CSIAM Trans. Life Sci.
doi: 10.4208/csiam-ls.SO-2024-0005

Vol. **1**, No. 1, pp. 67-92
March 2025

Persistence, Nonlocal Competition and Evolution of Movement: The Role of Principal Eigenvalues

Shuang Liu[1], Yuan Lou[2] and Shizhao Ma[3,4,*]

[1] *School of Mathematics and Statistics, Beijing Institute of Technology, Beijing 100081, China.*
[2] *School of Mathematical Sciences, CMA-Shanghai, Shanghai Jiao Tong University, Shanghai 200240, China.*
[3] *School of Mathematical Sciences, Shanghai Jiao Tong University, Shanghai 200240, China.*
[4] *Institute of Natural Sciences, Shanghai Jiao Tong University, Shanghai 200240, China.*

Received 27 May 2024; Accepted 30 July 2024

Abstract. How does the movement of individuals influence the persistence of a single species and the competition of multiple populations? Studies of such questions often involve the principal eigenvalues of the associated linear differential operators. We explore the significant roles of the principal eigenvalue by investigating two types of mathematical models for arbitrary but finite number of competing populations in spatially heterogeneous and temporally periodic environment. The interaction terms in these models are assumed to depend on the population sizes of all species in the whole habitat, representing some kind of nonlocal competition. For both models, the single species can persist if and only if the principal eigenvalue for the linearized operator is of negative sign, suggesting that the best strategy for the single species to invade when rare is to minimize the associated principal eigenvalue. For multiple populations, the global dynamics can also be completely characterized by the associated principal eigenvalues. Specifically, our results reveal that the species with the smallest principal eigenvalue among all competing populations, will gain a competitive advantage and competitively exclude other populations. This suggests that the movement strategies minimizing the corresponding principal eigenvalue are evolutionarily stable, echoing the persistence criteria for the single species.

AMS subject classifications: 35Q92, 35P15, 92D25, 35K57, 92D15

Key words: Principal eigenvalues, nonlocal competition, time-periodic, evolutionarily stable strategy.

---

[*]Corresponding author. *Email addresses:* `yuanlou@sjtu.edu.cn` (Y. Lou), `shizhaoma@sjtu.edu.cn` (S. Ma), `liushuangnqkg@bit.edu.cn` (S. Liu)

1 Introduction

Principal eigenvalue is a basic quantity associated with an elliptic or parabolic operator. The study of reaction diffusion equations in bounded domains often involves the principal eigenvalue of the associated linear differential operator. In this paper, we consider two types of mathematical models to illustrate the significant roles of the principal eigenvalue in determining the global dynamics of these nonlinear systems for arbitrary but finite number of competing populations. As applications, our results determine the optimal movement strategies for populations with dispersal and nonlocal competition in spatially heterogeneous and temporally varying environment.

1.1 Patch model

Consider the following single species model in K-patch landscapes:

$$\frac{\mathrm{d}\mathbf{u}}{\mathrm{d}t}=d\mathbf{L}\mathbf{u}+\mathrm{diag}\{m_j(t)-u_j\}\mathbf{u},\quad t>0, \tag{1.1}$$

where $\mathbf{u}=(u_1,\cdots,u_K)$, with $u_j(t)$ denoting the population size of the species in patch j at time t; $\mathbf{L}=(\ell_{ij})$ is a symmetric, cooperative and irreducible $K\times K$ matrix with constant entries, which satisfies $\ell_{ii}=-\sum_{j\neq i}\ell_{ij}$ for all $1\leq i\leq K$, referred as the discrete Laplacian. Here $\mathrm{diag}\{a_j\}$ denotes the $K\times K$ diagonal matrix with diagonal entries $a_1,\cdots,a_K$, and $m_j(t)$ is a T-periodic function representing the growth rate of the species in patch j, which measures the environmental heterogeneity in both space and time. Parameter $d>0$ is the migration rate of the species.

The dynamics of model (1.1) is related to the linear eigenvalue problem

$$\begin{cases}\dfrac{\mathrm{d}\boldsymbol{\varphi}}{\mathrm{d}t}=d\mathbf{L}\boldsymbol{\varphi}+\mathrm{diag}\{m_j(t)\}\boldsymbol{\varphi}+\lambda\boldsymbol{\varphi}, & t\in\mathbb{R},\\ \boldsymbol{\varphi}(t)=\boldsymbol{\varphi}(t+T), & t\in\mathbb{R},\end{cases} \tag{1.2}$$

which can be regarded as the linearization of the nonlinear model (1.1) at the trivial equilibrium $\mathbf{u}=\mathbf{0}$. By the Krein-Rutman theorem [19], problem (1.2) admits a principal eigenvalue, which is real and simple, and the corresponding eigenvector can be chosen to be positive; moreover, it has the smallest real part among all eigenvalues of (1.2).

Theorem 1.1. *For each $d>0$, let $\lambda(d)$ denote the principal eigenvalue of* (1.2).

(i) If $\lambda(d)<0$, then problem (1.1) *admits a unique positive T-periodic solution*

$$\mathbf{p}=\big(p_1(t),\cdots,p_K(t)\big)>0,$$

and $u_j(t)\to p_j(t)$ as $t\to+\infty$ for all $j=1,\ldots,K$.

(ii) If $\lambda(d)\geq 0$, then $u_j(t)\to 0$ as $t\to+\infty$ for all $j=1,\ldots,K$.

Theorem 1.1 is a direct consequence of the theory of monotone periodic systems established in [29, Chapter 3.1.2]. It is well known [4] that for an invading species to persist successfully, the population will increase when rare and eventually stabilize at an equilibrium state. Theorem 1.1 establishes a necessary and sufficient condition for the survival of an invading species, i.e. $\lambda(d)<0$, which establishes a strong connection between the dynamics of (1.1) and the principal eigenvalue of (1.2). The condition $\lambda(d)<0$ reflects many crucial information regarding the interaction between the movement of the species and the heterogeneity of environment. In particular, if $\inf_{d>0}\lambda(d)$ is negative, there exists some interval of diffusion rates for which the species can persist.

It is proved by [24, Theorem 2.1] that

$$\lambda(0):=\lim_{d\to 0}\lambda(d)=-\max_{1\le j\le K}\frac{1}{T}\int_0^T m_j(t)\mathrm{d}t. \tag{1.3}$$

In the special scenario when m_j is a constant (i.e. independent of t), the principal eigenvalue $\lambda(d)$ is the smallest eigenvalue of the symmetric matrix $-d\mathbf{L}-\mathrm{diag}\{m_j\}$ corresponding to a positive eigenvector. It turns out that $\lambda(d)$ is nondecreasing in diffusion rate d, so that by (1.3), the species can persist for some diffusion rate if and only if $\max_{1\le j\le K}m_j>0$. In the context of source-sink theory [18], this implies that the population can be sustained by immigrating among patches only when a source patch (in which $m_j>0$ for some j) exists.

The situation changes drastically when $m_j=m_j(t)$ varies periodically in time t. Even if $\lambda(0)>0$, i.e. all patches are sink (in which $\int_0^T m_j(t)\mathrm{d}t<0$ for all $j=1,\ldots,K$), it is still possible for species to persist through appropriate dispersal among patches. This surprising phenomenon has attracted attention in both theoretical and empirical studies [25,28] and is called dispersal-induced growth (DIG) in the literature [16, 17]. Mathematically, the DIG phenomenon occurs if $\lambda(0)>0$ but $\lambda(d)<0$ for certain positive diffusion rate d. By Theorem 1.1, this means that the population would become extinct if isolated, but dispersal, at an appropriate rate, can induce the persistence of the population. Hence, the dependence of principal eigenvalue $\lambda(d)$ on migration rate d plays a central role in this context. We refer to [3, 17] for more details.

To further understand the roles of the principal eigenvalue $\lambda(d)$ on the outcome of species interactions, we consider the following multiple competing species in K-patch landscapes:

$$\begin{cases}\dfrac{\mathrm{d}\mathbf{u}_i}{\mathrm{d}t}=d_i\mathbf{L}\mathbf{u}_i+\mathrm{diag}\left\{m_j-\displaystyle\sum_{i=1}^{N}\sum_{j=1}^{K}u_{ij}\right\}\mathbf{u}_i, & t>0,\quad i=1,\ldots,N,\\ \mathbf{u}_i(0)>0, & i=1,\ldots,N,\end{cases} \tag{1.4}$$

where $\mathbf{u}_i=(u_{i1},\cdots,u_{iK}),1\le i\le N$, with u_{ij} denoting the population sizes of competing species i in patch j, and m_j is a T-periodic function representing their common growth rate. These N species are assumed to be identical except for their migration rates, denoted by $d_i>0,1\le i\le N$.

For the classical Lotka-Volterra competition models, the competition among different species within a single patch is often assumed to depend only on the population sizes of all species in the same patch. However, the interaction terms in model (1.4) depend on the population sizes of all species in all patches, i.e. the effective growth rate of a species at a particular patch is not only determined by the total biomass in that patch, but also the total biomass in other patches. Such nonlocal competition effect is biologically reasonable, particularly when the depletion of the common resources in the whole habitat is incorporated. Specifically, nonlocal competition refers to interactions among species that are influenced not only by the local population sizes but also by the population sizes in other regions or patches. This type of competition can occur when species are affected by common resources that are shared across different patches or when individuals can move between patches, causing their presence in one patch to affect the competition dynamics in another. This concept is particularly relevant in ecosystems where resources are limited and the depletion or availability of resources in one area can impact species across a wider habitat. In this paper, we consider the nonlocal competition to better capture these realistic ecological scenarios, where the growth rate of a species at a specific location is influenced by the overall biomass distribution throughout the habitat. We refer to [12] for a spatially continuous nonlocal competition model.

What is the optimal migration rate in the sense that the species dispersing by it competitively excludes all other species with different migration rates? This question has been investigated in the context of two-patch models ($N=2$), see e.g. [7, 13, 21]. In particular, Hastings [13] showed that if the environment is spatially heterogeneous but temporally constant (i.e. m_j is time-independent for each patch j and $m_j \neq m_k$ for some $j \neq k$), then the slower diffuser can invade the faster diffuser when rare but not vice versa. In the context of the theory of adaptive dynamics [9], the result of Hastings implies that zero migration rate is a convergent stable strategy.

In this paper we study the question of selection on migration rates by considering model (1.4) with nonlocal competition, in spatially heterogeneous and temporally periodic environment.

Our first main result determines the global dynamics of model (1.4).

Theorem 1.2. *For each* $i=1,\ldots,N$, *let* $\mathbf{u}_i=(u_{i1},\cdots,u_{iK})$ *be the solution of* (1.4) *with positive initial data. Let* $\lambda(d_i)$ *be the principal eigenvalue of* (1.2) *with* $d=d_i$, *and the corresponding eigenvector is denoted by* $\boldsymbol{\varphi}_i=(\varphi_{i1},\cdots,\varphi_{iK})>0$. *Assume that* $\lambda(d_1)<0$ *and* $\lambda(d_1)<\lambda(d_j)$ *for* $j=2,\ldots,N$, *then*

$$\mathbf{u}_1 \;\to\; \frac{u_*(t)}{\sum_{j=1}^K \varphi_{1j}}\boldsymbol{\varphi}_1>0, \quad \mathbf{u}_2,\cdots,\mathbf{u}_N \;\to\; 0 \quad \text{as} \quad t \;\to\; +\infty,$$

whereas $u_*(t)$ *is the unique positive periodic solution of*

$$\frac{\mathrm{d}u}{\mathrm{d}t}=\left[\frac{\mathrm{d}}{\mathrm{d}t}\left(\ln\sum_{j=1}^K \varphi_{1j}(t)\right)-\lambda(d_1)-u\right]u, \quad u(t)=u(t+T), \quad t\in\mathbb{R}. \tag{1.5}$$

Theorem 1.2 implies that the migration rates, identified as the minimal points for the principal eigenvalue of (1.2), represent an optimal movement strategy. This strategy enables a species to competitively exclude other species whose migration rate is associated with larger $\lambda(d)$. It is referred to as an evolutionary stable strategy [26] in the theory of adaptive dynamics. When the environment is spatially heterogeneous but temporally constant, the principal eigenvalue $\lambda(d)$ is increasing in d, so that Theorem 1.2 implies the smaller migration rate has apparent competitive advantage, which is consistent with the findings of Hastings [13]. However, when the environment is spatially and temporally varying, the dependence of principal eigenvalue $\lambda(d)$ on migration rate d turns out to be more complicated. In particular, it was shown in [23, Theorem 1.3] that even in two-patch case ($K=2$), there are at least three different outcomes, including the evolution of slow dispersal, the evolution of intermediate dispersal, and the evolution branching. We refer to Section 3 for more details.

