A SPATIAL MODEL OF PLANTS WITH AN AGE-STRUCTURED SEED BANK AND JUVENILE STAGE

KIMBERLY I. MEYER† AND BINGTUAN LI†

Dedicated to Professor Hans F. Weinberger on the occasion of his 85th birthday

Abstract. We formulate an integro-difference model to predict the growth and spatial spread of a plant population with an age-structured seed bank and juvenile cohort. We allow the seeds in the bank to be of any age, producing a system of infinitely many equations. We assume that juvenile plants mature into adults at a particular age. The production of new seeds can be density-dependent and so the function describing this growth is allowed to be nonmonotone. The functions describing the seed bank and juvenile plants are linear. We show that when the system has a positive equilibrium, there is a spreading speed that can be computed using model parameters and that this spreading speed can be characterized as the slowest speed of a class of traveling wave solutions. The spreading speed results are obtained through linearization and comparison to an analogous finite system, while the existence of traveling wave solutions is shown by using an asymptotic fixed point theorem. We conduct numerical simulations of a truncated version of this model. These simulations show that both the perennial term and the seed bank can have a stabilizing effect on the population. On the other hand, traveling wave solutions may exhibit different patterns of fluctuations including periodic oscillations and chaotic tails.

Key words. integro-difference model, seed bank, spreading speed, traveling wave solution

AMS subject classifications. 92D40, 92D25

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1. Introduction. Dispersal of seed in plant populations can play a major role in the population dynamics and spatial spread of a species [3]. This process is difficult to quantify, and thus, historically, population models tend to ignore dispersal [24, 32, 34, 39]. In the past several decades integro-difference equations have emerged as a means of studying spatial spread of ecological populations [1, 2, 7, 9, 12, 13, 14, 15, 22, 25, 26, 35], among other applications. The main function of these types of models is to elucidate dispersal patterns by quantifying the rate of spread of populations and investigating traveling wave solutions, that is, solutions maintaining a fixed shape and fixed speed.

Integro-difference equations describe situations in which growth and dispersal occur independently, as is the case for annual and perennial plants. In the simplest case, an integro-difference model takes the form of a convolution integral with a density-dependent fecundity function and a flexible dispersal kernel. It has been shown (see Weinberger [41]) that if the fecundity function is a nondecreasing function, the integro-difference model predicts that there is a spreading speed that can be characterized as the slowest speed of a class of traveling wave solutions. Additionally, if the growth function does not exhibit an Allee effect, it can be computed from the linearization about zero [41]. This result has been extended to scalar models with nonmonotone growth functions [10, 19]. The case of a structured population (i.e., by

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†Department of Mathematics, University of Louisville, Louisville, KY 40292 (meyer.kimberly@gmail.com, bing.li@louisville.edu). The first author’s research was partially supported by the National Science Foundation under grant DMS-0616445. The second author’s research was partially supported by the National Science Foundation under grants DMS-0616445 and DMS-1225693.
age, size, etc.) can be modeled by a system of integro-difference equations; see, for example, Neubert and Caswell [25]. Spreading speeds of systems of integro-difference equations were analytically studied in Lui [21]. A rigorous treatment of spreading speeds and traveling wave solutions for abstract evolution systems can be found in Liang and Zhao [20].

In the context of plant populations, dispersal occurs through passive seed movement (wind, water, active agent, etc.). However, once a seed has been dispersed, it gets buried in the ground and can persist in dormancy for many years. This cohort of buried seed cannot disperse and comprises what is known as the seed bank. The longevity and viability of seeds in the seed bank are dependent upon the type of species, availability of resources, and natural environmental conditions. Seed banks may contain just a few hundred to over 100,000 seeds per square meter, and seeds may persist for hundreds or even thousands of years; see [6, Chapter 4] and [34]. This type of delay in germination can naturally have consequences on the overall population dynamics of the plant as well as the spatial spread of the population. Several nonspatial models for plants have been proposed (e.g., [24, 32, 34, 36, 37]). These models take the form of scalar difference equations or systems of finitely or infinitely many difference equations. Allen, Allen, and Gilliam [1] first studied the existence of traveling waves in integro-difference models with a seed bank. A thorough analysis for the existence of traveling waves in a scalar integro-difference model with a seed bank was given by Li [18]. It was shown that the model has a spreading speed that can be characterized as the slowest speed of a class of traveling wave solutions, despite the fact that the growth is allowed to be nonmonotone and the recursion operator is non-compact. Additionally, numerical simulations showed that in the presence of a seed bank, oscillations in the tails of traveling waves may be damped. Thus, the seed bank can have a stabilizing effect on the plant population. Lutscher and Van Minh [23] proposed a monotone integro-difference model for studying the spatial spread of an annual plant population with an infinite age-structured seed bank. The nonspatial version of the system was considered by Valleriani and Tielbörger [36]. Lutscher and Van Minh proved the existence of spreading speeds and traveling wave solutions for some special cases where the infinite system is reduced to a finite system. The problem of spreading speeds and traveling wave solutions for the full infinite system remains unsolved. Powell, Slapničar, and van der Werf [29] proposed a model for studying the spread of a lesion-forming plant pathogen with infinite age structure. However, the existence of spreading speed and traveling wave solutions for the model was not established analytically.

In this paper we study a nonmonotone spatial model for perennial and annual plants with an age-structured seed bank and a juvenile cohort in the form of an infinite integro-difference equation system. Our model has the benefit of synthesizing and generalizing many of the aforementioned models, while providing a clear focus on perennial plants. We provide a formula for the spreading speed of the model. We show that the spreading speed can be characterized as the slowest speed of a class of traveling wave solutions. The spreading speed results are obtained through linearization and comparison to an analogous finite system, while the traveling wave results make use of an asymptotic fixed point theorem. Our numerical simulations show that both the seed bank and the perennial term can have a stabilizing effect on the population, and that the tails of traveling wave solutions can take on many different patterns. (We will explain in more detail what we mean by the term stabilizing in section 6.)

The paper is arranged as follows. In section 2 we introduce an infinite integro-
difference system that models perennial and annual plants with an age-structured seed bank and juvenile cohort. We allow for density-dependent growth (a fundamental premise in plant population growth [8]). We also include a term that describes the survivorship of adults from generation to generation. Section 3 introduces notation and provides some preliminary results that set the stage for analysis in subsequent sections. We show the existence of a spreading speed in section 4, and in section 5 we present our results on the existence of traveling wave solutions. Section 6 is about numerical simulations of traveling wave solutions, and section 7 includes a discussion and some future directions.

2. The model. We begin with a general description of the life-cycle of an adult perennial plant. We follow the one-year life-cycle and assume the process begins at the end of summer. Adult plants produce seeds at the end of summer, the seeds lie dormant in the fall and winter, germinate in the spring, and finally become juvenile plants by the end of the next summer. Juvenile plants remain unable to produce seeds for a period of time dependent on the species. Upon maturation, juvenile plants become fecund adults. Since perennial plants can live for more than one year, also assume that a portion of the adult plants survive dormancy and are present in the next year.

Seeds that do not germinate during the spring but survive dormant in the ground contribute to the seed bank. To investigate the effect of the seed bank on the overall adult population, we distinguish seeds in the bank by age. Additionally, juvenile plants that do not mature remain juveniles into the next year, and so we distinguish juvenile plants by age. We assume that juvenile plants become mature in the \( \tau \)th year. Let \( A_n \) represent the density of adult plants at time \( n \) (\( n \in \{0, 1, 2, \ldots\} \)), let \( J^k_n \) represent the density of \( k \)-year-old juvenile plants at time \( n \) (\( k \in \{1, 2, \ldots, \tau\} \)), and let \( S^j_n \) represent the density of \( j \)-year-old seeds in the seed bank at time \( n \) (\( j \in \{1, 2, \ldots\} \)). The average number of seeds produced per adult individual is described by some function \( F \). We assume that survival and germination rates are constants for all cohorts of the population. The parameter \( \rho \) indicates a survival rate with a subscript of \( d \) signifying survival over the dormant period (\( \rho_d \)), a subscript of \( \nu \) signifying survival over the vegetative period (\( \rho_\nu \)), and a subscript of \( o \) signifying survival of adult plants over one year (\( \rho_o \)). The parameter \( b \) represents survivorship of juvenile plants over the span of a year. The parameter \( \beta \) indicates a germination probability. Assume that survivorship over the dormant period is age-dependent. Alternatively, we assume that the age of a germinating seed has no effect on survivorship over the vegetative period. Hence, we have only two survival rates associated with the vegetative period: one describing survival of germinated seed \( \rho_\nu \), and the other describing survival of nongerminated seed \( \rho_\nu/2 \). This assumption has been used in other plant population models as well [32, 36]. Many physical, physiological, and ecological processes related to germination are time-dependent. For example, over time, germination inhibitors decay and the seed coat becomes tainted [30]. Thus, seeds of varying ages will naturally have differing rates of germination. Thus, we assume that the seed germination rates are age-dependent.

The flow-chart in Figure 1 depicts the life-cycle of each cohort. The life-cycle goes from the end of summer in year \( n \) to the end of summer in year \( n + 1 \). Over the course of a year, adult plants can contribute to the next year’s population in two ways. First, because we consider perennial plants, a portion \( \rho_o \) of the adult population in year \( n \) will survive a year and again be part of the adult population in year \( n + 1 \). Second, adults produce new seeds, the number of which is determined by the function \( F \).
Fig. 1. Life-cycle of perennial plant population with a seed bank.

Age-Structured Juvenile and Seed Bank Model
Table 1: Seed bank model—parameter descriptions.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description of parameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \rho_0 )</td>
<td>probability an adult plant survives a full year</td>
</tr>
<tr>
<td>( \rho_j'^d )</td>
<td>probability a ( j )-year-old seed survives the dormant period</td>
</tr>
<tr>
<td>( \beta_j )</td>
<td>probability a ( j )-year-old seed germinates</td>
</tr>
<tr>
<td>( \rho_{v1} )</td>
<td>probability a germinated seed survives the vegetative period</td>
</tr>
<tr>
<td>( \rho_{v2} )</td>
<td>probability a nongerminating seed survives the vegetative period</td>
</tr>
<tr>
<td>( a_j = \rho_j'^d \beta_j \rho_{v1} )</td>
<td>probability a ( j )-year-old seed develops into a one-year-old juvenile plant</td>
</tr>
<tr>
<td>( s_j = \rho_j'^d (1 - \beta_j) \rho_{v2} )</td>
<td>probability a ( j )-year-old seed becomes a ((j+1))-year-old seed</td>
</tr>
<tr>
<td>( b_j ), for ( j \in {1, \ldots, \tau - 1} )</td>
<td>probability a ( j )-year-old juvenile becomes a ((j+1))-year-old juvenile</td>
</tr>
<tr>
<td>( b_{\tau} )</td>
<td>probability a ((\tau-1))-year-old juvenile matures into an adult plant</td>
</tr>
</tbody>
</table>

A portion of these new seeds will survive the dormant period with probability \( \rho_0'^d \), a portion \( \beta_0 \) will germinate, and a portion \( \rho_{v2} \) will survive the vegetative period. These surviving plants are now part of the one-year-old juvenile cohort \( J_{n+1}^1 \). The portion of nongerminated seeds \((1 - \beta_0)\) will survive the vegetative period with probability \( \rho_{v2} \) and become part of the one-year-old seed bank cohort \( S_{n+1}^1 \). To observe the life-cycle of the remaining seed bank cohorts, a similar logical flow can be applied.

