On spreading speeds and traveling waves for growth and migration models in a periodic habitat

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Abstract

It is shown that the methods previously used by the author [Wei82] and by R. Lui [Lui89] to obtain asymptotic spreading results and sometimes the existence of traveling waves for a discrete-time recursion with a translation invariant order preserving operator can be extended to a recursion with a periodic order preserving operator. The operator can be taken to be the time-one map of a continuous time reaction-diffusion model, or it can be a more general model of time evolution in population genetics or population ecology in a periodic habitat. Methods of estimating the speeds of spreading in various directions will also be presented.

1 Introduction

In 1937 R. A. Fisher [Fis37] introduced the model

$$u_{,t} = u_{,xx} + u(1-u),$$

where u is the frequency of one of two forms of a gene, for the evolutionary take-over of a habitat by a fitter genotype. He found traveling wave solutions of all speeds $c \geq 2$, and showed that there are no such waves of slower speed. Fisher conjectured that the take-over occurs at the asymptotic speed 2. This conjecture was proved in the same year by Kolmogorov, Petrowski, and Piscounov [KPP37][1] . More specifically, they proved a result which implies that if at time $t = 0$ u is 1 near $-\infty$ and 0 near ∞, then $\lim_{t\to\infty} u(x-ct)$ is 0 if $c > 2$ and 1 if $c < 2$. We call such a result, which states that a fitter state in the initial values spreads at a speed which is both no larger and no smaller than a certain spreading speed, a **spreading result**.

The results of Kolmogorov, Petrowski, and Piscounov for models of the form

$$u_{,t} = u_{,xx} + f(u)$$

were extended in a number of directions. (See, e.g., [Fif79]). [AW75] applied phase plane analysis to show that if $f(0) = f(1) = 0$ and f changes sign at most once in the interval (0,1), then there is a spreading speed c^* with the property that if $u(x,t)$ is a solution of this equation 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 go to 0, while an observer who travels with a speed below c^* eventually sees u approach 1. A stronger spreading result was proved by Fife and McLeod [FM77], who showed that for a large class of f the solution with such initial values approaches what looks like a juxtaposition of traveling waves. The results of [AW75] were extended to more general equations in [AW78], and it was shown that a spreading result also applies to solutions of the problem

$$u_{,t} = D\nabla^2 u + f(u) \tag{1.1}$$

in any number of dimensions. Because the equation is rotationally invariant, the spreading speed c^* is the same in all directions, and it is equal to that of the corresponding one-dimensional problem. It was also shown that there is a traveling wave of speed c^* in each direction, and that in the Fisher case there are also waves of all speeds greater than c^*. Equations of the form (1.1) serve as models for a number of situations in population genetics, population biology, and other fields.

It was shown in [Wei82] that many of these results could be carried over to recursions of the form

$$u_{n+1} = Q[u_n], \tag{1.2}$$

[1] [KPP37] was actually motivated by a similar model in which the growth term is $u(1-u)^2$, but the result applies to both models.

where u_n is a scalar-valued function on a Euclidean space or, more generally, a habitat $\mathcal{H}$ in such a space, while Q is a translation invariant order-preserving operator with the properties that $Q[0] = 0$, and $Q[\pi_1] = \pi_1$ for some positive constant π_1. If $u(x, t)$ is a solution of the equation (1.1) and τ is any positive number, then the sequence of functions $u_n(\mathbf{x}) := u(\mathbf{x}, n\tau)$ satisfies the recursion (1.2) with Q the operator which takes the initial values $u(\mathbf{x}, 0)$ to the values $u(\mathbf{x}, \tau)$ of the solution of (1.1) at time τ. This Q is called the **time-τ map** of the equation (1.1). It is easily seen that if $f(0) = f(1) = 0$ and $f'(1) < 0$, then this Q has the properties required of Q above, with $\pi_1 = 1$. In population genetics, one can think of u as a gene fraction. In population ecology, u can be thought of as the population density, or, if $\mathcal{H}$ is discrete, the population in the census tract centered at each point.

