

GLOBAL DYNAMICS OF A POPULATION MODEL FROM RIVER ECOLOGY*

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Abstract In this paper, we investigate the population dynamics of a two-species Lotka-Volterra competition system arising in river ecology. An interesting feature of this modeling system lies in the boundary conditions at the downstream end, where the populations may be exposed to differing magnitudes of loss of individuals. By applying the theory of principal eigenvalue and monotone dynamical systems, we obtain a complete understanding on the global dynamics, which suggests that slower dispersal is selected for. Our results can be seen as a further development of a recent work by Tang and Chen (J. Differential Equations, 2020, 2020(269), 1465–1483).

Keywords Lotka-Volterra competition, advection, evolution, global stability.

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1. Introduction

Recently, Tang etc [14] studied the following competition-diffusion system

$$\begin{cases} u_t = d_1 u_{xx} - \alpha u_x + u(r - u - v), & 0 < x < L, t > 0, \\ v_t = d_2 v_{xx} - \alpha v_x + v(r - u - v), & 0 < x < L, t > 0, \\ u_x(0, t) = v_x(0, t) = 0, & t > 0, \\ d_1 u_x(L, t) - \alpha u(L, t) = -b\alpha u(L, t), & t > 0, \\ d_2 v_x(L, t) - \alpha v(L, t) = -b\alpha v(L, t), & t > 0, \\ u(x, 0) = u_0(x) \geq, \neq 0, & 0 < x < L, \\ v(x, 0) = v_0(x) \geq, \neq 0, & 0 < x < L, \end{cases} \quad (1.1)$$

where $u(x, t)$ and $v(x, t)$ represent the population densities of two competing aquatic species at location x and time $t > 0$, respectively. It is assumed that two species are living in a river with unidirectional water flow which is abstracted here by an open interval $(0, L)$ and that both populations are taking some diffusive movements due to self-propelling with rates $d_1, d_2 > 0$ and also certain passive movements due

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to downstream water flow with advection speed $\alpha > 0$ (in this sense, $x = 0$ and $x = L$ are, respectively, upstream and downstream ends). The positive constant r accounts for the intrinsic growth rate. At $x = 0$, the zero Neumann (free-flow) boundary condition is imposed, which biologically means that the upstream end is connected to a big lake, while at the downstream end $x = L$, there appears an interesting parameter $b \geq 0$ measuring the loss rate of individuals relative to the flow rate (see Lutscher etc [11] for the derivation details based on the random walk).

The parameter b plays an important role in both mathematics and biology. Different values of b reflect different biological situations at the downstream end and also different types of boundary conditions (Robin, Neumann or Dirichlet); See, e.g. [6–8, 10, 15, 16, 19] for some previous discussion. Note that by $b = \infty$, we mean that Dirichlet boundary condition holds, that is, $u(L, t) = v(L, t) = 0$. We note here that the single species growth model (i.e., $v \equiv 0$) was firstly proposed by Speirs etc [13] with no-flux boundary condition at $x = 0$ and hostile (Dirichlet) boundary condition at $x = L$ to describe the scenario “stream to ocean”, and that the general two species competition model can be found in Lutscher etc [12, System (1)] and the general boundary conditions at both habitat ends can be seen from Lou etc [6, Equation (5)].

The main conclusion of Tang etc [14] can be summarized as follows: For $b \in [0, 1)$, larger diffusion rate is selected for, while for $b \in (1, \infty]$, slower diffuser has more competitive advantages. For $b = 1$, system (1.1) is degenerate in the sense that there is a compact global attractor consisting of a continuum of steady states.

Motivated by Tang etc [14], in the current paper, we aim to consider a more general and reasonable situation. Suppose $b > 1$, that is, in addition to the loss caused by water flow, diffusive movements would also cause a certain magnitude of loss at the downstream end $x = L$ as measured by $-(b-1)\alpha u(L)$ (or $-(b-1)\alpha v(L)$). Since the diffusion rates of two populations are different, it seems more reasonable to consider differing magnitudes of population loss at the downstream end $x = L$. Hence, we introduce two parameters b_1 and b_2 in the boundary conditions and formulate the following modeling system

