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Spreading Speed, Traveling Waves, and Minimal Domain Size in Impulsive Reaction-diffusion Models

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Spreading Speed, Traveling Waves, and Minimal Domain Size in Impulsive Reaction-diffusion Models

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Abstract

How growth, mortality, and dispersal in a species affect the species' spread and persistence constitutes a central problem in spatial ecology. We propose impulsive reaction-diffusion equation models for species with distinct reproductive and dispersal stages. These models can describe a seasonal birth pulse plus nonlinear mortality and dispersal throughout the year. Alternatively they can describe seasonal harvesting, plus nonlinear birth and mortality as well as dispersal throughout the year. The population dynamics in the seasonal pulse is described by a discrete map that gives the density of the population at the end stage as a possibly nonmonotone function of the density of the population at the beginning of the stage. The dynamics in the dispersal stage is governed by a nonlinear reaction-diffusion equation in a bounded or unbounded domain. We develop a spatially explicit theoretical framework that links species vital rates (mortality or fecundity) and dispersal characteristics with species' spreading speeds, traveling wave speeds, as well as and minimal domain size for species persistence. We provide an explicit formula for the spreading speed in terms of model parameters, and show that the spreading speed can be characterized as the slowest speed of a class of traveling wave solutions. We also determine an explicit formula for the minimal domain size using model parameters. Our results show how the diffusion coefficient, and

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the combination of discrete- and continuous-time growth and mortality determine the spread and persistence dynamics of the population in a wide variety of ecological scenarios. Numerical simulations are presented to demonstrate the theoretical results.

Key words. difference equation, reaction-diffusion equation, spreading speed, traveling wave, minimal domain size

AMS subject classification. 92D40, 92D25

Abbreviated title. waves and domain size in impulsive models

1 Introduction

Mathematical models have long been central to the development of spatial theory in ecology (e.g., Murray 2002, Okubo and Levin 2001, Tilman and Kareiva 1997, Shigesada and Kawasaki 1997, Skellam 1951, Cantrell and Cosner 2003). A large portion of the mathematical literature on spread and persistence is couched in terms of reaction-diffusion equations, which often yield appealingly tractable and compact models of spread and persistence. Reaction-diffusion equations assume that dispersal is governed by random diffusion and that dispersal and growth take place continuously in time and space. They have had remarkable success in explaining the rates at which species have invaded large open environments as well as spatial patterns that species have had established in bounded-patch habitats. It has been well-documented that the spatial theory about species spread and persistence matches the field observations well in a number of cases (Murray 2002, Shigesada and Kawasaki 1997, and Cantrell and Cosner 2003).

Many species such as fishes or large mammal populations exhibit what Gaughley termed a birth pulse growth pattern (Caswell 2001). That is, reproduction takes place in a relatively short period each year. In between these pulses of growth, mortality takes its toll, and the population decreases. The population dynamics consist of the within-season stage and the between-season stage . Within the season the population mortality is continuous while between the seasons population growth is discrete. Models incorporating both discrete and continuous components are referred to as semi-discrete models (Singh and Nisbet 2007, Pachepsky et al. 2008). There have been extensively studies regarding the dynamics of nonspatial semi-discrete models in the form of impulsive ordinary differential equations; see for example, Eskola and Geritz (2007), Eskola and Parvinen (2007, 2010), Pachepsky et al. (2008), Gyllenberg et al. (1997), Thieme (2003), Brauer and Castillo-Chávez (2001). The results given in these papers show that various discrete-time population models can be derived mechanistically just by altering the patterns of reproduction and interaction. These models include classical examples such as the Ricker model (Ricker 1954), the Beverton and Holt model (Beverton and Holt 1957), the Skellam model (Skellam 1951), and others, which generate equilibrium dynamics, limit cycles, and sometimes chaos. When population dynamics contain growth and dispersal, as well as continuous and discrete components, classical reaction-diffusion equations are not suitable to describe spread and persistence of the population, and impulsive reaction-diffusion equations (hybrid dynamical systems) provide a natural description of the spatial dynamics of the population. To the best of our knowledge, equations of this kind have not received attention in the development of spatial theory.

In this paper, we propose simple impulsive reaction-diffusion equation models to study persistence and spread of species with a reproductive stage and a dispersal stage in bounded and unbounded domains. It is assumed that a reproductive stage pulse growth occurs, and in the dispersal stage movement associated with mortality takes place. The formulations of the models consist of discrete maps and nonlinear reaction-diffusion equations. The discrete maps describe pulse growth, which are allowed to be nonmonotone (i.e., there may be overcompensation in population growth). We also show how the model can be extended to the case of impulsive harvesting in a continuously growing and dispersing population.

We shall address two fundamental questions for the models: what are the spreading speed and traveling wave speeds when a population invades a unbounded domain? and what is the minimal domain size in which the population can persist when the spatial domain is bounded and has a lethal exterior? We demonstrate that, although the underlying dynamics of the models can be complicated, explicit analytical solutions to the questions can be given. We particularly show that when a species spreads into an unbounded domain, there is a spreading speed that can be formulated in terms of species vital rates (survival, fecundity, or development rates) and dispersal characteristics, and the spreading speed can be characterized as the slowest speed of a class of traveling wave solutions. Loosely speaking, the spreading speed of a species is the asymptotic rate at which the species with uniformly positive initial distribution over a large interval and zero distribution outside an interval expands its spatial range. A traveling wave solution describes the propagation of a species as a wave with a fixed shape and a fixed speed. The spreading speeds and traveling wave solutions provide important insight into the spatial patterns and rates of invading species in space. In the case that the spatial domain of a population is bounded with a lethal exterior, we prove the existence of a minimal domain size that can be determined explicitly by the same set of model parameters used for computing the spreading speed. We present simulations for the models. We observe that the numerical solutions for the unbounded domain case can exhibit oscillations, and that the numerical solutions for the bounded domain case can have a variety of spatial patterns of species distributions.

This paper is organized as follows. In the next section we present an impulsive reaction-diffusion model with an unbounded domain, establish the existence of spreading speed and traveling wave solutions for the model, and provide a formula for the spreading speed. In Section 3, we provide an impulsive reaction-diffusion model in a bounded domain that has a lethal exterior, and determine the minimal domain size. Section 4 is about simulations for the models. Section 5 includes some concluding remarks and discussions. Section 6 contains a justification of nonlinearity of a reproduction function in the models and proofs of several theorems.

