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# ECOLOGICAL AND EVOLUTIONARY DYNAMICS IN PERIODIC AND ADVECTIVE HABITATS*

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*Dedicated to Professor Ling Hsiao on the Occasion of Her 80th Birthday*

**Abstract.** We study the dynamics of reaction-diffusion-advection models for single and two competing species in one-dimensional periodic habitats, where the individuals are subject to both diffusion and advection. We investigate the monotone dependence of the principal eigenvalue on diffusion and drift rates. As applications, we first consider the persistence and spatial spreading of a single species and establish the critical threshold for the persistence as well as the monotone dependence of the minimal wave speed on the drift rate. We also consider two competing species model and study the local and global stability of semi-trivial steady states. Furthermore, the existence of evolutionarily singular strategies is established, which helps gain deeper insight into the evolution of dispersal in advective environments.

**Key words.** Reaction-diffusion-advection, persistence, spreading, competition, singular strategy, periodic habitat.

**Mathematics Subject Classification.** 35Q92, 35P15, 92D25, 35K57, 92D15.

**1. Introduction.** In recent years there has been increasing interest in studying the dynamics of reaction-diffusion-advection systems of the form

$$\begin{cases} U_t = \nabla \cdot [\mu \nabla U + U\overrightarrow{\mathbf{b_1}}] + f(x, U, V) & \text{in } \Omega \times (0, \infty), \\ V_t = \nabla \cdot [\nu \nabla V + V\overrightarrow{\mathbf{b_2}}] + g(x, U, V) & \text{in } \Omega \times (0, \infty), \end{cases} \tag{1.1}$$

where $\Omega$ is a domain in $\mathbb{R}^N$ with smooth boundary $\partial\Omega$, $U(x,t)$ and $V(x,t)$ are the population densities of two species, parameters $\mu, \nu > 0$ are their diffusion rates, and vectors $\overrightarrow{\mathbf{b_i}}(x)$, $\mathbf{i} = 1, 2$, account for the advection of the species. Understanding the ecological and evolutionary impact of dispersal and advection on system (1.1) is a challenging issue [5, 8, 28, 31]. Some recent progress in this direction has been made for the case of $\overrightarrow{\mathbf{b_i}} = 0$ [15, 16, 17, 18, 33], the case of advection along resource gradient [1, 6, 7, 25, 26, 34], and the case of passive drift in water columns; see also [12, 29, 30, 32, 36, 37, 38, 39, 40, 45, 50, 51, 52, 53, 54, 55] and references therein.

We are interested in the situation when $\mathbf{b_i}$ describes a divergence free steady flow, i.e.

$$\nabla \cdot \overrightarrow{\mathbf{b_i}} = 0 \text{ in } \Omega, \quad \overrightarrow{\mathbf{b_i}} \cdot n = 0 \text{ on } \partial\Omega, \quad \mathbf{i} = 1, 2, \tag{1.2}$$

where $n(x)$ denotes the unit outward normal vector at $x \in \partial\Omega$. Our goal is to understand how such steady flow will affect the outcome of competitions. For river models in one-dimensional bounded interval with passive drift, $\overrightarrow{\mathbf{b_1}} = \alpha$ and $\overrightarrow{\mathbf{b_2}} = \beta$ for positive constants $\alpha, \beta$, thus $\nabla \cdot \overrightarrow{\mathbf{b_i}} = 0$ but they do not satisfy the boundary

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conditions $\overrightarrow{\mathbf{b_i}} \cdot n = 0$ on $\partial\Omega$. To this end, in this paper we consider the following two-species competition model in a one-dimensional, spatially periodic (i.e. with $\partial\Omega$ as an empty set) and advective environment to mimic (1.2):

$$\begin{cases} U_t = \mu U_{xx} + \alpha U_x + U[r_\ell(x) - U - V] & \text{in } \mathbb{R}\times(0,\infty), \\ V_t = \nu V_{xx} + \beta V_x + V[r_\ell(x) - U - V] & \text{in } \mathbb{R}\times(0,\infty), \\ U(x,t) = U(x+\ell,t),\ V(x,t) = V(x+\ell,t) & \text{in } \mathbb{R}\times(0,\infty), \end{cases} \tag{1.3}$$

where $r_\ell(x) := r(x/\ell)$ with some 1-periodic function $r \in C^2(\mathbb{R})$ accounts for the common local intrinsic growth rate, and $\alpha, \beta \in \mathbb{R}$ are their advection rates and are assumed to be constants. We assume that two species are neutral in competition, i.e. neither of them has advantage over the other in terms of the competitive ability.

In (1.3), as $\overrightarrow{\mathbf{b_1}} = \alpha$ and $\overrightarrow{\mathbf{b_2}} = \beta$, and $\partial\Omega$ can be viewed as an empty set, they satisfy (1.2). We envision that two competing species are subject to random diffusion and passive drift in a spatially periodic environment, for instance, in a circular tube. Surprisingly, even for such (deceptively) simple looking steady flow, full understanding the dynamics of (1.3) turns out to be quite challenging, as illustrated by the results in the rest of this section.

As the advection terms in system (1.3) describe passive flows (e.g. the drift due to the river flow), they are generally not correlated with the growth function $r_l$; i.e. the advection may not push the populations to move upward along the resource gradient. It will be of interest to consider the case of spatially heterogeneous and periodic drift rates, which is more practical biologically.

**1.1. Persistence and Spreading.** In this subsection, we focus on the logistic type single population models with diffusion and advection in the periodic habitat with the form

$$\begin{cases} u_t = \mu u_{xx} + \alpha u_x + u\,(r_\ell(x) - u) & \text{in } \mathbb{R}\times(0,\infty), \\ u(x,t) = u(x+\ell,t) & \text{in } \mathbb{R}\times(0,\infty). \end{cases} \tag{1.4}$$

Here $u(x,t)$ is the population density, $\mu > 0$ is the diffusion rate, and $r_\ell$ represents the growth rate of the population. The dynamics of (1.4) are not only of independent interest, they are also building blocks in studying the dynamics of (1.3), especially issues concerning the invasions of exotic species. The steady states of (1.4) are given by the solutions of

$$\mu\theta_{xx} + \alpha\theta_x + \theta(r_\ell - \theta) = 0 \quad \text{and} \quad \theta(x) = \theta(x+\ell) \quad \text{in } \mathbb{R}. \tag{1.5}$$

We denote the unique positive solution of (1.5), when it exists, as $\theta_\mu$.

Given any $\ell$-periodic function $p \in C(\mathbb{R})$, we define

$$p_{\min} := \min_{x\in[0,\ell]} p(x), \quad p_{\max} := \max_{x\in[0,\ell]} p(x), \quad \text{and} \quad \hat{p} := \frac{1}{\ell}\int_0^\ell p(x)\mathrm{d}x.$$

Our first result concerns the persistence of a single species.

Theorem 1.1 (Critical habitat period). *Assume $r_\ell(x) = r(x/\ell)$ for some 1-periodic function $r \in C(\mathbb{R})$. Then the followings hold.*

(1) *If $r_{\max} < 0$, then (1.5) has no positive solutions;*

(2) *If* $\hat{r} > 0$, *then for all* $\mu, \ell > 0$ *and* $\alpha \in \mathbb{R}$, (1.5) *has a unique positive solution* $\theta_\mu$ *which is globally asymptotically stable among all solutions of* (1.4) *with non-negative and not identically zero initial data;*

(3) *If* $\hat{r} < 0$ *and* $r_{\max} > 0$, *then there is a unique* $\ell^* = \ell^*(\mu, \alpha) \in (0, \infty)$ *such that if* $\ell > \ell^*$, (1.5) *has a unique positive solution* $\theta_\mu$ *which is globally asymptotically stable among all solutions of* (1.4) *with non-negative and not identically zero initial data; if* $\ell \leq \ell^*$, (1.5) *has no positive solutions. Furthermore,*

  (i) *for each* $\mu > 0$, $\ell^*(\mu, \alpha) = \ell^*(\mu, -\alpha)$, $\frac{\partial \ell^*}{\partial \alpha} > 0$ *for* $\alpha > 0$, *and* $\lim_{\alpha \to \infty} \ell^*(\mu, \alpha) = \infty$;

  (ii) *for each* $\alpha \in \mathbb{R}$, $\lim_{\mu \to 0} \ell^*(\mu, \alpha) = \lim_{\mu \to \infty} \ell^*(\mu, \alpha) = \infty$.

In case $\hat{r} < 0$ and $r_{\max} > 0$, Theorem 1.1 says that the species can persist if and only if the underlying spatial period is larger than the critical number $\ell^*$, which refers to the minimal period of the habitat required for population survival. Fix diffusion rate $\mu > 0$, then the critical habitat period $\ell^*$ is an increasing function of drift rate $\alpha > 0$, so that the faster drift decreases the likelihood of the persistence. We will see in Theorem 1.3 that it is competitively advantageous for species to adopt the slower drift. Fix drift rate $\alpha \in \mathbb{R}$, then Theorem 1.1(3)-(ii) indicates that there exists some $\mu_* = \mu_*(\alpha) \in (0, \infty)$ such that $\ell^*$ attains its minimum at $\mu_*$. Biologically, this suggests that there exists an intermediate diffusion rate $\mu_*$ which is the optimal strategy for population survival.

In what follows, we always assume that the positive steady state of (1.4) exists and consider the spreading properties related to (1.4). Of particular interest are the solutions connecting the two steady states 0, $\theta_\mu$ and propagating in a given direction with a constant average speed: the so-called pulsating front. It was shown in [3, 4] that there exists a critical speed $c^* = c^*(\mu, \alpha, \ell)$ such that a pulsating front with speed $c \geq c^*$ connecting two equilibria 0 and $\theta_\mu$ exists and no pulsating fronts exist when $c < c^*$. A variational formula established in [4] for the minimal speed $c^*$ is given by

$$c^*(\mu, \alpha, \ell) = \min_{\lambda > 0} \frac{\Lambda(\mu, \alpha, \ell, \lambda)}{\lambda}, \tag{1.6}$$

where $\Lambda(\mu, \alpha, \ell, \lambda)$ is the principal eigenvalue of the problem

$$\begin{cases} \mu \phi_{xx} + (\alpha + 2\mu\lambda)\, \phi_x + \left(\mu\lambda^2 + \alpha\lambda + r_\ell\right) \phi = \Lambda \phi & \text{in } \mathbb{R}, \\ \phi(x) = \phi(x + \ell) & \text{in } \mathbb{R}. \end{cases} \tag{1.7}$$

Our next result is concerned with the dependence of $c^*$ on the parameters $\mu, \alpha, \ell$.

THEOREM 1.2. *Assume* $r_\ell(x) = r(x/\ell)$ *for some* 1*-periodic function* $r \in C(\mathbb{R})$ *satisfying* $\hat{r} > 0$. *Let* $c^*(\mu, \alpha, \ell)$ *be the minimal speed given by* (1.6).

(1) *If* $r \equiv \hat{r}$ *is a constant, then* $c^* = 2\sqrt{\hat{r}\mu} + \alpha$ *for all* $\mu, \alpha, \ell > 0$;

(2) *If* $r$ *is non-constant, then* $c^*$ *is differentiable with respect to* $\mu, \alpha, \ell$, *and*

$$\frac{\partial c^*}{\partial \ell} > 0, \quad \frac{\partial (c^*/\alpha)}{\partial \alpha} < 0, \quad \textit{and} \quad \frac{\partial c^*}{\partial \alpha} > \frac{1}{2} \quad \textit{for all } \mu, \alpha, \ell > 0.$$

*Moreover,* $c^*/\alpha \to 1$ *as* $\alpha \to \infty$, *and*

$$\lim_{\ell \to 0} c^*(\mu, \alpha, \ell) = 2\sqrt{\mu \hat{r}} + \alpha \quad \textit{and} \quad \lim_{\ell \to \infty} c^*(\mu, \alpha, \ell) = 2\sqrt{\mu r_{\max}} + \alpha.$$

Generally, the presence of advection may enhance mixing [14, 56] and is expected to speed-up the spatial spreading. It was conjectured in [4, 14] that the minimal speed $c^*$ is increasing in $\alpha$, and $c^*/\alpha$ is decreasing in $\alpha$ for $\alpha > 0$. The monotonicity of $c^*/\alpha$ was completely solved in [35] for the general incompressible flow. We present a simpler proof for the specific flow given in (1.4). Yet, the monotonicity of $c^*$ in $\alpha$ was proved only for the shear flows in a straight cylinder [2, 43] and remains open for general case. Theorem 1.2 gives the first example to illustrate the monotonicity for non-shear flows.

The monotoncity of $c^*$ in $\ell$ and the asymptotic behavior as $\ell \to 0$ were initially proved by Nadin [42, 44]. It means that the fragmentation of environment may slow down the propagation [42, 47]. The differentiability of $c^*$, the monotonicity in $\alpha$, and the limit as $\ell \to \infty$ are new results. We also refer to [21, 48, 49] and references therein for some results on the dependence of $c^*$ on the diffusion rate $\mu$.

**1.2. Competition and Evolution.** We set $\ell = 1$ and $\hat{r} > 0$ throughout this subsection. System (1.3) has a trivial equilibrium $(0, 0)$, and two semi-trivial equilibria $(\theta_\mu, 0)$ and $(0, \theta_\nu)$, where $\theta_\mu$ is the unique positive solution of (1.5), and $\theta_\nu > 0$ solves

$$\nu(\theta_\nu)_{xx} + \beta(\theta_\nu)_x + \theta_\nu(r_\ell - \theta_\nu) = 0 \quad \text{and} \quad \theta_\nu(x) = \theta_\nu(x+\ell) \quad \text{in } \mathbb{R}. \tag{1.8}$$

In game theory, a player's strategy is defined as an option which the player chooses in a setting, where the final outcome depends on their own actions and the actions of other players. In our setting we regard parameters $\mu$ and $\alpha$ as strategies for the populations. As it is fairly challenging to consider the changes of two strategies simultaneously, in this paper we only consider the evolution of a single trait; i.e. we either set $\mu = \nu$ and consider the case $\alpha \neq \beta$, or consider the case $\alpha = \beta$ and $\mu \neq \nu$.

We study the evolution of dispersal for system (1.3) in the adaptive dynamics framework [10, 11]. A central concept of adaptive dynamics theory is the notation of an evolutionarily stable strategy (ESS), which was first introduced by Maynard Smith and Price in the seminal paper [41]. A strategy is said to be an ESS if the resident species playing it cannot be invaded by rare mutant species that plays any different strategies. For system (1.3), a strategy $\mu^*$ is a local ESS if $(\theta_\mu, 0)$ is locally stable whenever $\mu = \mu^*$ and $\nu \neq \mu^*$ but sufficiently close to $\mu^*$. Another important concept in adaptive dynamics theory is convergence stable strategy (CSS). Biologically, a strategy is a CSS if the strategies successively closer to it can invade a population using any nearby strategy value.

Our next result determines the global dynamics of (1.3) for the case $\mu = \nu$.

THEOREM 1.3. *Assume $\mu = \nu > 0$ and $0 \leq |\alpha| < |\beta|$ in (1.3). Then the semi-trivial state $(\theta_\mu, 0)$ is globally asymptotically stable, whenever it exists. In particular, the strategy $\alpha^* = 0$ is a global* ESS *and a global* CSS.

Theorem 1.3 shows that if two competing species have the same diffusion rate, then the species with the slower drift will be favored, regardless of the drift direction. Mathematically, the underlying one-dimensional domain can be identified as a circle due to the spatial periodicity. The drift along the circle may force individuals to depart from locations with more resources (and are thus favorable), and instead the populations are only accessible to the average resources in the habitat. Therefore, the slower drift could be more advantageous for the population to locate favorable regions, which in turn yields some competitive advantage for the species.

It is natural to inquire what happens if $\mu \neq \nu$. Concerning general $\mu, \nu, \alpha, \beta$, we have the following result:

THEOREM 1.4. *Assume $0 < \mu < \nu$. Let $\theta_\mu$ be the unique positive solution of* (1.5).

(1) *If $|\beta| \geq \sqrt{\frac{\nu}{\mu}}|\alpha|$, the semi-trivial state $(\theta_\mu, 0)$ is globally asymptotically stable;*

(2) *If $|\beta| < \sqrt{\frac{\nu}{\mu}}|\alpha|$, the stability of $(\theta_\mu, 0)$ and $(0, \theta_\nu)$ can be described as follows.*

(i) *For each $\alpha \in \mathbb{R}$, there is a unique $\beta^* = \beta^*(\alpha) \in [0, \sqrt{\frac{\nu}{\mu}}|\alpha|)$ such that $(\theta_\mu, 0)$ is linearly stable for $|\beta| > \beta^*$ and linearly unstable for $|\beta| < \beta^*$. Furthermore, there exists some constant $\epsilon_1 > 0$ such that $\beta^*(\alpha) \equiv 0$ for $\alpha \in [-\epsilon_1, \epsilon_1]$, and*

$$\lim_{|\alpha|\to\infty} \frac{\beta^*(\alpha)}{|\alpha|} = \sqrt{\frac{\nu}{\mu}}; \tag{1.9}$$

(ii) *For each $\beta \in \mathbb{R}$, there is a unique $\alpha^* = \alpha^*(\beta) \in (\sqrt{\frac{\mu}{\nu}}|\beta|, \infty)$ such that $(0, \theta_\nu)$ is linearly stable for $|\alpha| > \alpha^*$ and linearly unstable for $|\alpha| < \alpha^*$. Furthermore, there exists some constant $\epsilon_2 > 0$ such that $\alpha^*(\beta) > \epsilon_2$ for all $\beta \in \mathbb{R}$, and*

$$\lim_{|\beta|\to\infty} \frac{\alpha^*(\beta)}{|\beta|} = \sqrt{\frac{\mu}{\nu}}. \tag{1.10}$$

Theorem 1.4 gives a characterization of the local stability of two semi-trivial steady states of (1.3). For general $\mu, \nu, \alpha$ and $\beta$, it is unknown whether the global dynamics of (1.3) is determined by its local dynamics, i.e. any locally stable non-negative steady state of (1.3) may or may not be globally asymptotically stable among non-negative and non-trivial initial data. We give some illustrations of Theorem 1.4 in Fig. 1.