1.2 Reaction diffusion model

Consider the time-periodic reaction diffusion equation of the form

$$\begin{cases}\partial_t U=\nabla\cdot(d\nabla U-\alpha U\mathbf{b})+U(m(x,t)-U), & x\in\Omega, \quad t>0,\\ d\partial_\nu U-\alpha U(\mathbf{b}\cdot\nu)=0, & x\in\partial\Omega, \quad t>0,\\ U(x,0)=U_0(x)\geq\not\equiv 0, & x\in\Omega,\end{cases}\tag{1.6}$$

where Ω is a bounded domain in $\mathbb{R}^n$ with smooth boundary $\partial\Omega$ and $\nu(x)$ denotes the unit outward normal vector at $x\in\partial\Omega$. Eq. (1.6) serves as an important mathematical models for the persistence of single population with logistic growth, where $U(x,t)$ represents the density of the single species at location x and time t. The function $m\in C(\overline{\Omega}\times\mathbb{R})$ accounts for the local carrying capacity or the intrinsic growth rate of the species, which is assumed to be time-periodic with period $T>0$. Besides random diffusion, the population is also assumed to move along vector field $\mathbf{b}\in C^1(\Omega\times\mathbb{R};\mathbb{R}^n)$, which is T-periodic in t. Parameter $d>0$ and $\alpha\geq 0$ represent the diffusion and advection rates, respectively. When $m=m(x)$ is time-independent and $\mathbf{b}=\nabla m(x)$ is a time-independent gradient vector field, model (1.6) was first proposed by Belgacem and Cosner [2], see [5, 6, 8] and references therein for the further studies in this case.

The dynamics of problem (1.6) is related to the linear eigenvalue problem

$$\begin{cases}\partial_t\varphi=\nabla\cdot(d\nabla\varphi-\alpha\varphi\mathbf{b})+m(x,t)\varphi+\lambda\varphi, & x\in\Omega, \quad t\in\mathbb{R},\\ d\partial_\nu\varphi-\alpha\varphi(\mathbf{b}\cdot\nu)=0, & x\in\partial\Omega, \quad t\in\mathbb{R},\\ \varphi(x,t)=\varphi(x,t+T), & x\in\Omega, \quad t\in\mathbb{R}.\end{cases}\tag{1.7}$$

By the Krein-Rutman theorem, problem (1.7) admits a unique principal eigenvalue, which is simple, real and has the smallest real part among all eigenvalues of (1.7), and it corresponds to a positive eigenfunction, see [14, Proposition 16.1]. Similar to Theorem 1.1, the dynamics of problem (1.6) can be characterized by the following result.

Theorem 1.3. *For each* $d>0$ *and* $\alpha\geq 0$*, let* $\lambda(d,\alpha)$ *be the principal eigenvalue of* (1.7)*.*

- *(i) If* $\lambda(d,\alpha)<0$*, then problem* (1.7) *admits a positive* T*-periodic solution, which is unique and globally asymptotically stable among all non-negative and non-trivial (i.e. not identically zero) initial data.*
- *(ii) If* $\lambda(d,\alpha)\geq 0$*, the trivial solution* 0 *is globally asymptotically stable among all non-negative initial data.*

Theorem 1.3 can be proved by [14, Theorem 28.1] or [15, Proposition 3.1], where the case $\mathbf{b}=0$ is studied, but their proofs are applicable to our setting. Similar to Theorems 1.1, 1.3 implies that a population can persist if and only if the principal eigenvalue of (1.7) is negative, namely $\lambda(d,\alpha)<0$. This suggests that selecting the diffusion rate d and advection rate α that minimize principal eigenvalue $\lambda(d,\alpha)$ is always beneficial to the persistence of the population.

As in Section 1.1, regarding the diffusion and advection rate as a strategy of the population, we assess the effectiveness of such strategy by comparing it with other strategies. To this end, we consider the following nonlocal model of N competing species:

$$\begin{cases}\partial_t U_i=\nabla\cdot(d_i\nabla U_i-\alpha_i U_i\mathbf{b})+U_i\left[m_i(x,t)-\sum\limits_{j=1}^{N}\overline{U}_j(t)\right], & x\in\Omega, \quad t>0, \quad i=1,\dots,N,\\ d_i\partial_\nu U_i-\alpha_i U_i(\mathbf{b}\cdot\nu)=0, & x\in\partial\Omega, \quad t>0, \quad i=1,\dots,N,\\ U_i(x,0)=U_{i,0}(x), & x\in\Omega, \qquad\qquad i=1,\dots,N,\end{cases} \tag{1.8}$$

where $\overline{U}_j(t)$ denotes the total population density of j-th species at time t given by

$$\overline{U}_j(t):=\int_\Omega U_j(x,t)\mathrm{d}x, \quad 1\leq j\leq N. \tag{1.9}$$

Here $U_i(x,t)$ represents the density of the populations i at location x and time t. The diffusion rate and advection rate of population i are denoted by d_i and $\alpha_i, 1\leq i\leq N$, respectively. The growth rate of the i-th population at low densities is represented by function $m_i(x,t)$, which is time-periodic with common period $T>0$. No-flux type of boundary conditions imposed on $\partial\Omega$ represents the condition of no net migration across $\partial\Omega$. The initial data $\{U_{i,0}\}_{i=1}^N$ are assumed to be continuous and non-negative.

Similar to model (1.4), the intra- and inter-specidic competition effects in (1.8) are assumed to depend on an average population biomass in whole habitat. This is the nonlocal interspecific competition and is motivated by a more general nonlocal competition structure given by

$$\sum_{j=1}^{N}\int_\Omega K(x,y)U_j(y,t)\mathrm{d}y, \tag{1.10}$$

where $K\geq 0$ is a kernel function satisfying

$$\int_\Omega\int_\Omega K(x,y)\mathrm{d}x\mathrm{d}y=|\Omega|^2.$$

The competition component in (1.8) is a special form of (1.10) by choosing $K\equiv 1$. We refer to [12] for more discussions on nonlocal competition effects in biological interaction models.

Another special but important example is $K(x,y)=\delta(x-y)|\Omega|^2$ with the Dirac measure $\delta(\cdot)$ supported at 0. In this case, the competition (1.10) is simplified to $|\Omega|^2\sum_{j=1}^N U_j$, known as the Lotka-Volterra competition, which has been extensively investigated. For example, when the environment is spatially varying but temporally constant (i.e. $m_i=m_i(x)$ is independent of t), Dockery *et al.* [10] considered the case $\alpha=0$ and $N=2$, and proved that the population with the slower dispersal rate has the advantage, which is the so-called evolution of slow dispersal. However, when the environment varies both spatially and temporally, the dynamics become much more complicated. We refer to [1,15] for the study of the scenario involving two species, where it is shown that the coexistence of the two species is possible.

In this paper, the global dynamics of model (1.8), with the kernel $K\equiv 1$ in (1.10), is investigated. It appears interesting to investigate the dynamics of (1.8) incorporating a broader scope of competition as described by (1.10).

Theorem 1.4. *Let $U_i(x,t)$, $i=1,\ldots,N$, be the solution of* (1.8) *with nonnegative and non-trivial initial data. Denote by λ_i the principal eigenvalue of problem* (1.7) *with $d=d_i,\alpha=\alpha_i$, and m replaced by m_i, and the corresponding eigenfunction is denoted by $\varphi_i(x,t)>0$. Suppose that $\lambda_1<0$ and $\lambda_1<\lambda_j$ for all $j=2,\ldots,N$, then*

$$\begin{aligned} U_1(x,t) &\;\to\; \frac{\varphi_1(x,t)U_*(t)}{\int_\Omega\varphi_1(x,t)\mathrm{d}x}>0,\\ \int_\Omega U_2(x,t)\mathrm{d}x,\cdots,\int_\Omega U_N(x,t)\mathrm{d}x &\;\to\; 0 \end{aligned}$$

as $t\to+\infty$. Here $U_*>0$ is the unique positive periodic solution of

$$\frac{\mathrm{d}U}{\mathrm{d}t}=\left[\frac{\mathrm{d}}{\mathrm{d}t}\left(\ln\int_\Omega\varphi_1(x,t)\mathrm{d}x\right)-\lambda_1-U\right]U,\quad t>0. \tag{1.11}$$

Theorem 1.4 indicates that global dynamics of model (1.8) is completely determined by the principal eigenvalue $\lambda(d,\alpha)$ of problem (1.7). Assume that $m_1=\cdots=m_N$ in $\Omega\times\mathbb{R}$ so that these N populations share a common growth rate, which are identical except for their diffusion and advection rates. Theorem 1.4 implies that the population, that adapts its diffusion and advection rates to align with the smallest value of $\lambda(d,\alpha)$ among all populations, will gain a competitive advantage and competitively exclude all other populations. In particular, the populations are unable to coexist, differing from the results in [1,15] for Lotka-Volterra competition of two species. This finding is analogue to that of

Theorem 1.2 for patch model (1.4). Therefore, the dependence of the principal eigenvalue on diffusion and advection rates plays a central roles in understanding the evolution of dispersal.

When $\alpha=0$, the principal eigenvalue $\lambda(d,0)$ of problem (1.7) is studied in [22], which reveals at least three different outcomes, including the evolution of slow dispersal, the evolution of intermediate dispersal, and the evolution branching (though this is rare). For general vector field $\mathbf{b}$, it is thus of interest to understand the dependence of α on general values of d and α, in particular, to determine where $\lambda(d,\alpha)$ is locally minimized.

This paper is organized as follows. In Section 2, we provide some biological discussions and numerical simulations to further illustrate the results of the paper. In Section 3, we present the proofs of Theorems 1.2 and 1.4.

2 Biological discussions and numerical simulations

It is clear from previous section that the dependence of the principal eigenvalue $\lambda(d)$ on the diffusion rate d is critical: For both single and multiple competing species, it is better to minimize $\lambda(d)$. For single species, it is important to determine the sign of $\lambda(d)$ in order to ensure the persistence of the species; namely, the single species can persist if and only if $\lambda(d)$ is negative. Hence, if $\inf_{d>0}\lambda(d)$ is negative, there exists some interval of the diffusion rates in which the species can persist. The so-called question of "dispersal induced growth" asks whether it is possible for the species to persist for some diffusion rates, even though it can not persist without dispersal. If we translate it into mathematical terms, it essentially asks whether it is possible to have non-negative limit $\lim_{d\to 0}\lambda(d)$ but $\inf_{d>0}\lambda(d)$ is negative. In fact, one can further ask whether it is possible for a single species to persist for some diffusion rates even though it can not persist without dispersal or in well mixed environments; i.e. both limits $\lim_{d\to 0}\lambda(d)$ and $\lim_{d\to\infty}\lambda(d)$ are non-negative but $\inf_{d>0}\lambda(d)$ is negative. These questions beg for further studies of the dependence of $\lambda(d)$ on d, which is of independent interest mathematically.

