

## Persistence versus extinction for two competing species under a climate change\*

Zewei Zhang<sup>a,b</sup>, Wendi Wang<sup>a,1</sup>, Jiangtao Yang<sup>a</sup>

<sup>a</sup>Key Laboratory of Eco-environments in Three Gorges Reservoir Region,  
School of Mathematics and Statistics, Southwest University,  
Chongqing, 400715, China  
wendi@swu.edu.cn

<sup>b</sup>Department of Applied Mathematics,  
Xinjiang University of Finance and Economics,  
Urumqi 830012, China

**Received:** December 7, 2015 / **Revised:** September 15, 2016 / **Published online:** March 17, 2017

**Abstract.** This paper considers effects of a climate-induced range shift on outcomes of two competitive species, which is modeled by a reaction-diffusion system with the increasing growth rates of species along a shifting habitat gradient. Analytical conditions are established for the coexistence or competitive exclusion of two-competitors under the climate change, which present the control strategies to maintain the persistence of species.

**Keywords:** competition-diffusion system, climate change, persistence, spreading speed.

### 1 Introduction

In real ecological systems, issues of persistence of competing species and invasive spread of one species is fundamental. Ecologically, an understanding of spreading speeds of species can provide insights into invasion process [4, 22], for example, how quickly an introduced species can move into a novel landscape or how rapidly an extirpated species can recover to its previous range. Whether introduced purposely, accidentally or by natural means, the invasion of new species can have serious economic and ecological consequences.

There is an increasing acknowledgement that we are experiencing a period of rapid climate change. Meanwhile, an increasing appreciation that ecosystem responses to climate change are complex and widespread has promoted a focus on understanding and predicting biological impact [7, 9, 15, 18, 19, 26]. Whether populations and species will

---

\*This research was supported by National Science Found of China (11571284).

<sup>1</sup>Corresponding author.

persist at the local and global scale, respectively, depends on their abilities to endure future climate shifts. Thus, determining the rate of climate change that populations can cope with, therefore, is urgently needed.

Mathematical modeling is a powerful approach to understand the ecological effects of climate change. Early on, the issue of persistence in a changing landscape investigated by a number of papers [1, 3, 16, 23, 29] has primarily focused on the established species that exist at equilibrium distributions in a bounded domain prior to the onset of climate change. Few studies have considered the spread or invasion of an introduced species and how this might be impacted by shifts in habitat suitability. Recently, a number of studies have used analytical approaches to address the potential for the population persistence in asymmetric flow [8, 12–14, 25] or in the situation of changing climatic conditions, where the medium is static, but appropriate habitat is shifting [2, 5, 21, 32].

To explore the issue of species spread in the context of climate change, Li *et al.* [11] studied the spread of a single species over a region with varying habitat suitability, that is, shifting in time taking the form of

$$\frac{\partial u}{\partial t} = d \frac{\partial^2 u}{\partial x^2} + ur(x - ct) - u^2. \quad (1)$$

Here  $c > 0$  and  $r(\xi)$  is continuous and nondecreasing and bounded with  $r(-\infty) < 0$  and  $r(\infty) > 0$ . Thus,  $r(x - ct)$  divides the spatial domain into two parts: the region with the good-quality habitat suitable for growth (i.e.,  $r(x - ct) > 0$ ), and the region with the poor-quality habitat unsuitable for growth (i.e.,  $r(x - ct) < 0$ ). The edge of the habitat suitable for species is shifting at a speed  $c$ . Results in [11] have shown that the persistence and spreading dynamics of (1) depend on  $c$  and  $c^*(\infty)$ , that is, determined by the maximal linearized growth rate and the diffusion coefficient. More specifically, if  $c > c^*(\infty)$ , the species will become extinct in the habitat; if  $c < c^*(\infty)$ , then the species will persist and spread along the shifting habitat gradient at an asymptotic spreading speed  $c^*(\infty)$ . These results can be interpreted as whether a species is able to persist depend on its ability to outrun an encroaching boundary.

The purpose of the present paper is to extend the work in [11] to a two-competing species model. We will analyze the influence of climate change on the competition outcomes and characterize the spreading speeds of biological populations in response to both biological competitions and the shifting habitat under the climate change. We derive sufficient conditions for the coexistence of two species and show that there are switches in competitive dominance induced by different speeds of the shifting habitat edge. More precisely, if two species are initially restricted to and distributed over a band of suitable habitat, persistence then requires that the two species keep pace with the movement of its suitable habitat band. Indeed, we find that the interspecific competition slows the invasion speed of invasive species. Moreover, if the shifting of climate change moves slower than the minimum invasion rate of two species, coexistence of two species happens when the competition is weak; replacement happens when the shifting rate of climate change is medium; if the shifting rate of climate change is larger than the maximum invasion rate of two species, both species will go extinct.

The rest of this paper is organized as follows. In Section 2, we present our mathematical model and analyze its spatial dynamics. In Section 3, we provide a number of simulations to illustrate the results from Section 2. Section 4 gives a brief discussions.

## 2 Mathematical results

We consider the following competition model:

$$u_t = d_1 u_{xx} + u(r_1(x - ct) - u - a_1 v), \quad (2a)$$

$$v_t = d_2 v_{xx} + v(r_2(x - ct) - v - a_2 u) \quad (2b)$$

with the initial conditions  $u(0, x) = u_0(x)$ ,  $v(0, x) = v_0(x)$ . Here  $t \in \mathbb{R}_+$ ,  $-\infty < x < +\infty$ ;  $u := u(t, x)$ ,  $v := v(t, x)$  are the densities of two competing species respectively;  $d_1, d_2 > 0$  are their respective diffusion coefficients;  $a_1, a_2 > 0$  are interspecific competition coefficients;  $c > 0$  is a speed at which the edge of the habitat suitable for species growth is shifting. The per capita growth rates  $r_1(x - ct)$  and  $r_2(x - ct)$  satisfy the following standing hypothesis:

**Hypothesis 1.**  $r_i(x)$ ,  $i = 1, 2$ , are continuous, nondecreasing, and piecewise continuously differentiable for  $-\infty < x < \infty$  with  $0 < r_i(\infty) < \infty$  and  $-\infty < r_i(-\infty) < 0$ .

For  $0 \leq u_1, u_2 \leq r_1(\infty)$ ,  $0 \leq v_1, v_2 \leq r_2(\infty)$  with  $-\infty < x < \infty$  and  $t \geq 0$ , it is easy to examine

$$\begin{aligned} |u_1(r_1 - u_1 - a_1 v_1) - u_2(r_2 - u_2 - a_1 v_2)| &\leq \rho(|u_1 - u_2| + |v_1 - v_2|), \\ |v_1(r_2 - v_1 - a_2 u_1) - v_2(r_2 - v_2 - a_2 u_2)| &\leq \rho(|u_1 - u_2| + |v_1 - v_2|), \end{aligned}$$

where

$$\rho = \max\{3r_1(\infty) + a_1(r_1(\infty) + r_2(\infty)), 3r_2(\infty) + a_2(r_1(\infty) + r_2(\infty))\}.$$

Thus, the reaction terms in (2) are Lipschitz continuous in  $u, v$ . By adding dominant linear terms  $\rho u, \rho v$  to both sides of (2a) and (2b) respectively, model (2) can be written as

$$\begin{aligned} u_t + \rho u &= d_1 u_{xx} + u(\rho + r_1(x - ct) - u - a_1 v), \\ v_t + \rho v &= d_2 v_{xx} + v(\rho + r_2(x - ct) - v - a_2 u). \end{aligned}$$

