1. *Assume that* (H) *holds. Then the nontrivial nonnegative steady states of the system* (4.1) *are* $(u^*,v^*,0)$, $(0,0,w^*)$ *plus any positive steady states that exist.*

Next, we investigate the effects of diffusion rate d_3 on the local stability of $(u^*,v^*,0)$ and $(0,0,w^*)$, i.e., we fix the other parameters and let d_3 vary.

Lemma 4.2. *There exists* $d_c\in(d_1,\frac{\beta}{\alpha+\beta}d_1+\frac{\alpha}{\alpha+\beta}d_2)$, *such that* $(u^*,v^*,0)$ *is linearly unstable when* $d_3<d_c$ *and* $(u^*,v^*,0)$ *is linearly stable when* $d_3>d_c$.

Proof. To investigate the local stability of $(u^*, v^*, 0)$, we consider the eigenvalue problem

$$\begin{cases} \lambda\phi_1 = d_1\Delta\phi_1 + (m(x) - 2u^* - v^* - \alpha)\phi_1 + (\beta - u^*)\phi_2 - u^*\phi_3 & \text{in } \Omega, \\ \lambda\phi_2 = d_2\Delta\phi_2 + (\alpha - v^*)\phi_1 + (m(x) - u^* - 2v^* - \beta)\phi_2 - v^*\phi_3 & \text{in } \Omega, \\ \lambda\phi_3 = d_3\Delta\phi_3 + (m(x) - u^* - v^*)\phi_3 & \text{in } \Omega, \\ \dfrac{\partial\phi_1}{\partial n} = \dfrac{\partial\phi_2}{\partial n} = \dfrac{\partial\phi_3}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.4}$$

In view of Proposition 2.2(2), we have $u^* < \beta$ and $v^* < \alpha$, so this eigenvalue problem admits a principal eigenvalue which exactly is $\lambda(d_3, m - u^* - v^*)$ defined in Proposition 2.3. Since m is non-constant, it follows that (u^*, v^*) is a non-constant steady state (i.e., u^* and v^* are not both constant). Moreover, $m - u^* - v^*$ is also non-constant. Otherwise, suppose $m - u^* - v^* \equiv K$. Then adding the equations for the equilibria of (4.2) together and integrating, we get $K\int_\Omega [u^* + v^*] = 0$, and hence, $K = 0$. It follows that 0 is the principal eigenvalue of

$$\begin{cases} \lambda\phi_1 = d_1\Delta\phi_1 - \alpha\phi_1 + \beta\phi_2 & \text{in } \Omega, \\ \lambda\phi_1 = d_2\Delta\phi_2 + \alpha\phi_1 - \beta\phi_2 & \text{in } \Omega, \\ \dfrac{\partial\phi_1}{\partial n} = \dfrac{\partial\phi_2}{\partial n} = 0 & \text{on } \partial\Omega \end{cases}$$

associated with the positive eigenfunction (u^*, v^*). Note that (β, α) is another positive eigenfunction associated with the principal eigenvalue 0, and hence, $(u^*, v^*)^{\mathrm{T}} \in \mathrm{Span}\{(\beta, \alpha)^{\mathrm{T}}\}$, which is impossible.

Observe that $(u^*, v^*, 0)$ is independent of d_3. Then $\lambda(d_3, m - u^* - v^*)$ is continuous and strictly decreasing in d_3, i.e., it changes sign at most once.

Claim 1. $\lambda(d_3, m - u^* - v^*) > 0$ when $d_3 = d_1$.

Suppose by contradiction, $\lambda(d_1, m - u^* - v^*) \leqslant 0$. Note that the non-constant steady state (u^*, v^*) satisfies

$$\begin{cases} 0 = d_1\Delta u^* - \alpha u^* + \beta v^* + u^*(m(x) - u^* - v^*) & \text{in } \Omega, \\ 0 = d_2\Delta v^* + \alpha u^* - \beta v^* + v^*(m(x) - u^* - v^*) & \text{in } \Omega, \\ \dfrac{\partial u^*}{\partial n} = \dfrac{\partial v^*}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.5}$$

Multiplying the first and second equations by αu^* and βv^*, respectively, and then integrating over Ω and adding together, we see that

$$\begin{aligned} &\alpha\bigg[-d_1\int_\Omega |\nabla u^*|^2 + \int_\Omega (m - u^* - v^*)u^{*2}\bigg] + \beta\bigg[-d_2\int_\Omega |\nabla v^*|^2 + \int_\Omega (m - u^* - v^*)v^{*2}\bigg] \\ &\quad = \int_\Omega (\alpha u^* - \beta v^*)^2 \geqslant 0. \end{aligned} \tag{4.6}$$

Since $d_1 < d_2$, $\lambda(d_2, m^* - u^* - v^*) < \lambda(d_1, m^* - u^* - v^*) \leqslant 0$, and it follows from the variational formula for the principal eigenvalue $\lambda(d, m)$ that $-d_1\int_\Omega |\nabla u^*|^2 + \int_\Omega (m - u^* - v^*)u^{*2} \leqslant 0$ and $-d_2\int_\Omega |\nabla v^*|^2 + \int_\Omega (m - u^* - v^*)v^{*2} < 0$, in contradiction to (4.6).

Claim 2. $\lambda(d_3, m^* - u^* - v^*) < 0$ when $d_3 = \frac{\beta}{\alpha+\beta}d_1 + \frac{\alpha}{\alpha+\beta}d_2$.

By way of contradiction, assume that $\lambda(d_3^0, m - u^* - v^*) \geqslant 0$ where $d_3^0 = \frac{\beta}{\alpha+\beta}d_1 + \frac{\alpha}{\alpha+\beta}d_2$. Let ϕ^* be the positive eigenfunction associated with $\lambda(d_3^0, m - u^* - v^*)$; clearly, it is non-constant.

Let

$$L\begin{pmatrix}\phi_1 \\ \phi_2\end{pmatrix} = \begin{pmatrix} \alpha d_1\Delta\phi_1 + [(m - u^* - v^*)\alpha - \alpha^2]\phi_1 + \alpha\beta\phi_2 \\ \beta d_2\Delta\phi_2 + \alpha\beta\phi_1 + [(m - u^* - v^*)\beta - \beta^2]\phi_2 \end{pmatrix}.$$

Then L is a self-adjoint operator. The principal eigenvalue of L is 0 with (u^*, v^*) being the associated eigenfunction, and we have the variational formula for the principal eigenvalue of L:

$$0 = \lambda(L) = \sup_{(\phi_1,\phi_2)\in H^1(\Omega,\mathbb{R}^2)\setminus\{0\}} \bigg\{ \frac{\alpha[-d_1\int_\Omega |\nabla\phi_1|^2 + \int_\Omega (m - u^* - v^*)\phi_1^2]}{\int_\Omega (\phi_1^2 + \phi_2^2)}$$

$$+\frac{\beta[-d_2\int_\Omega|\nabla\phi_2|^2+\int_\Omega(m-u^*-v^*)\phi_2^2]}{\int_\Omega(\phi_1^2+\phi_2^2)}-\frac{\int_\Omega(\alpha\phi_1-\beta\phi_2)^2}{\int_\Omega(\phi_1^2+\phi_2^2)}\bigg\}.$$

Choose test functions $\phi_1=\frac{\phi^*}{\alpha}$ and $\phi_2=\frac{\phi^*}{\beta}$. It then follows that

$$\frac{-d_1\int_\Omega|\nabla\phi^*|^2+\int_\Omega(m-u^*-v^*)\phi^{*2}}{\alpha}+\frac{-d_2\int_\Omega|\nabla\phi^*|^2+\int_\Omega(m-u^*-v^*)\phi^{*2}}{\beta}<0. \tag{4.7}$$

The above strict inequality is due to the fact that $\alpha u^*-\beta v^*$ is not identically to zero and hence $(\phi_1,\phi_2)\neq(u^*,v^*)$. (If $\alpha u^*-\beta v^*\equiv 0$, it then follows that $\lambda(d_1,m-u^*-v^*)=\lambda(d_2,m-u^*-v^*)=0$ with $d_1<d_2$, which leads to a contradiction.)

Since we assumed $-d_3^0\int_\Omega|\nabla\phi^*|^2+\int_\Omega(m-u^*-v^*)\phi^{*2}\geqslant 0$, we have

$$\begin{aligned}&\left(\frac{d_3^0-d_1}{\alpha}+\frac{d_3^0-d_2}{\beta}\right)\int_\Omega|\nabla\phi^*|^2\\&\leqslant\frac{-d_1\int_\Omega|\nabla\phi^*|^2+\int_\Omega(m-u^*-v^*)\phi^{*2}}{\alpha}+\frac{-d_2\int_\Omega|\nabla\phi^*|^2+\int_\Omega(m-u^*-v^*)\phi^{*2}}{\beta}<0.\end{aligned} \tag{4.8}$$

This implies $d_3^0<\frac{\beta}{\alpha+\beta}d_1+\frac{\alpha}{\alpha+\beta}d_2$, which leads to a contradiction.