2 Spread in unbounded domain

2.1 Model formulation

We consider a population with two development stages: the reproductive stage and dispersal stage. In the reproductive stage, the population growth occurs impulsively via a discrete-time map. We use g to describe the population density at the end of reproductive stage as a function of the population density at the beginning of reproductive stage. The population diffuses with a diffusion coefficient d ($d > 0$) and dies continuously in the dispersal stage. For simplicity, we assume that the dispersal stage occurs for time $t \in [0, 1]$. For the dispersal stage, we use α to describe the death rate of the population due to the interaction of the population with the environment, and assume that the interspecific competition between individuals follows the mass action law and use γ to describe the effect of competition. Let $N_n(x)$ denote the density of the population at point x at the beginning of the reproductive season in the nth year. Then the mathematical model that describes the spatial dynamics of the population in a one-dimensional unbounded space is given by

$$\begin{aligned}
&\frac{\partial u}{\partial t} = d\frac{\partial u}{\partial x^2} + \alpha u - \gamma u^2, \quad -\infty < x < \infty, \\
&u(x, 0) = g(N_n(x)), \\
&N_{n+1}(x) = u(x, 1).
\end{aligned} \tag{2.1}$$

In this model, reproduction occurs only once a year, as with many mammal species or the spawning season for many fish species. Outside the production season mortality takes its toll, and the population decreases and diffuses continuously in time.

Model (2.1) can be also used to study the case that impulsive harvesting occurs periodically in a continuously growing and dispersing population. For such a case we assume that $\alpha > 0$ is the growth rate, and $0 < g(N)/N < 1$ so that $1 - g(N)/N$ represents the harvesting rate. Alternatively, it can be employed to describe the situation that the population dynamics is governed by a reaction-diffusion equation outside the winter, and during the winter the population stops reproducing and moving, and the population of the following season is recruited from the individuals that survive the winter.

We shall make the following assumptions on the model

Hypothesis 2.1.

i. *α is a real number, and γ is a positive number.*

ii. *$g(N)$ is a continuous function for $N \geq 0$, $g(0) = 0$, $g'(0) > 0$, $g(N) > 0$ for $N > 0$, and $g(N)/N$ is nonincreasing for $N > 0$.*

In the simplest case, $g(N) = aN$ where $a > 0$. If $\alpha > 0$ and $g(N) = N$, model (2.1) is essentially the classical Fisher equation. The reproductive process can be complicated by interactions between individuals, and $g(N)$ may be nonlinear. A nonlinear g can be derived in the context of competition for breeding sites and Poisson distributing of individuals in space; see Appendix A for a justification. Another approach involves the assumption that, in the reproductive stage, individuals are sessile, and new born juveniles are also immobile for some period of time. The results in Eskola and Parvinen (2007, 2010) show that $g(N)$ is the Beverton-Holt function if there is competition between reproductive adults in the reproductive stage, and $g(N)$ is given by the Ricker function if adults attack juveniles in the reproductive stage.

In the case of $d = 0$, i.e., individuals do not diffuse, we use $\bar{N}_n$ to denote the number of individuals at the beginning of reproductive stage in the nth year. $\bar{N}_n$ is described by

$$\begin{aligned} &\frac{du}{dt} = \alpha u - \gamma u^2, \\ &u(0) = g(\bar{N}_n), \\ &\bar{N}_{n+1} = u(1). \end{aligned} \tag{2.2}$$

For $\alpha \neq 0$, one can solve this problem and find that

$$\bar{N}_{n+1} = \frac{\alpha g(\bar{N}_n)}{(1 - e^{-\alpha})\gamma g(\bar{N}_n) + \alpha e^{-\alpha}}. \tag{2.3}$$

The limiting case of (2.3) is

$$\bar{N}_{n+1} = \frac{g(\bar{N}_n)}{\gamma g(\bar{N}_n) + 1} \tag{2.4}$$

which is the solution of (2.2) when $\alpha = 0$.

Note that the right-hand sides of both (2.3) and (2.4) are compositions of the Beverton-Holt function and g. Model (2.3) always has the trivial equilibria 0. In the case of $\alpha \neq 0$, a positive constant equilibrium of (2.1) or (2.3) is a root of the equilibrium equation

$$\frac{\alpha g(N)}{(1 - e^{-\alpha})\gamma g(N) + \alpha e^{-\alpha}} = N,$$

which is equivalent to

$$F(N, g(N)) = 0 \tag{2.5}$$

where

$$F(N, g(N)) := (1 - e^{-\alpha})\gamma N + \alpha e^{-\alpha} \frac{N}{g(N)} - \alpha. \tag{2.6}$$

We first consider the case of $\alpha > 0$. Since $N/g(N)$ is nondecreasing for $N > 0$, $F(N, g(N))$ increases to ∞ as $N \to \infty$. Consequently the above equation has a positive root if and only if the limit of $F(N, g(N))$ is negative as N approaches zero, that is

$$g'(0)e^{\alpha} > 1. \tag{2.7}$$

One can verify that (2.7) is also necessary and sufficient condition for (2.5) to have a positive root in the case of $\alpha \leq 0$. We use β to denote the smallest of such roots when (2.7) holds. Note that if (2.7) is not satisfied, then the solution $\bar{N}_n$ of (2.2) satisfies

$$\lim_{n\to\infty} \bar{N}_n = 0. \tag{2.8}$$

In order to understand the spatial dynamics of (2.1) we consider the case that g is monotone and the case that g is nonmonotone.

2.2 Monotone case

We begin with the hypothesis

Hypothesis 2.2. *$g(N)$ is nondecreasing for $N \geq 0$.*

The condition (2.7) is necessary for the population described by (2.1) to grow and spread in space. In fact, let $N_n(x)$ be a solution of (2.1) with $N_0(x)$ bounded above by a constant $\bar{N}_0 < \beta$. Then a simple comparison argument based on the maximum principle (Protter and Weinberger 1985) shows that the solution $N_n(x)$ of (2.1) and the solution of $\bar{N}_n$ of (2.2) satisfy $N_n(x) \leq \bar{N}_n$. It follows from (2.8) that if (2.7) is not satisfied, then $N_n(x)$ approaches zero uniformly in x as $n \to \infty$.

The following theorem shows that if (2.7) is satisfied, then model (2.1) has a positive asymptotic spreading speed given in terms of model parameters, and the spreading speed can be characterized as the slowest speed of a class of traveling wave solutions.

Theorem 2.1. *Assume that Hypotheses 2.1- Hypothesis 2.2, and (2.7) are satisfied. Then*

$$c^* := 2\sqrt{d \ln(g'(0)e^{\alpha})} \tag{2.9}$$

is the spreading speed of the system (2.1) in the following sense:

If the continuous initial function $u_0(x)$ is zero for all sufficiently large x, $u_0 \not\equiv 0$, and $0 \leq u_0(x) < \beta$, then for any positive ϵ the solution of u_n of (2.1) has the following properties

i.

$$\lim_{n\to\infty} \sup_{|x|\geq n(c^*+\epsilon)} N_n(x) = 0. \tag{2.10}$$

ii.

$$\lim_{n\to\infty} \sup_{|x|\leq n(c^*-\epsilon)} (\beta - u_n(x)) = 0. \tag{2.11}$$

Furthermore, for $c \geq c^*$, the system (2.1) has a continuous nonincreasing traveling wave $w_c(x-nc)$ with $w_c(-\infty) = \beta$ and $w_c(+\infty) = 0$. A continuous nonnegative traveling wave solution $w_c(x-nc)$ in (2.1) with $w_c(\infty) = 0$ and $\liminf_{x\to-\infty} w_c(x) > 0$ does not exist if $c < c^*$.