Under some technical conditions on Q which are satisfied by the time-τ map of (1.1) it was shown that the recursion (1.2) has a spreading speed in each direction, and that for large n, the part of u_n which lies above the largest equilibrium below π_1, which is denoted by π_0, spreads like the solution of a wave equation with these wave speeds in the various directions. It was also shown that the spreading speeds can be bounded above and below, and in some cases found explicitly, by solving linear problems. Under the additional condition that $Q[\alpha] > \alpha$ for every constant α in $(0, \pi_1)$ (the heterozygote intermediate or Fisher case) it was shown that there is a traveling wave of speed c in any direction if and only if c is at least as large as the spreading speed in this direction. Under other conditions, such as the heterozygote inferior or bistable case, the methods in [Wei82] still give the spreading result, but they provide no information about the existence of a traveling wave.

In 1979 Gärtner and Freidlin [GF79] used probabilistic methods to show that one can still obtain spreading results for an equation of Fisher type in which the mobility and the growth function vary periodically in space.

Shigesada, Kawasaki, and Teramoto [SKT86], [SK97] studied population spreading in a periodically varying habitat. They used the one-dimension model

$$u_{,t} = (D(x)u_{,x})_{,x} + u[\epsilon(x) - u],$$

where the mobility D and the growth rate ϵ are periodic functions of period 1, to model the growth and spread of an invading species in a forest which consists of trees planted in periodic rows when the population density u does not vary in the direction of the rows. They obtained a formula for the speeds of what they call periodic traveling waves of the linearization of this equation about $u = 0$. As Theorem 2.3 and Corollary 2.1 will show, this system is linearly determinate in the sense that its spreading speed is given by the slowest wave speed of this linearized system. The same is true of the two-dimensional version

$$u_{,t} = (D(x)u_{,x})_{,x} + (D(x)u_{,y})_{,y} + u[\epsilon(x) - u] \tag{1.3}$$

of this model, which has recently been treated by Kinezaki, Kawasaki, Takasu, and Shigesada [KKTS03]. They showed how to obtain spreading speeds not only in the direction perpendicular to the rows but in each direction.

The methods presented in the present paper permit the treatment of the periodic model (1.3) and of the more general model in which the mobility D and the carrying capacity ϵ are periodic functions of both x and y. Such models can be thought of as simple cases of growth and spread in a patchy environment.

As in [Wei82], we shall study such problems by considering a recursion of the form (1.2), but with an operator Q which is periodic but not necessarily translation invariant. That is, Q commutes with some but not all translations. As in the case of the equation (1.1), a continuous-time model like (1.3) can be reduced to a recursion of the form (1.2), where $u_n(\mathbf{x}) := u(\mathbf{x}, n\tau)$ and Q is the time-τ mapping of (1.3), which takes the initial values $u(\mathbf{x}, 0)$ of a solution of (1.3) to the values $u(\mathbf{x}, \tau)$ at time τ.

R. Lui [Lui89] showed that the discrete-time methods of [Wei82] can be extended to multispecies recursion systems of the form (1.2) in which u and $Q[u]$ are vector-valued functions and Q is translation invariant and order preserving, provided one makes suitable assumptions about Q. We shall obtain our results by showing that the methods of [Wei82] and [Lui89] can be extended to the case of a periodic operator.

The class of discrete-time models of population genetics or population ecology was introduced as a more flexible model in which one avoids the somewhat questionable assumption that the system is in equilibrium at every instant, which is implicit in any continuous-time diffusion model. However, it also permits the treatment of time-periodic models which allow for diurnal or annual variations. The fact that spatially discrete models are included permits models in which the required measurements involve only aggregate populations in census tracts. Such measurements are more likely to be possible than measurements at every point. Of course, numerical simulations of continuous models use discrete-time discrete-space models.

In all these cases it is shown that the spreading results obtained for translation invariant partial differential equation models are still valid. Lui's work on multispecies systems [Lui89] shows that one can also obtain these results for systems of partial differential, integro-differential, or finite difference equations where phase plane methods become difficult or impossible to apply. An extension of these results to more general systems which include models for invasion by a competing species was presented in [WLLnt] and [LLWnt]. The present work gives an extension in a different direction. It seems likely that the methods presented here can be combined with those found in these earlier papers to obtain corresponding results about models for two competing species or any number of cooperating species in a periodically varying environment. Such an extension might also provide sufficient conditions for the hairtrigger effect, which will not be discussed here.

