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QUALITATIVE ANALYSIS FOR A LOTKA-VOLTERRA COMPETITION SYSTEM IN ADVECTIVE HOMOGENEOUS ENVIRONMENT

Yuan Lou

Institute for Mathematical Sciences, Renmin University of China
Beijing, 100872, China
and
Department of Mathematics, Ohio State University
Columbus, OH 43210, USA

Dongmei Xiao

Department of Mathematics, Shanghai Jiao Tong University
Shanghai 200240, China

Peng Zhou[1]

Department of Mathematics and Statistics, Memorial University of Newfoundland
St. John's, NL A1C 5S7, Canada

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Abstract. We study a two-species Lotka-Volterra competition model in an advective homogeneous environment. It is assumed that two species have the same population dynamics and diffusion rates but different advection rates. We show that if one competitor disperses by random diffusion only and the other assumes both random and directed movements, then the one without advection prevails. If two competitors are drifting along the same direction but with different advection rates, then the one with the smaller advection rate wins. Finally we prove that if the two competitors are drifting along the opposite direction, then two species will coexist. These results imply that the movement without advection in homogeneous environment is evolutionarily stable, as advection tends to move more individuals to the boundary of the habitat and thus cause the distribution of species mismatch with the resources which are evenly distributed in space.

1. **Introduction.** We begin with the following logistic model proposed by Verhulst

$$u_t = u[r - u], \quad t > 0, \tag{1}$$

where $u(t)$ represents the total population number of a species at time t and r is a positive constant accounting for the carrying capacity of the environment. It is easy to observe that for any initial data $u(0) > 0$, problem (1) admits a unique positive solution satisfying $\lim_{t\to\infty} u(t) = r$, i.e., the equilibrium $u = r$ is globally asymptotically stable.

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[1] Corresponding author.

Taking migration into consideration, one can turn to the reaction-diffusion equation

$$u_t - d\triangle u = u[r-u], \qquad x \in \Omega,\ t>0, \tag{2}$$

where $u(x,t)$ denotes the population density of the species at location x and time t; the habitat Ω is a bounded domain in $\mathbb{R}^n$ with smooth boundary, denoted by $\partial\Omega$; $d>0$ is the dispersal rate, and $r>0$ signifies the intrinsic growth rate. Throughout this paper we assume that r is a positive constant to reflect a homogeneous environment with resources being evenly distributed across the space. We impose the zero Neumann boundary condition, i.e.,

$$\frac{\partial u}{\partial \nu} = 0, \qquad x\in\partial\Omega,\ t>0, \tag{3}$$

where ν is the outward unit normal vector on $\partial\Omega$. Similar to (1), all solutions of problem (2)-(3) with non-negative and not identically zero initial data will converge to the steady state $u=r$ as $t\to\infty$. Hence, the single species u can perfectly match the resource at the equilibrium, when the environment is homogeneous. We refer to [1, 7, 19] for the discussions of the heterogeneous case $r=r(x)$.

Besides the random movement, in some circumstances the species may also take directed movement towards more favorable habitats [2, 3, 4, 5, 6, 13, 14, 15, 20], or there exist some external environmental forces such as water flow [17, 18], wind [8, 9] and so on, which usually can be described by an advection term in the equation. Here we give a typical example. Let x denote the depth within a water column where x varies from 0 (water surface) to L (water bottom), and $u(x,t)$ be the population density of a single aquatic species at location x and time t. Due to self-propelling and/or water turbulence, individuals undergo diffusive movements with diffusion rate $d>0$. Additionally, they may be sinking (resp. buoyant) provided they are heavier (resp. lighter) than the water, with sinking velocity $\alpha>0$ (resp. buoyant velocity $\alpha<0$). Assume further that the species obeys the logistic growth law, then we obtain the following reaction-diffusion-advection model:

$$\begin{cases} u_t = du_{xx} - \alpha u_x + u[r-u], & 0<x<L, t>0,\\ du_x(0,t) - \alpha u(0,t) = 0, & t>0,\\ du_x(L,t) - \alpha u(L,t) = 0, & t>0, \end{cases} \tag{4}$$

where the no-flux boundary conditions mean that no individuals will pass through the water surface and bottom. The dynamics of problem (4) is trivial: all solutions of problem (4) will converge asymptotically to the unique positive steady state solution among all non-negative and non-trivial initial data. In particular, if the species has almost the same weight as the water, then the upward (or downward) movement caused by buoyancy (or gravity) can be ignored, i.e., $\alpha\approx 0$, and so in this case problem (4) reduces to problem (2)-(3). (We remark here that problem (4) with different boundary conditions has also been studied; see for example, Danckwerts condition in [23], hostile condition in [22], and a more general condition in [16].)

We consider two aquatic species which are competing for the same resources in the water column, as described by the following Lotka-Volterra competition model including advection forces:

$$\begin{cases} u_t = d_1u_{xx} - \alpha u_x + u[r-u-v], & 0<x<L, t>0,\\ v_t = d_2v_{xx} - \beta v_x + v[r-u-v], & 0<x<L, t>0,\\ d_1u_x(0,t) - \alpha u(0,t) = d_1u_x(L,t) - \alpha u(L,t) = 0, & t>0,\\ d_2v_x(0,t) - \beta v(0,t) = d_2v_x(L,t) - \beta v(L,t) = 0, & t>0,\\ u(x,0) = u_0(x) \geq, \not\equiv 0, & 0<x<L,\\ v(x,0) = v_0(x) \geq, \not\equiv 0, & 0<x<L. \end{cases} \tag{5}$$

For system (5), the case $d_1\neq d_2$ and $\alpha=\beta$ has recently been studied by the authors [16], where it is shown that the species with higher diffusion rate will always displace the one with the smaller rate, which indicates that in an advective environment, slow diffusers can be put at disadvantage and higher diffusion rate can evolve, in contrast to the evolution of slow diffusion rate in non-advective but spatially heterogeneous environment [10, 11].

In this paper, we continue to study system (5) under the hypothesis that the dispersal strategy of the two species only differs in their advection rate, that is,

$$d_1 = d_2 \text{ and } \alpha\neq\beta.$$

Then system (5) becomes

$$\begin{cases} u_t = du_{xx} - \alpha u_x + u[r-u-v], & 0<x<L, t>0, \\ v_t = dv_{xx} - \beta v_x + v[r-u-v], & 0<x<L, t>0, \\ du_x(0,t) - \alpha u(0,t) = du_x(L,t) - \alpha u(L,t) = 0, & t>0, \\ dv_x(0,t) - \beta v(0,t) = dv_x(L,t) - \beta v(L,t) = 0, & t>0, \\ u(x,0) = u_0(x) \geq, \not\equiv 0, & 0<x<L, \\ v(x,0) = v_0(x) \geq, \not\equiv 0, & 0<x<L. \end{cases} \tag{6}$$

Our main goal is to understand how different dispersal strategies affect the outcome of competition in a homogeneous environment. In particular, by the virtue of system (6), we will try to figure out whether strong or weak advection would help the species gain more competitive advantages.

