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ON THE PRINCIPAL EIGENVALUE OF COOPERATIVE ELLIPTIC SYSTEMS WITH APPLICATIONS TO A POPULATION MODEL WITH TWO REVERSIBLE STATES

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Abstract. We prove novel monotonic results of cooperative elliptic eigenvalue problems on a bounded one-dimensional domain under suitable conditions, which are then applied to analyze a population model with state-switching. Our results demonstrate that spatial heterogeneity alone can lead to selection of higher movement rate, which implies that the reduction phenomenon due to [L. Altenberg, Proc. Nat. Acad. Sci. (2012)] fails for general elliptic cooperative systems. This also provides a plausible mechanism for the differing effective growth rates of the high and low movement strains in different spatial placement of nutrients and toxins, as observed in recent biological experiments involving nematode populations.

1. Introduction.

Habitat heterogeneity is a common feature of natural environments. The overall growth rate of a given population depends on the spatial distribution of resources, and the manner individuals consume these resources as they move about in space [10, 21, 48]. Depending on the specific environmental conditions, there can be an evolutionary selection for or against dispersal. In spatially heterogeneous but temporally constant environments, and when only purely unconditional, or diffusive movement is considered, Hastings [29] proved that a lower movement rate is advantageous using an adaptive dynamics approach. This result is generalized in some situations in the mathematical context of N-species competition [15, 24, 36], and was demonstrated empirically in [51]. In fact, the reduction principle says that for a wide range of settings, increasing mixing, by diffusive or unconditional movement, in a spatially heterogeneous environment reduces overall growth rate [1]. In contrast, intermediate or higher movement rate can be selected when the environment has a uni-directional drift [38, 39], or when the organism has some form of directed movement [4, 11, 18, 19, 37]. Experimental results also

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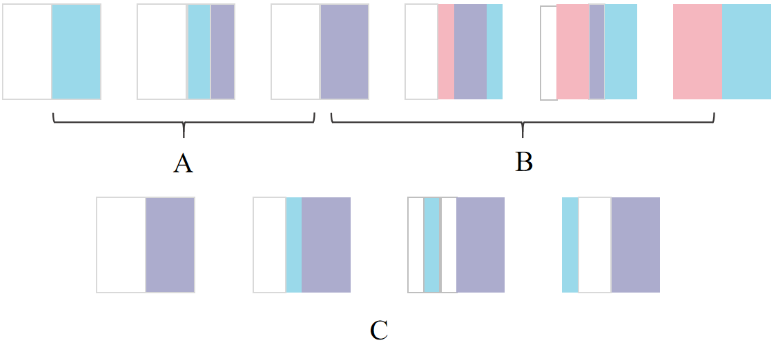

FIGURE 1. A schematic diagram of the experimental environment setup. A: Invasion of toxins–The coverage of toxins in the resource area (blue) gradually increases. B: Overlap between resources and toxins (pink)–Adjusting the degree of overlap between resources and toxins while keeping their total amounts constant. C: Position of refuge–The existence of the refuge (blue) and the variation in its distance from the mixed area(purple). Here, the blue zones represent resources, the pink zones represent toxins, the purple represent zones with both resources and toxins, and the white zones indicate no addition.

demonstrate that organisms adjust their movement rate based on the availability of resources [48], and that they have a tendency to avoid high concentration of environmental stressors or toxins [50]. Therefore, a natural question is how changes in the spatial placement of resources and particularly the inclusion of environmental stressors alter the selection of movement strategies of organisms.

In a recent study, Baragary et al. [7] investigated how the heterogeneity of resources and environmental stressors affect the population abundance of organisms. In these experiments, populations with distinct movement strategies are grown in isolation (i.e. each experiment involves only a single population), and the terminal population size of different experiments can be compared to gain insight into the relative advantage of fast versus slow movement rates in different environmental setting. Specifically, they designed three distinct spatial distribution patterns for resources and toxins (see Figure 1). For each particular resource/toxin distribution, nematode populations with differing movement rates were allowed to forage and grow, starting from six individuals, to their terminal population size which was then recorded. Experimental results show that adding toxins to the food patches is not conducive to the survival of nematode populations. Moreover, it was observed that increasing overlap of the toxin has a greater negative impact on the fast-moving nematodes. On the other hand, increasing the size of refuge is beneficial for the growth of nematode populations, and the location of the refuge determines which movement strategy is more fit, i.e., achieving greater growth rate. In contrary to previous results in the literature [51], it was found that faster diffuser grew to a larger final population size in the cases when toxins were added and allowed to overlap with the nutrient distribution. The goal of this paper is to propose a mathematical perspective to explain some of these intriguing experimental results.

To this end, we propose a possible mechanism for the relative advantage of having a higher versus lower movement rate in such experimental settings. First, we describe our main assumptions, which are motivated by the experimental conditions.

- The nematode strains are confined to the petri dish with a one-dimensional patterning of nutrient and toxin. In the absense of toxins, they perform unconditional movement modeled by diffusion with rate $\mu > 0$.
- The presence of toxin may induce a chemo-repulsive term that prompts nematodes to move away from toxin-rich location with rate $\alpha \geq 0$.
- The individual nematode switches between two reversible states: the state u with low internal reserve and the state v with high internal reserve.
- The nematode in state u switches to state v at a rate proportional to the nutrient distribution $r(x)$.
- At a rate $k > 0$ independent of the spatial location, an individual nematode in state v gives birth to (on average) $b(1-\sigma(x))$ offsprings, where a reduction of birth rate is caused by the toxin distribution $0 \leq \sigma(x) \leq 1$. Both the parent and offspring emerges in state u after reproduction event.
- For simplicity, the nutrient distribution $r(x)$ is taken to be spatially heterogeneous but temporally constant. This assumption is supported by the non-depletion of resource at the end of the 3-day experimental duration.

Guided by the above experimental assumptions, we introduce a novel reaction-diffusion model with two reversible state for the population dynamics of nematodes. This can be regarded as a simplified version of Droop models with only two distinct levels of internally stored nutrient [25]. We also mention the work of Cantrell et al. [14] concerning a two-state population model where the individuals switch between two different movement rate and also [9, 13] for other related works. Our model reads as follows:

$$\begin{cases} u_t = (\mu u_x + \alpha\sigma_x u)_x - r(x)u + kv + kb(1-\sigma(x))v, & 0 < x < L,\ t > 0,\\ v_t = (\mu v_x + \alpha\sigma_x v)_x - kv + r(x)u, & 0 < x < L,\ t > 0,\\ \mu u_x(x,t) + \alpha\sigma_x u(x,t) = 0, \mu v_x(x,t) + \alpha\sigma_x v(x,t) = 0, & x = 0,\ L,\ t > 0,\\ u(x,0) = u_0(x) \geq, \not\equiv 0, v(x,0) = v_0(x) \geq, \not\equiv 0, & 0 < x < L, \end{cases} \tag{1.1}$$

where $\mu, k, b, L \in (0,\infty)$ and $\alpha \in [0,\infty)$ are constants; $r \in C([0,L];[0,\infty))$ and $\sigma \in C([0,L];[0,1])$ are given functions whose meanings are as described above.

The main purpose of this paper is to understand the dependence of the effective population growth rate in model (1.1) on the diffusion rate μ and advection rate α in the context of spatially heterogeneous distributions of nutrients and toxins. For this purpose, we consider the principal eigenvalue λ_1 of the linearized elliptic problem associated with model (1.1), which characterizes the effective growth rate of the population (see [35] and (3.2) below) in the sense that

$$\lambda_1 = \lim_{t\to+\infty} \frac{1}{t} \log\left(\int_\Omega (u(x,t) + v(x,t))\, dx \right)$$

holds for every positive solution of the initial boundary problem (1.1). We will analyze how the principal eigenvalue λ_1 depends on the diffusion and advection rates, and interpret what this dependence means biologically. Although we are primarily analyzing the eigenvalue in this paper, we also mention that the eigenfunction associated with λ_1 carries crucial description of the distribution of the population in space.

A key result of this paper (Theorem 3.3) states that for organisms with two life stages, **spatial heterogeneity of resource/toxin distributions alone can be sufficient for the evolution of dispersal** (i.e., selection of higher movement rate), which extends an observation by [14] that the eigenvalue for cooperative systems may no longer be increasing in the movement rate. This should be compared to the classical results of Hastings [29] (see also [1, 24]), which state that unconditional movement is generally selected against in spatially heterogeneous but temporally constant environment. Here, the life-stage of the organism can be considered as a kind of intrinsic temporal heterogeneity even as the environment is temporally constant. Thus, the organisms has to be able to move between life stages to maximize its fitness, creating the opportunity for the selection of higher movement trait.

The rest of the paper is organized as follows. In Section 2, we investigate the properties of the principal eigenvalue for general cooperative systems. The asymptotic limits of the principal eigenvalue for small diffusion, large diffusion, and large advection rates are determined. Next, under the premise of large diffusion, monotonicity properties of the principal eigenvalue with respect to diffusion and advection rates are established in Theorem 2.5. (It can be compared with the recent results of Monmarché et al. [40] concerning the discretized problem with switching states. Therein the higher order expansion of the spectral bound is computed, where the monotonicity in given parameter is suggested by the sign of the first order expansion.) In Section 3, we apply our results to the nematode population model to achieve a mechanistic understanding of the experimental findings. Finally, we discuss the implications of our findings in Section 4.