For two or more competing species, it is important to determine how to minimize $\lambda(d)$ so that the optimal "trait" competitively excludes other species and to determine how trait will evolve in spatially and/or temporarily varying environments. When the environment is spatially heterogeneous but temporally constant, we know that $\lambda(d)$ is monotone increasing with respect to diffusion d, so slow diffusion rate is favored. When the environment is spatially and temporally varying, the dependence of principal eigenvalue on diffusion rate d becomes complicated.

2.1 Biological discussions on patch model

In this subsection, we apply the theory of adaptive dynamics to further illustrate Theorem 1.2. Model (1.4) has a trivial periodic solution $(0,\cdots,0)$, and N periodic solutions

$$(\mathbf{p}_1,0,\cdots,0),\cdots,(0,\cdots,\mathbf{p}_i,\cdots,0),\cdots,(0,\cdots,0,\mathbf{p}_N),$$

where only one population is present. For each $i=1,\dots,N$, $\mathbf{p}_i=(p_{i1},\cdots,p_{iK})$ is the unique positive periodic solution of the problem

$$\begin{cases} \dfrac{\mathrm{d}\mathbf{p}_i}{\mathrm{d}t}=d_i\mathbf{L}\mathbf{p}_i+\mathrm{diag}\left\{m_j-\sum\limits_{j=1}^{K}p_{ij}\right\}\mathbf{p}_i, & t\in\mathbb{R}, \\ \mathbf{p}_i(t)=\mathbf{p}_i(t+T), & t\in\mathbb{R}. \end{cases} \tag{2.1}$$

In the framework of adaptive dynamics, we can view the i_*-th species as a resident population with density $\mathbf{p}_{i_*}$, adopting a given strategy d_{i_*} at ecological equilibrium. Comparing (2.1) with eigenvalue problem (1.2), it can verified that

$$\lambda(d_{i_*})=-\frac{1}{T}\int_0^T\sum_{j=1}^{K}p_{i_*j}\mathrm{d}t \tag{2.2}$$

for some constant $c>0$, where $\lambda(d_{i_*})$ is the principal eigenvalue of problem (1.2) with $d=d_{i_*}$. Let the ℓ-th species be an invasive population (e.g. a rare mutant) with strategy d_ℓ. The outcome of the invasion is determined by the invasion fitness $\Lambda(d_\ell,d_{i_*})$, which measures the advantage to the invader species playing strategy d_l over the resident population playing strategy d_{i_*}. Mathematically, the fitness function $\Lambda(d_\ell,d_{i_*})$ can be given by the principal eigenvalue of the following problem:

$$\begin{cases} \dfrac{\mathrm{d}\boldsymbol{\varphi}}{\mathrm{d}t}=d_\ell\mathbf{L}\boldsymbol{\varphi}+\mathrm{diag}\left\{m_j-\sum\limits_{j=1}^{K}p_{i_*j}\right\}\boldsymbol{\varphi}-\Lambda\boldsymbol{\varphi}, & t\in\mathbb{R}, \\ \boldsymbol{\varphi}(t)=\boldsymbol{\varphi}(t+T), & t\in\mathbb{R}. \end{cases}$$

Together with (1.2) and (2.2), it is not difficult to observe that

$$\Lambda(d_\ell,d_{i_*})=\lambda(d_{i_*})-\lambda(d_\ell). \tag{2.3}$$

Equality (2.3) provides an explicit connection between the persistence criterion and the invasion fitness. Biologically, the invasion fitness $\Lambda(d_\ell,d_{i_*})$ represents the long-term exponential growth/decay rate of the mutant with strategy d_ℓ when it invades a resident population adopting strategy d_{i_*}. Hence, when $\Lambda(d_\ell,d_{i_*})>0$, the rare mutant strategy d_l experiences exponential growth, whereas it undergoes exponential decay when $\Lambda(d_\ell,d_{i_*})<0$. It follows by (2.3) that the invading population can invade successfully when rare only when $\lambda(d_\ell)<\lambda(d_{i_*})$, i.e. the strategy resulting in a smaller principal eigenvalue of (1.2) is favored. This observation is consistent with the findings in Theorem 1.2.

It is therefore of interest to investigate the dependence of principal eigenvalue of (1.2) on migration rate d. For two-patch case ($K=2$), such question was considered in [23]. It was shown in [23, Theorem 1.3] that there are at least three different outcomes, including

(1) $d\mapsto\lambda(d)$ is monotone increasing,

(2) $d\mapsto\lambda(d)$ is initially decreasing and then increasing,

(3) $d\mapsto\lambda(d)$ is initially increasing, then decreasing, and finally increasing.

See also Figs. 1 and 2 for some numerical examples.

The signs of fitness $\Lambda(d_\ell,d_{i_*})$ can be analysed graphically by means of "pairwise invasibility plot" (PIP). Based on (2.3), the graphs of $d\mapsto\lambda(d)$ and the corresponding PIPs can be illustrated in Figs. 1 and 2. In PIPs, the regions in which $\Lambda(d_\ell,d_{i_*})>0$ are illustrated by shaded components, while the regions in which $\Lambda(d_\ell,d_{i_*})<0$ are illustrated by blank ones. The boundaries of these regions consist of the zero sets of $\Lambda(d_\ell,d_{i_*})$, which always includes the diagonal due to $\Lambda(d_{i_*},d_{i_*})=0$ for all $d_{i_*}>0$. To see the evolutionary outcomes in PIPs from Figs. 1 and 2, we look along a vertical line through a point on the d_{i_*}-axis representing the strategy of resident population. The parts of this line located within a shaded area correspond to strategies on the d_ℓ-axis for which $\Lambda(d_\ell,d_{i_*})>0$, suggesting potentially invading populations. Conversely, the parts of the line inside a blank area correspond to strategies for which $\Lambda(d_\ell,d_{i_*})<0$, signifying populations that are unable to invade.

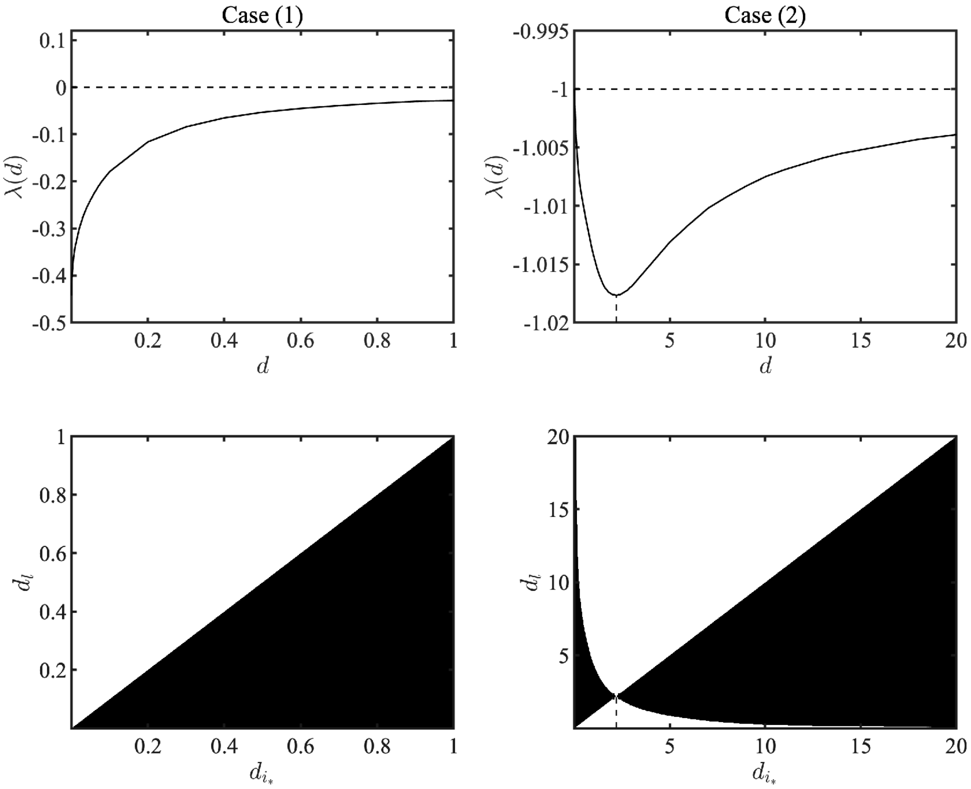

Figure 1: The numerical examples for Cases (1) and (2), where the graph of $d\mapsto\lambda(d)$ and the corresponding pairwise invasibility plots are illustrated. Here, we choose $K=21$, $m_j(t)=(j/10)\sin^2(2\pi t)$ for Case (1), $m_j(t)=1+\sin(\pi j/10)\sin(2\pi t)$ for Case (2), and $j=0,1,2,\ldots,20$.

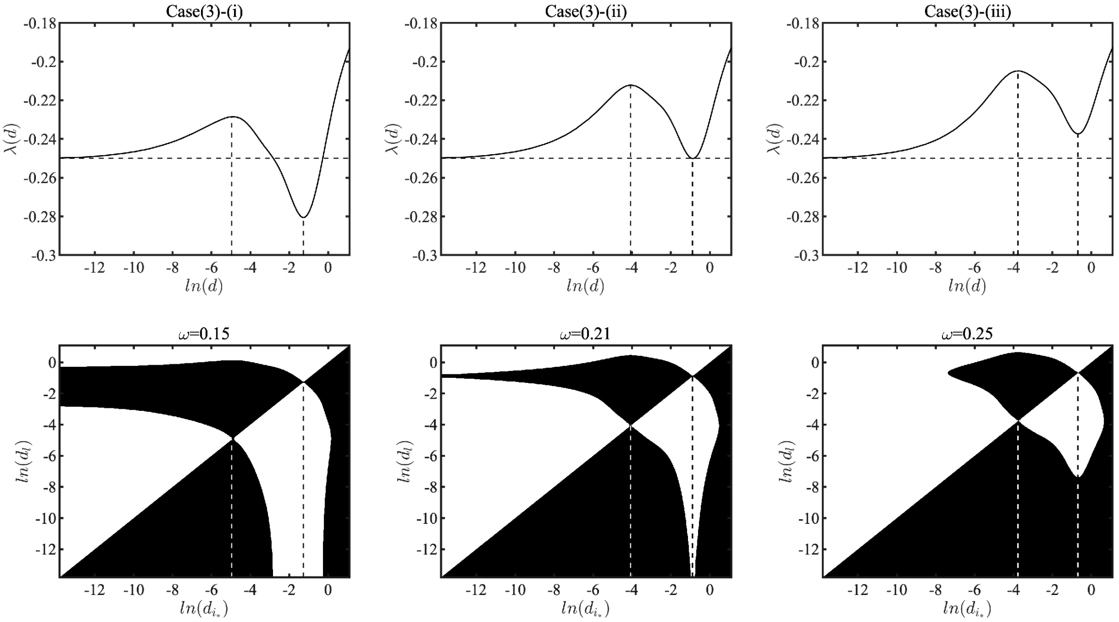

Figure 2: The numerical examples for Case (3), where the graph of $d \mapsto \lambda(d)$ and the corresponding pairwise invasibility plots are illustrated. Here, we choose $K=21$ and $m_j(t)=\cos(\pi j/20)/4+\sin(\pi j/10)\sin(2\pi\omega t)$ with $\omega=0.15,0.21,0.25$ and $j=0,1,2,\ldots,20$.