Section 2 formulates the problem in detail, and states all the theorems in this work. Section 3 shows how the spreading speed is defined, and the next two sections prove the spreading properties. Application of these results to a prescribed model requires a way of calculating the spreading speed. Proposition 3.1 at the end of section 3 shows how to obtain a lower bound for the spreading speed by means of numerical simulation. Section 6 shows how to obtain both upper and lower bounds for the spreading speed and the ray speed in terms of the eigenvalues of linear problems. Corollary 2.1 is the general version of linear determinacy, in which the spreading speed is equal to that of the linearization of the problem. It requires the assumption that the operator $Q[u]$ is bounded above by its linearization around $u = 0$, which can be interpreted as the absence of an Allee effect. This assumption is crucial to much of the work in this area, but it is not needed for any of our results other than Corollary 2.1.

Section 7 shows that for problems of Fisher type, the spreading speed in a direction is equal to the slowest speed of traveling waves in that direction. There is a large literature on the existence of traveling waves for continuous-time models in periodically varying Euclidean spaces of one or more dimensions. See, e.g., [Xin00], [PX91], [Xin91], [HZ95], [Hei01], [Nak00]. The speeds of these waves are upper bounds for the spreading speeds, but our result has the advantage of showing that the spreading speed is no slower than the slowest wave speed. The existence of traveling waves has also been proved for periodically varying discrete lattices. (See, e.g. [Kee87], [Zin92], [CMPS98], [MP99], [CMPvV99].) Some of these results include the sophisticated phenomenon of pinning, which does not appear to be obtainable from our methods.

The existence of traveling periodic waves has been extended to partially bounded domains such as strips and cylinders in [BL89], [BLL90], and [BN92]. Berestycki and Hamel [BH02] have recently extended these results to a rather general class of domains such as periodically varying strips or cylinders. In Section 8 we shall show how the results of the present work can be extended to such domains.

2 Formulation of the problem and statement of the results

We suppose that we are given an unbounded habitat $\mathcal{H}$, which is a closed d-dimensional subset of the Euclidean space R^d. We shall study a recursion of the form

$$u_{n+1} = Q[u_n], \tag{2.1}$$

where the operator Q takes a set $\mathcal{M}$ of uniformly bounded continuous functions into itself. The initial function u_0 is prescribed. We are interested in the asymptotic behavior of the function u_n for large n when u_0 vanishes outside a bounded set. We shall assume that Q is order preserving.

For any $\mathbf{a}$ in R^d we define the translation by $\mathbf{a}$ of a point $\mathbf{x}$ to be $\mathbf{x}-\mathbf{a}$. We also define the translation operator

$$T_{\mathbf{a}}[u](\mathbf{x}) := u(\mathbf{x} - \mathbf{a}).$$

We say that a set $\mathcal{L}$ of vectors is a **lattice** if $\mathbf{a} \pm \mathbf{b}$ is in $\mathcal{L}$ whenever $\mathbf{a}$ and $\mathbf{b}$ are in $\mathcal{L}$. That is, $\mathcal{L}$ is an additive group of vectors. Then the corresponding translations $T_{\mathbf{a}}$ also form a group.

This work is distinguished from earlier work by the fact that, instead of assuming Q to be translation invariant, we make the weaker assumption that it is periodic. We shall suppose that for some d-dimensional lattice $\mathcal{L}$ every translation $T_{\mathbf{a}}$ with $\mathbf{a} \in \mathcal{L}$ takes the habitat into itself, so that $\mathcal{H}$ is unbounded in all directions. Then $T_{\mathbf{a}}[u]$ is defined for all $u \in \mathcal{M}$, and we suppose that $\mathcal{M}$ contains all these translates. We say that u is **periodic with respect to $\mathcal{L}$** (or, more briefly, **$\mathcal{L}$-periodic**) if $T_{\mathbf{a}}[u] = u$ for all $\mathbf{a} \in \mathcal{L}$. We say that the operator Q is **periodic with respect to $\mathcal{L}$** if

$$Q[T_{\mathbf{a}}[u]] = T_{\mathbf{a}}[Q[u]] \text{ for all } \mathbf{a} \in \mathcal{L} \tag{2.2}$$

for every u. It is easily seen that if u and Q are periodic with respect to $\mathcal{L}$, then $Q[u]$ is also periodic with respect to $\mathcal{L}$.