From the above discussion, we see that given d_1,d_2,α,β, there exists a unique $d_c\in(d_1,\frac{\beta}{\alpha+\beta}d_1+\frac{\alpha}{\alpha+\beta}d_2)$, such that $\lambda(d_c,m-u^*-v^*)=0$. When $d_3<d_c$, $(u^*,v^*,0)$ is linearly unstable, while $d_3>d_c$, $(u^*,v^*,0)$ is linearly stable. □

Likewise, we check the local stability of $(0,0,w^*)$. The associated eigenvalue problem is

$$\begin{cases}\lambda\phi_1=d_1\Delta\phi_1+(m(x)-w^*-\alpha)\phi_1+\beta\phi_2 & \text{in }\Omega,\\ \lambda\phi_2=d_2\Delta\phi_2+\alpha\phi_1+(m(x)-\beta-w^*)\phi_2 & \text{in }\Omega,\\ \lambda\phi_3=d_3\Delta\phi_3-w^*\phi_1-w^*\phi_2+(m(x)-2w^*)\phi_3 & \text{in }\Omega,\\ \dfrac{\partial\phi_1}{\partial n}=\dfrac{\partial\phi_2}{\partial n}=\dfrac{\partial\phi_3}{\partial n}=0 & \text{on }\partial\Omega.\end{cases} \tag{4.9}$$

The principal eigenvalue λ_2 of (4.9) is determined by the sub-eigenvalue problem

$$\begin{cases}\lambda\phi_1=d_1\Delta\phi_1+(m(x)-w^*-\alpha)\phi_1+\beta\phi_2 & \text{in }\Omega,\\ \lambda\phi_2=d_2\Delta\phi_2+\alpha\phi_1+(m(x)-\beta-w^*)\phi_2 & \text{in }\Omega,\\ \dfrac{\partial\phi_1}{\partial n}=\dfrac{\partial\phi_2}{\partial n}=0 & \text{on }\partial\Omega.\end{cases} \tag{4.10}$$

This eigenvalue problem is equivalent to the weighted eigenvalue problem

$$\begin{cases}\lambda\alpha\phi_1=d_1\alpha\Delta\phi_1+(m(x)-w^*-\alpha)\alpha\phi_1+\alpha\beta\phi_2 & \text{in }\Omega,\\ \lambda\beta\phi_2=d_2\beta\Delta\phi_2+\alpha\beta\phi_1+(m(x)-\beta-w^*)\beta\phi_2 & \text{in }\Omega,\\ \dfrac{\partial\phi_1}{\partial n}=\dfrac{\partial\phi_2}{\partial n}=0 & \text{on }\partial\Omega.\end{cases} \tag{4.11}$$

The eigenvalue problem (4.11) is self-adjoint, so it admits a variational characterization, from which it is easy to see that λ_2 depends continuously on w^*. General properties of solutions to diffusive logistic equations imply that w^* depends smoothly on $d_3>0$ (see, for example, [4]). This implies λ_2 depends continuously on $d_3>0$. Now we have the following result.

Lemma 4.3. *Assume that* (H) *holds. If $d_3\leqslant d_1$, then $\lambda_2(d_3)<0$, i.e., $(0,0,w^*)$ is linearly stable. If $d_3\geqslant\frac{\beta}{\alpha+\beta}d_1+\frac{\alpha}{\alpha+\beta}d_2$, then $\lambda_2(d_3)>0$, i.e., $(0,0,w^*)$ is linearly unstable. Moreover, there exists $d_0\in(d_1,\frac{\beta}{\alpha+\beta}d_1+\frac{\alpha}{\alpha+\beta}d_2)$, such that $\lambda_2(d_0)=0$.*

Proof. Let (ϕ_1, ϕ_2) be the positive eigenfunction associated with λ_2. Then multiplying the first and second equations of (4.10) by $\alpha\phi_1$ and $\beta\phi_2$, respectively, and then integrating over Ω, we see that

$$\begin{aligned}\alpha&\bigg[-d_1\int_\Omega|\nabla\phi_1|^2+\int_\Omega(m-w^*)\phi_1^2\bigg]+\beta\bigg[-d_2\int_\Omega|\nabla\phi_2|^2+\int_\Omega(m-w^*)\phi_2^2\bigg]\\&=\int_\Omega(\alpha\phi_1-\beta\phi_2)^2+\lambda_2\int_\Omega(\alpha\phi_1^2+\beta\phi_2^2).\end{aligned}\tag{4.12}$$

In the case where $d_3 \leqslant d_1$, we claim that $\lambda_2 < 0$. Otherwise, there exists some $\tilde{d}_3 \leqslant d_1$ such that $\lambda_2 \geqslant 0$. It then follows from (4.12) that for $w^* = w^*(\tilde{d}_3)$,

$$\alpha\bigg[-d_1\int_\Omega|\nabla\phi_1|^2+\int_\Omega(m-w^*)\phi_1^2\bigg]+\beta\bigg[-d_2\int_\Omega|\nabla\phi_2|^2+\int_\Omega(m-w^*)\phi_2^2\bigg]\geqslant 0.$$

However, the fact $\lambda(\tilde{d}_3, m-w^*) = 0$ and $\tilde{d}_3 \leqslant d_1 < d_2$ implies that $\lambda(d_2, m-w^*) < \lambda(d_1, m-w^*) \leqslant 0$, and hence $-d_1\int_\Omega|\nabla\phi_1|^2+\int_\Omega(m-w^*)\phi_1^2 \leqslant 0$ and $-d_2\int_\Omega|\nabla\phi_2|^2+\int_\Omega(m-w^*)\phi_2^2 < 0$, which leads to a contradiction.

Suppose there exists some $d_3 \geqslant \frac{\beta}{\alpha+\beta}d_1 + \frac{\alpha}{\alpha+\beta}d_2$ such that $\lambda_2 \leqslant 0$. Adapting the previous analysis to (4.10) by writing down the variational formula arising from (4.11), we have

$$\begin{aligned}0\geqslant\lambda_2=\sup_{(\phi_1,\phi_2)\in H^1(\Omega,\mathbb{R}^2)\setminus\{0\}}&\bigg\{\frac{\alpha[-d_1\int_\Omega|\nabla\phi_1|^2+\int_\Omega(m-w^*)\phi_1^2]}{\int_\Omega(\alpha\phi_1^2+\beta\phi_2^2)}\\&+\frac{\beta[-d_2\int_\Omega|\nabla\phi_2|^2+\int_\Omega(m-w^*)\phi_2^2]}{\int_\Omega(\alpha\phi_1^2+\beta\phi_2^2)}-\frac{\int_\Omega(\alpha\phi_1-\beta\phi_2)^2}{\int_\Omega(\alpha\phi_1^2+\beta\phi_2^2)}\bigg\}.\end{aligned}$$

Choose test functions $\phi_1 = \frac{w^*}{\alpha}$ and $\phi_2 = \frac{w^*}{\beta}$. If $(\frac{w^*}{\alpha}, \frac{w^*}{\beta})$ were an eigenfunction for (4.11), we could substitute into the two equations in (4.11) and subtract to see that w^* would satisfy $(d_2 - d_1)\Delta w^* = 0$ with Neumann boundary conditions and hence would be constant, but w^* cannot be constant, so $(\frac{w^*}{\alpha}, \frac{w^*}{\beta})$ cannot be an eigenfunction for (4.11). Thus it follows that

$$\frac{-d_1\int_\Omega|\nabla w^*|^2+\int_\Omega(m-w^*)w^{*2}}{\alpha}+\frac{-d_2\int_\Omega|\nabla w^*|^2+\int_\Omega(m-w^*)w^{*2}}{\beta}<0.$$

Since $-d_3\int_\Omega|\nabla w^*|^2+\int_\Omega(m-w^*)w^{*2}=0$, we have

$$\begin{aligned}&\bigg(\frac{d_3-d_1}{\alpha}+\frac{d_3-d_2}{\beta}\bigg)\int_\Omega|\nabla w^*|^2\\&\leqslant\frac{-d_1\int_\Omega|\nabla w^*|^2+\int_\Omega(m-w^*)w^{*2}}{\alpha}+\frac{-d_2\int_\Omega|\nabla w^*|^2+\int_\Omega(m-w^*)\phi^{*2}}{\beta}<0.\end{aligned}\tag{4.13}$$

This implies $d_3 < \frac{\beta}{\alpha+\beta}d_1 + \frac{\alpha}{\alpha+\beta}d_2$, which leads to a contradiction.

