INVASION AND COEXISTENCE OF COMPETITION-DIFFUSION-ADVECTION SYSTEM WITH HETEROGENEOUS VS HOMOGENEOUS RESOURCES

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(Communicated by Yuan Lou)

Abstract. This paper mainly study the dynamics of a Lotka-Volterra reaction-diffusion-advection model for two competing species which disperse by both random diffusion and advection along environmental gradient. In this model, the species are assumed to be identical except spatial resource distribution: heterogeneity vs homogeneity. It is shown that the species with heterogeneous resources distribution is always in a better position, that is, it can always invade when rare. The ratio of advection strength and diffusion rate of the species with heterogeneous distribution plays a crucial role in the dynamics behavior of the system. Some conditions of invasion, driving extinction, and coexistence are given in term of this ratio and the diffusion rate of its competitor.

1. Introduction. The question of how the interactions between spatial heterogeneity and the organism’s dispersing affect the evolution of the population has fascinated ecologists and evolutionary biologists for many decades. For reaction-diffusion model, Hastings [15] and Dockery et al. [12] showed that, for two competing species with different (random) dispersal rate but otherwise identical in a heterogeneous environments, the slower diffuser always wins. To be more precise, consider the following Lotka-Volterra competition-diffusion system([12])

\[
\begin{align*}
U_t &= d_1 \Delta U + U(m(x) - U - V) & \text{in } \Omega \times \mathbb{R}^+ , \\
V_t &= d_2 \Delta V + V(m(x) - U - V) & \text{in } \Omega \times \mathbb{R}^+ , \\
\partial_n U &= \partial_n V = 0 & \text{on } \partial \Omega \times \mathbb{R}^+ , \\
U(x,0) &= U_0(x), V(x,0) &= V_0(x) & \text{in } \Omega ,
\end{align*}
\]

where the migration rates \(d_1, d_2\) are two positive constants, \(U(x,t), V(x,t)\) represent the densities of two species at location \(x\) and time \(t\), \(m(x)\) represents the intrinsic growth rate of species, which also reflects the environmental richness of the resources.
at location \( x \). The habitat \( \Omega \) is a bounded region in \( \mathbb{R}^N \) with smooth boundary \( \partial \Omega \), \( \partial_x = \nu \cdot \nabla \), where \( \nu \) denotes the unit normal vector on \( \partial \Omega \), and the no-flux boundary condition means no individuals cross the boundary. For simplicity, we will assume throughout this paper that the initial data \( U_0 \) and \( V_0 \) are nonnegative and nontrivial, i.e., not identically zero.

Let \( g(x) \in C^\infty(\Omega)(\alpha \in (0,1)) \) with \( \int_{\Omega} g(x)dx \geq 0 \) and \( g(x) \neq 0 \). It is well known that the problem

\[
d\Delta \theta + \theta(g(x) - \theta) = 0 \quad \text{in} \quad \Omega, \quad \partial_\nu \theta = 0 \quad \text{on} \quad \partial \Omega, \tag{2}
\]

has a unique positive solution (see, e.g., [4]), which is denoted by \( \theta_{d,g} \).

Then the following remarkable result is established by Hastings ([15]) and Dockery et al. ([12]):

**Theorem A.** Suppose that \( 0 < m(x) \neq \text{const} \) on \( \Omega \) and \( m(x) \in C^\infty(\Omega)(\alpha \in (0,1)) \). Then the semitrivial steady state \( (\theta_{d_1,m},0) \) of (1) is globally asymptotically stable when \( d_1 < d_2 \); i.e., every solution \((U,V) \) of (1) converges to \( (\theta_{d_1,m},0) \) as \( t \to \infty \) regardless of initial values \((U_0,V_0)\).

An intuitive explanation for this surprising result is that slow diffusion helps species to better track favorable regions whereas fast diffusion will move individuals away from such ideal regions and in so doing lose certain competitive advantages.

Recently, by allowing the species \( U \) and \( V \) to have different intrinsic growth rates or to have different distributions of resources, in a series of works, He and Ni [16, 17, 18, 19] studied the following Lotka-Volterra model of competition-diffusion system:

\[
\begin{aligned}
U_t &= d_1 \Delta U + U(m_1(x) - U - cV) \quad \text{in} \quad \Omega \times \mathbb{R}^+, \\
V_t &= d_2 \Delta V + V(m_2(x) - bU - V) \quad \text{in} \quad \Omega \times \mathbb{R}^+, \\
\partial_\nu U &= \partial_\nu V = 0 \quad \text{on} \quad \partial \Omega \times \mathbb{R}^+, \\
U(x,0) &= U_0(x), \quad V(x,0) = V_0(x) \quad \text{in} \quad \Omega,
\end{aligned}
\tag{3}
\]

where \( m_1(x) \) and \( m_2(x) \) represent the carrying capacities or intrinsic growth rates, which reflect the environmental influence on the species \( U \) and \( V \) respectively. The positive constants \( b \) and \( c \) are inter-specific competition coefficients, while both intra-specific competition coefficients are normalized to 1.

On the other hand, reaction-diffusion-advection equations nowadays seem more and more popular in spatial population dynamics. Belgacem and Cosner in [2] firstly proposed the single species model in the situation where individuals are very smart so that they can sense and follow gradients in resource distribution, and then Cantrell et al. [5] analyzed the corresponding two-species model. This topic has received considerable research attention; see, e.g., [4, 5, 6, 7, 8, 9, 10, 11, 14, 25, 26, 27, 31] and the references therein, for some latest advances, see [1].

