Spread and Persistence for Integro-Difference Equations with Shifting Habitat and Strong Allee Effect

Dedicated to Professor Mark A. Lewis on the occasion of his 60th birthday

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Abstract

We study an integro-difference equation model that describes the spatial dynamics of a species with a strong Allee effect in a shifting habitat. We examine the case of a shifting semi-infinite bad habitat connected to a semi-infinite good habitat. In this case we rigorously establish species persistence (non-persistence) if the habitat shift speed is less (greater) than the asymptotic spreading speed of the species in the good habitat. We also examine the case of a finite shifting patch of hospitable habitat, and find that the habitat shift speed must be less than the asymptotic spreading speed associated with the habitat and there is a critical patch size for species persistence. Spreading speeds and traveling waves are established to address species persistence. Our numerical simulations demonstrate the theoretical results and show the dependence of the critical patch size on the shift speed.

1 Introduction

In this paper, we are concerned with an integro-difference equation with a non-homogenous and temporally shifting habitat. Such an equation takes the form

$$u_{n+1}(x) = \int_{-\infty}^{\infty} k(x-y)g(y-nc, u_n(y))dy, \tag{1.1}$$

where $u_n(x)$ is the density of a population at x for the nth generation, $k(x-y)$ is the probability of dispersing from y to x, c is the speed of the habitat shift, and $g(y,u)$ describes the net fecundity at location y from the population u. We will study the case of a shifting gradient connecting unbounded poor habitat to unbounded high quality habitat, and the case of a shifting finite patch of high quality habitat.

Integro-difference equations model populations where a relatively synchronized reproduction process is followed by the spatial redistribution of the offspring. This has advantages over frameworks such as reaction-diffusion models in that it can model a wide variety dispersal behavior [18, 23, 37]. The flexibility of the integro-difference framework has made it possible to include a variety of biological details such as stage structure [37], mixed dispersal strategies [50], resource gradients [26], and over-compensation [40]. Therefore the integro-difference framework has been applied to a wide variety of ecological problems [13, 14, 15, 20, 21, 22, 23].

In this paper we are particularly interested in growth functions exhibiting a strong Allee effect. An Allee effect is said to occur if per-capita birth rates decline at low densities. A strong Allee effect occurs when there is a critical density below which the populations fails. A variety of biological factors can cause the Allee effect [1, 5, 6, 8, 41]. For the case of integro-difference equations with a strong Allee effect and a static and homogenous habitat, Lui [33] showed that there exists a spreading speed that is the unique speed for traveling waves connecting zero to the carrying capacity. Wang et al. [51] gave conditions, related to the integral of the growth function, under which the spreading speed is zero, positive, or negative. This can be interpreted as a static, advancing, or retreating invasion. These results have been used to study a variety of invasion processes [8, 23, 24, 29, 34, 36, 48, 49]. Recently Li and Otto [30] generalized the results in [33, 51] by removing some of the strong hypotheses. In this paper, the authors also showed that for habitats of finite size, a critical patch size is needed for survival. For a comprehensive treatment of integro-difference models, the reader should refer to the monograph by Lutscher [35].

With the acceleration of climate change, modeling the effects of non-static habitats has taken on greater importance. As is noted in an increasing number of ecological studies, climate change can impact invasion processes [16, 46]. These warming trends can result in habitat shifts [44, 43], expansion [11, 39], and contraction[11, 39, 43]. There are examples of climate change exacerbating invasions by non-native species [9, 47]; triggering an invasion by a range expansion of a native species [32, 52]; or even disrupting an invasion [4, 42]. Habitat gradients, whether climatological or otherwise, greatly impact the spatial structure of biodiversity. The location of some of these gradients have shifted substantially due to climate change processes. Temperature gradients have shifted polewards and to higher elevations. This has for example, resulted in coral communities on the west coast of Australia shifting southward [12], and has caused some insect populations to move to higher elevations in alpine habitat [17]. For more discussions with species specific examples, we would refer the reader to the papers [7, 27, 28] and the references cited therein.

Two early attempts at mathematically modeling the effects of habitat shifts in the framework of reaction-diffusion models were by Patapov and Lewis [45] and Berestycki et al. [2]. Patapov and Lewis considered the effects of a moving range boundary on the invasibility by a competing species, while Berestycki et al. considered if a single species can spread fast enough to keep up with a patch of suitable habitat. Zhou and Kot [53] later considered the question of a single species keeping up with a shifting finite patch of suitable habitat within the context of integro-difference equations. Their results established that if the asymptotic spreading speed is greater than the habitat shift speed and the size of the patch is greater than a critical size, the species persists. Li et al. [28] and Li and Wu [29] considered integro-difference equations in two connected static semi-infinite habitats with different levels of quality, and studied the existence of spreading speeds and traveling waves. Related results for reaction-diffusion models with an unbounded shifting habitat have also been obtained (e.g., Berestycki and Fang [3], Fang et al. [10], Hu et al. [19], and Li et al. [27]). In a recent paper by Lewis et al.[24] questions regarding persistence, neutral genetic diversity, and inside dynamics were addressed within the framework of integro-difference equations and shifting habitats. None of these works however, addressed questions about persistence of a species in a moving habitat if the growth function exhibits a strong Allee effect.

In this paper we will explore species persistence in the face of a shifting habitat and strong Allee effect in the integro-difference framework. We will examine the case of a shifting semi-infinite bad habitat connected to a semi-infinite good habitat. In this case we will rigorously establish persistence (non-persistence) if the habitat shift speed is less (greater) than the asymptotic spreading speed of the species in the good habitat. We will also examine the case of a finite shifting patch of hospitable habitat. Analogously to the results of Zhou and Kot [53], we find that with the presence of a strong Allee effect, in order for species to persist, the habitat shift speed must be less than the asymptotic spreading speed associated with the habitat. We also find that there is a critical patch size which depends on the shift speed.

This paper is organized as follows. In section 2 we present the hypotheses assumed for the growth function and dispersal kernel. In section 3 we present theorems and proofs related to the results for an unbounded habitat. In section 4 a theorem and its proof for a bounded habitat are provided. In section 5 numerical simulations supporting and complementing the theoretical results are presented. Finally, in section 6 a concluding discussion is given.

2 The hypotheses

For convenience, we use $Q^{(n)}$ as a shorthand for the nth year map, and define

$$Q^{(n)}[u](x) := \int_{-\infty}^{\infty} k(x-y)g(y-nc, u(y))dy,$$

so that (1.1) can be written in the form

$$u_{n+1}(x) = Q^{(n)}[u_n](x).$$

We make the following hypotheses on $k(x)$.

Hypotheses 2.1.

i. $k(x) \geq 0$ *and* $k(x)$ *is even. If* $B = \inf\{x : k(x) > 0\}$, *then* $k(x) > 0$ *in* $(-B, B)$. $B = \infty$ *is allowed so that* $k(x)$ *need not have compact support.*

ii. $k(x)$ *is continuous in* $\mathbb{R}$ *except possibly at* $-B, B$ *where* $lim_{x \to B^-} k(x) = p$. *Also* $k(x)$ *may be written in the form*

$$k(x) = k_a(x) - p\chi_{(-\infty,-B]} - p\chi_{[B,\infty)},$$

where $k_a(x)$ *is absolutely continuous and* χ_S *is the indicator function of the set* S.

iii. $\int_{\mathbb{R}} k(x)dx = 1$.

iv. $\int_{-\infty}^{\infty} e^{\mu x} k(x)dx$ *is finite for one nonzero* μ.

Hypotheses 2.1 are the same as Hypotheses 2.1 (i)-(iv) in [30] with $k(x)$ even. They are satisfied by many dispersal kernels used in applications. Recall that a function $\psi(x)$ is absolutely continuous if $\psi'(x)$ exists almost everywhere and for all s and t and $\psi(s) - \psi(t) = \int_s^t \psi'(x)dx$.

We first make the following hypotheses on $g(x, u)$.

Hypotheses 2.2.

i. $g(x, u)$ *is nonnegative and nondecreasing in* x *and* u *for* $-\infty < x < \infty$ *and* $u \geq 0$, *and* $g(x, u)$ *is continuous except at possibly the points in a finite number of sets in the form* $\{(x_i, u)|u > 0\}$ *where* x_i *is fixed.*

ii. There exists $\beta(\infty) > 0$ *such that* $g(\infty, u) = \lim_{x\to\infty} g(x, u)$ *uniformly for* $u \in [0, \beta(\infty)]$, *and* $g(\infty, \beta(\infty)) = \beta(\infty)$.

iii. $g(x, 0) = 0$ *for all* x, *and there exists* M *such that for* $x \geq M$, *there is* $\beta(x)$ *with* $\beta(\infty) \geq \beta(x) > 0$ *and* $g(x, \beta(x)) = \beta(x)$, *and for* $x \geq M$ *and* $x = \infty$, *the following statements hold:*

a. There exists $\alpha(x) \in (0, \beta(x))$ *such that* $g(x, \alpha(x)) = \alpha(x)$, $g(x, u) < u$ *for* $u \in (0, \alpha(x))$, *and* $g(x, u) > u$ *in* $u \in (\alpha(x), \beta(x))$;

b. $\frac{\partial g(x,u)}{\partial u}$ *is continuous in* u *and* $\frac{\partial g(x,u)}{\partial u} \geq 0$ *for* $u \in [0, \beta(x)]$, *and if*

$$\sigma_1(x) = \inf\{u : g(x, u) > 0\},\ \sigma_2(x) = \sup\{u : g(x, u) < \beta(x)\},$$

then $\frac{\partial g(x,u)}{\partial u} > 0$ *for* $u \in (\sigma_1(x), \sigma_2(x))$; *and*

c. $\frac{\partial g(x,0)}{\partial u} < 1$, $\frac{\partial g(x,\alpha(x))}{\partial u} > 1$, $\frac{\partial g(x,\beta(x))}{\partial u} < 1$.

iv. There exists $0 \leq r < 1$ *and* A *such that for* $x \leq A$ *and* $u \geq 0$, $g(x, u) \leq ru$.

In Hypotheses 2.2 (i) the monotonicity of $g(x,u)$ in x reflects that the quality of the habitat improves to the right along the x-axis, and the discontinuity of $g(x,u)$ in x implies that the environmental conditions may change abruptly at some points in space. This hypothesis is the same as Hypotheses 1 (i) in Li et al. [28] for the growth function of a model with a shifting habitat and no Allee effect. Hypotheses 2.1 (ii) shows that $g(x,u)$ converges to $g(\infty,u)$ uniformly in u. Hypotheses 2.1 (iii) indicates that the system exhibits a strong Allee effect for large x. This hypothesis is equivalent to Hypotheses 2.1 (v)-(ix) in Li and Otto [30] for the growth function of a model with a strong Allee effect and stationary habitat. Hypotheses 2.2 (iv) implies that the population declines near $-\infty$.

Hypotheses 2.2 (i)-(iii) shows $\alpha(x) \le \alpha(\tilde{x})$ and $\beta(x) \ge \beta(\tilde{x})$ for $x > \tilde{x} \ge M$, $\lim_{x\to\infty} \alpha(x) = \alpha(\infty)$, and $\lim_{x\to\infty} \beta(x) = \beta(\infty)$.

Alternatively, we make the following hypotheses for $g(x,u)$.