Note that in the frame of system (6), α and β are playing a symmetric role, hence without loss of generality, we may assume that $\alpha < \beta$. With this in mind, then mathematically we only need to deal with the following three cases:

$$\text{Case I}: \ 0 = \alpha < \beta; \ \text{Case II}: \ 0 < \alpha < \beta; \ \text{and Case III}: \ \alpha < 0 < \beta;$$

because $\alpha < \beta = 0$ and $\alpha < \beta < 0$ can be respectively converted to Case I and Case II by the transformation $x \mapsto -x$. Ecologically, Case I indicates that one species disperses by random diffusion only, and the other one takes both random and biased movements, hence we can call Case I: *Pure random diffusion versus mixed movement* for brevity. In Cases II and III, both species assume a combination of random and directed movements, but with the two competing species drifting in the same direction in Case II, and in the opposite direction in Case III. Hence, for the sake of simplicity, we may call Case II: *Advection along the same direction*, and Case III: *Advection along opposite direction*.

Before stating our main results, let us first introduce some notations. Throughout this paper, we denote by $(\widetilde{u}, 0)$ and $(0, \widetilde{v})$ the two semi-trivial steady states of system (6) (the existence of such solutions will be given later). In particular, we have $\widetilde{u} = r$ in Case I. In addition, we use (u^*, v^*) to denote any co-existence steady state (i.e., both components are positive) of system (6) if it exists.

Our first main result concerns Case I for system (6), where the global dynamics is completely determined.

Theorem 1.1. *Assume* $0 = \alpha < \beta$. *Then* $(\widetilde{u}, 0) = (r, 0)$ *is globally asymptotically stable, i.e., every solution of system (6) will converge to* $(r, 0)$ *as* $t \to \infty$ *for any non-negative and non-trivial initial condition.*

We mention here that for the case $\alpha < \beta = 0$, $(0, \widetilde{v}) = (0, r)$ will become globally asymptotically stable. Interchanging the role of α and β, one further finds that Theorem 1.1 holds actually for $0 = \alpha < |\beta|$, which gives us an information that *pure random diffusion wins*.

As a matter of fact, the conclusion of Theorem 1.1 can be generalized to system (5), where the restriction $d_1 = d_2$ is dropped.

Theorem 1.1* *For system (5), assume that* $d_1, d_2 > 0$ *and* $\alpha = 0 \neq |\beta|$. *Then* $(\widetilde{u}, 0) = (r, 0)$ *is globally asymptotically stable, i.e., every solution of system (5) will converge to* $(r, 0)$ *as* $t \to \infty$ *for any non-negative and non-trivial initial condition.*

Biologically, Theorem 1.1 and Theorem 1.1* are easy to understand. Since $0 = \alpha < |\beta|$, the species v has a tendency to move more individuals to the boundary $x = L$ or $x = 0$ due to gravity or buoyancy. As a result, the distribution of species v will more likely mismatch with the resources which are evenly distributed in space. In contrast, species u can perfectly match the resource at the equilibrium $u = r$. This explains why finally species u, which has no advective movement, has some competitive advantage over species v and it will win the competition finally.

We now turn to Case II, where we also obtain a complete understanding of the global dynamics of system (6).

Theorem 1.2. *Assume* $0 < \alpha < \beta$. *Then* $(\widetilde{u}, 0)$ *is globally asymptotically stable, i.e., every solution of system (6) will converge to* $(\widetilde{u}, 0)$ *as* $t \to \infty$ *for any non-negative and non-trivial initial condition.*

We remark here that for the case $\alpha < \beta < 0$, by the transformation $x \mapsto -x$, one can prove that $(0, \widetilde{v})$ will become globally asymptotically stable. Combining this result with Theorem 1.2, one finds that if the two competing species are drifting along the same direction, then larger advection rate causes species extinction; in other words, *small advection wins*.

Let us also give some biological explanations for this result: As now both species will move to the same end of the habitat, it will cause overcrowding and overmatching of resources at the boundary, which in turn results in the extinction of the species which has larger advection rate and can thus send more individuals to the boundary. Hence small advection will be selected.

Next, we discuss Case III for system (6).

Theorem 1.3. *Assume $\alpha < 0 < \beta$. Then system (6) has a (locally) stable co-existence steady state (u^*, v^*). In other words, in this situation, the two competing species may coexist finally.*

From the biological point of view, the above result is not difficult to understand since in the current scenario, u has a tendency to move to the boundary $x = 0$, while v prefers the other end $x = L$, hence both of them are able to boom themselves in their own favorable regions. We conjecture that (u^*, v^*) in the above theorem should be unique, and thereby it must be globally asymptotically stable.

We point out here that in this paper, the stability/instability of the semi-trivial stead states is given by two different methods: the first one uses the monotonicity of the principal eigenvalue on the advection parameter, and the second one rests on the essential structure feature of the system. Moreover, it seems nontrivial to prove the non-existence of any co-existence steady state for Case II, where we will introduce some new ideas and mathematical techniques.

The rest of this paper is arranged as follows. In Section 2 we present some preliminary results. In the next three consecutive sections, we will discuss Cases I, II and III and establish Theorems 1.1 (1.1*), 1.2 and 1.3, respectively.

2. Preliminary results.

In this section we present some preliminary results, which are useful in later analysis.

For any parameter $\gamma \in \mathbb{R}$, consider the problem

$$\begin{cases} dw_{xx} - \gamma w_x + w[r - w] = 0, & 0 < x < L, \\ dw_x(0) - \gamma w(0) = dw_x(L) - \gamma w(L) = 0. \end{cases} \tag{7}$$

Then we have

Lemma 2.1. *For any $\gamma \in \mathbb{R}$, problem (7) admits a unique positive solution $\widetilde{w}$.*

Proof. Set

$$\overline{w} = Me^{\frac{\gamma}{d}x} \quad \text{and} \quad \underline{w} = \varepsilon e^{\frac{\gamma}{d}x}.$$

It is easy to check that $\overline{w}$ and $\underline{w}$ are respectively an upper and lower solution to problem (7), provided $M \geq re^{\frac{|\gamma|}{d}L}$ and $\varepsilon \leq re^{-\frac{|\gamma|}{d}L}$. By the upper and lower solution method, problem (7) has a positive solution, denoted by $\widetilde{w}$.