Then  $u(\rho + r_1(x - ct) - u - a_1 v)$  is nondecreasing in  $u$  for  $0 \leq u \leq r_1(\infty)$  and  $v(\rho + r_2(x - ct) - v - a_2 u)$  is nondecreasing in  $v$  for  $0 \leq v \leq r_2(\infty)$ . It is clear that  $(0, 0)$  and  $(r_1(\infty), r_2(\infty))$  are a pair of lower and upper solutions of (2). It follows from [17, 20, 24, 27, 31] that the initial problem of (2) with  $(u(0, x), v(0, x)) = (u_0(x), v_0(x))$ , where  $u_0(x), v_0(x)$  are continuous and  $0 \leq u_0(x) \leq r_1(\infty)$ ,  $0 \leq v_0(x) \leq r_2(\infty)$  has a unique classical solution, which satisfies  $0 \leq u(t, x) \leq r_1(\infty)$ ,  $0 \leq v(t, x) \leq r_2(\infty)$ . We will consider only these solutions in what follows.

It is easily seen that a solution  $(u(t, x), v(t, x))$  of (2) takes the form of

$$\begin{aligned}
 u(t, x) &= \int_{-\infty}^{+\infty} k_1(t, x - y)u_0(y) \, dy \\
 &\quad + \int_0^t \int_{-\infty}^{+\infty} k_1(t - \tau, x - y)u(\tau, y) \\
 &\quad \quad \times [\rho + r_1(y - c\tau) - u(\tau, y) - a_1v(\tau, y)] \, dy \, d\tau, \\
 v(t, x) &= \int_{-\infty}^{+\infty} k_2(t, x - y)v_0(y) \, dy \\
 &\quad + \int_0^t \int_{-\infty}^{+\infty} k_2(t - \tau, x - y)v(\tau, y) \\
 &\quad \quad \times [\rho + r_2(y - c\tau) - v(\tau, y) - a_2u(\tau, y)] \, dy \, d\tau,
 \end{aligned}$$

where

$$k_1(s, y) = \frac{e^{-\rho s - y^2/(4\pi d_1 s)}}{\sqrt{4\pi d_1 s}}, \quad k_2(s, y) = \frac{e^{-\rho s - y^2/(4\pi d_2 s)}}{\sqrt{4\pi d_2 s}}.$$

To motivate our main results, we consider the homogeneous nonspatial case of system (2):

$$u_t = u(r_1(\infty) - u - a_1v), \quad v_t = v(r_2(\infty) - v - a_2u). \tag{3}$$

There are four constant equilibria: the unpopulated state  $(0, 0)$ ; the first-species monoculture state  $(r_1(\infty), 0)$ ; the second-species monoculture state  $(0, r_2(\infty))$ ; and the coexistence state  $(u^*, v^*)$ , where

$$u^* = \frac{r_1(\infty) - a_1r_2(\infty)}{1 - a_1a_2}, \quad v^* = \frac{r_2(\infty) - a_2r_1(\infty)}{1 - a_1a_2}. \tag{4}$$

We summarize the well-known facts for the existence and stability of the equilibria in the following:

1.  $(0, 0)$  always exists and is unstable.
2.  $(r_1(\infty), 0)$  always exists, and is stable if  $r_2(\infty) < a_2r_1(\infty)$ .
3.  $(0, r_2(\infty))$  always exists, and is stable if  $r_1(\infty) < a_1r_2(\infty)$ .
4.  $(u^*, v^*)$  exists if and only if  $[r_1(\infty) - a_1r_2(\infty)][r_2(\infty) - a_2r_1(\infty)] > 0$ .

In this paper, we are particularly interested in the weak competition case. Thus, the coexistence equilibrium  $(u^*, v^*)$  emerges and is stable if

$$0 < a_1a_2 < 1, \quad 0 < a_1 < \frac{r_1(\infty)}{r_2(\infty)}, \quad 0 < a_2 < \frac{r_2(\infty)}{r_1(\infty)}. \tag{5}$$

Furthermore, the coexistence state  $(u^*, v^*)$  disappears if

$$0 < a_1 a_2 < 1, \quad 0 < a_1 < \frac{r_1(\infty)}{r_2(\infty)}, \quad a_2 > \frac{r_2(\infty)}{r_1(\infty)}. \quad (6)$$

If  $v$  is the resident species and  $u$  is the invasive species, then (6) implies that the resident species is excluded by the invasive species because positive solutions of (3) tend to  $(r_1(\infty), 0)$  as  $t$  approaches  $\infty$ . From (4), it is also easy to see that  $(u^*, v^*) \rightarrow (0, r_2(\infty))$  if  $a_1 \rightarrow r_1(\infty)/r_2(\infty)$  and  $(u^*, v^*) \rightarrow (r_1(\infty), 0)$  if  $a_2 \rightarrow r_2(\infty)/r_1(\infty)$  under the condition that  $0 < a_1 a_2 < 1$ .

We now study how the outcomes of competing species  $u$  and  $v$  are affected by the climate changes. For  $r_i(x) - a_i r_j(\infty) > 0, i \neq j, i, j = 1, 2$ , we define

$$c_i^*(x) = 2\sqrt{d_i(r_i(x) - a_i r_j(\infty))}.$$

It is easily seen that

$$c_i^*(x) = \inf_{\mu > 0} \phi_i(x; \mu),$$

where

$$\phi_i(x; \mu) = \frac{d_i \mu^2 + r_i(x) - a_i r_j(\infty)}{\mu}.$$

The infimum occurs at  $\mu_i^*(x) = \sqrt{(r_i(x) - a_i r_j(\infty))/d_i}$ . We also define

$$\psi_i(\mu) = 2d_i \mu.$$

It is easily seen that  $\phi_i(x; \mu) > \psi_i(\mu)$  for  $0 < \mu < \mu_i^*(x)$  and  $\phi_i(x; \mu_i^*(x)) = \psi_i(\mu_i^*(x)) = c_i^*(x)$ .

The main results of this paper are stated in the following theorem.

**Theorem 1.** *Suppose that Hypothesis 1 is satisfied. Assume  $d_1 r_1(\infty) < d_2 r_2(\infty)$ . Then the following statements are valid:*

- (a) *Let  $c \in (0, c_1^*(\infty))$ . If  $0 < u(0, x) < u^*, v^* < v(0, x) \leq r_2(\infty)$  on a closed interval, and  $u(0, x) = v(0, x) \equiv 0$  for all sufficiently large  $x$ , we have*

- (i) *If (5) holds, then for  $0 < \varepsilon < (c_1^*(\infty) - c)/2$ ,*

$$\lim_{t \rightarrow \infty} \left[ \sup_{t(c+\varepsilon) \leq x \leq t(c_1^*(\infty) - \varepsilon)} \{|u^* - u(t, x)| + |v^* - v(t, x)|\} \right] = 0.$$

- (ii) *If (6) holds, then for  $0 < \varepsilon < (c_1^*(\infty) - c)/2$ ,*

$$\lim_{t \rightarrow \infty} \left[ \sup_{t(c+\varepsilon) \leq x \leq t(c_1^*(\infty) - \varepsilon)} \{|r_1(\infty) - u(t, x)| + |v(t, x)|\} \right] = 0.$$