Hypotheses 2.3.

$$g(x,u) = \begin{cases} g_0(u), & \text{for } -l \le x \le l, \quad l > 0, \\ 0, & \text{for } x < -l \text{ and } x > l, \end{cases}$$

and there exist $0 < \alpha_0 < \beta_0$ *such that* $g_0(0) = 0$, $g_0(\alpha_0) = \alpha_0$, $g_0(\beta_0) = \beta_0$, *and Hypotheses 2.2 (iii) (a)-(c) is satisfied with* $g(x,u)$ *replaced by* $g_0(u)$, $\alpha(x)$ *replaced by* α_0, *and* $\beta(x)$ *replaced by* β_0, *respectively.*

Under Hypothese 2.3, (1.1) becomes

$$u_{n+1}(x) = \int_{-l+nc}^{l+nc} k(x-y) g_0(u_n(y)) dy. \tag{2.1}$$

This model shows that the population growth with a strong Allee effect takes place in a bounded habitat $[-l+nc, l+nc]$ which shifts at the speed c. Problems in this form have been studied with no Allee effect (Zhou [53]), with no Allee effect and $c = 0$ (see Chapter 3 in Lutscher [35] for a review), and with growth exhibiting a strong Allee effect and $c = 0$ (Li and Otto [30], Section 4.5 and Section 6.4 in Lutscher [35]).

Lemma 2.1. *(Comparison principle) Assume that Hypotheses 2.1-2.2 or Hypotheses 2.1 and Hypotheses 2.3 hold. If* $u_n(x)$ *and* $v_n(x)$ *are two sequences of continuous and nonnegative functions with the properties* $v_{n+1}(x) \le Q^{(n)}[v_n](x)$ *and* $u_{n+1}(x) \ge Q^{(n)}[u_n](x)$ *for all nonnegative* n *and* $0 \le v_0(x) \le u_0(x) \le \beta$, *then* $0 \le v_n(x) \le u_n(x) \le \beta$ *with* $\beta = \beta(\infty)$ *or* $\beta = \beta_0$, *for all positive integer* n.

This lemma can be easily shown to be true by using the method of induction.

3 Spread and persistence with growth in an unbounded habitat

In this section we study population spread and persistence for (1.1) under Hypotheses 2.1 and Hypotheses 2.2. We first recall the framework developed in Lui [33]. For $\ell \ge M$ and $\ell = \infty$, we consider

$$u_{n+1}(x) = Q_\ell[u_n] := \int_{-\infty}^{\infty} k(x-y) g(\ell, u_n(y)) dy. \tag{3.1}$$

Let $\phi(\ell, x)$ be a continuous nonincreasing function such that $\phi(\ell, -\infty) \in (\alpha(\ell), \beta(\ell))$ and $\phi(\ell, x) = 0$ for $x \geq 0$. Define the sequence

$$a_{n+1}(\ell, \tilde{c}, x) = \max\{\phi(\ell, x), Q_\ell[a_n](\ell, \tilde{c}, x + \tilde{c})\}, \quad a_0(\ell, \tilde{c}, x) = \phi(\ell, x).$$

$a_n(\ell, \tilde{c}, x)$ is nondecreasing in n and x for each fixed $\tilde{c}$, and $a_n(\ell, \tilde{c}, x)$ increases to a limit function $a(\ell, \tilde{c}, x)$ as $n \to \infty$. Define

$$c^*(\ell) = \sup\{\tilde{c} : a(\ell, \tilde{c}, \infty) = \beta(\ell)\}. \tag{3.2}$$

Proposition 3.1. *Assume that Hypotheses 2.1-2.2 are satisfied. For $\ell \geq M$ and $\ell = \infty$, the following statements hold for (3.1):*

i. There exists a nonincreasing traveling wave solution $u_n(x) = w(x - nc^*(\ell))$ for (3.1) such that $w(-\infty) = \beta(\ell)$ and $w(\infty) = 0$, and $c^*(\ell)$ is the only wave speed for which a nonincreasing traveling wave with values $\beta(\ell)$ at $-\infty$ and 0 at ∞ can exist.

ii. a. $c^*(\ell) > 0$ if and only if $\int_0^{\beta(\ell)}[g(\ell, u) - u]du > 0$.

b. $c^*(\ell) = 0$ if and only if $\int_0^{\beta(\ell)}[g(\ell, u) - u]du = 0$.

c. $c^*(\ell) < 0$ if and only if $\int_0^{\beta(\ell)}[g(\ell, u) - u]du < 0$.

iii. Assume $\int_0^{\beta(\ell)}[g(\ell, u) - u]du > 0$. Let ϵ be any given small positive number.

a. If $u_0(x)$ is piecewise continuous, $u_0(x) = 0$ for large x, $0 \leq u_0(x) \leq \theta < \beta(\ell)$ in $\mathbb{R}$ with θ a constant, then the solution u_n satisfies

$$\lim_{n\to\infty} \sup_{x \geq n(c^*(\ell)+\epsilon)} u_n(x) = 0.$$

b. For any $\sigma > \alpha(\ell)$, there exists a constant $r_\sigma > 0$ such that if $u_0(x)$ is piecewise continuous and $\beta(\ell) \geq u_0(x) \geq \sigma$ on an interval of length equal to $2r_\sigma$, then the solution u_n satisfies

$$\lim_{n\to\infty} \min_{-n(c^*(\ell)-\epsilon) \leq x \leq n(c^*(\ell)-\epsilon)} u_n(x) = \beta(\ell).$$

In this proposition, statement (i) shows that $c^*(\ell)$ is the unique speed of nonincreasing traveling waves connecting 0 and $\beta(\ell)$, statement (ii) indicates that the sign of $c^*(\ell)$ is the same as that of $\int_0^{\beta(\ell)}[g(\ell, u) - u]du$, and statement (iii) shows that when $\int_0^{\beta(\ell)}[g(\ell, u) - u]du > 0$ (i.e., $c^*(\ell) > 0$), $c^*(\ell)$ is the asymptotic spreading speed for solutions with compact support and initial values larger than $\alpha(\ell)$ in a large interval.

Proposition 3.1 directly follows from Theorem 3.1 and Theorem 3.2 in Li and Otto [30].

Proposition 3.2. *Assume that Hypotheses 2.1-2.2 are satisfied. For $\ell \geq M$, if $w(x - n\hat{c})$ is a nonincreasing traveling wave of (3.1) with $w(-\infty) = \alpha(\ell)$ and $w(\infty) = 0$, then $\hat{c} < 0$.*

According to Hypotheses 2.2 (iii) (a), $\int_0^{\alpha(\ell)}[g(\ell, u) - u]du < 0$. This and a simplified version of the proof of Theorem 3.2 (iii) in [30] prove this proposition.

Lemma 3.1. *Assume that Hypotheses 2.1-2.2 are satisfied. Let $w(x - nc^*(\infty))$ be a nonincreasing traveling wave solution with $w(-\infty) = \beta(\infty)$ and $w(\infty) = 0$ for (3.1) with $\ell = \infty$. Let $c > c^*(\infty)$. If $u_0(x) = w(x)$, the solution u_n of (1.1) has the property that for any positive ε there exits an integer $N > 0$ such that for $n \geq N$, $u_n(x) < \varepsilon$ for all x.*

Proof. Since $g(\infty, u(x)) \geq g(x - nc, u(x))$ for $u(x) \geq 0$, the comparison principle shows $u_n(x) \leq w(x - nc^*(\infty))$, and thus

$$u_n(x) \leq \int_{-\infty}^{\infty} k(x-y)g(y-nc, w(y-nc^*(\infty)))dy = \int_{-\infty}^{\infty} k(x-y-nc^*(\infty))g(y+n(c^*(\infty)-c), w(y))dy.$$

Since $w(x)$ decreases to zero as $x \to \infty$, for a small $\epsilon > 0$ with $g(\infty, \epsilon) < \alpha(\infty)$, there exists x_1 such that $w(x) \leq \epsilon$ for $x \geq x_1$. On the other hand, $c > c^*(\infty)$, monotonicity of g and Hypotheses 2.1 (iv) indicate that there exists N_0 such that for $n \geq N_0$ and $x \leq x_1$, $g(x+n(c^*(\infty)-c), w(x)) \leq g(A, w(x)) < rw(x)$. It follows from this and $w(x) \leq \beta(\infty)$ that for $n \geq N_0$ and all x,

$$u_n(x) \leq \int_{-\infty}^{x_1} k(x-y-nc^*(\infty))rw(y)dy + \int_{x_1}^{\infty} k(x-y-nc^*(\infty))g(\infty, \epsilon)dy \leq \max\{r\beta(\infty), g(\infty, \epsilon)\}.$$

Particularly, $u_{N_0}(x) \leq \max\{r\beta(\infty), g(\infty, \epsilon)\}$ for all x. If $r\beta(\infty) > g(\infty, \epsilon)$ so that $\max\{r\beta(\infty), g(\infty, \epsilon)\} = r\beta(\infty)$, a similar argument shows $u_{N_0+1}(x) \leq \max\{r\max\{r\beta(\infty), g(\infty, \epsilon)\}, g(\infty, \epsilon)\} = \max\{r^2\beta(\infty), g(\infty, \epsilon)\}$. Induction shows $u_{N_0+j}(x) \leq \max\{r^{j+1}\beta(\infty), g(\infty, \epsilon)\}$ if $r^j\beta(\infty) > g(\infty, \epsilon)$. Since $0 \leq r < 1$, there must exist j_0 such that $r^{j_0}\beta(\infty) \leq g(\infty, \epsilon)$. We conclude that there exist $\tilde{N} \geq N_0$ such that $u_{\tilde{N}}(x) \leq g(\infty, \epsilon)$ for all x. It follows that for all x

$$u_{\tilde{N}+1}(x) \leq \int_{-\infty}^{\infty} k(x-y)g(y-nc, g(\infty, \epsilon))dy \leq \int_{-\infty}^{\infty} k(x-y)g(\infty, g(\infty, \epsilon))dy = g(\infty, g(\infty, \epsilon)).$$

Induction shows for all x,

$$u_{\tilde{N}+n}(x) \leq g^n(\infty, g(\infty, \epsilon)) \to 0, \quad \text{as} \quad n \to \infty.$$

Here $g^n(\infty, g(\infty, \epsilon))$ is the nth iteration of $g(\infty, u)$ at $g(\infty, \epsilon)$. The conclusion of this lemma follows immediately. The proof is complete. □

Theorem 3.1. *Assume that Hypotheses 2.1-2.2 are satisfied. Additionally, assume that $c > c^*(\infty)$. If the continuous initial function $u_0(x)$ is zero for sufficiently large x and $0 \leq u_0(x) \leq \rho < \beta(\infty)$ where ρ is a constant, then the solution $u_n(x)$ of (1.1) has the property that for any positive ε there exits an integer $N > 0$ such that for $n \geq N$, $u_n(x) < \varepsilon$ for all x.*

Proof. Let $w(x - nc^*(\infty))$ denote a nonincreasing traveling wave connecting 0 and $\beta(\infty)$ for (3.1) with $\ell = \infty$. Since $0 \leq u_0(x) \leq \rho < \beta(\infty)$ and $u_0(x)$ is zero for sufficiently large x, $u_0(x)$ is bounded above by $w(x - d)$ for some real number d. Note $w(x - d - nc^*(\infty))$ is also a traveling wave for (3.1) with $\ell = \infty$. Let $\tilde{u}_n(x)$ be the solution of (1.1) with $\tilde{u}_0(x) = w(x - d)$. The comparison principle shows $u_n(x) \leq \tilde{u}_n(x)$. The conclusion of the theorem follows from this and Lemm 3.1. The proof is complete. □

Theorem 3.1 indicates that a population with zero initial value for large x dies out eventually in space if $c > c^*(\infty)$.