We next prove $\widetilde{w}$ is unique, which can be done by a standard argument, and so we only sketch the main ideas here. Suppose for contradiction that problem (7) has two different positive solutions. Since M and ε can be chosen arbitrarily large and small, respectively, one can show that the maximal solution of problem (7), denoted by $\widetilde{w}_1$, and the minimal solution, denoted by $\widetilde{w}_2$, satisfy

$$\widetilde{w}_1 > \widetilde{w}_2 > 0 \text{ in } [0, L]. \tag{8}$$

Multiply the equation of $\widetilde{w}_1$ by $e^{-\frac{\gamma}{d}x}\widetilde{w}_2$ and the equation of $\widetilde{w}_2$ by $e^{-\frac{\gamma}{d}x}\widetilde{w}_1$, subtract the resulting equations and integrate over $[0, L]$, we obtain

$$\int_0^L e^{-\frac{\gamma}{d}x}\widetilde{w}_1\widetilde{w}_2[\widetilde{w}_1 - \widetilde{w}_2]\mathrm{d}x = 0,$$

which contradicts (8). This contradiction finishes the proof. □

Lemma 2.2. *$\widetilde{w}$ has the following properties:*

(a) $\widetilde{w}_x \equiv 0$ *in* $[0, L]$, *if* $\gamma = 0$;
(b) $\widetilde{w}_x > 0$ *in* $[0, L]$, *if* $\gamma > 0$;
(c) $\widetilde{w}_x < 0$ *in* $[0, L]$, *if* $\gamma < 0$.

Proof. Part (a) is easy to see and we turn to part (b).

Set $p := \frac{\widetilde{w}_x}{\widetilde{w}}$. After a series of computations we find

$$\begin{cases} -dp_{xx} + [\gamma - 2dp]p_x + \widetilde{w}p = 0, & 0 < x < L, \\ p(0) = p(L) = \frac{\gamma}{d} > 0. \end{cases}$$

By the maximum principle,

$$0 < p < \frac{\gamma}{d} \text{ in } (0, L),$$

which particularly implies

$$\widetilde{w}_x > 0 \text{ in } (0, L).$$

Thus part(b) is established. Part (c) can be verified similarly as part (b). The proof is complete. □

The following result is an immediate consequence of previous two lemmas.

Corollary 1. *For system (6), we have*

(a) *In Case I, system (6) has two semi-trivial steady states* $(\widetilde{u}, 0)$ *and* $(0, \widetilde{v})$ *with* $\widetilde{u} = r$ *and* $\widetilde{v}_x > 0$ *in* $[0, L]$*;*
(b) *In Case II, system (6) has two semi-trivial steady states* $(\widetilde{u}, 0)$ *and* $(0, \widetilde{v})$ *with* $\widetilde{u}_x > 0$ *and* $\widetilde{v}_x > 0$ *in* $[0, L]$*;*
(c) *In Case III, system (6) has two semi-trivial steady states* $(\widetilde{u}, 0)$ *and* $(0, \widetilde{v})$ *with* $\widetilde{u}_x < 0$ *and* $\widetilde{v}_x > 0$ *in* $[0, L]$.

Consider the linear eigenvalue problem

$$\begin{cases} -[d\zeta_x - \gamma\zeta]_x - m(x)\zeta = \tau\zeta, & 0 < x < L, \\ d\zeta_x(0) - \gamma\zeta(0) = d\zeta_x(L) - \gamma\zeta(L) = 0, \end{cases} \tag{9}$$

where $m(x) \in C^1([0, L])$. Denote by (τ_1, ζ_1) the first pair of eigenvalue-eigenfunction of problem (9). It is well known that (see, e.g., [12, 21]) τ_1 is simple and ζ_1 can be chosen strictly positive in $[0, L]$. In later analysis, sometimes we write τ_1 as $\tau_1(\gamma, m(x))$ to emphasize the dependence on γ and $m(x)$.

The following result concerns the monotonicity of τ_1 with respect to γ.

Lemma 2.3. *The following statements hold:*

(a) τ_1 *is a strictly increasing function of* $\gamma \in \mathbb{R}$ *if* $m_x \leq, \not\equiv 0$ *in* $[0, L]$*;*
(b) τ_1 *is a strictly decreasing function of* $\gamma \in \mathbb{R}$ *if* $m_x \geq, \not\equiv 0$ *in* $[0, L]$.

Proof. To establish part (a), we first prove the following fact

$$q \triangleq \frac{\zeta_{1x}}{\zeta_1} < \frac{\gamma}{d} \text{ in } (0, L). \tag{10}$$

Actually, by some tedious but straightforward calculations, we find

$$\begin{cases} -dq_{xx} + [\gamma - 2dq]q_x = m_x, & 0 < x < L, \\ q(0) = q(L) = \frac{\gamma}{d}. \end{cases} \tag{11}$$

Since $m_x \leq, \not\equiv 0$ in $[0, L]$, an application of the maximum principle to (11) immediately gives (10).

We next verify ${\tau_1}'(\gamma) > 0$ for $\gamma \in \mathbb{R}$.

Set $\vartheta = e^{-\frac{\gamma}{d}x}\zeta_1$. Then from the equation of (τ_1, ζ_1) we can deduce

$$\begin{cases} -[d\vartheta_x + \gamma\vartheta]_x - m(x)\vartheta = \tau_1\vartheta, & 0 < x < L, \\ \vartheta_x(0) = \vartheta_x(L) = 0. \end{cases} \tag{12}$$

Differentiating (12) with respect to γ produces

$$\begin{cases} -[d{\vartheta'}_x + \gamma\vartheta']_x - \vartheta_x - m(x)\vartheta' = {\tau_1}'\vartheta + \tau_1\vartheta', & 0 < x < L, \\ {\vartheta'}_x(0) = {\vartheta'}_x(L) = 0, \end{cases} \tag{13}$$

where the prime notation denotes the derivative with respect to γ. Multiplying (12) by $e^{\frac{\gamma}{d}x}\vartheta'$ and (13) by $e^{\frac{\gamma}{d}x}\vartheta$, subtracting the resulting equations and then integrating by parts over $(0, L)$ yield

$${\tau_1}'(\gamma) = -\frac{\int_0^L e^{\frac{\gamma}{d}x}\vartheta_x\vartheta \mathrm{d}x}{\int_0^L e^{\frac{\gamma}{d}x}\vartheta^2 \mathrm{d}x}. \tag{14}$$

Note that $\vartheta_x = e^{-\frac{\gamma}{d}x}[\zeta_{1x} - \frac{\gamma}{d}\zeta_1] < 0$ (due to (10)), we then see from (14) that

$${\tau_1}'(\gamma) > 0 \text{ for } \gamma \in \mathbb{R},$$

which completes the proof of part (a).