Since λ_2 depends continuously on d_0, there exists some $d_0 \in (d_1, \frac{\beta}{\alpha+\beta}d_1 + \frac{\alpha}{\alpha+\beta}d_2)$ such that $\lambda_2(d_0) = 0$. □

Remark 4.4. Here, we are unable to show that there exists a unique $d_3 > 0$ such that $\lambda_2(d_3) = 0$.

Next, we make an observation on the nonexistence of positive steady states of (4.1).

Lemma 4.5. *There exists a sufficiently small $\epsilon > 0$ such that the system* (4.1) *admits no positive steady state* (*i.e., no coexistence state*) *when* $d_3 \in (0, d_1+\epsilon) \cup (\frac{\beta}{\alpha+\beta}d_1 + \frac{\alpha}{\alpha+\beta}d_2 - \epsilon, \infty)$.

Proof. First, we prove that when $d_3 \leqslant d_1$ and $d_3 \geqslant \frac{\beta}{\alpha+\beta}d_1 + \frac{\alpha}{\alpha+\beta}d_2$, there is no positive steady state. The essential idea is similar to those in Lemmas 3.2 and 3.3. Suppose that, by contradiction, (u_0, v_0, w_0) is a positive steady state of (4.1). Then

$$\begin{cases}0=d_1\Delta u_0-\alpha u_0+\beta v_0+u_0(m(x)-u_0-v_0-w_0) & \text{in } \Omega,\\0=d_2\Delta v_0+\alpha u_0-\beta v_0+v_0(m(x)-u_0-v_0-w_0) & \text{in } \Omega,\\0=d_3\Delta w_0+w_0(m(x)-u_0-v_0-w_0) & \text{in } \Omega,\\\frac{\partial u_0}{\partial n}=\frac{\partial v_0}{\partial n}=\frac{\partial w_0}{\partial n}=0 & \text{on } \partial\Omega.\end{cases}\tag{4.14}$$

Note that $m - u_0 - w_0 - w_0$ is non-constant. Otherwise, as before, we can show u_0 and v_0 have to be constant. This implies m is constant, impossible.

Consider the case where $d_3 \leqslant d_1 < d_2$. Multiplying the first and second equations by αu_0 and βv_0, respectively, and then integrating over Ω, we see that

$$\begin{aligned}
&\alpha\bigg[-d_1\int_\Omega|\nabla u_0|^2+\int_\Omega(m-u_0-v_0-w_0)u_0^2\bigg]+\beta\bigg[-d_2\int_\Omega|\nabla v_0|^2+\int_\Omega(m-u_0-v_0-w_0)v_0^2\bigg]\\
&\quad=\int_\Omega(\alpha u_0-\beta v_0)^2\geqslant 0.
\end{aligned}\tag{4.15}$$

Since $0=\lambda(d_3,m-u_0-v_0-w_0)\geqslant\lambda(d_1,m-u_0-v_0-w_0)>\lambda(d_2,m-u_0-v_0-w_0)$, the variational formula of the principal eigenvalue implies that $-d_1\int_\Omega|\nabla u_0|^2+\int_\Omega(m-u_0-v_0-w_0)u_0^2\leqslant 0$ and $-d_2\int_\Omega|\nabla v_0|^2$ $+\int_\Omega(m-u_0-v_0-w_0)v_0^2<0$, which leads to a contradiction.

In the case where $d_3\geqslant\frac{\beta}{\alpha+\beta}d_1+\frac{\alpha}{\alpha+\beta}d_2$, let

$$L\begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix}=\begin{pmatrix}\alpha d_1\Delta\phi_1+[(m-u_0-v_0-w_0)\alpha-\alpha^2]\phi_1+\alpha\beta\phi_2\\ \beta d_2\Delta\phi_2+\alpha\beta\phi_1+[(m-u_0-v_0-w_0)\beta-\beta^2]\phi_2\end{pmatrix}.$$

Then L is a self-adjoint operator. The principal eigenvalue of L is 0, and we have the variational formula for the principal eigenvalue of L:

$$\begin{aligned}
\lambda(L)=\sup_{(\phi_1,\phi_2)H^1(\Omega,\mathbb{R}^2)\setminus\{0\}}&\bigg\{\frac{\alpha[-d_1\int_\Omega|\nabla\phi_1|^2+\int_\Omega(m-u_0-v_0-w_0)\phi_1^2]}{\int_\Omega(\phi_1^2+\phi_2^2)}\\
&+\frac{\beta[-d_2\int_\Omega|\nabla\phi_2|^2+\int_\Omega(m-u_0-v_0-w_0)\phi_2^2]}{\int_\Omega(\phi_1^2+\phi_2^2)}-\frac{\int_\Omega(\alpha\phi_1-\beta\phi_2)^2}{\int_\Omega(\phi_1^2+\phi_2^2)}\bigg\}.
\end{aligned}$$

Now let $\phi_1=\frac{w_0}{\alpha}$ and $\phi_2=\frac{w_0}{\beta}$. It follows that

$$\frac{-d_1\int_\Omega|\nabla w_0|^2+\int_\Omega(m-u_0-v_0-w_0)w_0^2}{\alpha}+\frac{-d_2\int_\Omega|\nabla w_0|^2+\int_\Omega(m-u_0-v_0-w_0)w_0^2}{\beta}$$

is negative. Since $-d_3\int_\Omega|\nabla w_0|^2+\int_\Omega(m-u_0-v_0-w_0)w_0^2=0$, it follows that $(\frac{d_3-d_1}{\alpha}+\frac{d_3-d_2}{\beta})\int_\Omega|\nabla w_0|^2$ <0. This yields that $d_3<\frac{\beta}{\alpha+\beta}d_1+\frac{\alpha}{\alpha+\beta}d_2$, which leads to a contradiction.

Motivated by [5], now we suppose that when $d_3\to d_1^+$, there exists a sequence of positive steady states, denoted by $(u^{d_3},v^{d_3},w^{d_3})$. By standard elliptic estimates, passing to a subsequence if necessary, we may assume that $(u^{d_3},v^{d_3},w^{d_3})\to(u_0,v_0,w_0)$ in $C^2(\bar\Omega)$ as $d_3\to d_1^+$ satisfying

$$\begin{cases}
0=d_1\Delta u_0-\alpha u_0+\beta v_0+u_0(m(x)-u_0-v_0-w_0) & \text{in } \Omega,\\
0=d_2\Delta v_0+\alpha u_0-\beta v_0+v_0(m(x)-u_0-v_0-w_0) & \text{in } \Omega,\\
0=d_1\Delta w_0+w_0(m(x)-u_0-v_0-w_0) & \text{in } \Omega,\\
\dfrac{\partial u_0}{\partial n}=\dfrac{\partial v_0}{\partial n}=\dfrac{\partial w_0}{\partial n}=0 & \text{on } \partial\Omega.
\end{cases}\tag{4.16}$$

It follows immediately from the previous analysis that when $d_3=d_1$ the non-negative steady state (u_0,v_0,w_0) cannot be component-wise positive.

Suppose that $(u_0,v_0,w_0)\equiv(0,0,0)$ and let

$$(\hat u^{d_3},\hat v^{d_3},\hat w^{d_3})=\bigg(\frac{u^{d_3}}{\|u^{d_3}\|_{L^\infty}+\|v^{d_3}\|_{L^\infty}},\frac{v^{d_3}}{\|u^{d_3}\|_{L^\infty}+\|v^{d_3}\|_{L^\infty}},\frac{w^{d_3}}{\|w^{d_3}\|_{L^\infty}}\bigg).$$

Divide the first two equations and the third equation of (4.16) by $\|u^{d_3}\|_{L^\infty}+\|v^{d_3}\|_{L^\infty}$ and $\|w^{d_3}\|_{L^\infty}$, respectively. Then using the elliptic estimates again, we may assume that $(\hat u^{d_3},\hat v^{d_3},\hat w^{d_3})\to(\hat u_0,\hat v_0,\hat w_0)$

in $C^2(\bar{\Omega})$ as $d_3 \to d_1^+$ satisfying

$$\begin{aligned} &0 = d_1\Delta\hat{u}_0 + \hat{u}_0(m(x)-\alpha) + \beta\hat{v}_0 && \text{in } \Omega,\\ &0 = d_2\Delta\hat{v}_0 + \alpha\hat{u}_0 + \hat{v}_0(m(x)-\beta) && \text{in } \Omega,\\ &0 = d_1\Delta\hat{w}_0 + \hat{w}_0 m(x) && \text{in } \Omega,\\ &\frac{\partial\hat{u}_0}{\partial n} = \frac{\partial\hat{v}_0}{\partial n} = \frac{\partial\hat{w}_0}{\partial n} = 0 && \text{on } \partial\Omega. \end{aligned} \tag{4.17}$$

The third equation in (4.17) implies that either $\int m < 0$ or $\hat{w}_0 \equiv 0$, which contradicts (H) or $\|\hat{w}_0\|_{L^\infty} = 1$. Thus (u_0, v_0, w_0) cannot be compnentwise-positive or have all components zero. Now if non-zero (u_0, v_0, w_0) has at least one component that is identically to zero, then (u_0, v_0, w_0) must be either $(u^*, v^*, 0)$ or $(0, 0, w^*_{d_1})$ in view of Proposition 4.1.