We now introduce truncated kernels to approximate $k(x)$. For an integro-differnce equation with dispersal kernel having compact support, a solution with compact initial data has the property that the (n+1)th generation density distribution is determined by the nth generation density distribution in a bounded interval. This is useful to establish population persistence for (1.1) when $c^*(\infty) > c > 0$.

Let $\zeta(s)$ be a differentiable nonincreasing function with the properties

$$\zeta(s) = \begin{cases} 1, & \text{for } s \le 1/2, \\ 0, & \text{for } s \ge 1. \end{cases}$$

For $m > 0$, let $k_m(x) = k(x)\zeta(\frac{|x|}{m})$ and $l_m = \int_{-\infty}^{\infty} k_m(x)dx$. Clearly $k_m(x)\to k(x)$ and $l_m \to 1$ as $m\to\infty$. Consider

$$v_{n+1}(x) = \int_{-\infty}^{\infty} \frac{k_m(x-y)}{l_m} l_m g(\ell, v_n(y))dy = \int_{-\infty}^{\infty} k_m(x-y)g(\ell, v_n(y))dy, \tag{3.3}$$

where $\frac{k_m(x)}{l_m}$ is a probability density with $\int_{\mathbb{R}} \frac{k_m(x)}{l_m}dx = 1$. Hypotheses 2.1 are satisfied with $k(x)$ replaced by $\frac{k_m(x)}{l_m}$. Hypotheses 2.2 (i)-(iii) show that there exist m_0 and $\ell_0 \ge M$ such that for $m \ge m_0$ and $x \ge \ell_0$, $l_m g(x,u)$ has three equilibria $0 < \alpha_m(x) < \beta_m(x)$, and Hypotheses 2.2 (i)-(ii) and (iii) (a)-(c) are satisfied with $g(x,u)$ replaced by $l_m g(x,u)$, $\alpha(x)$ replaced by $\alpha_m(x)$, and $\beta(x)$ replaced by $\beta_m(x)$, and $\int_0^{\beta(x)}[g(x,u)-u]du$ and $\int_0^{\beta_m(x)}[l_m g(x,u)-u]du$ have same sign in case of $\int_0^{\beta(x)}[g(x,u)-u]du \ne 0$. Clearly for $m > \tilde{m}$, $\alpha_m(x) \le \alpha_{\tilde{m}}(x)$, $\beta_m(x) \ge \beta_{\tilde{m}}(x)$, and $\alpha_m(x)\to\alpha(x)$ and $\beta_m(x)\to\beta(x)$ as $m\to\infty$. We use $c_m^*(\ell)$ to denote the wave speed for (3.3) for $m \ge m_0$ and $\ell \ge \ell_0$ and $\ell = \infty$. The definition (3.2) clearly shows $c^*(\ell) \ge c_m^*(\ell) \ge c_{\tilde{m}}^*(\tilde{\ell})$ for $m > \tilde{m} \ge m_0$ and $\ell > \tilde{\ell} \ge \ell_0$.

Lemma 3.2. *Assume that Hypotheses 2.1-2.2 are satisfied, and $\int_0^{\beta(\ell)}[g(\ell,u)-u]du > 0$ for $\ell \ge \ell_0$. The following statements hold:*

i. For $\ell \ge \ell_0$ and $\ell = \infty$, $c_m^*(\ell)\to c^*(\ell)$ as $m\to\infty$.

ii. For $m \ge m_0$ and $\ell \ge \ell_0$, $c_m^*(\ell)\to c_m^*(\infty)$ as $\ell\to\infty$.

Proof. Let $v_m(x-nc)$ be a nonincreasing traveling wave of (3.3) connecting 0 and $\beta_m(\ell)$. Then

$$v_m(x) = \int_{-\infty}^{\infty} k_m(x + c_m^*(\ell) - y)g(\ell, v_m(y))dy.$$

For $\eta > 0$,

$$\begin{aligned} |v_m(x+\eta) - v_m(x)| &= |\textstyle\int_{-\infty}^{\infty}(k_m(x+c_m^*(\ell)+\eta-y) - k_m(x+c_m^*(\ell)-y))g(\ell,v_m(y))dy| \\ &\le \beta(\ell)\textstyle\int_{-\infty}^{\infty}|k_m(y+\eta)-k_m(y)|dy, \end{aligned} \tag{3.4}$$

and

$$\begin{aligned} &|v_m(x+\eta) - v_m(x)| \\ &\le \beta(\ell)\textstyle\int_{-\infty}^{\infty}|k_m(y+\eta)-k_m(y)|dy \\ &\le \beta(\ell)[\textstyle\int_{-\infty}^{\infty}|k_m(y+\eta)-k(y+\eta)|dy + \int_{-\infty}^{\infty}|k(y+\eta)-k(y)|dy + \int_{-\infty}^{\infty}|k(y)-k_m(y)|dy] \\ &\le \beta(\ell)[\textstyle\int_{-\infty}^{\infty}|k_m(y+\eta)-k(y+\eta)|dy + \int_{-\infty}^{\infty}|k(y+\eta)-k(y)|dy + \int_{-\infty}^{\infty}|k(y)-k_m(y)|dy] \\ &\le \beta(\ell)[4\textstyle\int_{0.5m}^{\infty}k(y)dy + \int_{-\infty}^{\infty}|k(y+\eta)-k(y)|dy]. \end{aligned} \tag{3.5}$$

As indicated in Li et al. [25],

$$\lim_{\eta\to\infty}\int_{-\infty}^{\infty}|k_m(y+\eta)-k_m(y)|dy=0 \text{ for every } m,\quad \lim_{\eta\to 0}\int_{-\infty}^{\infty}|k(y+\eta)-k(y)|dy=0. \tag{3.6}$$

The first statement is obvious, and the second statement lies in the convergence of $\int_{-\infty}^{\infty}k(y)dy$ and that continuity of $k(x)$ results in uniform continuity of $k(y)$ on a closed bounded interval. It follows from (3.4)-(3.6) that for any $\varepsilon>0$, there exist $m_1>m_0$ and positive numbers η_i, $i=1,2,...,m_0+1$, such that

$$|v_m(x+\eta)-v_m(x)|<\varepsilon,\quad 0<\eta<\eta_i,\ m=m_0,m_0+1,...m_1,$$

and

$$|v_m(x+\eta)-v_m(x)|<\varepsilon,\quad 0<\eta<\eta_{m_0+1},\ m>m_1.$$

Choose $\tilde{\eta}=\min\{\eta_i,\ i=1,2,...m_0+1\}$. Then

$$|v_m(x+\eta)-v_m(x)|<\varepsilon,\quad 0<\eta<\tilde{\eta},\ m\ge m_0.$$

This implies that the family $\{v_m(x),\ m=m_0,m_0+1,...\}$ is equicontinuous. Since each $v_m(x)$ decreases from $\beta_m(\ell)$ to 0 as x increases from $-\infty$ to ∞. We may assume $v_m(0)=v_0$ with $0<v_0<\alpha(\ell)$ (by a translation if necessary). Then Ascoli's theorem implies that every sequence $v_m(x)$ has a subsequenence $v_{m_j}(x)$ that converges to a nonincreasing function $w(x)$ uniformly on every bounded interval. Since $c^*_{m_j}(\ell)$ increases as m_j increases and $c^*_{m_j}(\ell)$ is bounded above by $c^*(\ell)$, $c^*_{m_j}(\ell)$ approaches $\hat{c}$ as $m_j\to\infty$. Since $c^*_m(\ell)>0$ for large m, $\hat{c}>0$.

We take the limit $m_j\to\infty$ in

$$v_{m_j}(x)=\int_{-\infty}^{\infty}k_{m_j}(x+c^*_{m_j}(\ell)-y)g(\ell,v_{m_j}(y))dy.$$

to find

$$w(x)=\int_{-\infty}^{\infty}k(x+\hat{c}-y)g(\ell,w(y))dy.$$

$w(x-n\hat{c})$ is a nonincreasing traveling wave of (3.3) with $w(0)=v_0$. By taking $y\to\pm\infty$ in (3.4), we find that $g(\ell,w(\pm\infty))=w(\pm\infty)$ so that $w(\pm\infty)$ are equilibria of $g(\ell,u)$. Since $w(\infty)\le v_0<\alpha(\ell)$, $w(\infty)=0$. $w(-\infty)$ is either $\alpha(\ell)$ or $\beta(\ell)$. If $w(-\infty)=\alpha(\ell)$, $w(x-n\hat{c})$ is a nonincreasing traveling wave connecting 0 and $\alpha(\ell)$ with a positive speed $\hat{c}$. This contradicts Proposition 3.2. Therefore $w(-\infty)=\beta(\ell)$. The uniqueness of traveling wave speed for (3.3) indicate $\hat{c}=c^*(\ell)$. The fact that $c^*_m(\ell)$ increases in m shows $c^*_m(\ell)\to c^*(\ell)$ as $m\to\infty$. This proves statement (i).

Let $v_{m,\ell}(x-nc^*_m(\ell))$ be a nonincreasing traveling wave of (3.3) connecting 0 and $\beta_m(\ell)$. Then

$$v_{m,\ell}(x)=\int_{-\infty}^{\infty}k_m(x+c^*_m(\ell)-y)g(\ell,v_{m,\ell}(y))dy.$$

For $\eta>0$,

$$\begin{aligned}|v_{m,\ell}(x+\eta)-v_{m,\ell}(x)| &\le \textstyle\int_{-\infty}^{\infty}|k_m(x+\eta+c^*_{m,\ell}-y)-k_m(x+c^*_{m,\ell}-y)|g(\ell,v_{m,\ell}(y))dy\\ &\le \beta(\infty)\textstyle\int_{-\infty}^{\infty}|k_m(y+\eta)-k_m(y)|dy.\end{aligned}$$

Since $\lim_{\eta\to0}\int_{-\infty}^{\infty}|(k_m(y+\eta)-k_m(y))|dy=0$, the sequence $v_{m,\ell}(x)$ is equicontinuous. The rest of the proof of statement (ii) is similar to the part of the proof of statement (i) after the equicontinuity of v_m is established. We omit the details here. □

Lemma 3.3. *Assume that Hypotheses 2.1-2.2 hold, and* $\int_0^{\beta(\infty)}[g(\infty,u)-u]du>0$*. For any* $\beta(\infty)>\sigma>\alpha(\infty)$ *and any small positive* $\epsilon>0$*, there exist* $r_\sigma>0$ *and* $m_1\geq m_0$ *and* $\ell_1\geq\ell_0$ *such that for any* x_1 *and* x_2 *with* $x_2-x_1\geq 2r_\sigma$ *and* $v_0(x)\equiv\sigma$ *on* $[x_1,x_2]$ *and* $v_0(x)\equiv 0$ *otherwise, and for* $m\geq m_1$ *and* $\ell\geq\ell_1$*, the solution* $v_n(x)$ *of (3.3) has the property that there exists* n_0 *such that for* $n\geq n_0$*,*

$$\min_{x_1-n(c^*(\infty)-\epsilon/2)\leq x\leq x_2+n(c^*(\infty)-\epsilon/2)} v_n(x)\geq\sigma. \tag{3.7}$$