2. A general cooperative system.

In this section, we consider the eigenvalue problem for a general linear cooperative elliptic system with Neumann boundary conditions in one space dimension.

$$\begin{cases} \mu\varphi_{i,xx} + \alpha m_x\varphi_{i,x} + c_{ij}(x)\varphi_j + \lambda\varphi_i = 0, & 0 < x < 1, \\ \varphi_{i,x}(0) = \varphi_{i,x}(1) = 0, & 1 \le i \le n, \end{cases} \tag{2.1}$$

where the constants $\mu > 0$ and $\alpha \in \mathbb{R}$ are diffusion and advection coefficients, respectively, and $m(x) \in C^2([0,1])$. Note that for (2.1) and hereafter summation are taken over repeated indices. Moreover, we assume that $c_{ij}(x) \in C^1([0,1])$ satisfy the following assumption:

$$C(x) := (c_{ij}(x))_{n\times n} \text{ is cooperative, i.e., } c_{ij}(x) \ge 0 \text{ for } i \ne j, \text{ and } x \in [0,1],$$

and is irreducible. The existence of the principal eigenvalue $\lambda_1(\mu,\alpha)$, which is simple and has a componentwise positive eigenfunction (φ_i), follows from the Krein-Rutman theorem [46] (see also [35, Chapter 3]). We normalize (φ_i) by $\int_0^1 \varphi_i^2 dx = 1$.

This principal eigenvalue describes the long term exponential growth (or decay) rate of population in the sense that for any nonnegative, nontrivial solution $\{u_i(x,t)\}$ of the corresponding initial value problem

$$\begin{cases} \partial_t u_i = \mu u_{i,xx} + \alpha m_x u_{i,x} + c_{ij}u_j & \text{for } 0 < x < 1,\ t > 0, \\ u_{i,x} = 0 & \text{for } x = 0, 1,\ t > 0, \end{cases} \tag{2.2}$$

it holds that

$$\lambda_1 = \lim_{t\to\infty} \frac{1}{t} \log\left(\sum_i \int_0^1 u_i\, dx\right). \tag{2.3}$$

There has been considerable work devoted to studying such eigenvalue problems. For the case of a scalar equation, the asymptotic behavior of the principal eigenvalue and its dependence on parameters are quite well understood, thanks to the availability of a variational characterization; see [19, 20, 42, 43] and references therein. Regarding eigenvalue problems of cooperative reaction-systems, a series of studies [2, 3, 16, 23] have examined the dependence of the principal eigenvalue with respect to the zero-th order coefficient under Dirichlet boundary conditions. Dancer analyzed the asymptotic properties of the principal eigenvalue when the diffusion rate approaches zero under Dirichlet boundary conditions [22], which was later improved by Lam and Lou [34]. More recently, Bai et al. [5] established the concentration of eigenfunction in the vanishing viscosity limit. We also mention related works on time-periodic cooperative systems with diffusion [6, 52] and their nonlocal dispersal counterparts [26, 44, 45, 47].

However, few works have been devoted to studying the monotonicity properties of the principal eigenvalue with respect to diffusion rate μ, and the asymptotic properties of the principal eigenvalue with respect to advection rate α, even though the qualitative properties of the principal eigenvalue with respect to μ and α play an important role in analyzing the influence of random and directional motion on the population's movement strategy. Therefore, for the cooperative system eigenvalue problem (2.1) with advection term $m(x)$, we aim to investigate the asymptotic and monotonicity properties of the principal eigenvalue $\lambda_1(\mu,\alpha)$ with respect to diffusion and advection rates.

In the following, define the constant matrices $C^* = (c^*_{ij})_{n\times n}$ and $C_* = (c_{ij*})_{n\times n}$ by

$$c^*_{ij} = \max_{x\in[0,1]} c_{ij}(x) \quad \text{and} \quad c_{ij*} = \min_{x\in[0,1]} c_{ij}(x) \qquad \text{for } \ i,j = 1,2,\cdots,n.$$

Lemma 2.1. *For each $\mu > 0$, $\alpha \in \mathbb{R}$, the principal eigenvalue $\lambda_1(\mu,\alpha)$ of (2.1) satisfies*

$$-\Lambda_1(C^*) \le \lambda_1(\mu,\alpha) \le -\Lambda_1(C_*), \tag{2.4}$$

where $\Lambda_1(C^*)$ and $\Lambda_1(C_*)$ are the Perron-Frobenius eigenvalue for the given cooperative matrix C^* and C_*, respectively.

Proof. Let $(w_i) \in \mathbb{R}^n_+$ be the positive eigenvector of C^* that is uniquely identified by $\sum_{i=1}^n w_i = 1$. Then we have

$$\begin{cases} \mu w_{i,xx} + \alpha m_x w_{i,x} + c_{ij}(x) w_j \le c^*_{ij} w_j = \Lambda_1(C^*) w_i, & 0 < x < 1, \\ w_{i,x}(x) = 0, & x = 0,\ 1. \end{cases}$$

By [35, Lemma 3.2.9], it follows that $\lambda_1(\mu,\alpha) \ge -\Lambda_1(C^*)$. The proof of upper bound of $\lambda_1(\mu,\alpha)$ is analogous to that of the lower bound and uses [35, Lemma 3.2.10], and therefore we omit it here. □

Remark 2.2. Hereafter, we refer to [35, Lemmas 3.2.9 and 3.2.10] as eigenvalue comparison lemmas.

2.1. Effect of μ on λ_1 when $\alpha = 0$.

When $\alpha = 0$, we obtain the following asymptotic behaviors of $\lambda_1(\mu,\alpha)$ with respect to μ.

Lemma 2.3. *Suppose that $\alpha = 0$. Then the principal eigenvalue $\lambda_1(\mu,0)$ of (2.1) satisfies*

$$\lim_{\mu\to 0} \lambda_1(\mu,0) = \min_{x\in[0,1]} (-\Lambda_1(C(x))); \tag{2.5}$$

and

$$\lim_{\mu\to\infty} \lambda_1(\mu, 0) = -\Lambda_1(\bar{C}), \tag{2.6}$$

where $\bar{C} := \left(\int_0^1 c_{ij}(x)dx\right)_{1\le i,j\le n}$.

Proof. The first assertion is based on [34, Theorem 1.4] (see also [35, Theorem 3.2.8]). For the second assertion, see [12, Lemma 9]. □

Now, we focus on the monotonicity of the principal eigenvalue $\lambda_1(\mu, \alpha)$ with respect to the diffusion rate. In the case of a scalar equation, it is well known that if $\alpha = 0$, the principal eigenvalue is monotone increasing in μ (see, e.g. [35, 41]).

Lemma 2.4. *Let* $\lambda_1(\mu)$ *be the principal eigenvalue of*

$$\mu\varphi_{xx} + c(x)\varphi + \lambda\varphi = 0 \quad \text{in } (0,1), \quad \text{and} \quad \varphi_x = 0 \quad \text{for } x = 0, 1.$$

If $c(x) \in C([0,1])$ *is nonconstant, then* $\partial_\mu \lambda_1(\mu) > 0$ *for* $\mu > 0$.

This monotonicity of $\mu \mapsto \lambda_1(\mu)$ can be traced back to Karlin [32] in the matrix form (see also [1, 17, 33, 49]) and is used in proving the reduction principle in evolutionary biology: greater mixing reduces effective growth rate.

However, the above discussion is limited to the scalar case (where individuals can move between patches, but they do not switch between states) and does not generalize to general cooperative systems when the zero-th order term is coupled by a matrix multiplication $c_{ij}\varphi_j$. Recently, Cantrell et al. [12] demonstrated that the principle does not hold for a two-stage population model, by determining the asymptotic limits as the diffusion rate tends to zero or infinity. Here, we give sufficient conditions for cooperative systems to be monotonically increasing or decreasing in μ, for large enough μ.

Theorem 2.5. *Suppose that* $\alpha = 0$ *and* $\lambda_1(\mu, 0)$ *is the principal eigenvalue of* (2.1). *Let* (a_j), (a_j^*) *be, respectively, the positive right and left eigenvectors of the constant matrix*

$$\bar{C} := \left(\int_0^1 c_{ij}(x)dx\right)_{1\le i,j\le n}.$$

Then the following statements hold.

(i) $\partial_\mu \lambda_1(\mu, 0) < 0$ *for* $\mu \gg 1$ *provided that we have, for each* i,

$$(c_{ij})_x a_j \ \ge\ 0\ \ge\ (c_{ji})_x a_j^* \quad \forall x \quad \text{or} \quad (c_{ij})_x a_j\ \le\ 0\ \le\ (c_{ji})_x a_j^* \quad \forall x,$$

and there is an i *such that* $(c_{ij})_x a_j \not\equiv 0$ *and* $(c_{ji})_x a_j^* \not\equiv 0$.

