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SPREADING SPEED REVISITED: ANALYSIS OF A FREE BOUNDARY MODEL

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Abstract. We investigate, from a more ecological point of view, a free boundary model considered in [11] and [8] that describes the spreading of a new or invasive species, with the free boundary representing the spreading front. We derive the free boundary condition by considering a "population loss" at the spreading front, and correct some mistakes regarding the range of spreading speed in [11]. Then we use numerical simulation to gain further insights to the model, which may help to determine its usefulness in concrete ecological situations.

Dedicated to Professor Hiroshi Matano on the occasion of his 60th birthday

1. Introduction.

Understanding the nature of spreading of invasive species is a central problem in invasion ecology. It is known that many animal species spread to their new environment in a linear fashion, namely the range radius eventually exhibits a linear growth curve against time ([28, 24]). A well known example is due to Skellam [29] concerning the spreading of muskrat in Europe in the early 1900s: He calculated the area of the muskrat range from a map obtained from field data, took the square root and plotted it against years, and found that the data points lay on a straight line.

Several mathematical models have been proposed to describe this phenomenon and a number of them may be found in [28]. One of the most successful mathematical approaches to this problem is based on the investigation of front propagation governed by the following diffusive logistic equation over the entire space $\mathbb{R}^N$:

$$u_t - d\Delta u = u(a - bu),\ t > 0,\ x \in \mathbb{R}^N. \tag{1.1}$$

Here $u = u(t, x)$ may be regarded as the population density of a spreading species with diffusion rate d, intrinsic growth rate a and habitat carrying capacity a/b. If the population density at time $t = 0$ is given by a nonnegative function $u_0(x)$ (i.e., $u(0, x) = u_0(x)$), with $u_0(x)$ not identically zero but vanishes outside some bounded

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domain Ω of $\mathbb{R}^N$, then a well known result of Aronson and Weinberger [2] (see also Section 4 in [1] for the one space dimension case) states that, with $c^* := 2\sqrt{ad}$,

$$\lim_{t\to\infty,\ |x|\le(c^*-\epsilon)t} u(t,x) = a/b, \qquad \lim_{t\to\infty,\ |x|\ge(c^*+\epsilon)t} u(t,x) = 0$$

for any small $\epsilon > 0$. This means that if an observer travels in the direction of propagation at a speed c which is below c^*, then he would find that the population is close to the positive steady-state level a/b, while if his speed is above c^*, he would observe that the population is nearly 0. Therefore the transition phase of the solution, which is used to represent the propagation front here, propagates linearly in t at the speed c^* (for large time). The number c^* is usually called the (asymptotic) spreading speed of the species.

The intrinsic growth rate a and diffusion rate d in (1.1) can often be calculated from field data for specific animal species, which then yield a theoretical spreading speed c^* through the formula $c^* = 2\sqrt{ad}$. This theoretical rate has been compared with observed spreading rate in a number of works, and on page 55 of [28] one may find a comparison table. For most species listed in this table the theoretical rate c^* agrees reasonably well with the observed rate, with one exception where the theoretical rate is one magnitude smaller than the observed one.

The proof of the above Aronson-Weinberger result is based on the theory of traveling waves. In the pioneering works of Fisher [16] and Kolmogorov et al [19], for space dimension $N = 1$, traveling wave solutions have been found for (1.1): For any $c \ge c^* := 2\sqrt{ad}$, there exists a solution $u(t,x) := w(x-ct)$ with the property that

$$w'(y) < 0 \text{ for } y \in \mathbb{R}^1,\ w(-\infty) = a/b,\ \ w(+\infty) = 0;$$

no such solution exists if $c < c^*$. The number c^* in this context is called the minimal speed of the traveling waves. Thus the spreading speed coincides with this minimal speed. Based on these classical works, extensive further development on traveling wave solutions and the spreading speed has been achieved in several directions (e.g., [3, 4, 5, 22, 30, 31, 32]).

We note that the above mathematical result predicts successful spreading and establishment of the new species with any nontrivial initial population $u(0,x)$ (namely $u(t,x) \to a/b$ as $t \to \infty$), regardless of its initial size and supporting area. This is not consistent to numerous empirical evidences; for example, the introduction of several bird species from Europe to North America in the 1900s was successful only after many initial attempts. Indeed, there is a widely accepted law in ecology, called the "10s law": Of all the alien species found at a given time in a given habitat, about one tenth of them develop into an invasive species, and of these invasive species, about one tenth are established eventually.

1.1. **Allee effect.** The above mentioned draw back would disappear if the nonlinear term $u(a-bu)$ in (1.1) is suitably modified to reflect the "Allee effect" on the growth rate of the species. The key feature of the Allee effect is that populations shrink at very low densities because, on average, individuals cannot replace themselves. This can be represented by replacing the logistic reaction term $u(a-bu)$ in (1.1) by a function $f(u)$ with the following properties:

$$f(0) = f(\theta) = f(a/b) = 0,\ f(u) < 0 \text{ in } (0,\theta) \cup (a/b,\infty),\ f(u) > 0 \text{ in } (\theta, a/b),$$

where $\theta \in (0, a/b)$ is a threshold constant for the Allee effect, and one usually further requires that

$$\int_0^{a/b} f(u)du > 0.$$

Such a function $f(u)$ is called a bistable nonlinearity (see, e.g., [13]), while a function behaving like $u(a - bu)$ is called a monostable nonlinearity. This is because in the former case both the equilibria $u = 0$ and $u = a/b$ are stable for the ODE $u' = f(u)$, while in the latter case, only $u = a/b$ is stable. A widely used example of bistable nonlinearity is

$$f_0(u) = au(1 - u)(u - \theta),\ \theta \in (0, 1/2).$$

It is well known that for a bistable nonlinear term $f(u)$ as described above,

$$u_t - du_{xx} = f(u)$$

has a unique traveling wave solution (up to translation) $u(t, x) = w(x-ct)$ satisfying $w(-\infty) = a/b$ and $w(\infty) = 0$ when c takes a certain positive value c_0, and no such solution exists for other values of c (see, e.g., [1]). The value of c_0 is usually difficult to calculate, but when the special form $f_0(u)$ is used, then (see [17, 21])

$$c_0 = (1/2 - \theta)\sqrt{2ad}.$$

The number c_0 is known as the spreading speed for the model with Allee effect ([21]), since any solution of

$$u_t - d\Delta u = f(u)$$

with $u(0, x) \equiv 0$ outside a finite ball $|x| \le R$ satisfies

$$\lim_{t\to\infty,\ |x|\ge(c^*+\epsilon)t} u(t, x) = 0,$$

and if

$$\liminf_{t\to\infty} u(t, x) \ge a/b \text{ for every } x, \tag{1.2}$$

then

$$\lim_{t\to\infty,\ |x|\le(c^*-\epsilon)t} u(t, x) = a/b,$$

where $\epsilon > 0$ is an arbitrary small number. Various sufficient conditions for (1.2) in terms of the initial function $u(0, x)$ are known (see, e.g., [2]), and sharp threshold result is obtained in [13] when the space dimension is 1.

The Allee effect is generally believed to play a crucial role at the early stage of establishment of a spreading species, and once establishment is guaranteed, the spreading process of the species is not expected to be greatly influenced by the Allee effect. Therefore one may think that the asymptotic spreading speed for an establishing invading species should not be affected in a significant manner by the Allee effect. However, this may not to be the case. Lewis and Kareiva in [21] demonstrate that the Allee effect may significantly reduce the spreading speed. On the other hand, no Allee effect has been observed in some invading species (e.g., [14]). One may find further discussions on Allee effects in the review article [20] and references therein.