Proof. In view of Lemma 3.2, for any $\beta(\infty)>\sigma>\alpha(\infty)$ and small positive $\epsilon>0$, we may chose $m_1>m_0$ and $\ell_1>\ell_0$ so large that $c^*_{m_1}(\infty)-c^*_{m_1}(\ell)<\epsilon/16$, $c^*(\infty)-c^*_{m_1}(\infty)<\epsilon/4$, and $\beta_{m_1}(\ell)>\sigma>\alpha_{m_1}(\ell)$. Note $c^*_{m_1}(\ell)>0$. By Proposition 3.1 (iii), there exists $r_\sigma>0$ that depends on m_1 and ℓ_1 such that for $v_0(x)\equiv\sigma>\alpha_{m_1}(\ell)$ on $[-r_\sigma,r_\sigma]$ and $v_0(x)\equiv 0$ outside $[-r_\sigma,r_\sigma]$, the solution $v_n(x)$ of (3.3) with $m=m_1$ and $\ell=\ell_1$ satisfies

$$\lim_{n\to\infty}\min_{-n(c^*_{m_1}(\ell)-\epsilon/16)\leq x\leq n(c^*_m(\ell_1)-\epsilon/16)} v_n(x)=\beta_{m_1}(\ell_1).$$

It follows that there exists n_0 such that for $n\geq n_0$,

$$\min_{-n(c^*_{m_1}(\infty)-\epsilon/8)\leq x\leq n(c^*_{m_1}(\infty)-\epsilon/8)} v_n(x)\geq\sigma.$$

We may choose $n_0>\frac{8r_\sigma}{\epsilon}$ so that for $n\geq n_0$,

$$\min_{-r_\sigma-n(c^*_{m_1}(\infty)-\epsilon/4)\leq x\leq r_\sigma+n(c^*_{m_1}(\infty)-\epsilon/4))} v_n(x)\geq\sigma,$$

and thus

$$\min_{-r_\sigma-n(c^*(\infty)-\epsilon/2)\leq x\leq r_\sigma+n(c^*(\infty)-\epsilon/2))} v_n(x)\geq\sigma.$$

This and homogeneity of (3.3) show that for $v_0(x)=\sigma$ on $[x_1,x_2]$ with $x_2-x_1\geq 2r_\sigma$, there exists n_0 such that for $n\geq n_0$,

$$\min_{x_1-n(c^*(\infty)-\epsilon/2)\leq x\leq x_2+n(c^*(\infty)-\epsilon/2)} v_n(x)\geq\sigma. \tag{3.8}$$

Since $k_m(x)$ increases as m increases and $g(\ell,u)$ increases as ℓ increase, (3.8) holds for the solution $v_n(x)$ of (3.3) with $m\geq m_1$ and $\ell\geq\ell_1$ and the same $v_0(x)$. This completes the proof. ☐

Theorem 3.2. *Assume that Hypotheses 2.1-2.2 hold,* $\int_0^{\beta(\infty)}[g(\infty,u)-u]du>0$*, and* $c^*(\infty)>c>0$*. For* $\beta(\infty)>\sigma>\alpha(\infty)$ *and any small positive* $\epsilon>0$*, there exist* $\tilde{x}_1$ *and* $r_\sigma>0$ *such that for* $u_0(x)\geq\sigma$ *on* $[\tilde{x}_1,\tilde{x}_1+2r_\sigma]$*, there exists a positive integer* n_0 *such that the solution* u_n *of (1.1) satisfies*

$$\lim_{n\to\infty}\left[\sup_{nn_0(c+\epsilon)\leq x\leq nn_0(c^*(\infty)-\epsilon)}|\beta(\infty)-u_{nn_0}(x)|\right]=0. \tag{3.9}$$

Proof. In view of Lemma 3.3, for $\beta(\infty)>\sigma>\alpha(\infty)$ and small positive $\epsilon>0$ with $c^*(\infty)-c-\epsilon/2>0$, there exist $r_\sigma>0$ and m_1 and ℓ_1 such that for any x_1 and x_2 with $x_2-x_1\geq 2r_\sigma$ and $v_0(x)\equiv\sigma$ on $[x_1,x_2]$ and $v_0(x)\equiv 0$ otherwise, and for $m\geq m_1$ and $\ell\geq\ell_1$, the solution $v_n(x)$ of (3.3) has the property that there exists n_0 such that for $n\geq n_0$, (3.7) holds, and particularly

$$\min_{x_1-n_0(c^*(\infty)-\epsilon/2)\leq x\leq x_2+n_0(c^*(\infty)-\epsilon/2)} v_{n_0}(x)\geq\sigma. \tag{3.10}$$

Since $c^*_m(\infty) \to c^*(\infty)$ as $m \to \infty$ and $c^*_m(\infty)$ is less than D_m, which denotes the size of the support of k_m (see Lui [33]), we may chose m_1 so large such that $2D_{m_1} - c^*(\infty) - \epsilon/2 > 0$. Consider

$$u_0(x) \geq v_0(x) \equiv \sigma, \quad x \in [\ell_1 + 3n_0 D_{m_1},\ \ell_1 + 3n_0 D_{m_1} + 2r_\sigma]. \tag{3.11}$$

Let $u_n(x)$ be the solution of (1.1) with $u_0(x)$ satisfying (3.11). Since $g(x,u) \geq g(\ell,u)$ for $x \geq \ell$ and $u \geq 0$, using the comparison principle and (3.10) with $x_1 = \ell_1 + 3n_0 D_{m_1}$ and $x_2 = \ell_1 + 3n_0 D_{m_1} + 2r_\sigma$, we have

$$u_{n_0}(x) \geq v_{n_0}(x) \geq \sigma, \quad x \in [\ell_1 + 3n_0 D_{m_1} - n_0(c^*(\infty) - \epsilon/2),\ \ell_1 + 3n_0 D_{m_1} + 2r_\sigma + n_0(c^*(\infty) - \epsilon/2)].$$

Note $3n_0 D_{m_1} - n_0(c^*(\infty) - \epsilon/2) > n_0 D_{m_1}$. We particularly have

$$u_{n_0}(x) \geq v_{n_0}(x) \geq \sigma, \quad x \in [\ell_1 + 3n_0 D_{m_1} + n_0 c,\ \ell_1 + 3n_0 D_{m_1} + 2r_\sigma + n_0(c^*(\infty) - \epsilon/2)].$$

By induction, for any positive integer j,

$$u_{jn_0}(x) \geq v_{jn_0}(x) \geq \sigma, \quad x \in [\ell_1 + 3n_0 D_{m_1} + jn_0 c,\ \ell_1 + 3n_0 D_{m_1} + 2r_\sigma + jn_0(c^*(\infty) - \epsilon/2)]. \tag{3.12}$$

For any small $\varepsilon > 0$, there exists $m_2 > m_1$ such that $\beta_{m_2}(\infty) > \beta(\infty) - \varepsilon/4$. Consequently there is $\ell_2 \geq \ell_1$ such that for $\ell \geq \ell_2$, $\beta_{m_2}(\ell) > \beta(\infty) - \frac{\varepsilon}{2}$. On the other hand, there exists a positive integer N_0 such that for $N \geq N_0$, $(l_{m_2} g(\ell_2, \sigma))^{(Nn_0)} \geq \beta(\infty) - \varepsilon$ with $(l_{m_2} g(\ell_2, \sigma))^{(Nn_0)}$ the Nn_0th iteration of $l_{m_2} g(\ell_2, u)$ at σ. We choose j_0 so large that for $j \geq j_0$, $\ell_1 + 3n_0 D_{m_1} + jn_0 c > \ell_2$ and $jn_0(c^*(\infty) - c - \epsilon/2) + 2r_\sigma > 2n_0 N_0 D_{m_2} + N_0 n_0 c$. It follows that for $j \geq j_0$,

$$u_{(j+N_0)n_0}(x) \geq \beta(\infty) - \varepsilon,$$

$$x \in [\ell_1 + 3n_0 D_{m_1} + jn_0 c + N_0 n_0 D_{m_2} + N_0 n_0 c,\ \ell_1 + 3n_0 D_{m_1} + 2r_\sigma + jn_0(c^*(\infty) - \epsilon/2) - N_0 n_0 D_{m_2}].$$

We may further choose $j_1 > j_0$ such that for $j > j_1$, $\ell_1 + 3n_0 D_{m_1} + jn_0 c + N_0 n_0 D_{m_2} + N_0 n_0 c < (j + N_0) n_0 (c + \epsilon)$ and $\ell + 3n_0 D_{m_1} + 2r_\sigma + jn_0(c^*(\infty) - \epsilon/2) - N_0 n_0 D_{m_2} > (j + N_0) n_0 (c^*(\infty) - \epsilon)$. It follows that for $n > j_1 + N_0$,

$$u_{nn_0}(x) \geq \beta(\infty) - \varepsilon, \quad x \in [nn_0(c + \epsilon), nn_0(c^*(\infty) - \epsilon)].$$

We conclude that for $\tilde{x}_1 = x_1 = \ell_1 + 3n_0 D_{m_1}$ and $u_0(x) \geq \sigma$ on $[\tilde{x}_1, \tilde{x}_1 + 2r_\sigma]$, $u_n(x)$ satisfies (3.9). The proof is complete. □

Theorem 3.2 shows that when $\int_0^{\beta(\infty)} [g(\infty, u) - u] du > 0$ (i.e., $c^*(\infty) > 0$) and $c^*(\infty) > c > 0$, a population with initial values above the Allee threshold on an appropriate large interval persists in space. This theorem and Theorem 3.1 imply that a population with a compact initial distribution with values above the Allee threshold on an appropriate large interval spreads rightward at the speed $c^*(\infty)$ in a weak sense. The proof of Theorem 3.2 shows that the interval $[\tilde{x}_1, \tilde{x}_1 + 2r_\sigma]$ can be replaced by $[\tilde{x}_2, \tilde{x}_2 + 2r_\sigma]$ for any $\tilde{x}_1 \geq \tilde{x}_1$.