In Case (1), the principal eigenvalue $\lambda(d)$ is increasing in d as illustrated in Fig. 1. For any resident population with diffusion rate d_{i_*}, the mutant adopting strategy d_ℓ can invade and have a positive fitness if and only if $d_\ell < d_{i_*}$, and hence $d_{i_*}=0$ is a convergence stable strategy [11]. This indicates the evolution of slower dispersal, as observed in spatially heterogeneous but temporally constant environment by Hastings [13]. In Case (2), diffusion rate $d_* > 0$ is the unique minimal point of $\lambda(d)$. The vertical line through d_* lies entirely inside the blank area in Fig. 1. This implies $\Lambda(d_\ell, d_*) < 0$ for all $d_\ell \neq d_*$, namely no mutant can invade the resident with rate d_*. The strategy d_* is identified as a global evolutionarily stable strategy (ESS) [26]. The evolution of intermediate dispersal happens in this case. In Case (3), diffusion rate d^* is a local maximal point of principal eigenvalue $\lambda(d)$ as illustrated in Fig. 2, so that (2.3) implies $\Lambda(d_\ell, d^*) > 0$ for all $d_\ell \neq d^*$ and $d_\ell \approx d^*$. Hence, for the resident with strategy $d_{i_*}=d^*$, all nearby mutants can invade and have a positive fitness. Hence, strategy d^* is not evolutionarily stable and the nearby population will evolve away and towards some ESS. In contrast, diffusion rates 0 and d_* are local minimal points of $\lambda(d)$ and exhibit evolutionary outcomes opposite to that of d^*. We shall discuss this in three different scenarios.

For Case (3)-(i), diffusion rate d_* is the minimal point of $\lambda(d)$ and serves as the global ESS as in Case (2). Unlike d_*, in the corresponding PIP of Fig. 2, the vertical line through $d_{i_*}=0$ lies inside both blank and shaded areas. This implies that the mutant with small diffusion rate d_ℓ will be unable to successfully invade the immobile resident ($d_{i_*}=0$), and thus 0 is a local ESS. This corresponds to the fact that 0 is a local minimal of principal eigenvalue $\lambda(d)$.

For Case (3)-(ii), it is illustrated in Fig. 2 that diffusion rates 0 and d_* are minimal points of $\lambda(d)$, both of which are local ESS. The resident adopting strategy 0 or d_* can resist the invasion of any other strategy with strategy $d_\ell > 0$ and $d_\ell \neq d_*$.

For Case (3)-(iii), diffusion rate 0 is the minimal point of $\lambda(d)$ and the vertical line through 0 lies entirely the blank area as in PIP of Fig. 2. Hence, any mutant is unable to invade the immobile resident, and strategy 0 is the global ESS. In contrast, strategy d_* is a local ESS in this case.

2.2 Numerical examples for reaction diffusion model

In this subsection, we perform some numerical simulations for multi-species competition model with more general nonlocal competition structure (1.10). Specifically, similar to (1.8) we consider the following model:

$$\begin{cases} \partial_t U_i = d_i \Delta U_i + U_i \left[m(x,t) - \sum_{j=1}^{N} \int_\Omega K(x,y) U_j(y,t) dy \right], & x \in \Omega, \quad t > 0, \quad i = 1,\dots,N, \\ \partial_\nu U_i = 0, & x \in \partial\Omega, \quad t > 0, \quad i = 1,\dots,N, \\ U_i(x,0) = U_{i,0}(x), & x \in \Omega, \quad\quad\quad\quad i = 1,\dots,N, \end{cases} \tag{2.4}$$

where $K \geq 0$ denotes the competition kernel satisfying

$$\int_\Omega \int_\Omega K(x,y) \mathrm{d}x \mathrm{d}y = |\Omega|^2,$$

and the time-periodic $m(x,t)$ is the common growth rate of competing species.

We assume $N = 2, \Omega = (-1,1)$, and $m(x,t) = 1 + \sin(\pi x)\sin(2\pi t)$. Moreover, for each $a \in (0,1)$, we define

$$K(x,y) = \left[\frac{(1-a)\pi}{2} \cos\left(\frac{\pi x}{2}\right) + a \right] G_a(y), \tag{2.5}$$

where $G_a : (-1,1) \mapsto [0,1]$ is defined by

$$G_a(y) = \begin{cases} \dfrac{1}{a}, & y \in [-a,a], \\ 0, & y \notin (-a,a). \end{cases}$$

Case 1: $a = 1$. When $a = 1$, it follows by (2.5) that $K(x,y) \equiv 1$. Hence, under the above assumptions, model (2.4) takes the following form:

$$\begin{cases}\partial_t U_1 = d_1 \Delta U_1 + U_1\left[m(x,t) - \sum\limits_{j=1}^{2}\displaystyle\int_{-1}^{1} U_j(x,t)\mathrm{d}x\right], & x\in(-1,1), \quad t>0,\\ \partial_t U_2 = d_2 \Delta U_2 + U_2\left[m(x,t) - \sum\limits_{j=1}^{2}\displaystyle\int_{-1}^{1} U_j(x,t)\mathrm{d}x\right], & x\in(-1,1), \quad t>0,\\ \partial_\nu U_1(\pm 1,t) = \partial_\nu U_2(\pm 1,t) = 0, & \qquad\qquad\quad t>0,\\ U_1(x,0) = U_{1,0}(x), U_2(x,0) = U_{2,0}(x), & x\in(-1,1),\end{cases} \tag{2.6}$$

which is a particular example for model (1.8). For each $d>0$, let $\lambda(d)$ be the principal eigenvalue of the problem

$$\begin{cases}\partial_t \varphi = d\partial_{xx}\varphi + \big(1+\sin(\pi x)\sin(2\pi t)\big)\varphi + \lambda\varphi, & x\in(-1,1), \quad t\in\mathbb{R},\\ \partial_x \varphi(\pm 1,t) = 0, & \qquad\qquad\quad t\in\mathbb{R},\\ \varphi(x,t) = \varphi(x,t+1), & x\in(-1,1), \quad t\in\mathbb{R}.\end{cases}$$

Theorem 1.4 implies that the dynamics of (2.6) are determined completely by principal eigenvalue $\lambda(d)$. We thus compute $\lambda(d)$ numerically and numerical simulations for the dependence of $\lambda(d)$ on diffusion rate d is shown in Fig. 3(A). This is consistent with the theoretical result in [22], namely function $d \mapsto \lambda(d)$ is initially decreasing and then increasing, and there is a minimum point $d_* \approx 2.2$ such that $\lambda(d_*) = \min_{d>0}\lambda(d)$. Next, we shall verify that $d_* \approx 2.2$ is a global evolutionarily stable strategy (ESS) as proved by Theorem 1.4, see also Section 3.

To this end, we perform some numerical simulations for the solution (U_1,U_2) of (2.6) with different diffusion rates $(d_1,d_2)\in[0,3]\times[0,3]$ as shown in Fig. 3(B). Therein the blank areas represent the regions where the species with diffusion rate d_1 wins the competition, while the shaded areas represent the regions where the species with diffusion rate d_2 wins. Observe that the vertical line through $d_1 = d_*$ lies entirely inside the blank area, signifying the dominance of the species with diffusion rate $d_1 = d_*$ over its competitor with a different diffusion rate. Hence, such d_* is a global ESS, which is consistent with the observations in Fig. 1.

Case 2: $a\in(0,1)$. When $a\in(0,1)$, model (2.4) can be rewritten as

$$\begin{cases}\partial_t U_1 = d_1 \partial_{xx} U_1 + U_1\left[m(x,t) - \dfrac{F_a(x)}{a}\sum\limits_{j=1}^{2}\displaystyle\int_{-a}^{a} U_j(y,t)\mathrm{d}y\right], & x\in(-1,1), \quad t>0,\\ \partial_t U_2 = d_2 \partial_{xx} U_2 + U_2\left[m(x,t) - \dfrac{F_a(x)}{a}\sum\limits_{j=1}^{2}\displaystyle\int_{-a}^{a} U_j(y,t)\mathrm{d}y\right], & x\in(-1,1), \quad t>0,\\ \partial_x U_1(\pm 1,t) = \partial_x U_2(\pm 1,t) = 0, & \qquad\qquad\quad t>0,\\ U_1(x,0) = U_2(x,0) = \exp(x^2), & x\in(-1,1),\end{cases} \tag{2.7}$$

where

$$F_a(x) = \frac{(1-a)\pi}{2}\cos\Big(\frac{\pi x}{2}\Big) + a.$$

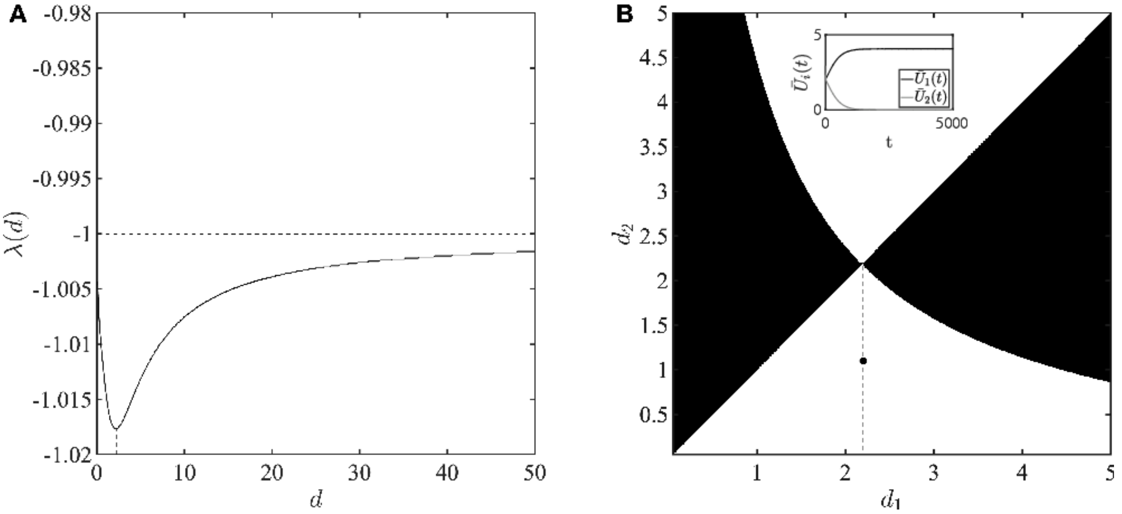

Figure 3: (A) The dependence of principal eigenvalue $\lambda(d)$ on diffusion rate d. The solid line indicates the value of λ against d, while the dashed line indicates $\lambda(0)=\lambda(+\infty)=-1$. (B) The competition results of (U_1,U_2) with different diffusion rates (d_1,d_2). The insert plot shows the long-time behaviors of (U_1,U_2) with different diffusion rates $(d_1,d_2)=(2.2,1.0)$. The black indicates $\overline{U}_1(t)=\int_0^1 U_1(x,t)dx$, while the grey indicates $\overline{U}_2(t)=\int_0^1 U_2(x,t)dx$.

In what follows, we will explore how kernel function $K(x,y)$ affect evolutionarily stable strategy (ESS).

We choose diffusion rates $(d_1,d_2)\in[0,3]\times[0,3]$ for given $a\in(0,1)$, the competition results of (U_1,U_2) with different (d_1,d_2) are shown in Fig. 4. The simulation results suggest that there exist two constants $0<a_*<a^*<1$ such that the followings hold:

(i) For $0<a<a_*$, diffusion rate $d=0$ is the unique singular strategy, which is globally evolutionarily stable. This implies the evolution of slow dispersal, see Fig. 4(A).