Part (b) can be proved similarly. In fact, under the condition in part (b), the inequality sign in (10) will be reversed, which together with the identity (14) directly gives the desired result. The proof is complete. □

Since problem (6) is a monotonic dynamical system, to a large extent, its dynamics can be determined by the stability/instability of steady states, which gives rise to the study of certain eigenvalue problems obtained by linearization.

At the end of this section, we are going to unify some symbols associated with the linearized problems for notation simplicity.

Linearizing system (6) at $(\widetilde{u}, 0)$ and $(0, \widetilde{v})$, respectively, we obtain the following two eigenvalue problems

$$\begin{cases} -[d\psi_x - \beta\psi]_x - [r - \widetilde{u}]\psi = \mu\psi, & 0 < x < L, \\ d\psi_x(0) - \beta\psi(0) = d\psi_x(L) - \beta\psi(L) = 0, \end{cases} \tag{15}$$

and

$$\begin{cases} -[d\varphi_x - \alpha\varphi]_x - [r - \widetilde{v}]\varphi = \lambda\varphi, & 0 < x < L, \\ d\varphi_x(0) - \alpha\varphi(0) = d\varphi_x(L) - \alpha\varphi(L) = 0. \end{cases} \tag{16}$$

Denote by (μ_1, ψ_1) and (λ_1, φ_1) the first pair of eigenvalue-eigenfunction of problem (15) and (16), respectively. (We underline that the symbols of μ_1, ψ_1, λ_1 and φ_1 appearing in later sections are defined the same as here.)

$(\widetilde{u}, 0)$ is called linearly stable (resp. linearly unstable) in $C(\bar{\Omega}) \times C(\bar{\Omega})$ provided $\mu_1 > 0$ (resp. $\mu_1 < 0$). The stability of $(0, \widetilde{v})$ can be defined in the same manner. Moreover, if a steady state is linearly stable (resp. linearly unstable), it is asymptotically stable (resp. unstable) (see, e.g., Theorem 7.6.2 in [21]).

3. Case I: Pure random diffusion versus mixed movement.

In this section we study the case $0 = \alpha < \beta$ and show that the species without directed movement (u) will win the competition finally.

We first investigate the stability/instability of $(0, \widetilde{v})$.

Lemma 3.1. *Assume $0 = \alpha < \beta$. Then the semi-trivial steady state $(0, \widetilde{v})$ is unstable.*

Proof. We prove this result by two different methods.

Method 1: Note that (λ_1, φ_1) defined in section 2 now satisfies $(\alpha = 0)$

$$\begin{cases} -d\varphi_{1xx} - [r - \widetilde{v}]\varphi_1 = \lambda_1\varphi_1, & 0 < x < L, \\ \varphi_{1x}(0) = \varphi_{1x}(L) = 0, \end{cases} \tag{17}$$

and that

$$\begin{cases} d\widetilde{v}_{xx} - \beta\widetilde{v}_x + \widetilde{v}[r - \widetilde{v}] = 0, & 0 < x < L, \\ d\widetilde{v}_x(0) - \beta\widetilde{v}(0) = d\widetilde{v}_x(L) - \beta\widetilde{v}(L) = 0. \end{cases} \tag{18}$$

Recall that τ_1 is defined in (9). We find

$$\lambda_1 = \tau_1(0, r - \widetilde{v}) \text{ and } 0 = \tau_1(\beta, r - \widetilde{v}).$$

By Corollary 1,

$$[r - \widetilde{v}]_x = -\widetilde{v}_x < 0,$$

which guarantees the validity of part (a) in Lemma 2.3, and then we have

$$\lambda_1 = \tau_1(0, r - \widetilde{v}) < \tau_1(\beta, r - \widetilde{v}) = 0.$$

Hence, $(0, \widetilde{v})$ is unstable.

Method 2: Dividing the first equation of (17) by φ_1 and then integrating the resulting equation over $[0, L]$ yield

$$\lambda_1 = -\frac{1}{L}\big\{d\int_0^L \frac{\varphi_{1x}^2}{\varphi_1^2}\mathrm{d}x + \int_0^L [r - \widetilde{v}]\mathrm{d}x\big\}. \tag{19}$$

From (18) one can easily deduce $\int_0^L \widetilde{v}[r - \widetilde{v}]\mathrm{d}x = 0$, and thus

$$\int_0^L [r - \widetilde{v}]\mathrm{d}x = \int_0^L \frac{[r - \widetilde{v}]}{r}[r - \widetilde{v}]\mathrm{d}x > 0, \tag{20}$$

due to $\widetilde{v} \not\equiv r$. Identity (19) and inequality (20) imply $\lambda_1 < 0$, as we wanted. The proof is complete. □

Next, we prove that in this situation, the two species cannot coexist.

Lemma 3.2. *Assume $0 = \alpha < \beta$. Then system (6) has no co-existence steady state.*

Proof. Arguing indirectly, we suppose that system (6) has a co-existence steady state (u^*, v^*). Then (u^*, v^*) satisfies

$$\begin{cases} du^*_{xx} + u^*[r - u^* - v^*] = 0, & 0 < x < L, \\ dv^*_{xx} - \beta v^*_x + v^*[r - u^* - v^*] = 0, & 0 < x < L, \\ u^*_x(0) = u^*_x(L) = 0, \\ dv^*_x(0) - \beta v^*(0) = dv^*_x(L) - \beta v^*(L) = 0. \end{cases}$$

By a direct integration, one finds

$$\int_0^L u^*[r - u^* - v^*]\mathrm{d}x = 0 \quad \text{and} \quad \int_0^L v^*[r - u^* - v^*]\mathrm{d}x = 0,$$

and thus

$$\int_0^L [r - u^* - v^*]\mathrm{d}x = \int_0^L \frac{[r - u^* - v^*]}{r}[r - u^* - v^*]\mathrm{d}x > 0, \tag{21}$$

where the fact that $r - u^* - v^*$ must change sign in $[0, L]$ is used.

On the other hand, divide the equation of u^* by u^* and then integrate over $[0, L]$ to obtain

$$\int_0^L [r - u^* - v^*]\mathrm{d}x = -d\int_0^L \frac{{u^*_x}^2}{{u^*}^2}\mathrm{d}x < 0,$$

which contradicts (21). This contradiction completes the proof. □

Proof of Theorem 1. By the theory of monotone dynamical system [21], Theorem 1.1 follows directly from part (a) of Corollary 1 and Lemmas 3.1 and 3.2. □

Remark 1. Actually, we can give a more direct proof for Theorem 1.1. Since $\alpha = 0$, system (6) has the following Lyapunov functional:

$$E(u, v)(t) = \int_0^L (u + v - r\ln u)\mathrm{d}x.$$

It is straightforward to check

$$\frac{dE}{dt} = -d\int_0^L \frac{{u_x}^2}{u^2}\mathrm{d}x - \int_0^L (r - u - v)^2\mathrm{d}x \le 0.$$

From this it then follows that $(r, 0)$ is locally stable in $C([0, L]) \times C([0, L])$ norm. Indeed, it can be further shown that $(r, 0)$ is globally convergent by LaSalle's invariance principle.