Motivated by the previous works, we introduce the following coupled reaction-diffusion-advection system

\[
\begin{aligned}
U_t &= \nabla \cdot (d_1 \nabla U - \alpha U \nabla m_1) + U(m_1(x) - U - cV) \quad \text{in} \quad \Omega \times \mathbb{R}^+, \\
V_t &= \nabla \cdot (d_2 \nabla V - \beta V \nabla m_2) + V(m_2(x) - bU - V) \quad \text{in} \quad \Omega \times \mathbb{R}^+, \\
(d_1 \nabla U - \alpha U \nabla m_1) \cdot \nu &= (d_2 \nabla V - \beta V \nabla m_2) \cdot \nu = 0 \quad \text{on} \quad \partial \Omega \times \mathbb{R}^+, \\
U(x,0) &= U_0(x), \quad V(x,0) = V_0(x) \quad \text{in} \quad \Omega,
\end{aligned}
\tag{4}
\]

where \( \alpha, \beta \) which are positive constants measure the speed of movement upward along the gradient of resources, respectively. Our main concern in paper is to pursue the dynamics of system (4), especially the effect of advection rates \( \alpha, \beta \) on the dynamics of this system.
When \( \alpha = \beta = 0 \), system (4) become the system (3), which is studied by He and Ni [16, 17, 18, 19] recently. By detailed computation and analysis, He and Ni [16, 17, 18, 19] obtained some dramatic picture of global dynamics of (3) based on diffusion rates \( d_1 \) and \( d_2 \). Especially, for the case of heterogeneity vs. homogeneity with equal amount of total resources and \( b = 1, c = 1 \), He and Ni [16, 19] obtained thoroughly complete global dynamics of (3). More precisely, in [16, 19], He and Ni proposed the following system

\[
\begin{align*}
U_t &= d_1 \Delta U + U(m(x) - U - V) \quad \text{in } \Omega \times \mathbb{R}^+, \\
V_t &= d_2 \Delta V + V(\bar{m} - U - V) \quad \text{in } \Omega \times \mathbb{R}^+, \\
\partial_t U &= \partial_n V = 0 \quad \text{on } \partial \Omega \times \mathbb{R}^+, \\
U(x, 0) &= U_0(x), V(x, 0) = V_0(x) \quad \text{in } \Omega,
\end{align*}
\]  

(5)

where \( m(x) \) is nonconstant in \( \Omega \) and \( \bar{m} \) is the average density of the resources \( m(x) \), i.e.

\[ \bar{m} = \frac{1}{|\Omega|} \int_{\Omega} m(x) dx. \]

The following notations of subsets of the first quadrant of the \( d_1d_2 \)-plane for (5) is also used in [16, 19]

\[ \Sigma_U := \{(d_1, d_2) \in \mathbb{Q} \mid (\theta_{d_1, m}, 0) \text{ is linearly stable}\}, \]

\[ \Sigma_V := \{(d_1, d_2) \in \mathbb{Q} \mid (0, \bar{m}) \text{ is linearly stable}\}, \]

\[ \Sigma_- := \{(d_1, d_2) \in \mathbb{Q} \mid \text{both } (\theta_{d_1, m}, 0) \text{ and } (0, \bar{m}) \text{ are linearly unstable}\}, \]

where

\[ \mathbb{Q} := \mathbb{R}^+ \times \mathbb{R}^+ \quad \text{and} \quad \mathbb{R}^+ := (0, \infty). \]

For the precise definition of linear stability/instability of a steady state and their characterization, see e.g., [4]. He and Ni obtained the following remarkable characterization of global dynamics result for system (5)

**Theorem B.** ([16, 19]) Assume that \( m \in C^\gamma(\bar{\Omega}) \) (\( \gamma \in (0, 1) \)), \( m > 0 \) in \( \bar{\Omega} \), and \( m \) is non-constant, then

(i) \( \Sigma_U = \emptyset \), namely, \( (0, \bar{m}) \) is always linearly unstable for all \( (d_1, d_2) \in \mathbb{Q} \);

(ii) \( \Sigma_U \neq \emptyset \), and \( (\theta_{d_1, m}, 0) \) is globally asymptotically stable for all \( (d_1, d_2) \in \Sigma_U \), where \( \Sigma_U \) denotes the closure of \( \Sigma_U \) in \( \mathbb{Q} \). Moreover, \( \Sigma_U \) can be characterized by

\[ \Sigma_U = \{(d_1, d_2) \in \mathbb{Q} \mid d_2 > \tilde{d}_2^*(d_1)\}, \]

where \( \tilde{d}_2^*(d_1) \) is a continuous function of \( d_1 \) defined in \( \mathbb{R}^+ \) with the property

\[ \tilde{d}_2^*(d_1) \rightarrow \infty, \quad \text{as } d_1 \rightarrow 0; \quad \tilde{d}_2^*(d_1) \rightarrow 0, \quad \text{as } d_1 \rightarrow \infty. \]

(iii) \( \Sigma_- \neq \emptyset \), and \( \mathbb{Q} = \Sigma_U \cup \Sigma_- \). Moreover, (5) has a unique coexistence steady state which is globally asymptotically stable for all \( (d_1, d_2) \in \Sigma_- = \mathbb{Q} \setminus \Sigma_U \).

Theorem B implies that for two competitive species having identical competition abilities and the same amount of total resources, the species with spatial heterogeneous distribution is always in a superior position to its homogenous counterpart: it is always guaranteed to survive, and it will often wipe out its competitor, so long as the diffusion point \((d_1, d_2)\) is above the critical line \( d_2 = \tilde{d}_2^*(d_1) \).
Following the idea of [17, 19], let \( m_1(x) = m(x), \) \( m_2(x) = \overline{m} = \frac{1}{|\Omega|} \int_{\Omega} m(x) dx, \) and \( b = c = 1, \) then system (4) change to the following coupled reaction-diffusion-advection system

\[
\begin{aligned}
U_t &= \nabla \cdot (d_1 \nabla U - \alpha U \nabla m) + U (m(x) - U - V) \quad \text{in } \Omega \times \mathbb{R}^+, \\
V_t &= d_2 \Delta V + V (\overline{m} - U - V) \quad \text{in } \Omega \times \mathbb{R}^+, \\
(d_1 \nabla U - \alpha U \nabla m) \cdot \nu &= \partial_\nu V = 0 \quad \text{on } \partial \Omega \times \mathbb{R}^+, \\
U(x, 0) &= U_0(x), \quad V(x, 0) = V_0(x) \quad \text{in } \Omega.
\end{aligned}
\]  

(6)

Note that since \( m_2(x) = \overline{m} \) is a constant, the gradient \( \nabla \overline{m} \equiv 0, \) and then advection rate \( \beta \) has no effect to the system (6).