$$\begin{cases} u_t = d_1 u_{xx} - \alpha u_x + u(r - u - v), & 0 < x < L, t > 0, \\ v_t = d_2 v_{xx} - \alpha v_x + v(r - u - v), & 0 < x < L, t > 0, \\ u_x(0, t) = v_x(0, t) = 0, & t > 0, \\ d_1 u_x(L, t) - \alpha u(L, t) = -b_1 \alpha u(L, t), & t > 0, \\ d_2 v_x(L, t) - \alpha v(L, t) = -b_2 \alpha v(L, t), & t > 0, \\ u(x, 0) = u_0(x) \geq, \neq 0, & 0 < x < L, \\ v(x, 0) = v_0(x) \geq, \neq 0, & 0 < x < L, \end{cases} \tag{1.2}$$

where all parameters can be understood in a similar biological manner as before. Moreover, it is easy to see that stronger diffusive movement should cause a greater loss of individuals, so mathematically we should assume that $b_1 < b_2$ provided $d_1 < d_2$. Indeed, in the sequel, we will deal with a more general mathematical setting as described by the following basic hypotheses

- (H₁) $0 < d_1 < d_2$;
- (H₂) $1 \leq b_1 \leq b_2 \leq \infty$ and $(b_1 - 1)^2 + (b_2 - 1)^2 \neq 0$.

Note that (H₁) is imposed without loss of generality due to the symmetry of system (1.2).

It should be pointed out that the new ingredient of system (1.2) lies in its boundary conditions at $x = L$, as one will observe the contest between Neumann and Robin type ($b_1 = 1 < b_2$), Robin and Robin type ($1 < b_1 < b_2 < \infty$), and Robin and Dirichlet type ($1 < b_1 < b_2 = \infty$), which have not been treated before.

Since system (1.2) generates a monotone dynamical system, the global dynamics of such systems is largely determined by the steady states and their qualitative properties (e.g., uniqueness and stability). By the general theory of abstract competitive systems developed in [2, 4], a critical issue in the application of monotone dynamical systems is the existence or non-existence of coexistence steady states. This requires us to figure out the (positive) solution structure of the following elliptic problem corresponding to system (1.2)

$$\begin{cases} d_1 u_{xx} - \alpha u_x + u(r - u - v) = 0, & 0 < x < L, \\ d_2 v_{xx} - \alpha v_x + v(r - u - v) = 0, & 0 < x < L, \\ u_x(0) = v_x(0) = 0, \\ d_1 u_x(L) - \alpha u(L) = -b_1 \alpha u(L), \\ d_2 v_x(L) - \alpha v(L) = -b_2 \alpha v(L), \end{cases} \quad (1.3)$$

which, in general, is highly nontrivial. We refer the interested readers to [9, 17, 18] for some previous discussion on this issue by considering the no-flux boundary conditions at both ends $x = 0$ and $x = L$. But now since the upstream end is imposed by the free flow type condition, we need to introduce new ingredients in the argument to solve the emerging difficulty. Moreover, although some basic ideas are borrowed from Tang etc [14], we have to refine the techniques due to the complexity of the boundary conditions at the downstream end $x = L$.

In the sequel, let us denote by $(\tilde{u}, 0)$ and $(0, \tilde{v})$ the two possible semi-trivial steady states of system (1.2) (note such solutions may not exist in Tang etc [14, Lemma 2.4]). In addition, there is a trivial steady state $(0, 0)$, which is always linearly unstable due to the positivity of r .

Our first main result presents a clear answer on the non-existence of positive solutions of system (1.3), which plays an important role in the determination of the global dynamics of system (1.2).

Theorem 1.1. *Assume that (H_1) and (H_2) hold. Then system (1.3) has no positive solution.*

Based on Theorem 1.1, we are able to give a complete classification on the global dynamics of system (1.2). See below.

Theorem 1.2. *Assume that (H_1) and (H_2) hold. Then the following statements on system (1.2) are valid:*

- (i) *If $(\tilde{u}, 0)$ does not exist, then $(0, \tilde{v})$ does not exist either, and so $(0, 0)$ is globally asymptotically stable;*
- (ii) *If $(\tilde{u}, 0)$ exists, then $(\tilde{u}, 0)$ is globally asymptotically stable.*

Theorem 1.2 implies some interesting biological interpretations. Statement (i) indicates that species who cannot survive without any competitor will definitely go to extinction when competition is involved in, which is easy to understand. Statement (ii) suggests that the slower diffuser u has more competitive advantages and will displace the faster one eventually. This is because faster diffusion will

more likely move populations to the downstream end, where there is relatively much severer loss rate of individuals ($b_2 \geq b_1$), hence the faster diffuser is put disadvantageous.