The properties (2.10) and (2.11) indicate that if $N_n(x)$ is a solution of (2.1) with nonnegative initial data which vanish outside a bounded interval, then an observer who travels to the left or right with speed greater than c^* will eventually see u going to 0, while an observer who travels with a speed below c^* will eventually see u approaching β.

The formula (2.9) shows that the spreading speed of (2.1) is determined by d, $g'(0)$, and α, which are all linerization parameters. It is well defined if (2.7) is satisfied. In the case of $\alpha > 0$ and $g'(0) = 1$, $c^* = 2\sqrt{d\alpha}$. This is the well-known spreading speed formula for the Fisher equation. Theorem 2.1 shows that c^* is also the slowest speed of traveling wave solutions connecting 0 with β.

2.3 Nonmonotone case

We make the following hypothesis

Hypothesis 2.3. *There is $\sigma > 0$ such that $g(N)$ is nondecreasing for $0 \leq N \leq \sigma$.*

This hypothesis assumes that $g(u)$ is nondecreasing near 0, which is weaker than Hypothesis 2.2. It is satisfied by biological meaningful models with overcompensation in growth. For example the Ricker function $g(N) = Ne^{r-bN}$ is increasing for $0 < bN < 1$ and decreasing for $bN > 1$.

Define

$$g^+(N) = \max_{0\leq u\leq N} g(u) \tag{2.12}$$

for $N \geq 0$. (This function is called $G(u, 0)$ in Thieme 1979.) It is easily seen that $g^+(N)$ is nondecreasing for $N \geq 0$, $g^+(N) \geq g(N)$ for $N \geq 0$, ${g^+}'(0) = g'(0)$, and $g^+(N) = g(N)$ for small positive N. The condition (2.7) ensures that the equilibrium equation (2.5) with g replaced by g^+ has a positive root. We use β^+ to denote the smallest of such roots. Clearly $\beta^+ \geq \beta$.

We next define

$$g^-(N) = \min_{N\leq u\leq \beta^+} g(u) \tag{2.13}$$

for $0 \leq N \leq \beta^+$. (This function is called $G(u, \alpha)$ in Thieme 1979.) It is easily seen that $g^-(N)$ is nondecreasing for $N \geq 0$, $g^-(N) \leq g(N)$ for $N \geq 0$, ${g^-}'(0) = g'(0)$, and $g^-(N) = g(N)$ for small positive N.

We have that $g^\pm$ are nondecreasing functions,

$$g^-(u) \leq g(u) \leq g^+(u),\ {g^\pm}'(0) = g'(0),\ g^\pm(N) \leq g'(0)N,$$

and there is $\sigma_0 > 0$ with $\sigma_0 < \sigma$ such that

$$g^{\pm}(N) = g(N) \tag{2.14}$$

for $0 \le N \le \sigma_0$.

We have two auxiliary systems

$$\begin{aligned} &\frac{\partial u}{\partial t} = d\frac{\partial u}{\partial x^2} + \alpha u - \gamma u^2, \quad -\infty < x < \infty \\ &u(x,0) = g^+(N_n^+(x)), \\ &N_{n+1}^+(x) = u(x,1), \end{aligned} \tag{2.15}$$

and

$$\begin{aligned} &\frac{\partial u}{\partial t} = d\frac{\partial u}{\partial x^2} + \alpha u - \gamma u^2, \quad -\infty < x < \infty \\ &u(x,0) = g^-(N_n^-(x)), \\ &N_{n+1}^-(x) = u(x,1). \end{aligned} \tag{2.16}$$

Comparison shows that if $N_n^+(x)$ is a solution of (2.15), $N_n^-(x)$ is a solution of (2.16), and $u_n(x)$ is a solution of (2.1), and if $0 \le u_0^-(x) \le u_0(x) \le u_0^+(x) \le \beta^+$, then

$$0 \le u_n^-(x) \le u_n(x) \le u_n^+(x) \le \beta^+ \tag{2.17}$$

for all and n.

Note that (2.15) and (2.16) have the same linearized system and thus have the same spreading speed given by (2.9). The property (2.17) implies that c^* given by (2.9) is also the spreading speed for (2.1). Furthermore we can show that c^* represents the slowest speed of a class of traveling wave solutions for (2.1).

Theorem 2.2. *Assume that Hypotheses 2.1 and Hypothesis 2.3, and (2.7) are satisfied. Then c^* given by (2.9) is the asymptotic spreading speed of the system (2.1) in the following sense:*

If the continuous initial function $u_0(x)$ is zero for all sufficiently large x, $u_0 \not\equiv 0$, and $0 \le u_0(x) \le \beta^+$, then for any positive ϵ the solution of u_n of (2.1) has the following properties

i.

$$\lim_{n\to\infty} \sup_{|x|\ge n(c^*+\epsilon)} N_n(x) = 0.$$

ii.

$$\lim_{n\to\infty} \inf_{|x|\le n(c^*-\epsilon)} u_n(x) \ge \beta^-. \tag{2.18}$$

Furthermore, for $c \geq c^*$*, the system (2.1) has a continuous traveling wave* $w_c(x-nc)$ *with* $w_c(\infty) = 0$ *and* $\liminf_{x\to-\infty} w_c(x) \geq \beta^-$*. A continuous nonnegative traveling wave solution* $w_c(x-nc)$ *in (2.1) with* $w_c(\infty) = 0$ *and* $\liminf_{x\to-\infty} w_c(x) > 0$ *does not exist if* $c < c^*$*.*

In the case that $g(N)$ is a nonmonotone function such as the Ricker function, the underlying dynamics of the model (2.1) can be complicated. Theorem 2.2 shows that for such a case the existence of traveling wave solutions can still be established. The numerical simulations provided in Section 4 demonstrate that (2.1) can have oscillating traveling waves if $g(N)$ is the Ricker function.

3 Minimal domain size

3.1 Model formulation

In this section, we consider the model

$$\begin{aligned}
&\frac{\partial u}{\partial t} = d\frac{\partial u}{\partial x^2} + \alpha u - \gamma u^2, \quad 0 < x < \ell,\\
&u(0,t) = u(\ell,t) = 0,\\
&u(x,0) = g(N_n(x)),\\
&N_{n+1}(x) = u(x,1).
\end{aligned} \tag{3.1}$$

Here we have assumed that the spatial domain of the population is the interval $[0, \ell]$ with a lethal exterior. We are interested in the minimal domain size for which the population can persist.