The dispersal process affects only newly produced seeds since older seed has already been set in the ground. We couple a dispersal kernel \( k(x) \) with the reproduction \( F \). We obtain the following model for the spatial spread of a plant population with a juvenile stage and age-structured seed bank:

\[
J_{n+1}^1(x) = a_0 \int_{-\infty}^{\infty} k(x-y) H(A_n(y)) dy + \sum_{j=1}^{\infty} a_j S_n^j(x),
\]

\[
J_{n+1}^2(x) = b_1 J_{n+1}^1(x)
\]

\[ \vdots \]

\[
J_{n+1}^\tau(x) = b_{\tau-1} J_{n+1}^{\tau-1}(x),
\]

\[
A_{n+1}(x) = b_\tau J_{n+1}^{\tau-1}(x) + \rho_0 A_n(x),
\]

\[
S_{n+1}^1(x) = s_0 \int_{-\infty}^{\infty} k(x-y) H(A_n(y)) dy,
\]

\[
S_{n+1}^2(x) = s_1 S_n^1(x)
\]

\[ \vdots \]

\[
S_{n+1}^{m+1}(x) = s_m S_n^m(x)
\]

where \( H(A) = F(A)A \), \( a_j = \rho_j'^d \beta_j \rho_{v1} \) for all \( j = 0, 1, \ldots \), and \( s_j = \rho_j'^d (1 - \beta_j) \rho_{v2} \) for all \( j = 0, 1, 2, \ldots \).

The parameters \( a_j \) and \( s_j \) are a product of survival and germination rates and may be interpreted as the age-dependent probabilities of contribution to either the juvenile population or the seed bank population (hence the choice of parameter \( s \)). Table 1 gives a description of each parameter. Age-dependent parameters are identified with superscripts indicating the age of the cohort that is related to the parameter.

We make the following assumptions on the model (2.1).
Hypotheses 2.1.

i. \(0 \leq \rho_0 < 1, 0 < \rho_1 \leq 1, 0 < \rho_2 \leq 1, 0 < \rho_j^I \leq 1, 0 \leq \beta_j < 1, \) and \(0 < b_j \leq 1\) for all \(j, s_i > 0\) for all \(i\), and \(a_i > 0\) for infinitely many \(i\).

ii. \(H(u)\) is continuous for \(u \geq 0\), \(H(0) = 0\), and \(H(u)\) is differentiable at 0.

iii. \(H(u)/u\) is nonincreasing for \(u > 0\) and \(\lim_{u \to \infty} H(u)/u = 0\).

iv. There are positive constants \(d\) and \(D\) such that
   \[ H(u) \text{ is nondecreasing for } 0 < u \leq d, \]  
   \[ H(u) \geq H'(0)u - Du^2 \text{ for } 0 \leq u \leq d. \]

v. \(1 < \rho_0 + (\prod_{i=1}^n b_i)H'(0)\left[a_0 + \sum_{j=1}^\infty a_j(\prod_{i=0}^{j-1}s_i)\right].\)

vi. \(k(x)\) is a nonnegative continuous function such that
   \[ a. \int k(x)dx = 1, \]  
   \[ b. \text{the integral } K(\mu) := \int \frac{k(x)e^{\mu x}dx}{x} \]
   converges for \(\mu \in I\), where \(I\) is an interval containing 0 as an interior point, and diverges for \(\mu \notin I\) if \(I \neq (-\infty, \infty).\)

vii. \(\sum_{j=1}^\infty (\prod_{i=0}^{j-1}s_i)\) is convergent, and if \(k(x)\) is asymmetric, then the series \(\sum_{j=1}^\infty (a_j \prod_{i=0}^{j-1}s_i)z^j\) is convergent for all \(z > 0.\)

The assumptions on the growth function \(H\) (Hypotheses 2.1 (ii–iv)) are common for ecological models of this type (see [16, 18, 19, 28]) and, specifically, are realized by the Beverton–Holt function and Ricker function. Particularly, they imply that \(H(u) \leq H'(0)u\) for \(u \geq 0\). Hypothesis 2.1 (v) guarantees that there exists a strictly positive constant equilibrium of the system (2.1). Hypothesis 2.1 (vii) will be needed in analyzing (2.1). One can use the ratio test and root test to find sufficient conditions under which the second part of Hypothesis 2.1 (vii) holds.

If \(\tau = 1\) and \(\rho_0 = 0\), model (2.1) is reduced to the infinite seed bank system introduced by Lutscher and Van Minh [23], where the growth function (i.e., \(H\)) is assumed to be monotone. We shall allow \(H\) to be nonmonotone in (2.1).

Remark 2.1. The assumption \(s_i > 0\) for all \(i\) and \(a_i > 0\) for infinitely many \(i\) in Hypothesis 2.1 (i) ensures that (2.1) is a system of infinite equations. If this assumption is not satisfied, then the model essentially involves only a finite number of equations. The analysis given below focuses on the case of infinite equations. However, it works for the case of finite equations. The theorems given in this paper are valid for a finite system if Hypotheses 2.1 (with the infinite sums replaced by appropriate finite sums) still hold.

We define the vector-valued operator

\[
Q[u](x) := \begin{pmatrix}
    a_0 \int_{-\infty}^{\infty} k(x-y)H(A(y))dy + \sum_{j=1}^\infty a_j S^j(x) \\
    b_1 J^1(x) \\
    \vdots \\
    b_{r-1} J^{r-1}(x) \\
    b_r J^r(x) + \rho_0 A(x) \\
    s_0 \int_{-\infty}^{\infty} k(x-y)H(A(y))dy \\
    s_1 S^1(x) \\
    \vdots \\
    s_m S^m(x) \\
    \vdots
\end{pmatrix},
\]
where \( u(x) = (u^{(1)}(x), u^{(2)}(x), \ldots) = (J^1(x), \ldots, J^r(x), A(x), S^1(x), \ldots) \). Thus \( (2.1) \) can be written in the more compact form
\[
 u_{n+1}(x) = Q[u_n](x).
\]

Model \( (2.1) \) is an infinite system, and \( Q \) is not compact due to the presence of the terms outside the integrals. \( Q \) satisfies the weak compactness assumption given in Liang and Zhao [20], and consequently the theory regarding spreading speeds and traveling waves for abstract monotone recursions developed by these authors applies to \( (2.1) \) when \( H \) is monotone. However, in [20] there is no spreading speed formula given for general recursions, and the spreading speed theory assumes that all components of the initial data are nonzero (that may be too strong for \( (2.1) \)). We shall develop a spreading speed formula for the spread of an invasion where only finitely many components of the initial data are required to be nonzero. We shall also take a more straightforward approach to prove the existence of traveling wave solutions in \( (2.1) \), for the case where \( H \) is monotone, and make use of some results for the monotone case to study the existence of traveling waves for the nonmonotone case.

We will sometimes refer to the \( m \)-dimensional analogue of system \( (2.1) \) \((m > \tau + 2)\), which we distinguish by using an additional subscript next to the time subscript:
\[
 J^1_{n+1|m}(x) = a_0 \int_{-\infty}^{\infty} k(x - y)H(A_{n|m}(y))dy + \sum_{j=1}^{m-\tau-1} a_j S^j_{n|m}(x),
\]
\[
 J^2_{n+1|m}(x) = b_1 J^1_{n|m}(x)
\]
\[
 \vdots
\]
\[
 J^{r}_{n+1|m}(x) = b_{r-1} J^{r-1}_{n|m}(x),
\]
\[
 A_{n+1|m}(x) = b_r J^r_{n|m}(x) + \rho_0 A_{n|m}(x),
\]
\[
 S^1_{n+1|m}(x) = s_0 \int_{-\infty}^{\infty} k(x - y)H(A_{n|m}(y))dy,
\]
\[
 S^2_{n+1|m}(x) = s_1 S^1_{n|m}(x)
\]
\[
 \vdots
\]
\[
 S^{m-\tau-1}_{n+1|m}(x) = s_{m-\tau-2} S^{m-\tau-2}_{n|m}(x).
\]

Similarly, we define the corresponding \( m \)-dimensional operator \( Q_m[u] \) so that
\[
 u_{n+1|m} = Q_m[u_{n|m}](x),
\]
where \( u_{n|m} = (u^{(1)}_{n|m}(x), \ldots, u^{(m)}_{n|m}(x)) = (J^1_{n|m}(x), \ldots, J^r_{n|m}(x), A_{n|m}(x), \ldots, S^{m-\tau-1}_{n|m}(x)) \).

Equation (2.4) is a truncated system of \( (2.1) \).

3. Preliminaries. We begin by introducing some notation. The space \( \ell_1 \) is a sequence space consisting of all real-valued sequences \( u = (u^{(1)}, u^{(2)}, u^{(3)}, \ldots) \) equipped with norm \( \|u\|_1 = \sum_{i=1}^{\infty} |u^{(i)}| \). Let \( u(x) \) and \( v(x) \) be two infinite-dimensional real-valued function sequences. The inequality \( u(x) \geq v(x) \) \((u \gg v)\) means that \( u^{(i)}(x) \geq v^{(i)}(x) \) for every \( i \). We define \( \max\{u(x), v(x)\} \) \((\min\{u(x), v(x)\}) \) to mean the vector-valued function whose \( i \)-th component at \( x \) is \( \max\{u^{(i)}(x), v^{(i)}(x)\} \) \((\min\{u^{(i)}(x), v^{(i)}(x)\}) \). We use the notation \( \mathbf{0} \) for the constant vector, all of whose components are 0.
A constant equilibrium \((J^1, \ldots, J^r, A, S^1, S^2, \ldots)\) of (2.1) satisfies
\[
(3.1) \quad J^i = \frac{1 - \rho_o}{b_i \cdots b_r} A, \quad S^j = \left( \prod_{i=0}^{j-1} s_i \right) H(A)
\]
and
\[
(3.2) \quad (1 - \rho_o) \left( \prod_{i=1}^{r} b_i \right)^{-1} A = \left[ a_0 + \sum_{j=1}^{\infty} a_j \left( \prod_{i=0}^{j-1} s_i \right) H(A) \right].
\]

We first observe that (3.1)–(3.2) have the trivial solution \(0\). It is easily seen that a nontrivial constant equilibrium must be an equilibrium that has all positive components. We rewrite (3.2) as
\[
(3.3) \quad \frac{H(A)}{A} = \frac{1 - \rho_o}{\left( \prod_{i=1}^{r} b_i \right) a_0 + \sum_{j=1}^{\infty} a_j \left( \prod_{i=0}^{j-1} s_i \right)}.
\]