Theorem 3.3. *Assume that Hypotheses 2.1-2.2 are satisfied. Assume in addition that $c^*(\infty) > c > 0$. Then there exists a nondecreasing traveling wave $w(x - nc)$ in (1.1) with $w(-\infty) = 0$ and $w(\infty) = \beta(\infty)$.*

Proof. In the proof of Theorem 3.2, (3.11) and (3.12) show that for $\beta(\infty) > \sigma > \alpha(\infty)$ and $\epsilon > 0$ with $c^*(\infty) - c - \epsilon > 0$, there exist positive numbers $\tilde{x}_1$ and r_σ, and positive integer n_0, such that for

$$u_0(x) = \sigma, \quad x \in [\tilde{x}_1,\ \tilde{x_1} + 2r_\sigma],$$

the solution $u_n(x)$ of (1.1) has the property that for $j = 1, 2, 3, ...,$

$$u_{jn_0}(x) \geq \sigma, \quad x \in [\tilde{x}_1 + jn_0 c,\ \tilde{x}_1 + 2r_\sigma + jn_0(c^*(\infty) - \epsilon/2)]. \tag{3.13}$$

A traveling wave $w(x - nc)$ of (1.1) satisfies

$$w(x) = S[w](x) := \int_{-\infty}^{\infty} k(x + c - y) g(y, w(y)) dy.$$

That is, $w(x)$ is a fixed point of S. Consider $w_{n+1}(x) = S[w_n](x)$ with $w_0(x) \equiv \beta(\infty)$. It is easy to see $w_1(x) \leq w_0(x)$. Induction shows $w_{n+1}(x) \leq w_n(x)$. Clearly $w_0(x)$ is nondecreasing in x. If $w_n(x)$ is nondecreasing in x, since $g(x, u)$ is nondecreasing in x and u, for $t_1 > t_2$,

$$\begin{aligned} w_{n+1}(t_1) - w_{n+1}(t_2) &= S[w_n](t_1) - S[w_n](t_2) \\ &= \textstyle\int_{-\infty}^{\infty} k(y)[g(t_1 + c - y, w_n(t_1 + c - y)) - g(t_2 + c - y, w(t_2 + c - y))]dy \geq 0, \end{aligned}$$

so that $w_{n+1}(x)$ is nondecreasing in x. We therefore conclude that $\lim_{n\to\infty} w_n(x) = w(x)$ exists and $w(x)$ is nondecreasing in x. Taking the limit $n\to\infty$ in $w_{n+1}(x) = S[w_n](x)$ and using the dominate convergence theorem, we find that $w(x) = S[w](x)$ thus $w(x - nc)$ is a traveling wave of (1.1). Taking $x \to \pm\infty$ in $w(x) = S[w](x)$ we see $w(\pm\infty) = g(\pm\infty, u)$. Hypotheses 2.2 (iv) show that there exists $0 \leq r_1 < 1$ such that $w(-\infty) \leq r_1 w(-\infty)$, leading to $w(-\infty) = 0$.

Consider $\tilde{w}_{n+1}(x) = S[\tilde{w}_n](x)$ with $\tilde{w}_0(x) = u_0(x)$, Since $w_0(x) > \tilde{w}_0(x)$, comparison shows

$$w_n(x) \geq \tilde{w}_n(x). \tag{3.14}$$

On the other hand, $\tilde{w}_n(x) = u_n(x - nc)$ so that by (3.13), for any j,

$$\tilde{w}_{jn_0}(x) \geq \sigma, x \in [\tilde{x_1},\ \tilde{x_1} + 2r_\sigma + jn_0(c^*(\infty) - c - \epsilon/2)],$$

and particularly,

$$\tilde{w}_{jn_0}(x) \geq \sigma, x \in [\tilde{x_1},\ \tilde{x_1} + 2r_\sigma].$$

This and (3.14) shows $w(x) \geq \sigma$ on $[\tilde{x_1},\ \tilde{x_1} + 2r_\sigma]$, so that $w(\infty) = \beta(\infty)$. This completes the proof. □

Theorem 3.3 states that if $c^*(\infty) > c > 0$, (1.1) has a nondecreasing traveling wave connecting 0 to $\beta(\infty)$.

4 Persistence with growth in a bounded habitat

In this section, we study (1.1) under Hypotheses 2.1 and Hypotheses 2.3. In this case, (1.1) becomes (2.1) where population growth takes place in a bounded habitat which shifts at a speed c. We establish persistence of solutions and existence of a positive traveling wave. A positive traveling wave is a nontrivial nonnegative traveling wave.

Let c^* denote the spreading speed of

$$u_{n+1}(x) = \int_{-\infty}^{\infty} k(x-y)g_0(u_n(y))dy, \tag{4.1}$$

and c^* is the unique speed of nonincreasing traveling waves connecting 0 and β_0. The sign of c^* is the same as that of $\int_0^{\beta_0}[g_0(u)-u]du$.

Theorem 4.1. *Assume that Hypotheses 2.1 and Hypotheses 2.3 hold.*

i. For $c^* > c > 0$, there exists $l^* > 0$ such that

  a. if $l > l^*$, (2.1) has a positive traveling wave $w(x-nc)$; and

  b. if $l < l^*$, there is no positive traveling wave for (2.1) with speed c, and every solution $u_n(x)$ of (2.1) with $0 \le u_0(x) \le \beta_0$ converges to zero as $n \to \infty$.

ii. For $c^* < c$, there is no positive traveling wave with speed c for (2.1), and in this case every solution $u_n(x)$ of (2.1) with $0 \le u_0(x) \le \rho < \beta_0$ converges to zero as $n \to \infty$.

Proof. We first assume $c^* > c > 0$. A traveling wave $w(x-nc)$ of (2.1) satisfies

$$w(x) = T_l[w](x) := \int_{-l}^{l} k(x+c-y)g_0(w(y))dy.$$

We consider the operators

$$T_{l,m}[w](x) := \int_{-l}^{l} k_m(x+c-y)g_0(w(y))dy,$$

and

$$v_{n+1}(x) = Q_{c,m}[v_n](x) := \int_{-\infty}^{\infty} k_m(x+c-y)g_0(v_n(y))dy. \tag{4.2}$$

For large m, the traveling wave speed of (4.2) is $c_m^* - c$ where c_m^* is the traveling wave speed for the operator

$$Q_m[u](x) =: \int_{-\infty}^{\infty} k_m(x-y)g_0(u(y))dy.$$

A proof similar to that of Lemma 3.2 (ii) shows $\lim_{m\to\infty} c_m^* = c^*$. A proof similar to that of Lemma 3.3 shows that for $\beta_0 > \sigma > \alpha_0$ and any given positive $\epsilon > 0$ with $c^* - c - \epsilon > 0$, there exist $r_\sigma > 0$ and m_1 such that for $v_0(x) \equiv \sigma$ on $[-r_\sigma, r_\sigma]$ and $v_0(x) \equiv 0$ otherwise, and for $m \ge m_1$, the solution $v_n(x)$ of (4.2) has the property that there exists n_0 such that

$$\min_{-r_\sigma - n_0(c^*-c-\epsilon) \le x \le r_\sigma + n_0(c^*-c-\epsilon)} v_{n_0}(x) \ge \sigma. \tag{4.3}$$

Choose $l_0 = r_\sigma + n_0(c^*-c-\epsilon) + n_0 D_m$ where D_m is the size of the support of k_m. Then for the given $v_0(x)$, $T^j_{l_0,m}[v_0](x) = Q^j_{c,m}[v_0](x)$, where $j = 1, 2, ..., n_0$, $T^j_{l_0,m}$ is the jth iteration of $T_{l_0,m}$, and $Q^j_{c,m}$ is the jth iteration of $Q_{c,m}$. This, the comparison principle, and (4.3) show that

$$u_{n_0}(l_0, x) \ge v_0(x), \quad x \in [-r_\sigma, r_\sigma],$$

where $u_n(l_0, x)$ satisfies $u_{n+1}(l_0, x) = T_{l_0}[u_n](l_0, x)$ and $u_0(l_0, x) = v_0(x)$. Induction shows

$$u_{jn_0}(l_0, x) \geq v_{jn_0}(x) \geq v_0(x), \quad x \in [-r_\sigma, r_\sigma]. \tag{4.4}$$

Consider $w_{n+1}(l, x) = T_l[w_n](l, x)$ with $w_0(x) \equiv \beta_0$. Induction shows $w_{n+1}(l, x) \leq w_n(l, x)$, so that $\lim_{n\to\infty} w_n(l, x) = w(l, x)$ exists. It is easy to see that $w(l, x)$ satisfies $w(l, x) = T_l[w(l, \cdot)](x)$. On the other hand, the comparison principle and (4.4) show $w_{jn_0}(l_0, x) \geq u_{jn_0}(l_0, x) \geq v_0(x)$ for any j, and thus $w(l_0, x) \geq v_0(x)$. We conclude that $w(l_0, x)$ is a positive fixed point for T_{l_0}.

On the other hand, since $g_0(u) \in C^1[0, \beta_0]$, there exists $A_0 > 0$ such that $g_0(u) \leq A_0 u$ for $u \in [0, \beta_0]$. Let K_0 denote the maximum value of $k(x)$. $w(l, x) = T_l[w(l, \cdot)](x)$ shows $w(l, x) \leq 2\ell A_0 K_0 \beta_0$. Let $\tilde{l}_0 = \frac{1}{4A_0K_0}$. $w(\tilde{l}_0, x) = T_{\tilde{l}_0}[w(\tilde{l}_0, \cdot)](x)$ and induction shows $w(\tilde{l}_0, x) \leq (2\tilde{l}_0 A_0 K_0)^n \beta_0 = \frac{\beta_0}{2^n}$ for any positive integer n, so that $w(\tilde{l}_0, x) \equiv 0$.

It is easily seen that $w_n(l, x)$ is nondecreasing in l. So $w(l, x)$ is nondecreasing in l. $w(l_0, x)$ is a positive fixed point, and $w(\tilde{l}_0, x) \equiv 0$. Therefore

$$l^* = \inf\{l, w(l, x) \not\equiv 0\}$$

is well defined and $0 < \tilde{l}_0 \leq l^* \leq l_0$, and furthermore $w(l, x)$ is a positive fixed point if $l > l^*$ and $w(l, x) \equiv 0$ if $l < l^*$. We have shown statement (i) (a). For any solution $u_n(l, x)$ of (2.1) with $u_0(x) \leq \beta_0$, $u_n(x - nc) \leq w_n(l, x)$, which leads to statement (i) (b). We have proven statement (i).

We now prove statement (ii). Let $w(x - nc^*)$ be a nonincreasing traveling wave solution of (4.1) with $w(-\infty) = \beta_0$ and $w(\infty) = 0$. Since $0 \leq u_0(x) \leq \rho < \beta_0$, there exists a number h such that $u_0(x) < w(x - h)$. We have that for $x \in [-l, l]$,

$$u_1(x - c) = T_l[u_0](x - c)) \leq T_l[w](x - c - h) \leq \int_{-\infty}^{\infty} k(x - h - y) g_0(w(y)) dy = w(x - c^* - h),$$

so that $u_1(x) \leq w(x - (c^* - c) - h)$. Induction shows $u_n(x) \leq w(x - n(c^* - c) - h)$. Since $c^* - c < 0$ and $w(\infty) = 0$, as $n \to \infty$, $w(x - n(c^* - c) - h) \to 0$ for $x \in [-l, l]$ and thus $u_n(x) \to 0$ for $x \in [l + nc, l - nc]$ and there is no nonnegative nontrivial equilibrium. The proof is complete. □

Theorem 4.1 states (i) if c is less than c^*, the wave speed of the corresponding model on $(-\infty, \infty)$, then there is a critical patch size l^* such that the population can persist when $l > l^*$ and dies out eventually if $l < l^*$, and (ii) if c is greater than c^* then the population dies out eventually.

5 Simulations

All simulations in this section were conducted in Matlab. The source code can be viewed at *https://github.com/glotto01/shifting-habitat-Journal-of-Mathematical-Biology*. The solutions to the integro-difference equations where computed using a mid-point rule with uniform spatial discretization with $\Delta x = 0.008$. This corresponds to the error tolerance (epsilon) being set at 0.0001 in the function *setglobal.m*.