For simplicity, we assume \( m(x) \) satisfies the following assumption in the rest of this paper, unless otherwise specified.

(\( \mathbf{M} \)) \( m \in C^{2+\gamma}(\Omega) \) \((\gamma \in (0, 1))\), \( m \) is non-constant, and \( \int_{\Omega} m > 0. \)

We assume that the initial data \( U_0, V_0 \) of (6) are non-negative and not identically zero, then by maximum principle [34], we can obtain \( U > 0, V > 0. \) Under assumption (\( \mathbf{M} \)), (6) have two semi-trivial steady states for all \( d_1, d_2 > 0 \) and \( \alpha > 0 \) (see [4], [11]), denoted by \((\hat{u}, 0), (0, \overline{m})\), respectively, where \( \hat{u} \) is the unique positive solution (see [2]) of

\[
\begin{aligned}
\nabla \cdot (d_1 \nabla \hat{u} - \alpha \hat{u} \nabla m) + \hat{u} (m - \hat{u}) = 0, \quad &\text{in } \Omega, \\
(d_1 \nabla \hat{u} - \alpha \hat{u} \nabla m) \cdot \nu = 0, \quad &\text{on } \partial \Omega,
\end{aligned}
\]  

(7)

and \( \overline{m} \) is the unique positive solution of

\[
\begin{aligned}
d_2 \Delta \overline{v} + \overline{v} (\overline{m} - \overline{v}) = 0, \quad &\text{in } \Omega, \\
\partial_\nu \overline{v} = 0, \quad &\text{on } \partial \Omega.
\end{aligned}
\]  

(8)

Now we state our first result

**Theorem 1.1.** Suppose that \( \mathbf{(M)} \) holds. Then \((0, \overline{m})\) is unstable for every \( d_1, d_2, \alpha > 0. \)

Theorem 1.1 implies that species \( V \) can never exclude species \( U. \) In other words, species \( U \) with small amount can always successfully invade the habitat occupied with \( V. \)

When the ratio \( \alpha/d_1 \) is small, we have

**Theorem 1.2.** Suppose that \( \mathbf{(M)} \) holds, and

\[
\frac{\alpha}{d_1} \leq \frac{1}{\max_\Omega m(x)}.
\]  

(9)

Then there exists an positive constant \( d_2^* = d_2^*(d_1, \alpha), \) such that

(i) \((\hat{u}, 0)\) is stable for \( d_2 > d_2^* \).

(ii) \((\hat{u}, 0)\) is unstable for \( d_2 < d_2^* \).

Theorem 1.2 implies that, when the ratio \( \alpha/d_1 \) is small, the species \( V \) can invade when rare if and only if it’s diffusion rate \( d_2 \) is less than the critical value \( d_2^*. \) By the theory of monotone dynamical systems, we have the following coexistence result.

**Theorem 1.3.** Suppose that \( \mathbf{(M)} \) holds, and

\[
\frac{\alpha}{d_1} \leq \frac{1}{\max_\Omega m(x)}.
\]  

(10)

Then there exists a positive constant \( d_2^* = d_2^*(d_1, \alpha), \) such that (6) has at least one stable positive coexistence steady state for \( d_2 < d_2^*. \)
Furthermore, when \( d_2 \) is large enough, we also have the following global asymptotically stability.

**Theorem 1.4.** Suppose that (M) holds, and
\[
\frac{\alpha}{d_1} \leq \frac{1}{\max_{\Omega} m(x)}.
\]
Then \((\bar{u}, 0)\) is globally asymptotically stable if \( d_2 \) is sufficiently large.

When the ratio \( \alpha/d_1 \) is large, we have

**Theorem 1.5.** Suppose that (M) holds, and \( m(x) > 0 \) for all \( x \in \overline{\Omega} \). If
\[
\frac{\alpha}{d_1} \geq \frac{1}{\min_{\Omega} m(x)},
\]
then \((\bar{u}, 0)\) is unstable for any \( d_2 > 0 \), and \((\bar{u})\) has at least one stable positive coexistence steady state.

Theorem 1.5 implies that when the ratio \( \alpha/d_1 \) is large, then for any \( d_2 > 0 \), species \( V \) can invade when rare, and the two species coexist.

The rest of this paper is organized as follows. Section 2 contains some preliminaries. In Section 3, we devote to establish our main results. Some concluding remarks are included in section 4.

2. Preliminaries. The stability of \((\bar{u}, 0)\) is determined by the principal eigenvalue, denoted by \( \mu_1(d_2, \overline{m} - \bar{u}) \), of the elliptic eigenvalue problem
\[
\begin{cases}
  d_2 \Delta \psi + (\overline{m} - \bar{u})\psi + \mu \psi = 0 & \text{in } \Omega, \\
  \partial_{\nu} \psi = 0 & \text{on } \partial \Omega.
\end{cases}
\]

Similarly, the stability of \((0, \overline{m})\) is determined by the principal eigenvalue, denoted by \( \mu_1(d_1, \alpha, m - \overline{m}) \), of the linear problem as follows:
\[
\begin{cases}
  \nabla \cdot (d_1 \nabla \psi - \alpha \psi \nabla m) + \psi(m - \overline{m}) + \mu \psi = 0 & \text{in } \Omega, \\
  (d_1 \nabla \psi - \alpha \psi \nabla m) \cdot \nu = 0 & \text{on } \partial \Omega.
\end{cases}
\]

More precisely, we have the following well known criterion

**Lemma 2.1.** \((\bar{u}, 0)\) is linearly stable if \( \mu_1(d_2, \overline{m} - \bar{u}) > 0 \) and is linearly unstable if \( \mu_1(d_2, \overline{m} - \bar{u}) < 0 \). Similarly, \((0, \overline{m})\) is linearly stable if \( \mu_1(d_1, \alpha, m - \overline{m}) > 0 \) and is linearly unstable if \( \mu_1(d_1, \alpha, m - \overline{m}) < 0 \).