By Hypothesis 2.1 (iii), \(H(A)/A \to 0\) as \(A \to \infty\), so that in (3.3) the right-hand side is greater than the left-hand side when \(A\) is large. On the other hand, \(H(A)/A \to H'(0)\) as \(A \to 0\), which, together with Hypothesis 2.1 (v), shows that in (3.3) the right-hand side is less than the left-hand side when \(A\) is positive and small. Since \(H(A)/A\) is continuous for \(A > 0\), the intermediate value theorem shows that (3.3) has a positive root. We use \(A_*\) to denote the smallest of such positive roots. Hence there exists a positive steady-state \(u_* = (J_*^1, \ldots, J_*^r, A_*, S_*^1, S_*^2, \ldots)\), where \(J_*^1\) and \(S_*^1\) are determined by (3.1) with \(A\) replaced by \(A_*\). Hypothesis 2.1 (vii) shows that \(u_* \in \ell_1\). For sufficiently large \(m\), Hypothesis 2.1 (v) shows that (2.4) has a positive constant equilibrium \(u_{*|m} = (J_{*|m}^1, \ldots, J_{*|m}^r, A_{*|m}, S_{*|m}^1, \ldots, S_{*|m}^{m-1})\), where \(J_{*|m}^i = \frac{1 - \rho_o}{b_i \cdots b_r} A_{*|m}, S_{*|m}^i = \left( \prod_{i=0}^{i-1} s_i \right) H(A_{*|m})\), and \(A_{*|m}\) satisfies
\[
H(A_{*|m})/A_{*|m} = \frac{1 - \rho_o}{\left( \prod_{i=1}^{r} b_i \right) a_0 + \sum_{j=1}^{m-1} a_j \left( \prod_{i=0}^{j-1} s_i \right)}.
\]
It is easily seen that \((u_{*|m}, 0, \ldots)\) approaches \(u_*\) as \(m \to \infty\) with respect to \(\| \cdot \|_1\).

If \(H(A)\) is a nondecreasing function for \(A > 0\), it is easily shown that a solution \(u_{0|m}\) of (2.4) with \(0 < u_{0|m} < u_{*|m}\) and \(u_{0|m}\) a constant vector satisfies \(\lim_{m \to \infty} u_{*|m} = u_{*|m}\). This and the fact that \((u_{*|m}, 0, \ldots) \to u_*\) as \(m \to \infty\) with respect to \(\| \cdot \|_1\) imply that a solution \(u_0\) of (2.1) with \(0 < u_0 < u_*\) and \(u_0\) a constant vector satisfies \(\lim_{n \to \infty} u_n = u_*\) with respect to \(\| \cdot \|_1\).

Observe that the linearization of \(Q\) about \(0\) is given by
\[
L[u](x) = \begin{pmatrix}
a_0 H'(0) \int_{-\infty}^{x} k(x - y) A(y) dy + \sum_{i=1}^{\infty} a_i S^i(x) \\
b_i J^1 \\
\vdots \\
b_{r-1} J^{r-1} \\
b_r J^r + \rho_o A \\
s_0 H'(0) \int_{-\infty}^{x} k(x - y) A(y) dy \\
s_1 S^1(x) \\
\vdots
\end{pmatrix}.
\]
where \( u(x) = (J^1(x), \ldots, J^\tau(x), A(x), S^1(x), S^2(x), \ldots) \). We introduce the moment generating matrix \( B_\mu \) for the linearization operator as

\[
B_\mu \alpha = \mathbf{L}[\alpha e^{-\mu x}]
\]

for every constant vector \( \alpha \). \( B_\mu \) is given by

\[
(3.4) \quad B_\mu := \begin{pmatrix}
0 & \cdots & 0 & 0 & a_0 H'(0) K(\mu) & a_1 & a_2 & \cdots \\
b_1 & \cdots & 0 & 0 & 0 & 0 & 0 & \cdots \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots \\
0 & \cdots & b_{\tau-1} & 0 & 0 & 0 & 0 & \cdots \\
0 & \cdots & 0 & b_{\tau} & \rho_o & 0 & 0 & \cdots \\
0 & \cdots & 0 & 0 & s_0 H'(0) K(\mu) & 0 & 0 & \cdots \\
0 & \cdots & 0 & 0 & 0 & s_1 & 0 & \cdots \\
0 & \cdots & 0 & 0 & 0 & 0 & s_2 & \cdots \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots
\end{pmatrix},
\]

where \( K(\mu) \) is defined as in (2.2). \( B_\mu \) is an infinite matrix.

An eigenvalue \( \lambda(\mu) \) of \( B_\mu \) satisfies

\[
B_\mu u = \lambda(\mu) u,
\]

where \( u = (J^1, \ldots, J^\tau, A, S^1, S^2, \ldots) \). This equation can be written as

\[
a_0 H'(0) K(\mu) A + \sum_{i=1}^{\infty} a_i S^i = \lambda(\mu) J^1, \\
b_1 J^1 = \lambda(\mu) J^2 \\
\vdots \\
b_{\tau-1} J^{\tau-1} = \lambda(\mu) J^{\tau}, \\
b_{\tau} J^{\tau} + \rho_o A = \lambda(\mu) A, \\
s_0 H'(0) K(\mu) A = \lambda(\mu) S^1, \\
s_1 S^1 = \lambda(\mu) S^2, \\
s_2 S^2 = \lambda(\mu) S^3 \\
\vdots
\]

(3.5)

For every \( i \) and \( m \), we solve (3.5) for \( j^i \) and \( S^m \) in terms of \( A \), substitute the results into the first equation of (3.5), and then divide the resulting equation by \( A \) to obtain

\[
(3.6) \quad 1 = \frac{\rho_o}{\lambda(\mu)} + \left( \prod_{i=1}^{\tau} b_i \right) H'(0) K(\mu) \left[ \frac{a_0}{\lambda^{\tau+1}(\mu)} + \sum_{i=1}^{\infty} a_i \left( \prod_{j=0}^{i-1} s_j \right) \varphi^{\tau+1+i}(\mu) \right],
\]

Define

\[
G(\mu, \varphi(\mu)) = -1 + \rho_o \varphi(\mu) + \left( \prod_{i=1}^{\tau} b_i \right) H'(0) K(\mu) \left[ a_0 \varphi^{\tau+1}(\mu) + \sum_{i=1}^{\infty} a_i \left( \prod_{j=0}^{i-1} s_j \right) \varphi^{\tau+1+i}(\mu) \right],
\]
where $\varphi(\mu) = \frac{1}{\lambda(\mu)}$. Clearly $G(\mu, 0) = -1$. If $k(x)$ is symmetric, then $K(\mu) > 1$ if $\mu \neq 0$. This and Hypotheses 2.1 (v), (vii) show that $G(\mu, 1) > 0$. By the intermediate value theorem the equation $G(\mu, \frac{1}{\lambda(\mu)}) = 0$ has a root $\lambda(\mu) > 1$. If $k(x)$ is asymmetric, $K(\mu) > 1$ for $\mu \neq 0$ cannot be ensured. In this case Hypotheses 2.1 (vii) and the intermediate value theorem imply that $G(\mu, \frac{1}{\lambda(\mu)}) = 0$ has a root $\lambda(\mu) > 0$. In what follows we use $\lambda(\mu)$ to denote the positive root of $G(\mu, \frac{1}{\lambda(\mu)}) = 0$. Clearly $\lambda(\mu) > \rho_o$.

We see from (3.5) that an eigenvector $\xi(\mu) = (\xi(1)(\mu), \xi(2)(\mu), \ldots)$ corresponding to $\lambda(\mu)$ satisfies

$$\xi(j)(\mu) = \frac{\lambda^{j-1}(\mu)(\lambda(\mu) - \rho_o)\xi(j+1)(\mu)}{b_j \cdots b_r}, \quad 1 \leq j \leq \tau,$$

and

$$\xi(j)(\mu) = \left(\frac{j}{\prod_{i=0}^{j-2} s_i}\right) H'(0) \frac{K(\mu)\xi(\tau+1)(\mu)}{(\lambda^{\tau-1}(\mu))}, \quad j \geq \tau + 2,$$

for the choice of $\xi(\tau+1)(\mu) > 0$. Clearly $\xi(j)(\mu) > 0$ for all $j \in \mathbb{N}$.

For $m > \tau + 1$, the $m$-dimensional analogue of matrix $B_\mu$ is

$$B_{\mu|m} := \left(\begin{array}{cccccc} 0 & \cdots & 0 & a_0 H'(0)K(\mu) & a_1 & \cdots & a_{m-\tau-1} \\ b_1 & \cdots & 0 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & \cdots & 0 & b_{\tau-1} & 0 & \cdots & 0 \\ 0 & \cdots & 0 & s_0 H'(0)K(\mu) & 0 & \cdots & 0 \\ 0 & \cdots & 0 & 0 & s_1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & \cdots & 0 & 0 & 0 & \cdots & s_{m-\tau-1} \end{array}\right).$$

(3.7)

Since $B_{\mu|m}$ is irreducible, by the Perron–Frobenius theorem, it has a positive, simple, strictly dominant eigenvalue with a corresponding positive eigenvector. We denote this eigenvalue as $\lambda_m(\mu)$. $\lambda_m(\mu)$ satisfies $G_m(\mu, \frac{1}{\lambda_m(\mu)}) = 0$, where $G_m(\mu, \varphi) = -1 + \rho_o \varphi(\mu) + \left(\prod_{i=1}^\tau h_i\right)H'(0)K(\mu)(a_0 \varphi^{\tau+1}(\mu) + \sum_{i=1}^{m-\tau-1} a_i (\prod_{j=0}^{i-1} s_j) \varphi^{i+1}(\mu)).$

It is easily seen that $\lambda_m(\mu)$ is nondecreasing in $m$ and $\lambda_m(\mu) \leq \lambda(\mu)$.

**Proposition 3.1.** Suppose Hypotheses 2.1 hold. Then as $m \to \infty$, $\lambda_m(\mu)$ converges uniformly to $\lambda(\mu)$ on every closed interval in the domain where $K(\mu)$ is convergent. Furthermore, $\lambda(\mu)$ and $\lambda_m(\mu)$ with large $m$ are strictly log convex.