(ii) For $a_*<a<a^*$, there are three singular strategies $d=0,d^*,d_*$ for some $0<d^*<d_*$ depending on a. It can be observed in Figs. 4(B-J) that while strategy $d=0$ is a global ESS, strategy $d=d_*$ severs as a local ESS and is a increasing function of a. In contrast, strategy $d=d^*$ is not evolutionarily stable and all nearby mutants can invade it, which can be decreasing in a and $d^*\searrow 0$ as $a\nearrow a^*$.

(iii) For $a^*<a<1$, diffusion rate $d=d_*$ is the unique singular strategy and serves as a global ESS, see Figs. 4(K-L).

Hence, the dynamics of (2.7) are rather rich and interesting for different $a\in(0,1)$. It will be of interest to generalize Theorem 1.4 to more general problem (2.4) and to investigate the impact of competition kernel on the evolution outcomes.

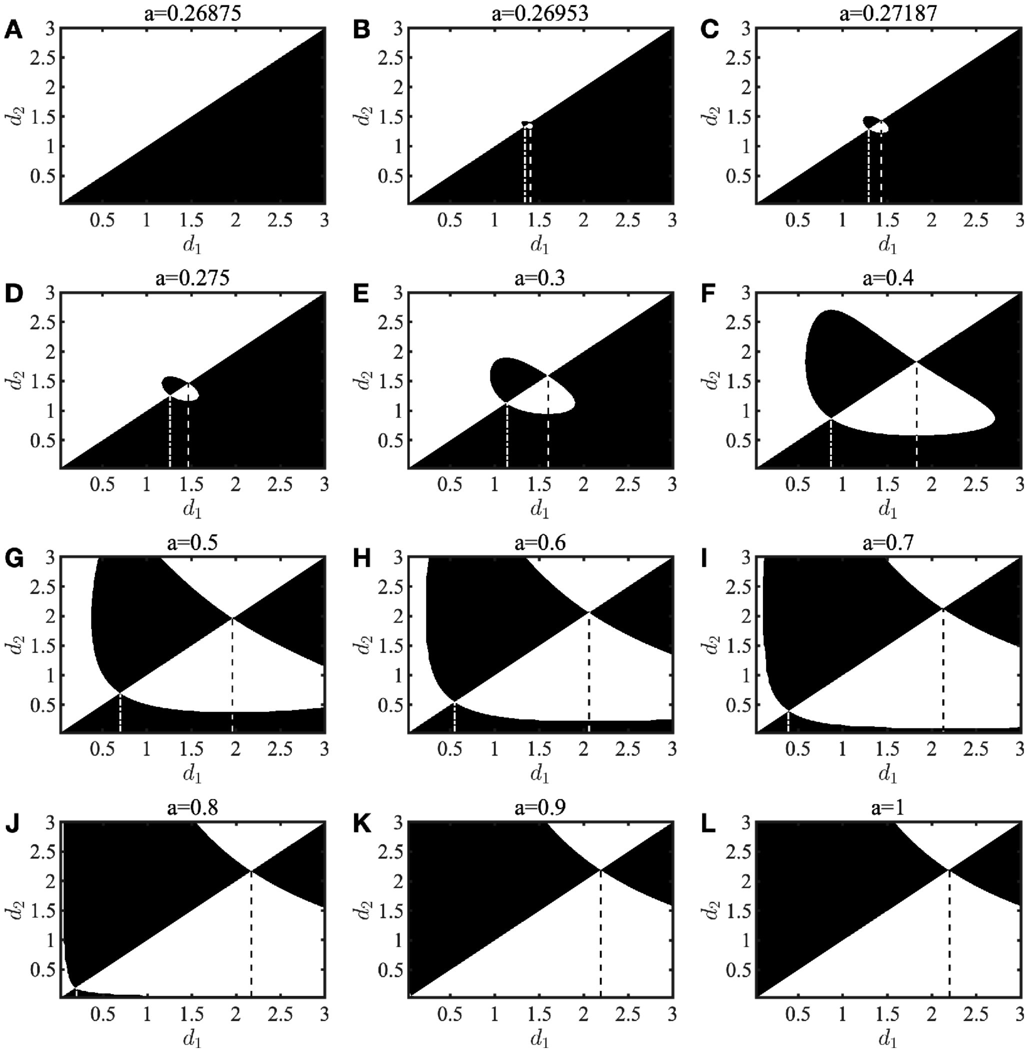

Figure 4: The competition results of (U_1,U_2) with different diffusion rates d_1,d_2 for given a. The blank areas represent the regions where $(U_1^*,0)$, while the shaded areas represent where $(0,\bar{U}_2^*)$. The dash-dotted line indicates $d_1 \approx d^*$, while the dashed line indicates $d_1 \approx d_*$.

3 Mathematical proofs

3.1 Proof of Theorem 1.2

In this subsection, we will prove Theorem 1.2. We first prepare the following result.

Lemma 3.1. *For each* $i=1,\ldots,N$, *let* $\boldsymbol{\varphi}_i=(\varphi_{i1},\cdots,\varphi_{iK})>0$ *denote the principal eigenvector of problem* (1.2) *with* $d=d_i$. *Then* $\mathbf{v}=\boldsymbol{\varphi}_i/\sum_{j=1}^{K}\varphi_{ij}$ *is the unique positive periodic solution of the problem*

$$\begin{cases}\dfrac{\mathrm{d}\mathbf{v}}{\mathrm{d}t}=d_i\mathbf{L}\mathbf{v}+\mathrm{diag}\left\{m_j-\displaystyle\sum_{j=1}^{K}m_jv_j\right\}\mathbf{v}, & t\in\mathbb{R},\\ \mathbf{v}(t)=\mathbf{v}(t+T), & t\in\mathbb{R}.\end{cases}\tag{3.1}$$

Proof. For each $i=1,\ldots,N$, let λ_i be the principal eigenvalue of problem (1.2). Set $\overline{\varphi}_i:=\sum_{j=1}^{K}\varphi_{ij}$. Similar to (3.7), by (1.2) one can calculate $\mathbf{v}=\boldsymbol{\varphi}_i/\sum_{j=1}^{K}\varphi_{ij}$ satisfies

$$\begin{aligned}\frac{\mathrm{d}\mathbf{v}}{\mathrm{d}t}&=\frac{1}{\overline{\varphi}_i}\frac{\mathrm{d}\boldsymbol{\varphi}_i}{\mathrm{d}t}-\frac{\boldsymbol{\varphi}_i}{(\overline{\varphi}_i)^2}\sum_{j=1}^{K}\frac{\mathrm{d}\varphi_{ij}}{\mathrm{d}t}\\ &=\frac{d_i\mathbf{L}\boldsymbol{\varphi}_i}{\overline{\varphi}_i}+\mathrm{diag}\{m_j\}\frac{\boldsymbol{\varphi}_i}{\overline{\varphi}_i}+\lambda_i\frac{\boldsymbol{\varphi}_i}{\overline{\varphi}_i}-\frac{\boldsymbol{\varphi}_i}{(\overline{\varphi}_i)^2}\left[\sum_{j=1}^{K}m_j\varphi_{ij}+\lambda_i\overline{\varphi}_i\right]\\ &=d_i\mathbf{L}\mathbf{v}+\mathrm{diag}\left\{m_j-\sum_{j=1}^{K}m_jv_j\right\}\mathbf{v}.\end{aligned}$$

This verifies that $\mathbf{v}=\boldsymbol{\varphi}_i/\sum_{j=1}^{K}\varphi_{ij}$ is a positive solution of (3.1). It remains to show the uniqueness of the solution to (3.1).

To this end, let $\mathbf{v}=(v_1,\cdots,v_K)$ be any positive solution of (3.1). We observe that

$$\frac{\mathrm{d}}{\mathrm{d}t}\sum_{j=1}^{K}v_j=\left(1-\sum_{j=1}^{K}v_j\right)\sum_{j=1}^{K}m_jv_j,\quad \sum_{j=1}^{K}v_j(t)=\sum_{j=1}^{K}v_j(t+T),$$

from which one can deduce

$$\sum_{j=1}^{K}v_j(t)\equiv 1,\quad \forall t\in\mathbb{R}.\tag{3.2}$$

Next we assume that $\mathbf{v}^+=(v_1^+,\cdots,v_K^+)$ and $\mathbf{v}^-=(v_1^-,\cdots,v_K^-)$ are two positive periodic solutions of (3.1). Set

$$f^{\pm}(t):=\exp\left\{\sum_{j=1}^{k}\left[\int_0^t m_j(s)v_j^{\pm}(s)\mathrm{d}s-\frac{t}{T}\int_0^T m_j(s)v_j^{\pm}(s)\mathrm{d}s\right]\right\},\tag{3.3}$$

Define $\mathbf{w}^+:=f^+\mathbf{v}^+$ and $\mathbf{w}^-:=f^-\mathbf{v}^-$, then we calculate that

$$\begin{cases}\dfrac{\mathrm{d}\mathbf{w}^+}{\mathrm{d}t}=d\mathbf{L}\mathbf{w}^++\mathrm{diag}\{m_j\}\mathbf{w}^+-\dfrac{\mathbf{w}^+}{T}\displaystyle\int_0^T\sum_{j=1}^{K}m_jv_j^+\mathrm{d}t, & t\in\mathbb{R},\\ \dfrac{\mathrm{d}\mathbf{w}^-}{\mathrm{d}t}=d\mathbf{L}\mathbf{w}^-+\mathrm{diag}\{m_j\}\mathbf{w}^--\dfrac{\mathbf{w}^-}{T}\displaystyle\int_0^T\sum_{j=1}^{K}m_jv_j^-\mathrm{d}t, & t\in\mathbb{R},\\ \mathbf{w}^+(t)=\mathbf{w}^+(t+T),\quad \mathbf{w}^-(t)=\mathbf{w}^-(t+T), & t\in\mathbb{R}.\end{cases}\tag{3.4}$$

Recall that λ_i is the principal eigenvalue of (1.2). By the uniqueness of principal eigenfunction of (1.2) up to some constant multiplier, we observe from (3.4) that $\mathbf{w}^+(t)=c\mathbf{w}^-(t)$ for some constant $c>0$ and

$$\frac{1}{T}\int_0^T\sum_{j=1}^K m_j v_j^+ \mathrm{d}t=\frac{1}{T}\int_0^T\sum_{j=1}^K m_j v_j^- \mathrm{d}t=-\lambda_i. \tag{3.5}$$

It follows by (3.2) that

$$\sum_{j=1}^k v_j^+\equiv\sum_{j=1}^k v_j^-\equiv 1,\quad \forall t\in\mathbb{R},$$

and thus by definition, $\sum_{j=1}^k w_j^+=f^+$ and $\sum_{j=1}^k w_j^-=f^-$. This together with $\mathbf{w}^+(t)=c\mathbf{w}^-(t)$ implies $f^+(t)=cf^-(t)$ for all $t\in\mathbb{R}$. Using (3.3) and (3.5), we deduce

$$\sum_{j=1}^K\int_0^t m_j(s)\big(v_j^+(s)-v_j^-(s)\big)\mathrm{d}s\equiv\log c,\quad \forall t\in\mathbb{R},$$

whence we derive that

$$\sum_{j=1}^K m_j(t)v_j^+(t)\equiv\sum_{j=1}^K m_j(t)v_j^-(t),\quad \forall t\in\mathbb{R}. \tag{3.6}$$

Define $\underline{\mathbf{v}}:=\mathbf{v}^+-\mathbf{v}^-$. By (3.6), we see that

$$\begin{cases}\dfrac{\mathrm{d}\underline{\mathbf{v}}}{\mathrm{d}t}=d\mathbf{L}\underline{\mathbf{v}}+\mathrm{diag}\left\{A_i-\displaystyle\sum_{j=1}^K m_j v_j^+\right\}\underline{\mathbf{v}}, & t\in\mathbb{R},\\ \underline{\mathbf{v}}(t)=\underline{\mathbf{v}}(t+T),\quad \displaystyle\sum_{j=1}^K\underline{v}_j(t)\equiv 0, & t\in\mathbb{R},\end{cases}$$

which implies $\underline{\mathbf{v}}(t)\equiv 0$, and hence $\mathbf{v}^+\equiv\mathbf{v}^-$ as desired. The proof is now complete. □

Next, we prove the following asymptotic result.