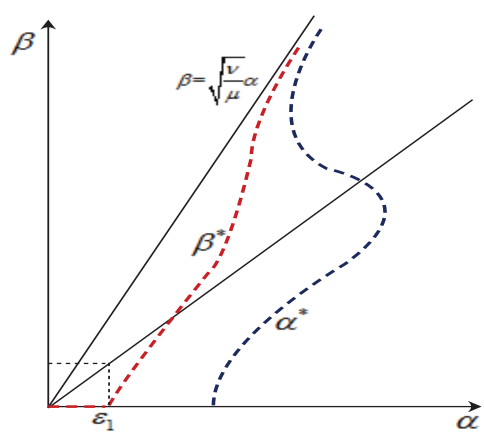


FIG. 1. *Illustrations of the curves of $\beta^*(\alpha)$ and $\alpha^*(\beta)$ determined by Theorem 1.4 in the first quadrant of $\alpha - \beta$ plane. In the region above the curve $\beta = \beta^*(\alpha)$ including the small square $(0, \epsilon_1) \times (0, \epsilon_1)$, the semi-trivial state $(\theta_\mu, 0)$ is linearly stable, whereas it is globally stable in the region above the ray $\beta = \sqrt{\frac{\mu}{\nu}}\alpha$. In the region below the curve $\alpha = \alpha^*(\beta)$, $(0, \theta_\nu)$ is linearly stable. Both curves approach the ray $\beta = \sqrt{\frac{\mu}{\nu}}\alpha$ asymptotically as $\alpha, \beta \to \infty$ and intersect the diagonal at some point, as proved by* (1.9) *and* (1.10). *However, it remains open to determine the relationship between the two curves.*

It is well known that if $\alpha = \beta = 0$ and $r$ is non-constant, then $(\theta_\mu, 0)$ is globally stable when $\mu < \nu$, and $(0, \theta_\nu)$ is globally stable when $\mu > \nu$. That is, the slower diffuser is favored [9, 13]. The following result concerns the drift case $\alpha = \beta \neq 0$:

THEOREM 1.5. *Given any $\alpha = \beta \neq 0$ and non-constant $r$, there exists some $\delta > 0$ such that the followings hold:*
(1) *If $\mu < \nu < \delta$, then $(0, \theta_\nu)$ is globally stable;*
(2) *If $\nu > \mu > 1/\delta$, then $(\theta_\mu, 0)$ is globally stable.*

Theorem 1.5 says the faster diffuser can confer some competition advantages provided that the underlying diffusion rates are both small, while the slower diffuser turns out to be competitively advantageous if the diffusion rates are both large. Therefore, neither large nor small diffusion rate is always beneficial to the competing species. We conjecture naturally that for each $\alpha = \beta \neq 0$, there is an intermediate diffusion rate $\mu^*(\alpha) > 0$ which is a ESS.

Let $\lambda(\mu, \nu)$ denote the principal eigenvalue of the problem

$$\begin{cases} \nu\varphi_{xx} + \beta\varphi_x + (r - \theta_\mu)\varphi = \lambda\varphi & \text{in } \mathbb{R}, \\ \varphi(x) = \varphi(x+1) & \text{in } \mathbb{R}. \end{cases} \tag{1.11}$$

Assume $\alpha = \beta$. It is clear that $\lambda(\mu, \mu) = 0$ for all $\mu > 0$ by regarding $\theta_\mu$ as the corresponding eigenfunction. We say $\mu^* > 0$ is an evolutionarily singular strategy if $\lambda_\nu(\mu^*, \mu^*) = 0$. Therefore, if some $\mu^* > 0$ is an evloutionarily stable strategy, it is necessarily a singular strategy. Our next result gives a partial answer to the conjecture by establishing the existence of singular strategy and determining some of its asymptotic behaviors.

THEOREM 1.6. *Suppose that $\beta = \alpha$ and $r$ is non-constant. Then for each $\alpha \neq 0$, there exists some $\mu^* = \mu^*(\alpha) \in (0, \infty)$ such that it is a singular strategy and satisfies*

$$\lambda_\nu(\mu, \mu) = \begin{cases} + & \mu < \mu^* \textit{ and } \mu \textit{ close to } \mu^*, \\ 0 & \mu = \mu^*, \\ - & \mu > \mu^* \textit{ and } \mu \textit{ close to } \mu^*. \end{cases} \tag{1.12}$$

*Moreover, $\mu^*(\alpha) \to 0$ as $\alpha \to 0$ and $\mu^*(\alpha) \to \infty$ as $|\alpha| \to \infty$. Furthermore, if $r(x) > 0$ for all $x \in \mathbb{R}$, then there exists some positive constant $C$ such that for all small $|\alpha| > 0$,*

$$C^{-1}|\alpha| \le \mu^*(\alpha) \le C|\alpha|. \tag{1.13}$$

Theorem 1.6 shows that a singular strategy $\mu^*$ exists for each $\alpha \in \mathbb{R}$, and moreover satisfies (1.12). It is natural to inquire whether such a singular strategy $\mu^*$ is also evolutionarily stable. Our numerical simulations in Fig. 2 suggest that $\mu^*$ is a local ESS but not necessarily a global ESS generally. Biologically, the estimate (1.13) says that diffusion and advection have to be properly balanced in order to be evolutionarily stable strategies.

The rest of this paper is organized as follows: In Section 2 we study the principal eigenvalue of a linear problem in one-dimensional periodic domain and establish the monotone dependence of the principal eigenvalue on diffusion and drift rates. Furthermore, we characterize the level sets of the principal eigenvalue in terms of diffusion and drift rates. In Section 3, we consider the persistence and spatial spreading of a

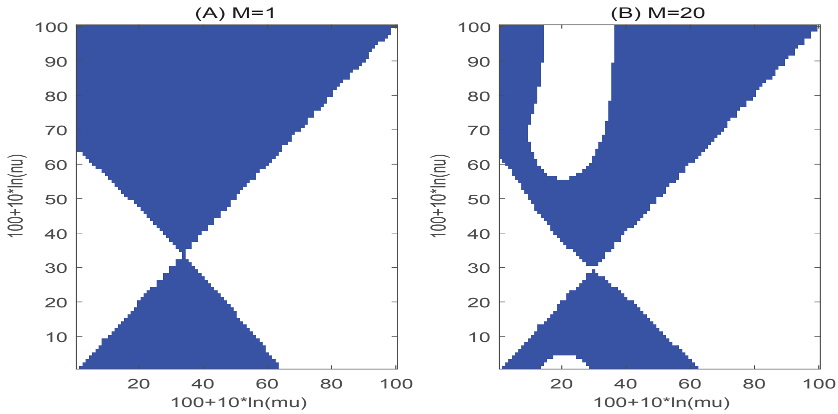


FIG. 2. *Numerical diagram of $\lambda(\mu,\nu)$ in $\mu-\nu$ plane under $r(x)=1+M(\sin(2\pi x)+\cos(2\pi x)+\cos(4\pi x))$ and $\alpha=\beta=2$. The dyed parts correspond to the parameter regions whereas $\lambda(\mu,\nu)<0$. When the amplitude of $r$ is small ($M=1$), $\mu^*$ found in Theorem 1.6 is a global ESS, as illustrated in Fig. 2*(A)*. As the amplitude increases, $\mu^*$ may no longer be a global ESS; see Fig. 2*(B)*.*

single species in one-dimensional periodic domain to establish Theorems 1.1 and 1.2. In Sections 4 and 5 we consider two competing species in one-dimensional periodic domain. Section 4 is devoted to the study of local and global stability of semi-trivial steady states, and Theorems 1.3 and 1.4 are established there. In Section 5 we study the evolution of dispersal in one-dimensional periodic habitat with drift and prove Theorems 1.5 and 1.6. Finally in the Appendix we present the Taylor expansion of some principal eigenvalue for sufficiently large drift rates.

**2. An eigenvalue problem in periodic domain.** In this section, we consider the principal eigenvalue of the following problem:

$$\begin{cases} \mu\varphi_{xx}+\alpha\varphi_x+V\varphi=\lambda\varphi & \text{in } \mathbb{R},\\ \varphi(x)=\varphi(x+1) & \text{in } \mathbb{R}, \end{cases} \tag{2.1}$$

where $V\in C(\mathbb{R})$ is assumed to be 1-periodic. By the Krein-Rutman Theorem [23], problem (2.1) admits a real and simple eigenvalue (called *principal eigenvalue*), denoted by $\lambda_1(\mu,\alpha)$, which corresponds to a positive eigenfunction (called *principal eigenfunction*). Furthermore, $\lambda_1(\mu,\alpha)$ has the smallest real part among all eigenvalues of (2.1).

Our main result can be stated as follows.

THEOREM 2.1. *Suppose that $\mu=\mu(\alpha)\in C^1(\mathbb{R}_+;\mathbb{R}_+)$, $\mu'(\alpha)\ge 0$, and $\left[\mu(\alpha)/\alpha^2\right]'\le 0$ in* (2.1)*. Set $\lambda(\alpha):=\lambda_1(\mu(\alpha),\alpha)$. Then $\lambda'(\alpha)\le 0$ for each $\alpha\ge 0$, and either $\lambda'(\alpha)<0$ for all $\alpha>0$, or $\lambda'(\alpha)\equiv 0$. Furthermore, $\lambda'(\alpha)\equiv 0$ if and only if $V$ is a constant. In particular, for each $\mu>0$, $\lambda_1(\mu,\alpha)$ is strictly decreasing in $\alpha>0$, provided that $V$ is non-constant.*

*Proof.* Let $\psi>0$ denote the principal eigenfunction of the adjoint problem to (2.1) associated with eigenvalue $\lambda(\alpha)$, which is given by

$$\begin{cases} \mu\psi_{xx}-\alpha\psi_x+V\psi=\lambda(\alpha)\psi & \text{in } \mathbb{R},\\ \psi(x)=\psi(x+1) & \text{in } \mathbb{R}. \end{cases} \tag{2.2}$$

Define $\varphi > 0$ as the principal eigenfunction of (2.1). Differentiate both sides of (2.1) with respect to $\alpha$ and denote $\varphi' = \frac{\partial \varphi}{\partial \alpha}$, we arrive at

$$\mu'(\alpha)\varphi_{xx} + \mu(\alpha)\varphi'_{xx} + \varphi_x + \alpha\varphi'_x + V\varphi' = \lambda'(\alpha)\varphi + \lambda(\alpha)\varphi'.$$

Multiply the above equation by $\psi$ and (2.2) by $\varphi'$, respectively, subtract the resulting equations, and integrate over $[0,1]$, then

$$\lambda'(\alpha)\int \varphi\psi = -\mu'(\alpha)\int \varphi_x\psi_x + \int \psi\varphi_x. \tag{2.3}$$

**Step 1.** We show that

$$\lambda'(\alpha)\int \varphi\psi = -\mu'(\alpha)\int \left[\partial_x\sqrt{\varphi\psi}\right]^2 + \frac{\alpha^2}{4}\left[\frac{\mu(\alpha)}{\alpha^2}\right]'\int \varphi\psi\left[\partial_x \log\left(\frac{\varphi}{\psi}\right)\right]^2. \tag{2.4}$$

It suffices to prove that

$$\int \psi\varphi_x = -\frac{\mu(\alpha)}{2\alpha}\int \varphi\psi\left[\partial_x \log\left(\frac{\varphi}{\psi}\right)\right]^2. \tag{2.5}$$

Then substituting (2.5) into (2.3) gives

$$\begin{aligned}
\lambda'(\alpha)\int \varphi\psi &= -\mu'(\alpha)\int \varphi_x\psi_x - \frac{\mu(\alpha)}{2\alpha}\int \varphi\psi\left[\partial_x \log\left(\frac{\varphi}{\psi}\right)\right]^2 \\
&= -\mu'(\alpha)\left\{\int \varphi_x\psi_x + \frac{1}{4}\int \varphi\psi\left[\partial_x \log\left(\frac{\varphi}{\psi}\right)\right]^2\right\} \\
&\quad + \frac{\alpha^2}{4}\left[\frac{\mu(\alpha)}{\alpha^2}\right]'\int \varphi\psi\left[\partial_x \log\left(\frac{\varphi}{\psi}\right)\right]^2,
\end{aligned}$$

which implies (2.4) immediately.

To establish (2.5), we set $\mathbb{S} := \{\zeta \in C^2(\mathbb{R}) : \zeta(x) > 0 \text{ and } \zeta(x) = \zeta(x+1) \text{ for } x \in \mathbb{R}\}$ and define the functional $F$ on $\mathbb{S}$ by

$$F(\zeta) := \int \varphi\psi\left[\frac{\mu\zeta_{xx} + \alpha\zeta_x}{\zeta}\right], \quad \zeta \in \mathbb{S}. \tag{2.6}$$

Direct calculation yields

$$F(\varphi) - F(\psi) = 2\alpha\int \psi\varphi_x.$$

Thus to prove (2.5), it remains to show

$$F(\psi) - F(\varphi) = \mu(\alpha)\int \varphi\psi\left[\partial_x \log\left(\frac{\varphi}{\psi}\right)\right]^2. \tag{2.7}$$

This can be proved by the similar arguments developed in [35], and we sketch the proof for completeness. By definition (2.6), we observe that

$$F(\zeta) = \mu\int \varphi\psi(\partial_x \log\zeta)^2 + \int \left[\alpha\varphi\psi - \mu(\varphi\psi)_x\right]\cdot(\partial_x \log\zeta), \tag{2.8}$$

from which the Fréchet derivation $F'(\varphi)$ at point $\varphi$ can be written as

$$F'(\varphi)\eta = 2\mu \int \varphi\psi(\partial_x \log\varphi) \cdot \left(\frac{\eta}{\varphi}\right)_x + \int \Big[\alpha\varphi\psi - \mu(\varphi\psi)_x\Big] \left(\frac{\eta}{\varphi}\right)_x \tag{2.9}$$

for all 1-periodic function $\eta \in C^1(\mathbb{R})$. Using (2.8), we can calculate

$$\begin{aligned}
&F(\psi) - F(\varphi)\\
&= \mu \int \varphi\psi\partial_x \log(\varphi\psi) \cdot \partial_x \log\left(\frac{\psi}{\varphi}\right) + \int \Big[\alpha\varphi\psi - \mu(\varphi\psi)_x\Big] \cdot \partial_x \log\left(\frac{\psi}{\varphi}\right)\\
&= \mu \int \varphi\psi \left[\partial_x \log\left(\frac{\psi}{\varphi}\right) + 2\partial_x \log\varphi\right] \cdot \partial_x \log\left(\frac{\psi}{\varphi}\right) + \int \Big[\alpha\varphi\psi - \mu(\varphi\psi)_x\Big] \cdot \partial_x \log\left(\frac{\psi}{\varphi}\right)\\
&= \mu \int \varphi\psi \left[\partial_x \log\left(\frac{\psi}{\varphi}\right)\right]^2 + 2\mu \int \varphi\psi(\partial_x \log\varphi) \cdot \partial_x \log\left(\frac{\psi}{\varphi}\right)\\
&\quad + \int \Big[\alpha\varphi\psi - \mu(\varphi\psi)_x\Big] \cdot \partial_x \log\left(\frac{\psi}{\varphi}\right).
\end{aligned}$$

Therefore, choosing $\eta = \varphi \log\left(\frac{\psi}{\varphi}\right)$ in (2.9), we find

$$F(\psi) - F(\varphi) = \mu \int \varphi\psi \left[\partial_x \log\left(\frac{\psi}{\varphi}\right)\right]^2 + F'(\varphi)\eta. \tag{2.10}$$

For any 1-periodic function $\eta \in C^1(\mathbb{R})$, by definition (2.6) we calculate

$$\begin{aligned}
F'(\varphi)\eta &= \int \varphi\psi \left[\frac{\mu\eta_{xx} + \alpha\eta_x}{\varphi} - \frac{\eta(\mu\varphi_{xx} + \alpha\varphi_x)}{\varphi^2}\right]\\
&= \int \eta\Big[\mu\psi_{xx} - \alpha\psi_x + V\psi - \lambda(\alpha)\psi\Big]\\
&= 0,
\end{aligned}$$

which together with (2.10) proves (2.7). Hence (2.4) is proved and Step 1 is complete.

**Step 2.** In view of $\mu'(\alpha) \geq 0$ and $\big[\mu(\alpha)/\alpha^2\big]' \leq 0$, (2.4) implies that $\lambda'(\alpha) \leq 0$ for each $\alpha \geq 0$. It remains to show $\lambda'(\alpha) = 0$ for some $\alpha > 0$ if and only if $V$ is constant.