**Proof.** Assume that $m$ is sufficiently large. Let $\varphi_m(\mu) = 1/\lambda_m(\mu)$. The mean value theorem shows that there is $\bar{\varphi}$ with $\varphi(\mu) \leq \bar{\varphi} \leq \varphi_m(\mu)$ such that

$$(\varphi_m(\mu) - \varphi(\mu)) \left(\frac{\partial G_m(\mu, \varphi)}{\partial \varphi}\right) = G_m(\mu, \varphi_m(\mu)) - G_m(\mu, \varphi(\mu)) = G(\mu, \varphi(\mu)) - G_m(\mu, \varphi(\mu)) = \left(\prod_{i=1}^\tau h_i\right) H'(0) K(\mu) \sum_{i=1}^{m-\tau} a_i (\prod_{j=0}^{i-1} s_j) \varphi^{i+1}(\mu).$$
It follows that

\[(3.8) \quad \lambda(\mu) - \lambda_m(\mu) = \frac{(\prod_{i=1}^\tau b_i)\lambda_m(\mu)\lambda(\mu)H'(0)K(\mu)\sum_{i=m-i}^\infty a_i(\prod_{j=0}^{i-1} s_j)\varphi^{i+1}(\mu)}{\partial G_m(\mu, \varphi)}.
\]

\(K(\mu)\) is continuous in \(\mu\), \(0 < \lambda_m(\mu) \leq \lambda(\mu)\), and \(\lambda(\mu)\) is continuous in \(\mu\). Since \(\frac{\partial G_m(\mu, \varphi)}{\partial \varphi}\) is nondecreasing in \(\varphi\), \(\frac{\partial G_m(\mu, \varphi(\mu))}{\partial \varphi} \geq \frac{\partial G_m(\mu, \varphi(\mu))}{\partial \varphi}\). \(K(\mu)\) and \(\lambda(\mu)\) are bounded on any given closed interval in which \(K(\mu)\) converges. Equation (3.8) shows that as \(m \to \infty\), \(\lambda_m(\mu)\) converges to \(\lambda(\mu)\) uniformly on bounded intervals.

Lemma 6.4 in Li [21] shows that \(\lambda_m(\mu)\) is log convex. The uniform convergence of \(\lambda_m(\mu)\) to \(\lambda(\mu)\) on bounded intervals implies that \(\lambda(\mu)\) is log convex; i.e., for \(0 < t < 1\), and \(\mu_1 \neq \mu_2\) with \(\mu_1\) and \(\mu_2\) in the domain where \(K(\mu)\) is convergent,

\[(3.9) \quad \lambda(t\mu_1 + (1 - t)\mu_2) \leq \lambda^t(\mu_1)\lambda^{1-t}(\mu_2).
\]

If the equal sign in (3.9) holds, from (3.6) we have that

\[
1 = \frac{\rho}{\lambda^t(\mu_1)\lambda^{1-t}(\mu_2)} + \left(\prod_{i=1}^\tau b_i\right) H'(0)K(t\mu_1 + (1 - t)\mu_2)
\]

\[(3.10) \quad \times \left[\frac{a_0\rho_{0}^{1-t}}{\lambda^t(\mu_1)\lambda^{1-t}(\mu_2)} + \sum_{i=1}^\infty \frac{a_i(\prod_{j=0}^{i-1} s_j)^t(a_i(\prod_{j=0}^{i-1} s_j))^{1-t}}{\lambda^{t+1+i}(\mu_1)\lambda^{1-t+i}(\mu_2)}\right].
\]

Using the fact that \(K(t\mu_1 + (1 - t)\mu_2) < K^t(\mu_1)\lambda^{1-t}(\mu_2)\) (see the first paragraph on page 328 in Li, Lewis, and Weinberger [19]) and applying Hölder’s inequality in (3.10), we obtain

\[
1 < \left\{\frac{\rho}{\lambda(\mu_1)} + \left(\prod_{i=1}^\tau b_i\right) H'(0)K(\mu_1) \left[\frac{a_0}{\lambda^t(\mu_1)} + \sum_{i=1}^\infty \frac{a_i(\prod_{j=0}^{i-1} s_j)}{\lambda^{t+1+i}(\mu_1)}\right]^{t}\right\}
\]

\[
\times \left\{\frac{\rho}{\lambda(\mu_2)} + \left(\prod_{i=1}^\tau b_i\right) H'(0)K(\mu_2) \left[\frac{a_0}{\lambda^t(\mu_2)} + \sum_{i=1}^\infty \frac{a_i(\prod_{j=0}^{i-1} s_j)}{\lambda^{t+1+i}(\mu_2)}\right]^{1-t}\right\}.
\]

It follows from this and (3.6) that \(1 < 1\), a contradiction. We therefore conclude that the inequality in (3.9) must be strict so that \(\lambda(\mu)\) is strictly log convex. Similarly, one can show that \(\lambda_m(\mu)\) is strictly log convex. The proof is complete.

Define

\[(3.11) \quad c^* := \inf_{\mu > 0} \phi(\mu),
\]

where

\[
\phi(\mu) = \frac{\ln(\lambda(\mu))}{\mu},
\]

and define

\[(3.12) \quad c^*_m := \inf_{\mu > 0} \phi_m(\mu),
\]
where
\[
\phi_m(\mu) = \frac{\ln(\lambda_m(\mu))}{\mu}.
\]

Hypotheses 2.1 (v) shows that \(\lambda(0) > 1\). The strict log convexity of \(\phi(\mu)\) and Lemma 6.5 in Lui [21] imply that either \(\phi(\mu)\) has the global minimum value \(c^*\) at a finite number \(\bar{\mu}\) in \((0, \infty)\) such that \(\phi(\mu)\) is strictly decreasing for \(0 < \mu < \bar{\mu}\) and strictly increasing for \(\mu > \bar{\mu}\), or \(\phi(\mu)\) is strictly decreasing for all \(\mu > 0\) and \(c^* = \lim_{\mu \to \infty} \phi(\mu)\). The same property holds for \(\phi_m(\mu)\) for large \(m\). The uniform convergence of \(\lambda_m(\mu)\) to \(\lambda(\mu)\) on closed intervals shows that \(c^*_m \to c^*\) as \(m \to \infty\).

Define \(c^*(-1)\) by (3.11) with \(\lambda(\mu)\) replaced by \(\lambda(-\mu)\), and define \(c^*_m(-1)\) by (3.12) with \(\lambda_m(\mu)\) replaced by \(\lambda_m(-\mu)\). Proposition 3.1 implies that \(c^*_m(-1) \to c^*(-1)\) as \(m \to \infty\), and \(\lambda(-\mu)\) and \(\lambda_m(-\mu)\) with large \(m\) are strictly log convex. The argument given in the second paragraph on page 328 in [19] shows that \(c^* + c^*(-1) > 0\) and \(c^*_m + c^*_m(-1) > 0\) for large \(m\).

4. The spreading speed. The following theorem states that \(c^*_m\) is the asymptotic rightward spreading speed of the monotone truncated system (2.4) for a certain class of initial data.

THEOREM 4.1. Suppose that Hypotheses 2.1 hold and that \(H\) is nondecreasing. Let \(m\) be sufficiently large. Then \(c^*_m\) given by (3.12) is the asymptotic rightward spreading speed of the \(m\)-dimensional truncated system (2.4) in the following sense:

If \(u_{0|m}(x)\) is continuous, \(0 \leq u_{0|m}(x) \ll u_{*|m}, u_{0|m}^{(i)}(x)\) is positive on a set with positive measure for some \(i\), and \(u_{0|m}(x) \equiv 0\) outside a bounded domain, then for any \(\epsilon > 0\) the solution \(u_{n|m}\) of system (2.4) has the following properties:

i. \[
\lim_{n \to \infty} \left\{ \sup_{x \geq n(c^*_m + \epsilon)} u_{n|m}^{(i)}(x) \right\} = 0 \quad \text{for } i \in \{1, 2, \ldots, m\}.
\]

ii. \[
\lim_{n \to \infty} \left\{ \sup_{-n(c^*_m(-1) - \epsilon) \leq x \leq n(c^*_m - \epsilon)} |u_{n|m}^{(i)}(x) - u_{*|m}^{(i)}(x)| \right\} = 0 \quad \text{for } i \in \{1, 2, \ldots, m\}.
\]

Proof. Since \(u_{0|m}^{(i)}(x)\) is positive on a set with positive measure for some \(i\), (2.4) shows that there exists \(N\) such that \(u_{N|m}^{(j)}(x)\) is positive on a set with positive measure for each \(j \in \{0, 1, \ldots, m\}\). Without loss of generality, assume that \(u_{0|m}^{(r+1)}(x) = A_{0|m}(x) > 0\) on \([x_1, x_2]\) with \(x_2 > x_1\) and that \(a_k \prod_{l=0}^{r-1} s_l \neq 0\) for some \(1 \leq k \leq m\). Let \(k(x) > 0\) on \([a, b]\) with \(b > a\). It follows from (2.4) that \(A_{0|m} > 0\) on \([na+x_1, nb+x_2]\). This and (2.4) show that \(u_{n|m}(x) \gg 0\) on an interval with length increasing to infinity as \(n \to \infty\). This theorem follows from Theorems 3.1-3.4 and Proposition 3.3 in Lui [21] if \(I = (-\infty, \infty)\), where \(I\) is as described in Hypotheses 2.1 (vi) (b). The proof for \(I \neq (-\infty, \infty)\) is similar to a simplified version of the proof of Theorem 2.1 in Weinberger and Zhao [42], where a scalar recursion is studied. We provide the details of the proof for the case of \(I = (-\Lambda_1, \Lambda_2)\) with \(0 < \Lambda_1 \leq \Lambda_2 < \infty\). The proofs for the other cases are similar and omitted.

The proof of Theorem 3.4 in Lui [21] still works to show that the rightward spreading speed of (2.4), denoted by \(\bar{c}\), satisfies
\[
\bar{c} \leq c^*_m.
\]
We next show that the inequality can be reversed. For this purpose we use the continuous cutoff function

$$
\eta(x) = \begin{cases} 
1 & \text{when } |x| \leq 1, \\
2 - x & \text{when } 1 < |x| \leq 2, \\
0 & \text{when } |x| > 2
\end{cases}
$$

introduced in [42]. Define the operator sequence

$$Q_m^{(j)}[u](x) = Q_m[\eta(x/j)u(x + \cdot)](0).$$

Because the sequence $\eta(x/j)$ increases to 1 uniformly on every bounded interval, we see that for each $0 \leq u(x) \leq u_{*m}$, $Q_m^{(j)}(u)$ increases to $Q_m[u]$ uniformly on every bounded interval. The formula for the linearization of $Q_m^{(j)}$ can easily be found, and the moment generating matrix $B_{\mu|m}^{(j)}$ is given by (3.7) with $K(\mu)$ replaced by $K^{(j)}(\mu) = \int_{\mathbb{R}} e^{\mu y} \eta(y/k(y)dy$. Because $e^{\mu y} \eta(y)$ is bounded for every $\mu \in \mathbb{R}$, $K^{(j)}(\mu)$ is well defined, continuous, and nondecreasing in $j$. Clearly, $K^{(j)}(\mu)$ increases to $K(\mu)$ as $j \to \infty$ for $-\Lambda_1 < \mu < \Lambda_2$, and $K^{(j)}(\mu)$ approaches $+\infty$ as $j \to \infty$ for $\mu \notin (-\Lambda_1, \Lambda_2)$.