Proof of Theorem 1.1*. Though now the condition $d_1 = d_2$ is dropped, one can easily check that the second proof of Lemma 3.1 and the proof of Lemma 3.2 are still valid. Hence Theorem 1.1* holds by the monotone theory.

In addition, the Lyapunov functional constructed in Remark 1 works also for $d_1 \neq d_2$. This provides another proof of this theorem. □

4. Case II: Advection along the same direction.

In this section we study the case $0 < \alpha < \beta$. Our goal is to show that the species with smaller advection rate will wipe out the other species eventually. To this end, we investigate the stability of semi-trivial steady states in Subsection 4.1. In Subsection 4.2 we establish the non-existence of co-existence steady state.

4.1. Stability of semi-trivial steady states.

We first analyze the stability of $(\widetilde{u}, 0)$.

Lemma 4.1. *If $0 < \alpha < \beta$, the semi-trivial steady state $(\widetilde{u}, 0)$ is (locally) stable.*

Proof. We prove this result by two different methods.

Method 1: Observe that (μ_1, ψ_1) defined in section 2 satisfies

$$\begin{cases} -[d{\psi_1}_x - \beta\psi_1]_x - [r - \widetilde{u}]\psi_1 = \mu_1\psi_1, & 0 < x < L, \\ d{\psi_1}_x(0) - \beta\psi_1(0) = d{\psi_1}_x(L) - \beta\psi_1(L) = 0, \end{cases} \tag{22}$$

and that

$$\begin{cases} d\widetilde{u}_{xx} - \alpha\widetilde{u}_x + \widetilde{u}[r - \widetilde{u}] = 0, & 0 < x < L, \\ d\widetilde{u}_x(0) - \alpha\widetilde{u}(0) = d\widetilde{u}_x(L) - \alpha\widetilde{u}(L) = 0. \end{cases} \tag{23}$$

By the definition of τ_1 in (9), we see

$$\mu_1 = \tau_1(\beta, r - \widetilde{u}) \quad \text{and} \quad 0 = \tau_1(\alpha, r - \widetilde{u}).$$

Since
$$[r-\widetilde{u}]_x = -\widetilde{u}_x < 0 \text{ (Corollary 1)},$$
part (a) of Lemma 2.3 is applicable, and thus
$$\mu_1 = \tau_1(\beta, r-\widetilde{u}) > \tau_1(\alpha, r-\widetilde{u}) = 0,$$
which shows that $(\widetilde{u}, 0)$ is locally stable.

Method 2: Rewrite (22) and (23) as
$$\begin{cases} -d\big\{e^{\frac{\beta}{d}x}[e^{-\frac{\beta}{d}x}\widetilde{u}]_x\big\}_x - [r-\widetilde{u}]\widetilde{u} = [\beta-\alpha]\widetilde{u}_x, & 0<x<L, \\ -d\big\{e^{\frac{\beta}{d}x}[e^{-\frac{\beta}{d}x}\psi_1]_x\big\}_x - [r-\widetilde{u}]\psi_1 = \mu_1\psi_1, & 0<x<L, \\ d\widetilde{u}_x(0) - \beta\widetilde{u}(0) = (\alpha-\beta)\widetilde{u}(0), \\ d\widetilde{u}_x(L) - \beta\widetilde{u}(L) = (\alpha-\beta)\widetilde{u}(L), \\ d{\psi_1}_x(0) - \beta\psi_1(0) = d{\psi_1}_x(L) - \beta\psi_1(L) = 0. \end{cases}$$

Multiplying the first equation by $e^{-\frac{\beta}{d}x}\psi_1$ and the second one by $e^{-\frac{\beta}{d}x}\widetilde{u}$, subtracting the resulting equations and then integrating over $[0,L]$, we obtain
$$\begin{aligned} \mu_1\int_0^L e^{-\frac{\beta}{d}x}\widetilde{u}\psi_1 \mathrm{d}x =& [\beta-\alpha]\int_0^L \widetilde{u}_x e^{-\frac{\beta}{d}x}\psi_1\mathrm{d}x + \Big\{[d\widetilde{u}_x - \beta\widetilde{u}]e^{-\frac{\beta}{d}x}\psi_1\Big\}\big|_0^L \\ =& [\beta-\alpha]\Big\{\widetilde{u}e^{-\frac{\beta}{d}x}\psi_1\Big\}\big|_0^L - [\beta-\alpha]\int_0^L \widetilde{u}[e^{-\frac{\beta}{d}x}\psi_1]_x\mathrm{d}x \\ &+ \Big\{[\alpha-\beta]\widetilde{u}e^{-\frac{\beta}{d}x}\psi_1\Big\}\big|_0^L \\ =& -[\beta-\alpha]\int_0^L \widetilde{u}e^{-\frac{\beta}{d}x}[{\psi_1}_x - \frac{\beta}{d}\psi_1]\mathrm{d}x, \end{aligned} \tag{24}$$
where the second identity used integration by parts and the boundary conditions.

Set $m(x) = r - \widetilde{u}$ and $\gamma = \beta$ in (9). Then similarly as the proof of (10), we can demonstrate
$$\frac{{\psi_1}_x}{\psi_1} < \frac{\beta}{d},$$
which together with (24) implies $\mu_1 > 0$, as we desired. The proof is complete. □

We now turn to the investigation of the stability of $(0, \widetilde{v})$.

Lemma 4.2. *If $0<\alpha<\beta$, the semi-trivial steady state $(0,\widetilde{v})$ is unstable.*

Proof. One can use the same methods as in Lemma 4.1 to prove that λ_1 defined in section 2 satisfies $\lambda_1 < 0$, i.e., $(0,\widetilde{v})$ is unstable. For brevity we omit the details here. □

4.2. **Nonexistence of co-existence steady state.** This subsection is devoted to the proof of the nonexistence of positive steady state, which shows that the two competing species cannot coexist.