If the former case occurs, we have $0 = d_1\Delta\hat{w}_0 + \hat{w}_0(m(x) - u^* - v^*)$ with the zero Neumann boundary condition, where $\hat{w}_0$ is the limit of $\hat{w}^{d_3} = \frac{w^{d_3}}{\|w^{d_3}\|_{L^\infty}}$ as $d_3 \to d_1^+$. Since $\|\hat{w}_0\|_{L^\infty} = 1$, we see from the strong maximum principle (looking at $w_t = d_1\Delta\hat{w}_0 + \hat{w}_0(m(x) - u^* - v^*)$) that $\hat{w}_0 > 0$ in $\bar{\Omega}$, and hence, $\lambda(d_1, m - u^* - v^*) = 0$, which contradicts Lemma 4.2.

Likewise, if the latter case occurs, we have

$$\begin{aligned} &0 = d_1\Delta\hat{u}_0 - \alpha\hat{u}_0 + \beta\hat{v}_0 + \hat{u}_0(m(x) - w^*_{d_1}) && \text{in } \Omega,\\ &0 = d_2\Delta\hat{v}_0 + \alpha\hat{u}_0 - \beta\hat{v}_0 + \hat{v}_0(m(x) - w^*_{d_1}) && \text{in } \Omega,\\ &\frac{\partial\hat{u}_0}{\partial n} = \frac{\partial\hat{v}_0}{\partial n} = 0 && \text{on } \partial\Omega. \end{aligned} \tag{4.18}$$

Now $\|\hat{u}_0\|_{L^\infty} + \|\hat{v}_0\|_{L^\infty} = 1$ and $\hat{u}_0 \geqslant 0, \hat{v}_0 \geqslant 0$. Then $\hat{u}_0 > 0$ and $\hat{v}_0 > 0$ on $\bar{\Omega}$ due to the maximum principle. This implies that $\lambda_2 = 0$ in (4.9) if $d_3 = d_1$, which contradicts Lemma 4.3.

We can use a similar indirect argument to prove that when $d_3 \to d^-$ where $d = \frac{\beta}{\alpha+\beta}d_1 + \frac{\alpha}{\alpha+\beta}d_2$, there is no positive steady state. For simplicity, we use the exact notation as before. Following the same process, we show that the non-zero limiting steady state (u_0, v_0, w_0) must be either $(u^*, v^*, 0)$ or $(0, 0, w^*_d)$. If the former case happens, it gives $\lambda(d, m - u^* - v^*) = 0 < \lambda(d_c, m - u^* - v^*) = 0$, which leads to a contradiction. If the latter case happens, it implies $\lambda_2 = 0$ when $d_3 = d$, which also leads to a contradiction.

Based on the above discussion, the result follows. □

We can combine the results on the stability or instability of semi-trivial steady states with monotone dynamical systems theory to obtain some results on the dynamics of (4.1). Let $X_1 = C(\bar{\Omega}, \mathbb{R})$, $X_2 = C(\bar{\Omega}, \mathbb{R}^2)$, $X_1^+ = C(\bar{\Omega}, \mathbb{R}^2_+)$ and $X_2^+ = C(\bar{\Omega}, \mathbb{R}^2_+)$. As noted previously, (4.1) generates a monotone semi-flow on $X_1 \times X_2$ with respect to the cooperative cooperative-competitive ordering.

Theorem 4.6. *Assume that* (H) *holds. Then there exist* $d_1 < C_1 \leqslant C_2 < \frac{\beta}{\alpha+\beta}d_1 + \frac{\alpha}{\alpha+\beta}d_2$ *such that the following statements are valid for the system* (4.1):

(i) $(0, 0, w^*)$ *is globally asymptotically stable in* $X_1^+ \times (X_2^+ \setminus \{0\})$ *when* $d_3 \in (0, C_1)$.

(ii) $(u^*, v^*, 0)$ *is globally asymptotically stable in* $(X_1^+ \setminus \{0\}) \times X_2^+$ *when* $d_3 \in (C_2, \infty)$.

Sketch of proof. We utilize the theory developed in [24] for abstract competitive systems (see also [23]) to prove the global stability of one of the boundary steady states. Set $X = X_1 \times X_2$, $K = X_1^+ \times (-X_2^+)$ and $\mathrm{Int}K = \mathrm{Int}X_1^+ \times (-\mathrm{Int}X_2^+)$. Then K generates the partial order relations $\leqslant_K$, $<_K$, $\ll_K$ on X. To prove (i) or (ii), we might set $E_0 = (0, 0)$, $E_1 = (0, w^*)$, $E_2 = (\hat{u}, 0)$ with $\hat{u} = (u^*, v^*)$.

Clearly, [24, (H1)–(H4)] are valid (see also [28]). Lemmas 4.2, 4.3 and 4.5, together with [24, Theorem B], imply (i) or (ii) is valid when $d_3 \in (0, d_1 + \epsilon)$ or $d_3 \in (\frac{\beta}{\alpha+\beta}d_1 + \frac{\alpha}{\alpha+\beta}d_2 - \epsilon, \infty)$. Now define

$$C_1 := \sup\{d : \text{there is no-coexistence steady state for } d_3 \in (0, d)\}$$

and

$$C_2 := \inf\{d : \text{there is no-coexistence steady state for } d_3 \in (d, \infty)\}.$$

Then it easily follows that $d_1 < C_1 \leqslant d_3^0 \leqslant C_2 < \frac{\beta}{\alpha+\beta}d_1 + \frac{\alpha}{\alpha+\beta}d_2$. □

Remark 4.7. We expect that there are conditions under which the system (4.1) has a coexistence state but we will not pursue that point here.

5 Effects of switching rates on the dynamics

Throughout this section, we assume that hypothesis (H) holds, so the results of Section 3 apply. When $d_3 \leqslant d_1$ or $d_3 \geqslant d_2$, the species having slower diffusion also wins the competition. In order to study the effects of switching rate on the competition we only focus on the case when $d_1 < d_3 < d_2$.

Lemma 5.1. *Assume that $d_1 < d_3 < d_2$ and $\max_{x\in\bar{\Omega}} m(x) \leqslant \alpha$. Then the following statements are valid*:

(i) *There exists a unique $\beta_c \in (0, \frac{d_2-d_3}{d_3-d_1}\alpha)$, such that $(0,0,w^*)$ is linearly stable when $\beta \in (0,\beta_c)$, and linearly unstable when $\beta \in (\beta_c,\infty)$.*

(ii) *$(u^*,v^*,0)$ is linearly unstable if β is small enough, and linearly stable if $\beta \in [\frac{d_2-d_3}{d_3-d_1}\alpha,\infty)$.*

(iii) *There exists small $\epsilon > 0$, such that the system (4.1) admits no positive steady state when $\beta \in (0,\epsilon) \cup (\frac{d_2-d_3}{d_3-d_1}\alpha - \epsilon,\infty)$.*

Proof. For the statement (i), it suffices to check the principal eigenvalue λ_2 of (4.9) (equivalently (4.10) or (4.11)) in terms of β. We prove that λ_2 is continuously differentiable on $\beta > 0$ by the implicit function theorem. Let $E = C^{2+\nu}(\bar{\Omega},\mathbb{R}) \times C^{2+\nu}(\bar{\Omega},\mathbb{R}) \times \mathbb{R}$ and $F = C^{\nu}(\bar{\Omega},\mathbb{R}) \times C^{\nu}(\bar{\Omega},\mathbb{R}) \times \mathbb{R}$, $0 < \nu < 1$, and consider a mapping $\Phi : E \times (0,\infty) \to F$ given by

$$\Phi(v_1,v_2,s,\beta) = \begin{pmatrix} d_1\Delta v_1 + (m-w^*-\alpha)v_1 + \beta v_2 - sv_1 \\ d_2\Delta v_2 + (m-w^*-\beta)v_2 + \alpha v_1 - sv_2 \\ \int_\Omega (v_1^2+v_2^2) - 1 \end{pmatrix}.$$