- (b) Let  $c \in (2\sqrt{d_1 r_1(\infty)}, 2\sqrt{d_2 r_2(\infty)})$ . If  $0 \leq u(0, x) \leq r_1(\infty)$ ,  $0 \leq v(0, x) \leq r_2(\infty)$ ,  $u(0, x), v(0, x)$  are zero for all sufficiently large  $x$ ,  $v(0, x) > 0$  for other values of  $x$ , then for every  $\varepsilon > 0$ , there exists  $T > 0$  such that the solution  $(u(t, x), v(t, x))$  of (2) satisfies

$$u(t, x) \leq \varepsilon \quad \text{for } t \geq T, x \in (-\infty, \infty), \tag{7}$$

$$\lim_{t \rightarrow \infty} \left[ \sup_{(c+\varepsilon)t \leq x \leq (2\sqrt{d_2 r_2(\infty)} - \varepsilon)t} |r_2(\infty) - v(t, x)| \right] = 0. \tag{8}$$

- (c) Let  $c > 2\sqrt{d_2 r_2(\infty)}$ . If  $0 \leq u(0, x) \leq r_1(\infty)$ ,  $0 \leq v(0, x) \leq r_2(\infty)$ , and  $u(0, x) = v(0, x) \equiv 0$  for all sufficiently large  $x$ , then for every  $\varepsilon > 0$ , there exists  $T > 0$  such that for  $t > T$ , the solution  $(u(t, x), v(t, x))$  of (2) satisfy  $u(t, x) < \varepsilon$  and  $v(t, x) < \varepsilon$  for all  $x$ .

Before the proof of Theorem 1, we present a few preliminaries. The first one is an auxiliary function proposed by Weinberger [28]. For  $\gamma > 0$  and  $\mu > 0$ , we define

$$w(\mu; x) = \begin{cases} e^{-\mu x} \sin \gamma x & \text{if } 0 \leq x \leq \frac{\pi}{\gamma}, \\ 0 & \text{elsewhere.} \end{cases} \tag{9}$$

Clearly,  $w(\mu; x)$  is a continuous function in  $x$ , and its second-order derivative in  $x$  exists and is continuous when  $x \neq 0, \pi/\gamma$ . The maximum of  $w(\mu; x)$  occurs at  $\sigma(\mu) = (1/\gamma) \tan^{-1}(\gamma/\mu)$ , which is a strictly decreasing function of  $\mu$ .

Secondly, we need to derive certain properties for a lower solution. Let  $(u(t, x), v(t, x))$  be a solution of (2) with  $(u(0, x), v(0, x)) = (u_0(x), v_0(x))$  that satisfies  $0 \leq u_0(x) \leq r_1(\infty)$  and  $0 \leq v_0(x) \leq r_2(\infty)$ . We denote by  $\underline{u}(t, x)$  the solution of

$$\underline{u}_t = d_1 \underline{u}_{xx} + \underline{u}(r_1(x - ct) - \underline{u} - a_1 r_2(\infty)) \tag{10}$$

with  $\underline{u}(0, x) = u_0(x)$ . Since  $0 \leq v(t, x) \leq r_2(\infty)$ , which implies  $u(r_1(x - ct) - u - a_1 v) \geq u(r_1(x - ct) - u - a_1 r_2(\infty))$ , it follows that  $\underline{u}(t, x)$  satisfies

$$u(t, x) \geq \underline{u}(t, x) \quad \text{for all } (t, x) \in [0, \infty) \times \mathbb{R}.$$

Similar to [11], we have the following useful lemma for (10).

**Lemma 1.** Assume that  $0 \leq c < c_1^*(\infty) = 2\sqrt{d_1(r_1(\infty) - a_1 r_2(\infty))}$ . For any  $\epsilon$  satisfying  $0 < \epsilon < (c_1^*(\infty) - c)/3$ , let  $l$  be a positive number such that  $c_1^*(l) = c_1^*(\infty) - \epsilon$ . Select  $0 < \mu_1 < \mu_2 < \mu_1^*(l)$  with  $\psi_1(\mu_1) = c + \epsilon$  and  $\psi_1(\mu_2) = c_1^*(\infty) - 2\epsilon$ . Then for any  $\mu \in [\mu_1, \mu_2]$ , there exist  $a > 0$  and  $\gamma > 0$  sufficiently small such that  $aw(\mu; x - l - \psi_1(\mu)t)$  with  $w$  given by (9) is a continuous weak lower solution of (10) in the distributional sense, i.e., for any  $T > 0$  and any  $\eta \in C^{2,1}((-\infty, \infty) \times [0, T])$  with  $\eta \geq 0$  and  $\text{supp } \eta(\cdot, t)$  being a bounded interval for all  $t \in [0, T]$ ,

$$\int_{-\infty}^{\infty} \tilde{u}(\mu; t, x) \eta(t, x) dx \Big|_{t=0}^{t=T_1} \leq \int_0^{T_1} \int_{-\infty}^{\infty} [\tilde{u}(\mu; s, x)(d\eta_{xx} + \eta_t)(s, x) + \eta(s, x) \tilde{u}(\mu; s, x) \times (r_1(x - cs) - \tilde{u}(\mu; s, x) - a_1 r_2(\infty))] dx ds,$$

where  $\tilde{u}(\mu; t, x) = aw(\mu; x - l - \psi_1(\mu)t)$  and  $T_1 \in [0, T]$ . Furthermore, if  $\underline{u}(0, x) \geq aw(\mu; x - l)$ , then  $\underline{u}(t, x) \geq aw(\mu; x - l - \psi_1(\mu)t)$  for all  $t > 0, x \in \mathbb{R}$ .

We are now able to present the proof of Theorem 1.

*Proof of Theorem 1.* Note that  $c_1^*(\infty)$  is well defined when either (5) or (6) holds. If  $c \in (0, c_1^*(\infty))$ , we choose a small constant  $\epsilon$  with  $0 < \epsilon < \min\{(c_1^*(\infty) - c)/3, r_1(\infty)/3\}$  so that Lemma 1 applies. Then we select  $\mu \in [\mu_1, \mu_2]$  and small  $\alpha > 0$  and  $\gamma > 0$  such that  $\alpha w(\mu; x - l - \psi_1(\mu)t)/w(\mu; \sigma(\mu))$  with  $w$  given by (9) is a continuous weak lower solution of (10).

Let  $\underline{u}(t, x) > 0$  be a solution of (10) with  $\underline{u}(0, x) = u(0, x)$ . Since  $u(0, x) \geq 0$  and  $u(0, x) \not\equiv 0$ , it follows from the maximal principle that  $\underline{u}(t, x) > 0$  for all  $x$  and any  $t > 0$ . Choose  $0 < t_0 < \sigma(\mu_1)/\psi_1(\mu_1)$ , and choose  $\alpha$  and  $\gamma$  sufficiently small such that  $\underline{u}(t_0, x) \geq \alpha$  for  $x \in [l, l + 4\pi/\gamma]$ . Set

$$z(0, x) = \begin{cases} \frac{\alpha w(\mu_1; x-l)}{w(\mu_1; \sigma(\mu_1))}, & l \leq x \leq l + \sigma(\mu_1), \\ \alpha, & l + \sigma(\mu_1) \leq x \leq l + \frac{3\pi}{\gamma} + \sigma(\mu_2), \\ \frac{\alpha w(\mu_2; x-l-\frac{3\pi}{\gamma})}{w(\mu_2; \sigma(\mu))}, & l + \frac{3\pi}{\gamma} + \sigma(\mu_2) \leq x \leq l + \frac{4\pi}{\gamma}, \\ 0 & \text{elsewhere.} \end{cases}$$