1.2. **Spreading front as a free boundary.** The main purpose of this paper is to further examine the free boundary models investigated recently in [11] and [8], where the authors use a free boundary to represent the spreading front of the population (which is the edge of the expanding population range), but the nonlinearity in (1.1) is not changed. So the population vanishes at the front, and is governed by (1.1) in the region enclosed by the front. It is assumed that the front invades at a rate that is proportional to the magnitude of the spatial population gradient there. It turns out that this free boundary approach gives rise to a spreading-vanishing dichotomy for the spreading species, and so it also does not have the problem of persistent spreading and establishment associated with the Cauchy problem of (1.1). We note that in this approach the spreading front is precisely described by the free boundary for any given time t, while the Cauchy problem of (1.1) uses an unspecified level set of the solution to describe the front.

More precisely, the model in [11] is given by the following diffusive logistic problem:

$$\begin{cases} u_t - du_{rr} = u(a-bu), & t>0,\ 0<r<h(t), \\ u_r(t,0)=0,\ u(t,h(t))=0, & t>0, \\ h'(t) = -\mu u_r(t,h(t)), & t>0, \\ h(0)=h_0, u(0,r)=u_0(r), & 0\le r\le h_0, \end{cases} \tag{1.3}$$

where $r=h(t)$ is the moving boundary to be determined, h_0, μ, d, a and b are given positive constants, and the initial function $u_0(r)$ satisfies

$$u_0\in C^2([0,h_0]),\ u_0'(0)=u_0(h_0)=0, \quad u_0>0 \text{ in } [0,h_0). \tag{1.4}$$

Here $u(t,r)$ stands for the population density of a new or invasive species over a one dimensional habitat, and the initial function $u_0(r)$ stands for the population of the species in the very early stage of its introduction, which occupies an initial region $[0,h_0]$. It is assumed that the species can only invade further into the environment from the right end of the initial region, and the spreading front expands at a speed that is proportional to the population gradient at the front, which gives rise to the free boundary condition $h'(t)=-\mu u_r(t,h(t))$.

In [8], the situation of higher space dimensions and heterogeneous environment is considered, under the restriction that the environment and the solution are radially symmetric. In [8], the positive solution is written as $u(t,r)$, $r=|x|$, $x\in\mathbb{R}^N$ ($N\ge 2$), and it satisfies

$$\begin{cases} u_t - d\Delta u = u(\alpha(r)-\beta(r)u), & t>0,\ 0<r<h(t), \\ u_r(t,0)=0,\ u(t,h(t))=0, & t>0, \\ h'(t) = -\mu u_r(t,h(t)), & t>0, \\ h(0)=h_0, u(0,r)=u_0(r), & 0\le r\le h_0, \end{cases} \tag{1.5}$$

where due to the radial symmetry, $\Delta u = u_{rr}+\frac{N-1}{r}u_r$, $r=h(t)$ is the moving boundary to be determined, h_0, μ and d are given positive constants, $\alpha,\beta\in C^{\nu_0}([0,\infty))$ for some $\nu_0\in(0,1)$, and there are positive constants $\kappa_1\le\kappa_2$ such that

$$\kappa_1\le\alpha(r)\le\kappa_2, \quad \kappa_1\le\beta(r)\le\kappa_2 \quad \text{for } r\in[0,\infty). \tag{1.6}$$

The initial function $u_0(r)$ satisfies (1.4). Thus problem (1.5) describes the spreading of a new or invasive species with population density $u(t,|x|)$ over an N-dimensional habitat, which is radially symmetric but heterogeneous. The initial function $u_0(|x|)$ stands for the population in the very early stage of its introduction, which occupies an initial region B_{h_0}. Here and in what follows we use B_R to stand for the ball with center at 0 and radius R. The spreading front is represented by the free boundary $|x| = h(t)$, which is the N-dimensional sphere $\partial B_{h(t)}$ whose radius $h(t)$ grows at a speed that is proportional to the population gradient at the front: $h'(t) = -\mu u_r(t, h(t))$. The coefficient function $\alpha(|x|)$ represents the intrinsic growth rate of the species, $\beta(|x|)$ measures its intra-specific competition, and d is the diffusion rate.

So to understand the evolution of the population $u(t, r)$ based on the models of [11, 8], instead of a Cauchy problem one considers a free boundary problem, where both $u(t, r)$ and $h(t)$ are unknown functions. We note that in this approach the spreading front is given explicitly by the moving boundary $r = h(t)$ of the population range, which more closely resembles the real spreading process than the Cauchy problem approach where the spreading front is described by an unspecified level set of the solution. The results of [11, 8] show that even with the original logistic nonlinear function, the dynamics of the population determined by the free boundary model exhibits a spreading-vanishing dichotomy, namely the population either spreads to all the available space ($\lim_{t\to\infty} h(t) = \infty$) and stabilizes at the steady state solution $u \equiv a/b$ ($\lim_{t\to\infty} u(t, r) = a/b$), or it fails to spread to all the space ($\lim_{t\to\infty} h(t) < \infty$) and vanishes as $t \to \infty$ ($\lim_{t\to\infty} u(t, r) = 0$). Moreover, when spreading happens, the propagation speed of the front $r = h(t)$ approaches a positive constant k_0 as $t \to \infty$ (provided that $\lim_{r\to\infty} \alpha(r)$ and $\lim_{r\to\infty} \beta(r)$ exist in the case of (1.5)). Qualitatively, these appear to agree well with many spreading processes of the natural world.

A mathematical theory for the free boundary model in a general non-symmetric setting has been established in [9]. The results in [8] have been extended to the case that the environment is time-periodic ([10]), and more recently to environments with seasonal succession ([26]). In one space dimension, [12] considers more general nonlinear terms for (1.3), including general monostable, bistable and combustion types of nonlinearities.

1.3. **Deduction of the free boundary condition.** Due to the lack of first principles for the ecological situation under consideration, a thorough justification of the free boundary condition used in (1.3) and (1.5) is difficult to supply. Nevertheless, we present here a deduction of the free boundary condition based on the consideration of "population loss" at the front. In the process of population range expansion, near the propagating front, where population density is assumed to be close to zero, the individuals of the species are suffering from the Allee effect. Moreover, as the front enters new unpopulated environment, the pioneering members at the front, with very low population density, are particularly vulnerable. (Note that since only one species is considered here, some existing interacting species are regarded as part of the environment.) Therefore it is plausible to assume that as the expanding front propagates, the population suffers a loss of k units per unit volume at the front. (A related discussion can be found in [15], where "forces" that oppose range limitation such as random dispersal and density regulation, and those that promote range limitation such as maladaptation of the genetic trait of the species, are considered near the edge of the population range, and an equation representing the balance between these forces is given; see eq. (5) there.)

For simplicity we assume that k is a constant for a given species in a given homogeneous environment. We now examine the case of (1.5). By Fick's first law, for a small time increment Δt, during the period from t to $t + \Delta t$, the number of individuals of the population that enters the region (through diffusion, or random walk) bounded by the old front $|x| = h(t)$ and new front $|x| = h(t + \Delta t)$ is approximated by

$$d|\nabla_x u|\Delta t \times (\text{surface area of } \{|x| = h(t)\}) = d|\nabla_x u|\Delta t \cdot N\omega_N h(t)^{N-1},$$

where ω_N denotes the volume of the N-dimensional unit ball, and $\nabla_x u$ is calculated at $|x| = h(t)$. (Note that the contribution of population from the reaction term can be ignored near the front, since $u(a - bu)$ is close to 0 there.)