Note that Φ is a continuous map and that the linearization of Φ with respect to E at (v_1,v_2,s,β), denoted $D_1\Phi(v_1,v_2,s,\beta) : E \to F$, is given by

$$[D_1\Phi(v_1,v_2,s,\beta)](w_1,w_2,t) = \begin{pmatrix} d_1\Delta w_1 + (m-w^*-\alpha)w_1 + \beta w_2 - sw_1 - tv_1 \\ d_2\Delta w_2 + (m-w^*-\beta)w_2 + \alpha w_1 - sw_2 - tv_2 \\ 2\int_\Omega (v_1w_1+v_2w_2) \end{pmatrix}.$$

Let $(v_{10},v_{20}) = (\phi_1(\beta_0),\phi_2(\beta_0))$ and $s_0 = \lambda_2(\beta_0)$. Here, $(\phi_1(\beta_0),\phi_2(\beta_0))$ is the positive eigenfunction corresponding to $\lambda_2(\beta_0)$ with $\int_\Omega [\phi_1(\beta_0)]^2 + [\phi_2(\beta_0)]^2 = 1$. Our next goal is to show that $D_1\Phi(v_1,v_2,s,\beta)$ is a bijection.

Suppose then that $D_1\Phi(v_{10},v_{20},\lambda_2(\beta_0),\beta_0)(w_1,w_2,t) = (0,0,0)$. Then

$$d_1\Delta w_1 + (m-w^*-\alpha-\lambda_2(\beta_0))w_1 + \beta_0 w_2 = tv_{10}, \quad d_2\Delta w_2 + (m-w^*-\beta_0-\lambda_2(\beta_0))w_2 + \alpha w_1 = tv_{20}$$

with the zero Neumann boundary condition, and $\int_\Omega w_1v_{10} + w_2v_{20} = 0$.

Direct calculations similar to those in Proposition 3.1 indicate that

$$\begin{aligned} &d_1\nabla\cdot(v_{10}\nabla w_{10} - w_{10}\nabla v_{10}) + \beta_0(w_2v_{10} - v_{20}w_1) = tv_{10}^2, \\ &d_2\nabla\cdot(v_{20}\nabla w_{20} - w_{20}\nabla v_{20}) + \alpha(w_1v_{20} - v_{10}w_2) = tv_{20}^2, \\ &\frac{\partial w_1}{\partial n} = \frac{\partial w_2}{\partial n} = 0. \end{aligned} \tag{5.1}$$

Multiply the equations of (5.1) by α and β_0, respectively, then integrate over Ω, and lastly add together. It then follows that $0 = t[\int_\Omega (\alpha v_{10}^2 + \beta_0 v_{20}^2)]$, and hence, $t = 0$. Since $\lambda_2(\beta_0)$ is the principal eigenvalue of (4.10), we see from the algebraic simplicity of $\lambda_2(\beta_0)$ that $(w_{10},w_{20}) \in \mathrm{Span}\ \{(v_{10},v_{20})\}$. Let $\frac{w_{10}}{v_{10}} = \frac{w_{20}}{v_{20}} = c$. Then the fact $\int_\Omega(w_1v_{10} + w_2v_{20}) = 0$ implies $c = 0$, and hence, $w_{10} = w_{20} = 0$.

Let $(h_1,h_2,r) \in F$. Then consider equations

$$d_1\Delta w_1 + (m-w^*-\alpha-\lambda_2(\beta_0))w_1 + \beta_0 w_2 - tv_{10} = h_1,$$

$$
\begin{aligned}
&d_2\Delta w_2 + (m - w^* - \beta_0 - \lambda_2(\beta_0))w_2 + \alpha w_1 - tv_{20} = h_2, \\
&2\int_\Omega (w_1v_{10} + w_2v_{20}) = r, \quad \frac{\partial w_i}{\partial n} = 0, \quad i = 1, 2.
\end{aligned}
\tag{5.2}
$$

For simplicity, we use the inner product $\langle \phi, \psi\rangle = \int_\Omega \phi^{\mathrm{T}}\psi$. Denote $w = (w_1, w_2)^{\mathrm{T}}$ and $v_0 = (v_{10}, v_{20})^{\mathrm{T}}$. Then solving (5.2) is equivalent to solving the inhomogeneous equation $Lw = G$ with the zero Neumann condition and the constraint $2\langle w, v_0\rangle = r$, where the self-adjoint operator $L : C^{2+\nu}(\bar\Omega, \mathbb{R})^2 \to C^\nu(\bar\Omega, \mathbb{R})^2$ is given by

$$
L\begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix} = \begin{pmatrix}\alpha d_1\Delta\phi_1 + \alpha[m - w^* - \alpha - \lambda_2(\beta_0)]\phi_1 + \alpha\beta_0\phi_2\\ \beta_0 d_2\Delta\phi_2 + \alpha\beta_0\phi_1 + \beta_0[m - w^* - \beta_0 - \lambda_2(\beta_0)]\phi_2\end{pmatrix},
$$

and G is given by

$$
G = \begin{pmatrix}\alpha tv_{10} + \alpha h_1\\ \beta_0 tv_{20} + \beta_0 h_2\end{pmatrix}.
$$

Since the solution set of the homogeneous equation $Lw = 0$ is $\mathrm{Span}\{v_0\}$, the solvability criterion for $Lw = G$ is

$$
\langle G, v_0\rangle = \langle Lw, v_0\rangle = \langle w, Lv_0\rangle = 0.
$$

A simple calculation shows that $t = -\frac{\int_\Omega(\alpha v_{10}h_1 + \beta_0 v_{20}h_2)}{\int_\Omega(\alpha v_{10}^2 + \beta_0 v_{20}^2)}$. Moreover, solutions of $Lw = G$ with the zero Neumann boundary conditions can be written in the form $z + kv_0$, where k is an arbitrary constant and z is uniquely determined by the requirement $\langle z, v_0\rangle = 0$. Now choose $k = \frac{r}{2}$. Then $w = z + kv_0$ is a solution of (5.2). It then follows from the implicit function theorem that $\lambda_2(\beta)$ and $(\phi_1(\beta), \phi_2(\beta))$ are continuously differentiable in β.

Taking the derivative with respect to β in (4.10) (or equivalently in $L\phi = 0$), we obtain a system equivalent to $L\tilde\phi = f$ with $\tilde\phi = (\phi_1'(\beta), \phi_2'(\beta))^{\mathrm{T}}$, and $f = (\lambda_2'(\beta)\alpha\phi_1 - \alpha\phi_2, \lambda_2'(\beta)\beta\phi_2 + \beta\phi_2)^{\mathrm{T}}$. A simple computation shows that

$$
0 = \langle L\phi, \tilde\phi\rangle = \langle \phi, L\tilde\phi\rangle = \langle \phi, f\rangle,
$$

i.e., $\lambda_2'(\beta) = \frac{\int_\Omega(\alpha\phi_1\phi_2 - \beta\phi_2^2)}{\int_\Omega(\alpha\phi_1^2 + \beta\phi_2^2)}$. Since $\lambda(d_2, m - w^*) < \lambda(d_3, m - w^*) = 0$, we see from the second equation of (4.10) that

$$
\lambda_2(\beta)\int_\Omega \phi_2^2 - \int_\Omega(\alpha\phi_1\phi_2 - \beta\phi_2^2) = -d_2\int_\Omega |\nabla\phi_2|^2 + \int_\Omega (m - w^*)\phi_2^2 < 0.
$$

This shows if $\lambda_2(\beta) \geqslant 0$, then $\lambda_2'(\beta) > 0$. Moreover, $\lambda_2(\beta)$ changes sign at most once.