It is easily seen that for  $0 \leq s \leq 2\pi/\gamma$ ,

$$z(0, x) \geq \frac{\alpha w(\mu_1; x - l - s)}{w(\mu_1; \sigma(\mu_1))},$$

and

$$z(0, x) \geq \frac{\alpha w(\mu_2; x - l - \frac{3\pi}{\gamma} + s)}{w(\mu_2; \sigma(\mu))}.$$

Since  $\underline{u}(t_0, x) \geq \alpha$  for  $x \in [l, l + 4\pi/\gamma]$ , Lemma 1 implies that for  $t \geq t_0$  and  $0 \leq s \leq 2\pi/\gamma$ ,

$$\underline{u}(t, x) \geq \frac{\alpha w(\mu_1; x - l - \psi_1(\mu_1)(t - t_0) - s)}{w(\mu_1; \sigma(\mu_1))}, \tag{11}$$

and

$$\underline{u}(t, x) \geq \frac{\alpha w(\mu_2; x - l - \frac{3\pi}{\gamma} - \psi_1(\mu_2) + s)}{w(\mu_2; \sigma(\mu))}. \tag{12}$$

It follows from (11) that for  $t \geq t_0$ ,

$$\underline{u}(t, x) \geq \begin{cases} \frac{\alpha w(\mu; x-l-\psi_1(\mu_1)(t-t_0))}{w(\mu_1; \sigma(\mu_1))}, & x \geq l + \psi_1(\mu_1)(t - t_0), \\ & x \leq l + \psi_1(\mu_1)(t - t_0) + \sigma(\mu_1); \\ \alpha, & x \geq l + \psi_1(\mu_1)(t - t_0) + \sigma(\mu_1), \\ & x \leq l + \frac{2\pi}{\gamma} + \psi_1(\mu_1)(t - t_0) + \sigma(\mu_1); \\ 0 & \text{elsewhere.} \end{cases} \tag{13}$$

On the other hand, (12) indicates that for  $t \geq t_0$ ,

$$\underline{u}(t, x) \geq \begin{cases} \alpha, & x \geq l + \frac{\pi}{\gamma} + \psi_1(\mu_2)(t - t_0) + \sigma(\mu_2), \\ & x \leq l + \frac{3\pi}{\gamma} + \psi_1(\mu_2)(t - t_0) + \sigma(\mu_2); \\ \frac{\alpha w(\mu_2; x - l - \frac{3\pi}{\gamma} - \psi_1(\mu_2)(t - t_0))}{w(\mu_2; \sigma(\mu_2))}, & x \geq l + \frac{3\pi}{\gamma} + \psi_1(\mu_2)(t - t_0) + \sigma(\mu_2), \\ & x \leq l + \frac{4\pi}{\gamma} + \psi_1(\mu_2)(t - t_0); \\ 0 & \text{elsewhere.} \end{cases} \quad (14)$$

Let

$$h = \frac{\frac{\pi}{\gamma} + \sigma(\mu_1) - \sigma(\mu_2)}{\psi_1(\mu_2) - \psi_1(\mu_1)}.$$

Note that

$$l + \frac{2\pi}{\gamma} + \psi_1(\mu_1)(t - t_0) + \sigma(\mu_1) \geq l + \frac{\pi}{\gamma} + \psi_1(\mu_2)(t - t_0) + \sigma(\mu_2)$$

for  $t_0 \leq t \leq t_0 + h$ . It follows from (13) and (14) that for  $t_0 \leq t \leq t_0 + h$ , we have

$$\underline{u}(t, x) \geq z(t - t_0, x), \quad (15)$$

where

$$z(t - t_0, x) = \begin{cases} \frac{\alpha w(\mu; x - l - \psi_1(\mu_1)(t - t_0))}{w(\mu_1; \sigma(\mu_1))}, & x \geq l + \psi_1(\mu_1)(t - t_0), \\ & x \leq l + \psi_1(\mu_1)(t - t_0) + \sigma(\mu_1); \\ \alpha, & x \geq l + \psi_1(\mu_1)(t - t_0) + \sigma(\mu_1) \\ & x \leq l + \frac{3\pi}{\gamma} + \psi_1(\mu_2)(t - t_0) + \sigma(\mu_2); \\ \frac{\alpha w(\mu_2; x - l - \frac{3\pi}{\gamma} - \psi_1(\mu_2)(t - t_0))}{w(\mu_2; \sigma(\mu_2))}, & x \geq l + \frac{3\pi}{\gamma} + \psi_1(\mu_2)(t - t_0) + \sigma(\mu_2), \\ & x \leq l + \frac{4\pi}{\gamma} + \psi_1(\mu_2)(t - t_0); \\ 0 & \text{elsewhere.} \end{cases} \quad (16)$$

By similar arguments to those in [11], we see that (15) is valid for all  $t \geq t_0$ .

For the chosen  $\epsilon > 0$ , we select  $L > 0$  large enough such that

$$\int_{-L}^L \frac{1}{\sqrt{\pi}} e^{-x^2} dx \geq 1 - \epsilon.$$

Note that for any  $s > 0$ ,

$$\int_{-L\sqrt{4ds}}^{L\sqrt{4ds}} \frac{1}{\sqrt{4\pi ds}} e^{-x^2/(4ds)} dx = \int_{-L}^L \frac{1}{\sqrt{\pi}} e^{-\xi^2} d\xi.$$



Let  $t_1 > t_0$  be a sufficiently large number. For  $t > t_1$ , the solution  $(u(t, x), v(t, x))$  satisfies the integral equations

$$\begin{aligned} u(t, x) = & \int_{-\infty}^{+\infty} k_1(t - t_1, x - y)u(t_1, y) \, dy \\ & + \int_{t_1}^t \int_{-\infty}^{+\infty} k_1(t - \tau, x - y)u(\tau, y) \\ & \times [\rho + r_1(y - c\tau) - u(\tau, y) - a_1v(\tau, y)] \, dy \, d\tau, \end{aligned} \quad (17)$$

$$\begin{aligned} v(t, x) = & \int_{-\infty}^{+\infty} k_2(t - t_1, x - y)v(t_1, y) \, dy \\ & + \int_{t_1}^t \int_{-\infty}^{+\infty} k_2(t - \tau, x - y)v(\tau, y) \\ & \times [\rho + r_2(y - c\tau) - v(\tau, y) - a_2u(\tau, y)] \, dy \, d\tau. \end{aligned} \quad (18)$$

Since  $u(t, x) \geq \underline{u}(t, x)$  for all  $t \geq 0$  and all  $x$ , it follows from (17) and (15) that for  $t > t_1$ ,

$$\begin{aligned} u(t, x) \geq & \int_{-\infty}^{+\infty} k_1(t - t_1, x - y)z(t_1 - t_0, y) \, dy \\ & + \int_{t_1}^t \int_{-\infty}^{+\infty} k_1(t - \tau, x - y)z(\tau - t_0, y) \\ & \times [\rho + r_1(y - c\tau) - z(\tau - t_0, y) - a_1v(\tau, y)] \, dy \, d\tau. \end{aligned}$$