An **equilibrium** $\theta(\mathbf{x})$ is a fixed point of Q: $Q[\theta] = \theta$. We shall deal with two or three equilibria $\phi(\mathbf{x}) \leq \theta_0(\mathbf{x}) < \theta_1(\mathbf{x})$ which are periodic with respect to $\mathcal{L}$. By changing the variable from u_n to $v_n = u_n - \phi$ and writing the recursion (2.1) in the form $v_{n+1} = Q[\phi + v_n] - \phi$ we can (and shall) assume without loss of generality that $\phi = 0$. Note that the new operator $Q[\phi + v] - \phi$ is again order preserving and periodic with respect to $\mathcal{L}$ and has the equilibrium 0. We denote the other resulting equilibria $\theta_i - \phi$ by π_i. We shall assume that π_0 is unstable and π_1 is stable in a very strong sense. We shall take the domain $\mathcal{M}$ of Q to be the set

$$\mathcal{M} = \{u(\mathbf{x}) : u \text{ continuous on } \mathcal{H},\ 0 \leq u(\mathbf{x}) \leq \pi_1(\mathbf{x})\}.$$

We write down our basic assumptions about the operator Q.

Hypotheses 2.1 *i. The habitat $\mathcal{H}$ is a closed subset of R^d, which is not contained in any lower-dimensional linear subspace of R^d.*

ii. Q is order preserving in the sense that if $u(\mathbf{x}) \leq v(\mathbf{x})$ on $\mathcal{H}$, then $Q[u](\mathbf{x}) \leq Q[v](\mathbf{x})$. That is, an increase throughout $\mathcal{H}$ in the population u_n at time $n\tau$ increases the population $u_{n+1} = Q[u_n]$ throughout $\mathcal{H}$ at the next time step.

iii. There is a closed d-dimensional lattice $\mathcal{L}$ such that $\mathcal{H}$ is invariant under translation by any element of $\mathcal{L}$, and Q is periodic with respect to $\mathcal{L}$ in the sense that (2.2) holds for all $u \in M$ and $\mathbf{a} \in \mathcal{L}$. Moreover, there is a bounded subset P of $\mathcal{H}$ such that every $\mathbf{x} \in \mathcal{H}$ has a unique representation of the form $\mathbf{x} = \mathbf{z} + \mathbf{p}$ with $\mathbf{z}$ in $\mathcal{L}$ and $\mathbf{p}$ in P.

iv. $Q[0] = 0$, and there are $\mathcal{L}$-periodic equilibria $\pi_0(\mathbf{x})$ and $\pi_1(\mathbf{x})$ such that $0 \leq \pi_0 < \pi_1$, $Q[\pi_0] = \pi_0$ and $Q[\pi_1] = \pi_1$. Moreover if $\pi_0 \leq u_0 \leq \pi_1$, u_0 is periodic with respect to $\mathcal{L}$, and $u_0 \not\equiv \pi_0$, then the solution u_n of the recursion (2.1), which is again periodic with respect to $\mathcal{L}$, converges to π_1 as $n \to \infty$ uniformly on $\mathcal{H}$. (That is, π_0 is unstable and π_1 is stable.) In addition, any $\mathcal{L}$-periodic equilibrium π other than π_1 which satisfies the inequalities $0 \leq \pi \leq \pi_1$ also satisfies $\pi \leq \pi_0$.

v. *Q is continuous in the sense that if the sequence $u_m \in \mathcal{M}$ converges to $u \in \mathcal{M}$, uniformly on every bounded subset of $\mathcal{H}$, then $Q[u_m]$ converges to $Q[u]$, uniformly on every bounded subset of $\mathcal{H}$. That is, a change in u far from the point $\mathbf{x}$ has very little effect on the value of $Q[u]$ at $\mathbf{x}$.*

vi. *Every sequence $\{u_m\}$ of functions in $\mathcal{M}$ contains a subsequence $\{u_{n_i}\}$ such that $\{Q[u_{n_i}]\}$ converges to some function, uniformly on every bounded set.*