By essentially the same argument as in Lemma 4.3, we obtain that when $\beta \geqslant \frac{d_2 - d_3}{d_3 - d_1}\alpha$, $\lambda_2(\beta) > 0$. Suppose that $\lambda_2(\beta)$ does not change sign. Then $\lambda_2(\beta)$ is bounded from below by zero, and there exists $\beta_n > 0$ and (ϕ_{1n}, ϕ_{2n}) with $\int_\Omega(\phi_{1n}^2 + \phi_{2n}^2) = 1$ such that $\lambda_2(\beta_n) \to A \geqslant 0$ as $\beta_n \to 0$. One may use the elliptic regularity to assume that $(\phi_{1n}, \phi_{2n}) \to (\hat\phi_1, \hat\phi_2)$ in $C^2(\bar\Omega)$ satisfying

$$
\begin{cases}
A\hat\phi_1 = d_1\Delta\hat\phi_1 + (m(x) - w^* - \alpha)\hat\phi_1 & \text{in } \Omega,\\
A\hat\phi_2 = d_2\Delta\hat\phi_2 + \alpha\hat\phi_1 + (m(x) - w^*)\hat\phi_2 & \text{in } \Omega,\\
\dfrac{\partial\hat\phi_1}{\partial n} = \dfrac{\partial\hat\phi_2}{\partial n} = 0 & \text{on } \partial\Omega.
\end{cases}
\tag{5.3}
$$

Since $\hat\phi_i \geqslant 0, i = 1, 2$, and $\int_\Omega(\hat\phi_1^2 + \hat\phi_2^2) = 1$, A is either $\lambda(d_1, m - w^* - \alpha) < \lambda(d_1, m - \alpha) \leqslant 0$ or $\lambda(d_2, m - w^*) < \lambda(d_3, m - w^*) = 0$, and hence, $A < 0$, which leads to a contradiction. Statement (i) holds true.

For the statement (ii), we claim there exists some $\epsilon > 0$ such that $\lambda(d_3, m - u^*(\beta) - v^*(\beta)) > 0$ if $\beta \in (0, \epsilon)$. If it is not true, then there exists $\beta_n \to 0 (n \to \infty)$, $\lambda(d_3, m - u_n^* - v_n^*) \leqslant 0$ and $(u_n^*, v_n^*) \in (0, \beta_n) \times (0, \alpha)$. Since $\lambda(d_3, m - u_n^* - v_n^*)$ depends continuously on $m - u_n^* - v_n^*$, we might assume that (up to a subsequence if necessary) $(u_n^*, v_n^*) \to (0, v_\infty^*)$ in $C^2(\bar\Omega)$ satisfying $d_2\Delta v_\infty^* + (m - v^*)v_\infty^* = 0$ and

$\lambda(d_3, m - v_n^* - u_n^*) \to \lambda(d_3, m - v_\infty^*) \leqslant 0$. If $v_\infty^* \equiv 0$, then $\lambda(d_3, m) > 0$ due to the assumption (H), which leads to a contradiction. Otherwise, v_∞^* is positive, $m - v_\infty^*$ is non-constant and $\lambda(d_2, m - v_\infty^*) = 0 < \lambda(d_3, m - v_\infty^*)$, which leads to a contradiction again.

In the case that $\beta \geqslant \frac{d_2-d_3}{d_3-d_1}\alpha$, it follows directly from Lemma 4.2 that $\lambda(d_3, m - u^* - v^*) < 0$, i.e., $(u^*, v^*, 0)$ is linearly stable.

For the statement (iii), we show that when $\beta \to 0^+$, there is no coexistence steady state. If not, then there exists $\beta_n \to 0$ $(n \to \infty)$, positive steady states (u_n^0, v_n^0, w_n^0) and $(u_n^0, v_n^0) \in (0, \beta_n) \times (0, \alpha)$. Passing to the limit, we might assume that (up to a subsequence if necessary) $(u_n^0, v_n^0, w_n^0) \to (0, v_\infty^0, w_\infty^0)$ in $C^2(\bar{\Omega})$ satisfying

$$\begin{cases} 0 = d_2\Delta v_\infty^0 + v_\infty^0(m(x) - v_\infty^0 - w_\infty^0) & \text{in } \Omega, \\ 0 = d_3\Delta w_\infty^0 + w_\infty^0(m(x) - v_\infty^0 - w_\infty^0) & \text{in } \Omega, \\ \dfrac{\partial v_\infty^0}{\partial n} = \dfrac{\partial w_\infty^0}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{5.4}$$

Clearly, v_∞^0, w_∞^0 cannot be both positive. There will be three possible cases, i.e., (a) $(v_\infty^0, w_\infty^0) = (0, 0)$; (b) $(v_\infty^0, w_\infty^0) = (0, w^*(d_3))$; (c) $(v_\infty^0, w_\infty^0) = (v(d_2), 0)$. However, essentially the same proof as in [43, Lemma 4.5] implies that none of them can happen. Suppose that the case (a) occurs. Let $\widehat{v}_n = \frac{v_n^0}{\|v_n^0\|_{L^\infty}}$. We have

$$0 = d_2\Delta\widehat{v}_n + (m(x) - u_n^0 + v_n^0 - w_n^0)\widehat{v}_n.$$

We can assume, by passing to a subsequence if necessary, that $\widehat{v}_n \to \widehat{v}^*$ with $\|\widehat{v}^*\|_{L^\infty} = 1$, where $\widehat{v}^*$ satisfies $0 = d_2\Delta\widehat{v}^* + (m(x) - w^*(d_3))\widehat{v}^*$. However, $0 = d_3\Delta w^*(d_3) + (m(x) - w^*(d_3))w^*(d_3)$, so the principal eigenvalue of the operator $Lw = d_3\Delta w + (m(x) - w^*(d_3))w$ is 0, so the strict monotonicity of the principal eigenvalue with respect to the diffusion coefficient gives a contradiction to $0 = d_2\Delta\widehat{v}^* + (m(x) - w^*(d_3))\widehat{v}^*$. The argument for the case (b) is very similar so we omit it. In the case (c) we use $\widehat{w}_n = \frac{w_n^0}{\|w_n^0\|_{L^\infty}}$ and pass to a limit $\widehat{w}^*$. An argument analogous to the one given previously for $\widehat{v}^*$ leads to the equation $0 = d_3\Delta\widehat{w}^* + (m(x) - v(d_2))\widehat{w}^*$ with $\|\widehat{w}^*\|_{L^\infty} = 1$, but since $0 = d_2\Delta v(d_2) + (m(x) - v(d_2))\widehat{w}^* v(d_2)$ and $d_3 \neq d_2$ this also leads to a contradiction. Hence none of (a), (b) or (c) is possible, so there cannot be a coexistence state as $\beta \to 0^+$. Following the same idea as in the proof of Lemma 4.5, we can see that $\beta \to \beta_0^-$ with $\beta_0 = \frac{d_2-d_3}{d_3-d_1}\alpha$, there is no coexistence steady state. □

A parallel result is stated below when α varies.

Lemma 5.2. *Assume that $d_1 < d_3 < d_2$ and $\max_{x\in\bar{\Omega}} m(x) \leqslant \beta$. Then the following statements are valid*:

(i) *There exists a unique $\alpha_c \in (\frac{d_3-d_1}{d_2-d_3}\beta, \infty)$, such that $(0, 0, w^*)$ is linearly unstable when $\alpha \in (0, \alpha_c)$, and linearly stable when $\alpha \in (\alpha_c, \infty)$.*

(ii) *$(u^*, v^*, 0)$ is linearly stable when α is small enough, and linearly unstable when $\alpha \in [\frac{d_3-d_1}{d_2-d_3}\beta, \infty)$.*

(iii) *There exists small $\epsilon > 0$, such that the system (4.1) admits no positive steady state when $\alpha \in (0, \epsilon) \cup (\frac{d_3-d_1}{d_2-d_3}\beta - \epsilon, \infty)$.*

Proof. We only prove the statement (i) when α is large, as the other cases are analogous to the proof in Lemma 5.1. By an argument similar to those in Lemma 5.1, we have $\lambda_2(\alpha)$ is continuously differentiable in $\alpha > 0$, and $\lambda(\alpha) > 0$ when $\alpha \leqslant \frac{d_3-d_1}{d_2-d_3}\beta$. A direct computation shows that $\lambda_2'(\alpha) = \frac{\int_\Omega(\beta\phi_1\phi_2 - \alpha\phi_1^2)}{\int_\Omega(\alpha\phi_1^2 + \beta\phi_2^2)}$. If $\lambda_2(\alpha) = 0$ for some $\alpha > 0$, then we see from (4.10) and (4.12) that

$$\int_\Omega(\alpha\phi_1^2 - \beta\phi_1\phi_2) = -d_1\int_\Omega|\nabla\phi_1|^2 + \int_\Omega(m - w^*)\phi_1^2 > 0.$$