Let \( \lambda_1(h) \) denote the unique nonzero principal eigenvalue of
\[
\begin{cases}
  \Delta \varphi + \lambda h(x) \varphi = 0 & \text{in } \Omega, \\
  \partial_{\nu} \varphi = 0 & \text{on } \partial \Omega,
\end{cases}
\]
where \( h \neq \text{Constant} \), could change sign. The following results are well known, see e.g., [3, 35, 33].

**Lemma 2.2.** The problem (15) has a nonzero principal eigenvalue \( \lambda_1 = \lambda_1(h) \) if and only if \( h \) changes sign and \( \int_{\Omega} h \neq 0 \). More precisely, if \( h \) changes sign, then
\[
\begin{align*}
  \text{(i)} & \quad \int_{\Omega} h = 0 \iff \lambda_1(h) = 0 \text{ is the only principal eigenvalue.} \\
  \text{(ii)} & \quad \int_{\Omega} h > 0 \iff \lambda_1(h) < 0. \\
  \text{(iii)} & \quad \int_{\Omega} h < 0 \iff \lambda_1(h) > 0. \\
  \text{(iv)} & \quad \lambda_1(h_1) > \lambda_1(h_2) \text{ if } h_1 \leq h_2, h_1 \neq h_2 \text{ a.e., and } h_1, h_2 \text{ both change sign.} \\
  \text{(v)} & \quad \lambda_1(h) \text{ is continuous in } h; \text{ more precisely, } \lambda_1(h_t) \to \lambda_1(h) \text{ if } h_t \to h \text{ in } L^\infty(\Omega).
\end{align*}
\]
In order to analyze the principal eigenvalue of problem (13), it is more convenient to consider the following more general form of eigenvalue problem:
\[
\begin{align*}
\left\{ \begin{array}{ll}
d\Delta \psi + h(x)\psi + \mu \psi = 0 & \text{in } \Omega, \\
\partial_{\nu} \psi = 0 & \text{on } \partial \Omega.
\end{array} \right.
\end{align*}
\] (16)

The principal eigenvalue of problem (16), denoted by \( \mu_1(d,h) \), is expressed by the following variational equation (see, e.g. [4])
\[
\mu_1(d,h) = \inf \left\{ \int_{\Omega} \left( d|\nabla \psi|^2 - h(x)\psi^2 \right) \, dx \mid \int_{\Omega} \psi^2 = 1, \psi \in H^1(\Omega) \right\}.
\] (17)

The following lemma collects some useful properties of \( \mu_1(d,h) \) (see Proposition 4.4 in [33]).

**Lemma 2.3.** The first eigenvalue \( \mu_1(d,h) \) of (16) has the following properties:
(i) \[ \int_{\Omega} h \geq 0 \Rightarrow \mu_1(d,h) < 0 \text{ for all } d > 0 \]
(ii) \[ \int_{\Omega} h < 0 \Rightarrow \begin{cases} 
\mu_1(d,h) < 0 & \text{for all } d < \frac{1}{\lambda_1(h)}, \\
\mu_1(d,h) = 0 & \text{for all } d = \frac{1}{\lambda_1(h)}, \\
\mu_1(d,h) > 0 & \text{for all } d > \frac{1}{\lambda_1(h)}.
\end{cases} \]
(iii) \( \mu_1(d,h) \) is strictly increasing and concave in \( d > 0 \). Moreover
\[ \lim_{d \to 0} \mu_1(d,h) = \min_{\Omega} (-h) \quad \text{and} \quad \lim_{d \to \infty} \mu_1(d,h) = -\overline{h} \]
where \( \overline{h} \) is the average of \( h \).
(iv) \( \mu_1(d,h) < \mu_1(d,k) \) if \( h \geq k \) and \( h \neq k \).

3. **Proofs of the main results.** We first prove Theorem 1.1.

**Proof of Theorem 1.1.** Let \( \lambda_1 = \lambda_1(d_1, \alpha, m - \overline{m}) \) be the principal eigenvalue of (14) and \( \psi > 0 \) be the corresponding eigenfunction, then
\[
\begin{align*}
\left\{ \begin{array}{ll}
\nabla \cdot (d_1 \nabla \psi - \alpha \psi \nabla m) + \psi (m - \overline{m}) + \lambda_1 \psi = 0 & \text{in } \Omega, \\
(d_1 \nabla \psi - \alpha \psi \nabla m) \cdot \nu = 0 & \text{on } \partial \Omega,
\end{array} \right.
\end{align*}
\] (18)

Set \( \varphi = e^{-\frac{\alpha}{d_1}m} \psi \), then \( \varphi \) satisfies
\[
\begin{align*}
\left\{ \begin{array}{ll}
d_1 \nabla \cdot (e^{\frac{\alpha}{d_1}m} \nabla \varphi) + e^{\frac{\alpha}{d_1}m} (m - \overline{m}) \varphi + \lambda_1 e^{\frac{\alpha}{d_1}m} \varphi = 0 & \text{in } \Omega, \\
\partial_{\nu} \varphi = 0 & \text{on } \partial \Omega.
\end{array} \right.
\end{align*}
\] (19)

Dividing (19) by \( \varphi \), integrating in \( \Omega \), we have
\[
d_1 \int_{\Omega} e^{\frac{\alpha}{d_1}m} |\nabla \varphi|^2 \, \varphi^{-2} + \int_{\Omega} (m - \overline{m}) e^{\frac{\alpha}{d_1}m} \varphi + \lambda_1 \int_{\Omega} e^{\frac{\alpha}{d_1}m} \varphi = 0.
\] (20)

Define
\[ \Omega^+ = \{ x \in \Omega \mid m(x) \geq \overline{m} \}, \quad \Omega^- = \{ x \in \Omega \mid m(x) < \overline{m} \}, \]
then \( \Omega = \Omega^+ \cup \Omega^- \), and
\[
\int_{\Omega} (m - \overline{m}) e^{(\alpha/d_i)m} = \int_{\Omega^+} (m - \overline{m}) e^{(\alpha/d_i)m} + \int_{\Omega^-} (m - \overline{m}) e^{(\alpha/d_i)m} > \int_{\Omega^+} (m - \overline{m}) e^{(\alpha/d_i)m} + \int_{\Omega^-} (m - \overline{m}) e^{(\alpha/d_i)m} = e^{(\alpha/d_i)m} \left[ \int_{\Omega^+} (m - \overline{m}) + \int_{\Omega^-} (m - \overline{m}) \right]
\]
(21)

It follows from (20) and (21) that \( \lambda_1 < 0 \), and then by Lemma 2.1, \((0, \overline{m})\) is linearly unstable.