3.2 Monotone case

We first assume that Hypothesis 2.2 is satisfied so that $g(N)$ is a nondecreasing function for $N \geq 0$. In order to determine the minimal domain size we need the following hypothesis

Hypothesis 3.1. *There are positive numbers* D, $\delta < \sigma$, *and* $\nu > 1$ *such that* $g(u) \geq g'(0)u - Du^\nu$ *for* $0 \leq u \leq \delta$.

This is a smoothness assumption for $g(u)$ near 0, which is satisfied by biologically reasonable growth functions.

Theorem 3.1. *Assume that Hypotheses 2.1, Hypothesis 2.2, Hypothesis 3.1, and (2.7) are satisfied. Then*

$$\ell^* := \pi\sqrt{\frac{d}{\ln(g'(0)e^\alpha)}} \tag{3.2}$$

represents the minimal domain size for (3.1) in the following sense:

i. if $\ell < \ell^*$, then the solution $N_n(x)$ of (3.1) satisfies

$$\lim_{n\to\infty} N_n(x) = 0$$

for all x; and

ii. if $\ell > \ell^*$, then (2.1) has a minimal positive equilibrium $\underline{N}(x)$, and if $N_0(x)$ is positive on an open subinterval of $(0, \ell)$ then the solution sequence $N_n(x)$ satisfies

$$\liminf_{n\to\infty} N_n(x) \geq \underline{N}(x).$$

If $g'(0)e^{\alpha} \leq 1$ then $g'(0)e^{\lambda_1} < 1$ is automatically true. In this case, the proof presented in Appendix C shows that the solution $N_n(x)$ satisfies $\lim_{n\to\infty} N_n(x) = 0$. It follows that if (2.7) is not satisfied, then the population cannot persist in space no matter how big ℓ is.

Observe that the minimal domain size ℓ^* for (3.1) is determined by the same set of parameters used for computing the spreading speed c^* for (2.1). It is interesting to note that $c^*\ell^* = 2d\pi$. When d is fixed, increasing $g'(0)e^{\alpha}$ will increase the spreading speed but will decrease the minimal domain size.

3.3 Nonmonotone case

We now assume that Hypothesis 2.3 is satisfied so that g is a nondecreasing for small u. We consider two auxiliary systems

$$\begin{aligned}
&\frac{\partial u}{\partial t} = d\frac{\partial u}{\partial x^2} + \alpha u - \gamma u^2, \quad 0 < x < \ell \\
&u(0,t) = u(\ell,t) = 0, \\
&u(x,0) = g^+(N_n^+(x)), \\
&N_{n+1}^+(x) = u(x,1),
\end{aligned} \tag{3.3}$$

and

$$\begin{aligned}
&\frac{\partial u}{\partial t} = d\frac{\partial u}{\partial x^2} + \alpha u - \gamma u^2, \quad 0 < x < \ell \\
&u(0,t) = u(\ell,t) = 0, \\
&u(x,0) = g^-(N_n^-(x)), \\
&N_{n+1}^-(x) = u(x,1),
\end{aligned} \tag{3.4}$$

where $g^{\pm}$ are defined by (2.12) and (2.13). Recall that $g^{-}(u) \leq g(u) \leq g^{+}(u)$ for $u \geq 0$. Comparison shows that if $N_n^{+}(x)$ is a solution of (3.3), $N_n^{-}(x)$ is a solution of (3.4), and $u_n(x)$ is a solution of (3.1), and if $0 \leq u_0^{-}(x) \leq u_0(x) \leq u_0^{+}(x) \leq \beta^{+}$, then

$$0 \leq u_n^{-}(x) \leq u_n(x) \leq u_n^{+}(x) \leq \beta^{+} \tag{3.5}$$

for all n.

Observe that the models (3.3) and (3.4) have the same minimal domain size given by (3.2) according to Theorem 3.1. By using this and (3.5), we immediately obtain the following theorem.

Theorem 3.2. *Assume that Hypotheses 2.1, Hypothesis 2.2, Hypothesis 3.1, and (2.7) are satisfied. Then*

$$\ell^{*} := \pi \sqrt{\frac{d}{\ln(g'(0)e^{\alpha})}}.$$

represents the minimal domain size for (3.1) in the following sense:

i. if $\ell < \ell^{*}$, then the solution $N_n(x)$ of (3.1) satisfies

$$\lim_{n\to\infty} N_n(x) = 0$$

for all x; and

ii. if $\ell > \ell^{*}$, then (3.1) has a minimal positive equilibrium $\underline{N}(x)$, and if $N_0(x)$ is positive on an open subinterval of $(0, \ell)$ then the solution sequence $N_n(x)$ satisfies

$$\liminf_{n\to\infty} N_n(x) \geq \underline{N}(x).$$

This theorem shows that when $g(N)$ is nonmonotone, the minimal domain size for (3.1) can still be completely determined. Our numerical simulations in Section 4 show that different spatial patterns of solutions for (3.1) can be found when $g(N)$ is the Ricker function with different parameter values.

3.4 Numerical simulations

In this section, we present some approximations to the solutions of the models (2.1) and (3.1). We first consider the case where g is the Beverton-Holt function

$$g(N) = mN/(a+N). \tag{3.6}$$

Clearly $g(N)$ is a monotone function for all $N \geq 0$, $g'(0) = m/a$, and $g(N) \leq g'(0)N$ for all $N \geq 0$. In this case (2.7) becomes $(m/a)e^{\alpha} > 1$, under which the model (2.1) has a positive equilibrium

$$\beta = \frac{\alpha(m - ae^{-\alpha})}{m\gamma(1-e^{-\alpha}) + \alpha e^{-\alpha}}.$$

Theorem 2.1 shows that the model (2.1) has a spreading speed given by (2.9) that is also the slowest speed of nondecreasing traveling wave solutions connecting 0 with β.

We choose $\alpha = -1$, $\gamma = 0.01$, $m = 8$, and $a = 0.2$. Then $\beta = 2.61100$, and $c^* = 3.27956$. Fig. 1 and Fig. 2 show solutions of (2.1) for this set of parameter values.

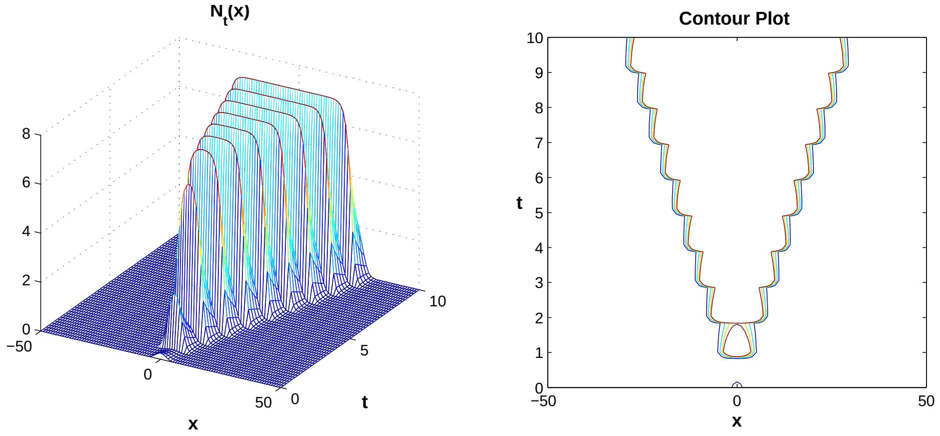

Figure 1: A numerical approximation to the graph of $N_n(x)$ for (2.1) with $d = 1$, $\alpha = -1$, $\gamma = 0.01$, and g given by (3.6) where $m = 8$ and $a = 0.2$. $N_0(x)$ is chosen to be a cosine function with a compact support from -5 to 5. The left figure depicts the spread of the solution in two directions; and the right figure shows the contour plots of the wave front.