The population loss in this region is approximated by

$$k \times (\text{volume of the region}) = k \times [\omega_N h(t + \Delta t)^N - \omega_N h(t)^N].$$

So the average density of the population in the region bounded by the two fronts is given by

$$d|\nabla_x u|N\omega_N h(t)^{N-1}\Delta t[\omega_N h(t + \Delta)^N - \omega_N h(t)^N]^{-1} - k.$$

Clearly the limit of this quantity as $\Delta t \to 0$ is the population density at the front, namely $u(t, h(t))$, which by assumption is 0. It is easily checked that this limit equals

$$d|\nabla_x u|/h'(t) - k \text{ with } |x| = h(t).$$

Therefore

$$d|\nabla_x u| = kh'(t) \text{ at } |x| = h(t),$$

or

$$h'(t) = -\mu u_r(t, r) \text{ at } r = h(t) \ \text{ with } \mu = dk^{-1}.$$

Clearly μ is reversely proportional to the population loss at the spreading front.

It can be shown that the Cauchy problem for (1.1) corresponds to the limiting case that $\mu = \infty$ ([9]), that is, the free boundary problem reduces to the Cauchy problem (1.1) if the population loss at the front is 0.

The free boundary condition here coincides with the one-phase Stefan condition arising from the investigation of the melting of ice in contact with water ([27]), where justification can be done based on the physical principles of heat conduction. Similar free boundary conditions also arise in the modeling of wound healing ([6]). For population models, [23] used such a condition for a predator-prey system over a bounded interval, showing the free boundary reaches the fixed boundary in finite time, and in [25], a two phase Stefan condition was used for a competition system over a bounded interval, where the free boundary separates the two competitors from each other in the interval. In these latter cases, justification of the free boundary conditions is much more difficult to obtain. In [18], the free boundary problem of [25] was shown to be the singular limit of a competition system with standard boundary conditions as the competition parameter goes to ∞. The works mentioned in this paragraph all have very different purposes from that of the current paper.

1.4. **Theoretical results for (1.3) and (1.5).** For simplicity, from now on, we always make the following extra assumption

$$\alpha(r) \equiv a > 0, \ \ \beta(r) \equiv b > 0$$

for (1.5).

We now recall explicitly the main results obtained in [11, 8] (under the above extra assumption for (1.5)).

Theorem 1 (Global existence): For the free boundary problem (1.3) or (1.5), there is a unique solution $(u(t, r), h(t))$ defined for all $t > 0$, with $u(t, r) > 0$ and $h'(t) > 0$ for $r \in [0, h(t))$ and $t > 0$.

Hence $\lim_{t\to\infty} h(t) = h_\infty \in (h_0, \infty]$ always exists.

Theorem 2 (Spreading-vanishing dichotomy): Let $(u(t,r), h(t))$ be the solution of the free boundary problem (1.3) or (1.5). Then the following alternative holds:

Either

(i) **Spreading:** $h_\infty = +\infty$ and $\lim_{t\to+\infty} u(t,r) = \frac{a}{b}$ uniformly for r in any bounded set of $[0,\infty)$;

or

(ii) **Vanishing:** $h_\infty < +\infty$ and $\lim_{t\to+\infty} \|u(t,\cdot)\|_{C([0,h(t)])} = 0$.

Theorem 3 (Spreading-vanishing criteria): There exists $R^* > 0$ with the following properties.

- If $h_0 \geq R^*$, then $h_\infty = +\infty$ and spreading happens.
- If $h_0 < R^*$, then there exists $\mu^* > 0$ depending on u_0 such that $h_\infty \leq R^*$ and vanishing happens if $\mu \leq \mu^*$; $h_\infty = +\infty$ and spreading happens if $\mu > \mu^*$.

If spreading occurs, it was shown in [11, 8] that the expanding front $r = h(t)$ moves at a constant speed for large time, namely

$$h(t) = \big(k_0 + o(1)\big)t \text{ as } t \to \infty.$$

The constant k_0 is called the **asymptotic spreading speed** and it is determined by the following auxiliary elliptic problem

$$-dU'' + kU' = aU - bU^2, \quad r > 0, \quad U(0) = 0. \tag{1.7}$$

The positive constant R^* in Theorem 3 is determined in the following way:

$$R^* = \sqrt{\lambda_1}\sqrt{\frac{d}{a}},$$

where λ_1 is the first eigenvalue of the problem

$$-\Delta u = \lambda u \text{ for } |x| < 1, \ u = 0 \text{ for } |x| = 1.$$

Thus, for (1.3), $R^* = \frac{\pi}{2}\sqrt{\frac{d}{a}}$.

The part in [11] that discusses the determination of the asymptotic speed k_0 contains some mistakes. These will be corrected in the next section. In section 3, we will make use of numerical calculations to obtain further insights to the model. Among other things, we will examine how the spreading speed k_0 varies with the parameters, how the critical value μ^* in Theorem 3 can be estimated, and how $u(t,r)$ evolves with time near the front $r = h(t)$. It is our hope that the numerical analysis may help to determine the usefulness of the model in concrete ecological problems.

2. **Semi-waves and the spreading speed.** Recall that for each $c \geq c^* := 2\sqrt{ad}$, the following problem

$$-dw'' - cw' = aw - bw^2, \ w(-\infty) = a/b, \ w(\infty) = 0$$

has a unique solution $w(x)$ (up to translation in x), and moreover, $w'(x) < 0$ for all x. If $c < c^*$, then no such solution exists. Such a solution is called a traveling wave of (1.1) with speed c because $u(t,x) := w(x - ct)$ satisfies

$$u_t - du_{xx} = au - bu^2 \ \text{ for all } t, \ x \in \mathbb{R}^1,$$

and as t increases, the curve $u = u(t,x)$ in the ux-plane resembles a wave which does not change its shape but travels to the right at speed c.

For fixed $k \geq 0$, we now consider the following problem over the half line:

$$-dV'' - kV' = aV - bV^2 \quad \text{in } (-\infty, 0), \quad V(-\infty) = a/b, \ V(0) = 0. \tag{2.1}$$

If V is a solution to (2.1), then clearly $v(t,x) := V(x - kt)$ satisfies

$$v_t - dv_{xx} = av - bv^2 \ \text{ for } t \in \mathbb{R}^1, x < kt; \ v(t, kt) = 0.$$

We will call V a **semi-wave**, since as t increases the graph of the curve $v = v(t,x)$, which is defined on the half line $x < kt$, resembles a wave traveling to the right at speed k, with the wave front at $x = kt$.

Set $U(x) = V(-x)$; then clearly (2.1) is equivalent to

$$-dU'' + kU' = aU - bU^2 \quad \text{in } (0, \infty), \quad U(0) = 0, \ U(\infty) = a/b. \tag{2.2}$$

For convenience of comparison with results in [11], we will use (2.2) instead of (2.1) in the following discussions.

We have the following result, which is a correction of Proposition 4.1 in [11].

Proposition 2.1. *For any given constants $a > 0$, $b > 0$, $d > 0$ and $k \in [0, 2\sqrt{ad})$, problem (2.2) admits a unique positive solution $U = U_k$, and it satisfies $U_k'(x) > 0$ for $x \geq 0$, $U_{k_1}'(0) > U_{k_2}'(0)$, $U_{k_1}(x) > U_{k_2}(x)$ for $x > 0$ and $0 \leq k_1 < k_2 < 2\sqrt{ad}$.*

Moreover, for each $\mu > 0$, there exists a unique $k_0 = k_0(\mu) \in (0, 2\sqrt{ad})$ such that $\mu U_{k_0}'(0) = k_0$.