We will use the Laplace dispersal kernel, $k(x) = \frac{b}{2} e^{-b|x|}$, $b > 0$ in all simulations except the one corresponding to Fig. 12 . By scaling, we may assume $b = 1$ without loss of generality. This corresponds to a variance of 2.

Case 1: Shifting habitat conforming to Hypotheses 2.2. For the growth function we will use

$$g(x,u) = \begin{cases} \frac{m_0 u^2}{1+(m_1-1)u^2} & x < 0, \\ \frac{m_1 u^2}{1+(m_1-1)u^2} & x \geq 0. \end{cases}$$

To satisfy Hypotheses 2.2, it is necessary for $m_1 > 2$ and $0 < m_0 < 2\sqrt{m_1 - 1}$. The equilibria of $g(\infty, u)$ are 0, $\frac{1}{m_1-1}$, and 1. To insure $\int_0^1 [g(\infty, u) - u]\mathrm{d}u > 0$ and therefore $c^*(\infty) > 0$ it is necessary for $m_1 > 3.295$.

We will simulate the scenario where $c < c^*(\infty)$ and where $c > c^*(\infty)$. We will also examine the relation between initial conditions, the habitat shift speed and persistence by finding the critical support , d^*, where the initial condition

$$u_0(x) = u_{\{d\}}(x) := \begin{cases} 1 & 0 \leq x \leq d, \\ 0 & \text{otherwise}, \end{cases}$$

leads to persistence.

For these simulations we choose the parameters $m_0 = 5$ and $m_1 = 15$. The graphs of $g(-\infty, u)$ and $g(\infty, u)$ can be seen in Fig. 1. For this choice of parameters $c^*(\infty) = .9982$. A graph of $c^*(\infty)$ vs. m_1 can be seen in Fig. 2. The speed was determined by iterating the model, and back-shifting the solution so that the value of $u_n(0)$ remains fixed, until a fixed point condition is met. The degree of backshift is $c^*(\infty)$.

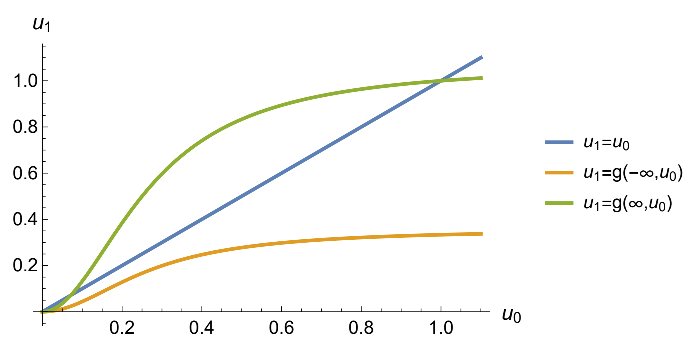


Figure 1: The graphs of $g(-\infty, u)$ and $g(\infty, u)$ with $m_0 = 5$ and $m_1 = 15$.

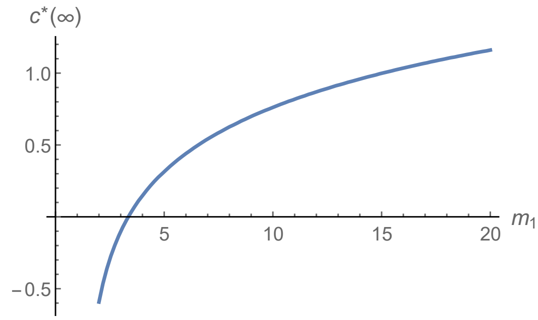
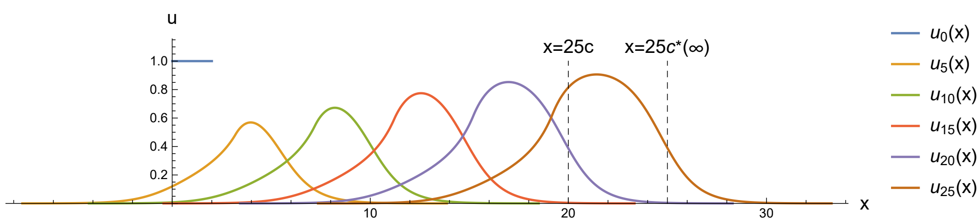
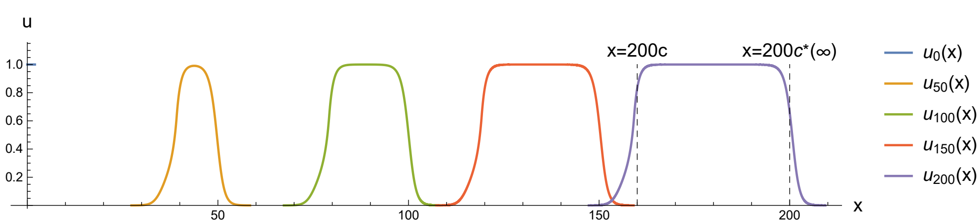


Figure 2: A graph of $c^*(\infty)$ versus m_1.

In Fig. 3 we show how a solution evolves when $c < c^*(\infty)$ and the initial condition is adequate to ensure persistence. Here $c = 0.8$, and $u_0(x) = u_{\{2\}}(x)$. We see as time becomes large the trailing edge of the population tracks closely with $x = c\,n$ and the leading edge tracks closely with $x = c^*(\infty)\,n$. Panel (a) of Fig. 3 show details of the early evolution of the solutions while panel (b) shows the evolution for later times. In Fig. 4 we show a solution where $c > c^*(\infty)$. The population spread cannot keep up with good habitat and it goes extinct. This will be true regardless of initial conditions, but the time till extinction will increase as the support of the initial condition increases.



(a) early evolution of the solution: $n = 0, 5, \cdots, 25$



(b) later evolution of the solution: $n = 0, 50, \cdots, 200$

Figure 3: The evolution of the solution for $u_0(x) = u_{\{2\}}(x)$ and $c = 0.8$. The dashed vertical line at $x = 200c$ in panel b corresponds to the boundary between the good and bad habitat for $u_{200}(x)$. Here $c^*(\infty) = .9982$, $m_0 = 5$ and $m_1 = 15$. We see the population persists as $c < c^*(\infty)$.

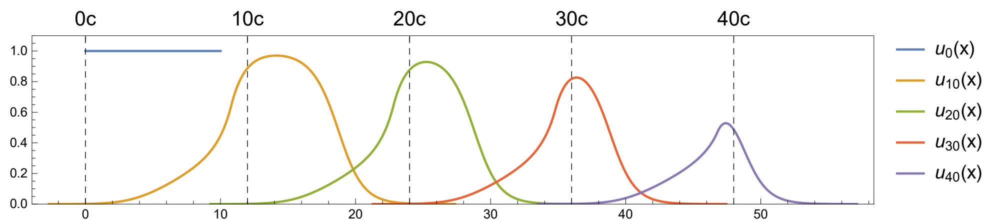


Figure 4: A plot of the solution where $c > c^*(\infty)$. Here $u_0(x) = u_{\{10\}}(x)$, $c = 1.2$, $c^*(\infty) = .9982$, $m_0 = 5$ and $m_1 = 15$. We see the population goes extinct.

In Fig. 5 we examine how the minimum support for the initial condition $u_0(x) = u_{\{d\}}(x)$ depends on the speed of the habitat shift. We define this threshold value as d^*. To conduct the simulation we characterized solutions where the total population increased consecutively 50 times in a row as persisting, and those where the maximum density is less than the Allee threshold as being effectively extinct. We then used a bisection algorithm until the difference between the upper and lower bound for d^* is less than 0.001. We see that d^* increases rapidly as c approaches $c^*(\infty)$. Due to limitations of numerical accuracy we did not attempt to compute d^* for values of c greater than $0.99c^*(\infty)$.

In Fig. 6 we examine the effect of shifting the initial condition, $u_0(x) = u_{\{d\}}(x)$, to the left by the amount $\tilde{x}_1$ for several values of habitat shift speed. The initial condition is thus $u_0(x) = u_{\{d\}}(x - \tilde{x}_1)$. We see that as the shift becomes large, the required initial support asymptotically approaches the value of 0.3359 regardless of the speed of the habitat shift. This is illustrative of Theorem 3.2, which to paraphrase, states that for a sufficiently large shift ($\tilde{x}_1$) and an interval of sufficient size above the Allee threshold ($[\tilde{x}_1, \tilde{x}_1 + 2r_\sigma]$) the population can survive for any value of c less than $c^*(\infty)$.

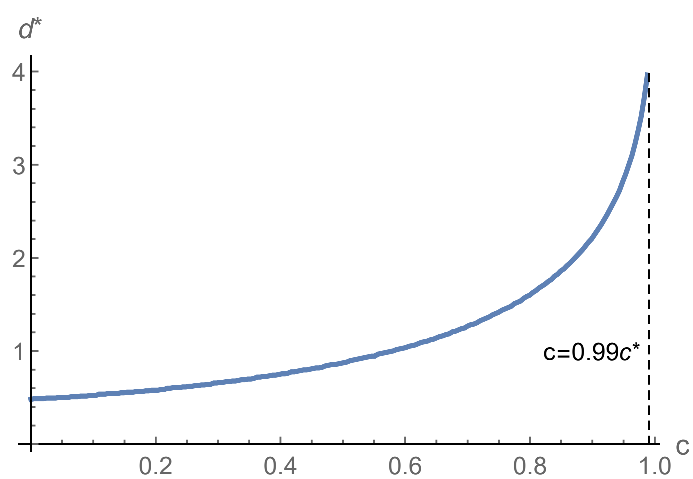


Figure 5: A plot of the critical initial support size for $u_0(x) = u_{\{d\}}(x)$ versus the habitat shift speed c. Here $m_0 = 5$ and $m_1 = 15$.

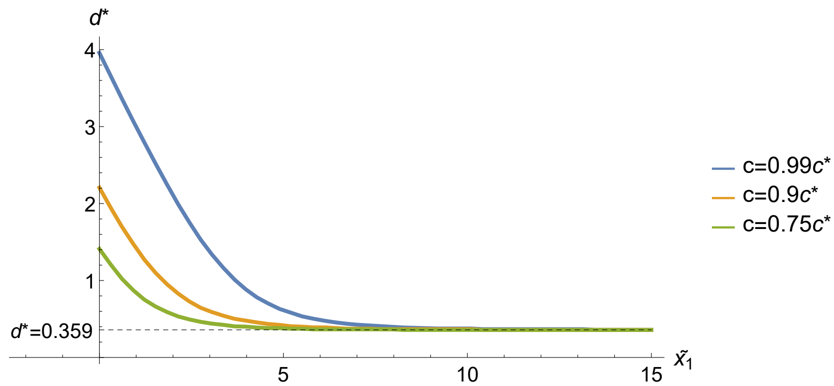


Figure 6: A plot of the critical support size for the initial condition versus the left-most position of the initial support. $u_0(x) = u_{\{d\}}(x - \tilde{x}_1)$. Here $m_0 = 5$ and $m_1 = 15$.