For  $t > t_1$ ,  $x$  satisfying

$$\begin{aligned} l + \sigma(\mu_1) + \psi_1(\mu_1)(t - t_0) + L\sqrt{4d_1(t - t_1)} \\ \leq x \leq l + \frac{3\pi}{\gamma} + \sigma(\mu_2) + \psi_1(\mu_2)(t - t_0) - L\sqrt{4d_1(t - t_1)}, \end{aligned} \quad (19)$$

and  $y$  satisfying

$$-L\sqrt{4d_1(t - t_1)} \leq y \leq L\sqrt{4d_1(t - t_1)},$$

we have

$$l + \sigma(\mu_1) + \psi_1(\mu_1)(t - t_0) \leq x - y \leq l + \frac{3\pi}{\gamma} + \sigma(\mu_2) + \psi_1(\mu_2)(t - t_0),$$

and

$$x - y - ct \geq l + \sigma(\mu_1) + \psi_1(\mu_1)(t - t_0) - ct = l + \epsilon t + \sigma(\mu_1) - \psi_1(\mu_1)t_0 > l.$$

This, together with (16), implies that for  $x$  satisfying (19),

$$\begin{aligned}
 & \int_{-\infty}^{+\infty} k_1(t-t_1, x-y)z(t_1-t_0, y) \, dy \\
 &= \int_{-\infty}^{+\infty} k_1(t-t_1, y)z(t_1-t_0, x-y) \, dy \\
 &\geq e^{-\rho(t-t_1)} \int_{-L\sqrt{4d_1(t-t_1)}}^{L\sqrt{4d_1(t-t_1)}} \frac{e^{-y^2/(4d_1(t-t_1))}}{\sqrt{4\pi d_1(t-t_1)}} z(t_1-t_0, x-y) \, dy \\
 &\geq \alpha e^{-\rho(t-t_1)} \int_{-L\sqrt{4d_1(t-t_1)}}^{L\sqrt{4d_1(t-t_1)}} \frac{e^{-y^2/(4d_1(t-t_1))}}{\sqrt{4\pi d_1(t-t_1)}} \, dy \\
 &\geq (1-\epsilon)\alpha e^{-\rho(t-t_1)}, \tag{20}
 \end{aligned}$$

and

$$\begin{aligned}
 & \int_{t_1}^t \int_{-\infty}^{+\infty} k_1(t-\tau, x-y)z(\tau-t_0, y) [\rho + r_1(y-c\tau) - z(\tau-t_0, y) - a_1v(\tau, y)] \, dy \, d\tau \\
 &\geq (1-\epsilon)\alpha \int_{t_1}^t e^{-\rho(t-\tau)} [\rho + r_1(\infty) - \epsilon - \alpha - a_1r_2(\infty)] \, d\tau. \tag{21}
 \end{aligned}$$

It follows from (18) that for  $x$  satisfying (19),

$$\begin{aligned}
 & \int_{t_1}^t \int_{-\infty}^{+\infty} k_2(t-\tau, x-y)v(\tau, y) [\rho + r_2(y-c\tau) - v(\tau, y) - a_2u(\tau, y)] \, dy \, d\tau \\
 &\leq r_2(\infty) \int_{t_1}^t e^{-\rho(t-\tau)} [\rho - a_2\alpha] \, d\tau, \tag{22}
 \end{aligned}$$

and

$$\int_{-\infty}^{+\infty} k_2(t-t_1, x-y)v(t_1, y) \, dy \leq r_2(\infty)e^{-\rho(t-t_1)}. \tag{23}$$

Here we use the simple fact that

$$\int_{-\infty}^{+\infty} k_2(t, y) \, dy = e^{-\rho t}.$$

It follows from (20), (21) and (22), (23) that for  $t \geq t_1$  and  $x$  satisfying (19),

$$u(t, x) \geq \tilde{u}^{(1)}(t), \quad v(t, x) \leq \tilde{v}^{(1)}(t),$$

where

$$\begin{aligned} \tilde{u}^{(1)}(t) &= (1 - \epsilon)\alpha e^{-\rho(t-t_1)} \\ &\quad + (1 - \epsilon)\alpha \int_{t_1}^t e^{-\rho(t-\tau)} [\rho + r_1(\infty) - \epsilon - \alpha - a_1 r_2(\infty)] d\tau, \\ \tilde{v}^{(1)}(t) &= r_2(\infty)e^{-\rho(t-t_1)} + r_2(\infty) \int_{t_1}^t e^{-\rho(t-\tau)} [\rho - a_2\alpha] d\tau. \end{aligned}$$

Equations (17) and (18) and induction arguments show that for  $t \geq t_1$  and  $x$  satisfying

$$\begin{aligned} l + \sigma(\mu_1) + \psi_1(\mu_1)(t - t_0) + nL\sqrt{4d_1(t - t_1)} \\ \leq x \leq l + \frac{3\pi}{\gamma} + \sigma(\mu_2) + \psi_1(\mu_2)(t - t_0) - nL\sqrt{4d_1(t - t_1)}, \end{aligned} \quad (24)$$

we have

$$u(t, x) \geq \tilde{u}^{(n)}(t), \quad v(t, x) \leq \tilde{v}^{(n)}(t), \quad (25)$$

where  $\tilde{u}^{(n)}(t)$  and  $\tilde{v}^{(n)}(t)$  satisfy

$$\begin{aligned} \tilde{u}^{(n)}(t) &= (1 - \epsilon)\alpha e^{-\rho(t-t_1)} + (1 - \epsilon) \\ &\quad \times \int_{t_1}^t e^{-\rho(t-\tau)} \tilde{u}^{(n-1)}(\tau) [\rho + r_1(\infty) - \epsilon - \tilde{u}^{(n-1)}(\tau) - a_1 \tilde{v}^{(n-1)}(\tau)] d\tau, \\ \tilde{v}^{(n)}(t) &= r_2(\infty)e^{-\rho(t-t_1)} \\ &\quad + \int_{t_1}^t e^{-\rho(t-\tau)} \tilde{v}^{(n-1)}(\tau) [\rho + r_2(\infty) - \tilde{v}^{(n-1)}(\tau) - a_2 \tilde{u}^{(n-1)}(\tau)] d\tau. \end{aligned}$$

Direct calculations and induction show that

$$\tilde{u}^{(n)}(t) = f_n + b_n(t)e^{-\rho(t-t_1)}, \quad \tilde{v}^{(n)}(t) = g_n + e_n(t)e^{-\rho(t-t_1)}, \quad (26)$$

where

$$\begin{aligned} f_n &= \frac{(1 - \epsilon)f_{n-1}(\rho + r_1(\infty) - \epsilon - f_{n-1} - a_1 g_{n-1})}{\rho}, \\ f_1 &= \frac{(1 - \epsilon)\alpha(\rho + r_1(\infty) - \epsilon - \alpha - a_1 r_2(\infty))}{\rho}, \\ g_n &= \frac{g_{n-1}(\rho + r_2(\infty) - g_{n-1} - a_2 f_{n-1})}{\rho}, \\ g_1 &= \frac{r_2(\infty)(\rho - a_2\alpha)}{\rho}. \end{aligned} \quad (27)$$