We use $\lambda_m^{(j)}(\mu)$ to denote the principal eigenvalue of $B_{\mu|m}^{(j)}$. We have that $\lambda_m^{(j)}(\mu) \leq \lambda_m(\mu)$ and $\lambda_m^{(j)}(\mu)$ approaches $\lambda_m(\mu)$ as $j \to \infty$ for $\mu \in (-\Lambda_1, \Lambda_2)$ and $\lambda_m^{(j)}(\mu) \to \infty$ as $j \to \infty$ for $\mu \notin (-\Lambda_1, \Lambda_2)$. For convenience, we shall also use the notation

$$\phi_m^{(j)}(\mu) = \frac{\ln(\lambda_m^{(j)}(\mu))}{\mu}$$

and

$$\phi_m(\mu) = \frac{\ln(\lambda_m(\mu))}{\mu}$$

with the convention that $\phi_m(\mu) = \infty$ when $\lambda_m(\mu) = \infty$. For large $j$, $\lambda_m^{(j)}(0) > 1$, $\lambda_m^{(j)}(\mu)$ is strictly convex, and $\inf_{\mu > 0} \frac{\ln(\lambda_m^{(j)}(\mu))}{\mu} + \inf_{\mu > 0} \frac{\ln(\lambda_m^{(j)}(\mu))}{\mu} > 0$. Note that

$$\lim_{\mu \to 0^+] \phi_m^{(j)}(\mu) = \infty.$$

There exists a positive integer $J$ such that for $j \geq J$,

$$\lambda_m^{(j)}(0) > 1, \quad \phi_m^{(j)}(\Lambda_2) > c^*_m.$$

Let $\bar{c}_j$ be the rightward spreading speed of $Q_m^{(j)}$. The definition of spreading speed given in [21] and the fact that $Q_m^{(j)}[u] \leq Q_m[u]$ show that $\bar{c}_j \leq \bar{c} \leq c^*_m$. Since $\phi_m(\Lambda_2) = \infty$, there exists $\mu_m \in (0, \Lambda_2)$ such that $\phi_m(\mu_m) = c^*_m$. We have that $\phi_m^{(j)}(\mu_m) \leq \phi_m(\mu_m) = c^*_m$. It follows from this, (4.1), Theorem 3.4 in [21], and the fact that $\phi_m^{(j)}(\mu)$ has no local maximum value that

$$\phi_m^{(j)}(\mu_j) = \bar{c}_j \quad \text{for some } \mu_j \in (0, \Lambda_2).$$

Since $\phi_m^{(j)}$ is nondecreasing in $j$, we see that if $\kappa \geq j \geq J$,

$$\phi_m^{(j)}(\mu_\kappa) \leq \phi_m^{(\kappa)}(\mu_\kappa) = \bar{c}_\kappa \leq \bar{c}.$$
Let \( \bar{\mu} \) be one accumulation point of \( \mu_\kappa \) so that there is a subsequence \( \mu_{\kappa_i} \) of \( \mu_\kappa \) such that \( \mu_{\kappa_i} \rightarrow \bar{\mu} \) as \( i \rightarrow \infty \). So now we see that

\[
\phi^{(j)}_{m}(\bar{\mu}) \leq \bar{c} \quad \text{for all } j \geq J.
\]

Let \( j \rightarrow \infty \) to obtain \( \phi_{m}(\bar{\mu}) \leq \bar{c} \), which implies that

\[ c_{m}^{*} = \inf_{\mu > 0} \phi_{m}(\mu) \leq \phi_{m}(\bar{\mu}) \leq \bar{c}. \]

This completes the proof. \( \square \)

Our next theorem states that \( c^{*} \) is the asymptotic rightward spreading speed of the monotone infinite model (2.1) when finitely many components of the species are initially concentrated in a bounded region of space.

**Theorem 4.2.** Suppose that Hypotheses 2.1 hold and that \( H \) is nondecreasing. Then \( c^{*} \) given by (3.11) is the asymptotic rightward spreading speed of the system (2.1) in the following sense: If \( u_{0}(x) \) is continuous, \( 0 \leq u_{0}(x) \ll u_{0}^{(i)}(x) \) is positive on a set with positive measure for finitely many \( i \), and \( u_{0}(x) \equiv 0 \) outside a bounded domain, then for any \( \epsilon > 0 \) the solution \( u_{n} \) of system (2.1) has the following properties:

i. 

\[
\lim_{n \rightarrow \infty} \left\{ \sup_{x \geq n(c^{*} + \epsilon)} u_{n}^{(i)}(x) \right\} = 0 \quad \text{for all } i \in \mathbb{N}.
\]

ii. 

\[
\lim_{n \rightarrow \infty} \left\{ \sup_{-n(c^{*} - 1 - \epsilon) \leq x \leq n(c^{*} - \epsilon)} \left| u_{n}^{(i)}(x) - u_{*}^{(i)} \right| \right\} = 0 \quad \text{for all } i \in \mathbb{N}.
\]

**Proof.** Let \( \bar{\mu} \) be the smallest positive number such that \( \phi(\bar{\mu}) = c^{*} + \epsilon/2 \). It is easy to see that \( L[e^{-\bar{\mu}x} \xi(\bar{\mu})] = B_{\mu}e^{-\bar{\mu}x} \xi(\bar{\mu}) \). Since \( \xi(\bar{\mu}) \gg 0 \), we may choose a constant \( \rho \) such that \( u_{0}(x) \leq \rho e^{-\bar{\mu}x} \xi(\bar{\mu}) \). Observe that

\[
u_{1}(x) = Q[u_{0}(x)] \leq L[u_{0}(x)] \leq \rho L[e^{-\bar{\mu}x} \xi(\bar{\mu})] = \rho B_{\mu} e^{-\bar{\mu}x} \xi(\bar{\mu}) = \rho e^{-\bar{\mu}(x-c^{*}-\epsilon/2)} \xi(\bar{\mu}).
\]

By induction we have that for all \( x \geq n(c^{*} + \epsilon) \),

\[
u_{n}(x) \leq \rho e^{-\bar{\mu}(n(c^{*} + \epsilon)-n(c^{*}+\epsilon/2))} \xi(\bar{\mu}) = \rho e^{-\bar{\mu}n\epsilon/2} \xi(\bar{\mu}).
\]

Therefore,

\[
\sup_{x \geq n(c^{*} + \epsilon)} u_{n}^{(i)}(x) \leq \rho e^{-\bar{\mu}n\epsilon/2} \xi^{(i)}(\bar{\mu}) \quad \text{for all } i \in \mathbb{N},
\]

and so

\[
\lim_{n \rightarrow \infty} \left\{ \sup_{x \geq n(c^{*} + \epsilon)} u_{n}^{(i)}(x) \right\} = 0 \quad \text{for all } i \in \mathbb{N}.
\]

We now show that (4.3) holds. Let \( u_{0|m}(x) = (u_{0|m}^{(1)}(x), \ldots, u_{0|m}^{(m)}(x)) \) with \( u_{0|m}^{(i)}(x) > 0 \) at some point for some \( i \in \{1, 2, \ldots, m\} \). Thus,

\[
u_{n}(x) \geq \bar{u}_{n|m}(x) \quad \text{for all } n,
\]

\[
u_{n}(x) \geq \bar{u}_{n|m}(x) \quad \text{for all } n.
\]
where \( \mathbf{u}_{n|m}(x) = (\mathbf{u}_{n|m}(x), 0, \ldots) \) with \( \mathbf{u}_{n|m}(x) \) being the solution of the \( m \)-dimensional recursion (2.4).

Let \( \varepsilon > 0 \) and \( \epsilon > 0 \). Since \( c_m^* \rightarrow c^* \) and \( c_m^*(-1) \rightarrow c^*(-1) \) as \( m \rightarrow \infty \), we choose \( M_1 \in \mathbb{N} \) such that for all \( m \geq M_1 \),

\[
|c_m^* - c^*| < \frac{\epsilon}{2}, \quad |c_m^*(-1) - c^*(-1)| < \frac{\epsilon}{2}.
\]

Since \( \mathbf{u}_{n|m} = (\mathbf{u}_{n|m}, 0, \ldots) \) converges to \( \mathbf{u}_* \) with respect to \( \| \cdot \|_1 \) as \( m \rightarrow \infty \), we may choose \( M_2 \in \mathbb{N} \) such that for all \( m \geq M_2 \),

\[
\| \mathbf{u}_{n|m} - \mathbf{u}_* \|_1 < \frac{\varepsilon}{2}.
\]

Theorem 4.1 shows that there exists \( M_3, N \in \mathbb{N} \) such that for \( m \geq M_3, n \geq N \), and \( 1 \leq i \leq m \),

\[
|\tilde{e}_{n|m}^{(i)} - \bar{e}_{n}^{(i)}| < \frac{\varepsilon}{2} \quad \text{for all} \quad -n(c_m^*(-1) - \epsilon/2) \leq x \leq n \left( c_m^* - \frac{\epsilon}{2} \right).
\]

Let \( M = \max\{M_1, M_2, M_3\} \). Equations (4.4)-(4.7) imply that for \( n \geq N \) and

\[
0 \leq u_i^{(i)} - u_n^{(i)}(x) = (u_i^{(i)} - \bar{u}_n^{(i)}(x)) + (\bar{u}_n^{(i)}(x) - \bar{u}_n^{(i)}(x)) + (\bar{u}_n^{(i)}(x) - u_n^{(i)}(x)) < \varepsilon.
\]

This implies that (4.3) holds, and the theorem is proved.

We now show that \( c^* \) is the spreading speed for the system (2.1) when \( H \) is nonmonotone. We first introduce some auxiliary functions. Define

\[
H^+(u) := \max_{0 \leq v \leq u} H(v)
\]

for \( u \geq 0 \) (denoted by \( G(u, 0) \) in [35]). \( H^+(u) \) is a continuous and nondecreasing function. The definition of \( H^+ \) and Hypotheses 2.1 (iii) show that \( H^+(A)/A \rightarrow 0 \) as \( A \rightarrow \infty \). This, the fact that \( H'(0) = H^+'(0) \), and Hypotheses 2.1 (vi) imply that (3.3) with \( H(A) \) replaced by \( H^+(A) \) has a positive root, and thus (2.1) with \( H \) by \( H^+ \) has a strictly positive constant equilibrium. Call the smallest of such equilibria \( u_+^* \) and the \((\tau + 1)\)th component of this positive solution \( A_+^* \).

Now define the function

\[
H^-(u) := \min_{0 \leq v \leq A_+^*} H(v) \quad \text{for} \quad 0 \leq u \leq A_+^*.
\]

(This function is denoted by \( G(u, a) \) in [35].) \( H^-(u) \) is nondecreasing and continuous on \([0, A_+^*] \). An argument similar to that used to prove that (2.1) with \( H \) replaced by \( H^+ \) has a strictly positive constant equilibrium shows that (2.1) with \( H \) replaced by \( H^- \) has a strictly positive constant equilibrium. Denote the smallest of such equilibria as \( u_-^* \) and the \((\tau + 1)\)th component of this positive solution as \( A_-^* \).