Therefore, $\lambda_2'(\alpha) < 0$ when $\lambda_2(\alpha) = 0$. This implies that $\lambda_2(\alpha)$ can change signs at most once. Suppose $\lambda_2(\alpha)$ does not change signs, i.e., $\lambda_2(\alpha) > 0$, $\forall\, \alpha > 0$. Since

$$\int_\Omega(\beta\phi_2^2 - \alpha\phi_1\phi_2) + \lambda_2\int_\Omega\phi_2^2 = -d_2\int_\Omega|\nabla\phi_2|^2 + \int_\Omega(m - w^*)\phi_2^2 < 0$$

and

$$\alpha\left[\int_\Omega(\alpha\phi_1^2-\beta\phi_1\phi_2)\right]+\beta\left[\int_\Omega(\beta\phi_2^2-\alpha\phi_1\phi_2)\right]\geqslant 0,$$

we have $\int_\Omega(\alpha\phi_1^2-\beta\phi_1\phi_2)>0$, so is $\lambda'(\alpha)<0$. Hence $\lambda_2(\alpha)$ is strictly decreasing in $\alpha>0$ and uniformly bounded from below. Let $(\phi_{1\alpha},\phi_{2\alpha})\in C^{2,\nu}(\bar\Omega,\mathbb{R})_+^2)$ with $\int_\Omega(\alpha\phi_{1\alpha}^2+\beta\phi_{2\alpha}^2)=1$ be the associated eigenfunction with $\lambda_2(\alpha)$. Then $\lambda_2(\alpha)\to\lambda_\infty\geqslant 0$, as $\alpha\to\infty$.

A straightforward calculation indicates that

$$\begin{aligned}\int_\Omega\phi_{1\alpha}^2&=\frac{-d_1\int_\Omega|\nabla\phi_{1\alpha}|^2+\int_\Omega((m-w^*-\lambda_2)\phi_{1\alpha}^2+\beta\phi_{1\alpha}\phi_{2\alpha})}{\alpha}\\&\leqslant\frac{\bar m+\beta}{\alpha}\to 0,\quad \alpha\to\infty,\end{aligned}$$

and

$$0<\int_\Omega(\alpha\phi_{1\alpha}^2-\beta\phi_{1\alpha}\phi_{2\alpha})=-d_1\int_\Omega|\nabla\phi_{1\alpha}|^2+\int_\Omega(m-w^*-\lambda_2)\phi_{1\alpha}^2\leqslant\bar m\int_\Omega\phi_{1\alpha}^2$$

which yields that $\lim_{\alpha\to\infty}\int_\Omega\alpha\phi_{1\alpha}^2=0$ and $\lim_{\alpha\to\infty}\int_\Omega\alpha|\nabla\phi_{1\alpha}|^2=0$ due to the fact from (4.12) that

$$-\alpha d_1\int_\Omega|\nabla\phi_{1\alpha}|^2+\alpha\int_\Omega(m-w^*)\phi_{1\alpha}^2>0.$$

In view of identity (4.12) again, we have

$$\int_\Omega(\alpha\phi_{1\alpha}-\beta\phi_{2\alpha})^2\leqslant\int_\Omega(m-w^*)\alpha\phi_{1\alpha}^2\leqslant\bar m\int_\Omega\alpha\phi_{1\alpha}^2\to 0,\quad\alpha\to\infty.$$

Therefore, $\|\alpha\phi_{1\alpha}-\beta\phi_{2\alpha}\|_{L^2(\Omega)}\to 0$ as $\alpha\to\infty$.

Now replace λ_2 and (ϕ_1,ϕ_2) by $\lambda_2(\alpha)$ and $(\phi_{1\alpha},\phi_{2\alpha})$ in (4.12) and let $\alpha\to\infty$. Then we obtain

$$\lim_{\alpha\to\infty}-d_2\int_\Omega|\nabla\phi_{2\alpha}|^2+\int_\Omega(m-w^*)\phi_{2\alpha}^2=\lambda_\infty\geqslant 0.$$

Indeed, $\lambda_\infty=0$ due to the fact that $-d_2\int_\Omega|\nabla\phi_{2\alpha}|^2+\int_\Omega(m-w^*)\phi_{2\alpha}^2<0$ for any $\alpha>0$. Now we see that $\phi_{2\alpha}$ is bounded in $H^1(\Omega)$ when α is large. This implies (up to a subsequence if necessary) $\phi_{2\alpha}\to\phi_\infty$ in $L^2(\Omega)$ with $\|\sqrt{\beta}\phi_\infty\|_{L^2(\Omega)}=1$. Let $A\phi:=-d_2\Delta\phi-(m-C)\phi$ for some large $C>\lambda(d_2,m)$. Then $A^{-1}:L^2(\Omega)\to H^2(\Omega)$ is a continuous operator. Passing to the limit in

$$\phi_{2\alpha}=A^{-1}[\alpha\phi_{1\alpha}-\beta\phi_{2\alpha}+(C-\lambda_2(\alpha))\phi_{2\alpha}],$$

we get $\phi_\infty=A^{-1}((C-\beta)\phi_\infty)$. The standard elliptic regularity implies $\phi_\infty\in C^{1,\nu}(\bar\Omega)$, and hence,

$$-d_2\int_\Omega|\nabla\phi_\infty|^2+\int_\Omega(m-w^*)\phi_\infty^2=0$$

and $\phi_\infty\not\equiv 0$, i.e., $0\leqslant\lambda(d_2,m-w^*)<\lambda(d_3,m-w^*)=0$, which leads to a contradiction.

It follows immediately that $\lambda_2(\alpha)$ changes sign once and has a unique $\alpha_c\in(0,\frac{d_3-d_1}{d_2-d_3}\beta)$ such that $\lambda_2(\alpha_c)=0$. □

Now we are ready to state two parallel results on the global dynamics of the boundary steady state in terms of α and β, respectively. They follow from the same arguments based on monotone dynamical systems that are used in Theorem 3.6.

Theorem 5.3. *Assume that* $d_1<d_3<d_2$ *and* $\max_{x\in\bar\Omega}m(x)\leqslant\alpha$. *Then there exist some* $0<C_1\leqslant C_2<\frac{d_2-d_3}{d_3-d_1}\alpha$ *such that the following statements are valid*:

(i) $(0,0,w^*)$ *is globally asymptotically stable in* $X_1^+\times(X_2^+\setminus\{0\})$ *when* $\beta\in(0,C_1)$.

(ii) $(u^*,v^*,0)$ *is globally asymptotically stable in* $(X_1^+\setminus\{0\})\times X_2^+$ *when* $\beta\in(C_2,\infty)$.

Theorem 5.4. *Assume that* $d_1<d_3<d_2$ *and* $\max_{x\in\bar\Omega}m(x)\leqslant\beta$. *Then there exist some* $0<C_1\leqslant C_2<\frac{d_3-d_1}{d_2-d_3}\beta$ *such that the following statements are valid*:

(i) $(0,0,w^*)$ *is globally asymptotically stable in* $X_1^+\times(X_2^+\setminus\{0\})$ *when* $\alpha\in(C_2,\infty)$.

(ii) $(u^*,v^*,0)$ *is globally asymptotically stable in* $(X_1^+\setminus\{0\})\times X_2^+$ *when* $\alpha\in(0,C_1)$.

6 Conclusions

For the two-component subsystem (2.1) we have derived conditions under which it is asymptotically competitive or cooperative. In the asymptotically cooperative case we have derived further conditions implying the existence of a unique globally stable positive equilibrium. We have obtained various eigenvalue estimates that determine the stability of the trivial solution $(0, 0)$. Some of the results for (2.1) are extensions of those in [6] to cases where some coefficients may vary in x. We should note that we have not been able to give a complete analysis of the stability of $(0, 0)$ in the indefinite case, i.e., where the local population growth rate $m(x)$ can change sign, reflecting the presence of both sources and sinks in the overall environment. This is due to the fact that we do not know of an extension of a key result from [22] to systems of equations. A major reason why results implying that the sub-model (2.1) has a unique globally attracting positive equilibrium are interesting is that in such a case (2.1) behaves like a single logistic equation and hence it is reasonable to view the populations u and v together as a single population consisting of individuals that can switch their dispersal behavior.

The main problem motivating this paper was that of understanding how well a population whose members can switch between slow and fast diffusion rates d_1 and d_2 could compete against an ecologically identical population where all individuals diffuse at a single intermediate rate d_3. What we found was that if $d_3 < d_1 < d_2$ then the semi trivial equilibrium $(u^*, v^*, 0)$ of (4.1) is unstable and $(0, 0, w^*)$ is stable, while if $d_1 < (\alpha d_1 + \beta d_2)/(\alpha + \beta) < d_3$ then $(u^*, v^*, 0)$ stable and $(0, 0, w^*)$ is unstable. Furthermore, both semi trivial equilibria change their stability for some values of d_3 in the interval $(d_1, (\alpha d_1 + \beta d_2)/(\alpha + \beta))$. Thus, the size of the diffusion rate d_3 relative to the average of diffusion rates d_1 and d_2 weighted by the switching rates α and β seems to be informative about which of the populations (u, v) and w has the advantage. In some cases we were able to show the nonexistence of a positive (coexistence) equilibrium for (4.1), which then implies competitive exclusion when combined with suitable results on stability of semi trivial equilibria.