Furthermore,  $b_n(t)$  and  $e_n(t)$  in (26) are the sums of polynomials, and products of polynomials and exponential functions in the form of  $e^{-j(t-t_1)}$  with  $j$  a positive integer. Observe that  $\lim_{t \rightarrow \infty} \tilde{u}^{(n)}(t) = f_n$  and  $\lim_{t \rightarrow \infty} \tilde{v}^{(n)}(t) = g_n$ . Since  $f_n$  is increasing and  $g_n$  is decreasing, it is easy to see that the limits of  $f_n$  and  $g_n$  as  $n \rightarrow \infty$  exist. Taking the limits to both sides of the first equation and third equation of (27) and setting  $\lim_{n \rightarrow \infty} f_n = f^*$ ,  $\lim_{n \rightarrow \infty} g_n = g^*$ , we get

$$\begin{aligned} f^* &= \frac{(1 - \epsilon)f^*(\rho + r_1(\infty) - \epsilon - f^* - a_1g^*)}{\rho}, \\ g^* &= \frac{g^*(\rho + r_2(\infty) - g^* - a_2f^*)}{\rho}. \end{aligned} \tag{28}$$

If (5) holds, since  $\epsilon$  is sufficiently small, from (28) we get

$$\begin{aligned} f_n &\rightarrow \frac{r_1(\infty) - a_1r_2(\infty) - \epsilon - \frac{\epsilon\rho}{1-\epsilon}}{1 - a_1a_2}, \\ g_n &\rightarrow \frac{r_2(\infty) - a_2r_1(\infty) + a_2\epsilon + \frac{a_2\epsilon\rho}{1-\epsilon}}{1 - a_1a_2} \end{aligned}$$

as  $n \rightarrow \infty$ . If (6) holds, we have  $r_2(\infty) - a_2r_1(\infty) < 0$ . Note that the limit of  $g_n$  can not be negative due to the positivity of the solution  $(u(t, x), v(t, x))$  for  $t > 0$  and that  $\epsilon > 0$  is sufficiently small. It follows from (28) that

$$f_n \rightarrow \frac{r_1(\infty) - (1 + \rho)\epsilon}{1 - \epsilon}, \quad g_n \rightarrow 0$$

as  $n \rightarrow \infty$ . These and (26) indicate that there exist a positive integer  $N$  and  $t_2 > t_1$  such that for  $t > t_2$  and  $x$  satisfying (24) with  $n$  replaced by  $N$ , either

$$\begin{aligned} \tilde{u}^{(N)}(t) &\geq \frac{r_1(\infty) - a_1r_2(\infty) - \epsilon - \frac{\epsilon\rho}{1-\epsilon}}{1 - a_1a_2}, \\ \tilde{v}^{(N)}(t) &\leq \frac{r_2(\infty) - a_2r_1(\infty) + a_2\epsilon + \frac{a_2\epsilon\rho}{1-\epsilon}}{1 - a_1a_2} \end{aligned}$$

if (5) holds, or

$$\tilde{u}^{(N)}(t) \geq \frac{r_1(\infty) - (1 + \rho)\epsilon}{1 - \epsilon}, \quad \tilde{v}^{(N)}(t) \leq 0$$

if (6) holds. We choose  $t_1$  sufficiently large such that for  $t \geq t_1$ ,

$$\begin{aligned} &l + \sigma(\mu_1) + \psi_1(\mu_1)(t - t_0) + NL\sqrt{4d_1(t - t_1)} \\ &\leq x \leq l + \frac{3\pi}{\gamma} + \sigma(\mu_2) + \psi_1(\mu_2)(t - t_0) - NL\sqrt{4d_1(t - t_1)}. \end{aligned} \tag{29}$$

For any given  $\varepsilon$  with  $0 < \varepsilon < (c_1^*(\infty) - c)/2$ , we choose  $\epsilon$  sufficiently small such that  $\epsilon < \varepsilon/2$ . Since  $\psi_1(\mu_1) = c + \epsilon$  and  $\psi_1(\mu_2) = c_1^*(\infty) - 2\epsilon$ , there exists  $t_3 > t_2$  such that

for  $t > t_3$ ,  $t(c + \varepsilon) \leq x \leq t(c_1^*(\infty) - \varepsilon)$  is a subset of interval defined by (29). It follows from (25) and (26) that either

$$\begin{aligned} \lim_{t \rightarrow \infty} \left[ \inf_{t(c+\varepsilon) \leq x \leq t(c_1^*(\infty) - \varepsilon)} u(t, x) \right] &\geq \frac{r_1(\infty) - a_1 r_2(\infty) - \epsilon - \epsilon \rho / (1 - \epsilon)}{1 - a_1 a_2}, \\ \lim_{t \rightarrow \infty} \left[ \sup_{t(c+\varepsilon) \leq x \leq t(c_1^*(\infty) - \varepsilon)} v(t, x) \right] &\leq \frac{r_2(\infty) - a_2 r_1(\infty) + a_2 \epsilon + \frac{a_2 \epsilon \rho}{1 - \epsilon}}{1 - a_1 a_2} \end{aligned} \tag{30}$$

if (5) holds, or

$$\begin{aligned} \lim_{t \rightarrow \infty} \left[ \inf_{t(c+\varepsilon) \leq x \leq t(c_1^*(\infty) - \varepsilon)} u(t, x) \right] &\geq \frac{r_1(\infty) - (1 + \rho)\epsilon}{1 - \epsilon}, \\ \lim_{t \rightarrow \infty} \left[ \sup_{t(c+\varepsilon) \leq x \leq t(c_1^*(\infty) - \varepsilon)} v(t, x) \right] &\leq 0 \end{aligned} \tag{31}$$

if (6) holds. Since  $\epsilon$  is arbitrarily small, (30) and (31) show that statement (a) holds.

Let  $\bar{u}(t, x)$  with  $\bar{u}(0, x) = r_1(\infty)$  be the solution of

$$u_t = d_1 u_{xx} + u(r_1(x - ct) - u).$$

If  $c > 2\sqrt{d_1 r_1(\infty)}$ , it follows from Theorem 2.1 in [11] that for every  $\varepsilon > 0$ , there exists  $T > 0$  such that for  $t \geq T$ ,  $\bar{u}(t, x) < \varepsilon$  for all  $x$ . Since  $0 \leq u(0, x) \leq r_1(\infty)$  and

$$u_t \leq d_1 u_{xx} + u(r_1(x - ct) - u),$$

we get

$$u(t, x) \leq \bar{u}(t, x) < \varepsilon \quad \text{for } t > T, x \in \mathbb{R}.$$

As a consequence, (7) is verified. If  $c < 2\sqrt{d_2 r_2(\infty)}$ , by similar discussions to those for Theorem 2.2 in [11], we conclude that species  $v$  spreads at an asymptotic spreading speed  $2\sqrt{d_2 r_2(\infty)}$  and (8) holds. This proves statement (b).

Statement (c) is clearly an application of [11, Thm. 2.1]. The proof is complete.  $\square$

### 3 Simulations

In this section we present numerical simulations to demonstrate influences of climate changes on the dynamical behaviors of model (2). Fix

$$\begin{aligned} r_1(x - ct) &= \frac{1.62}{\pi} \arctan(x - ct), \\ r_2(x - ct) &= \frac{2}{\pi} \arctan(x - ct), \end{aligned}$$

where  $c > 0$ . Choose the initial data by

$$u(0, x) = \begin{cases} 0.4 \sin(x - 20) & \text{if } 20 \leq x \leq 20 + \pi, \\ 0 & \text{elsewhere,} \end{cases}$$

$$v(0, x) = \begin{cases} 1 & \text{if } 20 \leq x \leq 20 + \pi, \\ 0 & \text{elsewhere.} \end{cases}$$

Then profiles of advantageous reproduction areas of two competing species move to the right at a speed  $c$ , and the two species are initially distributed on the interval  $[20, 20 + \pi]$ . Let us fix  $d_1 = d_2 = 1$ . If  $a_1 = 0.21, a_2 = 0.2$ , then (5) holds,  $c_1^*(\infty) \simeq 1.55$ ,  $2\sqrt{d_1 r_1(\infty)} = 1.8$  and  $2\sqrt{d_2 r_2(\infty)} = 2$ .