The minimal domain size for (3.1) with g given by (3.6) is $\ell^* = \pi\sqrt{d/\ln(m/ae^\alpha)}$. It is 1.91586 for $d = 1,\ \alpha = -1,\ m = 8,\ a = 0.2$. Fig. 3 show a solution of (3.1) for this set of parameters.

We next choose $g(N)$ to be the Ricker function, i.e,

$$g(N) = Ne^{r-bN}. \tag{3.7}$$

The non-spatial dynamics of (2.1) with $d = 0$ and g given by (3.7) is described by (2.3). Clearly $g'(0) = e^r$ and $g(N) \leq g'(0)N$ for all $N \geq 0$. In this case (2.7) becomes $r + \alpha > 0$, under which the model (2.1) has a positive equilibrium. Theorem 2.2 shows that the model (2.1) has a spreading speed $c^* = 2\sqrt{d(r+\alpha)}$ that is also the slowest speed of positive traveling wave solutions with value 0 at ∞. Fig. 4, Fig. 5 and Fig. 6 show solutions of (2.1) spreading and interacting with the boundaries.

We note in these figures that the spatial patterns of solutions are different for the same growth function g given by (3.7) with different parameter values.

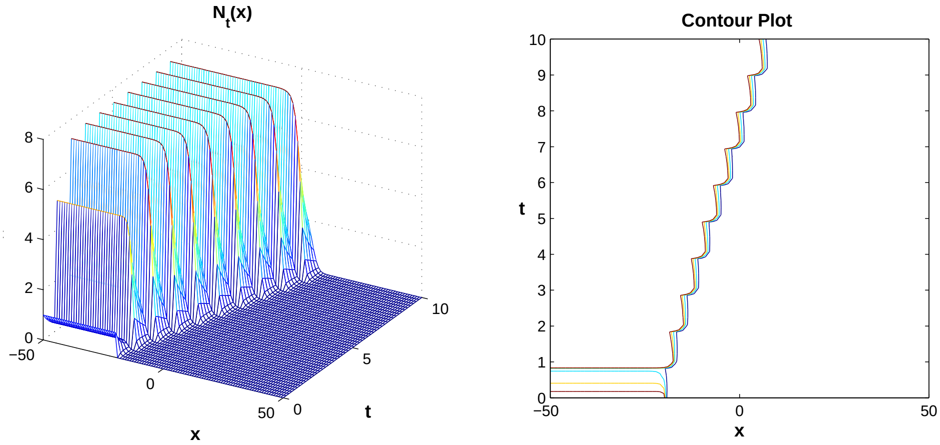

Figure 2: A numerical approximation to the graph of $N_n(x)$ for (2.1) with $d = 1$, $\alpha = -1$, $\gamma = 1$, and g given by (3.6) where $m = 8$ and $a = 0.2$. $N_0(x)$ is chosen to be a step function with a positive value for $x \leq -20$ and zero otherwise. The left figure depicts the rightward spread of the solution; and the right figure shows the contour plots of the wave front.

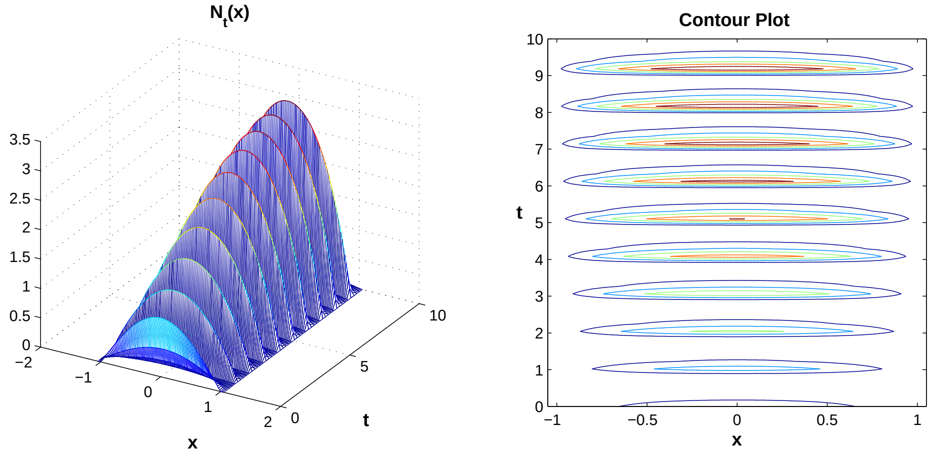

Figure 3: A numerical approximation to the graph of $N_n(x)$ for (3.1) with $d = 1$, $\alpha = -1$, $\gamma = 0.01$, and g given by (3.6) where $m = 8$ and $a = 0.2$. The domain is $[-1, 1]$. $N_0(x)$ is chosen to be a cosine function that becomes 0 at $[-1, 1]$. The left figure depicts the solution; and the right figure shows the contour plots of the solution.

4 Discussion

We studied impulsive reaction-diffusion models with a reproductive stage and a dispersal stage in bounded and unbounded domains. In the reproductive stage pulse growth occurs, and in the dispersal stage dispersal associated with mortality takes place. The models can be also used to describe a continuously growing and dispers-

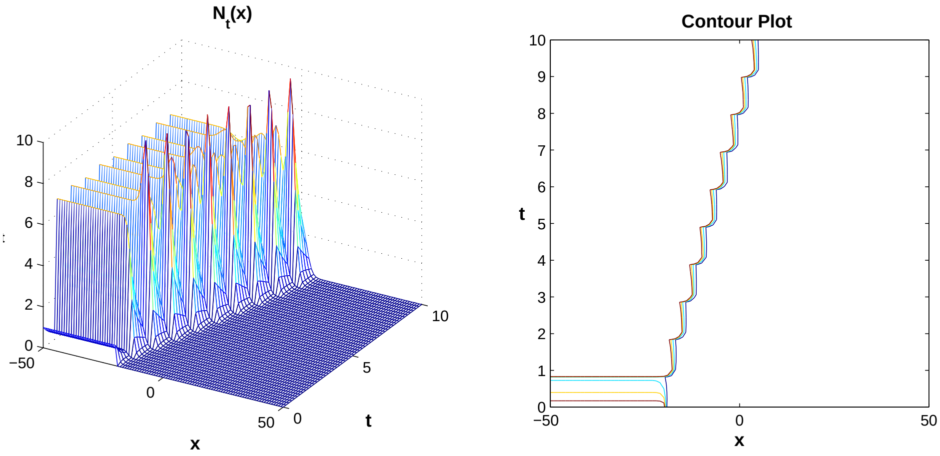

Figure 4: A numerical approximation to the graph of $N_n(x)$ with $d = 1$, $\alpha = -1$, $\gamma = 0.04$, and g given by (3.7) where $r = 3.3$ and $b = 1.0$, giving $c^* = 3.03315$. $N_0(x)$ is chosen to be a step function with a positive value for $x \leq -20$ and zero otherwise. The left figure depicts the rightward spread of the solution; and the right figure shows the contour plots of the wave front.