Clearly, \( H^-(u) \leq H(u) \leq H^+(u) \) for \( 0 \leq u \leq A_+^* \), and \( u_-^* \leq u \leq u_+^* \). It is easily seen that \( H^-(u) = H(u) = H^+(u) \) for \( u \) positive and small, \( H^+(0) = H^-'(0) \), and \( H^-(u) \leq H(u) \leq H^+(u) \leq H^+(0)u \) for \( u \geq 0 \). Theorem 4.2 shows that \( c^* \) given by (3.11) is the asymptotic spreading speed of the system (2.1) with \( H \) replaced by \( H^+ \) and \( H^- \), respectively. By comparing solutions of (2.1) and solutions of (2.1) with \( H \) replaced by \( H^+ \) and \( H^- \), one can easily obtain the following theorem.
Theorem 4.3. Suppose that Hypotheses 2.1 hold. Then \( c^* \) given by (3.11) is the asymptotic rightward spreading speed of the system (2.1) in the following sense: If \( 0 \leq u_0(x) \ll u^+ \), \( u_0(x) \) is continuous for all \( x \), \( u_0^{(i)}(x) \) is positive on a set with positive measure for finitely many \( i \), and \( u_0(x) \equiv 0 \) outside a bounded domain, then for any \( \epsilon > 0 \) the solution \( u_n \) of system (2.1) has the following properties:

i. \( u_n(x) \leq u_\star^+ \) for all \( x \in \mathbb{R} \) and \( n \in \mathbb{N} \).

ii. \( \lim_{n \to \infty} \left\{ \sup_{x \geq n(c^* + \epsilon)} u_n^{(i)}(x) \right\} = 0 \) for all \( i \in \mathbb{N} \),

iii. \( \liminf_{n \to \infty} \left\{ \inf_{-n(c^* - \epsilon) \leq x \leq n(c^* - \epsilon)} u_n^{(i)}(x) \right\} \geq u_\star^{-(i)} \) for all \( i \in \mathbb{N} \).

5. Traveling wave solutions. In this section we establish the existence of traveling wave solutions for system (2.1). We need the following lemma.

Lemma 5.1. Let \( u_n(x) \) be a sequence of nonnegative nonincreasing functions, and let \( \bar{a}_n \) be a sequence of nonnegative numbers. Suppose that there exists some nonincreasing function \( u(x) \) that is the limit of \( u_n(x) \) as \( n \to \infty \) and \( u_n(x) \leq u(x) \) for all \( n \). If \( u(x) \) is bounded above by \( U \in L_1 \), then

i. \( \lim_{n \to \infty} \sum_{i=1}^{\infty} \bar{a}_i u_n^{(i+1)}(x) = \sum_{i=1}^{\infty} \bar{a}_i u^{(i+1)}(x) \).

ii. \( \lim_{x \to -\infty} \sum_{i=1}^{\infty} \bar{a}_i u^{(i+1)}(x) = \sum_{i=1}^{\infty} \bar{a}_i \lim_{x \to -\infty} u^{(i+1)}(x) \).

This lemma follows from Lebesgue’s dominated convergence theorem.

A traveling wave solution of (2.1) with speed \( c \) satisfies \( w(x - c) = Q[w](x) \) or, equivalently,

\[
\begin{align*}
J^1(x - c) &= a_0 \int_{-\infty}^{\infty} k(x - y)H(A(y))dy + \sum_{j=1}^{\infty} a_j S^j_n(x), \\
J^2(x - c) &= b_1 J^1(x) \\
&\vdots \\
J^\tau(x - c) &= b_{\tau-1} J^{\tau-1}(x), \\
A(x - c) &= b_{\tau} J^\tau(x) + p_0 A(x), \\
S^1(x - c) &= s_0 \int_{-\infty}^{\infty} k(x - y)H(A(y))dy, \\
S^2(x - c) &= s_1 S^1(x), \\
S^3(x - c) &= s_2 S^2(x) \\
&\vdots
\end{align*}
\]
where \( w = (J^1, \ldots, J^\tau, A, S^1, S^2, \ldots) \). This implies that

\[
J^i(x) = \frac{1}{b_i \cdots b_1} [A(x - (\tau + 1 - i)c) - \rho_0 A(x - (\tau - i)c)],
\]

(5.2)

\[
S^i(x) = \left( \prod_{j=0}^{i-1} s_j \right) \int_{\mathbb{R}} k(x + ic - y) H(A(y)) dy.
\]

Hence system (5.1) can be reduced to

\[
A(x - c) = \rho_0 A(x) + \left( \prod_{i=1}^{\tau} b_i \right) \left[ a_0 \int_{\mathbb{R}} k(x + \tau c - y) H(A(y)) dy \right. \\
+ \sum_{i=1}^{\infty} a_i \left( \prod_{j=0}^{i-1} s_j \right) \int_{\mathbb{R}} k(x + (\tau + i)c - y) H(A(y)) dy \left].
\]

(5.3)

We have that the traveling wave system (5.1) is equivalent to the scalar equation (5.3) with \( J^i(x), S^i(x) \) given by (5.2).

Similarly, a traveling wave solution \( w_m = (J^1_m, \ldots, J^\tau_m, A_m, S^1_m, \ldots, S^{m-\tau-1}_m) \) of (2.4) satisfies

\[
A_m(x - c) = \rho_0 A_m(x) + \left( \prod_{i=1}^{\tau} b_i \right) \left[ a_0 \int_{\mathbb{R}} k(x + \tau c - y) H(A_m(y)) dy \right. \\
+ \sum_{i=1}^{m-\tau-1} a_i \left( \prod_{j=0}^{i-1} s_j \right) \int_{\mathbb{R}} k(x + (\tau + i)c - y) H(A_m(y)) dy \left].
\]

(5.4)

with \( J^i(x), S^i(x) \) given by (5.2) for \( 1 \leq i \leq \tau \) and \( 1 \leq j \leq m - \tau - 1 \).

**Lemma 5.2.** If \( \{ A_{cn}(x) \} \) is a sequence of nonnegative nonincreasing functions with \( A_{cn}(-\infty) \leq A \), that satisfy

\[
A_{cn}(x - c_n) = \rho_0 A_{cn}(x) + \left( \prod_{i=1}^{\tau} b_i \right) \left[ a_0 \int_{\mathbb{R}} k(x + \tau c_n - y) H(A_{cn}(y)) dy \right. \\
+ \sum_{i=1}^{m_n} a_i \left( \prod_{j=0}^{i-1} s_j \right) \int_{\mathbb{R}} k(x + (\tau + i)c_n - y) H(A_{cn}(y)) dy \left].
\]

(5.5)

with \( m_n \) a large number or \( m_n = \infty \), then \( \{ A_{cn}(x) \} \) is an equicontinuous family of functions.
Proof. It follows from (5.5) that
\[
|A_{c_n}(x + \delta - c_n) - A_{c_n}(x - c_n)|
\leq \rho_0 |A_{c_n}(x + \delta) - A_{c_n}(x)|
+ \left( \prod_{i=1}^{\tau} b_i \right) H(A_x) \left[ a_0 \int_{\mathbb{R}} |k(x + \tau c_n + \delta - y) - k(x + \tau + c_n - y)|dy \right]
+ \sum_{i=1}^{m_n} a_i \left( \prod_{j=0}^{i-1} s_j \right) \int_{\mathbb{R}} |k(x + \delta + (\tau + i)c_n - y) - k(x + (\tau + i)c_n - y)|dy
\leq \rho_0 |A_{c_n}(x + \delta) - A_{c_n}(x)|
+ \left( \prod_{i=1}^{\tau} b_i \right) H(A_x) \left[ a_0 + \sum_{i=1}^{\infty} a_i \left( \prod_{j=0}^{i-1} s_j \right) \right] \int_{\mathbb{R}} |k(\zeta + \delta) - k(\zeta)|d\zeta.
\]
This implies that
\[
\sup_{x \in \mathbb{R}} |A_{c_n}(x + \delta) - A_{c_n}(x)| \leq \frac{(\prod_{i=1}^{\tau} b_i) H(A_x) [a_0 + \sum_{i=1}^{\infty} a_i (\prod_{j=0}^{i-1} s_j)]}{1 - \rho_0} \int_{\mathbb{R}} |k(\zeta + \delta) - k(\zeta)|d\zeta.
\]

A result in the proof of Theorem 4.1 in [19] (see page 331) shows that \( \lim_{\delta \to 0} \int_{\mathbb{R}} |k(\zeta + \delta) - k(\zeta)|d\zeta = 0 \). Thus we have that \( \{A_{c_n}(x)\} \) is an equicontinuous family of functions. The proof is complete. \( \square \)

**Theorem 5.1.** Let Hypotheses 2.1 be satisfied. Assume that \( H(A) \) is nondecreasing. Then the following statements hold for the spatial system (2.1):

1. For \( c \geq c^* \) there exists a nonincreasing traveling wave \( u_n(x) = \mathbf{w}(x - nc) \) with \( \mathbf{w}(\infty) = \mathbf{0} \) and \( \mathbf{w}(-\infty) = u_* \).

2. A nonincreasing traveling wave solution \( \mathbf{w}(x - nc) \) with \( \mathbf{w}(\infty) = \mathbf{0} \) and \( \mathbf{w}(-\infty) = u_* \) does not exist if \( c < c^* \).

**Proof.** We first show that statement (i) is true. For \( c > c^* \), there exists a large positive \( M \) such that for \( m \geq M, c > c^*_m \). Define \( \mu_c \) to be the smallest positive number such that \( \phi_{\mu_c}(\mu_c) = c \). Choose \( \mu_c < s < \min\{\bar{\mu}, 2\mu_c\} \) with \( \bar{\mu} \) the extended positive number at which the infimum in (3.12) is attained. We use \( \mu_c \) to denote the principal eigenvector of \( B_m \) corresponding to \( \lambda_m(\mu_c) \). Define \( \mathbf{w}^+(x) = \min\{e^{-\mu_c x} \mathbf{w}_m(\mu_c, u_*), u_*\}, \mathbf{w}^-(x) = \max\{e^{-\mu_c x} \mathbf{w}_m(\mu_c) - e^{-\mu_c x} \mathbf{w}(s), 0\} \), where \( \epsilon \) is a small positive number. \( \mathbf{w}^+ \) is a nonincreasing function. Construct the sequence \( \{z_n(x)\} \) generated by \( z_{n+1}(x) = Q_m[z_n](x + c) \) with \( z_0(x) = \mathbf{w}_m^+(x) \). Induction and Hypotheses 2.1 (iv) (b) show that for \( \epsilon \) sufficiently small, \( \mathbf{w}_m^-(x) \leq z_{n+1}(x) \leq z_n(x) \leq \mathbf{w}_m^+(x) \) for all \( n \). Let \( \mathbf{w}_n(x) = \lim_{n \to \infty} z_n(x) \). \( \mathbf{w}_m \) is a nonincreasing function and satisfies \( Q_m[w](x) = \mathbf{w}(x - c) \), \( \mathbf{w}_m(-\infty) = u_{\epsilon\mu} \), and \( \mathbf{w}_m(\infty) = \mathbf{0} \). The details of the proof are very similar to those in the proof of Theorem 5 in [40], Theorem 3.1 in [38], and Lemma 3.3 and Theorem 3.1 in [5], and thus shall be omitted here.