(ii) $\partial_\mu \lambda_1(\mu, 0) > 0$ *for* $\mu \gg 1$ *provided that we have, for each* i,

$$\min\left\{(c_{ij})_x a_j\,,\ (c_{ji})_x a_j^*\right\}\ \ge\ 0 \quad \forall x \quad \text{or} \quad \max\left\{(c_{ij})_x a_j\,,\ (c_{ji})_x a_j^*\right\}\ \le\ 0 \quad \forall x,$$

and there is an i *such that* $(c_{ij})_x a_j \not\equiv 0$ *and* $(c_{ji})_x a_j^* \not\equiv 0$.

Remark 2.6. We conjecture that if $(c_{ij})_x > 0$ for all i, j, then $\partial_\mu \lambda_1(\mu, 0) > 0$ for all $\mu > 0$. Our result says that this is true at least for μ sufficiently large.

Proof of Theorem 2.5. The proof is inspired by [28, Lemma A.2]. Note that when $\alpha = 0$, the adjoint problem of (2.1) is

$$\mu\varphi^*_{i,xx} + c_{ji}(x)\varphi^*_j + \lambda\varphi^*_i = 0, \quad \text{in } (0,1),\ \ \varphi^*_{i,x}(x) = 0,\ \ x = 0,\ 1, \tag{2.7}$$

and $\varphi^*_i > 0$ in $[0, 1]$, where $1 \le i \le n$. We normalize φ^*_i by $\int_0^1 \varphi_i\varphi^*_i dx = 1$, with φ_i being the eigenfunction of (2.1).

Claim 1. $\partial_\mu\lambda_1(\mu,0) = \displaystyle\int_0^1 \varphi_{i,x}\varphi^*_{i,x}dx.$

Indeed, differentiating both sides of (2.1) with respect to μ, we obtain

$$\begin{cases} \mu(\partial_\mu\varphi_i)_{xx} + c_{ij}(x)\partial_\mu\varphi_j + \lambda_1\partial_\mu\varphi_i = -\varphi_{i,xx} - \partial_\mu\lambda_1\varphi_i, & 0 < x < 1, \\ \partial_\mu\varphi_{i,x}(x) = 0, & x = 0,\ 1. \end{cases} \tag{2.8}$$

Claim 1 follows by multiplying (2.7) by $\partial_\mu\varphi_i$ and (2.8) by φ^*_i , and then integrating each by parts and summing over i.

In the following, we consider the Taylor expansion of the eigenvalue and eigenfunction of problem (2.1) in $\mu \gg 1$.

$$\varphi_i = a_i + \frac{\hat{\varphi}_i}{\mu} + o\left(\frac{1}{\mu^2}\right), \quad \text{and} \quad \lambda_1(\mu) = \bar{\lambda} + \frac{\hat{\lambda}}{\mu} + o\left(\frac{1}{\mu^2}\right), \tag{2.9}$$

where $\bar{\lambda}$ and $(a_i) \in \mathbb{R}^n_+$ are the principal eigenvalue and the corresponding unit right positive eigenvector of matrix $\bar{C} = (\int_0^1 c_{ij}\, dx)_{1\le i,j\le n}$. We have used the fact that $\varphi_i \to a_i$ and $\lambda_1(\mu) \to \bar{\lambda}$ as $\mu \to \infty$.

We will determine the first order approximation $\hat{\varphi}_i$ and $\hat{\lambda}$ by grouping the lowest order terms to get

$$\begin{cases} \hat{\varphi}_{i,xx} + c_{ij}(x)a_j + \bar{\lambda}a_i = 0, & 0 < x < 1, \\ \hat{\varphi}_{i,x}(x) = 0, & x = 0,\ 1. \end{cases} \tag{2.10}$$

Taking the derivative of the first equation of (2.10) with respect to x, and noting that a_i is constant in x, we have

$$\begin{cases} (\hat{\varphi}_{i,x})_{xx} = -(c_{ij}(x))_x a_j, & 0 < x < 1, \\ \hat{\varphi}_{i,x}(x) = 0, & x = 0,\ 1. \end{cases} \tag{2.11}$$

Hence, it follows from the maximum principle that

$$\pm(\hat{\varphi}_i)_x > 0 \ \text{ in } \ (0,1) \ \text{ for some } i \quad \text{if} \ \ \pm(c_{ij}(x))_x a_j \ge 0, \not\equiv 0 \ \text{ in } \ (0,1). \tag{2.12}$$

Thanks to (2.9), we have

$$\pm(\varphi_i)_x > 0 \ \text{ in } \ (0,1) \ \text{ for } \ \mu \gg 1 \ \text{ for some } i \ \text{ if } \ \pm(c_{ij}(x))_x a_j \ge 0, \not\equiv 0 \ \text{ in } \ (0,1). \tag{2.13}$$

Similarly, we can prove via the Taylor expansion of the adjoint problem (2.7) that

$$\pm(\varphi^*_i)_x > 0 \ \text{ in } \ (0,1) \ \text{ for } \ \mu \gg 1 \ \text{ for some } i \ \text{ if } \ \pm(c_{ji}(x))_x a^*_j \ge 0, \not\equiv 0 \ \text{ in } \ (0,1), \tag{2.14}$$

where $(a^*_j) \in \mathbb{R}^n_+$ is the unit left eigenvector of $\bar{C}$ corresponding to the eigenvalue $\bar{\lambda}$. The conclusion now follows from Claim 1, (2.13) and (2.14). □

When $n = 2$, the principal eigenvalue $\lambda_1(\mu,0)$ has global monotonicity with respect to μ in some special cases.

Theorem 2.7. *Suppose that $\alpha = 0$ and there exists a $k > 0$ such that $c_{12}(x) = kc_{21}(x)$ on $[0,1]$. Then the principal eigenvalue $\lambda_1(\mu,0)$ of (2.1) satisfies $\partial_\mu\lambda_1(\mu,0) \ge 0$ for all $\mu > 0$.*

Proof. Let $\varphi_1 = \sqrt{k}\phi_1$. If $c_{12}(x) = kc_{21}(x)$ on $[0,1]$, then (ϕ_1, φ_2) satisfies

$$\begin{cases} \mu\phi_{1,xx} + c_{11}(x)\phi_1 + \sqrt{k}c_{21}(x)\varphi_2 + \lambda\phi_1 = 0, & 0 < x < 1, \\ \mu\varphi_{2,xx} + \sqrt{k}c_{21}(x)\phi_1 + c_{22}(x)\varphi_2 + \lambda\varphi_2 = 0, & 0 < x < 1, \\ \phi_{1,x}(x) = 0, \ \varphi_{2,x}(x) = 0, & x = 0, \ 1. \end{cases} \tag{2.15}$$

Since the above system is self-adjoint, it follows from Claim 1 above that

$$\partial_\mu \lambda_1(\mu, 0) = \int_0^1 |\phi_{1,x}|^2 + |\varphi_{2,x}|^2 \, dx \geq 0,$$

Moreover, the equality holds if and only if $c_{11} + c_{12}\beta = \gamma = \frac{c_{21}}{\beta} + c_{22}$ for some constants $\gamma \in \mathbb{R}$ and $\beta > 0$.

□

2.2. **Effect of α on λ_1.** Here we consider the qualitative behavior when $\alpha \neq 0$ varies. First, we study the limiting behavior of the principal eigenvalue in the case of large α.

Lemma 2.8. *Suppose that $\mu > 0$ is fixed and there exists $x_0 \in (0,1)$ such that $m_x = 0$ for $x = x_0$, $m_x > 0$ for $x \in [0, x_0)$ and $m_x < 0$ for $x \in (x_0, 1]$. Then the principal eigenvalue $\lambda_1(\mu, \alpha)$ of (2.1) satisfies*

$$\lim_{\alpha \to \infty} \lambda_1(\mu, \alpha) = -\Lambda_1(C(x_0)). \tag{2.16}$$

Proof. In case of a scalar equation, the above result is proved in [19, 42] by exploiting the variational structure. In contrast, the proof for the system case at hand relies on the eigenvalue comparison lemma, which is achieved by constructing generalized super- and subsolutions (see [8, Definition 4.2] or [35, Definition 1.1.1]). We first prove that

$$\limsup_{\alpha \to \infty} \lambda_1(\mu, \alpha) \leq -\Lambda_1(C(x_0)). \tag{2.17}$$

Given any small $\varepsilon > 0$, we construct a nonnegative generalized subsolution $\underline{\varphi}_i$ such that for sufficiently large α,

$$\begin{cases} \mu\underline{\varphi}_{i,xx} + \alpha m_x \underline{\varphi}_{i,x} + c_{ij}(x)\underline{\varphi}_j - \Lambda_1(C(x_0))\underline{\varphi}_i + \varepsilon\underline{\varphi}_i \geq 0, & 0 < x < 1, \\ \underline{\varphi}_{i,x}(0) \geq 0, \ \underline{\varphi}_{i,x}(1) \leq 0. \end{cases} \tag{2.18}$$

Let $(\psi_i^{(2)}) \in \mathbb{R}^n_+$ be the (constant) eigenvector of $(c_{ij}(x_0))$, i.e., $c_{ij}(x_0)\psi_j^{(2)} = \Lambda_1(C(x_0))\psi_i^{(2)}$. By the continuity of $c_{ij}(x)$, for any $\varepsilon > 0$, there exists a $\delta_0 := \delta_0(\varepsilon)$ and $|x - x_0| \leq \delta_0$ such that

$$|c_{ij}(x)\psi_j^{(2)} - \Lambda_1(C(x_0))\psi_i^{(2)}| < \frac{\varepsilon}{2}\psi_i^{(2)} \ \mathit{for} \ x \in [x_0 - \delta_0, x_0 + \delta_0], \ 1 \leq i \leq n. \tag{2.19}$$

Fix $M > 1$ such that $(M-1)\varepsilon > \delta_0\mu$, and define $\underline{\varphi}_i := \psi_i^{(2)} p(x)$, where

$$p(x) := \begin{cases} \frac{\delta_0^2}{2}x + M - \frac{\delta_0^3}{4} - \frac{\delta_0^2}{2}(x_0 - \delta_0), & x \in [0, x_0 - \delta_0], \\ M - \delta_0\frac{(x-x_0)^2}{4}, & x \in [x_0 - \delta_0, x_0 + \delta_0], \\ -\frac{\delta_0^2}{2}x + M - \frac{\delta_0^3}{4} + \frac{\delta_0^2}{2}(x_0 + \delta_0), & x \in [x_0 + \delta_0, 1]. \end{cases}$$

Note that $\underline{\varphi}_i \in C^1([0,1])$ and $\underline{\varphi}_i \geq (M-1)\psi_i^{(2)}$.