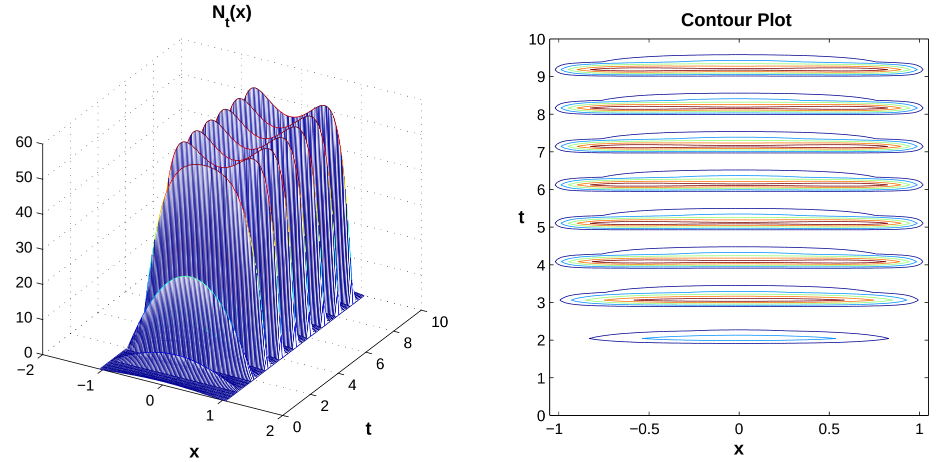

Figure 5: A numerical approximation to the graph of $N_n(x)$ for (3.1) with domain $[-1, 1]$, $d = 1$, $\alpha = -1$, $\gamma = 0.04$, and g given by (3.7) where $r = 5$. $N_0(x)$ is chosen to be a cosine function that becomes 0 at $[-1, 1]$. The right figure depicts the solution; and the left figure shows the contour plots of the solution.

ing population with pulse harvesting and a population with individuals immobile during the winter. In the case where the spatial domain is unbounded, we provided a formula for the spreading speed in terms of the linearization parameters in the models including the pulse recruitment rate of the population about zero, the diffusion coefficient, and the death rate of the population about zero in the dispersal stage stage. We showed the spreading speed can be characterized as the slowest speed

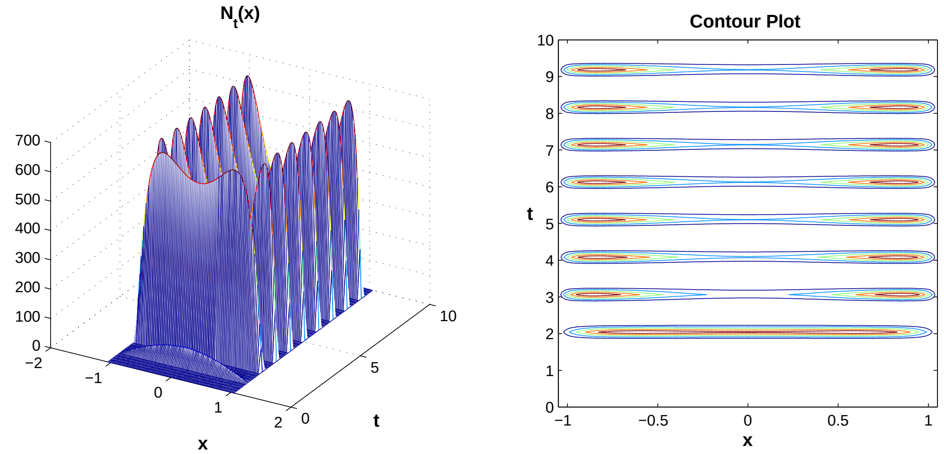

Figure 6: A numerical approximation to the graph of $N_n(x)$ for (3.1) with domain $[-1,1]$, $d = 1$, $\alpha = -1$, $\gamma = 0.04$, and g given by (3.7) where $r = 7.5$ and $b = 1.0$. $N_0(x)$ is chosen to be a cosine function that becomes 0 at $[-1,1]$. The right figure depicts the solution; and the left figure shows the contour plots of the solution.

of a class of traveling wave solutions. When the spatial domain is bounded with a lethal exterior, we found a formula for the minimal domain size in terms of the same set of model parameters used for computing the spreading speed. Our numerical simulations suggest that different spatial patterns of solutions can be obtained even for the same (nonmonotone) growth function with different parameters.

The model formulations of the present investigation could be generalized in several biologically meaningful ways. It was assumed in the models that in the reproductive stage and dispersal stage, all individuals have the same growth and mortality rate, as well as the same dispersal rate. These rates, however, are likely depend on the age of individuals in the populations, and the reproductive stage and dispersal stage could be age-structured. While the single species model were considered here, more general models could include two species and competition interaction between them.

The present paper only treated one-dimension habitats. However, it is known (Weinberger 1982) how to use the one-dimensional results to determine the spreading speeds and traveling waves in higher-dimensional habitats by looking at one direction at a time. In the case that the domain in (3.1) is two or three-dimensional, one might use the framework developed in this paper to determine the minimal domain size.

5 Appendix

In this section provide a justification for nonlinearity of g and the proofs for Theorem 2.1-Theorem 3.1.

5.1 Justification of nonlinearity of g

We consider a population with the following properties: (i) reproduction requires units of resource, i.e., breeding territories; (ii) an individual needs a unit of resource to produce offspring; and (iii) each resource unit occupies area b and the mean density of individuals in space is N. Suppose that the population is randomly distributed in space via a Poisson process and individuals are sessile in productive stage. Then the number of individuals in each unit is a Poisson RV with mean Nb. The probability of k individuals in a unit is

$$(Nb)^k e^{-Nb}/k!$$

Suppose that there is contest competition. If there is more than one individual per unit, then they compete so that only one reproduces. Then the expected number of offspring arising from the unit would be R times the probability that the unit is occupied, where R is the number offspring per adult:

$$R(1 - e^{-bN}).$$

This is the Skellam function (Skellam, 1951), which is qualitatively similar to the Beverton-Holt function (3.6).