There remain many challenging open questions about (4.1) and related models. In the case where $m(x)$ changes sign, we do not have a uniqueness result for the principal eigenvalue of the linearized model corresponding to the sub model (2.1). Since we can show that the semi trivial equilibria can change stability as d_3 or α or β vary we expect that the system (4.1) will have bifurcations that produce coexistence states (which might be unstable), but we have not explored a bifurcation theoretic approach, and we do not have enough information about the relative locations relative to d_3 of the points where the stabilities of $(u^*, v^*, 0)$ and $(0, 0, w^*)$ change to use monotone methods to show the presence of coexistence states. It should be possible to address these and other questions but that will require additional research. In a different direction, it would be interesting to consider models with different types of dispersal operators, boundary conditions, or interaction terms. Another topic of interest would be to try to see if and when adaptive switching that mimics area restricted search (i.e., switching that is biased toward slower diffusion at locations where $m(x)$ is large, but toward faster diffusion where $m(x)$ is small) is advantageous versus diffusion at a fixed rate everywhere. Some numerical results about this type of phenomenon in a more realistic dispersal model are given in [12]. In general, the idea that organisms switch between different movement modes has considerable empirical support and leads to mathematical models whose analysis is challenging but within the scope of current mathematical methods. For those reasons we think dispersal models with switching are an interesting topic for further study.

Acknowledgements This work was supported by National Science Foundation of USA (Grant No. DMS-1514752).

References

1 Amann H. Maximum principles and principal eigenvalues. In: 10 Mathematical Essays on Approximation in Analysis and Topology. Amsterdam: Elsevier, 2005, 1–60

2 Brown K J, Zhang Y. On a system of reaction-diffusion equations describing a population with two age groups. J Math Anal Appl, 2003, 282: 444–452

3 Cantrell R S, Cosner C. On the steady-state problem for the Volterra-Lotka competition model with diffusion. Houston J Math, 1987, 13: 337–352

4 Cantrell R S, Cosner C. Spatial Ecology via Reaction-diffusion Equations. Chichester: John Wiley & Sons, 2003

5 Cantrell R S, Cosner C, Lou Y. Advection-mediated coexistence of competing species. Proc Roy Soc Edinburgh Sect A, 2007, 137: 497–518

6 Cantrell R S, Cosner C, Yu X. Dynamics of populations with individual variation in dispersal on bounded domains. J Biol Dyn, 2018, 12: 288–317

7 Conway E, Smoller J. A comparison technique for systems of reaction-diffusion equations. Comm Partial Differential Equations, 1977, 2: 679–697

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

9 Dancer E. On the principal eigenvalue of linear cooperating elliptic systems with small diffusion. J Evol Eqn, 2009, 9: 419–428

10 Dockery J, Hutson V, Mischaikow K, et al. The evolution of slow dispersal rates: A reaction-diffusion model. J Math Biol, 1998, 37: 61–83

11 Elliot E C, Cornell S J. Dispersal polymorphism and the speed of biological invasions. PLoS One, 2012, 7: e40496

12 Fagan W F, Hoffman T, Dahiya D, et al. Improved foraging by switching between diffusion and advection: Benefits from movement that depends on spatial context. Theor Ecol, 2019, in press

13 Fleming C H, Calabrese J M, Mueller T, et al. From fine-scale foraging to home ranges: A semivariance approach to identifying movement modes across spatiotemporal scales. Am Nat, 2014, 5: E154–E167

14 Fryxell J, Hazell M, Borger L, et al. Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proc Natl Acad Sci USA, 2008, 49: 19114–19119

15 Girardin L. Non-cooperative Fisher-KPP systems: Traveling waves and long-time behavior. Nonlinearity, 2018, 31: 108–164

16 Girardin L. Non-cooperative Fisher-KPP systems: Asymptotic behavior of traveling waves. Math Models Methods Appl Sci, 2018, 28: 1067–1104

17 Girardin L. Two components is too simple: An example of oscillatory Fisher-KPP system with three components. ArXiv:1812.05336, 2018

18 Hastings A. Can spatial variation alone lead to selection for dispersal? Theor Pop Biol, 1983, 24: 244–251

19 He X, Ni W-M. Global Dynamics of the Lotka-Volterra competition-diffusion system: Diffusion and spatial heterogeneity I. Comm Pure Appl Math, 2016, 69: 981–1014

20 Hei L J, Wu J H. Existence and stability of positive solutions for an elliptic cooperative system. Acta Math Sin Engl Ser, 2005, 21: 1113–1120

21 Hess P. Periodic-Parabolic Boundary Value Problems and Positivity. Pitman Search Notes in Mathematics Series, vol. 247. Harlow: Longman Scientific Technical, 1991

22 Hess P, Kato T. On some linear and nonlinear eigenvalue problems with an indefinite weight function. Comm Partial Differential Equations, 1980, 10: 999–1030

23 Hess P, Lazer A C. On an abstract competition model and applications. Nonlinear Anal, 1991, 16: 917–940

24 Hsu S B, Smith H L, Waltman P. Competitive exclusion and coexistence for competitive systems on ordered Banach spaces. Trans Amer Math Soc, 1996, 348: 4083–4094

25 Kato T. Superconvexity of the spectral radius, and convexity of the spectral bound and the type. Math Z, 1982, 180: 265–273

26 Kato T. Perturbation Theory for Linear Operators. Berlin-New York: Springer-Verlag, 1984

27 Lam K-Y, Lou Y. Asymptotic behavior of the principal eigenvalue for cooperative elliptic systems and applications. J Dynam Differential Equations, 2016, 28: 29–48

28 Lam K-Y, Munther D. A remark on the global dynamics of competitive systems on ordered Banach spaces. Proc Amer Math Soc, 2016, 144: 1153–1159

29 López-Gómez J, Fernández-Rincón S. A singular perturbation result in competition theory. J Math Anal Appl, 2017, 445: 280–296

30 López-Gómez J, Molina-Meyer M. The maximum principle for cooperative weakly coupled elliptic systems and some applications. Differential Integral Equations, 1994, 7: 383–398

31 Morris A L, Börger L, Crooks E. Individual variability in dispersal and invasion speed. ArXiv:1612.06768, 2016

32 Newlands N K, Lutcavage M E, Pitcher T J. Analysis of foraging movements of Atlantic Bluefin tuna (Thunnus thynnus): Individuals switch between two modes of search behaviour. Pop Ecol, 2004, 46: 39–53

33 Prevedello J A, Forero-Medina G, Vieira M V. Does land use affect perceptual range? Evidence from two marsupials of the Atlantic Forest. J Zool, 2011, 284: 53–59

34 Rodríguez J P, Fernández-Gracia J, Thums M, et al. Big data analyses reveal patterns and drivers of the movements of southern elephant seals. Sci Rep, 2017, 7: 112

35 Skalski G, Gilliam J F. Modeling diffusive spread in a heterogeneous population: A movement study with stream fish. Ecology, 2000, 81: 1685–1700
36 Skalski G, Gilliam J F. A diffusion-based theory of organism dispersal in heterogeneous populations. Am Nat, 2003, 161: 441–458
37 Smith H L. Competing subcommunities of mutualists and a generalized Kamke theorem. SIAM J Appl Math, 1986, 46: 856–874
38 Smith H L. Systems of ordinary differential equations that generate an order preserving flow. A Survey of results. SIAM Rev, 1988, 30: 87–113
39 Smith H L. Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems. Mathematical Surveys and Monographs, vol. 41. Providence: Amer Math Soc, 1995
40 Smith H L, Zhao X-Q. Robust persistence for semidynamical systems. Nonlinear Anal, 2001, 47: 6169–6179
41 Tyson R C, Wilson J B, Lane W D. Beyond diffusion: Modelling local and long-distance dispersal for organisms exhibiting intensive and extensive search modes. Theor Pop Biol, 2011, 79: 70–81
42 Ward D, Saltz D. Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev desert. Ecology, 1994, 75: 48–58
43 Zhao X-Q, Zhou P. On a Lotka-Volterra competition model: the effects of advection and spatial variation. Calc Var Partial Differential Equations, 2016, 55: 73