Example 2.1 *We consider a stepping stone model for growth and spread of a population in the Euclidean plane. The plane is broken into unit squares, which can be thought of as census tracts. Let $u_n(i,j)$ denote the population of the nth synchronized generation of some species in the square $i \le x < i+1, j \le y < j+1$. We associate this square and its population with the center $(i+\frac{1}{2}, j+\frac{1}{2})$. Thus we let $\mathcal{H}$ be the set of points with coordinates of the form $(i+\frac{1}{2}, j+\frac{1}{2})$ where i and j are integers. We assume that if $u_n(i,j)$ is the population in the square with center $(i+1/2, j+1/2)$ at the nth time step, the population grows or decays to the value $g(i,j,u_n(i,j))$, after which a positive fraction $d(i,j) < 1/4$ of this population migrates to each of the four adjacent squares. Then*

$$\begin{aligned} u_{n+1}(i,j) = [1-4d(i,j)]g(i,j,u_n(i,j) + d(i-1,j)g(i-1,j,u_n(i-1,j)) \\ + d(i+1,j)g(i+1,j,u_n(i+1,j)) + d(i,j-1)g(i,j-1,u_n(i,j-1)) \\ + d(i,j+1)g(i,j+1,u_n(i,j+1)). \end{aligned} \tag{2.3}$$

This is a recursion of the form (2.1), where $Q[u_n]$ is the function of i and j on the right. We shall use the growth function

$$g(i,j,u) := \frac{e^{r(i,j)}u + t(i,j)s(i,j)u^2}{1+s(i,j)u} \quad \text{where } s(i,j) > 0 \text{ and } 0 \le t(i,j) < 1. \tag{2.4}$$

Here $r(i,j)$ is the growth rate when the population is small, $s(i,j) > 0$ is a logistic parameter, and $-\ln t(i,j)$ is the decay rate when the population is large. When $t(i,j) = 0$, this is just the Beverton-Holt growth law. $0 < d(i,j) < 1/4$ is the mobility. Because $g(i,j,u)$ is increasing in u and $d(i,j) < 1/4$, Q is order preserving.

We now suppose that for some positive integers N_1 and N_2 the square $[i, i+1) \times [j, j+1)$ has the same growth and dispersion properties as the square $[i+N_1, i+N_1+1) \times [j+N_2, j+N_2+1)$. That is, the functions $r(i,j))$, $s(i,j)$, $t(i,j)$, and $d(i,j)$ are periodic of period N_1 in i and of period N_2 in j. We define the lattice $\mathcal{L} := \{(kN_1, \ell N_2) : k, \ell \text{ integers}\}$. It is easily verified that Q is $\mathcal{L}$-periodic. Hypothesis 2.1.iii is satisfied with the set $P = \{(i-1/2, j-1/2) : i = 1, \cdots, N_1,\ j = 1, \cdots, N_2\}$. Since $\mathcal{H}$ is discrete, all functions are continuous, and Hypotheses 2.1.v and 2.1.vi are trivially satisfied. Thus all the Hypotheses 2.1 are valid with the possible exception of Hypothesis 2.1.iv.

It only remains to verify Hypothesis 2.1.iv. 0 is clearly an equilibrium. Arguments of maximum principle type show that there is at most one other nonnegative periodic *equilibrium, and that if it exists, it is strictly positive. Since $t(i,j) < 1$, the population decreases if it is large. From this we can obtain the existence of a positive N-periodic equilibrium $\pi_1(i,j)$ such that Hypothesis 2.1.iv is valid with $\pi_0(i,j) \equiv 0$ if and only if the equilibrium 0 is unstable. One can determine whether or not this is the case by looking at the stability of the linearization M of Q, which is obtained by replacing the function $g(i,j,u)$ in (2.3) by its linearization $e^{r(i,j)}u$. This problem will be discussed in Example 6.1 in the special case where $N_2 = 1$, so that the parameters are independent of j, and the set P is one-dimensional. The methods presented there serve to show that, even without this special assumption, Hypotheses 2.1 are satisfied if $r(i,j) > 0$ everywhere, and that there is no positive equilibrium if $r(i,j) < 0$ everywhere.*