We next assume that there is scramble competition. If two or more individuals chose the same unit then they would each get a smaller amount of resource, but not enough to reproduce, and so none would reproduce. In this case the expected number of offspring arising from a unit would be R time the probability that there was one individual occupying the location:

$$RbNe^{-bN}.$$

Choosing $r = \log Rb$ yields the Ricker equation (3.7).

The first model would apply to animals such as birds which have contest competition for nesting sites, and the second to animals such as salmon, where they spawn in river beds and can spawn on top of a previous site.

B. Proof of Theorem 2.1

Let Q denote the time one solution operator of the reaction-diffusion equation in (2.1). It is well-known that Q is continuous and compact in the topology of uniform convergence on every bounded interval, and Q is monotone in the sense $Q[u](x) \geq Q[v](x)$ if $u(x) \geq v(x) \geq 0$. $N_n(x)$ satisfies the abstract recursion

$$N_{n+1}(x) = Q[g(N_n)](x). \tag{5.8}$$

We use $M[N]$ to denote the linearization of $Q[g(N)]$ about 0. M is the solution operator of the problem

$$\begin{aligned}
&\frac{\partial u}{\partial t} = \frac{\partial u}{\partial x^2} + \alpha u, \quad -\infty < x < \infty, \\
&u(x,0) = g'(0)N_n(x), \qquad\qquad\qquad\qquad\qquad\qquad (5.9)\\
&N_{n+1}(x) = u(x,1).
\end{aligned}$$

The condition $g(N) \leq g'(0)N$ and the fact that $\alpha u - \gamma u^2 \leq \alpha u$, as well as comparison show that

$$Q[g(N)](x) \leq M[N](x).$$

Theorem 6.1 - Theorem 6.4 in Weinberger (1982) show that the system (5.8) has a spreading speed c^* satisfying (2.10) and (2.11), which can be computed through linearization.

Solving the linear problem (5.9) explicitly, we obtain that

$$N_{n+1}(x) = M[N_n](x) := \int_{-\infty}^{+\infty} k(x-y)g'(0)e^{\alpha}N_n(y)dy \tag{5.10}$$

where $k(x)$ is the normal distribution given by

$$k(x) = \frac{1}{\sqrt{2\pi d}}e^{-\frac{x^2}{4d}}.$$

The moment generating function of $k(x)$ is

$$K(x) = \int_{-\infty}^{\infty} e^{\mu x}k(x)dx = e^{d\mu^2}.$$

It follows from the results in Weinberger (1982) that

$$c^* = \inf_{\mu>0} \ln[g'(0)e^{\alpha}K(\mu)]/\mu = \inf_{\mu>0}(1/\mu)[\ln(g'(0)e^{\alpha}) + d\mu^2] = 2\sqrt{d\ln(g'(0)e^{\alpha})}.$$

The second part of the Theorem follows immediately from Theorem 6.6 in Weinberger (1982). The proof is complete.

B. Proof of Theorem 2.2

An argument that makes use of property (2.17) and comparison, similar to the proof of Proposition 3.1 in Li et al. (2009), shows that c^* is the spreading speed of (2.1). We shall omit the details here.

The nonexistence of traveling wave solutions with speeds $c < c^*$ is similar to the second part of the proof of in Li et al. (2009) and is omitted here. We now establish the existence of traveling wave solutions with speeds $c \geq c^*$.

We first show that the time one solution operator Q has the property that for $0 < \rho < 1$,

$$Q[\rho N](x) \geq \rho Q[N](x). \tag{5.11}$$

In fact we consider the initial value problem

$$\begin{aligned} &\frac{\partial p}{\partial t} = d\frac{\partial p}{\partial x^2} + \alpha p - \gamma p^2, \quad -\infty < x < \infty, \\ &p(x,0) = \rho N(x). \end{aligned} \tag{5.12}$$

Then $v := p/\rho$ satisfies

$$\begin{aligned} &\frac{\partial v}{\partial t} = d\frac{\partial v}{\partial x^2} + \alpha v - \gamma \rho v^2, \quad -\infty < x < \infty, \\ &v(x,0) = N(x). \end{aligned} \tag{5.13}$$

We introduce the system

$$\begin{aligned} &\frac{\partial u}{\partial t} = d\frac{\partial u}{\partial x^2} + \alpha u - \gamma u^2, \quad -\infty < x < \infty \\ &u(x,0) = N(x). \end{aligned} \tag{5.14}$$

which is comparable with (5.13). Since $0 < \rho < 1$, comparision shows the solution $v(x,t)$ of (5.13) and the solution $u(x,t)$ of (5.14) satisfy $v(x,t) \geq u(x,t)$ for $t > 0$, and particularly,

$$v(x,1) \geq u(x,1),$$

so that $p(x,1) \geq \rho u(x,1)$ where $p(x,t)$ is the solution of (5.12). This shows that (5.11) holds.

Hypotheses 2.1 ii implies that for $0 < \rho < 1$,

$$g(\rho u) \geq \rho g(u). \tag{5.15}$$

By combining (5.11) and (5.15) we have that for $0 < \rho < 1$

$$Q[g(\rho N)](x) \geq \rho Q[g(N)](x). \tag{5.16}$$

The results about the traveling wave solutions obtained in Section 2.2 show that for $c \geq c^*$, the system (2.15) has a nonincreasing traveling solution $N_n(x) = w^+(x - nc)$ with $w^+(-\infty) = \beta^+$ and $w^+(\infty) = 0$. We now choose a positive number $0 < \rho < 1$ so small such that $\rho w^+(x) \leq \sigma^0$ and $g(\rho w^+(x)) \leq \sigma_0$. It follows that

$$\rho w^+(x - c) = \rho Q[g^+(w^+)] \leq Q[g^+(\rho w^+)](x) = Q[g(\rho w^+)](x), \tag{5.17}$$

and

$$w^+(x - c) = Q[g^+(w^+)] \geq Q[g(w^+)](x). \tag{5.18}$$

It follows that the set

$$E_c = (u(x) : u(x) \text{ is continuous },\rho w^+(x) \leq u(x) \leq w^+(x)$$

is an invariant set for the operator $T_c[Q[(g(\cdot))]$ with $T_c[u](x) = u(x+c)$. Since g is continuous and Q is compact, the composition operator $Q[(g(\cdot))]$ is compact. It follows that the image of E_c under $T_c[Q[(g(\cdot))]$ is compact in the topology of uniform convergence on every bounded interval. Because the set of bounded vector-valued functions with this topology is a locally convex topological vector space, the existence of a solution of the equation $T_c[Q[(g(w))] = w$ follows from what Rudin (1991) calls the Schauder-Tychonoff fixed point theorem. The proof is complete.