Regarding the existence/non-existence of $(\tilde{u}, 0)$ (or similarly $(0, \tilde{v})$), one can turn to study the corresponding single equation. Indeed, it is well known (see, e.g., Cantrell etc [1]) that the existence of \tilde{u} is equivalent to determining the sign of the principle eigenvalue of the associated linearized problem at the trivial solution $u = 0$; See $\lambda_1(d_1, \alpha, r, b_1)$ below defined for problem (2.1). We refer to Tang etc [14, Lemma 2.4] for a detailed description on how to use the diffusion rate to determine the sign of $\lambda_1(d_1, \alpha, r, b_1)$.

The remainder of this paper is organized as follows. In section 2 below, we mainly discuss an auxiliary eigenvalue problem and establish several important properties of its principal eigenvalue, which play a significant role in later analysis. In section 3, we prove our main results by employing the theory of principal eigenvalue and the theory of monotone dynamical systems.

2. Preliminaries

Let us consider the following auxiliary eigenvalue problem

$$\begin{cases} d\varphi_{xx} - \alpha\varphi_x + m(x)\varphi + \lambda\varphi = 0, & 0 < x < L, \\ \varphi_x(0) = 0, \\ d\varphi_x(L) - \alpha\varphi(L) = -b\alpha\varphi(L), \end{cases} \tag{2.1}$$

where $d, \alpha, L > 0$, $b \in [1, \infty]$ and $m(x) \in L^\infty(0, L)$.

By the celebrated Krein-Rutman Theorem [3], problem (2.1) has a principal eigenvalue denoted by λ_1 , and its corresponding eigenvalue φ can be chosen strictly positive in $(0, L)$.

To stress the dependence on parameters, in the sequel we mainly write λ_1 as $\lambda_1(d, \alpha, m, b)$, but sometimes for simplicity we also adopt the notation “ $\lambda_1(\kappa)$ ” to mean that λ_1 is regarded as a function of κ with other parameters fixed.

The following properties of λ_1 are very useful in later analysis.

Proposition 2.1. *The following statements on λ_1 are true:*

- (i) *Suppose $m(x) \equiv m_0$ with m_0 being a constant and $b \in (1, \infty]$. Regard λ_1 as a function of d (with others fixed), then $\lambda_1'(d) > 0$.*
- (ii) *Suppose that $m(x)$ is non-constant and positive in $[0, L)$ and that $b \in [1, \infty]$. Regard λ_1 as a function of d (with others fixed). If there exists $d^* > 0$ such that $\lambda_1(d^*) = 0$, then $\lambda_1'(d^*) > 0$.*
- (iii) *Regard λ_1 as a function of b (with others fixed), then λ_1 is strictly increasing in b . That is, if $b_1 < b_2$, then $\lambda_1(b_1) < \lambda_1(b_2)$.*

Proof. We first prove statement (i). Differentiating (2.1) with respect to d , one has

$$\begin{cases} d\varphi'_{xx} - \alpha\varphi'_x + \varphi_{xx} + m(x)\varphi' + \lambda_1\varphi' + \lambda'_1\varphi = 0, & 0 < x < L \\ \varphi'_x(0) = 0, \\ d\varphi'_x(L) - \alpha\varphi'(L) + \varphi_x(L) = -b\alpha\varphi'(L), \end{cases} \tag{2.2}$$

where the prime notation means the derivative in d . Multiplying the first equation in (2.2) by $e^{-\frac{\alpha}{d}x}\varphi$ and the first equation in (2.1) by $e^{-\frac{\alpha}{d}x}\varphi'$, subtracting the resulting equations, and then integrating over $[0, L]$, one gets

$$\int_0^L [d\varphi'_x - \alpha\varphi']_x e^{-\frac{\alpha}{d}x} \varphi dx - \int_0^L [d\varphi_x - \alpha\varphi]_x e^{-\frac{\alpha}{d}x} \varphi' dx + \int_0^L \varphi_{xx} e^{-\frac{\alpha}{d}x} \varphi dx + \lambda'_1(d) \int_0^L e^{-\frac{\alpha}{d}x} \varphi^2 dx = 0.$$