Lemma 3.2. *Let* $\mathbf{u}_i=(u_{i1},\cdots,u_{iK})>0$ *be the solution of* (1.4). *Then for any* $t\in[0,T]$,

$$\lim_{n\to+\infty}\left|\frac{\mathbf{u}_i(t+nT)}{\sum_{j=1}^K u_{ij}(t+nT)}-\frac{\boldsymbol{\varphi}_i(t)}{\sum_{j=1}^K\varphi_{ij}(t)}\right|=0,\quad i=1,\dots,N,$$

where $\boldsymbol{\varphi}_i=(\varphi_{i1},\cdots,\varphi_{iK})>0$ *denotes the principal eigenvector of problem* (1.2).

Proof. For any $i=1,\dots,N$, define

$$\overline{u}_i(t):=\sum_{j=1}^K u_{ij}(t),\quad \mathbf{v}_i:=\frac{\mathbf{u}_i(t)}{\overline{u}_i(t)},\quad t>0. \tag{3.7}$$

By (1.4) and (3.7), direct calculations yield

$$\frac{\mathrm{d}\mathbf{v}_i}{\mathrm{d}t}=\frac{1}{\overline{u}_i}\frac{\mathrm{d}\mathbf{u}_i}{\mathrm{d}t}-\frac{\mathbf{u}_i}{(\overline{u}_i)^2}\sum_{j=1}^K\frac{\mathrm{d}u_{ij}}{\mathrm{d}t}$$

$$
\begin{aligned}
&=\frac{d_i\mathbf{L}\mathbf{u}_i}{\overline{u}_i}+\operatorname{diag}\left\{m_j-\sum_{i=1}^N\overline{u}_i\right\}\frac{\mathbf{u}_i}{\overline{u}_i}-\frac{\mathbf{u}_i}{(\overline{u}_i)^2}\left[\sum_{j=1}^K m_ju_{ij}-\overline{u}_i\sum_{i=1}^N\overline{u}_i\right]\\
&=d_i\mathbf{L}\mathbf{v}_i+\operatorname{diag}\left\{m_j-\sum_{j=1}^K m_jv_{ij}\right\}\mathbf{v}_i. \qquad (3.8)
\end{aligned}
$$

It follows from (3.7) that

$$
\sum_{j=1}^K v_{ij}(t)\equiv 1, \quad \forall t\in\mathbb{R}, \quad i=1,\dots,N, \tag{3.9}
$$

which implies that $\mathbf{v}_i(t)$ is uniformly bounded in $t\in(0,+\infty)$. Hence, it follows by (3.8) that $\mathrm{d}\mathbf{v}_i(t+nT)/\mathrm{d}t$ is uniformly bounded for all $n\geq 1$. Up to extraction, $\mathbf{v}_i(t+nT)$ converges uniformly on any bounded interval of $t\in\mathbb{R}$ to some T-periodic vector $\mathbf{p}_i=(p_{i1},\cdots,p_{iK})\geq 0$ as $n\to\infty$, which satisfies (3.1) and $\sum_{j=1}^K p_{ij}(t)\equiv 1$ for all $t\in\mathbb{R}$ (due to (3.9)). By the irreducibility of migration matrix $\mathbf{L}$, it is easily seen that $\mathbf{p}_i>0$, i.e. vector $\mathbf{p}_i$ is a positive periodic solution to (3.1). A direct application of Lemma 3.1 yields $\mathbf{p}_i=\boldsymbol{\varphi}_i/\sum_{j=1}^K\varphi_{ij}$, which completes the proof. ☐

Finally, we are in a position to prove Theorem 1.2.

Proof of Theorem 1.2. **Step 1.** Recalling the definitions in (3.7), we show that

$$
\overline{u}_1(t) \;\to\; u_*(t) \quad \text{and} \quad \overline{u}_2(t),\cdots,\overline{u}_N(t) \;\to\; 0 \quad \text{as} \quad t \;\to\; +\infty, \tag{3.10}
$$

where $u_*(t)$ is the unique positive periodic solution of (1.5).

By (3.7), we calculate from (1.4) that

$$
\frac{\mathrm{d}\overline{u}_i}{\mathrm{d}t}=\left(\sum_{j=1}^K m_jv_{ij}-\sum_{i=1}^N\overline{u}_k\right)\overline{u}_k, \quad t>0, \quad i=1,\dots,N. \tag{3.11}
$$

Denote $\boldsymbol{\varphi}_i=(\varphi_{i1},\cdots,\varphi_{iK})>0$ by the principal eigenvector of the problem (1.2). Summing both sides of (1.2) from $j=1$ to K gives

$$
\frac{\mathrm{d}}{\mathrm{d}t}\sum_{j=1}^K\varphi_{ij}=\sum_{j=1}^K m_j\varphi_{ij}+\lambda_i\sum_{j=1}^K\varphi_{ij}, \quad t\in\mathbb{R}. \tag{3.12}
$$

Applying Lemma 3.2, we derive from (3.12) that

$$
\lim_{n\to+\infty}\sum_{j=1}^K m_j(t)v_{ij}(t+nT)=\sum_{j=1}^K\frac{m_j(t)\varphi_{ij}(t)}{\sum_{j=1}^K\varphi_{ij}(t)}=\frac{\mathrm{d}}{\mathrm{d}t}\left(\ln\sum_{j=1}^K\varphi_{ij}(t)\right)-\lambda_i.
$$

Hence, the limiting system of (3.11) can be written as

$$\frac{\mathrm{d}w_i}{\mathrm{d}t}=\left[\frac{\mathrm{d}}{\mathrm{d}t}\left(\ln\sum_{j=1}^{K}\varphi_{ij}(t)\right)-\lambda_i-\sum_{k=1}^{N}w_k\right]w_i,\quad t>0,\quad i=1,\ldots,N. \tag{3.13}$$

Let $(w_1,\cdots,w_N)$ be the solution to (3.13) with any positive initial data. We shall show

$$w_1(t)\ \to\ u_*(t)>0 \quad\text{and}\quad w_2(t),\cdots,w_N(t)\ \to\ 0 \quad\text{as}\quad t\ \to\ +\infty. \tag{3.14}$$

Then (3.10) can be proved by a direct application of the theory of asymptotically periodic systems established in [29, Chapter 3.2.2] (see, e.g. [29, Theorem 3.2.2]). To this end, set

$$W_i(t):=\frac{w_i(t)}{\sum_{j=1}^{K}\varphi_{ij}(t)},\quad t>0,\quad i=1,\ldots,N. \tag{3.15}$$

By (3.13), direct calculations yields

$$\frac{\mathrm{d}W_i}{\mathrm{d}t}=\left(-\lambda_i-\sum_{k=1}^{N}w_k\right)W_i,\quad t>0,\quad i=1,\ldots,N. \tag{3.16}$$

In particular, $\mathrm{d}W_1/\mathrm{d}t\le(-\lambda_1-w_1)W_1$ for all $t>0$, and thus $W_1(t)$ is uniformly bounded in $t\in(0,+\infty)$. Define $Z_i:=W_i/W_1$ for any $i=2,\ldots,N$. It follows from (3.16) that

$$\frac{\mathrm{d}Z_i}{\mathrm{d}t}=(\lambda_1-\lambda_i)Z_i,\quad \forall t>0,\quad i=2,\ldots,N.$$

Due to $\lambda_1<\lambda_i$ for all $i=2,\ldots,N$, we deduce

$$Z_i(t)=\frac{W_i(0)}{W_1(0)}\exp\{(\lambda_1-\lambda_i)t\}\ \to\ 0\quad\text{as}\quad t\ \to\ +\infty.$$

Since $W_1(t)$ is uniformly bounded, we derive that $W_i(t)\to0$ for all $i=2,\ldots,N$, and thus by (3.15) one obtains $w_2,\cdots,w_n\to0$ as $t\to+\infty$. Hence, the limiting equation of w_1 in (3.13) is the desired (1.5). Due to $\lambda_1<0$, the periodic solution $u_*>0$ of (1.5) is asymptotically stable, and thus $w_1\to u_*$ as $t\to+\infty$, which verifies (3.14). Hence, (3.10) holds.

Step 2. It follows from (3.10) that $\mathbf{u}_2,\cdots,\mathbf{u}_N\to0$ as $t\to+\infty$ and the limiting equation of $\mathbf{u}_1$ in (1.4) can be written as the following linear equation:

$$\frac{\mathrm{d}\mathbf{w}}{\mathrm{d}t}=d_1\mathbf{L}\mathbf{w}+\mathrm{diag}\{m_j-u_*\}\mathbf{w},\quad \sum_{j=1}^{K}w_j(t)=u_*(t),\quad t>0. \tag{3.17}$$

Applying the theory of asymptotically periodic systems in [29, Chapter 3.2.2] again, it suffices to show that for any solution $\mathbf{w}$ of (3.17) with positive initial data,

$$\mathbf{w}\ \to\ \boldsymbol{\psi}:=\frac{u_*(t)}{\sum_{j=1}^{K}\varphi_{1j}}\boldsymbol{\varphi}_1\quad\text{as}\quad t\ \to\ +\infty. \tag{3.18}$$

By (1.2) and (1.5), we calculate that

$$\begin{aligned}
&\frac{\mathrm{d}\boldsymbol{\psi}}{\mathrm{d}t}-d_1\mathbf{L}\boldsymbol{\psi}-\mathrm{diag}\{m_j-u_*\}\boldsymbol{\psi}\\
=&\frac{u_*(t)}{\sum_{j=1}^K\varphi_{1j}}\left[\frac{\mathrm{d}\boldsymbol{\varphi}_1}{\mathrm{d}t}-d_1\mathbf{L}\boldsymbol{\varphi}_1-\mathrm{diag}\{m_j(t)\}\boldsymbol{\varphi}_1\right]\\
&\quad+\frac{\boldsymbol{\varphi}_1}{\sum_{j=1}^K\varphi_{1j}}\left[\frac{\mathrm{d}u_*(t)}{\mathrm{d}t}+u_*^2(t)\right]-\frac{\mathrm{d}}{\mathrm{d}t}\left(\ln\sum_{j=1}^K\varphi_{1j}(t)\right)\boldsymbol{\psi}\\
=&\lambda(d_1)\boldsymbol{\psi}+\left[\frac{\mathrm{d}}{\mathrm{d}t}\left(\ln\sum_{j=1}^K\varphi_{1j}(t)\right)-\lambda(d_1)\right]\boldsymbol{\psi}-\frac{\mathrm{d}}{\mathrm{d}t}\left(\ln\sum_{j=1}^K\varphi_{1j}(t)\right)\boldsymbol{\psi}\\
=&0,
\end{aligned}$$

which implies that $\boldsymbol{\psi}$ is a positive periodic solution of (3.17). Hence, the principal eigenvalue of the operator $\partial_t-d_1\mathbf{L}-\mathrm{diag}\{m_j-u_*\}$ is 0 corresponding to eigenvector $\boldsymbol{\psi}>0$. Since the principal eigenvalue is simple due to the Krein-Rutman theorem, it is easily seen that $\boldsymbol{\psi}$ is the unique positive periodic solution to (3.17). Then by the classical arguments we can conclude that $\mathbf{w}(t+nT)\to\boldsymbol{\psi}(t)$ as $n\to+\infty$, which proves (3.18). The proof is now complete. □

3.2 Proof of Theorem 1.4

In this subsection, we are concerned with the global dynamics of problem (1.8) and prove Theorem 1.4. For each $i=1,\ldots,N$, we rewrite problem (1.7) as

$$\begin{cases}\partial_t\varphi=\nabla\cdot(d_i\nabla\varphi-\alpha_i\varphi\mathbf{b})+m_i(x,t)\varphi+\lambda\varphi, & x\in\Omega,\quad t\in\mathbb{R},\\ d_i\partial_\nu\varphi-\alpha_i\varphi(\mathbf{b}\cdot\nu)=0 & x\in\partial\Omega,\quad t\in\mathbb{R},\\ \varphi(x,t)=\varphi(x,t+T), & x\in\Omega,\quad t\in\mathbb{R},\end{cases}\tag{3.19}$$

where m_i is a time-periodic function given in (1.8).