Proof. For large $l > 0$ and $k \in [0, 2\sqrt{ad})$, we consider the problem

$$-dU'' + kU' = aU - bU^2, \quad 0 < x < l, \quad U(0) = U(l) = 0. \tag{2.3}$$

Define

$$\lambda = \frac{k}{\sqrt{ad}} \ \text{ and } W(x) = \frac{b}{a} e^{-\frac{\lambda}{2}x} U\Big(\sqrt{\frac{d}{a}}\, x\Big).$$

Then (2.3) is changed to the equivalent problem

$$-W'' = \Big(1 - \frac{\lambda^2}{4}\Big) W - e^{\frac{\lambda}{2}x} W^2 \text{ in } (0, \tilde{l}), \ W(0) = W(\tilde{l}) = 0, \tag{2.4}$$

where

$$\tilde{l} := \sqrt{\frac{a}{d}}\, l.$$

By our assumption on k, we find that $1 - \frac{\lambda^2}{4} > 0$, and hence for all large l, by a well-known result (see, e.g., Theorem 5.1 in [7]), the logistic type problem (2.4) has a unique positive solution W^l, which in turn defines a unique positive solution U^l for (2.3).

The proof now proceeds as in the proof of Proposition 4.1 in [11] until the discussion for the function

$$\sigma(k) := k - \mu U_k'(0)$$

near the end of the proof there. The function $\sigma(k)$ now is defined for $k \in [0, 2\sqrt{ad})$, and by the monotonicity of $U_k'(0)$ on k, we know that $\sigma(k)$ is strictly increasing with $\sigma(0) < 0$. Therefore there exists a unique $k_0 \in (0, 2\sqrt{ad})$ such that $\sigma(k_0) = 0$ provided that we can show

$$\lim_{k \nearrow 2\sqrt{ad}} \sigma(k) > 0. \tag{2.5}$$

To complete the proof, it remains to prove (2.5). To this end, we choose an arbitrary sequence $\{k_n\}$ of positive numbers that increases to $2\sqrt{ad}$ as $n \to \infty$ and consider the corresponding sequence of solutions $\{U_{k_n}\}$. Since $0 < U_{k_n}(x) < a/b$ for $x \in (0, \infty)$, and $U_{k_n}(x)$ is decreasing in n, the limit

$$U_*(x) := \lim_{n\to\infty} U_{k_n}(x)$$

exists and satisfies $0 \le U_*(x) < a/b$ for $x \in (0, \infty)$. Moreover, applying standard L^p estimates to the equation for U_{k_n} and then the Sobolev embedding theorem, we easily see that $U_{k_n} \to U_*$ in $C^1_{loc}([0, \infty))$. Hence U_* satisfies in the week sense (and also classical sense)

$$-dU_*'' + 2\sqrt{ad}U_*' = aU_* - bU_*^2 \text{ in } (0, \infty),\ U_*(0) = 0.$$

Define

$$W_*(x) = \frac{b}{a} e^{-x} U_*\Big(\sqrt{\frac{d}{a}}\, x\Big).$$

Then one readily checks that

$$W_*'' = e^x W_*^2,\ 0 \le W_* < 1 \text{ in } (0, \infty),\ W_*(0) = 0.$$

We claim that $U_* \equiv 0$. Otherwise by the strong maximum principle we have $U_*(x) > 0$ for $x > 0$ and $U_*'(0) > 0$. It follows that

$$W_*''(x) = e^x W_*^2(x) > 0 \text{ for } x > 0, \text{ and } W_*'(0) > 0.$$

This implies that $W_*(x) \to \infty$ as $x \to \infty$, a contradiction to the fact that $W_*(x) < 1$ for $x > 0$. Thus we must have $U_* \equiv 0$.

Since $\{k_n\}$ is an arbitrary sequence increasing to $2\sqrt{ad}$, the above discussion shows that $U_k \to 0$ as $k \to 2\sqrt{ad}$ in $C^1_{loc}([0, \infty))$. In particular, $U_k'(0) \to 0$ as $k \to 2\sqrt{ad}$. Therefore

$$\lim_{k\nearrow 2\sqrt{ad}} \sigma(k) = 2\sqrt{ad} > 0,$$

as we wanted. □

The number k_0 is the asymptotic spreading speed for the free boundary problems in [11] and [8]. The mistake in Proposition 4.1 of [11] affects a few conclusions given in [11] about k_0, which we now correct. These are only concerned with the asymptotic behavior of k_0 when some of the parameters are large or small; for example, the second half of Proposition 4.3 in [11] needs to be changed. The rest of [11] remains valid as they are not affected by the mistake in Proposition 4.1 there.

By Proposition 2.1 above, for any $\lambda \in [0, 2)$, the problem

$$-\tilde{V}'' + \lambda \tilde{V}' = \tilde{V} - \tilde{V}^2 \text{ in } (0, \infty),\ \tilde{V}(0) = 0 \tag{2.6}$$

has a unique positive solution $\tilde{V}_\lambda$, and for each $\alpha > 0$, the equation

$$\lambda = \alpha \tilde{V}_\lambda'(0) \tag{2.7}$$

has a unique solution $\lambda = \lambda_0(\alpha) \in (0, 2)$.

From the proof of Proposition 2.1 we know that the function

$$\eta(\lambda) := \tilde{V}_\lambda'(0)$$

is strictly decreasing (and continuous) for $\lambda \in [0, 2)$, and

$$\eta(0) > 0,\ \eta(2 - 0) = 0.$$

Hence for each fixed $\alpha > 0$, $(\lambda_0(\alpha), \lambda_0(\alpha)/\alpha)$ is the unique intersection point of the increasing line $\eta = \frac{1}{\alpha}\lambda$ with the decreasing curve $\eta = \eta(\lambda)$ in the $\eta - \lambda$ plane. Clearly

$$\lim_{\alpha\to 0}(\lambda_0(\alpha), \lambda_0(\alpha)/\alpha) = (0, \eta(0)),\ \lim_{\alpha\to\infty}(\lambda_0(\alpha), \lambda_0(\alpha)/\alpha) = (2, 0). \tag{2.8}$$

A simple calculation confirms that for each $k > 0$,

$$\tilde{V}_{\frac{k}{\sqrt{ad}}}(x) = \frac{b}{a}U_k\Big(\sqrt{\frac{d}{a}}\,x\Big). \tag{2.9}$$

Hence

$$\tilde{V}'_{\frac{k}{\sqrt{ad}}}(0) = \frac{b}{a}\sqrt{\frac{d}{a}}\,U_k'(0),$$

and $\mu U_k'(0) = k$ is equivalent to

$$\frac{a\mu}{bd}\tilde{V}'_{\frac{k}{\sqrt{ad}}}(0) = \frac{k}{\sqrt{ad}}.$$

It follows that

$$\frac{k_0}{\sqrt{ad}} = \lambda_0\big(\frac{a\mu}{bd}\big). \tag{2.10}$$

We can now use (2.8) to obtain

$$\lim_{\frac{a\mu}{bd}\to\infty}\frac{k_0}{\sqrt{ad}} = 2,\ \lim_{\frac{a\mu}{bd}\to 0}\frac{k_0}{\sqrt{ad}}\frac{bd}{a\mu} = \eta(0).$$

We show next that $\eta(0) = 1/\sqrt{3}$. Indeed, by definition, $\eta(0) = \tilde{V}_0'(0)$ and $\tilde{V}_0$ satisfies

$$-\tilde{V}_0'' = \tilde{V}_0 - \tilde{V}_0^2,\ \tilde{V}_0 > 0 \text{ in } (0,\infty),\ \tilde{V}_0(0) = 0,\ \tilde{V}_0(\infty) = 1.$$

Hence

$$\int_0^\infty (-\tilde{V}_0'')\tilde{V}_0'dx = \int_0^\infty (\tilde{V}_0 - \tilde{V}_0^2)\tilde{V}_0'dx.$$

We have

$$\int_0^\infty (-\tilde{V}_0'')\tilde{V}_0'dx = \tilde{V}_0'(0)^2/2,$$

and

$$\int_0^\infty (\tilde{V}_0 - \tilde{V}_0^2)\tilde{V}_0'dx = \int_0^1 (v - v^2)dv = 1/6.$$

Therefore

$$\tilde{V}_0'(0) = 1/\sqrt{3}.$$

Summarizing, we have proved the following result.