For $x \in [x_0 - \delta_0, x_0 + \delta_0]$, $\alpha m_x \underline{\varphi}_{i,x} \geq 0$, by using (2.19), we obtain

$$\begin{aligned}
&\mu \underline{\varphi}_{i,xx} + \alpha m_x \underline{\varphi}_{i,x} + c_{ij}(x)\underline{\varphi}_j - \Lambda_1(C(x_0))\underline{\varphi}_i + \varepsilon \underline{\varphi}_i \\
&\geq \frac{-\delta_0}{2}\mu\psi_i^{(2)} + \frac{\varepsilon}{2}\underline{\varphi}_i \geq -\frac{\delta_0}{2}\mu\psi_i^{(2)} + \frac{\varepsilon}{2}(M-1)\psi_i^{(2)} > 0 \qquad \text{for all } \alpha > 0.
\end{aligned}$$

For $x \in [0, x_0 - \delta_0]$, $m_x > 0$, we choose α_0 is sufficiently large such that

$$\frac{1}{2M}\alpha_0\delta_0^2\big(\inf_{[0,x_0-\delta_0]} m_x\big) + \min_i\left(\frac{1}{\psi_i^{(2)}}c_{ij*}\psi_j^{(2)}\right) - \Lambda_1(C(x_0)) > 0.$$

Then for $\alpha \geq \alpha_0$, we have

$$\begin{aligned}
&\mu \underline{\varphi}_{i,xx} + \alpha m_x \underline{\varphi}_{i,x} + c_{ij}(x)\underline{\varphi}_j - \Lambda_1(C(x_0))\underline{\varphi}_i + \varepsilon \underline{\varphi}_i \\
&= \frac{1}{2}\alpha\delta_0^2 m_x\psi_i^{(2)} + c_{ij}(x)\underline{\varphi}_j - \Lambda_1(C(x_0))\underline{\varphi}_i + \varepsilon\underline{\varphi}_i \\
&\geq \underline{\varphi}_i\left\{\frac{1}{2M}\alpha_0\delta_0^2\big(\inf_{[0,x_0-\delta_0]} m_x\big) + \min_i\left(\frac{1}{\psi_i^{(2)}}c_{ij*}\psi_j^{(2)}\right) - \Lambda_1(C(x_0)) + \varepsilon\right\} > 0.
\end{aligned}$$

Similarly, the desired differential inequality holds for $x \in [x_0 + \delta_0, 1]$. Therefore, according to eigenvalue comparison lemma, we obtain $\lambda_1(\mu, \alpha) \leq -\Lambda_1(C(x_0)) + \varepsilon$ for sufficiently large α. Since $\varepsilon > 0$ is arbitrary, (2.17) follows.

We now turn to prove that

$$\liminf_{\alpha\to\infty} \lambda_1(\mu, \alpha) \geq -\Lambda_1(C(x_0)). \tag{2.20}$$

We shall construct a positive generalized supersolution $\bar{\varphi}_i$ such that for sufficiently large α,

$$\begin{cases}
\mu\bar{\varphi}_{i,xx} + \alpha m_x\bar{\varphi}_{i,x} + c_{ij}(x)\bar{\varphi}_j - \Lambda_1(C(x_0))\bar{\varphi}_i - \varepsilon\bar{\varphi}_i \leq 0, & 0 < x < 1, \\
\bar{\varphi}_{i,x}(0) \leq 0, \ \bar{\varphi}_{i,x}(1) \geq 0.
\end{cases} \tag{2.21}$$

Define $\bar{\varphi}_i(x) := \psi_i^{(2)} q(x)$, where

$$q(x) := \begin{cases}
-\frac{\delta_0^2}{2}x + M + \frac{\delta_0^3}{4} + \frac{\delta_0^2}{2}(x_0 - \delta_0), & x \in [0, x_0 - \delta_0], \\
M + \delta_0\frac{(x-x_0)^2}{4}, & x \in [x_0 - \delta_0, x_0 + \delta_0], \\
\frac{\delta_0^2}{2}x + M + \frac{\delta_0^3}{4} - \frac{\delta_0^2}{2}(x_0 + \delta_0), & x \in [x_0 + \delta_0, 1],
\end{cases}$$

Note that $\bar{\varphi}_i \in C^1[0,1]$ and $\bar{\varphi}_i \leq (M+1)\psi_i^{(2)}$.

For $x \in [x_0 - \delta_0, x_0 + \delta_0]$, $\alpha m_x\bar{\varphi}_{i,x} \leq 0$, by (2.19), we obtain

$$\begin{aligned}
&\mu\bar{\varphi}_{i,xx} + \alpha m_x\bar{\varphi}_{i,x} + c_{ij}(x)\bar{\varphi}_j - \Lambda_1(C(x_0))\bar{\varphi}_i - \varepsilon\bar{\varphi}_i \\
&\leq \frac{\delta_0}{2}\mu\psi_i^{(2)} - \frac{\varepsilon}{2}\bar{\varphi}_i \leq \frac{\delta_0}{2}\mu\psi_i^{(2)} - \frac{\varepsilon}{2}M\psi_i^{(2)} < 0 \qquad \text{for all } \alpha > 0.
\end{aligned}$$

For $x \in [0, x_0 - \delta_0]$, $m_x > 0$, we choose α_0 is sufficiently large such that for every i,

$$-\frac{\alpha_0\delta_0^2}{2(M+1)}\big(\inf_{[0,x_0-\delta_0]} m_x\big)\psi_i^{(2)} + \left(c_{ij}^*\psi_j^{(2)}\right) - \Lambda_1(C(x_0))\psi_i^{(2)} < 0.$$

Then for $\alpha \ge \alpha_0$, we have

$$\begin{aligned}
&\mu\bar\varphi_{i,xx} + \alpha m_x \bar\varphi_{i,x} + c_{ij}(x)\bar\varphi_j - \Lambda_1(C(x_0))\bar\varphi_i - \varepsilon\bar\varphi_i\\
&= -\frac{1}{2}\alpha\delta_0^2 m_x \psi_i^{(2)} + c_{ij}(x)\bar\varphi_j - \Lambda_1(C(x_0))\bar\varphi_i - \varepsilon\bar\varphi_i\\
&\le -\frac{\alpha_0\delta_0^2}{2(M+1)}\big(\inf_{[0,x_0-\delta_0]} m_x\big)\bar\varphi_i + c^*_{ij}\bar\varphi_j - \Lambda_1(C(x_0))\bar\varphi_i - \varepsilon\bar\varphi_i\\
&\le -\frac{\alpha_0\delta_0^2}{2(M+1)}\big(\inf_{[0,x_0-\delta_0]} m_x\big)\psi_i^{(2)} + \Big(c^*_{ij}\psi_j^{(2)}\Big) - \Lambda_1(C(x_0))\psi_i^{(2)} - \varepsilon\psi_i^{(2)}\\
&< 0,
\end{aligned}$$

where we used $\bar\varphi_i \le (M+1)\psi_i^{(2)}$.

Similarly, one can show the desired differential inequality in $x \in [x_0 + \delta_0, 1]$. By using eigenvalue comparison lemma, we have $\lambda_1(\mu,\alpha) \ge -\Lambda_1(C(x_0)) - \varepsilon$ for α is sufficiently large. Since $\varepsilon > 0$ is arbitrary, (2.20) follows. Combing (2.17) and (2.20), we obtain (2.16). □

By similar arguments as in Lemma 2.8, we can deduce that the following corollary holds.

Corollary 2.9. *Let $\lambda_1(\mu,\alpha)$ be the principal eigenvalue of* (2.1)*. Then the following statements hold.*

(i) *If $m(x)$ satisfies $m_x < 0$ for $x \in (0,1]$, then we have*

$$\lim_{\alpha\to\infty}\lambda_1(\mu,\alpha) = -\Lambda_1(C(0)).$$

(ii) *If $m(x)$ satisfies $m_x > 0$ for $x \in [0,1)$, then we have*

$$\lim_{\alpha\to\infty}\lambda_1(\mu,\alpha) = -\Lambda_1(C(1)).$$

When the advection term $m(x)$ is spatially degenerate, e.g., $m(x)$ is constant in an interval of $[0,1]$, we obtain the following result.