Figure 1 displays the numerical solutions when  $c = 1.4 < c_1^*(\infty)$ , which shows that two species with the weak competition coexist in an asymptotic region  $t(c + \varepsilon) \leq x \leq t(c_1^*(\infty) - \varepsilon)$  by expanding its spatial range to the right at the asymptotic speed  $c_1^*(\infty)$ .

Figure 2 demonstrates the numerical solutions when  $c = 1.4 < c_1^*(\infty)$  with  $a_1 = 0.21, a_2 = 1.5$  satisfying (6), which shows that in a region of asymptotic size  $(c_1^*(\infty) - c)t$ , the superior competitor  $u$  displaces the well established species  $v$ .

In Fig. 3, we consider the case where  $c = 1.9 \in (2\sqrt{d_1 r_1(\infty)}, 2\sqrt{d_2 r_2(\infty)})$ . Note that  $2\sqrt{d_1 r_1(\infty)}$  is the asymptotic invasion speed of  $u$  in (1) without competition (in the absence of individuals of species  $v$ ). Thus,  $u$  becomes extinct and only species  $v$  persists in the suitable habitat through expanding its spatial range to the right at the asymptotic speed  $2\sqrt{d_2 r_2(\infty)}$ .

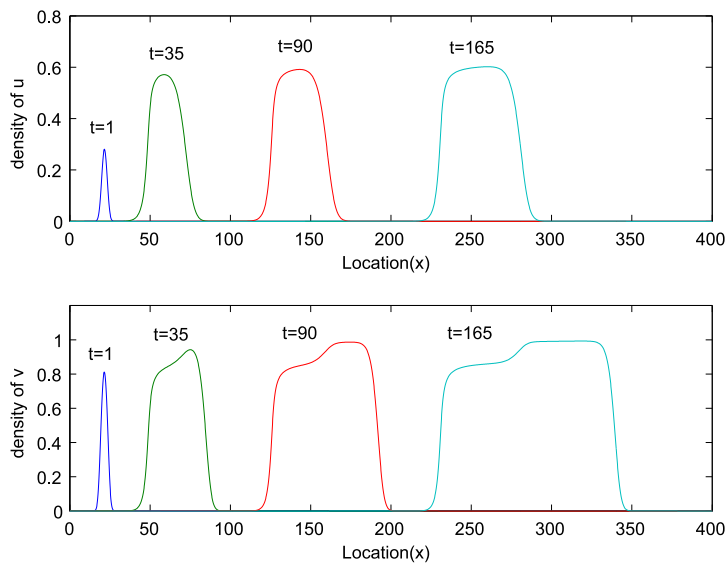
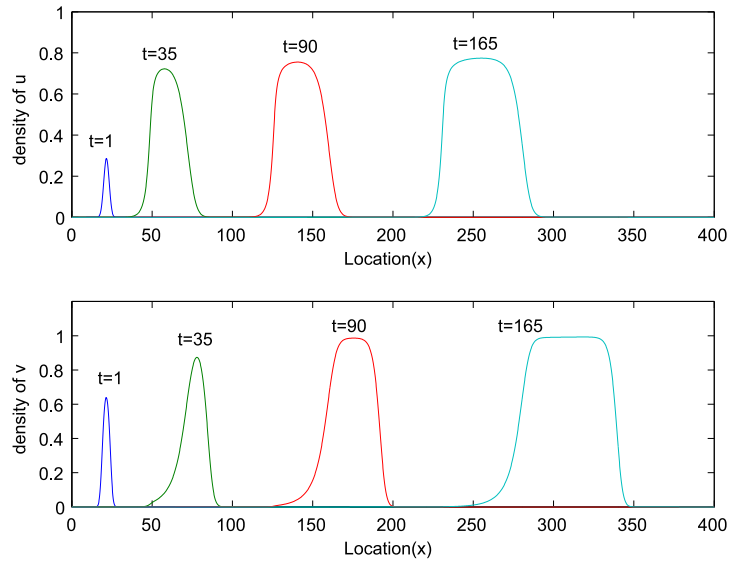
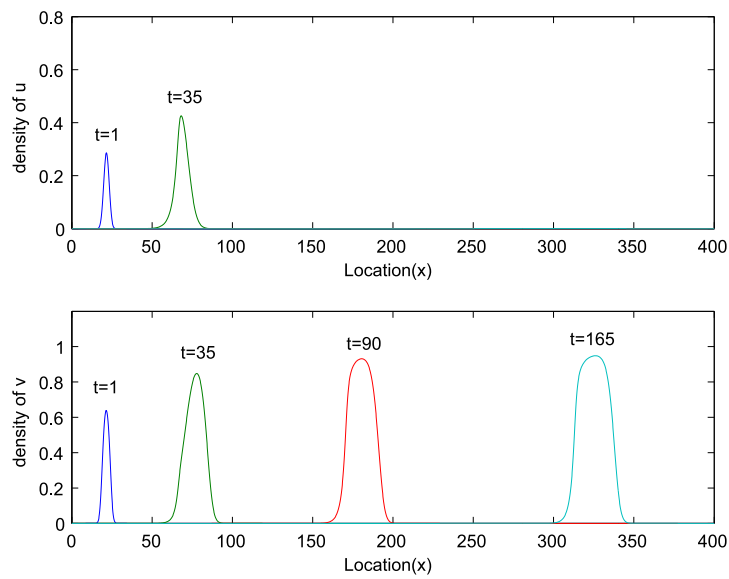


Figure 1. Densities of  $u$  and  $v$  with  $a_1 = 0.21, a_2 = 0.2$  when  $c = 1.4$ .

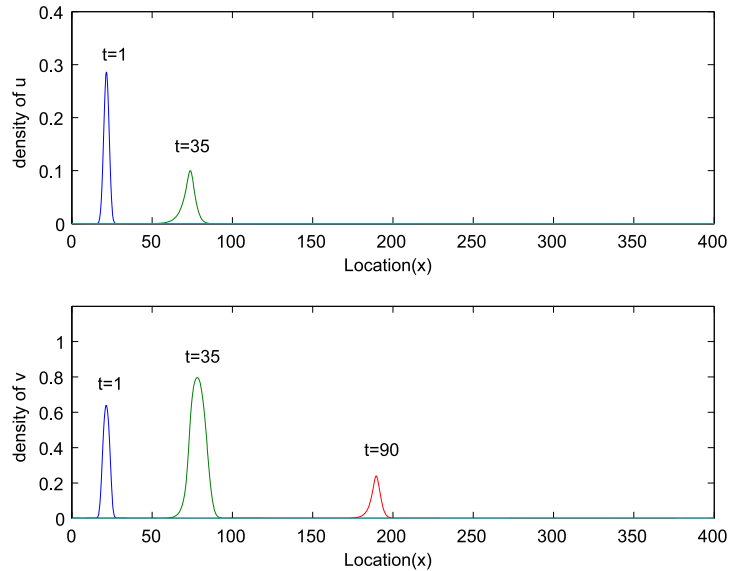


**Figure 2.** Densities of  $u$  and  $v$  with  $a_1 = 0.21, a_2 = 1.5$  when  $c = 1.4$ .



**Figure 3.** Densities of  $u$  and  $v$  with  $a_1 = 0.21, a_2 = 0.2$  when  $c = 1.9$ .

Lastly, Fig. 4 presents the case  $c = 2.1 > \sqrt{d_2 r_2(\infty)}$  where both species cannot keep a pace with a shifting climate and, finally, become extinct.