Proposition 2.2. *Let k_0 be the spreading speed determined by Proposition 2.1. Then*

$$\lim_{\frac{a\mu}{bd}\to\infty}\frac{k_0}{\sqrt{ad}} = 2,\ \lim_{\frac{a\mu}{bd}\to 0}\frac{k_0}{\sqrt{ad}}\frac{bd}{a\mu} = 1/\sqrt{3}.$$

Let us note that Proposition 2.2 indicates that when the quantity $\frac{a\mu}{bd}$ is large, then the spreading speed k_0 is well approximated by the formula

$$k_0 \approx 2\sqrt{ad}, \tag{2.11}$$

while when this quantity is small, k_0 is well approximated by the formula

$$k_0 \approx \frac{1}{\sqrt{3}}\frac{a\mu}{bd}\sqrt{ad}. \tag{2.12}$$

In particular, for fixed $a, b, \mu > 0$, if we regard k_0 as a function of d, then

$$\lim_{d\to 0} \frac{k_0}{\sqrt{d}} = 2\sqrt{a}, \ \lim_{d\to\infty} k_0\sqrt{d} = \frac{\mu a^{3/2}}{\sqrt{3}\, b}.$$

These limits correct those in Proposition 4.3 of [11].

Let us note that from Proposition 2.1 above we always have $0 < k_0 < 2\sqrt{ad}$. That is the spreading speed determined by the free boundary model is always smaller than that determined by the Cauchy problem of (1.1). The following remark indicates a possible approach to determine the spreading speed k_0 based on ecological considerations and (2.10).

Remark 2.3. *Recall that $\mu = d/k$, where k is the preferred population density of the species. If we assume that k is the carrying capacity of the environment, namely $k = \frac{a}{b}$, then*

$$\frac{a\mu}{bd} = 1 \ \text{and} \ k_0 = \lambda_0(1)\sqrt{ad}.$$

More generally, if we assume that the ratio of the carrying capacity to the preferred population density is a constant γ, then

$$\frac{a\mu}{bd} = \gamma \ \text{and} \ k_0 = \lambda_0(\gamma)\sqrt{ad}.$$

3. **Numerical analysis.** In this section, we use numerical analysis to obtain various quantitative estimates which are missing from the theoretical results described above for (1.3) and (1.5). These provide further insights to the model and may help to determine its usefulness in concrete ecological problems.

3.1. **Calculation of spreading speed.** In this subsection, through numerical calculations we indicate how the spreading speed k_0 can be calculated. In particular, we determine the ranges of $\frac{a\mu}{bd}$ for which (2.11) and (2.12) give good approximations of the spreading speed k_0, respectively.

Let us recall from the previous section that the asymptotic spreading speed for (1.3) and (1.5) (with $\alpha(r) \equiv a,\ \beta(r) \equiv b$) is given by, due to (2.10),

$$k_0 = \lambda_0\left(\frac{a\mu}{bd}\right)\sqrt{ad},$$

where the function $\lambda = \lambda_0(\alpha),\ \alpha > 0$, is uniquely determined by (2.7). From (2.9) we find that

$$U_k(x) = \frac{a}{b}\tilde{V}_{\frac{k}{\sqrt{ad}}}\left(\sqrt{\frac{a}{d}}x\right),$$

where $\tilde{V}_\lambda, \lambda \in [0, 2)$, is the unique positive solution of (2.6).

Table 3.1 below shows how $\lambda_0(\alpha)$ varies as α varies in $[1, \infty)$. In particular, it shows that $2 > \lambda_0(\alpha) > 1.84$ for $\alpha > 10^4$. This indicates that when $\frac{a\mu}{bd} > 10^4$, the formula (2.11), namely $k_0 \approx 2\sqrt{ad}$, is a reasonable approximation of the spreading speed.

The changes of $\lambda_0(\alpha)$ and $\frac{\lambda_0(\alpha)}{\alpha}$ for $\alpha \in (0, 1]$ are described by Table 3.2. We find

$$\frac{1}{\sqrt{3}} > \frac{\lambda_0(\alpha)}{\alpha} > \frac{0.84}{\sqrt{3}}$$

for $0 < \alpha < 0.3$. Thus the formula (2.12) gives a reasonable approximation of the spreading speed in the parameter regime $\frac{a\mu}{bd} < 0.3$.

α	1	10	10^2	10^3	10^4	10^5	10^6	10^7	10^8
$\lambda_0(\alpha)$	0.36	1.01	1.49	1.72	1.84	1.90	1.93	1.95	1.96
α	10^9	10^{10}	10^{11}	10^{12}	10^{13}	10^{14}	10^{15}	10^{16}	∞
$\lambda_0(\alpha)$	1.97	1.98	1.98	1.99	1.99	1.99	1.99	1.99	2.00

TABLE 3.1. $\lambda_0(\alpha)$ for $\alpha \geq 1$

α	0	0.01	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
$\lambda_0(\alpha)$	0	0.006	0.05	0.10	0.15	0.19	0.22	0.25	0.28	0.31	0.34	0.36
$\frac{\lambda_0(\alpha)}{\alpha}\sqrt{3}$	1	0.99	0.94	0.89	0.84	0.80	0.77	0.73	0.70	0.68	0.65	0.63

TABLE 3.2. $\lambda_0(\alpha)$ for $\alpha \leq 1$

3.2. **Evolution of the population and the front.** Though a rigorous theoretical proof is lacking, our numerical simulation indicates that when spreading happens, near the spreading front, the density function $u(t,r)$ approaches $U_{k_0}(r) = \frac{a}{b}\tilde{V}_{\frac{k_0}{\sqrt{ad}}}\left(\sqrt{\frac{a}{d}}r\right)$ in the following sense

$$\lim_{t\to\infty}[u(t,r) - U_{k_0}(h(t)-r)] = 0.$$

The behavior of the standard semi-wave $\tilde{V}_\lambda(-r)$ for various values of $\lambda \in [0,2)$ is described in Figure 3.3 below.