Lemma 2.10. *Assume that there exist x_1, x_2 such that $0 \le x_1 < x_2 \le 1$ and*

$$\begin{cases} m_x > 0, & \text{for } x \in [0,x_1),\\ m_x = 0, & \text{for } x \in [x_1,x_2],\\ m_x < 0, & \text{for } x \in (x_2,1]. \end{cases}$$

Then the principal eigenvalue $\lambda_1(\mu,\alpha)$ of (2.1) *satisfies*

$$\lim_{\alpha\to\infty}\lambda_1(\mu,\alpha) = -\lambda^{\mathcal{N}\mathcal{N}}(x_1,x_2),$$

where $\lambda^{\mathcal{N}\mathcal{N}}(x_1,x_2)$ is the principal eigenvalue of

$$\mu\psi_{i,xx} + c_{ij}(x)\psi_j = \lambda\psi_i \quad \text{in } (x_1,x_2), \quad \text{and} \quad \psi_{i,x}(x) = 0 \quad \text{for } x = x_1,\ x_2.$$

Proof. We are going to prove that

$$\liminf_{\alpha\to\infty}\lambda_1(\mu,\alpha) \ge -\lambda^{\mathcal{N}\mathcal{N}}(x_1,x_2). \tag{2.22}$$

For each $\varepsilon > 0$, we shall construct a positive generalized supersolution $\bar\varphi_i > 0$ such that

$$\begin{cases} \mu\bar\varphi_{i,xx} + \alpha m_x\bar\varphi_{i,x} + c_{ij}(x)\bar\varphi_j - \lambda^{\mathcal{N}\mathcal{N}}(x_1,x_2)\bar\varphi_i - \varepsilon\bar\varphi_i \le 0, \quad 0 < x < 1,\\ \bar\varphi_{i,x}(0) \le 0,\ \ \bar\varphi_{i,x}(1) \ge 0, \end{cases} \tag{2.23}$$

provided that α is sufficiently large.

First, for a principal eigenfunction ψ_i corresponding to $\lambda^{\mathcal{NN}}(x_1,x_2)$, we extend ψ_i across $x\in\{x_1,x_2\}$ by reflection:

$$\psi_i(x):=\begin{cases}\psi_i(x_2-x) & \text{for } x\in(x_2,2x_2-x_1)\,,\\ \psi_i(x-x_1) & \text{for } x\in(2x_1-x_2,x_1).\end{cases}$$

By continuity, there exists a small $\delta_1>0$ such that

$$\mu\psi_{i,xx}+c_{ij}\psi_j-\lambda^{\mathcal{NN}}(x_1,x_2)\psi_i-\tfrac{\varepsilon}{2}\psi_i<0 \quad\text{and}\quad \psi_i>0 \text{ in } [x_1-\delta_1,x_2+\delta_1]. \tag{2.24}$$

Next, fix a small $\delta\in(0,\delta_1)$ such that $\tilde\psi_i(x)=\psi_i(x)+\delta(x-\frac{1}{2}(x_1+x_2))^2$ satisfies

$$\begin{cases}\mu\tilde\psi_{i,xx}+c_{ij}\tilde\psi_j-\lambda^{\mathcal{NN}}(x_1,x_2)\tilde\psi_i-\varepsilon\tilde\psi_i<0 \quad\text{and}\quad \tilde\psi_i>0 \quad \text{in } [x_1-\delta,x_2+\delta],\\ \tilde\psi_{i,x}<0 \quad \text{in } [x_1-\delta,x_1], \quad\text{and}\quad \tilde\psi_{i,x}>0 \quad \text{in } [x_2,x_2+\delta].\end{cases} \tag{2.25}$$

Assertion (2.25) also follows from continuity, where we used $\psi_{i,x}(x_1)=\psi_{i,x}(x_2)=0$.

Next, define the supersolution $\bar\varphi_i$ by

$$\bar\varphi_i=\begin{cases}\tilde\psi_i(x_1-\delta)+(x-x_1+\delta)\tilde\psi_{i,x}(x_1-\delta) & \text{for } x\in[0,x_1-\delta],\\ \tilde\psi_i(x) & \text{for } x\in[x_1-\delta,x_2+\delta],\\ \tilde\psi_i(x_2+\delta)+(x-x_2-\delta)\tilde\psi_{i,x}(x_2+\delta) & \text{for } x\in[x_2+\delta,1].\end{cases} \tag{2.26}$$

It follows from (2.25) that $\bar\varphi_i$ is a supersolution in the interval $[x_1-\delta,x_2+\delta]$.

For $x\in[0,x_1-\delta]$, $m_x>0$, $\bar\varphi_{i,x}=\tilde\psi_{i,x}(x_1-\delta)<0$, we choose $\alpha_0\gg1$ such that, for every i,

$$\alpha_0\left(\inf_{[0,x_1-\delta]}m_x\right)\tilde\psi_{i,x}(x_1-\delta)+c^*_{ij}\bar\varphi_j-\lambda^{\mathcal{NN}}(x_1,x_2)\bar\varphi_i<0,$$

which is possible since $|\bar\varphi_j(x)|$ is bounded independently of α. Then for $\alpha\geq\alpha_0$, we have

$$\begin{aligned}&\mu\bar\varphi_{i,xx}+\alpha m_x\bar\varphi_{i,x}+c_{ij}(x)\bar\varphi_j-\lambda^{\mathcal{NN}}(x_1,x_2)\bar\varphi_i-\varepsilon\bar\varphi_i\\ &=\alpha m_x\tilde\psi_{i,x}(x_1-\delta)+c_{ij}(x)\bar\varphi_j-\lambda^{\mathcal{NN}}(x_1,x_2)\bar\varphi_i-\varepsilon\bar\varphi_i\\ &\leq\alpha_0\left(\inf_{[0,x_1-\delta]}m_x\right)\tilde\psi_{i,x}(x_1-\delta)+c^*_{ij}\bar\varphi_j-\lambda^{\mathcal{NN}}(x_1,x_2)\bar\varphi_i-\varepsilon\bar\varphi_i<0.\end{aligned}$$

Similarly, one can show the desired differential inequality in $[x_2+\delta,1]$. Since $\bar\varphi_i\in C^1([0,1])$ and satisfies $\bar\varphi_{i,x}(0)<0<\bar\varphi_{i,x}(1)$, we have verified (2.23). Hence, it follow from eigenvalue comparison lemma that $\varliminf\limits_{\alpha\to\infty}\lambda_1(\mu,\alpha)\geq-\lambda^{\mathcal{NN}}(x_1,x_2)-\varepsilon$. Since $\varepsilon>0$ is arbitrary, we have proven (2.22).

We then establish

$$\limsup_{\alpha\to\infty}\lambda_1(\mu,\alpha)\leq-\lambda^{\mathcal{NN}}(x_1,x_2). \tag{2.27}$$

For each $\varepsilon>0$, it suffices to construct a nonnegative generalized subsolution $\underline{\varphi}_i$ such that

$$\begin{cases}\mu\underline{\varphi}_{i,xx}+\alpha m_x\underline{\varphi}_{i,x}+c_{ij}(x)\underline{\varphi}_j-\lambda^{\mathcal{NN}}(x_1,x_2)\underline{\varphi}_i+\varepsilon\underline{\varphi}_i\geq0, \quad 0<x<1,\\ \underline{\varphi}_{i,x}(0)\geq0,\ \underline{\varphi}_{i,x}(1)\leq0,\end{cases} \tag{2.28}$$

provided that α is sufficiently large. To this end, we let

$$\hat\psi_i(x)=\psi_i(x)-\delta(x-\tfrac{1}{2}(x_1+x_2))^2,$$

and it satisfies

$$\begin{cases} \mu\hat{\psi}_{i,xx} + c_{ij}\hat{\psi}_j - \lambda^{\mathcal{N}\mathcal{N}}(x_1, x_2)\hat{\psi}_i + \varepsilon\hat{\psi}_i > 0 \quad \text{and} \quad \hat{\psi}_i > 0 \quad \text{in } [x_1 - \delta, x_2 + \delta], \\ \hat{\psi}_{i,x} > 0 \quad \text{in } [x_1 - \delta, x_1], \quad \text{and} \quad \hat{\psi}_{i,x} < 0 \quad \text{in } [x_2, x_2 + \delta]. \end{cases} \tag{2.29}$$

Now, define the subsolution $\underline{\varphi}_i$ by

$$\underline{\varphi}_i = \begin{cases} \hat{\psi}_i(x_1 - \delta) + (x - x_1 + \delta)\hat{\psi}_{i,x}(x_1 - \delta) & \text{for } x \in [0, x_1 - \delta], \\ \hat{\psi}_i(x) & \text{for } x \in [x_1 - \delta, x_2 + \delta], \\ \hat{\psi}_i(x_2 + \delta) + (x - x_2 - \delta)\hat{\psi}_{i,x}(x_2 + \delta) & \text{for } x \in [x_2 + \delta, 1]. \end{cases} \tag{2.30}$$

We claim that $\underline{\varphi}_i$ is a subsolution in $[0, 1]$ with the appropriate boundary conditions. We remark that this can be verified similar to the verification of supersolution, and omit the details.