By integration by parts and the boundary conditions, one can further derive

$$\lambda'_1(d) = \frac{\int_0^L \varphi_x (e^{-\frac{\alpha}{d}x} \varphi)_x dx}{\int_0^L e^{-\frac{\alpha}{d}x} \varphi^2 dx}. \quad (2.3)$$

We claim that $\varphi_x < 0$ in $(0, L]$. Otherwise, there exists $x_0 \in (0, L)$ such that

$$\varphi_x(x_0) = 0 > \varphi_x(L) \quad \text{and} \quad \varphi_x < 0 \quad \text{in} \quad (x_0, L],$$

where $\varphi_x(L) < 0$ is obvious if $b \in (1, \infty)$ and is due to Hopf boundary lemma if $b = \infty$. Consider $x \in (0, x_0)$, in which $\varphi > 0$ and set $Q = \frac{\varphi_x}{\varphi}$. Then

$$\begin{cases} -dQ_{xx} + [\alpha - 2dQ]Q_x = m'(x) \equiv 0, & 0 < x < x_0, \\ Q(0) = Q(x_0) = 0. \end{cases}$$

By the maximum principle, $Q \equiv 0$ in $[0, x_0]$, which implies $\varphi \equiv C_0$ in $[0, x_0]$ for some positive constant C_0 . By the equation of φ , $m + \lambda_1 \equiv 0$, so

$$d\varphi_{xx} - \alpha\varphi_x \equiv 0 \quad \text{in} \quad (0, L),$$

and so

$$d\varphi_x - \alpha\varphi \equiv C_1 \quad \text{in} \quad (0, L) \quad \text{for some constant } C_1.$$

By a direct integration,

$$\varphi(x) = \left[\frac{C_1}{\alpha} + \varphi(0) \right] e^{\frac{\alpha}{d}x} - \frac{C_1}{\alpha}, \quad x \in (0, L),$$

which, in view of $\varphi_x(0) = 0$, yields

$$\varphi(x) \equiv -\frac{C_1}{\alpha} \quad \text{in} \quad (0, L),$$

contradicting $\varphi_x(L) < 0$.

The above claim, together with (2.3), confirms statement (i).

We now verify statement (ii). Let φ^* be the eigenfunction corresponding to $\lambda_1(d^*)$. Since $\lambda_1(d^*) = 0$, we have

$$\begin{cases} d^* \varphi^*_{xx} - \alpha \varphi^*_x + m(x) \varphi^* = 0, & 0 < x < L \\ \varphi^*_x(0) = 0, \\ d^* \varphi^*_x(L) - \alpha \varphi^*(L) = -b \alpha \varphi^*(L). \end{cases}$$

In view of (2.3), it suffices to show $\varphi_x^*(x) < 0$ in $(0, L]$. If not, since $\varphi_{xx}^*(0) < 0$, there exists $x^* \in (0, L)$ such that

$$\varphi_x^*(0) = \varphi_x^*(x^*) = 0 \quad \text{and} \quad \varphi_x^*(x) < 0 \quad \text{in} \quad (0, x^*),$$

which implies $\varphi_{xx}^*(x^*) \geq 0$. But by the positivity of $m(x)$ and the equation of φ^* , one finds $\varphi_{xx}^*(x^*) < 0$, a contradiction.

For statement (iii), let $(\lambda_1(b_1), \varphi)$ and $(\lambda_1(b_2), \psi)$ be, respectively, the principal eigen-pair corresponding to $b = b_1$ and $b = b_2$. Then following the same idea as in the proof of (2.3), one can deduce that if $b_1 < b_2 < +\infty$,

$$[\lambda_1(b_2) - \lambda_1(b_1)] \int_0^L e^{-\frac{\alpha}{d}x} \varphi \psi dx = (b_2 - b_1) \alpha \varphi(L) \psi(L) e^{-\frac{\alpha}{d}L} > 0,$$

and if $b_1 < b_2 = \infty$,

$$[\lambda_1(b_2) - \lambda_1(b_1)] \int_0^L e^{-\frac{\alpha}{d}x} \varphi \psi dx = -d \psi_x(L) \varphi(L) e^{-\frac{\alpha}{d}L} > 0,$$

as desired. □

We end this section by including a basic estimate on the positive solution w of the following single equation problem

$$\begin{cases} dw_{xx} - \alpha w_x + w[r - w] = 0, & 0 < x < L \\ w_x(0) = 0, \\ dw_x(L) - \alpha w(L) = -b\alpha w(L), \end{cases} \tag{2.4}$$

where $d, \alpha, r, L > 0$ and $b \in (1, \infty]$.