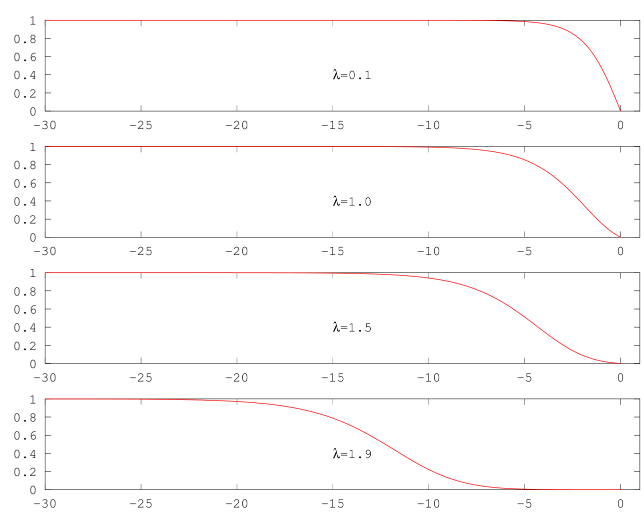
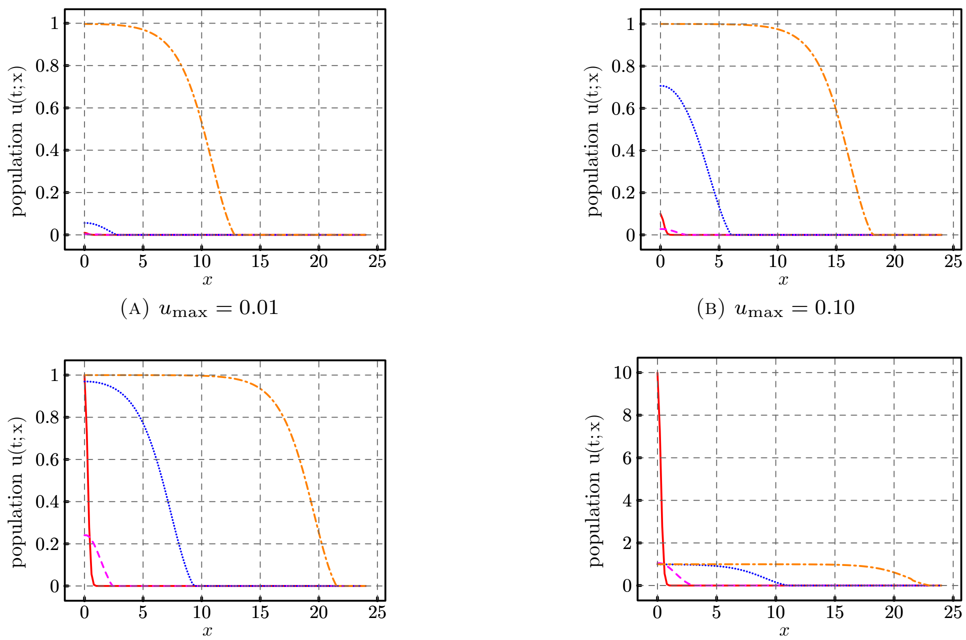


FIGURE 3.3. Shape of the semi-wave solution $\tilde{V}_\lambda(-r)$.

We note the significant change of the shape of the front in Figure 3.3 as λ varies. In particular, the slope of the front gets closer and closer to 0 as the traveling speed λ is increased closer and closer to the limiting speed 2.

We next examine the solutions of (1.3) and (1.5). The evolution with time t of the solution $(u(t,r),h(t))$ of (1.3) is represented by the graphs in Figure 3.4 and Figure 3.5, where $a=b=d=1$, $h_0=2$, $\mu=10$ and $u_0(r)=u_{\max}e^{-\frac{r^2}{2\sigma^2}}$ ($\sigma=0.25$)[1] and several different values of $u_{\max}$ are taken.



(A) $u_{\max}=0.01$ (B) $u_{\max}=0.10$

(C) $u_{\max}=1$ (D) $u_{\max}=10$

FIGURE 3.4. Snapshots for the evolution of $u(t,x)$ for the 1-d problem (1.3), at $t=0$, 0.64, 8.0 and 20.0, with parameters set to: $a=1$, $b=1$, $d=1$, $\mu=10$, $h_0=2$.

In space dimension 2, taking these same parameter values in (1.5), the corresponding graphs for the solution $(u(t,r),h(t))$ are given in Figures 3.6 and 3.7.

Let us note that with the above choices of the parameters, $k_0=1.01$ from Table 3.1, and the graphs of $U_{k_0}(h(t)-r)$ with the same t values are given in Figure 3.8 (in dotted line), where $h(t)$ is calculated with the parameters given in Figure 3.6 (D). The snapshots of the graphs of $u(t,r)$ in Figure 3.6 (D) is reproduced in Figure 3.8 (in solid line) using the new scales for convenience of comparison. It shows that from $t=8.0$, the fronts of $u(t,r)$ is already very well approximated by that of the semi-wave.

[1]The function $u_0(r)$ here does not satisfy $u_0(h_0)=0$. However, in the numerical simulations, this function is extended to be zero for $r\geq h_0$ and the discretization of this extended function is used. Therefore the assumptions in (1.4) for u_0 in (1.3) and (1.5) is not violated in the numerical simulation.

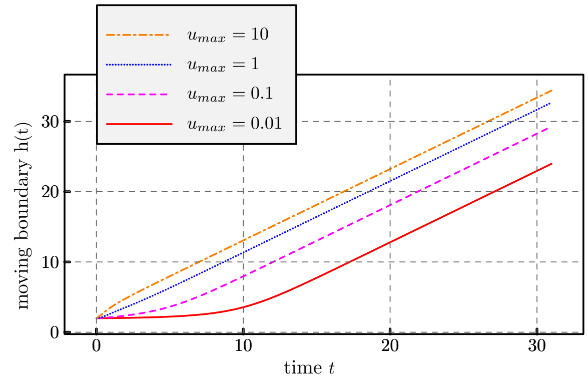
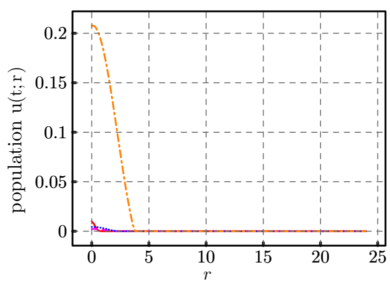
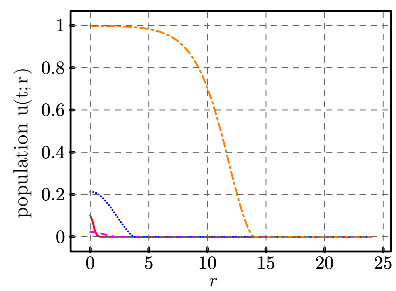


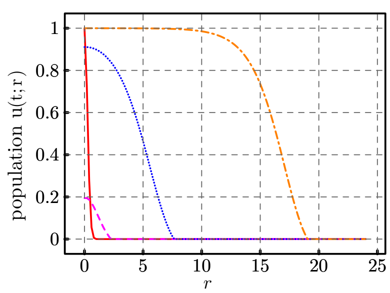
FIGURE 3.5. Spreading radius $h(t)$ for the 1-d problem (1.3), with parameters set to: $a = 1$, $b = 1$, $d = 1$, $\mu = 10$, $h_0 = 2$ and four different values of $u_{\max}$.



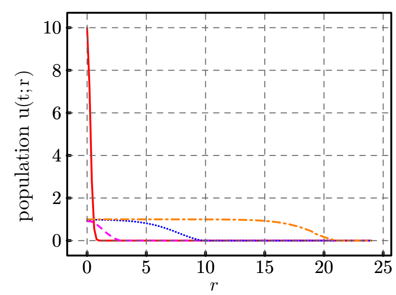
(A) $u_{\max} = 0.01$



(B) $u_{\max} = 0.10$



(C) $u_{\max} = 1$



(D) $u_{\max} = 10$

FIGURE 3.6. Snapshots of the evolution of $u(t, r)$ for the 2-d problem (1.5), at $t = 0$, 0.64, 8.0 and 20.0, with parameters set to: $a = 1$, $b = 1$, $d = 1$, $\mu = 10$, $h_0 = 2$.