The proofs of the rest results depend heavily on the following result.

**Lemma 3.1.** Assume that \( m(x) \in C^2(\Omega) \), \( m \neq \text{constant} \), and \( \int_{\Omega} m(x) dx \geq 0 \) (\( m \) may change sign). Then the steady state problem
\[
\begin{align*}
\nabla \cdot (d \nabla \tilde{u} - \alpha \tilde{u} \nabla m) + \tilde{u}(m - \tilde{u}) &= 0, & \text{in } \Omega, \\
(d \nabla \tilde{u} - \alpha \tilde{u} \nabla m) \cdot \nu &= 0 & \text{on } \partial \Omega.
\end{align*}
\]
(22)

has a unique positive solution \( \tilde{u} \). Moreover,
(i) if \( \alpha/d \leq 1/\max_\Omega m \), then \( \int_\Omega \tilde{u} > \int_\Omega m \);
(ii) if \( m > 0 \) in \( \Omega \), and \( \alpha/d \geq 1/\min_\Omega m \), then \( \int_\Omega \tilde{u} < \int_\Omega m \).

**Proof.** The existence and uniqueness of positive solution \( \tilde{u} \) is well known, for the proof, see [11]. For (ii), see Lemma 4.1 in [1]. For completeness, we give a proof of (i) by using the technique in [1].

Suppose that \( \alpha/d \leq 1/\max_\Omega m \). Let
\[ w = e^{-\eta m} \tilde{u}, \]
where \( \eta = \alpha/d \). Then \( w \) satisfies
\[
\begin{align*}
\nabla \cdot [e^{\eta m} \nabla w] + \tilde{u}(m - \tilde{u}) &= 0 & \text{in } \Omega, \\
\partial_\nu w &= 0 & \text{on } \partial \Omega.
\end{align*}
\]
(23)

Let \( w(x^*) = \max_\Omega w \), then we can always choose \( x^* \in \Omega \). If this is not the case, then \( x^* \in \partial \Omega \), and \( w(x) < w(x^*) \) for all \( x \in \Omega \). By the Hopf Boundary Lemma (see [13, 34]), \( \frac{\partial w}{\partial \nu}(x^*) > 0 \). But this contradicts the boundary condition of \( w \) on \( \partial \Omega \). This contradiction implies that we can choose the maximal value point \( x^* \) to be in \( \Omega \). For such \( x^* \in \Omega \), we have \( \Delta w(x^*) \leq 0, \nabla w(x^*) = 0 \). Hence, by equation (23) we have \( \tilde{u}(x^*) \leq m(x^*) \). Therefore
\[ \max_\Omega w = w(x^*) = e^{-\eta m(x^*)} \tilde{u}(x^*) \leq e^{-\eta m(x^*)} m(x^*) \leq 1/(\eta \epsilon), \]
(24)

where the last inequality follows from \( ye^{-\eta y} \leq 1/(\eta \epsilon) \). It follows that \( w(x) \leq 1/(\eta \epsilon) \) for every \( x \in \Omega \). Then by the assumption that \( \eta \max_\Omega m \leq 1 \), we have
\[ \tilde{u}(x) = e^{\eta m(x)} w(x) \leq e^{\eta \max_\Omega m} \max_\Omega w \leq 1/\eta \quad \text{for all } \ x \in \Omega. \]
(25)

Define a function \( F(y) = ye^{-\eta y}, \ y \in [0, 1/\eta] \). Since \( F'(y) > 0 \) for \( y \in [0, 1/\eta] \), \( F \) has an inverse function, denoted by \( G \). It is easy to see that \( G \) is defined in \([0, 1/(\eta \epsilon)]\), and its rang is \([0, 1/\eta] \). Hence \( G(w(x)) \) and \( F(\tilde{u}(x)) \) are always well defined by (24) and (25) for any \( x \in \Omega \).
Dividing (23) by $G(w)$ and integrating in $\Omega$,
\[
d \int_{\Omega} \frac{e^{\eta}G'(w)|\nabla w|^2}{G^2(w)} + \int_{\Omega} \frac{\tilde{u}}{G(w)} (m - \tilde{u}) = 0,
\]
which can be written as
\[
\int_{\Omega} (\tilde{u} - m) = d \int_{\Omega} \frac{e^{\eta}G'(w)|\nabla w|^2}{G^2(w)} + \int_{\Omega} \frac{\tilde{u} - G(w)}{G(w)} (m - \tilde{u}).
\]
Now we prove that
\[
[\tilde{u} - G(w)](m - \tilde{u}) \geq 0 \text{ in } \Omega.
\]
If $\tilde{u}(x) < m(x)$, then $F(\tilde{u}(x)) = \tilde{u}(x)e^{-\eta}(x) > \tilde{u}(x)e^{-\eta m(x)} = w(x)$. By the strictly monotone increasing property of $G$, we have $\tilde{u}(x) > G(w(x))$, and then (28) follows.

If instead $\tilde{u}(x) \geq m(x)$, then $F(\tilde{u}(x)) = \tilde{u}(x)e^{-\eta}(x) \leq \tilde{u}(x)e^{-\eta m(x)} = w(x)$. It follows that $\tilde{u}(x) \leq G(w(x))$, and then (28) holds either.

By $G' > 0$, (27), (28), we have $\int_{\Omega} \tilde{u} > \int_{\Omega} m$. This completes the proof of (i).

Now we are ready to establish Theorem 1.2 and Theorem 1.3.