First, if $V$ is constant, then $\lambda(\alpha) \equiv V$, and thus $\lambda'(\alpha) = 0$ for all $\alpha > 0$ with the principal eigenfunction $\varphi \equiv 1$. Next, we assume $\lambda'(\alpha) = 0$ for some $\alpha > 0$ and show $V$ is a constant. We shall claim that $\varphi = c\psi$ for some constant $c > 0$. Then plugging $\varphi = c\psi$ into the first equation in (2.1), and using (2.2) we can derive $\psi$ is a constant, which implies $V$ is a constant as desired. To this end, we consider the following two cases: (i) If $\big[\mu(\alpha)/\alpha^2\big]' > 0$, then from (2.4) we see that $\partial_x \log(\frac{\varphi}{\psi}) \equiv 0$ for all $x \in \mathbb{R}$, and thus $\varphi = c\psi$ for some $c > 0$; (ii) If $\mu'(\alpha) > 0$, then by (2.4), $\varphi\psi \equiv c_1$ for some constant $c_1 > 0$. From the definitions of $\varphi$ and $\psi$, it can be verified directly that

$$\alpha(\varphi\psi)_x = \mu \left[\varphi\psi\partial_x \log\left(\frac{\psi}{\varphi}\right)\right]_x.$$

This together with $\varphi\psi \equiv c_1$ implies $\partial_{xx} \log(\frac{\psi}{\varphi}) \equiv 0$, and thus $\varphi = c\psi$ for some $c > 0$. The proof is now complete. ∎

Our next result gives some asymptotic behaviors for the principal eigenvalue of (2.1).

THEOREM 2.2. *Let* $\lambda_1(\mu,\alpha)$ *be the principal eigenvalue of* (2.1). *Then for all* $\mu > 0, \alpha \neq 0$,

$$\lim_{|\alpha|\to\infty} \lambda_1(\mu,\alpha) = \lim_{\mu\to\infty} \lambda_1(\mu,\alpha) = \lim_{\mu\to 0} \lambda_1(\mu,\alpha) = \hat{V}.$$

*Proof.* By the maximum principle, it is straightforward to see that

$$V_{\min} \leq \lambda_1(\mu,\alpha) \leq V_{\max} \quad \text{for all } \mu > 0,\ \alpha \in \mathbb{R}. \tag{2.11}$$

Define $\varphi > 0$ as the principal eigenfunction corresponding to $\lambda_1(\mu,\alpha)$ such that $\int \varphi^2 = 1$.

**Step 1.** We show that for each $\mu > 0$, $\lambda_1(\mu,\alpha) \to \hat{V}$ as $\alpha \to \infty$. Multiply both sides of (2.1) by $\varphi_x$, and integrate the resulting equation over $[0,1]$. Then

$$\int |\varphi_x|^2 = -\frac{1}{\alpha}\int V\varphi\varphi_x \leq \frac{1}{2\alpha^2}\int V^2\varphi^2 + \frac{1}{2}\int |\varphi_x|^2. \tag{2.12}$$

This implies $\int |\varphi_x|^2 \to 0$ as $\alpha \to \infty$. Set $\zeta := \varphi - \hat{\varphi}$. The Poincaré inequality implies $\int \zeta^2 \to 0$ as $\alpha \to \infty$. Note that $\zeta$ solves

$$\mu\zeta_{xx} + \alpha\zeta_x + V\zeta + \hat{\varphi}V = \lambda\hat{\varphi} + \lambda\zeta \quad \text{in } \mathbb{R}. \tag{2.13}$$

Integrate both side of (2.13) over $[0,1]$, and send $\alpha \to \infty$ in the resulting equation. In view of $\int \zeta^2 \to 0$, one can deduce $\lambda_1(\mu,\alpha) \to \hat{V}$ as desired.

**Step 2.** We show that for each $\alpha \in \mathbb{R}$, $\lambda_1(\mu,\alpha) \to \hat{V}$ as $\mu \to \infty$. Multiply both sides of (2.1) by $\varphi$ and integrate over $[0,1]$, then we obtain

$$\int |\varphi_x|^2 = \frac{1}{\mu}\left[\lambda_1(\mu,\alpha) - \int V\varphi^2\right].$$

This together with (2.11) implies $\int |\varphi_x|^2 \to 0$ as $\mu \to \infty$. By the same arguments as in Step 1, we can derive $\lambda_1(\mu,\alpha) \to \hat{V}$ as $\mu \to \infty$.

**Step 3.** We show that for each $\alpha \neq 0$, $\lambda_1(\mu,\alpha) \to \hat{V}$ as $\mu \to 0$. By (2.12), $\varphi$ is uniformly bounded in $H^1((0,1))$ for all $\mu > 0$. Passing to a subsequence if necessary, we may assume $\varphi \rightharpoonup \phi$ weakly in $H^1((0,1))$ and $\lambda_1(\mu,\alpha) \to \lambda_*$ as $\mu \to 0$ for some $\phi \in H^1((0,1))$ and $\lambda_* \in \mathbb{R}$, which can be verified to satisfy

$$\alpha\phi_x + V\phi = \lambda_*\phi \quad \text{and} \quad \phi(x) = \phi(x+1) \quad \text{in } \mathbb{R}.$$

We divide the above by $\phi$ and integrate over $[0,1]$ to obtain $\lambda_* = \hat{V}$. Due to the arbitrariness of subsequence, we have $\lambda_1(\mu,\alpha) \to \hat{V}$ as $\mu \to 0$. The proof is now complete. ☐

We conclude this section by characterizing the level sets of the principal eigenvalue.

THEOREM 2.3. *Let* $\lambda_1(\mu,\alpha)$ *be the principal eigenvalue of* (2.1) *with non-constant* $V$. *Then* $\lambda_1 \in (\hat{V}, V_{\max})$ *for any* $\mu > 0$ *and* $\alpha \in \mathbb{R}$. *Furthermore, for any* $A \in (\hat{V}, V_{\max})$, *there exist a unique* $\mu_A \in (0,\infty)$ *and a unique continuous function* $\overline{\alpha}_A : [0,\mu_A] \to [0,\infty)$ *such that* $\lambda_1(\mu,\overline{\alpha}_A(\mu)) \equiv \lambda_1(\mu,-\overline{\alpha}_A(\mu)) \equiv A$ *for all* $\mu \in [0,\mu_A]$. *Moreover,*

(i) *$\mu_A$ is decreasing in $A$, $\mu_A \to \infty$ as $A \to \hat{V}$, and $\mu_A \to 0$ as $A \to V_{\max}$;*
(ii) *$\overline{\alpha}_A(0) = \overline{\alpha}_A(\mu_A) = 0$ and $\overline{\alpha}_A > 0$ in $(0, \mu_A)$;*
(iii) *for each $\mu \in (0, \infty)$, $\overline{\alpha}_A(\mu)$ is decreasing in $A \in (\hat{V}, A_*)$, where $A_* \in (\hat{V}, V_{\max})$ is uniquely determined such that $\mu_{A_*} = \mu$.*

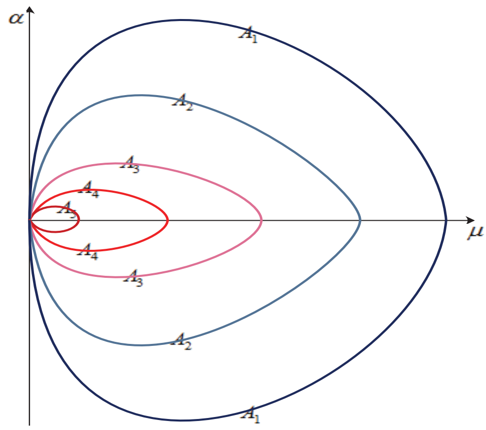


FIG. 3. *Illustrations of the level sets $\lambda_1(\mu, \alpha) = A$ in $\mu - \alpha$ plane, where $\hat{V} < A < V_{\max}$. The different colored curves in the first quadrant represent the graphs of function $\overline{\alpha}_A$ determined in Theorem 2.3, which intersects $\mu$ axis at the origin and $(\mu_A, 0)$. These closed curves of level sets will shrink to the origin as $A \to V_{\max}$; As $A \to \hat{V}$, they will expand and converge to $\{(0, \alpha) : \alpha \in \mathbb{R}\} \cup \{(+\infty, \alpha) : \alpha \in \mathbb{R}\} \cup \{(\mu, +\infty) : \mu > 0\} \cup \{(\mu, -\infty) : \mu > 0\}$ in proper sense, which is consistent with Theorem 2.2. Finally, Theorem 2.1 implies that $\lambda_1(\mu, \alpha)$ is increasing in $\alpha$, but as shown by Fig. 2, it is never monotone in $\mu$ when $V$ is non-constant.*

*Proof.* Let $\varphi > 0$ be the principal eigenfunction of (2.1). Divide both sides of (2.1) by $\varphi$ and integrate the resulting equation over $[0, 1]$, then using the periodicity of $\varphi$ we can deduce $\lambda_1 > \hat{V}$ for any $\mu > 0$ and $\alpha \in \mathbb{R}$. This together with (2.11) gives $\lambda_1 \in (\hat{V}, V_{\max})$.

Now we define $\mu_A$. Set $\alpha = 0$ in (2.1). The variational characterization of $\lambda_1(\mu, 0)$ implies that $\lambda_1(\mu, 0)$ is a decreasing function of $\mu$ [5, Corollary 2.2], and

$$\lim_{\mu \to 0} \lambda_1(\mu, 0) = V_{\max} \quad \text{and} \quad \lim_{\mu \to \infty} \lambda_1(\mu, 0) = \hat{V}. \tag{2.14}$$

Hence, for any $A \in (\hat{V}, V_{\max})$, we define the unique $\mu_A \in (0, \infty)$ such that $\lambda(\mu_A, 0) = A$. The monotonicity of $\lambda(\mu, 0)$ asserts that $\mu_A$ is decreasing in $A$, and (2.14) implies $\mu_A \to \infty$ as $A \to \hat{V}$ and $\mu_A \to 0$ as $A \to V_{\max}$. This proves (i).

Next, we define the function $\overline{\alpha}_A$. By the definition of $\mu_A$ and the monotonicity of $\lambda_1(\mu, 0)$ in $\mu$, it follows $\lambda_1(\mu, 0) > A$ for any $\mu \in (0, \mu_A)$. Using Theorem 2.2, we have $\lambda_1(\mu, \alpha) \to \hat{V} < A$ as $\alpha \to \infty$. Thus, by the monotonicity of $\lambda_1(\mu, \alpha)$ in $\alpha$ (Theorem 2.1), there is a unique $\overline{\alpha}_A(\mu) \in (0, \infty)$ such that $\lambda_1(\mu, \overline{\alpha}_A(\mu)) = A$. The continuity of $\overline{\alpha}_A(\mu)$ in $\mu$ follows from the implicit function theorem. Due to $\lambda_1(\mu_A, 0) = A$, by definition we see that $\overline{\alpha}_A(\mu_A) = 0$. Hence, to prove (ii), it remains to show $\overline{\alpha}_A \to 0$ as $\mu \to 0$.

Choose any sequence $\{\mu_n\}_{n=1}^{\infty}$ satisfying $\mu_n \to 0$ as $n \to \infty$. Assume by the contrary that $\overline{\alpha}_A(\mu_n) \to \alpha_*$ as $n \to \infty$ for some $\alpha_* \in (0, \infty]$ upon some subsequence. Fix some $\tilde{\alpha}_* \in (0, \infty)$ such that $\tilde{\alpha}_* < \alpha_*$. Using the monotonicity of $\lambda_1(\mu, \alpha)$ in $\alpha$

(Theorem 2.1), we derive

$$A = \lim_{n\to\infty} \lambda_1(\mu_n, \overline{\alpha}_A(\mu_n)) \le \lim_{n\to\infty} \lambda_1(\mu_n, \tilde{\alpha}_*). \tag{2.15}$$

Note that $\lambda_1(\mu_n, \tilde{\alpha}_*) \to \lambda_*$ as $n \to \infty$, where $\lambda_*$ is the principal eigenvalue of

$$\tilde{\alpha}_* \phi_x + V\phi = \lambda_* \phi \quad \text{and} \quad \phi(x) = \phi(x+1) \quad \text{in } \mathbb{R}.$$

Divide the above by $\phi$ and integrate over $[0, 1]$, then we deduce $\lambda_* = \hat{V}$ (see also Theorem 2.2), which together with (2.15) implies $A \le \hat{V}$. This is a contradiction and (ii) is proved.

It remains to prove (iii). Fix any $\mu \in (0, \infty)$. By (i), there is a unique $A_* \in (\hat{V}, V_{\max})$ such that $\mu_{A_*} = \mu$, then $\overline{\alpha}_A(\mu)$ is well defined in $(\hat{V}, A_*]$. In view of $\lambda_1(\mu, \overline{\alpha}_A(\mu)) \equiv A$, direct calculation gives $\frac{\partial \lambda_1}{\partial \alpha} \cdot \frac{\partial \overline{\alpha}_A(\mu)}{\partial A} = 1$. Since $\frac{\partial \lambda_1}{\partial \alpha} < 0$ as proved in Theorem 2.1, we have $\frac{\partial \overline{\alpha}_A(\mu)}{\partial A} < 0$ as desired. The proof is now complete. ∎

**3. Persistence and spreading for a single species.** In this section, we consider the persistence and spatial spreading of a single species modeled by (1.4) and prove Theorems 1.1 and 1.2. Mathematically, the persistence of species is equivalent to the instability of the trivial equilibrium, which is in turn characterized by the negativity of the principal eigenvalue, denoted by $\lambda(\mu, \alpha, \ell)$, of the following problem:

$$\begin{cases} \mu\varphi_{xx} + \alpha\varphi_x + r_\ell \varphi = \lambda\varphi & \text{in } \mathbb{R}, \\ \varphi(x) = \varphi(x+\ell) & \text{in } \mathbb{R}. \end{cases} \tag{3.1}$$

More precisely, we have the following persistence and extinction result:

Lemma 3.1. *Let $\lambda(\mu, \alpha, \ell)$ denote the principal eigenvalue of* (3.1).

(1) *If $\lambda(\mu, \alpha, \ell) > 0$, then* (1.4) *has a unique positive equilibrium $\theta_\mu(x)$ which attracts every non-trivial non-negative solution;*

(2) *If $\lambda(\mu, \alpha, \ell) \le 0$, then* (1.4) *has no positive equilibria and all non-negative solutions tend uniformly to zero as $t \to \infty$.*

Lemma 3.1 can be proved by the same arguments developed in [5, Propositions 3.1 and 3.2], and thus we omit the proof; see also [31].

Proposition 3.2. *Let $\lambda(\mu, \alpha, \ell)$ be the principal eigenvalue of* (3.1). *Then $\lambda(\mu, \alpha, \ell)$ is a non-decreasing function of $\ell$, and either $\frac{\partial \lambda}{\partial \ell} > 0$ or $\frac{\partial \lambda}{\partial \ell} \equiv 0$. Furthermore, $\frac{\partial \lambda}{\partial \ell} \equiv 0$ if and only if $r$ is a constant. Moreover,*

$$\lim_{\ell\to 0} \lambda(\mu, \alpha, \ell) = \hat{r} \quad \text{and} \quad \lim_{\ell\to\infty} \lambda(\mu, \alpha, \ell) = r_{\max}. \tag{3.2}$$

*Proof.* Let $\varphi > 0$ denote the principal eigenfuntion of (3.1) corresponding to $\lambda(\mu, \alpha, \ell)$. Set $r(x) = r_\ell(\ell x)$ and $\phi(x) = \varphi(\ell x)$, which are 1-periodic functions. Then $\phi$ defines the principal eigenfunction of the problem

$$\begin{cases} \frac{\mu}{\ell^2}\phi_{xx} + \frac{\alpha}{\ell}\phi_x + r(x)\phi = \lambda\phi & \text{in } \mathbb{R}, \\ \phi(x) = \phi(x+1) & \text{in } \mathbb{R}. \end{cases} \tag{3.3}$$

A direct application of Theorem 2.1 yields that $\lambda(\mu, \alpha, \ell)$ is non-increasing in $1/\ell$, and thus non-decreasing in $\ell$, and moreover, $\frac{\partial \lambda}{\partial \ell} = 0$ if and only if $r$ is a constant. It remains to show (3.2). Letting $\ell \to 0$ in (3.3) and using the same arguments as in Step 1 of Theorem 2.2, we can deduce $\lambda(\mu, \alpha, \ell) \to \hat{r}$. We next prove $\lambda(\mu, \alpha, \ell) \to r_{\max}$ as $\ell \to \infty$.

First, by the maximum principle, $\lambda(\mu, \alpha, \ell) \le r_{\max}$ for all $\ell > 0$. Thus it suffices to claim for each $\epsilon > 0$, there holds $\lambda(\mu, \alpha, \ell) \ge r_{\max} - \epsilon$ for large $\ell$. To this end, we choose some $x_* \in [0, 1]$ such that $r(x_*) = r_{\max}$. Choose $\delta > 0$ small such that $r(x) \ge r_{\max} - \epsilon/2$ for all $x \in [x_* - \delta, x_* + \delta]$. Define a non-negative 1-periodic function $\underline{\phi} \in C^2(\mathbb{R})$ satisfying $\int \underline{\phi}^2 = 1$ and $\mathrm{supp}\underline{\phi} \subset [x_* - \delta, x_* + \delta]$. Then we can choose $\ell$ large such that

$$(\mu/\ell^2)\underline{\phi}_{xx} + (\alpha/\ell)\underline{\phi}_x + r(x)\underline{\phi} \ge (r_{\max} - \epsilon)\underline{\phi} \quad \text{in } \mathbb{R}. \tag{3.4}$$

Let $\phi > 0$ be the principal eigenfunction of (3.3) for such chosen $\ell$. Set $w := \underline{\phi}/\phi \ge 0$. Then by (3.3) and (3.4) we derive that

$$(\mu/\ell^2)w_{xx} + \left[2\mu/\ell^2(\log \phi)_x + \alpha/\ell\right] w_x \ge [r_{\max} - \epsilon - \lambda(\mu, \alpha, \ell)]\, w \quad \text{in } \mathbb{R}. \tag{3.5}$$

The proof is completed by evaluating (3.5) at the maximum point of $w$. □

We are now in a position to prove Theorem 1.1.