Hence, we obtain (2.27) by using eigenvalue comparison lemma. Combing (2.22) and (2.27), we complete the proof. □

Next, we investigate the monotonicity of the principal eigenvalue $\lambda_1(\mu, \alpha)$ with respect to the advection rate. In the case of a scalar equation, if $c(x)$ is strictly decreasing, the principal eigenvalue is monotone increasing in α.

Lemma 2.11. *Let $\lambda_1(\alpha)$ be the principal eigenvalue of*

$$\mu\varphi_{xx} + \alpha\varphi_x + c(x)\varphi + \lambda\varphi = 0 \quad \text{in } (0, 1), \quad \text{and} \quad \varphi_x = 0 \quad \text{for } x = 0, 1.$$

If $c(x) \in C([0, 1])$ is strictly decreasing, then $\partial_\alpha\lambda_1(\alpha) > 0$ for $\mu > 0$ and $\alpha \in \mathbb{R}$.

Proof. See, e.g. ([30, 31, 35]). □

Here, we provide sufficient conditions for cooperative systems to be monotonically increasing or decreasing in α, for sufficiently large μ and sufficiently small $\frac{\alpha}{\mu}$.

Theorem 2.12. *Let $\lambda_1(\mu, \alpha)$ be the principal eigenvalue of (2.1). Then the following statements hold.*

(i) *$\partial_\alpha\lambda_1(\mu, \alpha) < 0$ for $\mu \gg 1$ and $\frac{\alpha}{\mu} \ll 1$ provided that we have, for each i,*

$$m_x > 0,\ (c_{ij})_x a_j \ \geq\ 0 \quad \forall x \quad \text{or} \quad m_x < 0,\ (c_{ij})_x a_j \ \leq\ 0 \quad \forall x,$$

and there is an i such that $(c_{ij})_x a_j \not\equiv 0$.

(ii) *$\partial_\alpha\lambda_1(\mu, \alpha) > 0$ for $\mu \gg 1$ and $\frac{\alpha}{\mu} \ll 1$ provided that we have, for each i,*

$$m_x > 0,\ (c_{ij})_x a_j \ \leq\ 0 \quad \forall x \quad \text{or} \quad m_x < 0,\ (c_{ij})_x a_j \ \geq\ 0 \quad \forall x,$$

and there is an i such that $(c_{ij})_x a_j \not\equiv 0$.

Here (a_j) is the positive right eigenvector of the constant matrix $\bar{C}$, respectively.

Remark 2.13. By considering the adjoint problem, one can also derive a different set of conditions based on a_j^*, the positive left eigenvector of the constant matrix $\bar{C}$. For example, a alternative condition for the conclusion of Theorem 2.12 (i) is given by

$$m_x > 0,\ (c_{ji})_x a_j^* \ \geq\ 0 \quad \forall x \quad \text{or} \quad m_x < 0,\ (c_{ji})_x a_j^* \ \leq\ 0 \quad \forall x,$$

and there is an i such that $(c_{ji})_x a_j^* \not\equiv 0$. When $c_{ij} = c_{ji}$, then these two conditions are the same. However, they represent different conditions when c_{ij} is asymmetric.

Proof. The adjoint problem of (2.1) is

$$\begin{cases} (\mu\phi^*_{i,x} - \alpha m_x \phi^*_i)_x + c_{ji}(x)\phi^*_j + \lambda\phi^*_i = 0, & 0 < x < 1, \\ \mu\phi^*_{i,x}(x) - \alpha m_x \phi^*_i(x) = 0, & x = 0,\ 1, \end{cases} \tag{2.31}$$

where $1 \le i \le n$, and the value of λ coincides with the principal eigenvalue of (2.1). We perform an exponential transformation on (2.31), such that $\varphi^*_i = e^{-\alpha m(x)/\mu}\phi^*_i$, to obtain

$$\begin{cases} \mu\varphi^*_{i,xx} + \alpha m_x \varphi^*_{i,x} + c_{ji}(x)\varphi^*_j + \lambda\varphi^*_i = 0, & 0 < x < 1, \\ \varphi^*_{i,x}(x) = 0, & x = 0,\ 1. \end{cases} \tag{2.32}$$

For simplicity, we further normalize φ^*_i by $\int_0^1 e^{(\alpha/\mu)m(x)}\varphi_i\varphi^*_i dx = 1$.

Claim 2. $\partial_\alpha\lambda_1(\mu,\alpha) = -\displaystyle\int_0^1 e^{(\alpha/\mu)m(x)} m_x \varphi_{i,x}\varphi^*_i dx = -\int_0^1 e^{(\alpha/\mu)m(x)} m_x \varphi^*_{i,x}\varphi_i dx.$

Differentiating both sides of (2.1) with respect to α, we have

$$\begin{cases} \mu(\partial_\alpha\varphi_i)_{xx} + m_x\varphi_{i,x} + \alpha m_x(\partial_\alpha\varphi_i)_x + c_{ij}(x)\partial_\alpha\varphi_j + \lambda_1\partial_\alpha\varphi_i = -\partial_\alpha\lambda_1\varphi_i, \\ \partial_\alpha\varphi_{i,x}(x) = 0,\ x = 0,\ 1. \end{cases} \tag{2.33}$$

Multiplying (2.33) by $e^{(\alpha/\mu)m(x)}\varphi^*_i$ and (2.32) by $e^{(\alpha/\mu)m(x)}\partial_\alpha\varphi_i$, respectively, then integrating each by parts and summing over i, we have

$$\partial_\alpha\lambda_1(\mu,\alpha) = -\int_0^1 e^{(\alpha/\mu)m(x)} m_x\varphi_{i,x}\varphi^*_i dx.$$

Similarly, taking the derivative of both sides of (2.32) with respect to α and then integrating and simplifying, we can obtain

$$\partial_\alpha\lambda_1(\mu,\alpha) = -\int_0^1 e^{(\alpha/\mu)m(x)} m_x\varphi^*_{i,x}\varphi_i dx.$$

Therefore, Claim 2 holds.

For given α, we still use the Taylor expansion (2.9) of the eigenvalue and eigenfunction for problem (2.1) in $\mu \gg 1$. Note that as $\mu \to \infty$ and $\frac{\alpha}{\mu} \to 0$, $\bar\lambda$ and $(a_i), (a^*_i) \in \mathbb{R}^n_+$ remain the principal eigenvalue and the corresponding unit right and left positive eigenvectors of matrix $\bar C$ based on Lemma 2.14. Thus, by using Claim 2 and (2.13)-(2.14), we deduce that the conclusions (of Theorem 2.12 as well as of Remark 2.13) hold. □

2.3. **Joint effects of μ and α.** We give one result when μ and α jointly varies.

Lemma 2.14. *For each $\zeta \in [0,\infty)$, the principal eigenvalue $\lambda_1(\mu,\alpha)$ of (2.1) satisfies*

$$\lim_{\mu\to\infty,\alpha/\mu\to\zeta} \lambda_1(\mu,\alpha) = -\Lambda_1(\bar C_\zeta), \tag{2.34}$$

where $\bar C_\zeta := \left(\dfrac{\int_0^1 e^{\zeta m(x)}c_{ij}(x)dx}{\int_0^1 e^{\zeta m(x)}dx}\right)_{1\le i,j\le n}$.

Proof. Multiplying the equation of (2.1) by $e^{(\alpha/\mu)m(x)}$, we have

$$\begin{cases}\mu(e^{(\alpha/\mu)m(x)}\varphi_{i,x})_x + e^{(\alpha/\mu)m(x)}c_{ij}(x)\varphi_j + \lambda e^{(\alpha/\mu)m(x)}\varphi_i = 0, & 0 < x < 1,\\ \varphi_{i,x}(x) = 0, & x = 0,\ 1.\end{cases} \tag{2.35}$$

Dividing (2.35) by μ, we have

$$\begin{cases}(e^{(\alpha/\mu)m(x)}\varphi_{i,x})_x + \frac{1}{\mu}(e^{(\alpha/\mu)m(x)}c_{ij}(x)\varphi_j + \lambda e^{(\alpha/\mu)m(x)}\varphi_i) = 0, & 0 < x < 1,\\ \varphi_{i,x}(x) = 0, & x = 0,\ 1.\end{cases} \tag{2.36}$$

By using elliptic L^p estimates and Sobolev embedding, there is a subsequence $\varphi_i \to \bar{\varphi}_i$ that is weakly convergent in $W^{2,p}(0,1)$ and strongly convergent in $C^1([0,1])$ as $\mu \to \infty, \alpha/\mu \to \zeta$, where $\bar{\varphi}_i$ satisfies

$$(e^{\zeta m(x)}\bar{\varphi}_{i,x})_x = 0,\ 0 < x < 1,\ \bar{\varphi}_{i,x}(x) = 0,\ x = 0,\ 1.$$

That is, $\bar{\varphi}_i$ is a constant. Integrating (2.35) over $(0,1)$, and letting $\mu \to \infty, \alpha/\mu \to \zeta$, we obtain

$$\int_0^1 e^{\zeta m(x)}c_{ij}(x)dx \cdot \bar{\varphi}_j + \bar{\lambda}\int_0^1 e^{\zeta m(x)}dx \cdot \bar{\varphi}_i = 0, \tag{2.37}$$

where $\bar{\lambda} = \lim\limits_{\mu\to\infty,\alpha/\mu\to\zeta} \lambda_1(\mu,\alpha)$. According to (2.37), $\bar{\lambda}$ is an eigenvalue of the cooperative matrix $\bar{C}_\zeta$ possessing a nonnegative eigenvector $(\bar{\varphi}_i)$. By the characterization of Perron-Frobenius eigenvalue [27], it follows that $\bar{\lambda} = -\Lambda_1(\bar{C}_\zeta)$. □

3. **Application to the nematode population model (1.1).**

This section is dedicated to applying the properties of the principal eigenvalue obtained in Section 2 to the two-state nematode population model (1.1), to explain which movement strategies are most beneficial under various nutrient and toxin distributions.