Let \( \gamma \) be a small positive number. By taking translations if necessary, we may assume that \( A_m \), the \((\tau + 1)\)th component of \( \mathbf{w}_m \), satisfies \( A_m(0) = \gamma \). Lemma 5.2
shows that \( \{A_m\}_{m \geq M} \) is an equicontinuous family of functions. Then there exists a subsequence \( A_{m_j} \) such that \( A_{m_j} \) converges to \( A(x) \) uniformly on every bounded interval. Note that 

\[
\sum_{i=m_j-\tau}^{\infty} a_i(\prod_{j=0}^{i-1} s_j) \int_{\mathbb{R}} k(x + (\tau + i)c - y)H(A_{m_j}(y))dy \leq H(A_\ast) \sum_{i=m_j-\tau}^{\infty} a_i(\prod_{j=0}^{i-1} s_j),
\]

which approaches 0 as \( m_j \to \infty \) according to Hypotheses 2.1 (vii). By using this and Lebesgue’s dominated convergence theorem, and by taking the limit \( m_j \to \infty \) in (5.4), we obtain that \( A \) satisfies (5.3) with \( A(0) = \gamma \). Since each \( A_{m_j}(x) \) is nonincreasing in \( x \), \( A(x) \) is nonincreasing in \( x \). On the other hand, by using Lemma 5.1, we have \( A(\pm \infty) = \rho_0 A(\pm \infty) + (\prod_{i=1}^{\infty} b_i) [a_0 H(A(\pm \infty)) + \sum_{i=1}^{\infty} a_i(\prod_{j=0}^{i-1} s_j) H(A(\pm \infty))] \) so that \( A(\pm \infty) \) are equilibria. Since \( A(\pm \infty) \geq \gamma \geq A(\ast) \) and \( \gamma \) is small, \( A(-\infty) = A_\ast \) and \( A(\infty) = 0 \).

We have shown that for \( c_n > c^\ast \) and \( c_n \to c^\ast \) as \( n \to \infty \), (5.3) has nonincreasing traveling wave solutions \( A_{c_n} \) with \( A_{c_n}(0) = \gamma \), \( A_{c_n}(\infty) = 0 \), and \( A_{c_n}(-\infty) = A_\ast \). Lemma 5.2 shows that there exists a subsequence \( n_j \) such that \( A_{c_{n_j}}(x) \) converges to a nonincreasing continuous function \( A(x) \) uniformly on every bounded interval. Taking the limit \( n \to \infty \) in (5.3) with \( A \) replaced by \( A_{c_n} \) and \( c \) replaced by \( c_n \) and using Lemma 5.1, we obtain that \( A \) satisfies (5.3) with \( c \) replaced by \( c^\ast \), \( A(-\infty) = A_\ast \), and \( A(\infty) = 0 \).

We have proven statement (i). To prove statement (ii) we obtain a contradiction by letting \( w(x) \) be a traveling wave solution with speed \( c < c^\ast \) such that \( w(-\infty) = u_\ast \) and \( w(\infty) = 0 \). Choose a nonincreasing function \( v_0(x) \) such that \( v_0(x) \leq w(x) \), \( v_0(x) < u_\ast \), and \( v_0(x) \equiv 0 \) outside of a bounded domain with \( v_0^{(i)}(x) \) positive on a set with positive measure for finitely many \( i \). Let \( v_n \) be defined by the recursion 

\[
(v_{n+1})(x) = Q[v_n](x).
\]

By induction and the fact that \( Q \) is order preserving, we have 

\[
v_n(x) \leq w(x - nc).
\]

Choose \( \epsilon = (c^\ast - c)/2 \). By Theorem 4.2, \( \lim_{n \to \infty} v_n^{(\tau+1)}(x_n) = A_\ast \) where \( x_n = n(c^\ast - \epsilon) \). Alternatively, \( \lim_{n \to \infty} u^{(\tau+1)}(x_n - nc) = u^{(\tau+1)}(\infty) = 0 \). But this contradicts (5.6), and so the statement is proved.

We now investigate the existence of traveling wave solutions for the more general case when the growth function \( H(u) = F(u)u \) is nonmonotone. We again consider the scalar traveling wave equation (5.3).

Define the operator 

\[
P[u] := T[u] + R[u],
\]

where 

\[
T[u](x) := \rho_0 u(x)
\]

and 

\[
R[u](x) := \left( \prod_{i=1}^{\tau} b_i \right) \left[ a_0 \int_{\mathbb{R}} k(x + \tau c - y)H(u(y))dy + \sum_{i=1}^{\infty} a_i \left( \prod_{j=0}^{i-1} s_j \right) \int_{\mathbb{R}} k(x + (\tau + i)c - y)H(u(y))dy \right].
\]

Define 

\[
P_\epsilon[u](x) := P[u](x + \epsilon).
\]
We let $P_c^+$ and $P_c^-$ be defined by (5.7) and (5.8) with $H$ replaced by $H^+$ and $H^-$, respectively. For all $x$, let $u(x)$ be continuous and let $0 \leq u(x) \leq A_c^+$. Since $H^-(u) \leq H(u) \leq H^+(u)$, we have

$$P_c^-[u] \leq P_c[u] \leq P_c^+[u].$$

**Theorem 5.2.** Let Hypotheses 2.1 be satisfied. Then the following hold for the spatial system (2.1):

i. For any $c \geq c^*$ there exists a traveling wave solution $u_c(x) = w(x - nc)$ with $w(x) \leq u_c^+$ for all $x$, $w(\infty) = 0$, and $\liminf_{x \to -\infty} w(x) \geq u_c^-$. 

ii. A traveling wave solution $w(x-nc)$ with $w(\infty) = 0$ and $\liminf_{x \to -\infty} w(x) \geq u_c^+$ does not exist if $c < c^*$.

**Proof.** According to (5.3), a traveling wave solution of system (2.1) is equivalent to a fixed point of $P_c$. Because $H^+$ is a monotone function, Theorem 5.1 shows that for $c \geq c^*$ there exists a nonincreasing function $A_c^+(x)$ such that

$$P_c^+[A_c^+](x) = A_c^+(x), A_c^+(-\infty) = A_c^+, A_c^+(\infty) = 0.$$ 

The definitions of $H^\pm$ and Hypotheses 2.1 show that the number

$$l := \sup\{u : 0 < u < d \text{ and } H(u) < H^-(d)\}$$ 

satisfies the inequalities $0 < l \leq d$, and

$$H^-(u) = H^+(u) = H(u) \quad \text{for } 0 \leq u \leq l.$$ 

Furthermore, Hypotheses 2.1 (iii) show that if $0 < \gamma < l/A_c^+$ and if $0 < u \leq A_c^+$, then $H^-(\gamma u) \geq \gamma H^+(u)$.

Denote the Banach space of bounded continuous functions with the supremum norm as $C(\mathbb{R})$. Let

$$E_c = \{u(x) : u \in C(\mathbb{R}), \quad \gamma A_c^+(x) \leq u(x) \leq A_c^+(x)\}$$

with $0 < \gamma < \min\{\frac{d}{A_c^+}\}$. It follows that $E_c$ is a bounded nonempty closed convex subset of $C(\mathbb{R})$. A simple argument similar to the proof of Lemma 4.3 in [19] shows that $P_c$ maps $E_c$ into $E_c$.

$P_c$ is of the form

$$P_c = T_c + R_c,$$

where $T_c[u](x) = T[u](x + c)$ and $R_c[u](x) = R[u](x + c)$.

By using an argument similar to the proof of Lemma 5.2, one can show

$$|R_c[u](x+\delta) - R_c[u](x)| \leq \left(\prod_{i=1}^{r} b_i\right) H(A_c^+) \left[a_0 + \sum_{i=1}^{\infty} a_i \left(\prod_{j=0}^{i-1} s_j\right)\right] \int_{\mathbb{R}} |k(\zeta+\delta)-k(\zeta)| d\zeta.$$ 

This shows that $\{R_c[u](x) : u \in E_c\}$ is an equicontinuous family of functions that is uniformly bounded by $A_c^+$. Further, $T_c$ is a $\rho_c$-contraction (i.e., $\|T_c u\|_c \leq \rho_c \|u\|_c$).

An asymptotic fixed point theorem by Cain and Nashed [4, Thm. 3.1, p. 583]) shows that $P_c$ has a fixed point $A_c(x) \in E_c$ that describes a traveling wave solution to system (2.1) with speed $c$. Since $A_c^+(x) \leq A_c^+$ for all $x$ and $A_c^+(\infty) = 0$, we have that $A_c(x) \leq A_c^+$ for all $x$ and $A_c(\infty) = 0$. 


Define $Q^-$ by (2.3) with $H$ replaced by $H^-$, and define $Q^- [u](x) = Q^- [u](x+c)$. To obtain the behavior of $A_c$ at $-\infty$, consider the infinite vector recursion $u_{n+1}^- = Q^- [u_n^-]$ with the initial condition $u_0^- (x) = \gamma w_c^+ (x)$, where $w_c^+$ is obtained by substituting $A_c^+$ for $A$ in (5.2) and $\gamma$ is a small positive number. We see that $Q^- [u_0^-] \geq u_0^-$ since $H^- (\gamma u) \geq \gamma H^+ (u)$. Thus by induction, $u_{n+1}^- \geq u_n^-$ for all $n$ and $u_n^-(x)$ is nonincreasing in $x$. Define $w_c$ by substituting $A_c$ for $A$ in (5.2). Since $Q^- [w_c] \leq Q_c [w_c] = w_c$ and $u_n^- \leq w_c$ induction shows that $u_n^- \leq w_c$ for all $n$. This implies that

$$\liminf_{x \to -\infty} w_c (x) \geq u_n^- (-\infty) \quad \text{for all } n.$$ 

By Lemma 5.1, for any fixed $n$,

$$u_{n+1}^- (-\infty) = \rho_o u_n^- (-\infty) + \left( \prod_{i=1}^{\tau} b_i \right) \left[ a_0 H^- (u_n^- (-\infty)) + \sum_{i=1}^{\infty} a_i \left( \prod_{j=0}^{i-1} s_j \right) H^- (u_n^- (\tau)) \right].$$

Since $u_0^- (-\infty) = \gamma A_c^+ (-\infty) > 0$ and $u_n^- (-\infty) \leq w_c$ are nondecreasing in $n$, they must converge to a number greater than or equal to the smallest positive solution of the equation $u = \rho_o u + a_0 H^- (u) + \sum_{i=1}^{\infty} a_i (\prod_{j=0}^{i-1} s_j) H^- (u)$. This solution has been defined to be $A_c^-$. Hence, $\liminf_{x \to -\infty} A_c (x) \geq A_c^-$. This completes the proof of statement (i).