Lemma 3.3. *For any $i=1,\ldots,N$, let $U_i(x,t)$ be the solution of problem* (1.8) *with nonnegative initial data and $\varphi_i>0$ be the principal eigenfunction of problem* (3.19). *Then for any $t\in[0,T]$, there holds*

$$\lim_{n\to+\infty}\left\|\frac{U_i(x,t+nT)}{\overline{U}_i(t+nT)}-\frac{\varphi_i(x,t)}{\int_\Omega\varphi_i(x,t)\mathrm{d}x}\right\|_{L^2(\Omega)}=0.$$

Proof. For each $i=1,\ldots,N$, define

$$V_i(x,t):=\frac{U_i(x,t)}{\overline{U}_i(t)},$$

where $\overline{U}_i(t)$ is defined by (1.9). Observe that

$$\int_\Omega V_i(x,t)\mathrm{d}x\equiv 1,\quad \forall t\geq 0,\quad i=1,\ldots,N. \tag{3.20}$$

Using (1.8), direct calculations yield

$$\begin{aligned}\partial_t V_i &= \frac{\partial_t U_i}{\overline{U}_i}-\frac{U_i\int_\Omega \partial_t U_i \mathrm{d}x}{\overline{U}_i^2}\\ &=\frac{1}{\overline{U}_i}[\nabla\cdot(d_i\nabla U_i-\alpha_i U_i\mathbf{b})]+\frac{U_i}{\overline{U}_i}\left[m_i(x,t)-\sum_{j=1}^N\overline{U}_j\right]-\frac{U_i}{\overline{U}_i^2}\left[\int_\Omega mU_i\mathrm{d}x-\overline{U}_i\sum_{j=1}^N\overline{U}_j\right]\\ &=\nabla\cdot(d_i\nabla V_i-\alpha_i V_i\mathbf{b})+\left[m_i(x,t)-\int_\Omega m_iV_i\mathrm{d}x\right]V_i. \end{aligned}\tag{3.21}$$

For any $i=1,\ldots,N$, let $\lambda_i\in\mathbb{R}$ be the principal eigenvalue of (3.19) and define

$$\tilde{V}_i(x,t):=\exp\left\{\lambda_i t+\int_0^t\int_\Omega m_i(x,s)V_i(x,s)\mathrm{d}x\mathrm{d}s\right\}V_i(x,t),\quad \forall (x,t)\in\Omega\times\mathbb{R}. \tag{3.22}$$

By (3.21), we calculate that $\tilde{V}_i$ solves

$$\begin{cases}\partial_t\tilde{V}_i=\nabla\cdot(d_i\nabla\tilde{V}_i-\alpha_i\tilde{V}_i\mathbf{b})+m_i(x,t)\tilde{V}_i+\lambda_i\tilde{V}_i, & x\in\Omega,\quad t>0,\\ d_i\partial_\nu\tilde{V}_i-\alpha_i\tilde{V}_i(\mathbf{b}\cdot\nu)=0, & x\in\partial\Omega,\quad t>0.\end{cases}\tag{3.23}$$

The adjoint problem of (3.19) can be written as

$$\begin{cases}-\partial_t\psi=d_i\Delta\psi-\alpha_i\mathbf{b}\cdot\nabla\psi+m_i(x,t)\psi+\lambda\psi, & x\in\Omega,\quad t\in\mathbb{R},\\ \partial_\nu\psi=0, & x\in\partial\Omega,\quad t\in\mathbb{R},\\ \psi(x,t)=\psi(x,t+T), & x\in\Omega,\quad t\in\mathbb{R}.\end{cases}\tag{3.24}$$

We denote $\psi_i>0$ by the principal eigenfunction of (3.24) associated to λ_i. By (3.23), it can be proved by [27, Lemma 6.4, Chapter 6.4.1] (see also [20, Lemma 4.3.1]) that for any convex C^2 function $H:\mathbb{R}\mapsto\mathbb{R}$, there holds

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_\Omega\varphi_i\psi_i H\left(\frac{\tilde{V}_i}{\varphi_i}\right)\mathrm{d}x=-d_i\int_\Omega\varphi_i\psi_i H''\left(\frac{\tilde{V}_i}{\varphi_i}\right)\left|\nabla\left(\frac{\tilde{V}_i}{\varphi_i}\right)\right|^2\mathrm{d}x,\quad\forall t>0. \tag{3.25}$$

Without loss of generality, we assume $\int_\Omega\varphi_i(x,0)\psi_i(x,0)\mathrm{d}x=1$ for all $i=1,\ldots,N$. Set

$$\rho_i:=\frac{1}{|\Omega|}\int_\Omega\psi_i(x,0)\tilde{V}_i(x,0)\mathrm{d}x,\quad i=1,\ldots,N.$$

By letting $H(x)=1$ and $H(x)=x$ in (3.25) respectively, we deduce that

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_\Omega\varphi_i(x,t)\psi_i(x,t)\mathrm{d}x=\frac{\mathrm{d}}{\mathrm{d}t}\int_\Omega\psi_i(x,t)\tilde{V}_i(x,t)\mathrm{d}x=0,\quad\forall t>0,$$

which implies that

$$\int_\Omega \varphi_i(x,t)\psi_i(x,t)\mathrm{d}x \equiv 1, \quad \frac{1}{|\Omega|}\int_\Omega \tilde{V}_i(x,t)\psi_i(x,t)\mathrm{d}x \equiv \rho_i, \quad \forall t>0. \tag{3.26}$$

Next we choose $H(x)=(x-\rho_i)^2$ in (3.25) and obtain

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_\Omega \frac{\psi_i}{\varphi_i}(\tilde{V}_i-\rho_i\varphi_i)^2\mathrm{d}x = -2d_i\int_\Omega \varphi_i\psi_i\left|\nabla\left(\frac{\tilde{V}_i}{\varphi_i}\right)\right|^2\mathrm{d}x, \quad \forall t>0.$$

Hence, by Poincaré inequality we deduce that there exists some constant $C>0$ such that

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}\int_\Omega \frac{\psi_i}{\varphi_i}(\tilde{V}_i-\rho_i\varphi_i)^2\mathrm{d}x &\le -2Cd_i\int_\Omega \varphi_i\psi_i\left[\frac{\tilde{V}_i}{\varphi_i}-\frac{1}{|\Omega|}\int_\Omega\left(\frac{\tilde{V}_i}{\varphi_i}\right)\mathrm{d}x\right]^2\mathrm{d}x \\ &= -2Cd_i\int_\Omega \frac{\psi_i}{\varphi_i}\left[\tilde{V}_i-\frac{\varphi_i}{|\Omega|}\int_\Omega\left(\frac{\tilde{V}_i}{\varphi_i}\right)\mathrm{d}x\right]^2\mathrm{d}x. \end{aligned}\tag{3.27}$$

It follows from (3.26) that

$$\begin{aligned}&\int_\Omega \frac{\psi_i}{\varphi_i}\left[\tilde{V}_i-\frac{\varphi_i}{|\Omega|}\int_\Omega\left(\frac{\tilde{V}_i}{\varphi_i}\right)\mathrm{d}x\right]^2\mathrm{d}x-\int_\Omega\frac{\psi_i}{\varphi_i}\left(\tilde{V}_i-\rho_i\varphi_i\right)^2\mathrm{d}x \\ =&\left(\rho_i-\frac{1}{|\Omega|}\int_\Omega\left(\frac{\tilde{V}_i}{\varphi_i}\right)\mathrm{d}x\right)\cdot\int_\Omega\psi_i\left[2\tilde{V}_i-\left(\rho_i+\frac{1}{|\Omega|}\int_\Omega\left(\frac{\tilde{V}_i}{\varphi_i}\right)\mathrm{d}x\right)\varphi_i\right]\mathrm{d}x \\ =&\left(\rho_i-\frac{1}{|\Omega|}\int_\Omega\left(\frac{\tilde{V}_i}{\varphi_i}\right)\mathrm{d}x\right)\cdot\left[2\int_\Omega\psi_i\tilde{V}_i\mathrm{d}x-\rho_i\int_\Omega\varphi_i\psi_i\mathrm{d}x-\frac{1}{|\Omega|}\int_\Omega\left(\frac{\tilde{V}_i}{\varphi_i}\right)\mathrm{d}x\right] \\ =&\left(\rho_i-\frac{1}{|\Omega|}\int_\Omega\left(\frac{\tilde{V}_i}{\varphi_i}\right)\mathrm{d}x\right)^2\ge 0.\end{aligned}$$

This together with (3.27) implies

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_\Omega\frac{\psi_i}{\varphi_i}\left(\tilde{V}_i-\rho_i\varphi_i\right)^2\mathrm{d}x\le -2Cd_i\int_\Omega\frac{\psi_i}{\varphi_i}\left(\tilde{V}_i-\rho_i\varphi_i\right)^2\mathrm{d}x, \quad \forall t>0,$$

for which we apply the Gronwall inequality to derive that

$$\int_\Omega\frac{\psi_i}{\varphi_i}(\tilde{V}_i-\rho_i\varphi_i)^2\mathrm{d}x\le C_1e^{-2Cd_it}, \quad \forall t>0$$

for some constant $C_1>0$. Hence, it holds

$$\|\tilde{V}_i(\cdot,t)-\rho_i\varphi_i(\cdot,t)\|_{L^2(\Omega)} \;\to\; 0 \quad \text{as} \quad t\;\to\;+\infty, \tag{3.28}$$

which together with (3.20) and (3.22) implies

$$\begin{aligned}&\exp\left\{\lambda_it+\int_0^t\int_\Omega m_i(x,s)V_i(x,s)\mathrm{d}x\mathrm{d}s\right\}-\rho_i\int_\Omega\varphi_i(x,t)\mathrm{d}x \\ =&\int_\Omega\tilde{V}_i(x,t)\mathrm{d}x-\rho_i\int_\Omega\varphi_i(x,t)\mathrm{d}x \;\to\; 0, \quad \text{as} \quad t\;\to\;\infty.\end{aligned}$$

Therefore, by (3.22) and (3.28) we can conclude that for any $t\in[0,T]$,

$$\begin{aligned}&\lim_{n\to+\infty}\left\|V_i(x,t+nT)-\frac{\varphi_i(x,t)}{\int_\Omega\varphi_i(x,t)\mathrm{d}x}\right\|_{L^2(\Omega)}\\=&\lim_{n\to+\infty}\left\|\frac{\tilde{V}_i(x,t+nT)}{\rho_i\int_\Omega\varphi_i(x,t)\mathrm{d}x}-\frac{\varphi_i(x,t)}{\int_\Omega\varphi_i(x,t)\mathrm{d}x}\right\|_{L^2(\Omega)}=0.\end{aligned}$$

The proof is now complete. ☐

We are in a position to prove Theorem 1.4.