Proof of Theorem 1.2. Consider the eigenvalue problem
\[
\begin{cases}
d_2 \Delta \psi + (\bar{m} - \bar{u})\psi + \mu \psi = 0 & \text{in } \Omega \\
\partial_\nu \psi = 0 & \text{on } \partial \Omega.
\end{cases}
\]
Suppose that $\frac{\alpha}{d_1} \leq \frac{1}{\max_{\Omega} m(x)}$, by Lemma 3.1,
\[
\int_{\Omega} (\bar{m} - \bar{u}) = \int_{\Omega} (m - \bar{u}) < 0.
\]
By Lemma 2.2 and Lemma 2.3, there exists $d^* = 1/\lambda_1(\bar{m} - \bar{u}) > 0$, which is dependent on $d_1, \alpha$, but is independent on $d_2$, such that the principal eigenvalue $\mu_1 = \mu_1(d_2, \bar{m} - \bar{u})$ of (29) satisfies
\[
\mu_1 < 0 \text{ for all } d_2 < d^*, \text{ and } \mu_1 > 0 \text{ for all } d_2 > d^*.
\]
This complete the proof of Theorem 1.2.

Proof of Theorem 1.3. It is known that (6) is a strongly monotone system, for a proof, refer to Lemma 2.2 in [6]. Assume that the conditions of Theorem 1.3 is satisfied, then by Theorem 1.2 (ii), for $d_2 < d^*_2$, the semi-trivial steady state $(\bar{u}, 0)$ is linearly unstable. By Theorem 1.1, the other semi-trivial steady state $(0, \overline{m})$ is always linear unstable for all $d_1, d_2, \alpha > 0$. Then by the theory of monotone dynamical system (see, e.g., [21, 22, 23, 36]), (6) has at least one stable positive coexistence steady state. This completes the proof.

To prove Theorem 1.4, we also need the following lemma.

Lemma 3.2. Suppose that $m \in C^{2+\gamma}(\Omega)$, and $\alpha/d_1 \leq \frac{1}{\max_{\Omega} m(x)}$. If $(\bar{U}, \bar{V})$ is a positive steady state solution of (6), then
\[
\|\bar{U}\|_{L^\infty} < \|m\|_{L^\infty}, \quad \|\bar{V}\|_{L^\infty} < \bar{m}.
\]

Proof. $(\bar{U}, \bar{V})$ satisfies the following elliptic system
\[
\begin{cases}
\nabla \cdot (d_1 \nabla \bar{U} - \alpha \bar{U} \nabla m) + \bar{U} (m(x) - \bar{U} - \bar{V}) = 0 & \text{in } \Omega, \\
d_2 \Delta \bar{V} + \bar{V} (\bar{m} - \bar{U} - \bar{V}) = 0 & \text{in } \Omega, \\
(d_1 \nabla \bar{U} - \alpha \bar{U} \nabla m) \cdot \nu = \partial_\nu \bar{V} = 0 & \text{on } \partial \Omega,
\end{cases}
\]
By the maximal principle and comparison theorem([13, 34]), we have that \( \| \tilde{V} \|_{L^\infty} < \bar{m} \), and
\[
\| \tilde{U} \|_{L^\infty} \leq \| \tilde{u} \|_{L^\infty},
\]
where \( \tilde{u} \) is the unique positive solution of the equation
\[
\nabla \cdot (d_1 \nabla \tilde{u} - \alpha \tilde{u} \nabla m) + \tilde{m}(x) - \tilde{u} = 0 \quad \text{in } \Omega, \quad (d_1 \nabla \tilde{u} - \alpha \tilde{u} \nabla m) \cdot \nu = 0 \quad \text{on } \partial \Omega.
\]
By Lemma 3.2, both \( \tilde{u} \) and \( \tilde{m} \) are uniformly bounded on \( \bar{\Omega} \) independent of \( k \). By Lemma 5.2 in [7], we have
\[
\tilde{u}(x) < \| m \|_{L^\infty} \cdot e(\alpha/d_1) \| m \|_{L^\infty} \quad \text{for all } x \in \bar{\Omega}.
\]
This completes the proof.

Now we are ready to prove Theorem 1.4.

**Proof of Theorem 1.4.** By Theorem 1.1, the semi-trivial steady state solution \((0, \bar{m})\) is linearly unstable for all \( d_1, d_2, \alpha > 0 \), then by the monotone dynamical system theory(see [21, 22, 23, 36]), to show that \((\tilde{u}, 0)\) is globally asymptotically stable, it suffices to show that (6) has no co-existence steady state for all \( d_2 \) sufficiently large. Suppose this is not true, then there exist some \( d_1 > 0 \), a positive sequence \( d_2^{(k)} \) of \( d_2 \) with \( d_2^{(k)} \rightarrow \infty \), such that (6) has a positive coexistence steady state \((\tilde{U}_k, \tilde{V}_k)\).

By passing to a subsequences if necessary, we may assume that
\[
\lim_{k \rightarrow \infty} (\tilde{U}_k, \tilde{V}_k) = (\bar{U}_\infty, \bar{V}_\infty).
\]
Dividing the second equation of (35) by \( d_2^{(k)} \) and letting \( k \rightarrow \infty \), we conclude that the limiting function \( \bar{V}_\infty \) satisfies that
\[
\Delta \bar{V}_\infty = 0 \quad \text{in } \Omega, \quad \partial_\nu \bar{V}_\infty = 0 \quad \text{on } \partial \Omega.
\]
Thus \( \bar{V}_\infty \equiv C \) for some constant \( C \geq 0 \). Setting \( \bar{V}_k^* \equiv \frac{\bar{V}_k}{\| \bar{V}_k \|_{L^\infty(\Omega)}} \), then \( \bar{V}_k^* \) satisfies
\[
\Delta \bar{V}_k^* + \frac{\bar{m} - \bar{U}_k - \bar{V}_k}{d_2^{(k)}} \bar{V}_k^* = 0 \quad \text{in } \Omega, \quad \partial_\nu \bar{V}_k^* = 0 \quad \text{on } \partial \Omega.
\]
By similar arguments as before, \( \bar{V}_k^* \) converges to some non-negative constant \( \bar{V}_\infty^* \) as \( k \rightarrow \infty \). Since \( \| \bar{V}_k^* \|_{L^\infty(\Omega)} = 1 \), \( \bar{V}_\infty^* \equiv 1 \).