*Proof of Theorem* 1.1. Let $\lambda(\mu, \alpha, \ell)$ be the principal eigenvalue of (3.1). Combining with the adjoint problem of (3.1), it is easily seen that $\lambda(\mu, \alpha, \ell) = \lambda(\mu, -\alpha, \ell)$ for any $\mu, \ell > 0$ and $\alpha \in \mathbb{R}$. Hence we only prove Theorem 1.1 in the case $\alpha > 0$. We claim that

$$\hat{r} \le \lambda(\mu, \alpha, \ell) \le r_{\max} \quad \text{for all } \mu, \alpha, \ell > 0. \tag{3.6}$$

The fact that $\lambda(\mu, \alpha, \ell) \le r_{\max}$ is a direct consequence of the maximum principle. For any $\mu, \ell > 0$, applying Theorem 2.1 (with $\mu'(\alpha) = 0$) and Theorem 2.2 gives

$$\lambda(\mu, \alpha, \ell) \ge \lim_{\alpha \to \infty} \lambda(\mu, \alpha, \ell) = \hat{r} \quad \text{for all } \alpha > 0.$$

Thus inequality (3.6) holds. From (3.6) we see that if $r_{\max} < 0$, then $\lambda(\mu, \alpha, \ell) < 0$, and if $\hat{r} > 0$, then $\lambda(\mu, \alpha, \ell) > 0$. By Lemma 3.1, this establishes Theorem 1.1(1) and (2).

In what follows, we assume $\hat{r} < 0$ and $r_{\max} > 0$. Proposition 3.2 implies $\frac{\partial \lambda}{\partial \ell} > 0$, and that there is a unique $\ell^* = \ell^*(\mu, \alpha) \in (0, \infty)$ such that $\lambda(\mu, \alpha, \ell^*) = 0$, and $\lambda(\mu, \alpha, \ell) > 0$ if $\ell > \ell^*$, and $\lambda(\mu, \alpha, \ell) < 0$ if $\ell < \ell^*$. Applying Lemma 3.1 again, this proves the first part of Theorem 1.1(3) and it remains to show (i) and (ii).

To establish (i), we fix $\mu > 0$. First, the assertion $\ell^*(\mu, \alpha) = \ell^*(\mu, -\alpha)$ is a direct consequence of $\lambda(\mu, \alpha, \ell) = \lambda(\mu, -\alpha, \ell)$ and $\frac{\partial \lambda}{\partial \ell} > 0$. Next, noting that $\lambda(\mu, \alpha, \ell^*) = 0$ for $\alpha > 0$, we have $\frac{\partial \lambda}{\partial \alpha} + \frac{\partial \lambda}{\partial \ell} \cdot \frac{\partial \ell^*}{\partial \alpha} = 0$. Using $\frac{\partial \lambda}{\partial \alpha} < 0$ and $\frac{\partial \lambda}{\partial \ell} > 0$, we deduce $\frac{\partial \ell^*}{\partial \alpha} > 0$ immediately, where $\frac{\partial \lambda}{\partial \alpha} < 0$ follows from Theorem 2.1. Finally, we claim $\ell^*(\mu, \alpha) = \infty$ as $\alpha \to \infty$. Suppose not. Then there exists some sequence $\{\alpha_n\}_{n=1}^{\infty}$ such that $\alpha_n \to \infty$ and $\ell^*(\mu, \alpha_n) \to L$ as $n \to \infty$ for some $L \in (0, \infty)$. The fact that $\frac{\partial \ell^*}{\partial \alpha} > 0$ implies $\ell^*(\mu, \alpha_n) \le L$, so that by $\frac{\partial \lambda}{\partial \ell} > 0$, we have $0 = \lambda(\mu, \alpha_n, \ell^*(\mu, \alpha_n)) \le \lambda(\mu, \alpha_n, L)$ for all $n \ge 1$, for which letting $n \to \infty$ and using $\lambda(\mu, \alpha_n, L) \to \hat{r}$ (Theorem 2.2), we arrive at $\hat{r} \ge 0$. This is a contradiction since it is assumed that $\hat{r} < 0$. The assertion (i) is now proved.

To establish (ii), we fix $\alpha \in \mathbb{R}$. We only prove $\ell^*(\mu, \alpha) \to \infty$ as $\mu \to 0$, and the assertion $\ell^*(\mu, \alpha) \to \infty$ as $\mu \to \infty$ follows from a similar argument. If not, then there exists a sequence $\{\mu_n\}_{n=1}^{\infty}$ such that $\mu_n \to 0$ and $\ell^*(\mu_n, \alpha) \to L$ as $n \to \infty$ for some $L \in (0, \infty)$. Thus there exists some $\tilde{L} > L$ such that $\ell^*(\mu_n, \alpha) \le \tilde{L}$ for all $n \ge 1$. Again by invoking the montonicity $\frac{\partial \lambda}{\partial \ell} > 0$, we deduce $0 = \lambda(\mu_n, \alpha, \ell^*(\mu_n, \alpha)) \le \lambda(\mu_n, \alpha, \tilde{L})$ for all $n \ge 1$. Letting $n \to \infty$, we reach $\hat{r} \ge 0$, a contradiction. Hence (ii) follows and Theorem 1.1 is proved. □

Next, we consider the spatial spreading of a single species and prove Theorem 1.2.

*Proof of Theorem* 1.2. Recall that $\Lambda = \Lambda(\mu, \alpha, \ell, \lambda)$ defines the principal eigenvalue of (1.7). If $r \equiv \hat{r}$ is constant, then it is clear that $\Lambda = \mu\lambda^2 + \alpha\lambda + \hat{r}$ independent of $\ell > 0$ with the principal eigenfunction $\phi \equiv 1$. By (1.6) we have

$$c^*(\mu, \alpha, \ell) = \min_{\lambda > 0} \left[ \mu\lambda + \frac{\hat{r}}{\lambda} + \alpha \right] = 2\sqrt{\mu \hat{r}} + \alpha,$$

which establishes Theorem 1.2(1). It remains to show Theorem 1.2(2).

It was shown in [46, Proposition 4.2] that the minimum in (1.6) can be attained uniquely at some $\lambda^* = \lambda^*(\mu, \alpha, \ell) \in (0, \infty)$ for any given $\mu, \alpha, \ell > 0$ such that

$$c^*(\mu, \alpha, \ell) = \frac{\Lambda(\mu, \alpha, \ell, \lambda^*)}{\lambda^*}. \tag{3.7}$$

Hence the map $(\mu, \alpha, \ell) \mapsto \lambda^*$ is well defined. At the minimal point $\lambda^*(\mu, \alpha, \ell)$, by the argument of extreme point we have

$$\lambda^* \frac{\partial \Lambda(\mu, \alpha, \ell, \lambda^*)}{\partial \lambda} = \Lambda(\mu, \alpha, \ell, \lambda^*). \tag{3.8}$$

Set $F(\mu, \alpha, \ell, \lambda) := \lambda \frac{\partial \Lambda(\mu, \alpha, \ell, \lambda)}{\partial \lambda} - \Lambda(\mu, \alpha, \ell, \lambda)$. Then $F(\mu, \alpha, \ell, \lambda^*) = 0$ and $\frac{\partial F}{\partial \lambda} = \frac{\partial^2 \Lambda(\mu, \alpha, \ell, \lambda)}{\partial \lambda^2}$. It was proved in [35, Proposition 6.2] that $\frac{\partial^2 \Lambda}{\partial \lambda^2} < 0$, so that $\frac{\partial F}{\partial \lambda} \neq 0$ particularly. The implicit function theorem implies that $\lambda^*(\mu, \alpha, \ell)$, and hence $c^*(\mu, \alpha, \ell)$, are differentiable with respect to $\mu, \alpha, \ell$.

**Step 1.** We prove $\frac{\partial c^*}{\partial \ell} > 0$. Differentiate both sides of (3.7) with respect to $\ell$, then at $(\mu, \alpha, \ell, \lambda^*)$ we have

$$\frac{\partial c^*}{\partial \ell} = \frac{1}{\lambda^*} \left[ \frac{\partial \Lambda}{\partial \ell} + \frac{\partial \Lambda}{\partial \lambda} \frac{\partial \lambda^*}{\partial \ell} - \frac{\Lambda \frac{\partial \lambda^*}{\partial \ell}}{\lambda^*} \right],$$

which together with (3.8) implies $\frac{\partial c^*}{\partial \ell} = \frac{1}{\lambda^*} \frac{\partial \Lambda}{\partial \ell}$. We apply Proposition 3.2 to (1.7) and deduce $\frac{\partial \Lambda}{\partial \ell} > 0$ as $r$ is non-constant. This gives $\frac{\partial c^*}{\partial \ell} > 0$ as desired.

**Step 2.** We show that $\frac{\partial (c^*/\alpha)}{\partial \alpha} < 0$ and $\frac{\partial c^*}{\partial \alpha} > \frac{1}{2}$. Set $\overline{\Lambda} := \Lambda - \mu\lambda^2 - \alpha\lambda$, which is the principal eigenvalue of the problem

$$\begin{cases} \mu\phi_{xx} + (\alpha + 2\mu\lambda)\, \phi_x + r_\ell \phi = \overline{\Lambda}\phi & \text{in } \mathbb{R}, \\ \phi(x) = \phi(x + \ell) & \text{in } \mathbb{R}. \end{cases} \tag{3.9}$$

A direct application of Theorem 2.1 to (3.9) yields

$$\frac{\partial \overline{\Lambda}}{\partial \alpha} = \frac{1}{2\mu} \frac{\partial \overline{\Lambda}}{\partial \lambda} < 0 \quad \text{for all } \mu, \alpha, \lambda, \ell > 0. \tag{3.10}$$

By (3.7) and (3.8), as in the calculation of $\frac{\partial c^*}{\partial \ell}$ we obtain

$$\frac{\partial c^*}{\partial \alpha} = \frac{\frac{\partial \Lambda}{\partial \alpha}}{\lambda^*} = \frac{\frac{\partial \overline{\Lambda}}{\partial \alpha}}{\lambda^*} + 1. \tag{3.11}$$

The fact that $\frac{\partial (c^*/\alpha)}{\partial \alpha} < 0$ has been proved in [35, Theorem 1.4] for the general incompressible steady flow. We here provide a simpler proof for (1.4) with a special incompressible flow in one dimension. Using (3.7) and (3.11) we can calculate

$$\frac{\partial (c^*/\alpha)}{\partial \alpha} = \frac{1}{\alpha}\left[\frac{\partial c^*}{\partial \alpha} - \frac{c^*}{\alpha}\right] = \frac{1}{\alpha}\left[\frac{\frac{\partial \overline{\Lambda}}{\partial \alpha}}{\lambda^*} - \frac{\overline{\Lambda}}{\alpha \lambda^*} - \frac{\mu \lambda^*}{\alpha}\right]. \tag{3.12}$$

Let $\phi > 0$ be the principal eigenfuntion of (3.9). Divide both sides of (3.9) by $\phi$ and integrate over $[0, \ell]$, then we deduce $\overline{\Lambda} \geq \hat{r} > 0$. This, along with (3.10) and (3.12), implies that $\frac{\partial (c^*/\alpha)}{\partial \alpha} < -\frac{\mu \lambda^*}{\alpha^2} < 0$ as desired.

It remains to show $\frac{\partial c^*}{\partial \alpha} > \frac{1}{2}$. Observe from (3.8) and the definition of $\overline{\Lambda}$ that at the minimal point $\lambda^*$, there holds $\frac{\partial \overline{\Lambda}}{\partial \lambda} + \mu \lambda^* = \frac{\overline{\Lambda}}{\lambda^*}$. This together with (3.10) and (3.11) implies

$$\frac{\partial c^*}{\partial \alpha} = \frac{\frac{\partial \overline{\Lambda}}{\partial \lambda}}{2\mu \lambda^*} + 1 = \frac{\overline{\Lambda}}{2\mu (\lambda^*)^2} + \frac{1}{2} > \frac{1}{2},$$

where the last inequity is due to $\overline{\Lambda} \geq \hat{r} > 0$. Step 2 is now complete.

**Step 3.** We prove the limit of $c^*/\alpha$ as $\alpha \to \infty$ and the limits of $c^*$ as $\ell \to 0$ and $\ell \to \infty$. Again recall that $\Lambda = \Lambda(\mu, \alpha, \ell, \lambda)$ denotes the principal eigenvalue of (1.7). Proposition 3.2 implies that $\frac{\partial \Lambda}{\partial \ell} > 0$ and

$$\lim_{\ell \to 0} \Lambda(\mu, \alpha, \ell, \lambda) = \mu \lambda^2 + \alpha \lambda + \hat{r} \quad \text{and} \quad \lim_{\ell \to \infty} \Lambda(\mu, \alpha, \ell, \lambda) = \mu \lambda^2 + \alpha \lambda + r_{\max}, \tag{3.13}$$

so that $\mu \lambda^2 + \alpha \lambda + \hat{r} < \Lambda < \mu \lambda^2 + \alpha \lambda + r_{\max}$ for all $\mu, \alpha, \ell, \lambda > 0$. By (1.6), this means

$$2\sqrt{\mu \hat{r}} + \alpha \leq c^* \leq 2\sqrt{\mu r_{\max}} + \alpha \quad \text{for all } \mu, \alpha, \ell > 0. \tag{3.14}$$

This implies $c^*/\alpha \to 1$ as $\alpha \to \infty$.

Set $\overline{\lambda} := \sqrt{\frac{\hat{r}}{\mu}}$. Then (1.6) implies that $c^* \leq \frac{\Lambda(\mu, \alpha, \ell, \overline{\lambda})}{\overline{\lambda}}$, for which letting $\ell \to 0$, we use (3.13) to obtain $\limsup_{\ell \to 0} c^* \leq 2\sqrt{\mu \hat{r}} + \alpha$. This together with (3.14) implies $\lim_{\ell \to 0} c^* = 2\sqrt{\mu \hat{r}} + \alpha$ as desired. It remains to consider the case $\ell \to \infty$.

Fix any sequence $\{\ell_n\}_{n=1}^{\infty}$ such that $\ell_n \to \infty$ as $n \to \infty$. By passing to a subsequence if necessary, we may assume the minimal point $\lambda^*(\mu, \alpha, \ell_n) \to \lambda^*_\infty$ as $n \to \infty$ for some $\lambda^*_\infty \in [0, \infty]$. By (3.7) and the definition of $\overline{\Lambda}$ given in Step 1, we see that

$$c^*(\mu, \alpha, \ell_n) = \frac{\overline{\Lambda}(\mu, \alpha, \ell_n, \lambda^*)}{\lambda^*(\mu, \alpha, \ell_n)} + \mu \lambda^*(\mu, \alpha, \ell_n) + \alpha. \tag{3.15}$$

Note from (3.9) that $\hat{r} \leq \overline{\Lambda} \leq r_{\max}$ for all $\mu, \alpha, \ell, \lambda > 0$. Letting $n \to \infty$ in (3.15), the uniform boundedness of $c^*$ in (3.14) implies $\lambda^*_\infty \in (0, \infty)$. Hence, by (3.13) we have

$$\lim_{n \to \infty} c^*(\mu, \alpha, \ell_n) = \frac{r_{\max}}{\lambda^*_\infty} + \mu \lambda^*_\infty + \alpha \geq 2\sqrt{\mu r_{\max}} + \alpha,$$

which together with (3.14) implies $c^*(\mu, \alpha, \ell_n) \to 2\sqrt{\mu r_{\max}} + \alpha$ as $n \to \infty$. This completes the proof by noting the arbitrariness of the sequence. ∎

**4. Ecological dynamics: Proofs of Theorems** 1.3 **and** 1.4**.** In this section, we apply Theorem 2.1 to (1.3) and establish the ecological dynamics given in Theorems 1.3 and 1.4. To this end, we first state the following result derived from the theory of monotone dynamical system [19].

LEMMA 4.1 ([20, 27]). *For any $\mu, \nu > 0$ and $\alpha, \beta \in \mathbb{R}$, suppose that system* (1.3) *has no positive steady state, then the followings hold:*

(i) *If $(0, \theta_\nu)$ is linearly unstable, then $(\theta_\mu, 0)$ is globally asymptotically stable;*
(ii) *If $(\theta_\mu, 0)$ is linearly unstable, then $(0, \theta_\nu)$ is globally asymptotically stable.*

We now prove Theorem 1.3.

*Proof of Theorem* 1.3. We first claim that the semi-trivial state $(0, \theta_\nu)$ is linearly unstable. The linear stability of $(0, \theta_\nu)$ is determined by the principal eigenvalue $\tilde{\lambda}(\mu, \nu, \alpha, \beta)$ of

$$\begin{cases} \mu\varphi_{xx} + \alpha\varphi_x + (r - \theta_\nu)\varphi = \tilde{\lambda}\varphi & \text{in } \mathbb{R}, \\ \varphi(x) = \varphi(x+1) & \text{in } \mathbb{R}, \end{cases} \tag{4.1}$$

where $\theta_\nu$ defines the unique positive solution of (1.8). Since $\mu = \nu$, it is convenient to write $\tilde{\lambda}(\alpha, \beta) = \tilde{\lambda}(\mu, \mu, \alpha, \beta)$. By definition, we can check that $\tilde{\lambda}(\alpha, \beta) = \tilde{\lambda}(-\alpha, \beta)$, and $\tilde{\lambda}(\beta, \beta) = 0$ by regarding $\theta_\nu$ in (1.8) as the corresponding eigenfunction. Thus it suffices to consider the case $0 < \alpha < \beta$.