Lemma 4.3. *If $0<\alpha<\beta$, system (6) has no co-existence steady state.*

Proof. We argue by contradiction. Suppose that system (6) has a co-existence steady state (u^*, v^*). For notational simplicity, we write it as (u,v). Then we have
$$\begin{cases} du_{xx} - \alpha u_x + u[r-u-v] = 0, & 0<x<L, \\ dv_{xx} - \beta v_x + v[r-u-v] = 0, & 0<x<L, \\ du_x(0) - \alpha u(0) = du_x(L) - \alpha u(L) = 0, \\ dv_x(0) - \beta v(0) = dv_x(L) - \beta v(L) = 0. \end{cases} \tag{25}$$

Let $T = \frac{u_x}{u}$ and $S = \frac{v_x}{v}$. Then after a series of computations, we arrive at
$$\begin{cases} -dT_{xx} + [\alpha - 2dT]T_x + uT + vS = 0, & 0<x<L, \\ -dS_{xx} + [\beta - 2dS]S_x + uT + vS = 0, & 0<x<L, \\ T(0) = T(L) = \frac{\alpha}{d} > 0, \\ S(0) = S(L) = \frac{\beta}{d} > 0. \end{cases} \tag{26}$$

Define
$$f(x) \triangleq du_x - \alpha u \text{ for } x\in[0,L],$$
and
$$g(x) \triangleq dv_x - \beta v \text{ for } x\in[0,L].$$

Clearly, $f(0) = f(L) = g(0) = g(L) = 0$ due to the boundary conditions.

For clarity, we divide the rest of the proof into several steps.

Step 1. $f'(x) > 0 \Leftrightarrow g'(x) > 0$, $f'(x) < 0 \Leftrightarrow g'(x) < 0$, $f'(x) = 0 \Leftrightarrow g'(x) = 0$.

By an inspection of (25), one easily sees that

$$f'(x) = u[u + v - r] \ \text{ and } \ g'(x) = v[u + v - r].$$

Since u and v are strictly positive in $[0, L]$, the sign of $f'(x)$ and $g'(x)$ is determined by the same function $u + v - r$, and hence Step 1 is established.

Step 2. f (or g) cannot be identically zero in any interval $[y_1, y_2] \subset [0, L]$.

We only prove this result for f, since g can be treated similarly.

Suppose for contradiction that $f \equiv 0$ in some interval $[y_1, y_2] \subset [0, L]$. Then $u_x \equiv \frac{\alpha}{d} u$ in $[y_1, y_2]$, and hence

$$u(x) = u(y_1)e^{\frac{\alpha}{d}x} \text{ for } x \in [y_1, y_2].$$

On the other hand, since $f \equiv 0$ in $[y_1, y_2]$, $f'(x) \equiv 0$ in $[y_1, y_2]$. By Step 1, we have $u+v-r \equiv 0$ in $[y_1, y_2]$, and so

$$g(x) \triangleq dv_x - \beta v \equiv C,$$

for some constant C. Substituting the expression of $v(x) = r - u(x) = r - u(y_1)e^{\frac{\alpha}{d}x}$ into $g(x) \equiv C$, one can easily deduce $\alpha = \beta$, a contradiction to our assumption. The proof of this step is finished.

Step 3. There exists small $\delta > 0$ such that $f(x) < 0$ in $(0, \delta] \cup [L - \delta, L)$ and $g(x) < 0$ in $(0, \delta] \cup [L - \delta, L)$.

We first claim that if the above conclusion for f is true, then the counterpart for g is also true. The reason is as follows: if $f(x) < 0$ in $(0, \delta] \cup [L - \delta, L)$, then by shrinking $\delta > 0$ if necessary, we may assume $f'(x) < 0$ in $(0, \delta]$ and $f'(x) > 0$ in $[L - \delta, L)$; by Step 1, $g'(x) < 0$ in $(0, \delta]$ and $g'(x) > 0$ in $[L - \delta, L)$, and thus $g(x) < 0$ in $(0, \delta] \cup [L - \delta, L)$.

Based on the above claim, in what follows, we only have to deal with f. Since the arguments treating $(0, \delta]$ and $[L - \delta, L)$ are exactly the same, we omit the details for the latter one.

If $f(x) < 0$ in $(0, \delta]$ for some $\delta > 0$ does not hold, then in view of Step 2, $f(x) > 0$ in $(0, \varepsilon]$ for some small $\varepsilon > 0$. By similar analysis as in the above claim, we see $g(x) > 0$ in $(0, \varepsilon]$ (shrinking $\varepsilon > 0$ if necessary).

Denote the first zero point of f in $(\varepsilon, L]$ by z_1, and the first one of g by $z_2 \in (\varepsilon, L]$ (both z_1 and z_2 must exist since $f(L) = g(L) = 0$). Without loss of generality, we may assume $z_1 \le z_2$. Then we have

$$f(0) = f(z_1) = 0, \ f(x) > 0 \text{ in } (0, z_1), \tag{27}$$

and

$$g(0) = 0, \ g(z_1) \ge 0, \ g(x) > 0 \text{ in } (0, z_1). \tag{28}$$

Recall T and S defined in (26). Then (27) guarantees

$$T(0) = T(z_1) = \frac{\alpha}{d} > 0, \ T(x) > \frac{\alpha}{d} > 0 \text{ in } (0, z_1), \tag{29}$$

and (28) guarantees

$$S(x) \ge \frac{\beta}{d} > 0 \text{ in } [0, z_1]. \tag{30}$$

Moreover, from (29) one sees that T must attain a positive local maximum in $(0, z_1)$, say $z_3 \in (0, z_1)$. Evaluating the first equation of (26) at z_3, one then easily finds $S(z_3) < 0$, a contradiction to (30). This contradiction completes the proof of this step.

Step 4. Both f and g must change sign in $[0, L]$.

We only deal with the case of g, since the case of f can be proved by similar arguments with easy modifications.

If the above conclusion for g is not valid, then in view of Steps 2 and 3,

$$g(x) \le, \not\equiv 0 \text{ in } [0, L],$$

and consequently

$$[e^{-\frac{\beta}{d}x} v]_x = e^{-\frac{\beta}{d}x}[v_x - \frac{\beta}{d} v] \le, \not\equiv 0 \text{ in } [0, L]. \tag{31}$$

Rewrite (25) as the following

$$\begin{cases} d\{e^{\frac{\beta}{d}x}[e^{-\frac{\beta}{d}x}u]_x\}_x + [r-u-v]u = [\alpha-\beta]u_x, & 0<x<L,\\ d\{e^{\frac{\beta}{d}x}[e^{-\frac{\beta}{d}x}v]_x\}_x + [r-u-v]v = 0, & 0<x<L,\\ du_x(0)-\beta u(0) = (\alpha-\beta)u(0), \\ du_x(L)-\beta u(L) = (\alpha-\beta)u(L), \\ dv_x(0)-\beta v(0) = dv_x(L)-\beta v(L) = 0. \end{cases} \tag{32}$$

Multiply the first equation of (32) by $e^{-\frac{\beta}{d}x}v$ and the second one by $e^{-\frac{\beta}{d}x}u$, subtract and integrate the resulting equations over $[0,L]$ to obtain

$$\Big\{[du_x-\beta u]e^{-\frac{\beta}{d}x}v\Big\}\,|_0^L = [\alpha-\beta]\int_0^L u_x e^{-\frac{\beta}{d}x}v\mathrm{d}x.$$

By the boundary conditions and integration by parts, we further find

$$\int_0^L u[e^{-\frac{\beta}{d}x}v]_x\mathrm{d}x = \int_0^L ue^{-\frac{\beta}{d}x}[v_x-\frac{\beta}{d}v]\mathrm{d}x = 0,$$

which contradicts (31). The proof of this step is complete.