Lemma 2.1. *Fix $d, \alpha, r, L > 0$ and $b \in (1, \infty]$. If problem (2.4) has a positive solution w , then*

- (i) $w(x) < r$ in $[0, L]$;
- (ii) $w_x(x) < 0$ in $(0, L]$.

Proof. We provide here a different proof from Tang etc [14, Lemma 2.2].

We first prove statement (i). By the maximum principle, $w(x) \leq r$ in $[0, L]$. If statement (i) is invalid, then there exists $x_1 \in [0, L]$ such that

$$w(x_1) = \max_{0 \leq x \leq L} w(x) = r.$$

Since $b \in (1, \infty]$, $x_1 \in [0, L)$. By the equation of w ,

$$w_x(x_1) = 0 \quad \text{and} \quad w_{xx}(x_1) = 0.$$

It then follows from the uniqueness of solutions of ODE that

$$w_x \equiv 0 \quad \text{in} \quad [0, L],$$

that is,

$$w \equiv C_0 \quad \text{in} \quad [0, L] \quad \text{for some positive constant } C_0.$$

This clearly is impossible due to the boundary condition of w at $x = L$.

For statement (ii), we use the contradiction argument. If not, there exists $x_2 \in (0, L)$ such that

$$w_x(0) = w_x(x_2) = 0 \quad \text{and} \quad w_x < 0 \quad \text{in} \quad (0, x_2),$$

which implies $w_{xx}(x_2) \geq 0$. Combining the equation of w with statement (i), one sees $w_{xx}(x_2) < 0$, a contradiction. □

3. Proof of Main results

Before proving Theorem 1.1, we need to make some a priori estimates on the positive solution (u, v) to system (1.3).

Suppose that (u, v) is a positive solution of system (1.3). Then, by the maximum principle, we have the following result. The proof is similar to that of Lou etc [10, Lemma 3.5].

Lemma 3.1. *Let $T := \frac{u_x}{u}$ and $S := \frac{v_x}{v}$. Then we have*

- (i) *If T achieves a positive local maximum at $x_0 \in (0, L)$, then $S(x_0) < 0$;*
- (ii) *If S achieves a positive local maximum at $x_0 \in (0, L)$, then $T(x_0) < 0$.*

Proof. By some straightforward computations, one finds

$$\begin{cases} -d_1 T_{xx} + [\alpha - 2d_1 T]T_x + uT + vS = 0, & 0 < x < L, \\ -d_2 S_{xx} + [\alpha - 2d_2 S]S_x + uT + vS = 0, & 0 < x < L. \end{cases}$$

The desired result would then follow directly from the maximum principle. \square

Now, we display a key estimate on (u, v) .

Lemma 3.2. *Suppose that (u, v) is a positive solution of system (1.3). Then it must hold that $r - u(x) - v(x) > 0$ in $[0, L]$.*

Proof. We divide the proof into three steps.

Step 1: $r - u(0) - v(0) \neq 0$.

If not, by the boundary condition $u_x(0) = v_x(0) = 0$ and the equations of u and v , one sees

$$u_{xx}(0) = v_{xx}(0) = 0.$$

Then, by the uniqueness of solutions of ODEs,

$$u_x = v_x \equiv 0 \quad \text{in } [0, L],$$

that is,

$$u \equiv c_1 \quad \text{and} \quad v \equiv c_2 \quad \text{for some positive constants } c_1 \text{ and } c_2,$$

contradicting the boundary condition at $x = L$.

Step 2: $r - u(0) - v(0) > 0$.