3.3. **Spreading and vanishing thresholds.** Taking $a = b = d = 1$ in (1.3), then Theorem 2 of section 1.4 above (see also Theorems 3.4 and 3.9 of [11]) indicates that spreading always happens when $h_0 \geq \pi/2$, and when $h_0 \in (0, \pi/2)$, there exists $\mu^* > 0$ depending on u_0 such that we have spreading when $\mu > \mu^*$, and vanishing when $\mu \in (0, \mu^*]$.

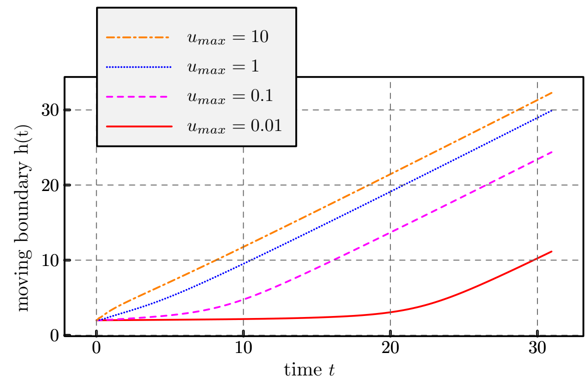


FIGURE 3.7. Spreading radius $h(t)$ for the 2-d problem (1.5), with parameters set to: $a = 1$, $b = 1$, $d = 1$, $\mu = 10$, $h_0 = 2$ and four different values of $u_{\max}$.

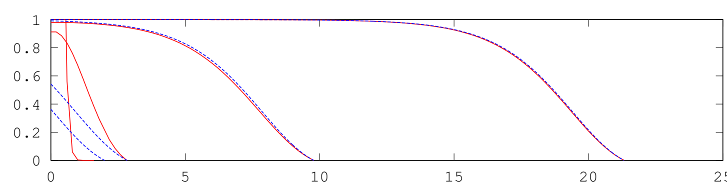


FIGURE 3.8. Shown in dotted line are snapshots of the graphs of the semi-wave $U_{k_0}(h(t) - r)$ with $k_0 = 1.01$ and $h(t)$ as in Figure 3.7 (with $u_{\max} = 10$), at $t = 0$, 0.64, 8.0 and 20.0. In solid line are the snapshots of $u(t, r)$ as in Figure 3.6 (D) (with different scales for clear comparison), at the same time moments $t = 0$, 0.64, 8.0 and 20.0.

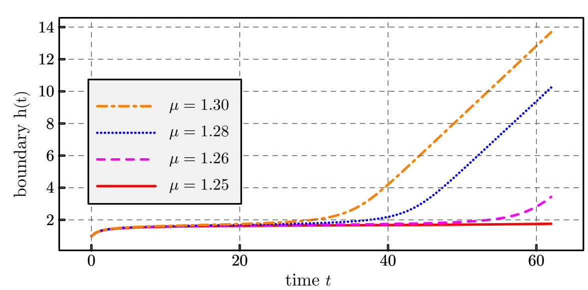


FIGURE 3.9. Evolution of $h(t)$ (position of the front) for the 1-d problem (1.3), with parameters set to: $a = 1$, $b = 1$, $d = 1$, $u_{\max} = 1$, $h_0 = 1$ and four values of μ, showing the existence of a threshold value μ^* between 1.25 and 1.26.

We now take $h_0 = 1 < \pi/2$ and as before $u_0(r) = \alpha e^{-\frac{r^2}{2\sigma^2}}$, $\sigma = 0.25$. Firstly we fix $\alpha = 1$ and use numerical simulation to find μ^*. Figures 3.9 and 3.10 give the graphs of $h(t)$ and $h'(t)$ for a sequence of suitable μ values, which suggest that μ^* is between 1.25 and 1.26.

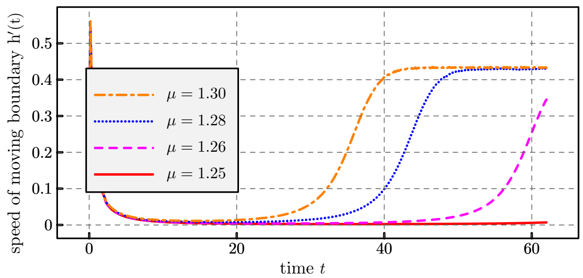


FIGURE 3.10. Evolution of $h'(t)$ (speed of the front) for the 1-d problem (1.3), with parameters set to: $a = 1$, $b = 1$, $d = 1$, $u_{\max} = 1$, $h_0 = 1$ and four values of μ, indicating the existence of a threshold value μ^* between 1.25 and 1.26..

Next we examine, with a, b, d and u_0 as given above and $h_0 = 1$, whether for fixed $\mu > 0$, there is a critical $\alpha^* > 0$ such that spreading happens for $\alpha > \alpha^*$, and vanishing happens for $\alpha < \alpha^*$. The existence of such an α^* is not known from the theoretical analysis in [11, 8]. On the other hand, in [12] it was shown that when the logistic term $u(a - bu)$ is replaced by $u(a - bu^p)$ with $p > 3 + \sqrt{13}$, then there exists some $h_0^* > 0$ so that when $h_0 \in (0, h_0^*]$, vanishing always happens no matter what α value is taken.

Figure 3.11 shows the graphs of $h(t)$ for fixed $\mu = 1.3$ and a sequence of values of α, which indicates that a critical value α^* exists, and its value lies between 1.0 and 1.1.

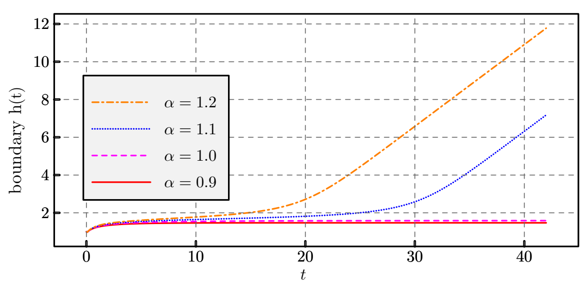


FIGURE 3.11. Evolution of spreading radius $h(t)$ for the 1-d problem (1.3), with parameters set to: $a = 1$, $b = 1$, $d = 1$, $h_0 = 1$, $\mu = 1.3$ and four values of $\alpha = u_{\max}$, indicating the existence of a threshold value α^* between 1.0 and 1.1.

In space dimension 2 we now consider (1.5) with the same parameter values (except that $h_0 = 0.3$) and the same u_0 as that in Figures 3.9 and 3.10. Let us recall that we assume $\alpha(r) \equiv a$ and $\beta(r) \equiv b$, and by Theorem 3 in section 1.4 above, there exists $R^* > 0$ such that spreading always happens when $h_0 \geq R^*$, while if $h_0 \in (0, R^*)$, then there exists $\mu^* > 0$ such that spreading happens when $\mu > \mu^*$, and vanishing happens when $\mu \in (0, \mu^*]$. The general formula for R^* is given by

$$R^* = (\lambda_1)^{1/2}(d/a)^{1/2},$$

where λ_1 is the first eigenvalue of the Laplacian operator $-\Delta$ over the unit ball in R^N with Dirichlet boundary conditions. Now $N = 2$ and so $\lambda_1 = j_{0,1}^2$, where $j_{0,1} = 2.4048...$ is the first zero of the Bessel function of order zero. Thus with the above choice of parameters, we have $R^* = 2.4048...$, and $h_0 = 0.3 < R^*$. Figure 3.12 below shows the graphs of $h(t)$ for a suitable sequence of μ values, which suggest that μ^* for (1.5) in this setting is between 8.2 and 8.3.