A direct application of Theorem 2.1 yields $\tilde{\lambda}(\alpha, \beta) \geq \tilde{\lambda}(\beta, \beta) = 0$. We claim $\tilde{\lambda}(\alpha, \beta) > 0$. Suppose by the contrary that $\tilde{\lambda}(\alpha, \beta) = 0$, then Theorem 2.1 implies $\tilde{\lambda}(\tilde{\alpha}, \beta) \equiv 0$ for all $\tilde{\alpha} \geq 0$. By (1.11) and Theorem 2.1, there holds $r - \theta_\nu$ is constant in $x$. Then using (1.8), we may deduce $\theta_\nu$, and thus $r$ are constant, which is a contradiction. Hence, $\tilde{\lambda}(\alpha, \beta) > 0$ so that $(0, \theta_\nu)$ is linearly unstable; see e.g. [5].

By Lemma 4.1, it remains to show that (1.3) has no positive steady states for $0 < \alpha < \beta$. Suppose not, then there exists solution $(U, V)$ with $U > 0, V > 0$ solving

$$\begin{cases} \mu U_{xx} + \alpha U_x + U[r(x) - U - V] = 0 & \text{in } \mathbb{R}, \\ \mu V_{xx} + \beta V_x + V[r(x) - U - V] = 0 & \text{in } \mathbb{R}, \\ U(x) = U(x+1), \ V(x) = V(x+1) & \text{in } \mathbb{R}. \end{cases}$$

This implies that the principal eigenvalues of operators $\mu\frac{\mathrm{d}^2}{\mathrm{d}x^2} + \alpha\frac{\mathrm{d}}{\mathrm{d}x} + (r - U - V)$ and $\mu\frac{\mathrm{d}^2}{\mathrm{d}x^2} + \beta\frac{\mathrm{d}}{\mathrm{d}x} + (r - U - V)$ are both zero. Since $\alpha > \beta$, applying Theorem 2.1, we derive that $r - U - V$ is a constant. This implies that $U$ and $V$ are both constant, and so is $r$, which is a contradiction. This proves the global stability of $(\theta_\mu, 0)$, and hence the strategy $\alpha^* = 0$ is a global ESS and a global CSS. Theorem 1.3 thus follows. □

Next, we turn to prove Theorem 1.4.

*Proof of Theorem* 1.4. We divide the proof into the three steps.

**Step 1.** We first consider the case $|\beta| \geq \sqrt{\frac{\nu}{\mu}}|\alpha|$ and establish the global stability of $(\theta_\mu, 0)$. Let $\tilde{\lambda}(\mu, \nu, \alpha, \beta)$ denote the principal eigenvalue of (4.1). By the definition of $\theta_\nu$ in (1.8), we see that $\tilde{\lambda}(\nu, \nu, \beta, \beta) = 0$ by regarding $\theta_\nu$ as the principal eigenfunction. Since $\tilde{\lambda}(\mu, \nu, \alpha, \beta) = \tilde{\lambda}(\mu, \nu, -\alpha, \beta)$ for all $\alpha \in \mathbb{R}$, there holds $\tilde{\lambda}(\nu, \nu, |\beta|, \beta) = \tilde{\lambda}(\nu, \nu, \beta, \beta) = 0$. In view of $|\beta| \geq \sqrt{\frac{\nu}{\mu}}|\alpha|$ and $\nu > \mu$, applying Theorem 2.1 we can derive

$$\tilde{\lambda}(\mu, \nu, \alpha, \beta) = \tilde{\lambda}(\mu, \nu, |\alpha|, \beta) \geq \tilde{\lambda}\left(\frac{\mu}{\nu}\nu, \nu, \sqrt{\frac{\mu}{\nu}}|\beta|, \beta\right) \geq \tilde{\lambda}(\nu, \nu, |\beta|, \beta) = 0. \tag{4.2}$$

We claim that $\tilde{\lambda}(\mu,\nu,\alpha,\beta) > 0$. If not, by (4.2), $\tilde{\lambda}(\frac{\mu}{\nu}\nu,\nu,\sqrt{\frac{\mu}{\nu}}|\beta|,\beta) = \tilde{\lambda}(\nu,\nu,|\beta|,\beta)$. Using Theorem 2.1 we find $r-\theta_\nu$ is a constant, i.e. $r-\theta_\nu \equiv c$ for some $c \in \mathbb{R}$. Substituting this into (1.8) gives

$$\nu r_{xx} + \beta r_x + c(r-c) = 0 \quad \text{in } \mathbb{R}. \tag{4.3}$$

If $c = 0$, i.e. $\theta_\nu \equiv r$, then (4.3) means $\nu r_{xx} + \beta r_x = 0$, which together with the periodicity of $r$ asserts that $r$ is constant, a contradiction. If $c \neq 0$, then integrating both sides of (4.3) yields $\hat{r} = c$, which is also a contradiction since $r(x) > c$ for all $x \in \mathbb{R}$ (due to $\theta_\nu = r - c > 0$). Hence, it follows $\tilde{\lambda}(\mu,\nu,\alpha,\beta) > 0$, i.e. the semi-trivial state $(0,\theta_\nu)$ is linearly unstable.

To establish the global stability of $(\theta_\mu, 0)$, by Lemma 4.1 it suffices to show that (1.3) has no positive periodic solutions. Suppose not, i.e. (1.3) admits some periodic solution $(U,V)$ with $U>0, V>0$. Define $\lambda(d,q)$ as the principal eigenvalue of the problem

$$\begin{cases} d\varphi_{xx} + q\varphi_x + (r-U-V)\varphi = \lambda\varphi & \text{in } \mathbb{R}, \\ \varphi(x) = \varphi(x+1) & \text{in } \mathbb{R}. \end{cases}$$

Then the definition of $(U,V)$ implies $\lambda(\mu,\alpha) = \lambda(\nu,\beta) = 0$. Since $|\beta| \geq \sqrt{\frac{\nu}{\mu}}|\alpha|$ and $\nu > \mu$, applying the monotonicity in Theorem 2.1 we find

$$\lambda(\nu,\beta) = \lambda(\nu,|\beta|) \leq \lambda\left(\tfrac{\nu}{\mu}\mu, \sqrt{\tfrac{\nu}{\mu}}|\alpha|\right) \leq \lambda(\mu,|\alpha|) = \lambda(\mu,\alpha),$$

which implies $\lambda(\frac{\nu}{\mu}\mu,\sqrt{\frac{\nu}{\mu}}|\alpha|) = \lambda(\mu,|\alpha|)$. Due to $\nu > \mu$, by Theorem 2.1 it must hold that $r-U-V$ is constant. Using the same arguments as above, we can reach a contradiction and Theorem 1.4(1) is proved.

**Step 2.** We assume $|\beta| < \sqrt{\frac{\nu}{\mu}}|\alpha|$ and prove Theorem 1.4(2)-(i). The stability of $(\theta_\mu, 0)$ can be determined by the principal eigenvalue $\lambda(\mu,\nu,\alpha,\beta)$ of (1.11) with $\theta_\mu$ defined by (1.5). Note that $\lambda(\mu,\nu,\alpha,\beta) = \lambda(\mu,\nu,\alpha,-\beta)$ for all $\mu,\nu>0$ and $\alpha,\beta \in \mathbb{R}$. We only consider the situation when $\alpha,\beta > 0$ and $\beta < \sqrt{\frac{\nu}{\mu}}\alpha$, and other cases can be proved similarly.

We first define the continuous function $\beta^*(\alpha)$ for $\alpha > 0$. Define

$$\mathcal{D}^+ := \{\alpha \in (0,\infty) : \lambda(\mu,\nu,\alpha,0) > 0\}, \tag{4.4}$$

where $\lambda(\mu,\nu,\alpha,0) := \lim_{\beta\to 0}\lambda(\mu,\nu,\alpha,\beta)$. As in (4.2), by Theorem 2.1 we find for any $\alpha > 0$,

$$\lambda(\mu,\nu,\alpha,\sqrt{\tfrac{\nu}{\mu}}\alpha) < \lambda(\mu,\mu,\alpha,\alpha) = 0.$$

Thus for each $\alpha \in \mathcal{D}^+$, the monotonicity in Theorem 2.1 implies that there exists a unique $\beta^*(\alpha) \in (0,\sqrt{\frac{\nu}{\mu}}\alpha)$ depending continuously on $\alpha$ such that

$$\lambda(\mu,\nu,\alpha,\beta^*(\alpha)) = 0. \tag{4.5}$$

Here the continuity follows from the implicit function theorem. It is clear that $\beta^*(\partial\mathcal{D}^+) = 0$. We extend $\beta^*$ to $(0,\infty)$ by setting $\beta^*(\alpha) := 0$ for $\alpha \in (0,\infty)\setminus\mathcal{D}^+$.

By construction, $\mathcal{D}^+ = \{\alpha \in (0,\infty) : \beta^*(\alpha) > 0\}$. By Theorem 2.1 and the symmetry of $\lambda(\mu,\nu,\alpha,\beta)$ in $\beta$, we see that $(\theta_\mu, 0)$ is linearly stable for $|\beta| > \beta^*$ and linearly unstable for $|\beta| < \beta^*$.

Setting $\alpha = \beta = 0$ in (1.5) and (1.11), it is easily seen that $\lambda(\mu,\nu,0,0)$ is decreasing in $\nu$ [5, Corollary 2.2], so that $\lambda(\mu,\nu,0,0) < \lambda(\mu,\mu,0,0) = 0$. By continuity, there exists some $\epsilon_1 > 0$ small such that $\lambda(\mu,\nu,\alpha,0) \le 0$ for $\alpha \in [0,\epsilon_1]$. The definition of $\mathcal{D}^+$ in (4.4) implies $\mathcal{D}^+ \cap [0,\epsilon_1] = \emptyset$, and thus $\beta^*(\alpha) \equiv 0$ for all $\alpha \in [0,\epsilon_1]$.

It remains to prove (1.9). We shall claim $\beta^*(\alpha) \to \infty$ as $\alpha \to \infty$, then (1.9) is a direct consequence of Theorem A.1 in the appendix section. Suppose by the contrary that $\beta^*(\alpha) \to \beta^*_\infty \in [0,\infty)$ as $\alpha \to \infty$ upon some subsequence. By Lemma 5.1, $\theta_\mu \to \hat{r}$ uniformly, so that we send $\alpha \to \infty$ in (1.11) to deduce $\lambda(\mu,\nu,\alpha,\beta^*(\alpha)) \to \lambda_\infty$, where $\lambda_\infty$ defines the principal eigenvalue of the problem

$$\begin{cases} \nu\phi_{xx} + \beta^*_\infty \phi_x + (r - \hat{r})\phi = \lambda_\infty \phi & \text{in } \mathbb{R}, \\ \phi(x) = \phi(x+1) & \text{in } \mathbb{R}. \end{cases} \tag{4.6}$$

The definition of $\beta^*(\alpha)$ in (4.5) implies $\lambda_\infty = 0$. Define $\phi > 0$ as the principal eigenfunction of (4.6) corresponding to $\lambda_\infty = 0$. Divide both sides of (4.6) by $\phi$ and integrate over $[0,1]$, then we have $\nu \int \frac{|\phi_x|^2}{\phi^2} = 0$, and thus $\phi \equiv c$ for some constant $c > 0$. Substituting this into (4.6) yields $r \equiv \hat{r}$, which is a contradiction. Hence, $\beta^*(\alpha) \to \infty$ as $\alpha \to \infty$ and (1.9) holds.

**Step 3.** We assume $|\beta| < \sqrt{\frac{\nu}{\mu}}|\alpha|$ and prove Theorem 1.4(2)-(ii). Let $\tilde{\lambda}(\mu,\nu,\alpha,\beta)$ denote the principal eigenvalue of (4.1). Due to $\tilde{\lambda}(\mu,\nu,\alpha,\beta) = \tilde{\lambda}(\mu,\nu,-\alpha,\beta)$ for all $\alpha \in \mathbb{R}$, we only consider the case $\alpha, \beta > 0$, and other situation follows by a similar argument.

Since $\mu < \nu$, choosing $\alpha = \sqrt{\frac{\mu}{\nu}}\beta$ in (4.2), we find $\tilde{\lambda}\left(\mu,\nu,\sqrt{\frac{\mu}{\nu}}\beta,\beta\right) > 0$ for all $\beta > 0$. Applying Theorem 2.2 we deduce from (1.8) that for $\beta \ge 0$,

$$\lim_{\alpha\to\infty} \tilde{\lambda}(\mu,\nu,\alpha,\beta) = \hat{r} - \hat{\theta}_\nu = -\nu \int \frac{(\theta_\nu)_x^2}{\theta_\nu^2} < 0. \tag{4.7}$$

Therefore, the monotonicity of $\tilde{\lambda}$ in $\alpha$ (Theorem 2.1) implies that there is a unique continuous function $\alpha^*(\beta) \in (\sqrt{\frac{\mu}{\nu}}\beta, \infty)$ such that $\tilde{\lambda}(\mu,\nu,\alpha^*(\beta),\beta) = 0$, and $(0,\theta_\nu)$ is linearly stable for $|\alpha| > \alpha^*$ and linearly unstable for $|\alpha| < \alpha^*$.

Set $\alpha = \beta = 0$ in (1.8) and (4.1). It is easily seen that $\tilde{\lambda}(\mu,\nu,0,0) > \tilde{\lambda}(\nu,\nu,0,0) = 0$. Since $\tilde{\lambda}(\mu,\nu,\alpha,0) < 0$ for large $\alpha$ as in (4.7), we have $\alpha^*(0) > 0$. Due to $\alpha^* > \sqrt{\frac{\mu}{\nu}}\beta$, it follows that $\alpha^*(\beta) > \epsilon_2$ for some $\epsilon_2 > 0$ independent of $\beta$. Also, $\alpha^* > \sqrt{\frac{\mu}{\nu}}\beta$ implies $\alpha^*(\beta) \to \infty$ as $\beta \to \infty$. By Theorem A.1 in the Appendix, we can deduce (1.10). $\square$

**5. Evolutionary dynamics: Proofs of Theorems 1.5 and 1.6.** In this section, we aim to study the evolution dynamics of (1.3), and establish Theorems 1.5 and 1.6. To this end, we first prepare the following result:

LEMMA 5.1. *Let $\theta_\mu$ be the unique positive solution of* (1.5). *Then $\theta_\mu \to \hat{r}$ in $H^2((0,1))$ as $\max\{\mu,|\alpha|\} \to \infty$. In particular, $\theta_\mu \to \hat{r}$ in $H^2((0,1))$ uniformly for $\alpha \in \mathbb{R}$ as $\mu \to \infty$, and $\theta_\mu \to \hat{r}$ in $H^2((0,1))$ uniformly for $\mu \in (0,\infty)$ as $|\alpha| \to \infty$.*

*Proof.* We write $\theta_\mu$ as $\theta$ for simplicity. Let $C$ denote a generic positive constant independent of $\mu > 0$ and $\alpha \in \mathbb{R}$. We first prove that there exists some $C$ such that

$$\max\{\mu,\alpha^2\} \int |\theta_x|^2 < C. \tag{5.1}$$

To establish (5.1), multiply both sides of (1.5) by $\theta$ and integrate over $[0,1]$, then $\mu\int|\theta_x|^2 = \int\theta^2(r-\theta)$. Since $r_{\min}\le\theta\le r_{\max}$ for all $\mu>0$ and $\alpha\le\mathbb{R}$, this implies $\mu\int|\theta_x|^2 < C$. Similarly, multiplying both sides of (1.5) by $\theta_x$ and integrating the resulting equation over $[0,1]$ yield $\alpha\int|\theta_x|^2 = -\int\theta\theta_x(r-\theta)$. By Hölder inequality and the uniform boundedness of $\theta$ in $L^\infty(\mathbb{R})$, we have $\alpha^2\int|\theta_x|^2 < C$ for some $C$. This proves (5.1).

Next, we show that there exists some $C$ such that

$$\max\{\mu^2,\alpha^2\}\int|\theta_{xx}|^2 < C\left(1+\frac{1}{\max\{\mu,\alpha^2\}}\right). \tag{5.2}$$

Multiply both sides of (1.5) by $\theta_{xx}$ and integrate over $[0,1]$, then $\mu\int|\theta_{xx}|^2 = \int\theta_{xx}\theta(\theta-r)$. By Hölder inequality and the uniform boundedness of $\theta$, this implies $\mu^2\int|\theta_{xx}|^2 < C$. To establish the rest of (5.2), differentiate (1.5) with respect to $x$, multiply the resulting equation by $\theta_{xx}$, and integrate over $[0,1]$. Then we derive

$$\alpha^2\int|\theta_{xx}|^2 \le C\left(1+\int|\theta_x|^2\right) < C\left(1+\frac{1}{\max\{\mu,\alpha^2\}}\right), \tag{5.3}$$

where the last inequality follows from (5.1). This proves (5.2).

It follows from (5.1) and (5.2) that if $\max\{\mu,|\alpha|\}\to\infty$, then $\int|\theta_x|^2\to0$ and $\int|\theta_{xx}|^2\to0$. Hence, Poincaré inequality implies $\theta-\hat\theta\to0$ in $L^2((0,1))$, so that via a compactness argument and subject to passing to a sequence, we have $\theta\to c$ in $L^2((0,1))$ for some positive constant $c$ as $\max\{\mu,|\alpha|\}\to\infty$. Integrate (1.5) in [0,1] then we find $\int\theta(r-\theta)=0$, from which it follows that $c=\hat r$. Since $c$ is independent of the choice of sequence, it thus follows that $\theta\to\hat r$ in $H^2((0,1))$ as $\max\{\mu,|\alpha|\}\to\infty$. ☐

We are in a position to prove Theorem 1.5.