In view of Steps 3 and 4, there exist $0<x_1<x_2\le L$ such that

$$g(0)=g(x_1)=g(x_2)=0,\ g(x)\le 0 \text{ in } (0,x_1),\ \text{and } g(x)>0 \text{ in } (x_1,x_2), \tag{33}$$

which particularly implies

$$S(x)\ge \frac{\beta}{d}>0 \text{ in } [x_1,x_2]. \tag{34}$$

Step 5. $f<0$ in $(0,x_1]$.

Otherwise, f has at least one zero point in $(0,x_1]$, and let x_0 be the first one. Then we have

$$f(0)=f(x_0)=0,\ f(x)<0 \text{ in } (0,x_0)\subset(0,x_1],$$

which infers that

$$[e^{-\frac{\alpha}{d}x}u]_x<0 \text{ in } (0,x_0). \tag{35}$$

Clearly, $g(x_0)\le 0$, that is,

$$dv_x(x_0)\le \beta v(x_0). \tag{36}$$

Now rearrange (25) as

$$\begin{cases} d\{e^{\frac{\alpha}{d}x}[e^{-\frac{\alpha}{d}x}u]_x\}_x + [r-u-v]u = 0, & 0<x<L,\\ d\{e^{\frac{\alpha}{d}x}[e^{-\frac{\alpha}{d}x}v]_x\}_x + [r-u-v]v = [\beta-\alpha]v_x, & 0<x<L. \end{cases} \tag{37}$$

Multiply the first equation of (37) by $e^{-\frac{\alpha}{d}x}v$ and the second one by $e^{-\frac{\alpha}{d}x}u$, subtract the resulting equations, and then integrate over $[0,x_0]$, one finally gets

$$\begin{aligned}[dv_x(x_0)-\alpha v(x_0)]&e^{-\frac{\alpha}{d}x_0}u(x_0)-[\beta-\alpha]u(0)v(0)\\ =&[\beta-\alpha]\int_0^{x_0} v_x e^{-\frac{\alpha}{d}x}u\mathrm{d}x\\ =&[\beta-\alpha]v(x_0)e^{-\frac{\alpha}{d}x_0}u(x_0)-[\beta-\alpha]u(0)v(0)\\ &-[\beta-\alpha]\int_0^{x_0} v[e^{-\frac{\alpha}{d}x}u]_x\mathrm{d}x,\end{aligned}$$

which can be reduced to

$$[dv_x(x_0)-\beta v(x_0)]e^{-\frac{\alpha}{d}x_0}u(x_0) = -[\beta-\alpha]\int_0^{x_0} v[e^{-\frac{\alpha}{d}x}u]_x\mathrm{d}x.$$

By inequality (36),

$$\int_0^{x_0} v[e^{-\frac{\alpha}{d}x}u]_x\mathrm{d}x\ge 0,$$

which leads to a contradiction with (35). The proof of this step is complete.

Step 6. $f\le 0$ in $[x_1,x_2]$ with $f(x_2)<0$.

We first prove $f\le 0$ in $[x_1,x_2]$.

If not, then there exist $x_1<x_3<x_4\le x_2$ such that

$$f(x)\le 0 \text{ in } [x_1,x_3],\ f(x_3)=0,\ f(x)>0 \text{ in } (x_3,x_4]\subset[x_1,x_2].$$

This particularly tells us that f has an increasing tendency when x crosses over x_3. On the other hand, since $g > 0$ in (x_1, x_2) and $g(x_2) = 0$ (see (33)), g has a decreasing tendency as $x \to x_2^-$. So does f due to Step 1. Therefore, f must attain at least one positive local maximum in (x_3, x_2). Let $x_5 \in (x_3, x_2)$ be the one that is closest to x_3. Clearly, $f(x) > 0$ in $(x_3, x_5]$ and $f'(x_5) = 0$.

Note that

$$f'(x) = du_{xx} - \alpha u_x = d\frac{u_{xx}u - \frac{\alpha}{d}u_x u}{u},$$

and

$$T'(x) = [\frac{u_x}{u}]_x = \frac{u_{xx}u - u_x^2}{u^2}.$$

Since $u_x > \frac{\alpha}{d}u > 0$ in $(x_3, x_5]$ ($f(x) > 0$ in $(x_3, x_5]$),

$$u_{xx}u - u_x^2 < u_{xx}u - \frac{\alpha}{d}u_x u \text{ in } (x_3, x_5].$$

In particular,

$$[u_{xx}u - u_x^2]|_{x=x_5} < [u_{xx}u - \frac{\alpha}{d}u_x u]|_{x=x_5} = \frac{f'(x_5)u(x_5)}{d} = 0,$$

and so $T'(x_5) < 0$.

Now restrict T on $[x_3, x_5]$. Then the following properties are easy to see

$$T(x_3) = [\frac{u_x}{u}]|_{x=x_3} = \frac{\alpha}{d} > 0, \ T(x) > \frac{\alpha}{d} > 0 \text{ in } (x_3, x_5], \ T'(x_5) < 0.$$

Hence, T must attain a positive local maximum in (x_3, x_5), say x_6. Evaluating the first equation of (26) at $x = x_6$, we find $S(x_6) < 0$, a contradiction to (34). This contradiction confirms $f \le 0$ in $[x_1, x_2]$.

Combining $f \le 0$ in $[x_1, x_2]$ with the fact that f has a decreasing tendency as $x \to x_2^-$, we see $f(x_2) < 0$. Thus Step 6 is established.

After x passes through x_2, we can find the next zero point of g. Denote it by $x_7 \in (x_2, L]$. In (x_2, x_7), clearly either $g > 0$ or $g < 0$.

Step 7. If $g > 0$ in (x_2, x_7), then $f \le 0$ in $[x_2, x_7]$ with $f(x_7) < 0$.

This result can be verified in the same spirit of Step 6.

Step 8. If $g < 0$ in (x_2, x_7), then $f < 0$ in $[x_2, x_7]$.