C. Proof of Theorem 3.1

Consider the eigenvalue problem

$$\begin{aligned} &\frac{d^2u}{\partial x^2} + \alpha u = \lambda u,\ 0 < x < \ell, \\ &u(0,t) = u(\ell,t) = 0. \end{aligned} \tag{5.19}$$

It is easily seen that

$$\lambda_1 = \alpha - d\pi^2/\ell^2$$

is the principle eigenvalue and a corresponding eigenfunction is

$$\phi(x) = \sin\frac{\pi}{\ell}.$$

Let

$$\tilde{N}_n(x) = \kappa(g'(0)e^{\lambda_1})^n\phi(x),\ n = 0, 1, ...$$

where κ is a positive constant. $\tilde{N}_n(x)$ is a solution of the linear problem

$$\begin{aligned} &\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} + \alpha u,\ 0 < x < \ell, \\ &u(0,t) = u(\ell,t) = 0, \\ &u(x,0) = g'(0)\tilde{N}_n(x), \\ &\tilde{N}_{n+1}(x) = u(x,1). \end{aligned} \tag{5.20}$$

In fact, $u(t,x) = \kappa g'(0)e^{\lambda_1 t}\phi(x)$ satisfies the linear reaction-diffusion equation and the boundary value condition in (5.20), as well as the initial condition $u(x,0) = g'(0)\tilde{N}_0(x) = \kappa g'(0)\phi(x)$. It follows that

$$u(x,1) = \kappa g'(0)e^{\lambda_1}\phi(x)$$

which is $\tilde{N}_1(x)$. Induction shows that $\tilde{N}_n(x)$ is a solution of (5.20).

For any given initial value function $u(x,0) = N_0(x)$ in (3.1), we can choose κ sufficiently large such that $N_0(x) \leq \tilde{N}_0(x)$. Since the reaction term in the equation (3.1) is no greater than that in (5.20) for nonnegative u, comparison and induction show that the solution $N_n(x)$ of (3.1) has the property that $N_n(x) \leq \tilde{N}_n(x)$ for all $n \geq 0$. If $g'(0)e^{\lambda_1} < 1$, then $\lim_{n\to\infty} \tilde{N}_n(x) = 0$ for all x and thus

$$\lim_{n\to\infty} N_n(x) = 0 \tag{5.21}$$

for all x. The proof of the statement (i) is complete.

We now assume $g'(0)e^{\lambda_1} > 1$ or equivalently $\ell > \pi\sqrt{\frac{d}{\ln g'(0)+\alpha}}$ and prove the statement (ii). We choose $\hat{\lambda} < \lambda_1$ and $\rho_1 < g'(0)$ such that $\rho_1 e^{\hat{\lambda}} > 1$. Let $v(x,t) = \epsilon\rho_1 e^{\hat{\lambda}t}\phi(x)$. Then for sufficiently small ϵ, $v(x,t) \leq \delta$ for $0 \leq t \leq 1$. It follows from (3.1) that for sufficiently small $\epsilon > 0$ and $0 < t \leq 1$

$$g(v(x,t)) \geq \rho_1 v(x,t) - \epsilon\{(g'(0)-\rho_1)e^{\hat{\lambda}t}\phi(x) - \epsilon^{\nu-1}D[e^{\hat{\lambda}t}\phi(x)]^\nu\} \geq \rho_1 v(x,t). \tag{5.22}$$

On the other hand, for $0 < t \leq 1$

$$\begin{aligned}
&\tfrac{\partial v}{\partial t} - [d\tfrac{\partial^2 v}{\partial x^2} + \alpha v - \gamma v^2]\\
&= \epsilon\rho_1 e^{\hat{\lambda}t}[\hat{\lambda}\phi - d\phi'' - \alpha\phi] + \epsilon^2\gamma(\rho_1)^2(e^{\hat{\lambda}t}\phi)^2\\
&= \epsilon\rho 1 e^{\hat{\lambda}t}[\lambda_1\phi - d\phi'' - \alpha\phi] + \epsilon\rho_1 e^{\hat{\lambda}t}(\hat{\lambda} - \lambda_1) + \epsilon^2\gamma(\rho_1)^2(e^{\hat{\lambda}t}\phi^2)\\
&= \epsilon\rho_1 e^{\hat{\lambda}t}(\hat{\lambda} - \lambda_1)e^{\hat{\lambda}t} + \epsilon^2\gamma(\rho_1)^2(e^{\hat{\lambda}t}\phi^2)\\
&= \epsilon\rho_1 e^{\hat{\lambda}t}\phi[\hat{\lambda} - \lambda_1 + \epsilon\gamma\rho_1 e^{\hat{\lambda}t}\phi]\\
&< 0
\end{aligned}$$

for sufficiently small ϵ. This shows that for $0 < t \leq 1$, $v(x,t)$ is a lower solution of

$$\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} + \alpha u - \gamma u^2,$$

$$u(0,t) = u(\ell,t) = 0.$$

We use S to denote the time 1 solution map of

$$\frac{\partial u}{\partial t} = d\frac{\partial u}{\partial x^2} + \alpha u - \gamma u^2$$

$$u(0,t) = u(\ell,t) = 0$$

$$u(x,0) = u_0(x).$$

Then $u(x,1) = S[u_0](x)$. A comparison argument shows that S is a monotone operator in the sense that $S[u_1](x) \geq S[u_2](x)$ whenever $u_1(x) \geq u_2(x) \geq 0$. Using S, we see that the solution $N_n(x)$ of (3.1) satisfies the abstract recursion

$$N_{n+1}(x) = S[g(N_n)](x).$$

Let $\underline{N}_0(x) = \epsilon\phi(x)$ and $\underline{N}_{n+1}(x) = S[g(\underline{N}_n](x)$. The properties of $v(x,t)$ show that for sufficiently small ϵ

$$S[g(\underline{N}_0)](x) \geq S[\rho_1 \underline{N}_0](x) \geq v(x,1) \geq \underline{N}_0(x).$$

Induction shows that $\underline{N}_{n+1}(x) \geq \underline{N}_n(x)$ for all $n \geq 0$.

On the other hand, for sufficiently small ϵ, the equilibrium value $\beta > \epsilon\phi(x)) = \underline{N}_0(x)$ is a super solution of (3.1). It follows that

$$\beta \geq \underline{N}_{n+1}(x) \geq \underline{N}_n(x)$$

for all $n \geq 0$. We therefore have that $\underline{N}_n(x)$ increases to a limit function $\underline{N}(x)$, which is the minimum positive equilibrium solution of (3.1). If $N_0(x)$ in (3.1) is initially nonnegative and is positive on an open subinterval of $(0,\ell)$, then the strong maximum principle shows that $N_1(x) > 0$ for $0 < x < \ell$. Choose ϵ sufficiently small so that $\underline{N}_0(x) = \epsilon\phi(x) < N_1(x)$. Then comparison shows that $\underline{N}_{n+1} \leq N_n(x)$ for all $n \geq 0$, and thus $\liminf_{n\to\infty} \underline{N}_n(x) \geq \underline{N}(x)$. The proof is complete.

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