*Proof of Theorem* 1.5. **Step 1.** We prove (i). Since $\beta=\alpha$, (1.11) becomes

$$\begin{cases}\nu\varphi_{xx}+\alpha\varphi_x+(r-\theta_\mu)\varphi=\lambda\varphi & \text{in }\mathbb{R},\\ \varphi(x)=\varphi(x+1) & \text{in }\mathbb{R}.\end{cases} \tag{5.4}$$

Let $(\lambda(\mu,\nu),\varphi)$ denote the principal eigenpair of (5.4) such that $\int\varphi^2=\int\theta_\mu^2$. We define $\psi$, normalized by $\int\varphi\psi=1$, as the principal eigenfunction of the adjoint problem

$$\begin{cases}\nu\psi_{xx}-\alpha\psi_x+(r-\theta_\mu)\psi=\lambda\psi & \text{in }\mathbb{R},\\ \psi(x)=\psi(x+1) & \text{in }\mathbb{R}.\end{cases} \tag{5.5}$$

Differentiate both sides of (5.4) with respect to $\nu$ and multiply the resulting equation by $\psi$, then by (5.5) we obtain

$$\lambda_\nu(\mu,\nu) = -\int\varphi_x\psi_x. \tag{5.6}$$

Multiply both sides of (5.4) by $\varphi_x$, then integrate the resulting equation over $[0,1]$. By Hölder inequality and the boundedness of $\theta_\mu$ in $L^\infty(\mathbb{R})$, we can derive that $\varphi$ is uniformly bounded in $H^1((0,1))$ independent of $\mu,\nu>0$. Letting $\mu,\nu\to0$ in (5.4) and (5.5), by the standard arguments one can conclude that $\varphi\rightharpoonup\theta^*$ and $\psi\rightharpoonup\tilde\theta^*$

weakly in $H^1((0,1))$ and strongly in $L^2((0,1))$, where $\theta^*$ and $\tilde{\theta}^*$ satisfying $\int \theta^*\tilde{\theta}^* = 1$ define the unique positive solutions of

$$\begin{cases} \alpha\theta^*_x + (r-\theta^*)\theta^* = 0 & \text{in } \mathbb{R}, \\ \theta^*(x) = \theta^*(x+1) & \text{in } \mathbb{R}, \end{cases} \quad \text{and} \quad \begin{cases} -\alpha\tilde{\theta}^*_x + (r-\theta^*)\tilde{\theta}^* = 0 & \text{in } \mathbb{R}, \\ \tilde{\theta}^*(x) = \tilde{\theta}^*(x+1) & \text{in } \mathbb{R}. \end{cases} \tag{5.7}$$

We claim that $r-\theta^*$ is non-constant. Indeed, if $r-\theta^*$ is a constant, then integrating the first equation in (5.7) over $[0,1]$ gives $r \equiv \theta^*$. Substituting this in (5.7) yields $\theta^*$, and thus $r$ are constants, contrary to our assumption. Hence, using (5.6) we find

$$\lim_{(\mu,\nu)\to(0,0)} \lambda_\nu(\mu,\nu) = -\int \theta^*_x\tilde{\theta}^*_x = \frac{1}{\alpha^2}\int (r-\theta^*)^2\theta^*\tilde{\theta}^* > 0,$$

where the last inequality holds since $r-\theta^*$ is non-constant and $\theta^*, \tilde{\theta}^* > 0$. This implies that there exists some $\delta_1 > 0$ such that $\lambda_\nu(\mu,\nu) > 0$ for all $\mu,\nu \in (0,\delta_1)$. Due to $\lambda(\mu,\mu) = 0$, we deduce $\lambda(\mu,\nu) > 0$ for all $\mu < \nu < \delta_1$, i.e. the semi-trivial state $(\theta_\mu, 0)$ is unstable. Therefore, by Lemma 4.1, it remains to find some $\delta \in (0,\delta_1)$ such that (1.3) has no positive steady states for any $\mu < \nu < \delta$.

Suppose there exist $\mu_k < \nu_k$ and solution $(U_k, V_k)$ with $U_k > 0, V_k > 0$ such that $(\mu_k,\nu_k) \to (0,0)$ as $k \to \infty$ and

$$\begin{cases} \mu_k(U_k)_{xx} + \alpha(U_k)_x + U_k[r(x) - U_k - V_k] = 0 & \text{in } \mathbb{R}, \\ \nu_k(V_k)_{xx} + \alpha(V_k)_x + V_k[r(x) - U_k - V_k] = 0 & \text{in } \mathbb{R}, \\ U_k(x) = U_k(x+1), \ V_k(x) = V_k(x+1) & \text{in } \mathbb{R}. \end{cases} \tag{5.8}$$

By the maximum principle, we see that $U_k$ and $V_k$ are uniformly bounded in $L^\infty(\mathbb{R})$ for all $k \geq 1$. Multiply the first and second equations in (5.8) by $(U_k)_x$ and $(V_k)_x$, respectively, and integrate over $[0,1]$, then by adding the resulting equations we can derive $\alpha^2\int\left[(U_k)^2_x + (V_k)^2_x\right] \leq \int (U_k^2+V_k^2)(r-U_k-V_k)^2$. This implies that $U_k$ and $V_k$ are uniformly bounded in $H^1((0,1))$ for all $k \geq 1$. Hence, there holds $U_k + V_k \to W$ weakly in $H^1((0,1))$ and strongly in $L^2((0,1))$ as $k \to \infty$ for some non-negative 1-periodic function $W \in H^1((0,1))$. We claim that $r - W$ is non-constant. Indeed, if $W \equiv 0$, the assertion follows from the assumption that $r$ is non-constant. If $W \not\equiv 0$, then $W = \theta^*$, where $\theta^*$ is the unique positive solution of the first equation in (5.7), and thus the assertion holds since $r-\theta^*$ is non-constant.

Let $\lambda(d, W)$ be the principal eigenvalue of the problem

$$\begin{cases} d\phi_{xx} + \alpha\phi_x + (r-W)\phi = \lambda\phi & \text{in } \mathbb{R}, \\ \phi(x) = \phi(x+1) & \text{in } \mathbb{R}. \end{cases}$$

Since $r-W$ is non-constant, we may apply the same arguments as above to derive $\frac{\partial\lambda}{\partial d} > 0$ for all $d \in (0,\delta)$ with some $\delta \in (0,\delta_1)$. By continuity, we can choose $k$ large such that $\mu_k,\nu_k < \delta/2$ and $\frac{\partial\lambda}{\partial d}(d, U_k+V_k) > 0$ for all $d \in (0,\delta/2)$. For the chosen $k$, (5.8) implies $\lambda(\mu_k, U_k+V_k) = \lambda(\nu_k, U_k+V_k) = 0$, which contradicts $\frac{\partial\lambda}{\partial d} > 0$ and $\mu_k < \nu_k$. Therefore, (1.3) has no positive steady states for $\mu < \nu < \delta$ and Theorem 1.5(i) follows from Lemma 4.1.

**Step 2.** We prove (ii). Let $\alpha = \beta$ in (4.1), then $\tilde{\lambda}(\mu,\nu)$ is the principal eigenvalue of

$$\begin{cases} \mu\varphi_{xx} + \beta\varphi_x + (r-\theta_\nu)\varphi = \tilde{\lambda}\varphi & \text{in } \mathbb{R}, \\ \varphi(x) = \varphi(x+1) & \text{in } \mathbb{R}. \end{cases} \tag{5.9}$$

Denote by $\varphi > 0$ the principal eigenfunction of (5.9) such that $\int \varphi^2 = \int \theta_\nu^2$. We define $\psi > 0$, normalized by $\int \varphi\psi = 1$, as the principal eigenfunction of the adjoint problem

$$\begin{cases} \mu\psi_{xx} - \beta\psi_x + (r - \theta_\nu)\psi = \tilde{\lambda}\psi & \text{in } \mathbb{R}, \\ \psi(x) = \psi(x+1) & \text{in } \mathbb{R}. \end{cases} \tag{5.10}$$

Since $\varphi$ is periodic, there exists some $x_* = x_*(\mu, \nu) \in (0, 1]$ such that $\varphi_x(x_*) = 0$. Integrating both sides of (5.9) and (5.10) from $x_*$ to $x$ gives

$$\mu\varphi_x + \beta(\varphi - \varphi(x_*)) + \int_{x_*}^{x} (r - \theta_\nu)\varphi = \tilde{\lambda} \int_{x_*}^{x} \varphi, \tag{5.11}$$

$$\mu(\psi_x - \psi_x(x_*)) - \beta(\psi - \psi(x_*)) + \int_{x_*}^{x} (r - \theta_\nu)\psi = \tilde{\lambda} \int_{x_*}^{x} \psi. \tag{5.12}$$

By (5.9) and (5.10), direct calculation yields

$$\begin{aligned} \mu^2 \tilde{\lambda}_\mu(\mu, \nu) &= -\mu^2 \int \varphi_x \psi_x = -\mu^2 \int \varphi_x (\psi_x - \psi_x(x_*)) \\ &= -\int \left[\int_{x_*}^{x} (r - \theta_\nu)\varphi\right] \cdot \left[\int_{x_*}^{x} (r - \theta_\nu)\psi\right] + R(\mu, \nu), \end{aligned} \tag{5.13}$$

where the remainder term $R(\mu, \nu)$ can be expressed explicitly from (5.11) and (5.12). By the Sobolev embedding theorem [24], Lemma 5.1 implies $\theta_\mu \to \hat{r}$ uniformly as $\mu \to \infty$. Thus letting $(\mu, \nu) \to (\infty, \infty)$ in (5.9) and (5.10), we deduce from Theorem 2.2 that $\tilde{\lambda} \to 0$, and hence it can be verified readily that $\varphi \to \hat{r}$ and $\psi \to 1/\hat{r}$ uniformly as in Lemma 5.1. This implies $R \to 0$ uniformly. Thus one can send $(\mu, \nu) \to (\infty, \infty)$ in (5.13) to deduce

$$\limsup_{(\mu,\nu)\to(\infty,\infty)} \mu^2 \tilde{\lambda}_\mu(\mu, \nu) \le -\min_{y\in[0,1]} \left\{ \int \left[\int_y^x (r - \hat{r})\right]^2 \right\} < 0,$$

which implies that there exists some $\delta_2 > 0$ small such that $\tilde{\lambda}_\mu(\mu, \nu) < 0$ for all $\mu, \nu > 1/\delta_2$. Since $\tilde{\lambda}(\nu, \nu) = 0$, we have $\tilde{\lambda}(\mu, \nu) > 0$ for all $\nu > \mu > 1/\delta_2$, i.e. $(0, \theta_\nu)$ is linearly unstable. As in Step 1, we may use a similar argument to show that there is some $\delta \in (0, \delta_2)$ such that (1.3) has no positive steady states for any $\nu > \mu > 1/\delta$. Then Theorem 1.5(ii) is a direct consequence of Lemma 4.1. The proof is now complete. □

In what follows, we turn to establish Theorem 1.6. By the definition of $\lambda(\mu, \nu)$ in (1.11) with $\beta = \alpha$, direct calculation yields that for each $\mu > 0$,

$$\lambda_\nu(\mu, \mu) = -\frac{\int \theta_x \tilde{\theta}_x}{\int \theta\tilde{\theta}}, \tag{5.14}$$

where $\theta = \theta_\mu$ is the unique positive solution of (1.5) and $\tilde{\theta} = \tilde{\theta}_\mu$ is the unique positive solution of the adjoint problem

$$\begin{cases} \mu\tilde{\theta}_{xx} - \alpha\tilde{\theta}_x + \tilde{\theta}(r - \theta) = 0 \ \text{ in } \mathbb{R}, \\ \tilde{\theta}(x) = \tilde{\theta}(x+1) \ \text{ in } \mathbb{R} \quad \text{and} \quad \int \tilde{\theta}^2 = 1. \end{cases} \tag{5.15}$$

We first establish the existence of evolutionarily singular strategies.

PROPOSITION 5.2. *Assume $\beta = \alpha$ and $r$ is non-constant. Then for each $\alpha \neq 0$, there exists some $\mu^* = \mu^*(\alpha) \in (0, \infty)$ such that it is a singular strategy and* (1.12) *holds.*

*Proof.* Recall that $\theta$ defines the unique positive solution of (1.5). It is straightforward to verify that $\theta \rightharpoonup \vartheta$ weakly in $H^1((0,1))$ and strongly in $L^2((0,1))$ as $\mu \to 0$, where $\vartheta$ is the unique positive solution of the problem

$$\alpha\vartheta_x + \vartheta(r - \vartheta) = 0 \quad \text{and} \quad \vartheta(x) = \vartheta(x+1) \quad \text{in } \mathbb{R}. \tag{5.16}$$

Similarly, it can be shown that $\tilde{\theta} \rightharpoonup \tilde{\vartheta}$ weakly in $H^1((0,1))$ and strongly in $L^2((0,1))$ as $\mu \to 0$, where $\tilde{\theta}$ is given by (5.15) and $\tilde{\vartheta} > 0$ solves

$$-\alpha\tilde{\vartheta}_x + \tilde{\vartheta}(r - \vartheta) = 0, \quad \tilde{\vartheta}(x) = \tilde{\vartheta}(x+1) \quad \text{in } \mathbb{R}, \quad \text{and} \quad \int \tilde{\vartheta}^2 = 1. \tag{5.17}$$

By (5.16) and (5.17), we use (5.14) to deduce

$$\lim_{\mu\to 0} \lambda_\nu(\mu, \mu) = -\frac{\int \vartheta_x\tilde{\vartheta}_x}{\int \vartheta\tilde{\vartheta}} = \frac{\int \vartheta\tilde{\vartheta}(r-\vartheta)^2}{\alpha^2 \int \vartheta\tilde{\vartheta}} > 0, \tag{5.18}$$

where the strict inequality holds since $r$ is non-constant. Hence, to establish Proposition 5.2, it suffices to show $\lambda_\nu(\mu, \mu) < 0$ for large $\mu$.

By the periodicity of $\theta$, we may assume $\theta_x(x_*) = 0$ for some $x_* \in [0,1]$ depending on $\mu$. Integrating both sides of (1.5) and (5.15) from $x_*$ to $x$, we obtain

$$\mu\theta_x + \alpha\left[\theta - \theta(x_*)\right] + \int_{x_*}^{x} \theta(r - \theta) = 0$$
$$\text{and } \mu\left[\tilde{\theta}_x - \tilde{\theta}_x(x_*)\right] - \alpha\left[\tilde{\theta} - \tilde{\theta}(x_*)\right] + \int_{x_*}^{x} \tilde{\theta}(r - \theta) = 0,$$

which together with (5.14) implies that

$$\begin{aligned}\mu^2\lambda_\nu(\mu,\mu) &= -\frac{\mu^2}{\int \theta\tilde{\theta}} \int \theta_x \left[\tilde{\theta} - \tilde{\theta}(x_*)\right] \\ &= -\frac{1}{\int \theta\tilde{\theta}} \int \left[\int_{x_*}^{x} \theta(r-\theta)\right] \cdot \left[\int_{x_*}^{x} \tilde{\theta}(r-\theta)\right] + R_2.\end{aligned} \tag{5.19}$$

Here the remainder term $R_2$ can be calculated explicitly. By the Sobolev embedding theorem [24], Lemma 5.1 implies $\theta \to \hat{r}$ uniformly as $\mu \to \infty$. Direct calculation yields that the remainder term $R_2$ in (5.19) satisfies $R_2 \to 0$ as $\mu \to \infty$. Letting $\mu \to \infty$ in (5.19), we apply Lemma 5.1 again to deduce

$$\limsup_{\mu\to\infty} \mu^2\lambda_\nu(\mu,\mu) \le -\min_{y\in[0,1]} \left\{ \int \left[\int_y^x (r - \hat{r})\right]^2 \right\} < 0. \tag{5.20}$$

As both $\theta$ and $\tilde{\theta}$ are analytic functions of $\mu \in (0, \infty)$, by (5.14) we conclude that $\lambda_\nu(\mu, \mu)$ is also analytic in $\mu$. Hence, by (5.18) and (5.20), there exists some singular strategy, denoted by $\mu^*$, such that (1.12) holds. ◻

Our next result concerns the limits of the singular strategies for small and large $|\alpha|$.

PROPOSITION 5.3. *Assume $\beta = \alpha \neq 0$ and $r$ is non-constant. Let $\mu^*$ be any evolutionarily singular strategy given in Proposition* 5.2. *Then $\mu^*(\alpha) \to 0$ as $\alpha \to 0$ and $\mu^*(\alpha) \to \infty$ as $|\alpha| \to \infty$.*

*Proof.* Let $K$ denote any compact subset of $(0, \infty)$. Multiply both sides of (1.5) by $\theta$ and integrate over $[0, 1]$, then we observe that $\theta$ is bounded in $H^1((0, 1))$ uniformly for $\mu \in K$ and uniformly for $\alpha \in \mathbb{R}$. Let $\theta_0$ be the unique positive solution of (1.5) with $\alpha = 0$. By $L^p$-estimate and the embedding theorems [24], we derive that $\theta \to \theta_0$ in $H^1((0, 1))$ as $\alpha \to 0$, uniformly for $\mu \in K$. Similarly, $\tilde{\theta} \to \frac{\theta_0}{(\int \theta_0^2)^{1/2}}$ in $H^1((0, 1))$ as $\alpha \to 0$ uniformly for $\mu \in K$, where $\tilde{\theta}$ is defined by (5.15). Hence letting $\alpha \to 0$ in (5.14) we find $\lim_{\alpha\to 0} \lambda_\nu(\mu, \mu) < 0$ uniformly for $\mu \in K$. This asserts that $\mu^*(\alpha) \to 0$ or $\mu^*(\alpha) \to \infty$ as $\alpha \to 0$. If $\mu^*(\alpha) \to \infty$, we use (5.20) to derive $(\mu^*)^2\lambda_\nu(\mu^*, \mu^*) < 0$ for small $|\alpha|$, which contradicts $\lambda_\nu(\mu^*, \mu^*) \equiv 0$ for all $\alpha \in \mathbb{R}$. Thus, we conclude $\mu^*(\alpha) \to 0$ as $\alpha \to 0$.