Integrating the second equation of (35) and then dividing by \( \| \bar{V}_k \|_{L^\infty(\Omega)} \), we have
\[
\int_{\Omega} \bar{V}_k^*(\bar{m} - \bar{U}_k - \bar{V}_k) = 0.
\]
Letting \( k \rightarrow \infty \), we obtain that
\[
\int_{\Omega} (\bar{m} - \bar{U}_\infty - C) = 0.
\]
Thus \( \int_{\Omega}(m - C) = \int_{\Omega}(m - C) = \int_{\Omega} \bar{U}_\infty \geq 0 \). By letting \( k \rightarrow \infty \) in the first equation of (35), we have
\[
\begin{align*}
\nabla \cdot (d_1 \nabla \bar{U}_\infty - \alpha \bar{U}_\infty \nabla m) + \bar{U}_\infty (m(x) - C - \bar{U}_\infty) = 0 & \quad \text{in } \Omega, \\
(d_1 \nabla \bar{U}_\infty - \alpha \bar{U}_\infty \nabla m) \cdot \nu = 0 & \quad \text{on } \partial \Omega.
\end{align*}
\]
Since \( m - C \) is nonconstant, and \( \alpha/d_1 \leq 1/\max_\Omega m \leq 1/\max_\Omega (m - C) \), it follows from (37) and Lemma 3.1 that \( \int_\Omega \tilde{U}_\infty > \int_\Omega (m - C) \), which is a contradiction to (36). This completes the proof of Theorem 1.4. 

Finally, we prove Theorem 1.5.

**Proof of Theorem 1.5.** It suffices to show that principal eigenvalue \( \mu_1 \) of the problem

\[
\begin{align*}
\begin{cases}
d_2 \Delta \psi + (m - \tilde{u}) \psi + \mu_1 \psi = 0 & \text{in } \Omega, \\
\frac{\partial \psi}{\partial n} = 0 & \text{on } \partial \Omega,
\end{cases}
\end{align*}
\]

(38)

is negative. Dividing (38) by \( \psi \), integrating in \( \Omega \), we obtain

\[
\int_\Omega (\tilde{u} - m) - d_2 \int_\Omega \frac{|\nabla \psi|^2}{\psi^2} = \int_\Omega \mu_1.
\]

(39)

Since \( \alpha/d_1 \geq 1/\max_\Omega m \), we have \( \int_\Omega (\tilde{u} - m) < 0 \) by Lemma 3.1, Then \( \mu_1 < 0 \) by (39).

The proof of the coexistence part is similar to that in the proof of Theorem 1.3 and is thus omitted.  

4. **Concluding remarks.** We study the dynamics of the Lotka-Volterra reaction-diffusion-advection model, in which the two competing species have equal total resources but different strategy of resource distribution. The two species adopt the dispersal strategy of a combination of random dispersal and biased movement upward along the resource gradient (moving to the location with better resource). In this paper, we mainly study the situation that one species, species \( V \), adopts the homogenous distribution, and its competitor, species \( U \), adopts heterogeneous distribution.

We are interest to know how the resource distribution, the random dispersal rate, and the advection rate affect the dynamics of the system. The species \( U \) with heterogeneous distribution is always in a better position than its competitor \( V \) with homogenous distribution (Theorem 1.1), that is, the semi-trivial steady state \((\tilde{u},0)\) is always unstable. Then the dynamics of (6) is mainly depending on the stability of the other semi-trivial steady state \((\tilde{u},0)\). It turns out that the ratio \( \alpha/d_1 \) plays a crucial role on the stability of \((\tilde{u},0)\). Our main results can be interpreted biologically in the following statements:

(i) The species \( U \) can always invade when rare the species \( V \) for any \( d_1, d_2 > 0 \), and \( \alpha \geq 0 \).

(ii) For \( \alpha/d_1 \leq 1/\max_\Omega m \) and \( d_2 < d_2^* \), the species \( V \) can invade when rare the species \( U \), and the two species will coexist.

(iii) For \( \alpha/d_1 \leq 1/\max_\Omega m \) and \( d_2 > d_2^* \), the species \( V \) can not invade when rare the species \( U \) near \((\tilde{u},0)\), and species \( U \) will drive \( V \) to extinction for any initial value if \( d_2 \) is sufficiently large.

In case (ii) and (iii), the species \( U \) has relatively weak advection, its competitor \( V \) can evolve if and only if by adopting slow diffusion strategy.

(iv) If \( m > 0 \) in \( \Omega \), and \( \alpha/d \geq 1/\min_\Omega m \), then the two species always coexist for any \( d_2 > 0 \). In this case, the species \( U \) has relatively strong advection, and then it left sufficient habitat for \( V \) evolving.

These results provide some new mechanisms for the dynamics of competition system (see, e.g., [6, 8, 16, 17, 18, 19, 20]). For \( \alpha/d_1 \) in the interval \((1/\max_\Omega m, 1/\min_\Omega m)\), the dynamics behavior of (6) is more complicated, and it is likely depend upon the the geometry of \( \Omega \) and the specific distribution of the resources.
The results about the dynamics of the general form of system (4) are known very limited. We hope to explore further in this direction in a future paper.