Otherwise, by Step 1 and the equations of u and v , one finds

$$u_{xx}(0) > 0 \quad \text{and} \quad v_{xx}(0) > 0.$$

Since $u_x(L) < 0$ and $v_x(L) < 0$, without loss of generality, we may assume that there exists $x_1 \in (0, L)$ such that

$$u_x(0) = u_x(x_1) = 0 \quad \text{and} \quad u_x > 0 \quad \text{in } (0, x_1),$$

and

$$v_x(0) = 0 \leq v_x(x_1) \quad \text{and} \quad v_x > 0 \quad \text{in } (0, x_1).$$

This particularly implies that T achieves a positive local maximum in $(0, x_1)$, in which S is positive, contradicting Lemma 3.1(i).

Step 3: $u_x < 0, v_x < 0$ in $(0, L]$.

By Step 2, it is easy to see that

$$u_{xx}(0) < 0 = u_x(0) \quad \text{and} \quad v_{xx}(0) < 0 = v_x(0),$$

so this step is true for $x > 0$ small. Suppose by contradiction that Step 3 is not true. Then, without loss of generality, we may assume that there exists $x_2 \in (0, L)$ such that

$$u_x(0) = u_x(x_2) = 0, \quad u_x(x) < 0 \quad \text{in} \quad (0, x_2),$$

and

$$v_x < 0 \quad \text{in} \quad (0, x_2),$$

which, in view of Step 2, implies

$$u_{xx}(x_2) \geq 0 \quad \text{and} \quad r - u(x_2) - v(x_2) > 0.$$

But, by the equation of u , one sees $u_{xx}(x_2) < 0$, a contradiction.

The desired result follows directly from Steps 2 and 3. □

We now prove *Theorem 1.1* as follows.

Proof of Theorem 1.1. Arguing indirectly, we suppose that system (1.3) has a positive solution (u, v) . By the equations of (u, v) , one sees

$$\lambda_1(d_1, \alpha, r - u - v, b_1) = \lambda_1(d_2, \alpha, r - u - v, b_2) = 0. \tag{3.1}$$

If $b_1 = b_2$, combing $d_1 < d_2$, Lemma 3.2, and Proposition 2.1 (ii) together, one gets a contradiction with (3.1). If $b_1 < b_2$, one can further use Proposition 2.1 (iii) to derive the same contradiction. □

We next turn to prove Theorem 1.2. Before doing this, we first study the local stability of the two semi-trivial steady states.

Lemma 3.3. *Assume that (H_1) - (H_2) hold. Then we have*

- (i) *If $(\tilde{u}, 0)$ exists, then it must be linearly stable;*
- (ii) *If $(0, \tilde{v})$ exists, then it must be linearly unstable.*

Proof. We only deal with $(\tilde{u}, 0)$ since $(0, \tilde{v})$ can be treated similarly.

Suppose that $(\tilde{u}, 0)$ exists. By the equation of $(\tilde{u}, 0)$, one sees

$$\lambda_1(d_1, \alpha, r - \tilde{u}, b_1) = 0.$$

On the other hand, as we know (see, e.g., Lam etc [5, Corollary 2.10]), the linear stability of $(\tilde{u}, 0)$ is determined by the sign of $\lambda_1(d_2, \alpha, r - \tilde{u}, b_2)$, which, in view of $d_1 < d_2$, Lemma 2.1 and Proposition 2.1 (ii) and (iii), must satisfy

$$\lambda_1(d_2, \alpha, r - \tilde{u}, b_2) > 0.$$

Hence $(\tilde{u}, 0)$ is linearly stable. □

We finally justify *Theorem 1.2*.

Proof of Theorem 1.2. The global stability in statements (i) and (ii) can be verified by the standard comparison argument; See, e.g., [10, Theorem 3.1] or [19, Lemma 5.1]. What we need to illustrate is why the non-existence of $(\tilde{u}, 0)$ implies the non-existence of $(0, \tilde{v})$. Indeed, if $(\tilde{u}, 0)$ does not exist, then

$$\lambda_1(d_1, \alpha, r, b_1) \geq 0.$$

Since $d_1 \leq d_2$ and $b_1 \leq b_2$, by Proposition 2.1 (i) and (iii), one finds

$$\lambda_1(d_2, \alpha, r, b_2) > 0,$$

hence $(0, \tilde{v})$ does not exist.

Statement (iii) follows directly from Theorem 1.1 and the theory of monotone dynamical systems [2, 4]. \square

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