To prove $\mu^*(\alpha) \to \infty$ as $|\alpha| \to \infty$, it suffices to show that for each $\bar{\mu} > 0$, there holds

$$\lim_{\alpha\to\infty} \alpha^2\lambda_\nu(\mu, \mu) > 0 \quad \text{uniformly for } \mu \in (0, \bar{\mu}]. \tag{5.21}$$

By definitions (1.5) and (5.15), we use (5.14) to calculate

$$\alpha^2\lambda_\nu(\mu, \mu) = \frac{1}{\int \theta\tilde{\theta}} \int [\mu\theta_{xx} + \theta(r - \theta)] \cdot \left[\mu\tilde{\theta}_{xx} + \tilde{\theta}(r - \theta)\right] = \frac{\int \tilde{\theta}\theta(r - \theta)^2}{\int \theta\tilde{\theta}} + \mu R_3, \tag{5.22}$$

where $R_3 = \frac{1}{\int \theta\tilde{\theta}} \left[\mu \int \theta_{xx}\tilde{\theta}_{xx} + \int \theta_{xx}\tilde{\theta}(r - \theta) + \int \tilde{\theta}_{xx}\theta(r - \theta)\right]$. Thus,

$$R_3 \leq C(\mu + 1) \left(\|\theta_{xx}\|_{L^2((0,1))} + \|\tilde{\theta}_{xx}\|_{L^2((0,1))}\right) \tag{5.23}$$

for some constant $C > 0$ independent of $\alpha > 0$ and $\mu \in \mathbb{R}$. We claim that for any given $\bar{\mu} > 0$, $R_3 \to 0$ uniformly for $\mu \in (0, \bar{\mu}]$ as $\alpha \to \infty$. It follows from Lemma 5.1 that $\int |\theta_{xx}|^2 \to 0$ uniformly for $\mu \in (0, \infty)$ as $\alpha \to \infty$. Similar to the proof of Lemma 5.1, we have $\int |\tilde{\theta}_{xx}|^2 \to 0$ uniformly for $\mu \in (0, \infty)$ as $\alpha \to \infty$, and thus the claim is a direct consequence of (5.23).

By Lemma 5.1, $\theta \to \hat{r}$ in $L^2((0, 1))$ uniformly for $\mu \in (0, \infty)$ as $\alpha \to \infty$. Similarly, $\tilde{\theta} \to 1$ in $L^2((0, 1))$ uniformly for $\mu \in (0, \infty)$ as $\alpha \to \infty$. Thus letting $\alpha \to \infty$ in (5.22) we have

$$\lim_{\alpha\to\infty} \alpha^2\lambda_\nu(\mu, \mu) = \int (r - \hat{r})^2 > 0$$

uniformly for $\mu \in (0, \bar{\mu}]$, where the last inequality holds since $r$ is non-constant. Therefore, (5.21) holds and Proposition 5.3 is proved. ◻

To further study the asymptotic behaviors of the singular strategies as $\alpha \to 0$, we prepare the following result:

LEMMA 5.4. *Let $\mu^*(\alpha)$ be any evolutionarily singular strategy. Suppose that $\alpha/\mu^*(\alpha)$ is bounded for small $\alpha$. Then $\theta \to r$ (strongly) in $H^1((0, 1))$ as $\alpha \to 0$, where $\theta$ is the unique positive solution of* (1.5) *with $\mu = \mu^*(\alpha)$.*

*Proof.* By (1.5) we observe that

$$\mu^*(\theta - r)_{xx} + \alpha(\theta - r)_x + \theta(r - \theta) + \mu^* r_{xx} + \alpha r_x = 0.$$

Multiply the above by $\theta - r$ and integrate the resulting equation over $[0, 1]$, then

$$\int |\theta_x - r_x|^2 \le \int r_{xx}(\theta - r) + \frac{\alpha}{\mu^*} \int r_x(\theta - r). \tag{5.24}$$

Since $\mu^*/\alpha$ is uniformly bounded, (5.24) implies

$$\int |\theta_x - r_x|^2 \le C \int |\theta - r|,$$

where $C$ is some positive constant independent of $\alpha \in \mathbb{R}$. In view of $\theta \to r$ in $L^2((0, 1))$, we deduce $\theta_x \to r_x$ in $L^2((0, 1))$ as $\alpha \to 0$. This completes the proof. ◻

Proposition 5.5. *Let $\mu^*(\alpha)$ be any evolutionarily singular strategy given in Proposition* 5.2. *If $r(x) > 0$ for all $x \in \mathbb{R}$, then there exists some $C > 0$ independent of $\alpha$ such that $C^{-1}|\alpha| \le \mu^*(\alpha) \le C|\alpha|$ for small $|\alpha| > 0$.*

*Proof.* We divide the proof into two steps.

**Step 1.** We show that there exists some $C > 0$ independent of $\alpha$ such that $\mu^*(\alpha) \le C\alpha$ for small $\alpha > 0$. Suppose not, then by passing to some subsequence if necessary, we may assume $\mu^*(\alpha)/\alpha \to \infty$ as $\alpha \to 0$. Set $P := \frac{\theta - r}{\mu^*}$. By (1.5) we see that $P$ satisfies

$$\begin{cases} \mu^* P_{xx} + \alpha P_x - P\theta = -r_{xx} - \frac{\alpha}{\mu^*} r_x & \text{in } \mathbb{R}, \\ P(x) = P(x+1) & \text{in } \mathbb{R}. \end{cases} \tag{5.25}$$

Note that $0 < r_{\min} \le \theta \le r_{\max}$ for all $\alpha \in \mathbb{R}$. Applying the maximum principle to (5.25), we deduce $|P| \le C$ for some $C > 0$ independent of $\alpha$.

Rewrite the equation of $\tilde\theta$ in (5.15) as $\tilde\theta_{xx} - \frac{\alpha}{\mu^*}\tilde\theta_x - \tilde\theta P = 0$. Multiply the above by $\tilde\theta$ and then integrate the resulting equation over $[0, 1]$. In light of $\int \tilde\theta^2 = 1$ and $|P| \le C$, we derive $\int \left|\tilde\theta_x\right|^2 = -\int P\tilde\theta^2 \le C$ for all $\alpha \in \mathbb{R}$, which means that $\tilde\theta$ is uniformly bounded in $H^1((0, 1))$. Thus by passing to a subsequence if necessary, we assume $\tilde\theta$ converges weakly in $H^1((0, 1))$ to some $\tilde\theta^* \in H^1((0, 1))$ as $\alpha \to 0$ such that $\int (\tilde\theta^*)^2 = 1$. Observe that $\tilde\theta$ also solves

$$\tilde\theta_{xx} - \frac{\alpha}{\mu^*}\tilde\theta_x - \tilde\theta \left[\frac{\theta_{xx} + \frac{\alpha}{\mu^*}\theta_x}{\theta}\right] = 0.$$

Using $\alpha/\mu^* \to 0$ and $\theta \to r$ in $H^1((0, 1))$ (Lemma 5.4), one can deduce

$$\tilde\theta^*_{xx} - \left[\frac{r_{xx}}{r}\right]\tilde\theta^* = 0 \quad \text{and} \quad \tilde\theta^*(x) = \tilde\theta^*(x+1) \quad \text{for } x \in \mathbb{R}.$$

Due to $\int (\tilde\theta^*)^2 = 1$, we have $\tilde\theta^* = \frac{r}{\sqrt{\int r^2}}$. Since $\lambda_\nu(\mu^*, \mu^*) \equiv 0$, letting $\alpha \to 0$ in (5.14) gives

$$0 = \lim_{\alpha \to 0} \lambda_\nu(\mu^*, \mu^*) = -\frac{\int |r_x|^2}{\int r^2},$$

which contradicts our assumption that $r$ is non-constant. Step 1 is thus complete.

**Step 2.** We show that there exists some $c > 0$ independent of $\alpha$ such that $\mu^*(\alpha) \geq c\alpha$ for small $\alpha$. Assume on the contrary that $\mu^*(\alpha)/\alpha \to 0$ as $\alpha \to 0$ for some subsequence. Define $Q := \frac{\theta - r}{\alpha}$, which satisfies

$$\begin{cases} \mu^* Q_{xx} + \alpha Q_x - Q\theta = -\frac{\mu^*}{\alpha} r_{xx} - r_x & \text{in } \mathbb{R}, \\ Q(x) = Q(x+1) & \text{in } \mathbb{R}. \end{cases}$$

As in Step 1, applying the maximum principle we derive $|Q| \leq C$ for some $C > 0$ independent of $\alpha$. Observe from (1.5) that $\frac{\mu^*}{\alpha}\theta_{xx} + \theta_x - Q\theta = 0$, for which multiplying both sides by $\theta_x$ gives $\int |\theta_x|^2 = \int Q\theta\theta_x \leq C \int |\theta\theta_x|$. This together with Hölder inequality implies that $\int |\theta_x|^2 \leq C \int \theta^2$. Thus $\theta$ is uniformly bounded in $H^1((0,1))$ for all $\alpha \in \mathbb{R}$. Noting that $\theta \to r$ in $L^2((0,1))$, we deduce $\theta \rightharpoonup r$ weakly in $H^1((0,1))$ as $\alpha \to 0$.

From (5.15) we see that $\tilde\theta$ satisfies $\frac{\mu^*}{\alpha}\tilde\theta_{xx} - \tilde\theta_x - Q\tilde\theta = 0$. By the same arguments as above, it follows that $\|\tilde\theta\|_{H^1((0,1))}$ is uniformly bounded with respect to $\alpha$. So $\tilde\theta \rightharpoonup \tilde\theta^{**}$ weakly in $H^1((0,1))$ as $\alpha \to 0$ for some $\tilde\theta^{**} \in H^1((0,1))$ satisfying $\int (\tilde\theta^{**})^2 = 1$. Note that $\tilde\theta$ solves

$$\frac{\mu^*}{\alpha}\tilde\theta_{xx} - \tilde\theta_x - \tilde\theta\left[\frac{\frac{\mu^*}{\alpha}\theta_{xx} + \theta_x}{\theta}\right] = 0. \tag{5.26}$$

Letting $\alpha \to 0$ in (5.26), since $\theta \rightharpoonup r$ and $\frac{\mu^*}{\alpha} \to 0$, we find that $\tilde\theta^{**}$ satisfies

$$\tilde\theta^{**}_x + \left[\frac{r_x}{r}\right]\tilde\theta^{**} = 0 \quad \text{and} \quad \tilde\theta^{**}(x) = \tilde\theta^{**}(x+1) \quad \text{for } \ x \in \mathbb{R},$$

from which we deduce $\tilde\theta^{**} = \frac{1}{r\sqrt{\int \frac{1}{r^2}}}$. Thus letting $\alpha \to 0$ in (5.14) gives

$$0 = \lim_{\alpha \to 0} \lambda_\nu(\mu^*, \mu^*) = \int \frac{|r_x|^2}{r^2},$$

which is also a contradiction. The proof is now complete. □

Finally, Theorem 1.6 is a direct consequence of Propositions 5.2, 5.3, and 5.5.

**Appendix A. Taylor expansion of the principal eigenvalue for $\alpha, \beta \gg 1$.** By [5, Proposition 3.6], the unique positive solution $\theta = \theta_\mu$ of (1.5) depends smoothly on $\alpha \in \mathbb{R}$. Thus the principal eigenpair $(\lambda, \varphi)$ of (1.11) depends smooth on $\alpha, \beta \in \mathbb{R}$. Our main result in this section can be stated as follows:

THEOREM A.1. *Let $\lambda(\mu, \nu, \alpha, \beta)$ be the principal eigenvalue of* (1.11)*. Then for $\alpha, \beta \gg 1$,*

$$\lambda(\mu, \nu, \alpha, \beta) = -\frac{\mu \int (r - \hat r)^2}{\alpha^2} + \frac{\nu \int (r - \hat r)^2}{\beta^2} + O\left(\frac{1}{\alpha^3} + \frac{1}{\beta^3}\right).$$

To prove Theorem A.1, we first Taylor expand the unique positive solution $\theta$ of (1.5).

LEMMA A.2. *Let* $\theta(x) = \vartheta_0(x) + \frac{\vartheta_1(x)}{\alpha} + \frac{\vartheta_2(x)}{\alpha^2} + \frac{\vartheta_3(x)}{\alpha^3} + O(\frac{1}{\alpha^4})$ *as* $\alpha \to \infty$ *for* 1*-periodic smooth functions* $\vartheta_i$, $i = 0, 1, 2, 3$. *Then*

$$\vartheta_0 \equiv \hat{r}, \quad \hat{\vartheta}_1 = 0, \quad \textit{and} \quad \hat{\vartheta}_2 = \mu \int (r - \hat{r})^2.$$

*Proof.* First, we observe from Lemma 5.1 that $\vartheta_0 \equiv \hat{r}$. Using this in (1.5), we obtain

$$\begin{aligned} 0 = \mu\tfrac{(\vartheta_1)_{xx}}{\alpha} + \mu\tfrac{(\vartheta_2)_{xx}}{\alpha^2} + (\vartheta_1)_x + \tfrac{(\vartheta_2)_x}{\alpha} + \tfrac{(\vartheta_3)_x}{\alpha^2} + O\left(\tfrac{1}{\alpha^3}\right) \\ + \left[r - \hat{r} - \tfrac{\vartheta_1}{\alpha} - \tfrac{\vartheta_2}{\alpha^2} + O(\tfrac{1}{\alpha^3})\right] \cdot \left[\hat{r} + \tfrac{\vartheta_1}{\alpha} + \tfrac{\vartheta_2}{\alpha^2} + O(\tfrac{1}{\alpha^3})\right]. \end{aligned} \tag{A.1}$$

Consider the zero order terms in (A.1), then

$$(\vartheta_1)_x + \hat{r}(r - \hat{r}) = 0. \tag{A.2}$$

By the periodicity of $\vartheta_1$, we observe that $\int (r - \hat{r})\vartheta_1 = \int (r - \hat{r})\vartheta_1^2 = 0$. From (A.1) we derive the first order equation given by

$$\mu(\vartheta_1)_{xx} + (\vartheta_2)_x + (r - 2\hat{r})\vartheta_1 = 0. \tag{A.3}$$

Integrating both sides of (A.3) gives $\hat{r}\hat{\vartheta}_1 = \int \vartheta_1(r - \hat{r}) = 0$, i.e. $\hat{\vartheta}_1 = 0$.

It remains to show $\hat{\vartheta}_2 = \mu \int (r - \hat{r})^2$. Consider the second order equation in (A.1):

$$\mu(\vartheta_2)_{xx} + (\vartheta_3)_x + (r - 2\hat{r})\vartheta_2 = \vartheta_1^2. \tag{A.4}$$

Integrate both sides of (A.4) over $[0, 1]$, then by (A.2) we have

$$\hat{r}^2\hat{\vartheta}_2 = -\hat{r}\int \vartheta_1^2 + \int \hat{r}(r - \hat{r})\vartheta_2 = -\hat{r}\int \vartheta_1^2 + \int (\vartheta_2)_x\vartheta_1. \tag{A.5}$$

Multiplying both sides of (A.3) by $\vartheta_1$ and integrating over $[0, 1]$ yield

$$\int (\vartheta_2)_x\vartheta_1 = \mu\int (\vartheta_1)_x^2 - \int (r - \hat{r})\vartheta_1^2 + \hat{r}\int \vartheta_1^2 = \mu\int (\vartheta_1)_x^2 + \hat{r}\int \vartheta_1^2, \tag{A.6}$$

where the last equality is due to $\int (r - \hat{r})\vartheta_1^2 = 0$. Combining (A.5) and (A.6) with (A.2), we deduce $\hat{\vartheta}_2 = \frac{\mu}{\hat{r}^2}\int (\vartheta_1)_x^2 = \mu\int (r - \hat{r})^2$ as desired. Lemma A.2 is thus proved. □

We are in a position to prove Theorem A.1.