REFERENCES

[1] I. Averill, K.-Y. Lam and Y. Lou, The role of advection in a two-species competition model: A bifurcation approach, *Mem. Am. Math. Soc.*, 245 (2017), v+117 pp.
[2] F. Belgacem and C. Cosner, The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environment, *Canadian Appl. Math. Quarterly*, 3 (1995), 379–397.
[3] K. J. Brown and S. S. Lin, On the existence of positive eigenfunctions for an eigenvalue problem with indefinite weight function, *J. Math. Anal. Appl.*, 75 (1980), 112–120.
[4] R. S. Cantrell and C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*, Series in Mathematical and Computational Biology, John Wiley and Sons, Chichester, UK, 2003.
[5] R. S. Cantrell, C. Cosner and Y. Lou, Movement towards better environments and the evolution of rapid diffusion, *Math. Biosciences*, 204 (2006), 199–214.
[6] R. S. Cantrell, C. Cosner and Y. Lou, Advection mediated coexistence of competing species, *Proc. Roy. Soc. Edinb. Sect. A*, 137 (2007), 497–518.
[7] X. F. Chen, R. Hambrock and Y. Lou, Evolution of conditional dispersal: A reaction-diffusion-advection model, *J. Math. Biol.*, 57 (2008), 361–386.
[8] 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), 3841–3859.
[9] X. F. Chen and Y. Lou, Principal eigenvalue and eigenfunctions of an elliptic operator with large advection and its application to a competition model, *Indiana Univ. Math. J.*, 57 (2008), 627–658.
[10] X. F. Chen and Y. Lou, Effects of diffusion and advection on the smallest eigenvalue of an elliptic operator and their applications, *Indiana Univ. Math. J.*, 61 (2012), 45–80.
[11] C. Cosner and Y. Lou, Does movement toward better environments always benefit a population?, *J. Math. Anal. Appl.*, 277 (2003), 489–503.
[12] J. Dockery, V. Hutson, K. Mischaikow and M. Pernarowski, The evolution of slow dispersal rates: A reaction-diffusion model, *J. Math. Biol.*, 37 (1998), 61–83.
[13] D. Gilbarg and N. Trudinger, *Elliptic Partial Differential Equations of Second Order*, Springer-Verlag, Berlin, 1983.
[14] R. Hambrock and Y. Lou, The evolution of conditional dispersal strategy in spatially heterogeneous habitats, *Bull. Math. Biol.*, 71 (2009), 1793–1817.
[15] A. Hastings, Can spatial variation alone lead to selection for dispersal?, *Theor. Pop. Biol.*, 24 (1983), 244–251.
[16] X. Q. He and W.-M. Ni, The effects of diffusion and spatial variation in Lokta-Volterra competition-diffusion system, I: Heterogeneity vs. homogeneity, *J. Diff. Eqs.*, 254 (2013), 528–546.
[17] X. Q. He and W.-M. Ni, The effects of diffusion and spatial variation in Lokta-Volterra competition-diffusion system, II: The general case, *J. Diff. Eqs.*, 254 (2013), 4088–4108.
[18] X. Q. He and W.-M. Ni, Global dynamics of the Lokta-Volterra competition-diffusion system: Diffusion and spatial heterogeneity, I, *Comm. Pure Appl. Math.*, 69 (2016), 981–1014.
[19] X. Q. He and W.-M. Ni, Global dynamics of the Lotka-Volterra competition-diffusion system with equal amount of total resources, II, *Calc. Var. Partial Diff. Equ.*, 55 (2016), Art. 25, 20 pp.
[20] X. Q. He and W.-M. Ni, Global dynamics of the Lotka-Volterra competition-diffusion system with equal amount of total resources, III, *Calc. Var. Partial Diff. Equ.*, 56 (2017), Art. 13, 26 pp.
[21] P. Hess, *Periodic-parabolic Boundary Value Problems and Positivity*, Pitman Research Notes in Mathematics, Vol. 247, Longman, Harlow, UK, 1991.
[22] M. W. Hirsch, Stability and convergence in strongly monotone dynamical systems, *J. Reine Angew. Math.*, 383 (1988), 1–51.
[23] S. Hsu, H. Smith and P. Waltman, Competitive exclusion and coexistence for competitive systems on ordered Banach spaces, *Trans. Amer. Math. Soc.*, 348 (1996), 4083–4094.
[24] V. Hutson, Y. Lou and K. Mischaikow, Spatial heterogeneity of resources versus Lotka-Volterra dynamics, *J. Diff. Eqs.*, 185 (2002), 97–136.
[25] K.-Y. Lam, Concentration phenomena of a semilinear elliptic equation with large advection in an ecological model, *J. Differ. Equ.* 250 (2011), 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), 1808–1830.

[27] K.-Y. Lam and W.-M. Ni, Limiting profiles of semilinear elliptic equations with large advection in population dynamics, *Discrete Contin. Dyn. Syst. A*, 28 (2010), 1051–1067.

[28] K.-Y. Lam and W.-M. Ni, Uniqueness and complete dynamics in the heterogeneous competition-diffusion systems, *SIAM J. Appl. Math.*, 72 (2012), 1695–1712.

[29] K.-Y. Lam and W.-M. Ni, Advection-mediated competition in general environments, *J. Differ. Equ.*, 257 (2014), 3466–3500.

[30] Y. Lou, On the effects of migration and spatial heterogeneity on single and multiple species, *J. Diff. Eqs.*, 223 (2006), 400–426.

[31] Y. Lou, Some challenging mathematical problems in evolution of dispersal and population dynamics, in *Tutorials in Mathematical Biosciences IV, Lecture Notes in Math.*, 1922, Springer, Berlin, 2008, 171–205.

[32] Y. Lou and W. M. Ni, Diffusion, self-diffusion and cross-diffusion. *J. Diff. Equs.*, 131 (1996), 79–131.

[33] W.-M. Ni, *The Mathematics of Diffusion*, CBMS-NSF Regional Conf. Ser. in Appl. Math., Vol. 82, SIAM, Philadelphia, 2011.

[34] M. H. Protter and H. F. Weinberger, *Maximum Principles in Differential Equations*, 2nd Ed. Springer, Berlin, 1984.

[35] S. Senn and P. Hess, On positive solutions of a linear elliptic eigenvalue problem with Neumann boundary conditions. *Math. Ann.*, 258 (1982), 459–470.

[36] H. Smith, *Monotone Dynamical Systems, An Introduction to the Theory of Competitive and Cooperative Systems*, Math. Survey Monogr. 41, American Mathematical Society, Providence, RI, 1995.

Received September 2017; revised December 2017.

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