Proof of Theorem 1.4. Recalling definition (1.9), we shall prove that

$$\overline{U}_1(t)\ \to\ U_*(t)>0\quad\text{and}\quad\overline{U}_2(t),\cdots,\overline{U}_N(t)\ \to\ 0\quad\text{as}\quad t\ \to\ +\infty.\tag{3.29}$$

Then Theorem 1.4 can be proved by the same arguments as in Step 2 of Theorem 1.2. By (1.8), we calculate that

$$\frac{\mathrm{d}\overline{U}_i}{\mathrm{d}t}=\left[\int_\Omega m_i(x,t)V_i(x,t)\mathrm{d}x-\sum_{j=1}^N\overline{U}_j(t)\right]\overline{U}_i,\quad\forall t>0,\quad i=1,\ldots,N.\tag{3.30}$$

A direct application of Lemma 3.3 yields

$$\lim_{n\to+\infty}\int_\Omega m_i(x,t)V_i(x,t+nT)\mathrm{d}x=\frac{\displaystyle\int_\Omega m_i(x,t)\varphi_i(x,t)\mathrm{d}x}{\displaystyle\int_\Omega\varphi_i(x,t)\mathrm{d}x},\quad\forall t\in[0,T],\tag{3.31}$$

where $\varphi_i>0$ is the principal eigenfunction of problem (3.19) corresponding to principal eigenvalue λ_i. Integrate both sides of (3.19) with respect to x over Ω, then

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_\Omega\varphi_i(x,t)\mathrm{d}x=\int_\Omega m_i(x,t)\varphi_i(x,t)\mathrm{d}x+\lambda_i\int_\Omega\varphi_i(x,t)\mathrm{d}x,$$

which together with (3.31) implies

$$\lim_{n\to+\infty}\int_\Omega m_i(x,t)V_i(x,t+nT)\mathrm{d}x=\frac{\mathrm{d}}{\mathrm{d}t}\left(\ln\int_\Omega\varphi_i(x,t)\mathrm{d}x\right)-\lambda_i,\quad\forall t\in[0,T].\tag{3.32}$$

Hence, the limiting system of (3.30) can be written as

$$\frac{\mathrm{d}W_i}{\mathrm{d}t}=\left[\frac{\mathrm{d}}{\mathrm{d}t}\left(\ln\int_\Omega\varphi_i(x,t)\mathrm{d}x\right)-\lambda_i-\sum_{j=1}^N W_j(t)\right]W_i,\quad t>0.\tag{3.33}$$

Given any constant vector $u=(u_1,\cdots,u_N)>0$, we define $S_i(t,s,u)$ and $W_i(t,u)$ as the solutions of (3.30) and (3.33) satisfies $S_i(s,s,u)=W_i(0,u)=u_i$, respectively. By (3.32), we can derive that

$$\lim_{n\to+\infty}|S_i(t+nT,nT,u)-W_i(t,u)|=0 \quad \text{uniformly for} \quad t\in[0,T].$$

In particular, letting $u=\overline{U}_i(nT)$ gives

$$\lim_{n\to+\infty}\left|\overline{U}_i(t+nT)-W_i\big(t,\overline{U}_i(nT)\big)\right|=0.$$

Therefore, $\overline{U}_i(t+nT)$ is asymptotic to an solution of limiting system (3.33).

Next, we shall show that for any $u=(u_1,\cdots,u_N)>0$,

$$W_1(t,u) \ \to \ U_*(t) \quad \text{and} \quad W_2(t,u),\cdots,W_N(t,u) \ \to \ 0 \quad \text{as} \quad t \ \to \ +\infty, \tag{3.34}$$

where $U_*>0$ is the unique positive periodic solution of (1.11). Then we can apply the theory of asymptotically periodic systems established in [29, Chapter 3.2.2] (see e.g. [29, Theorem 3.2.2]) to complete the proof of (3.29). To this end, we define

$$\tilde{W}_i(t,u):=\frac{W_i(t,u)}{\int_\Omega \varphi_i(x,t)\,\mathrm{d}x}, \quad \forall t>0.$$

By (3.33) we can calculate that

$$\frac{\mathrm{d}\tilde{W}_i}{\mathrm{d}t}=\left[-\lambda_i-\sum_{j=1}^N W_j(t)\right]\tilde{W}_i, \quad t>0. \tag{3.35}$$

In particular, we have

$$\frac{\mathrm{d}\tilde{W}_1}{\mathrm{d}t}\le\left[-\lambda_1-\tilde{W}_1\int_\Omega \varphi_i(x,t)\,\mathrm{d}x\right]\tilde{W}_1, \quad t>0,$$

which implies that $\tilde{W}_1(t)$ is bounded as $t\to+\infty$.

Set $Z_i:=\tilde{W}_i/\tilde{W}_1$ for any $i=2,\dots,N$. By (3.35) direct calculation yields

$$\frac{\mathrm{d}Z_i}{\mathrm{d}t}=(\lambda_1-\lambda_i)Z_i, \quad \forall t>0, \quad i=2,\dots,N.$$

Due to $\lambda_1<\lambda_j$ for all $j=2,\dots,N$, this implies

$$Z_j(t)=\frac{\tilde{W}_j(0)}{\tilde{W}_1(0)}\exp\{(\lambda_1-\lambda_j)t\} \ \to \ 0 \quad \text{as} \quad t \ \to \ +\infty, \quad j=2,\dots,N.$$

Since $\tilde{W}_1(t)$ is bounded as $t\to+\infty$, we thus deduce that $\tilde{W}_j(t)\to 0$ for all $2\le j\le N$, and thus $W_2,\cdots,W_n\to 0$ as $t\to+\infty$. Hence, the limiting equation of W_1 in (3.33) is desired (1.11). Since $\lambda_1<0$, (1.11) admits a unique positive periodic solution denoted by U_*, which is asymptotic stable. Therefore, $W_1\to U_*$ as $t\to+\infty$, which proves (3.34). Hence, (3.29) holds. The proof is now complete. □

Acknowledgments

S. Liu is partially supported by the NSFC (Grant No. 12201041), by the China National Postdoctoral Program for Innovative Talents (Grant No. BX20220377), by the China Postdoctoral Science Foundation (Grant No. 2022M710391) and by the Beijing Institute of Technology Research Fund Program for Young Scholars. Y. Lou is partially supported by the NSFC (Grant Nos. 12250710674, 12261160366). S. Ma is partially supported by the China Postdoctoral Science Foundation (Grant No. 2024M751949) and by the NSFC (Grant Nos. 12171478, 12071476).

References

[1] X. Bai, X. He, and W.-M. Ni, *Dynamics of a periodic-parabolic Lotka-Volterra competition-diffusion system in heterogeneous environments*, J. Eur. Math. Soc., 25:4583–4637, 2023.
[2] F. Belgacem and C. Cosner, *The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environments*, Can. Appl. Math. Q., 3:379–397, 1995.
[3] M. Benaim, C. Lobry, T. Sari, and E. Strickler, *When can a population spreading across sink habitats persist?*, J. Math. Biol., 88:19, 2024.
[4] R. S. Cantrell and C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*, Wiley Series in Mathematical and Computational Biology, John Wiley & Sons, 2003.
[5] R. S. Cantrell, C. Cosner, and Y. Lou, *Advection-mediated coexistence of competing species*, P. Roy. Soc. Edinb. A, 137(3):497–518, 2007.
[6] X. F. Chen and Y. Lou, *Principal eigenvalue and eigenfunctions of an elliptic operator with large advection and its application to a competition model*, Indiana Univ. Math. J., 57:627–657, 2008.
[7] D. Cohen and S. A. Levin, *The interaction between dispersal and dormancy strategies in varying and heterogeneous environments*, in: Mathematical Topics in Population Biology, Morphogenesis and Neurosciences. Lecture Notes in Biomathematics, Springer, 71:110–122, 1987.
[8] C. Cosner and Y. Lou, *Does movement toward better environments always benefit a population?* J. Math. Anal. Appl., 277:489–503, 2003.
[9] O. Diekmann, *A beginner's guide to adaptive dynamics*, Banach Cent. Publ., 63:47–86, 2003.
[10] J. Dockery, V. Hutson, K. Mischaikow, and M. Pernarowski, *The evolution of slow dispersal rates: A reaction-diffusion model*, J. Math. Biol., 37:61–83, 1998.
[11] I. Eshel and U. Motro, *Kin selection and strong evolutionary stability of mutual help*, Theor. Popul. Biol., 19:420–433, 1981.
[12] J. Furter and M. Grinfeld, *Local vs. non-local interactions in population dynamics*, J. Math. Biol., 27:65–80, 1989.
[13] A. Hastings, *Can spatial variation alone lead to selection for dispersal?* Theor. Popul. Biol. 24:244–251, 1983.
[14] P. Hess, *Periodic-Parabolic Boundary Value Problems and Positivity*, Pitman Reseach Notes in Mathematics, Vol. 247, Longman Scientific & Technical, 1991.
[15] V. Hutson, K. Mischaikow, and P. Poláčik, *The evolution of dispersal rates in a heterogeneous time-periodic environment*, J. Math. Biol., 43:501–533, 2001.
[16] V. A. Jansenand and J. Yoshimura, *Populations can persist in an environment consisting of sink habitats only*, Proc. Natl. Acad. Sci. USA, 95:3696–3698, 1988.
[17] G. Katriel, *Dispersal-induced growth in a time-periodic environment*, J. Math. Biol., 85:24, 2022.

[18] T. J. Kawecki, *Ecological and evolutionary consequences of source-sink population dynamics*, in: Ecology, genetics and evolution of metapopulations, Academic Press, 387–414, 2004.

[19] M. G. Krein and M. A. Rutman, *Linear Operators Leaving Invariant a Cone in a Banach Space*, AMS, 1950.

[20] K.-Y. Lam and Y. Lou, *Introduction to Reaction-Diffusion Equations: Theory and Applications to Spatial Ecology and Evolutionary Biology*, Lecture Notes on Mathematical Modelling in the Life Sciences, Springer, 2022.

[21] S. A Levin, D. Cohen, and A. Hastings, *Dispersal strategies in patchy environments*, Theor. Popul. Biol., 26:165–191, 1984.

[22] S. Liu and Y. Lou, *Classifying the level set of principal eigenvalue for time-periodic parabolic operators and applications*, J. Funct. Anal., 282:109338, 2022.

[23] S. Liu and Y. Lou, *On the principal eigenvalues for a class of time-periodic and spatially discrete problems*, Sci. Sin. Math., 54(3):483–514, 2024 (in Chinese).

[24] S. Liu, Y. Lou, and P. Song, *A new monotonicity for principal eigenvalues with applications to time-periodic patch models*, SIAM J. Appl. Math., 82:576–601, 2022.

[25] D. P. Matthews and A. Gonzalez, *The inflationary effects of environmental fluctuations ensure the persistence of sink metapopulations*, Ecology, 88:2848–2856, 2007.

[26] J. Smith and G. Price, *The logic of animal conflict*, Nature, 246:15–18, 1973.

[27] B. Perthame, *Transport Equations in Biology*, Springer Science & Business Media, 2007.

[28] M. Roy, R. D. Holt, and M. Barfield, *Temporal autocorrelation can enhance the persistence and abundance of metapopulations comprised of coupled sinks*, Am. Nat., 166:246–261, 2005.

[29] X.-Q. Zhao, *Dynamical Systems in Population Biology*, CMS Books in Mathematics, Springer, 2017.