To prove statement (ii) we obtain a contradiction by letting $w(x)$ be a traveling wave solution with speed $c < c^*$ such that $\liminf_{x \to -\infty} w(x) \geq u_n^-$ and $w(\infty) = 0$. Choose a nonincreasing function $v_0 (x)$ such that $v_0 (x) \leq w(x)$, $v_0 (x) \leq u_n^-$, $v_0 (x) \equiv 0$ outside of a bounded domain, and $v_0 (x)$ is positive on a set with positive measure for some $i$. Let $v_n$ be defined by the recursion $v_{n+1} (x) = Q^- [v_n] (x)$. By induction and the fact that $Q^-$ is order preserving and $Q^- \leq Q$, we have that $v_n (x) \leq w(x - nc)$. The rest of the proof follows the last part of the proof of statement (ii) in Theorem 5.1. The proof is complete.

6. Numerical simulations. In this section we conduct numerical simulations of the growth and spread of perennial and annual plant populations with an age-structured seed bank. For the purpose of these simulations we consider the four-dimensional truncated model:

$$A_{n+1} (x) = \rho_o A_n (x) + a_0 \int_{-\infty}^{\infty} k(x-y) H(A_n (y)) dy + \sum_{j=1}^{3} a_j S_n^j (x),$$

$$S_{n+1}^1 (x) = s_0 \int_{-\infty}^{\infty} k(x-y) H(A_n (y)) dy,$$

$$S_{n+1}^2 (x) = s_1 S_n^1 (x),$$

$$S_{n+1}^3 (x) = s_2 S_n^2 (x).$$

Here $\tau = 1$ (i.e., there is no juvenile), and the oldest possible age of a seed in the bank is three years. This perennial model is relevant for many species of herbs which can go from germination to maturation within one growing season. It is an annual plant population model if $\rho_o = 0$, and a perennial plant population model if $0 < \rho_o < 1$. 

Fig. 2. Annual plants. Traveling waves for (6.1) when the perennial term is 0 ($\rho_o = 0$). Top row: no seed bank. Bottom row: seed bank.

We simulate traveling wave solutions for the spatial system. Traveling wave solutions are modeled using an approximation to the convolution integral based on an algorithm motivated by the methods used in [2, 19].

We use the Laplace dispersal kernel

$$k(|x - y|) = 100e^{-200|x - y|}$$

and the Ricker growth function

$$H(u) = ue^{r-u}$$

with $r > 0$. Note that $K(\mu)$ for the above Laplace kernel converges for $-\Lambda < \mu < \Lambda$ with $\Lambda = 200$ and that Hypotheses 2.1 are satisfied.

Parameters that remain consistent in each simulation are $\rho_o = 0$, $\beta_1 = 0.9$, $\beta_2 = 0.9$, $\beta_3 = 0.9$, $\beta_4 = 0.9$, and $\beta_5 = 0.9$. We investigate the effect of the perennial term $\rho_o$ and the growth function parameter $r$ so these will vary by diagram.

A positive constant equilibrium of the system (6.1) is given by $(A_*, S_1^*, S_2^*, S_3^*)$, where

$$A_* = r - \ln\left(\frac{1 - \rho_o}{a_0 + a_1s_0 + a_2s_1s_0 + a_3s_2s_1s_0}\right)$$

and $S_1^* = s_0F(A_*)A_*$, $S_2^* = s_2S_2^*$, and $S_3^* = s_2S_3^*$.

Figures 2 and 3 show some approximations to traveling wave solutions for $(A_*, S_1^*, S_2^*, S_3^*)$. We use different types of lines to represent the distribution of each population cohort. Solid lines represent the adult population, dashed lines represent the one-year-old seed bank population ($S_1^*$), dotted lines represent the two-year-old seed bank population ($S_2^*$), and the dotted/dashed lines represent the three-year-old seed bank population ($S_3^*$). In each caption we indicate values for the growth function parameter $r$, the perennial term $\rho_o$, and the spreading speed of the traveling wave $c$. 
Fig. 3. Perennial plants. Traveling waves for the model (6.1) when the perennial term is 0.5 ($\rho_o = 0.5$). Top row: no seed bank. Bottom row: seed bank.

We make a few general observations about the system. First, traveling waves for each population cohort in the seed bank model take on qualitatively similar shapes; see the second row of Figures 2 and 3. This can be seen by observing that, in any single diagram, all four distributions look very similar. Second, the maximum density of the seed bank populations decreases with age. The maximum seed bank density follows this order as well, with dashed lines the highest, dotted lines the middle, and dashed/dotted lines the lowest. The adult plant distribution (solid lines) does not follow a particular pattern. Its position, relative to the seed bank distributions, is related to the choice of survival and germination parameters. Finally, in both Figures 2 and 3 the shape of the traveling waves is related to the growth function parameter $r$. We see that as the parameter $r$ increases, the tail of the traveling waves becomes increasingly unstable.

We now examine the role of the seed bank and perennial term $\rho_o$. The diagrams in Figure 2 represent traveling waves for annual plants (the perennial term $p_o$ is 0). Alternatively, the diagrams in Figure 3 represent traveling waves for perennial plants (the perennial term $p_o$ is 0.5). Both figures follow the same type of flow: The top row displays traveling wave solutions when there is no seed bank present (i.e., $s_i = 0$ for $i = 1, 2, 3$) and the bottom row displays traveling wave solutions when an age-structured seed bank exists for seeds up to age three. Moving across a row from left to right the growth function parameter $r$ is increased ($r = 1.5, 3.5, 6$) and all other parameters are held constant. In this way we can observe the effect of the perennial term by comparing diagrams in Figure 2 to diagrams in Figure 3 that have the same relative position. We can observe the effect of the seed bank by comparing the top row to the bottom row in each figure.

The effect of increasing the perennial survival term $\rho_o$ is clear: comparing diagrams in Figure 2 to those in Figure 3 with the same relative position, we see that the distribution increases in magnitude and stabilizes in shape. Thus, a perennial plant...
with strong survivorship throughout the years will tend to have a more stable and higher density distribution.

Comparing diagrams in the top row with those in the bottom row for Figures 2 and 3 we see that having a seed bank can increase the overall adult plant density. Also, when \( r = 1.5 \) the shape of the adult plant distribution is the same for both the case of having a seed bank (bottom row) and not having a seed bank (top row). However, when \( r \) is increased we see that the seed bank can have a stabilizing effect on the adult plant distribution. The diagram in Figure 2b representing no seed bank appears to have oscillations in the tail of period 4, while the corresponding diagram in Figure 2e representing a seed bank has oscillations of period 2.

For the case of perennial plants (\( \rho_o = 0.5 \)), we see from Figure 3 that the shape of traveling waves is the same when a seed bank is present and when it is absent (compare Figure 3a to 3d, Figure 3b to 3e, and Figure 3c to 3f). Thus, when the perennial survival rate is large enough, the stabilizing effect of this term washes out the effects of the seed bank, creating qualitatively similar traveling waves for both the case of having a seed bank and not having one.

In summary, when comparing an annual model with no seed bank to a perennial model with no seed bank (all other parameters equal), the perennial term can have a stabilizing effect on the traveling waves and increase the maximum plant density. Similarly, when comparing an annual model with no seed bank to an annual model with a seed bank, the seed bank can have a stabilizing effect on the traveling waves and increase the maximum plant density. When comparing a perennial model with no seed bank to a perennial model with a seed bank, the traveling waves look very similar. Thus, the effect of the perennial term may have washed out the stabilizing effect of the seed bank.

7. Discussion. In this paper we formulated a system of infinite integro-difference equations that serve to model growth and spread of perennial and annual plants with an age-structured seed bank and juvenile cohort. This model is an extension of the models studied in Li [18] and Lutscher and Van Minh [23]. The underlying dynamics are very complicated when the growth function is nonmonotone. However, we can still give a complete description of the spreading speed and traveling wave solutions. The techniques developed in this paper can be used to analytically determine the spreading speed and traveling wave solutions in the model given in Powell, Slapničar, and van der Werf [29] that is used to study the spread of a lesion-forming plant pathogen with infinite age structure.

In section 3 we showed that system (2.1) has a strictly positive constant equilibrium. We also established the existence and properties of a positive eigenvalue and eigenvector for the infinite moment generating matrix \( B_\mu \). In section 4 we showed that the spreading speed \( c^* \) of the system is given by \( c^* = \inf_{\mu > 0} \frac{\ln \lambda(\mu)}{\mu} \), where \( \lambda(\mu) \) is the principal eigenvalue \( \lambda(\mu) \) of \( B_\mu \).

In section 5 we proved the existence of traveling wave solutions when \( c \geq c^* \) and showed that traveling wave solutions do not exist when \( c < c^* \). This shows that the spreading speed can be characterized as the slowest speed of a class of traveling wave solutions.

In section 6, we conducted numerical simulations of traveling wave solutions for a four-dimensional truncated version of the model so that seeds in the bank can only survive up to three years. The Ricker function is used as the growth function. This function has been used to study plant populations (see [16, 28]). From these simulations we observe that the tail of traveling wave solutions can take on many different
patterns, determined in large part by the value of the growth function parameter $r$. We also see that the seed bank and the perennial term can have a stabilizing effect on the traveling waves. Additionally, when the perennial term $\rho_0$ is large enough, the stabilizing effect of this term washes out the effect of the seed bank, effectively making the seed bank versus no seed bank models indistinguishable.

This model can be extended in several different directions. We may add further structure to model perennial plants with age-structure in the adult plant population. Perennial plants may stop producing seeds when they get too old, and seed production may be age-dependent. To model this type of situation we could add a cohort in the adult population in which adult plants are divided into groups with distinct seed production functions and survival rates.

We may permit density-dependent survival and germination parameters to account for crowding. Crowding describes the effect that high population density has on the reproductive output and adaptive strategies of ecological populations. It is known that crowding in plant populations oftentimes has a negative effect on reproductive output [31]. Additionally, it has also been shown that crowding can cause insects to have a more detrimental effect on the crowded plants [11]. By permitting the survival and germination parameters in (2.1) to be density-dependent we may study the effects of crowding and how it relates to the spatial spread of plant populations.

We may consider stochastic fluctuations in population growth. Environmental variability including climate effects, effects of human interaction, and effects of competitors are stochastic. One year may see booming reproduction due to a particularly agreeable climate, while the next year may bring drought or flooding resulting in a large number of deaths and low reproductive output. Presently our model assumes the environment is temporally constant, using a specific function $H(A) = F(A)A$ to model growth. We may replace the growth function with a stochastic variable to model these random effects, similar to the approaches used in [27, 36].

We may allow for an Allee effect. An Allee effect refers to the observed effect that “under-crowding” or low population densities correspond with low reproduction or decreased fitness [33]. There are many reasons why a population might exhibit this Allee effect including an individual’s inability to replace itself in low densities (“pollen limitation”), inbreeding depression, and more [17]. We may incorporate this effect into our model (2.1) by replacing the requirement that the growth function be bounded above by its linearization ($H(A) \leq H'(0)A$) with a weaker condition.

Finally, we may consider a two-species model. Analyzing how species interact and compete upon invasion has been of long standing interest in ecology. By coupling two systems of the form (2.1) we may study species interaction and examine the speed at which the invading species spreads into its competitor’s habitat.

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**REFERENCES**