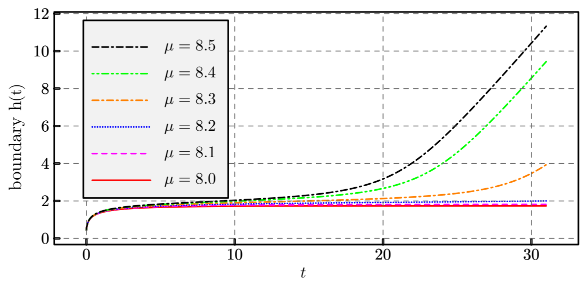


FIGURE 3.12. Evolution of spreading radius $h(t)$ for the 2-d problem (1.5), with parameters set to: $a = 1$, $b = 1$, $d = 1$, $u_{\max} = 1$, $h_0 = 0.3$ and six values of μ, suggesting the existence of a threshold value μ^* lying between 8.2 and 8.3.

3.4. **Strategies for spreading or vanishing.** Depending on circumstances, spreading or vanishing may be favored for a new species. If all the parameters are the same, what shape of the initial distribution of the species better serves the spreading of the species? We now look at how the shape of u_0 affects the threshold value μ^*. Note that the shape of u_0 matters for deciding spreading or vanishing only if h_0 is below the threshold value R^*.

Here we only consider the case (1.5) in space dimension 2. We take $a = b = d = 1$, $h_0 = 0.3 < R^*$, and [2]

$$u_0(r) = u_{\max} \exp\left(-\frac{(r-\bar{r})^2}{2\sigma^2}\right), \ \sigma = 1/8.$$

A sequence of values for the pair $(u_{\max}, \bar{r})$ are taken so that the total initial population

$$\int_{|x|<h_0} u_0(|x|)dx = 2\pi \int_0^{h_0} u_0(r) r dr$$

is kept the same ($\approx 2\pi \cdot 0.032078$); see Figure 3.13.

The estimated values of μ^* for these different set of values of $(u_{\max}, \bar{r})$ are given in Table 3.14.

This table suggests that the threshold value μ^* decreases as the maximum point $\bar{r}$ of $u_0(r)$ is shifted towards h_0, and thus the chance of spreading of the species is increased under such a change of u_0.

[2]This $u_0(r)$ does not satisfy $u_0'(0) = u_0(h_0) = 0$. However, as before, in the numerical simulations, $u_0(r)$ is first extended to be 0 for $r \geq h_0$, and then a discretization of the extended function is used. Therefore the assumption $u_0(h_0) = 0$ in (1.4) is not violated in the numerical simulations. Moreover, one could modify $u_0(r)$ locally near $r = 0$ to make it satisfy $u_0'(0) = 0$. But such local modification makes no difference to the descretized version of the function used in the simulation.

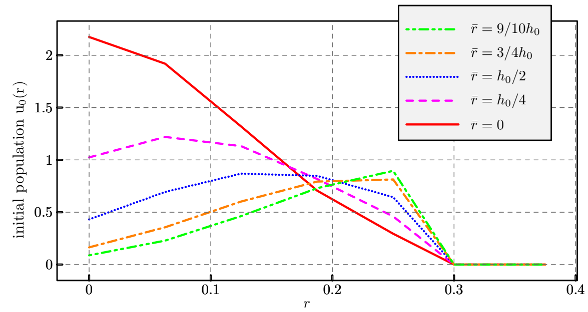


FIGURE 3.13. Initial population $u_0(r)$ (discretized) for the 2-d problem (1.5), with $h_0 = 0.3$ and five sets of values for $(u_{\max}, \bar{r})$.

$\bar{r}$	0	$\frac{1}{4}h_0$	$\frac{1}{2}h_0$	$\frac{3}{4}h_0$	$\frac{9}{10}h_0$
$u_{\max}$	2.175	1.226	0.887	0.829	0.907
estimated μ^*	14.0	11.0	8.5	6.25	5.75

TABLE 3.14. Numerically estimated values of μ^* as u_0 in (1.5) varies.

3.5. **The value of h_∞ when it is finite.** When h_∞ is finite, Theorem 3 of section 1.4 implies that $h_0 < h_\infty \leq R^*$. However, whether and how h_∞ varies with the parameters in the model is unclear from the theoretical result. We now use numerical simulation to check how h_∞ changes as μ is varied below the threshold μ^*. Figure 3.15 shows the behavior of $h(t)$ for (1.5) with $a = b = d = 1,\ h_0 = 0.3$, $u_0(r) = 2.175 \exp\left(-\frac{r^2}{2\sigma^2}\right)$, $\sigma = 1/8$, for a sequence of suitable values of μ, which indicates that h_∞ can take various values in (h_0, R^*).

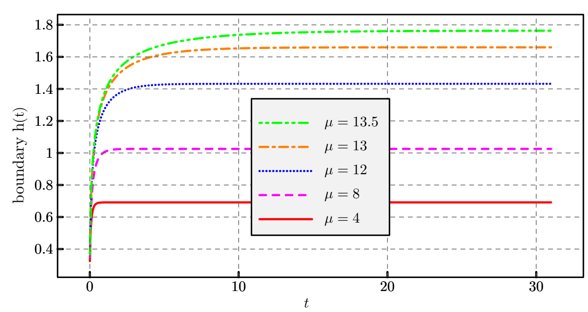


FIGURE 3.15. Evolution of spreading radius $h(t)$ for the 2-d problem (1.5) for some values of μ, with other parameters set to: $a = 1$, $b = 1$, $d = 1$, $u_{\max} = 2.175$ and $h_0 = 0.3$.

3.6. **Numerical algorithms.** The numerical analysis for (1.3) and (1.5) was performed with Scilab, the free software for numerical computation (http://www.scilab.org). Our algorithm is a modification of the standard finite-difference method for *reaction-diffusion equations* over a fixed interval with suitable boundary conditions. The modification is due to the moving boundary nature of our problem. We first choose grid points to divide a large interval $[0, H]$ into small intervals of equal length dx, and extend the initial function $u_0(r)$ from $[0, h_0]$ to $[0, H]$ by the value 0 to obtain $u(t_0, \cdot)$ with $t_0 = 0$. We then redefine the grid point x_i which is closest to h_0 by $x_i = h_0$. We next calculate $u(t, x)$ for the time step $t = t_1$ according to the reaction-diffusion equation for u over the space interval $[0, h_0]$ with the boundary conditions $u_r = 0$ at $r = 0$, and $u = 0$ at $r = h_0$. We then use the free boundary condition $h'(t) = -\mu u_r(t, h(t))$ to determine the next position of the free boundary, denoted by h_1, namely

$$h_1 = h_0 + (dt)u_r(t_1, h_0),$$

where $dt = t_1 - 0 (= t_{k+1} - t_k)$ is the size of time step, and the value of $u_r(t_1, h_0)$ is calculated from $u(t_1, \cdot)$ obtained in the previous step. (It turns out that the value of $u_r(t_1, h_0)$ should be calculated with great care to avoid unwanted oscillations in the simulation; in our calculation $u(t_1, \cdot)$ is first suitably smoothed over several grid intervals to the left of $r = h_0$ before $u_r(t_1, h_0)$ is evaluated.) With the new boundary position h_1 determined, we repeat the above procedure (starting by making h_1 a grid point) until the moving boundary is close to the predetermined value H, or a suitable time step t_m.

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