**Figure 4.** Densities of  $u$  and  $v$  with  $a_1 = 0.21$ ,  $a_2 = 0.2$  when  $c = 2.1$ .

## 4 Discussion

One crucial measure of a species' invasiveness is the rate at which it spreads into a competitor's environment, so that the spreading speed which reflecting the invasion speed of the invader becomes a hot topic in the past decades [6, 10, 30]. In this paper, we focus on the effect of climate change on two species interacting through Lotka–Volterra competition with different dispersal and competitive abilities with varying habitat suitability, that is, shifting in time.

By applying the methods developed in Li et al. [11], we have determined the critical invasion speed for each species, and have found that two competing species become extinct if the habitat boundary moves at speeds greater than the fastest speed of expansion of species population. On the other hand, two competing species coexist and spread if the habitat boundary moves at speeds lower than the slowest speed of expansion of species population when the competition is weak. If the rate of shifting habitat edge is medium, then more adapted species survives. As we have pointed out earlier, the persistence conditions in our theorem requires weak interactions between two competitors (i.e.,  $a_1 a_2 < 1$ ), and we shall consider the strong competition in future.

**Acknowledgment.** We are very grateful to the anonymous referees for careful reading and valuable comments which have led to important improvements of our original manuscript.



## References

1. D.A. Andow, P.M. Kareiva, S.A. Levin, A. Okubo, Spread of invading organisms, *Landscape Ecol.*, **4**(2):177–188, 1990.
2. H. Berestycki, O. Diekmann, C.J. Nagelkerke, P.A. Zegeling, Can a species keep pace with a shifting climate?, *Bull. Math. Biol.*, **71**(2):399–429, 2009.
3. W.F. Fagan, R.S. Cantrell, C. Cosner, S. Ramakrishnan, Interspecific variation in critical patch size and gap-crossing ability as determinants of geographic range size distributions, *Am. Nat.*, **173**(3):363–375, 2009.
4. W.F. Fagan, M.A. Lewis, M.G. Neubert, P. van Den Driessche, Invasion theory and biological control, *Ecology Letters*, **5**(1):148–157, 2002.
5. J. Huang, W. Shen, Speeds of spread and propagation for KPP models in time almost and space periodic media, *SIAM J. Appl. Dyn. Syst.*, **8**(3):790–821, 2009.
6. W. Huang, Problem on minimum wave speed for a Lotka–Volterra reaction–diffusion competition model, *J. Dyn. Differ. Equations*, **22**(2):285–297, 2010.
7. S.T. Jackson, D.F. Sax, Balancing biodiversity in a changing environment: Extinction debt, immigration credit and species turnover, *Trends Ecol. Evol.*, **25**(3):153–160, 2010.
8. Y. Jin, M.A. Lewis, Seasonal influences on population spread and persistence in streams: Spreading speeds, *J. Math. Biol.*, **65**(3):403–439, 2012.
9. E. Kintisch, Impacts research seen as next climate frontier, *Science*, **322**(5899):182–183, 2008.
10. M.A. Lewis, B. Li, H.F. Weinberger, Spreading speed and linear determinacy for two-species competition models, *J. Math. Biol.*, **45**(3):219–233, 2002.
11. B. Li, S. Bewick, J. Shang, W.F. Fagan, Persistence and spread of a species with a shifting habitat edge, *SIAM J. Appl. Math.*, **74**(5):1397–1417, 2014.
12. B. Li, W.F. Fagan, G. Otto, C. Wang, Spreading speeds and traveling wave solutions in a competitive reaction–diffusion model for species persistence, *Dyn. Contin. Discrete Impuls. Syst., Ser. B, Appl. Algorithms*, **19**(10):3267–3281, 2014.
13. F. Lutscher, M.A. Lewis, E. McCauley, Effects of heterogeneity on spread and persistence in rivers, *Bull. Math. Biol.*, **68**(8):2129–2160, 2006.
14. F. Lutscher, R.M. Nisbet, E. Pachevsky, Population persistence in the face of advection, *Theor. Ecol.*, **3**(4):271–284, 2010.
15. C. Moritz, J.L. Patton, C.J. Conroy, J.L. Parra, G.C. White, S.R. Beissinger, Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA, *Science*, **322**(5899):261–264, 2008.
16. E. Pachevsky, F. Lutscher, R. Nisbet, M.A. Lewis, Persistence, spread and the drift paradox, *Theor. Popul. Biol.*, **67**(1):61–73, 2005.
17. C.V. Pao, *Nonlinear Parabolic and Elliptic Equations*, Plenum Press, New York, 1992.
18. C. Parmesan, Ecological and evolutionary responses to recent climate change, *Annu. Rev. Ecol. Evol. Syst.*, **37**:637–669, 2006.
19. C. Parmesan, G. Yohe, A globally coherent fingerprint of climate change impacts across natural systems, *Nature*, **421**(6918):37–42, 2003.

20. A. Pazy, *Semigroups of Linear Operators and Applications to Partial Differential Equations*, Springer-Verlag, New York, 1983.
21. A.B. Potapov, M.A. Lewis, Climate and competition: the effect of moving range boundaries on habitat invasibility, *Bull. Math. Biol.*, **66**(5):975–1008, 2004.
22. N. Shigesada, K. Kawasaki, *Biological Invasions: Theory and Practice*, Oxford University Press, Oxford, 1997.
23. N. Shigesada, K. Kawasaki, E. Teramoto, Traveling periodic waves in heterogeneous environments, *Theor. Popul. Biol.*, **30**(1):143–160, 1986.
24. J. Smoller, *Shock Waves and Reaction–Diffusion Equations*, Springer-Verlag, New York, 1994.
25. D.C. Speirs, W.S.C. Gurney, Population persistence in rivers and estuaries, *Ecology*, **82**(5):1219–1237, 2001.
26. G.R. Walther, E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J.M. Fromentin, O. Hoegh-Guldberg, F. Bairlein, Ecological responses to recent climate change, *Nature*, **416**(6879):389–395, 2002.
27. X. Wang, On the Cauchy problem for reaction–diffusion equations, *Trans. Am. Math. Soc.*, **337**(2):549–590, 1993.
28. H.F. Weinberger, Long-time behavior of a class of biological models, *SIAM J. Math. Anal.*, **13**(3):353–396, 1982.
29. H.F. Weinberger, On spreading speeds and traveling waves for growth and migration models in a periodic habitat, *J. Math. Biol.*, **45**(6):511–548, 2002.
30. R. Xu, M.A.J. Chaplain, F.A. Davidson, Travelling wave and convergence in stage-structured reaction–diffusion competitive models with nonlocal delays, *Chaos Solitons Fractals*, **30**(4):974–992, 2006.
31. Q. Ye, Z. Li, M. Wang, Y. Wu, *Introduction to Reaction-Diffusion Equations*, Science Press, Beijing, 2011.
32. Y. Zhou, M. Kot, Discrete-time growth-dispersal models with shifting species ranges, *Theor. Ecol.*, **4**(1):13–25, 2011.