Example 2.2 *Let $\mathcal{H}$ be the Euclidean plane, and consider the equation (2.1) of [KKTS03]*

$$u_{,t} = [D(x)u_{,x}]_{,x} + [D(x)u_{,y}]_{,y} + u(\epsilon(x) - u), \tag{2.5}$$

where the functions $D(x)$ and $\epsilon(x)$ are independent of y and periodic of period 1 in x. Then $\mathcal{L}$ is the set of vertical lines $\{(i,y) : i \text{ an integer}\}$. Hypothesis 2.1.iii is satisfied with P the segment $P = \{(x,y) : 0 \leq x < 1,\ y = 0\}$. Well-known properties of parabolic equations show that the time-one map Q of this equation satisfies all the Hypotheses 2.1 with the possible exception of Hypothesis 2.1.iv. As in the preceding example, the existence of a periodic $\pi_1(x)$ such that Hypothesis 2.1.iv is satisfied with $\pi_0 \equiv 0$ is equivalent to the linear instability of the equilibrium 0. It is easily seen that this property is valid when $\epsilon(x) > 0$ and invalid when $\epsilon(x) < 0$, but needs to be investigated numerically as in Example 6.2 when ϵ changes sign.

We remark that when $\pi_1(x) > 0$ is known, the variable $v := u/\pi_1$ satisfies a periodic equation of the form

$$v_{,t} = D(x)[v_{,xx} + v_{,yy}] - e_1(x)v_{,x} - e_2(x)v_{,y} + r(x)v(1 - v), \tag{2.6}$$

which is of the type treated by probabilistic means by Gärtner and Freidlin [GF79], [Fre84]. The equation

$$U_{,t} = \{D(x)U\}_{,xx} + \{D(x)U\}_{,yy} + R(x)U - [1 - T(x)]S(x)U^2,$$

is obtained as a formal limit of the preceding example with $N_2 = 1$ by shrinking the sides of the squares and the time interval by the factor N_1, scaling the parameters suitably, and letting N_1 approach infinity. This equation can also be put into the form (2.6) by letting $v := U/\pi_1$ when a positive equilibrium π_1 is known.

Our principal results will be stated in terms of spreading speeds, which are defined and characterized by the following theorem.

Theorem 2.1 *For each unit vector $\boldsymbol{\xi}$ there exists a* **spreading speed** $c^*(\boldsymbol{\xi}) \in (-\infty, \infty]$ *such that solutions of the recursion (2.1) have the following spreading properties:*

1. *If* $u_0(\mathbf{x}) \geq 0$*,* $\inf[\pi_1(\mathbf{x}) - u_0(\mathbf{x})] > 0$*, and* $u_0(\mathbf{x}) = 0$ *in a half-space of the form* $\boldsymbol{\xi}\cdot\mathbf{x} \geq L$ *and if* $c^*(\boldsymbol{\xi}) < \infty$*, then for every* $c > c^*(\boldsymbol{\xi})$

$$\limsup_{n\to\infty}\left[\sup_{\boldsymbol{\xi}\cdot\mathbf{x}\geq nc}[u_n(\mathbf{x}) - \pi_0(\mathbf{x})]\right] \leq 0; \tag{2.7}$$

and

2. *If* $0 \leq u_0 \leq \pi_1$ *and there is a constant* K *such that* $\inf_{\boldsymbol{\xi}\cdot\mathbf{x}\leq -K}[u_0(\mathbf{x}) - \pi_0(\mathbf{x})] > 0$*, then for every* $c < c^*(\boldsymbol{\xi})$

$$\lim_{n\to\infty}\left[\sup_{\boldsymbol{\xi}\cdot\mathbf{x}\leq nc}[\pi_1(\mathbf{x}) - u_n(\mathbf{x})]\right] = 0. \tag{2.8}$$

This theorem states that if u_0 is zero for all large values of $\boldsymbol{\xi}\cdot\mathbf{x}$ and uniformly above π_0 for all sufficiently negative values of $\boldsymbol{\xi}\cdot\mathbf{x}$, then an observer who moves in a direction $\boldsymbol{\xi}$ with a speed above $c^*(\boldsymbol{\xi})$ will see the solution go down to at most π_0, while an observer who moves in this direction at a speed slower than $c^*(\boldsymbol{\xi})$ sees the solution approach π_1. It should be noted that if the model includes a phenomenon such as a prevailing wind, $c^*(\boldsymbol{\xi})$ may be negative in some directions. In this case an observer who stands still sees the solution go down to or below the unstable state π_0 because the cloud of growing population gets blown away.