Let $\tilde{\lambda}_1(\mu,\alpha)$ be the principal eigenvalue of

$$\begin{cases}(\mu\tilde{\phi}_x + \alpha\sigma_x\tilde{\phi})_x - r(x)\tilde{\phi} + k\tilde{\varphi} + kb(1-\sigma(x))\tilde{\varphi} + \tilde{\lambda}\tilde{\phi} = 0, & 0 < x < L,\\ (\mu\tilde{\varphi}_x + \alpha\sigma_x\tilde{\varphi})_x - k\tilde{\varphi} + r(x)\tilde{\phi} + \tilde{\lambda}\tilde{\varphi} = 0, & 0 < x < L,\\ \mu\tilde{\phi}_x(x) + \alpha\sigma_x\tilde{\phi}(x) = \mu\tilde{\varphi}_x(x) + \alpha\sigma_x\tilde{\varphi}(x) = 0, & x = 0,\ L.\end{cases} \tag{3.1}$$

The principal eigenvalue $\tilde{\lambda}_1(\mu,\alpha)$ governs the long-time asymptotics of (1.1). A classical result (see, e.g. [35, Ch. 4]) states that any positive solution (u,v) of (1.1) satisfies

$$\underline{c}e^{-\tilde{\lambda}_1(\mu,\alpha)t} \leq \min\{u,v\} \leq \max\{u,v\} \leq \bar{c}e^{-\tilde{\lambda}_1(\mu,\alpha)t} \tag{3.2}$$

for some constants $\bar{c} \geq \underline{c} > 0$.

We use the transformation $\phi = e^{(\alpha/\mu)\sigma(x)}\tilde{\phi}$ and $\varphi = e^{(\alpha/\mu)\sigma(x)}\tilde{\varphi}$. Then (3.1) becomes

$$\begin{cases}\mu\phi_{xx} - \alpha\sigma_x\phi_x - r(x)\phi + k\varphi + kb(1-\sigma(x))\varphi + \tilde{\lambda}\phi = 0, & 0 < x < L,\\ \mu\varphi_{xx} - \alpha\sigma_x\varphi_x - k\varphi + r(x)\phi + \tilde{\lambda}\varphi = 0, & 0 < x < L,\\ \phi_x(x) = 0,\ \varphi_x(x) = 0, & x = 0,\ L.\end{cases} \tag{3.3}$$

Note that the cooperative system (3.3) can be regarded as a special case of (2.1) with $n = 2$, and

$$m(x) = -\sigma(x),\ C(x) = (c_{ij}(x))_{2\times 2} = \begin{pmatrix} -r(x) & k + kb(1-\sigma(x))\\ r(x) & -k\end{pmatrix}.$$

The following result shows that the sign of the principal eigenvalue $\tilde{\lambda}_1(\mu,\alpha)$ of (3.3) depends on the distribution of the toxins. Specifically, when toxins are uniformly distributed throughout the entire interval such that $\sigma(x)\equiv 1$, $\tilde{\lambda}_1(\mu,\alpha)=0$. This means that no new nematodes will be born in the population, and the number of nematodes will always remain the same as at the beginning of the experiment.

Lemma 3.1. *For each $\mu>0$, $\alpha\in\mathbb{R}$ and $0\le\sigma(x)\le 1$, the principal eigenvalue $\tilde{\lambda}_1(\mu,\alpha)$ of (3.3) satisfies $\tilde{\lambda}_1(\mu,\alpha)\le 0$, and equality holds if and only if $\sigma(x)\equiv 1$ on $[0,L]$.*

Proof. Let (ϕ_1,φ_1) be the principal eigenfunction of (3.3). Multiplying the equations of (3.3) by $e^{-(\alpha/\mu)\sigma(x)}$, integrating over $[0,L]$, and adding the result, we obtain

$$\int_0^L e^{-(\alpha/\mu)\sigma(x)}kb(1-\sigma(x))\varphi_1dx+\tilde{\lambda}_1\int_0^L e^{-(\alpha/\mu)\sigma(x)}(\phi_1+\varphi_1)dx=0.$$

Since $0\le\sigma(x)\le 1$, we have $\tilde{\lambda}_1(\mu,\alpha)\le 0$ and equality holds if and only if $\sigma(x)\equiv 1$ on $[0,L]$. □

Based on Lemma 2.3, we obtain the following result.

Lemma 3.2. *Suppose that $\alpha=0$. Then the principal eigenvalue $\tilde{\lambda}_1(\mu,0)$ of (3.3) satisfies*

$$\lim_{\mu\to 0}\tilde{\lambda}_1(\mu,0)=\min_{x_0\in[0,L]}\frac{1}{2}[k+r(x_0)-\sqrt{(k+r(x_0))^2+4kbr(x_0)(1-\sigma(x_0))}],\tag{3.4}$$

and

$$\lim_{\mu\to\infty}\tilde{\lambda}_1(\mu,0)=\frac{1}{2}[k+\bar{r}-\sqrt{(k+\bar{r})^2+4kb\bar{r}(1-\bar{\sigma})}],\tag{3.5}$$

where $\bar{r}=\frac{\int_0^L r(x)dx}{L}$, $\bar{\sigma}=\frac{\int_0^L\sigma(x)dx}{L}$.

The above mathematical results can, to some extent, explain some experimental results in [7].

- If there is a point x_0 such that $\sigma(x_0)=\min\limits_{x_0\in[0,L]}\sigma(x)$, $r(x_0)=\max\limits_{x_0\in[0,L]}r(x)$, then the right side of (3.4) attains its minimum value at x_0, which means that the effective growth rate of nematodes $-\tilde{\lambda}_1(\mu,0)$ reaches its maximum value under these conditions, and that the nematode distribution has a local maximum near x_0. Therefore, we can conclude that nematodes exhibit a higher effective growth rate in areas with abundant nutrients and fewer toxins when their diffusion rate is small.
- Obviously, as the toxin covered area gradually increases (see Figure 1 A), the value of $\bar{\sigma}$ continues to increase. According to (3.5), we know that the effective growth rate $-\tilde{\lambda}_1(\mu,0)$ of the nematode gradually decreases. Thus, it can be conclude that when the diffusion rate of nematodes is large, the increase of toxins coverage can lead to a sustained decline in population abundance.

Next, we derive sufficient conditions for the monotonicity of $\tilde{\lambda}_1(\mu,\alpha)$ in $\mu\gg 1$:

Theorem 3.3. *Suppose that $\alpha=0$ and $\tilde{\lambda}_1(\mu,0)$ is the principal eigenvalue of (3.3). Then the following statements hold.*

(i) *If $r_x\ge 0,\not\equiv 0$, and $\sigma_x\ge 0,\not\equiv 0$ for $0<x<L$, then $\partial_\mu\tilde{\lambda}_1(\mu,0)<0$ for $\mu\gg 1$.*

(ii) *If* $r_x \leq 0, \not\equiv 0$, *and* $\sigma_x \leq 0, \not\equiv 0$ *for* $0 < x < L$, *then* $\partial_\mu \tilde{\lambda}_1(\mu, 0) < 0$ *for* $\mu \gg 1$.

(iii) *If* $r_x \geq 0$, $\sigma_x \leq 0$, *and* $a_1 r_x + a_2 k b \sigma_x \leq 0$ *for* $0 < x < L$, *such that* $r_x \sigma_x \not\equiv 0$ *for some* $x \in (0, L)$, *then* $\partial_\mu \tilde{\lambda}_1(\mu, 0) > 0$ *for* $\mu \gg 1$.

(iv) *If* $r_x \leq 0$, $\sigma_x \geq 0$, *and* $a_1 r_x + a_2 k b \sigma_x \geq 0$ *for* $0 < x < L$, *such that* $r_x \sigma_x \not\equiv 0$ *for some* $x \in (0, L)$, *then* $\partial_\mu \tilde{\lambda}_1(\mu, 0) > 0$ *for* $\mu \gg 1$.