*Proof of Theorem* A.1. Fix any $\mu, \nu > 0$ and let $(\lambda, \varphi)$ be the principal eigenpair of (1.11) such that $\int \varphi^2 = 1$. By Theorem 2.2 and Lemma 5.1, we see that $\lambda(\mu, \nu, \alpha, \beta) \to 0$ and $\varphi \to 1$ uniformly as $\alpha, \beta \to \infty$. Thus, by smoothness we may assume that for $\alpha, \beta \gg 1$,

$$\lambda(\mu, \nu, \alpha, \beta) = \frac{\Lambda_1}{\alpha} + \frac{\Lambda_2}{\beta} + \frac{\Lambda_3}{\alpha^2} + \frac{\Lambda_4}{\beta^2} + \frac{\Lambda_5}{\alpha\beta} + O\left(\frac{1}{\alpha^3} + \frac{1}{\alpha^2\beta} + \frac{1}{\alpha\beta^2} + \frac{1}{\beta^3}\right), \tag{A.7}$$

and

$$\varphi(x) = 1 + \frac{p_1(x)}{\alpha} + \frac{q_1(x)}{\beta} + \sum_{i=2}^{\infty}\left[\frac{p_i(x)}{\alpha^i} + \frac{q_i(x)}{\beta^i} + \sum_{\substack{k+h=i \\ k,h\geq 1}} \frac{z_{kh}(x)}{\alpha^k\beta^h}\right], \tag{A.8}$$

for 1-periodic smooth functions $p_i$, $q_i$ and $z_{kh}$ $(i,k,h\geq 1)$. It suffices to show

$$\Lambda_1=\Lambda_2=\Lambda_5=0,\quad \Lambda_3=-\mu\int(r-\hat{r})^2,\quad \text{and}\quad \Lambda_4=\nu\int(r-\hat{r})^2. \tag{A.9}$$

To this end, dividing both sides of (1.11) by $\beta$ and substituting (A.7) and (A.8) into the resulting equation, we obtain

$$\begin{aligned}
&\nu\frac{(p_1)_{xx}}{\alpha\beta}+\nu\frac{(q_1)_{xx}}{\beta^2}+\nu\frac{(p_2)_{xx}}{\alpha^2\beta}+\nu\frac{(q_2)_{xx}}{\beta^3}+\nu\frac{(z_{11})_{xx}}{\alpha\beta^2}+O\left(\frac{1}{\alpha^3\beta}+\frac{1}{\alpha^2\beta^2}+\frac{1}{\alpha\beta^3}+\frac{1}{\beta^4}\right)\\
&\quad+\frac{(p_1)_x}{\alpha}+\frac{(q_1)_x}{\beta}+\frac{(p_2)_x}{\alpha^2}+\frac{(z_{11})_x}{\alpha\beta}+\frac{(q_2)_x}{\beta^2}+\frac{(p_3)_x}{\alpha^3}+\frac{(z_{12})_x}{\alpha\beta^2}+\frac{(z_{21})_x}{\alpha^2\beta}+\frac{(q_3)_x}{\beta^3}v\\
&\quad+\frac{1}{\beta}\left[r-\hat{r}-\frac{\vartheta_1}{\alpha}-\frac{\vartheta_2}{\alpha^2}+O(\frac{1}{\alpha^3})\right]\cdot\left[1+\frac{p_1}{\alpha}+\frac{q_1}{\beta}+\frac{p_2}{\alpha^2}+\frac{z_{11}}{\alpha\beta}+\frac{q_2}{\beta^2}\right]\\
&=\frac{1}{\beta}\left[\frac{\Lambda_1}{\alpha}+\frac{\Lambda_2}{\beta}+\frac{\Lambda_3}{\alpha^2}+\frac{\Lambda_4}{\beta^2}+\frac{\Lambda_5}{\alpha\beta}\right]\cdot\left[1+\frac{p_1}{\alpha}+\frac{q_1}{\beta}+\frac{p_2}{\alpha^2}+\frac{z_{11}}{\alpha\beta}+\frac{q_2}{\beta^2}\right].
\end{aligned}\tag{A.10}$$

For $i=1,2,3$, we collect the coefficients of the term $\frac{1}{\alpha^i}$ in (A.10) to obtain $(p_i)_x=0$, whence the periodicity of $p_i$ implies $p_i\equiv c_i$ for some constant $c_i\in\mathbb{R}$. Considering the terms including $\frac{1}{\beta}$, we deduce

$$(q_1)_x+(r-\hat{r})=0. \tag{A.11}$$

Using the periodicity of $q_1$, this implies $\int(r-\hat{r})q_1=\int(r-\hat{r})q_1^2=0$. Then we collect the coefficients of $\frac{1}{\alpha\beta}$ to derive that

$$\nu(p_1)_{xx}+(z_{11})_x+(r-\hat{r})p_1-\vartheta_1=\Lambda_1. \tag{A.12}$$

Since $p_1\equiv c_1$, integrating (A.12) over $[0,1]$ gives $\Lambda_1=-\hat{\vartheta}_1=0$, where $\hat{\vartheta}_1=0$ is proved in Lemma A.2. Also, we collect the terms of $\frac{1}{\beta^2}$ in (A.10) and obtain

$$\nu(q_1)_{xx}+(q_2)_x+(r-\hat{r})q_1=\Lambda_2. \tag{A.13}$$

Integrating in $x$ over $[0,1]$, this implies $\Lambda_2=\int(r-\hat{r})q_1=0$. Hence, we have deduced $\Lambda_1=\Lambda_2=0$.

Now, we claim $\Lambda_3=-\mu\int(r-\hat{r})^2$. Collect the terms including $\frac{1}{\alpha^2\beta}$ in (A.10) to find

$$\nu(p_2)_{xx}+(z_{21})_x+(r-\hat{r})p_2-p_1\vartheta_1-\vartheta_2=\Lambda_1p_1+\Lambda_3.$$

In view of $p_2\equiv c_2$ and $\Lambda_1=0$, integrating the above over $[0,1]$ we deduce $\Lambda_3=-\hat{\vartheta}_2$, so that Lemma A.2 implies $\Lambda_3=-\mu\int(r-\hat{r})^2$.

Next, we show $\Lambda_4=\mu\int(r-\hat{r})^2$. Considering the coefficients of $\frac{1}{\beta^3}$, it follows that

$$\nu(q_2)_{xx}+(q_3)_x+(r-\hat{r})q_2=\Lambda_2q_1+\Lambda_4. \tag{A.14}$$

Due to $\Lambda_2=0$, using (A.11) and (A.13), we deduce from (A.14) that

$$\Lambda_4=\int(r-\hat{r})q_2=\int q_1(q_2)_x=\nu\int(q_1)_x^2-\int(r-\hat{r})q_1^2=\nu\int(r-\hat{r})^2,$$

where the last equality holds since $\int(r-\hat{r})q_1^2=0$.

Finally, we prove $\Lambda_5 = 0$. Collecting the coefficients of $\frac{1}{\alpha\beta^2}$ in (A.10) yields

$$\nu(z_{11})_{xx} + (z_{12})_x + (r - \hat{r})z_{11} - q_1\vartheta_1 = \Lambda_1 q_1 + \Lambda_2 p_1 + \Lambda_5. \tag{A.15}$$

Since $\Lambda_1 = \Lambda_2 = 0$, (A.15) implies $\Lambda_5 = \int(r - \hat{r})z_{11} - \int q_1\vartheta_1$. By (A.11) and (A.12), in view of $p_1 \equiv c_1$ we have

$$\Lambda_5 = \int (z_{11})_x q_1 - \int q_1\vartheta_1 = -c_1 \int (r - \hat{r})q_1 = 0.$$

Therefore, (A.9) holds and Theorem A.1 is proved. ◻

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REFERENCES

[1] I. Averill, K.-Y. Lam, and Y. Lou, *The role of advection in a two-species competition model: a bifurcation approach*, Mem. Amer. Math. Soc., 245 (2017), 1161.

[2] H. Berestycki, *The influence of advection on the propagation of fronts in reaction-diffusion equations*, Nonlinear PDE's in Condensed Matter and Reactive Flows, 569 (2002), pp. 11–48.

[3] H. Berestycki and F. Hamel, *Front propagation in periodic excitable Media*, Comm. Pure Appl. Math., 60 (2002), pp. 949–1032.

[4] H. Berestycki, F. Hamel, and N. Nadirashvili, *The speed of propagation for KPP-type problems. I. Periodic framework*, J. Eur. Math. Soc., 7 (2005), pp. 173–213.

[5] R. S. Cantrell and C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*, Wiley Series in Mathematical and Computational Biology, John Wiley & Sons, Ltd., Chichester, 2003.

[6] R. S. Cantrell, C. Cosner, M. A. Lewis, and Y. Lou, *Evolution of dispersal in spatial population models with multiple timescales*, J. Math. Biol., 80 (2020), pp. 3-37.

[7] X. F. Chen, K.-Y. Lam, and Y. Lou, *Dynamics of a reaction-diffusion-advection model for two competing species*, Discrete Contin. Dyn. Syst., 32 (2012), pp. 3841–3859.

[8] C. Cosner, *Reaction-diffusion-advection models for the effects and evolution of dispersal*, Discrete Contin. Dyn. Syst., 34 (2014), pp. 1701-1745.

[9] J. Dockery, V. Hutson, K. Mischaikow, and M. Pernarowski, *The evolution of slow dispersal rates: a reaction-diffusion model*, J. Math. Biol., 37 (1998), pp. 61–83.

[10] U. Dieckmann and R. Law, *The dynamical theory of coevolution: A derivation from stochastic ecological processes*, J. Math. Biol., 34 (1996), pp. 579–612.

[11] S. A. H. Geritz, E. Kisdi, G. Meszena, and J. A. J. Metz, *Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree*, Evol. Ecol., 12 (1998), pp. 35–57.

[12] W. Hao, K.-Y. Lam, and Y. Lou, *Ecological and evolutionary dynamics in advective environments: Critical domain size and boundary conditions*, Discrete Contin. Dyn. Syst. Ser.-B, 26 (2021), pp. 367–400.

[13] A. Hastings, *Can spatial variation alone lead to selection for dispersal?*, Theor. Pop. Biol., 24 (1983), pp. 244–251.

[14] F. Hamel and A. Zlatoš, *Speed-up of combustion fronts in shear flows*, Math. Ann., 356 (2013), pp. 845–867.

[15] X. He and W.-M. Ni, *The effects of diffusion and spatial variation in LotkaVolterra competitiondiffusion system I: heterogeneity vs. homogeneity*, J. Differential Equations, 254 (2013), pp. 528-546.

[16] X. He and W.-M. Ni, *The effects of diffusion and spatial variation in Lotka-Volterra competition-diffusion system II: the general case*, J. Differential Equations, 254 (2013), pp. 4088-4108.

[17] X. He and W.-M. Ni, *Global dynamics of the Lotka-Volterra competitiondiffusion system: diffusion and spatial heterogeneity I*, Comm. Pure Appl. Math., 69 (2016), pp. 981-1014.

[18] X. He and W.-M. Ni, *Global dynamics of the LotkaVolterra competition-diffusion system with equal amount of total resources, III*, Calc. Var. Partial Differential Equations, 56 (2017), 132.

[19] P. Hess, *Periodic-Parabolic Boundary Value Problems and Positivity*, vol. 247 of Pitman Research Notes in Mathematics Series, Longman Scientific & Technical, Harlow; published in the United States with John Wiley & Sons, Inc., New York, 1991.

[20] S.-B. Hsu, H. L. Smith, and P. Waltman, *Competitive exclusion and coexistence for competitive systems on ordered Banach spaces*, Trans. Amer. Math. Soc., 348 (1996), pp. 4083–4094.

[21] R. Ito, *Determining the optimal coefficient of the spatially periodic FisherKPP equation that minimizes the spreading speed*, J. Math. Biol., 80 (2020), pp. 1953-1970.

[22] N. Kinezaki, K. Kawasaki, F. Takasu, and N. Shigesada, *Modeling biological invasions into periodically fragmented environments*, Theor. Popul. Biol., 64 (2003), pp. 291–302.

[23] M. G. Krein and M. A. Rutman, *Linear Operators Leaving Invariant a Cone in a Banach Space*, American Mathematical Society, New York, 1950.

[24] O. Ladyzenskaja, V. Solonnikov, and N. Uralceva, *Linear and Quasi-Linear Equations of Parabolic Type*, Amer. Math. Soc., Transl. Math. Monogr. 1967.

[25] K.-Y. Lam, *Concentration phenomena of a semilinear elliptic equation with large advection in an ecological model*, J. Differential Equations, 250 (2011), pp. 161–181.

[26] K.-Y. Lam, *Limiting profiles of semilinear elliptic equations with large advection in population dynamics II*, SIAM J. Math. Anal., 44 (2012), pp. 1808–1830.

[27] K.-Y. Lam and D. Munther, *A remark on the Global dynamics of competitive systems on ordered Banach spaces*, Proc. Amer. Math. Soc., 144 (2016), pp. 1153–1159.

[28] K.-Y. Lam, S. Liu, and Y. Lou, *Selected topics on reaction-diffusion-advection models from spatial ecology*, Math. Appl. Sci. Eng., 1 (2020), pp. 150–180.

[29] K.-Y. Lam and Y. Lou, *Evolution of dispersal: evolutionarily stable strategies in spatial models*, J. Math. Biol., 68 (2014), pp. 851–877.

[30] K.-Y. Lam and Y. Lou, *Evolutionarily stable and convergent stable strategies in reaction-diffusion models for conditional dispersal*, Bull. Math. Biol., 76 (2014), pp. 261–291.

[31] K.-Y. Lam and Y. Lou, *Persistence, Competition and Evolution*, book chapter, The Dynamics of Biological Systems, A. Bianchi, T. Hillen, M. Lewis, Y. Yi eds., Springer Verlag. 2019.

[32] K.-Y. Lam, Y. Lou, and F. Lutscher, *Evolution of dispersal in closed advective environments*, J. Biol. Dyn., 9 (2015), pp. 188–212.

[33] K.-Y. Lam and W.-M. Ni, *Uniqueness and complete dynamics of the Lotka-Volterra competition diffusion system*, SIAM J. Appl. Math., 72 (2012), pp. 1695–1712.

[34] K.-Y. Lam and W.-M. Ni, *Advection-mediated competition in general environments*, J. Differential Equations, 257 (2014), pp. 3466–3500.

[35] S. Liu and Y. Lou, *A functional approach towards eigenvalue problems associated with incompressible flow*, Discrete Cont. Dyn. Syst., 40 (2020), pp. 3715–3736.

[36] Y. Lou and F. Lutscher, *Evolution of dispersal in advective environments*, J. Math. Biol., 69 (2014), pp. 1319–1342.

[37] Y. Lou, H. Nie, and Y. Wang, *Coexistence and bistability of a competition model in open advective environments*, Math. Biosciences, 306 (2018), pp. 10-19.

[38] Y. Lou, D. Xiao, and P. Zhou, *Qualitative analysis for a Lotka-Volterra competition system in advective homogeneous environment*, Discrete Contin. Dyn. Syst., 36 (2016), pp. 953–969.

[39] Y. Lou, X.-Q. Zhao, and P. Zhou, *Global dynamics of a Lotka-Volterre competition-diffusion-advection system in heterogeneous environments*, J. Math. Pure. Appl., 121 (2019), pp. 47–82.

[40] Y. Lou and P. Zhou, *Evolution of dispersal in advective homogeneous environments: The effect of boundary conditions*, J. Differential Equations, 259 (2015), pp. 141–171.

[41] J. Maynard Smith and G. Price, *The logic of animal conflict*, Nature, 246 (1973), pp. 15–18.

[42] G. Nadin, *The effect of the Schwarz rearrangement on the periodic principal eigenvalue of a nonsymmetric operator*, SIAM J. Math. Anal., 41 (2010), pp. 2388–2406.

[43] G. Nadin, *Some dependence results between the spreading speed and the coefficients of the space-time periodic Fisher-KPP equation*, Euro. J. Appl. Math., 22 (2011), pp. 169–185.

[44] G. Nadin, *How does the spreading speed associated with the Fisher-KPP equation depend on random stationary diffusion and reaction terms?*, Discrete Contin. Dyn. Syst. Ser.-B, 20 (2015), pp. 1785–1803.

[45] H. Nie, Y. Lou, and J. H. Wu, *Competition between two similar species in the unstirred*

*chemostat*, Discrete Contin. Dyn. Syst. Ser.-B, 21 (2016), pp. 621–639.
[46] J. Nolen, M. Rudd, and J. Xin, *Existence of KPP fronts in spatially-temporally periodic advection and variational principle for propagation speeds*, Dyn. Partial Differ. Equ., 2 (2005), pp. 1–24.
[47] N. Shigesada and K. Kawasaki, *Biological Invasions: Theory and Practice*, Oxford Series in Ecology and Evolution, Oxford University Press, Oxford, 1997.
[48] M. E. Smaily, *Pulsating travelling fronts: Asymptotics and homogenization regimes*, Eur. J. Appl. Math., 19 (2008), pp. 393–434.
[49] M. E. Smaily, *The non-monotonicity of the KPP speed with respect to diffusion in the presence of a shear flow*, Proc. Amer. Math. Soc., 141 (2013), pp. 3553-3563.
[50] O. Vasilyeva, *Population dynamics in river networks: analysis of steady states*, J. Math. Biol., 79 (2019), pp. 63–100.
[51] O. Vasilyeva and F. Lutscher, *Population dynamics in rivers: analysis of steady states*, Can. Appl. Math. Quart., 18 (2011), pp. 439–469.
[52] Y. Wang and J. P. Shi, *Persistence and extinction of population in reaction-diffusion-advection model with weak Allee effect growth*, SIAM J. Appl. Math., 79 (2019), pp. 1293-1313
[53] Y. Wang, J. P. Shi, and J. F. Wang, *Persistence and extinction of population in reaction-diffusion-advection model with strong Allee effect growth*, J. Math. Biol., 78 (2019), pp. 2093-2140.
[54] X.-Q. Zhao and P. Zhou, *On a Lotka-Volterra competition model: the effects of advection and spatial variation*, Calc. Var. Partial Differential Equations, 55 (2016), 73.
[55] P. Zhou, *On a Lotka-Volterra competition system: diffusion vs advection*, Calc. Var. Partial Differential Equations, 55 (2016), 137.
[56] A. Zlatoš, *Sharp asymptotics for KPP pulsating front speed-up and diffusion enhancement by flows*, Arch. Rat. Mech. Anal., 195 (2010), pp. 441–453.