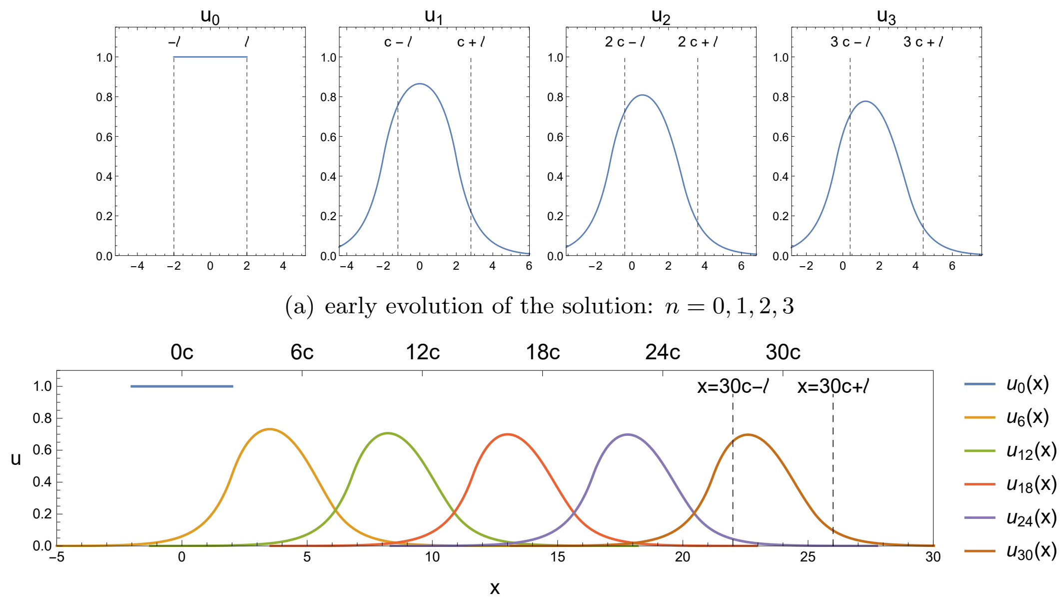
Case 2: Shifting habitat conforming to Hypotheses 2.3. We will use the growth function

$$g(x,u) = \begin{cases} \frac{mu^2}{1+(m-1)u^2} & |x| \leq l \\ 0 & \text{otherwise} \end{cases} . \tag{5.1}$$

As in Case 1, $\int_0^1 [g_0(u) - u]\mathrm{d}u > 0$ so by Theorem 4.1(i) we would expect a persistent solution for sufficiently large l. In these simulations we will examine how the habitat shift speed (c) and patch size (l) affect the persistence of solutions and the resulting stable traveling wave solutions. We will also present a graph showing the relation between c and l^*. The initial condition used in these simulations is

$$u_0(x) = u_{\{l\}}(x) := \begin{cases} 1 & |x| < l \\ 0 & \text{otherwise} \end{cases} .$$

In Fig. 7 we show the evolution of a solution where the habitat shift speed is less than $c^*(\infty)$, and the habitat size is larger than the critical size, l^*. In subfigure-a we use a moving reference frame in the four snapshots to better show detail. We see that the population persists and a stable traveling wave solution develops. In Fig. 8 we show the evolution of a case where the habitat moves at speed greater than $c^*(\infty)$. We see that the population can not keep up with the favorable habitat and goes extinct. In Fig. 9 we show a solution where the habitat size falls below the critical value l^*. The losses due to dispersal and habitat shift are too great, and the population goes extinct.



(a) early evolution of the solution: $n = 0, 1, 2, 3$

(b) later evolution of the solution: $n = 0, 6, \cdots, 30$

Figure 7: The evolution of a solution where $c < c^*(\infty)$ and $l > l^*$. Here $l^* = 1.76$, $l = 2$, $u_0(x) = u_{\{2\}}(x)$, $c^*(\infty) = .9982$, $c = 0.8$ and $m = 15$. The region between dashed vertical lines on panel (b) represents the habitat favorable to growth for $u_{30}(x)$.

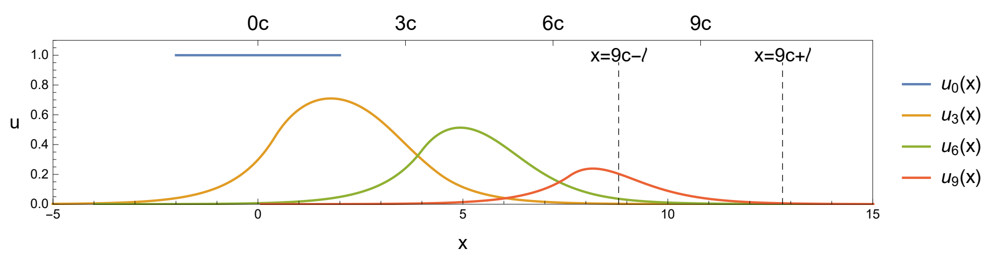


Figure 8: The evolution of a solution with $c > c^*(\infty)$. Here $l^* = 1.76$, $l = 2$, $u_0(x) = u_{\{2\}}(x)$, $c^*(\infty) = .9982$, $c = 1.2$ and $m = 15$. The region between the dashed vertical lines represents the habitat favorable to growth for $u_9(x)$.

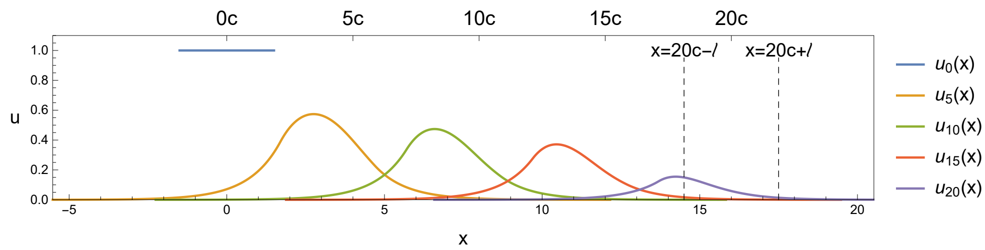
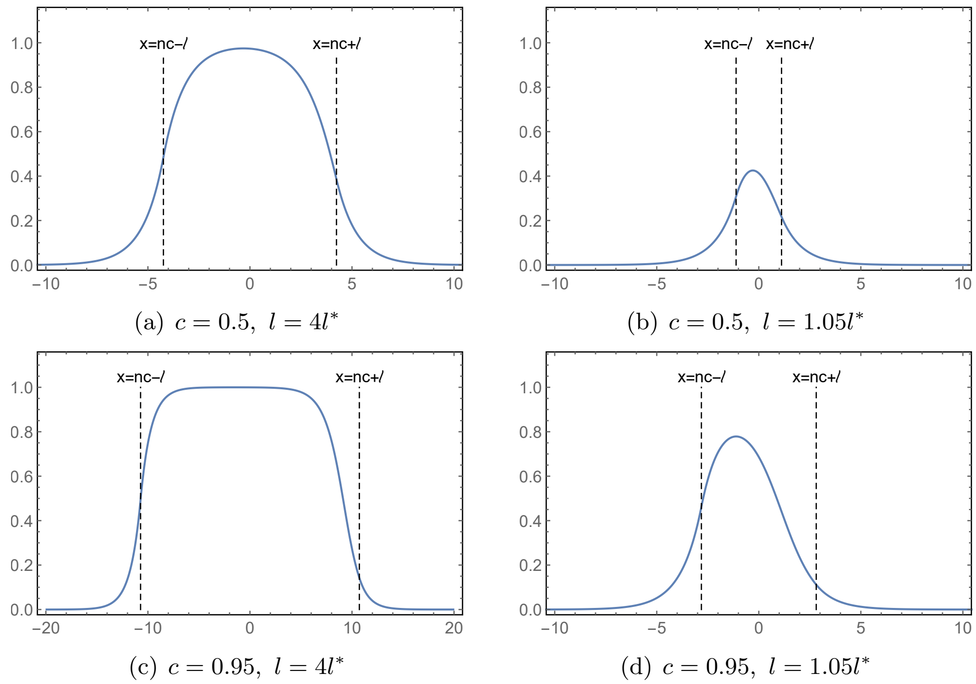


Figure 9: The evolution of a solution with $l < l^*$. Here $l^* = 1.76$, $l = 1.5$, $u_0(x) = u_{\{2\}}(x)$, $c^*(\infty) = .9982$, $c = 1.2$ and $m = 15$. The region between dashed vertical lines represents the habitat favorable to growth for $u_9(x)$.

In Fig. 10 we show the stable traveling wave solution for different values of c and l. To compute the stable travelling wave we iterated the solution with $u_0(x) = u_{\{l\}}(x)$ until $\max_{-l \le x \le l} |g(x, u_n(x + nc)) - g(x, u_{n-1}(x + (n-1)c)|$ meets a fixed point tolerance. We can see that when l is much larger than l^* then density has a broad plateau approaching the carrying capacity. As l approaches l^* we see the peak density decreases and the plateau becomes less pronounced. As the habitat shift speed approaches $c^*(\infty)$ we see the location of the peak becomes more biased to the left.

Fig. 11 shows how the total population of the stable travelling wave solution varies with the habitat shift speed. This is obtained by numerically integrating the solution over the spatial coordinate. The habitat size in this figure is fixed at $l = 2$ and $m = 15$. We see for low speeds population weakly decreases, however as c approaches 0.85 the population rapidly falls to zero. As can be seen from Fig. 12, $l^* = 2$ corresponds to $c \approx 0.85$. Due to limitations of the accuracy of the numerical methods, there is some amount of jitter in the plot, plot markers are thus used to indicate the actual sample points.



(a) $c = 0.5,\ l = 4l^*$

(b) $c = 0.5,\ l = 1.05l^*$

(c) $c = 0.95,\ l = 4l^*$

(d) $c = 0.95,\ l = 1.05l^*$

Figure 10: The stable traveling wave solutions for different habitat shift speeds and sizes. It should be noted the x-coordinates are labelled such that 0 corresponds to $c\,n$. $c^*(\infty) = .9982$ and $m = 15$ for all subfigures.

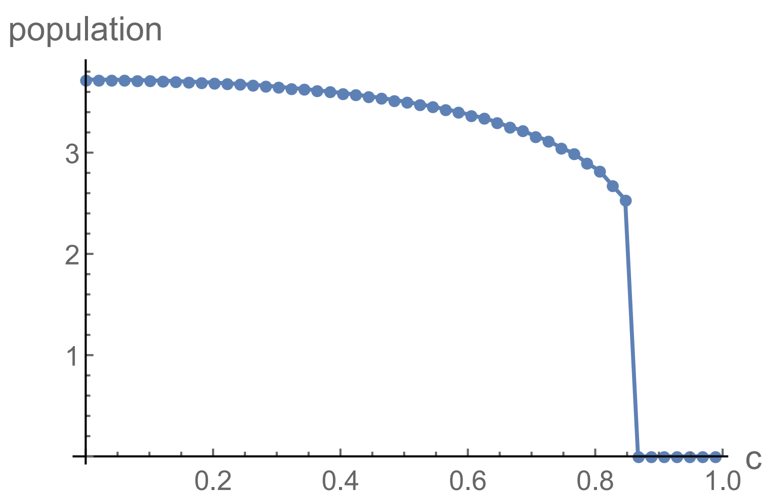


Figure 11: The total population of the stable travelling wave solution versus the habitat shift speed. The habitat size is $l = 2$ and $m = 15$.