If not, then in view of $f(x_2) < 0$, we can find the first zero point of f in $(x_2, x_7]$, denoted by x_8. Obviously,

$$f < 0 \text{ in } (x_2, x_8) \ \text{ and } \ g(x_8) < 0,$$

that is,

$$[e^{-\frac{\alpha}{d}x}u]_x < 0 \text{ in } (x_2, x_8) \ \text{ and } \ dv_x(x_8) < \beta v(x_8). \tag{38}$$

By using the same arguments as in Step 5, we now can derive from (37) the following identity

$$\begin{aligned}\Big\{[dv_x - \alpha v]e^{-\frac{\alpha}{d}x}u\Big\}|_{x_2}^{x_8} - &\Big\{[du_x - \alpha u]e^{-\frac{\alpha}{d}x}v\Big\}|_{x_2}^{x_8} \\ =&[\beta - \alpha]\int_{x_2}^{x_8} v_x e^{-\frac{\alpha}{d}x}u\mathrm{d}x \\ =&[\beta - \alpha]\Big\{ve^{-\frac{\alpha}{d}x}u\Big\}|_{x_2}^{x_8} - [\beta - \alpha]\int_0^{x_0} v[e^{-\frac{\alpha}{d}x}u]_x\mathrm{d}x,\end{aligned}$$

which can be reduced to

$$[dv_x(x_8) - \beta v(x_8)]e^{-\frac{\alpha}{d}x_8}u(x_8) + f(x_2)e^{-\frac{\alpha}{d}x_2}v(x_2) = -[\beta - \alpha]\int_0^{x_0} v[e^{-\frac{\alpha}{d}x}u]_x\mathrm{d}x.$$

By (38) and $f(x_2) < 0$, one can easily deduces a contradiction, which ends the proof of this step.

Step 9. We are now in a position to get the final conclusion.

Steps 7 and 8 imply $f \le 0$ in $[x_2, x_7]$. Actually, by repeating the same analysis, we can establish $f \le 0$ in $[x_7, L]$, which together with the previous results obtained in Steps 5 and 6 gives

$$f \le 0 \text{ in } [0, L].$$

However, this violates the conclusion obtained in Step 4, and this violation shows that (u, v), assumed in (25), does not exist. The proof of this lemma now is complete. □

Proof of Theorem 2. By the theory of monotone dynamical systems [21], Theorem 1.2 follows from Lemmas 4.1, 4.2 and 4.3. □

5. **Case III: Advection along opposite direction.** In this section we deal with the case $\alpha < 0 < \beta$. We will show that in this situation, two species could coexist.

As in previous sections, we first study the stability of $(\widetilde{u}, 0)$.

Lemma 5.1. *If $\alpha < 0 < \beta$, the semi-trivial steady state $(\widetilde{u}, 0)$ is unstable.*

Proof. This lemma can be established by the following two methods.

Method 1: The first method in Lemma 4.1 also works for this result. We mention here that since now $\alpha < 0$, part (b) of Lemma 2.3 will become true, and it is crucial in the proof.

Method 2: Observe that (μ_1, ψ_1) defined in section 2 satisfies

$$\begin{cases} -[d\psi_{1x} - \beta\psi_1]_x - [r - \widetilde{u}]\psi_1 = \mu_1\psi_1, & 0 < x < L, \\ d\psi_{1x}(0) - \beta\psi_1(0) = d\psi_{1x}(L) - \beta\psi_1(L) = 0. \end{cases} \tag{39}$$

Next, we only have to show $\mu_1 < 0$.

From the equation of $\widetilde{u}$ one can derive

$$\int_0^L \widetilde{u}[r - \widetilde{u}]\mathrm{d}x = 0 \text{ and} \int_0^L [r - \widetilde{u}]\mathrm{d}x = \int_0^L \frac{[r - \widetilde{u}]}{r}[r - \widetilde{u}]\mathrm{d}x > 0. \tag{40}$$

The former identity implies that $r - \widetilde{u}$ must change sign in $(0, L)$. Since $\widetilde{u}_x < 0$ in $[0, L]$ (Corollary 1), we see that $r - \widetilde{u}$ changes sign only once in $(0, L)$. Let $x_0 \in (0, L)$ be the unique zero point of $r - \widetilde{u}$. Then

$$[x - x_0][r - \widetilde{u}] > 0, \text{ for } x \in [0, L]\backslash\{x_0\}. \tag{41}$$

Let us define

$$h(\tau) \triangleq \int_0^L e^{\tau(x - x_0)}[r - \widetilde{u}]\mathrm{d}x, \ \tau \in \mathbb{R}.$$

Clearly, $h(0) > 0$ due to (40). By inequality (41),

$$h'(\tau) = \int_0^L e^{\tau(x - x_0)}[x - x_0][r - \widetilde{u}]\mathrm{d}x > 0, \ \tau \in \mathbb{R},$$

and thereby

$$h(\tau) > h(0) > 0, \text{ for } \tau > 0. \tag{42}$$

Set $\Psi = e^{-\frac{\beta}{d}x}\psi_1$, then (39) becomes

$$\begin{cases} -d[e^{\frac{\beta}{d}x}\Psi_x]_x - [r - \widetilde{u}]e^{\frac{\beta}{d}x}\Psi = \mu_1 e^{\frac{\beta}{d}x}\Psi, & 0 < x < L, \\ \Psi_x(0) = \Psi_x(L) = 0. \end{cases} \tag{43}$$

Dividing the first equation of (43) by Ψ and then integrating over $[0, L]$ yield

$$\begin{aligned} \mu_1 \int_0^L e^{\frac{\beta}{d}x}\mathrm{d}x =& -d\int_0^L e^{\frac{\beta}{d}x}\frac{\Psi_x^2}{\Psi^2}\mathrm{d}x - \int_0^L e^{\frac{\beta}{d}x}[r - \widetilde{u}]\mathrm{d}x \\ =& -d\int_0^L e^{\frac{\beta}{d}x}\frac{\Psi_x^2}{\Psi^2}\mathrm{d}x - e^{\frac{\beta}{d}x_0}\int_0^L e^{\frac{\beta}{d}(x - x_0)}[r - \widetilde{u}]\mathrm{d}x \\ =& -d\int_0^L e^{\frac{\beta}{d}x}\frac{\Psi_x^2}{\Psi^2}\mathrm{d}x - e^{\frac{\beta}{d}x_0}h(\frac{\beta}{d}) \\ <&0, \end{aligned}$$

where the last inequality used (42). Hence, $\mu_1 < 0$, as we wanted. The proof is finished. □

By the above two methods (with easy modifications), we can establish the instability of $(0, \widetilde{v})$ as follows.

Lemma 5.2. *If $\alpha < 0 < \beta$, the semi-trivial steady state is $(0, \widetilde{v})$ is unstable.*

Proof of Theorem 3. By the theory of monotone dynamical systems, system (6) must have a stable co-existence steady state due to Lemmas 5.1 and 5.2. Hence, the proof of this theorem is complete. □

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E-mail address: lou@math.ohio-state.edu
E-mail address: xiaodm@sjtu.edu.cn
E-mail address: pengzhou011@126.com