Here (a_1, a_2) *is a positive eigenvector of the constant matrix:*

$$A = \begin{pmatrix} -\bar{r} & k(1 + b(1 - \bar{\sigma})) \\ \bar{r} & -k \end{pmatrix}.$$

Proof. First, let $\bar{\lambda}$ and (a_1^*, a_2^*) be the principal eigenvalue and left positive eigenvector of A. It is easy to see that

$$\bar{\lambda} a_1^* = \bar{r}(-a_1^* + a_2^*) \quad \text{and} \quad \bar{\lambda} a_2^* = k(a_1^* - a_2^*) + kb(1 - \bar{\sigma}) a_1^*.$$

Since $kb(1 - \bar{\sigma}) > 0$, it follows that $\bar{\lambda} > 0$ and $a_2^* > a_1^*$. The desired conclusion now follows from Theorem 2.5. For example, to prove (i), we observe that (in the notation of Section 2)

$$(c_{11})_x a_1 + (c_{12})_x a_2 = -(a_1 r_x + a_2 k b \sigma_x) \leq 0, \qquad (c_{21})_x a_1 + (c_{22})_x a_2 = a_1 r_x \geq 0,$$

$$(c_{11})_x a_1^* + (c_{21})_x a_2^* = r_x(-a_1^* + a_2^*) \geq 0, \qquad (c_{12})_x a_1^* + (c_{22})_x a_2^* = -a_1^* k b \sigma_x \leq 0.$$

It then follows from Theorem 2.5(i) that $\partial_\mu \tilde{\lambda}_1(\mu, 0) < 0$ for $\mu \gg 1$. The proof of the other cases is analogous. ☐

Theorem 3.4. *Let* $\tilde{\lambda}_1(\mu, \alpha)$ *be the principal eigenvalue of* (3.3). *Then we have* $\partial_\alpha \tilde{\lambda}_1(\mu, \alpha) < 0$ *for* $\mu \gg 1$ *and* $\frac{\alpha}{\mu} \ll 1$ *if one of the following assumptions hold:*

(i) $\sigma_x < 0$, $r_x \geq 0$, *and* $a_1 r_x + a_2 k b \sigma_x \leq 0$ *for* $0 < x < L$, *such that* $r_x \sigma_x \not\equiv 0$ *for some* $x \in (0, L)$.

(ii) $\sigma_x > 0$, $r_x \leq 0$, *and* $a_1 r_x + a_2 k b \sigma_x \geq 0$ *for* $0 < x < L$, *such that* $r_x \sigma_x \not\equiv 0$ *for some* $x \in (0, L)$.

Proof. The proof is similar to Theorem 3.3, where we use Theorem 2.12 in place of Theorem 2.5. It should be noted that since $\sigma(x) = -m(x)$, the formula in Claim 2 of the proof of Theorem 2.12 for determining the monotonicity of $\tilde{\lambda}_1(\mu, \alpha)$ with respect to α can be written as

$$\partial_\alpha \tilde{\lambda}_1(\mu, \alpha) = \int_0^L e^{-(\alpha/\mu)\sigma(x)} \sigma_x \phi_x \phi^* \, dx + \int_0^L e^{-(\alpha/\mu)\sigma(x)} \sigma_x \varphi_x \varphi^* \, dx.$$

The rest of the proof is omitted. ☐

Theorems 3.3 – 3.4 well explain the optimal movement strategies of nematodes when nutrients and toxins exhibit different spatial distribution patterns in [7].

- When the spatial distribution of nutrients and toxins follows the same monotonicity, e.g., both monotone increasing (or both monotone decreasing) in one direction, the higher diffusion rate is advantageous (see Theorem 3.3(i)-(ii)).
- Conversely, when the spatial distribution of nutrients and toxins exhibits different monotonicity, e.g., the nutrient distribution is increasing and the toxin distribution is decreasing, and the gradient of the toxin concentration is greater relative to that of the nutrient (or vice versa), the lower diffusion

rate is advantageous (see Theorem 3.3 (iii)-(iv)). Furthermore, the higher advection rate is advantageous in such an environment (see Theorem 3.4).

Theorem 3.5. *Assume that $\sigma(x)$ satisfies $\sigma_x = 0$ for $x \in [0,a]$ and $\sigma_x > 0$ for $x \in (a,L]$. Then the principal eigenvalue $\tilde{\lambda}_1(\mu,\alpha)$ of (3.3) satisfies*

$$\lim_{\alpha\to\infty} \tilde{\lambda}_1(\mu,\alpha) = -\lambda^{\mathcal{N}\mathcal{N}}(0,a),$$

where $\lambda^{\mathcal{N}\mathcal{N}}(0,a)$ is the principal eigenvalue of the problem

$$\begin{cases} \mu\phi_{xx} - r(x)\phi + k\varphi + kb(1-\sigma(x))\varphi = \lambda\phi, & 0<x<a, \\ \mu\varphi_{xx} - k\varphi + r(x)\phi = \lambda\varphi, & 0<x<a, \\ \phi_x(x) = \varphi_x(x) = 0, & x = 0,\ a. \end{cases} \tag{3.6}$$

Furthermore, $\partial_\mu \lambda^{NN} > 0$ for $\mu \gg 1$ if $r_x \le 0, \not\equiv 0$ (or $r_x \ge 0, \not\equiv 0$) for $0<x<a$.

Proof. The first assertion is based on Lemma 2.10. Note that for the eigenvalue problem of (3.6), the formula Claim 1 for determining the monotonicity of $\lambda^{\mathcal{N}\mathcal{N}}(0,a)$ with respect to μ should be

$$\partial_\mu \lambda^{NN} = -\int_0^a \phi_x\phi_x^* + \varphi_x\varphi_x^*.$$

When $r_x \le 0, \not\equiv 0$ for $0<x<a$, by similar arguments as in Theorem 3.3, we have in the domain $[0,a]$,

$$(c_{11})_x a_1 + (c_{12})_x a_2 = -a_1 r_x \ge 0, \qquad (c_{21})_x a_1 + (c_{22})_x a_2 = a_1 r_x \le 0,$$

$$(c_{11})_x a_1^* + (c_{21})_x a_2^* = r_x(-a_1^* + a_2^*) \le 0, \qquad (c_{12})_x a_1^* + (c_{22})_x a_2^* = -a_1^* kb\sigma_x = 0.$$

It then follows from (2.13)-(2.14) that $\phi_x > 0$, $\phi_x^* < 0$ and $\varphi_x < 0$, $\varphi_x^* = 0$ for $\mu \gg 1$. Hence, we obtain $\partial_\mu \lambda^{NN} > 0$ for $\mu \gg 1$. ☐

Theorem 3.5 is consistent with the third set of experiment in [7], which involves adding nutrients next to areas contaminated by toxins (see Figure 1 C). In such an environment, the nematodes tend to concentrate in areas with only nutrients when the advection rate is large enough. Meanwhile, when the added nutrient distribution is monotone decreasing (or monotone increasing), the effective growth rate $\lambda^{\mathcal{N}\mathcal{N}}(0,a)$ is increasing with μ for large μ, i.e., the higher diffusion rate is advantageous.

4. **Discussion.**

In this paper, we propose a two-state population model (1.1) that is motivated by recent experiments on the population dynamics of nematodes by Baragary et al. [7]. In those experiment, it is shown that when nutrients and toxins are placed on the same side of the petri dish, then strains with higher movement rates achieve larger population growth relative to strains with lower movement rates. By contrast, lower movement rates are advantageous when the gradients of nutrients and toxins point in opposite directions. This motivates our study of the principal eigenvalue of (3.3).

Our approach is based on obtaining sufficient conditions for the principal eigenvalue of general linear cooperative elliptic system (2.1) to be increasing or decreasing with respect to the diffusion rate μ and advection rate α, for $\mu \gg 1$, $\frac{\alpha}{\mu} \ll 1$. In particular, our results show that increasing properties with respect to the diffusion and advection rates, which holds for the scalar case [35, 41, 30, 31], no longer holds in general for cooperative systems. It is a challenging open questions to obtain conditions to ensure the monotonicity of principal eigenvalue with respect to the diffusion and advection rates; see Remark 2.6 and Theorem 2.7.

Applying these results to the specific system (3.3), we showed the following:

(i) (Theorem 3.3(i)-(ii)) When the nutrient and toxin distribution are both monotone increasing (or both monotone decreasing) in one direction, then strains with higher diffusion rate have higher growth rates relative to strains with lower diffusion rate.

(ii) (Theorem 3.3(iii)-(iv)) Conversely, when the nutrient distribution is increasing and the toxin distribution is decreasing, and the gradient of the toxin concentration is greater relative to that of the nutrient (or vice versa), then strains with higher diffusion rate has lower growth rate relative to strains with lower diffusion rate.

(iii) (Theorem 3.4) Under the same conditions as in (ii) above, strains with higher advection rate have higher growth rates relative to strains with lower advection rate in such an environment.

(iv) (Theorem 3.5) Under the effect of large advection, when nutrients are added to a toxin-contaminated environment, and the added nutrient distribution is monotone decreasing (or monotone increasing), then strains with higher diffusion rate have higher growth rates relative to strains with lower diffusion rate.

Since the movement rates of the nematode strains are relatively large with respect to the size of the domain in the experiments, our results well explain the optimal movement strategies of organisms when nutrients and toxins exhibit different spatial distribution patterns. Therefore, the two-state reaction-diffusion model with internal food reserves offers an novel approach to understand experimental observations and how species with different movement strategies respond to habitat changes.

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