In Fig. 12 we see how the critical patch size depends on habitat shift speed for three different dispersal kernels. The kernels used are the Laplace, Gaussian, and Uniform distributions, all with mean zero and variance 2. These are members of the generalized Gaussian distribution with exponents

1 for Laplace, 2 for Gaussian, and the Uniform is the limiting case as the exponent approaches infinity. The kurtosis decreases as the exponent increases, thus the Laplace has more individuals dispersing extreme distances. See Otto et al. [40] for a more detailed discussion on this family of kernels.

The values of l^* were determined by using a bisection method similar to that for d^*. To determine persistence, solutions where iterated until a fixed point condition was met or the maximum density fell below the Allee threshold. The dashed vertical lines represent $c^*(\infty)$ for the respective distributions. As was the case for d^*, we see there is a rapid increase as c approached $c^*(\infty)$. Due to limits of numerical accuracy we did not attempt to compute l^* beyond $0.99c^*(\infty)$. It is interesting to note the curves become flatter as the kurtosis decreases, indicating species with leptokurtic dispersal may be more sensitive to patch size in a shifting habitat. The cause of this may have to do with the fact that extreme dispersal may cause more individuals to fall in sparsely populated regions where the population is below the Allee threshold.

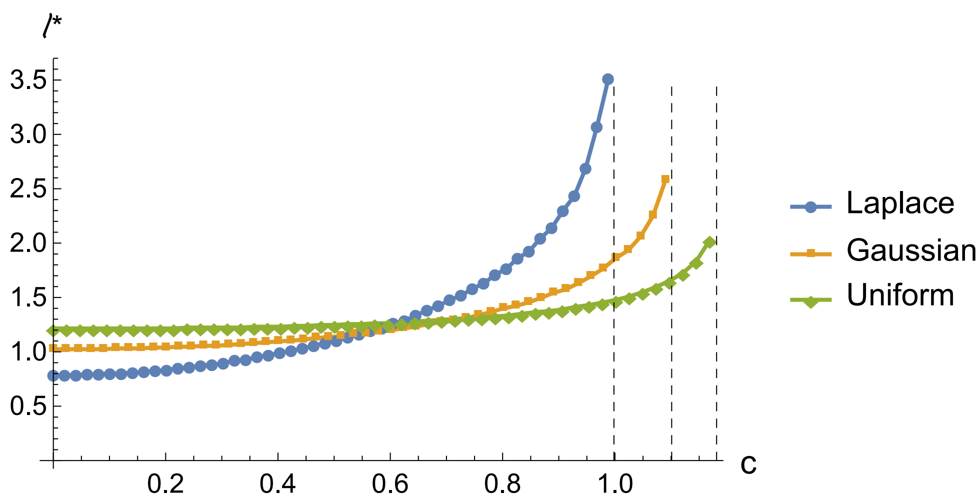


Figure 12: A plot of the critical habitat size (l^*) versus the habitat shift speed (c) for different dispersal kernels with mean 0 and variance 2. $m = 15$.

Finally, in Fig. 13 we show how l^* depends on the Allee threshold for the growth function given by (5.1) for a habitat shift speed fixed at $c = 0.5$. It should be noted that the Allee threshold (α_0) is related to the parameter m by $\alpha_0 = \frac{1}{m-1}$. As the Allee threshold approaches zero and thus m approaches infinity we see the critical habitat size approaches zero. The vertical asymptote at $\alpha_0 = 0.182$ corresponds to $m = 6.495$, which as can be seen on Fig. 2 corresponds to $c^*(\infty) = 0.5$.

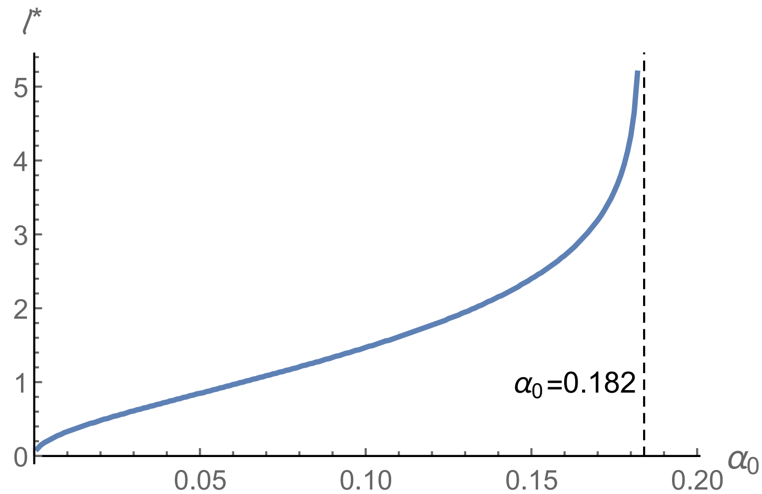


Figure 13: A plot of l^* versus the Allee threshold. The habitat shift speed is $c = 0.5$. It should be noted the Allee threshold is related to m by $\alpha_0 = \frac{1}{m-1}$.

6 Discussion

In this paper, we studied the population dynamics for (1.1) with a strong Allee effect in a shifting habitat in response to climate change. We investigated the case of a shifting semi-infinite bad habitat, where the species declines, connected to a semi-infinite good habitat, where the species grows. We found that the habitat shift speed c and the asymptotic spreading speed $c^*(\infty)$ in the good habitat determine species persistence. Particularly, we showed that if $c^*(\infty) > c > 0$ then a species with an initial distribution having values above the Allee threshold in an appropriately large interval will persist, and if $c^*(\infty) < c$ then extinction will take place. In the former case, a nondecreasing traveling wave with speed c connecting 0 and the equilibrium above the Allee threshold exists. We also examined the case of a shifting bounded habitat on which the species grows. We demonstrated that species persistence depends on the habitat size, shift speed c, and asymptotic spreading speed c^* for the corresponding model with the same growth function in the habitat $(-\infty, \infty)$. Particularly we showed (i) if $c^* > c$, there is a critical patch size l^* which is the minimal habitat size for species persistence, and (ii) if $c^* < c$ then species dies out eventually.

These results are in line with those for (1.1) with a shifting habitat and no Allee effect given in [28, 29, 53]. Similar results were obtained for reaction-diffusion equations without Allee effect [2, 3, 19, 27]. However, there are important differences between results of these papers and those in the present paper. Firstly, linearization about zero was used to study persistence of solutions for models without Allee effect, while a new approach is taken in this paper to study the case of strong Allee effect. Specifically, in this paper, with the presence of a strong Allee effect, long term behavior of solutions of homogeneous systems was used to study persistence for an unbounded habitat, and a limit process was employed to determine the critical habitat size for a bounded habitat. In contrast, without Allee effect, a lower solution with appropriate speed based on a linearized system plays a key role for establishing persistence in a shifting unbounded habitat [19, 27, 28], and the principal eigenvalue of a linearized system determines persistence in a shifting bounded habitat [2, 53]. The principal eigenvalue depends on the derivative of the growth function at zero, the shift speed c, patch size, and the dispersal kernel. The principal eigenvalue is set to 1 to find the critical patch size in terms of other components. In the presence of a strong Allee effect, linearizion is no longer valid to discuss the critical patch size. One has to consider the growth function on the entire domain from zero to the carrying capacity. This is seen from our definition of l^* where integrals of the growth function with appropriate density functions are involved. The methodology in this paper works for (1.1) in the case of weak Allee effect as well, and it also provides an alternative way to investigate the situation without Allee effect. Secondly, the persistence results for (1.1) with a strong Allee effect are more restrictive. When a strong Allee effect exists, the condition $\int_0^{\beta(\infty)}[g(\infty,u)-u]du \geq 0$ is necessary for persistence in a habitat. In an unbounded habitat, without Allee effect, persistence holds when the initial data has positive values in any small interval where growth is nonzero [28]; with a strong Allee effect, in order for persistence to take place, the initial data must have values above the Allee threshold in a large interval and the location of initial data matters in general. It should be also pointed out that the spreading speed established in this paper is in a weaker sense. Specifically (3.9) holds for a large fixed integer n_0, while $n_0 = 1$ is only needed in the absence of Allee effect [28].

We established the existence of traveling waves for both unbounded habitats and bounded habitats. The traveling waves are forced by the shifting habitats and their speeds are the same as the habitat shift speeds. Our analysis showed that traveling waves attracts solutions with initial data above them. Consequently for the bounded habitat case there exists a large class of initial distributions for which the solutions persist in space. Li and Wu [29] showed that for (1.1) with a shifting semi-infinite bad habitat and no Allee effect, besides existence of a monotone traveling wave, there are infinitely many pulse traveling waves. It is an open question if pulse traveling waves exist in the presence of a strong Allee effect for unbounded habitats. We conjecture that there is a second traveling wave for the case of bounded habitat and strong Allee effect. This was shown to be true for a corresponding reaction-diffusion model [31].

The numerical simulations provided in Section 5 supported the theoretical results obtained in Section 3 and Section 4. The Case 1 simulations corresponded to a semi-infinite high quality habitat. In Fig. 3 we showed the density curves of a solution persisting when $c < c^*(\infty)$. In Fig. 4 we showed a solution reaching extinction when $c > c^*(\infty)$. Fig. 5 and 6 explore the dependance of persistence on initial conditions. In Fig. 5 we observed that the minimum support for the initial condition with values above the Allee threshold depends on the speed of the habitat shift. It may be worth investigating the monotonicity of this relation analytically. Theorem 3.2 is supported by Fig. 6 which shows that for a sufficient left shift there is an initial domain size that leads to persistence regardless of c.

The Case 2 simulations corresponded to a finite interval of high quality habitat. In Fig. 7 we showed persistence when $c < c^*(\infty)$ and $l > l^*$. In Fig. 8 we showed non-persistence when $c > c^*(\infty)$. In Fig. 9 we showed non-persistence when $l < l^*$. Fig. 10 shows how the shape of the stable travelling wave depends on c and l. Fig. 11 shows how the total population depends on c, showing a very rapid decline as c approaches $c^*(\infty)$. In Fig. 12 we showed how l^* depends on c for 3 different dispersal kernels of the same variance. The monotone relation between c and population size, and c and l^* suggested by Fig. 11 and 12 warrants further analytical investigation. The relation between persistence and shape of dispersal also would be of interest for future investigations. Finally, in Fig. 13 we showed the critical patch size depends on the Allee threshold for the form of growth function we chose and a fixed c.

Papers [28] and [29] also considered the scenario where two semi-infinite habitats with different levels of good quality are connected. We plan to study this scenario when there is a strong Allee effect. This paper assumes that the growth function is monotone in species density. It is possible that a growth function is non-monotone in density, i.e., there exists overcompensation in population growth. It is known that a combination of strong Allee effect and overcompensation in a homogeneous integro-difference equation with the habitat $(-\infty, \infty)$ can produce oscillations in spreading speed (see Sullivan et al. [48] and Nestor and Li [38]), and oscillating nonspreading solutions (see Otto et al. [40]). It would be of great interest to investigate a system in the form of (1.1) with both strong Allee effect and overcompensation. We leave the problem for future investigations.

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