The next two theorems show that the spreading speeds also serve to describe the asymptotic location of any level surface between π_0 and π_1 of a solution of the recursion (2.1) in any number of dimensions when the initial function u_0 vanishes outside a bounded set. We first define the set

$$\mathcal{S} := \{\mathbf{x}\in R^d : \boldsymbol{\xi}\cdot\mathbf{x} \leq c^*(\boldsymbol{\xi}) \text{ for all unit vectors } \boldsymbol{\xi}\}. \tag{2.9}$$

If $c^*(\boldsymbol{\xi})$ were the propagation speed in the $\boldsymbol{\xi}$-direction of a wave equation, $\mathcal{S}$ would be the ray surface. (See, e.g., pp. 552-587 of [CH62].) This convex set can also be characterized by the **ray speed** $C(\boldsymbol{\eta})$ in the direction of the unit vector $\boldsymbol{\eta}$. $C(\boldsymbol{\eta})$ is defined to be the largest value of α such that $\alpha\boldsymbol{\eta}\in\mathcal{S}$. It is related to c^* by the formula

$$C(\boldsymbol{\eta}) = \inf_{\boldsymbol{\xi}\cdot\boldsymbol{\eta}>0}\frac{c^*(\boldsymbol{\xi})}{\boldsymbol{\xi}\cdot\boldsymbol{\eta}}, \tag{2.10}$$

where the right-hand side is defined to be $+\infty$ if the set of $\boldsymbol{\xi}$ where $c^*(\boldsymbol{\xi}) < \infty$ and $\boldsymbol{\xi}\cdot\boldsymbol{\eta} > 0$ is empty. When $\mathcal{S}$ contains the origin so that $c^*(\boldsymbol{\xi}) \geq 0$, $C(\boldsymbol{\eta})$ is defined and nonnegative for all directions $\boldsymbol{\eta}$. If $c^*(\boldsymbol{\xi}_0) < 0$, then $C(\boldsymbol{\eta}) < 0$ for all $\boldsymbol{\eta}$ such that $\boldsymbol{\eta}\cdot\boldsymbol{\xi} > 0$. Moreover, if $\boldsymbol{\eta}\cdot\boldsymbol{\xi}_0 = 0$, then the line $\alpha\boldsymbol{\eta}$ does not intersect $\mathcal{S}$, so that $C(\boldsymbol{\eta})$ is undefined.

For any positive β we define the dilation $\beta\mathcal{S}$ to be the set of points of the form $\beta\mathbf{x}$ with $\mathbf{x}\in\mathcal{S}$. Clearly, $\beta\mathcal{S} = \{\mathbf{x}\in R^k : \boldsymbol{\xi}\cdot\mathbf{x} \leq \beta c^*(\boldsymbol{\xi}) \text{ for all } \boldsymbol{\xi}\}$.

Theorem 2.2 *Let $u_n(\mathbf{x})$ be a solution of the recursion (2.1). Suppose that u_0 vanishes outside a bounded set, and that $0 \le u_0(\mathbf{x}) < \pi_1(\mathbf{x})$. Then*

1. *If $C(\boldsymbol{\eta})$ is defined and finite, then for any $c > C(\boldsymbol{\eta})$*

$$\limsup_{n\to\infty} \left[\sup_{\beta \ge c}[u_n(n\beta\boldsymbol{\eta}) - \pi_0(n\beta\boldsymbol{\eta})]\right] \le 0, \tag{2.11}$$

and if $C(\boldsymbol{\eta})$ is undefined,

$$\limsup_{n\to\infty} \left[\sup_{\beta}[u_n(\beta\boldsymbol{\eta}) - \pi_0(\beta\boldsymbol{\eta})]\right] \le 0. \tag{2.12}$$

2. *Suppose in addition that the set $\mathcal{S}$ is nonempty and bounded, and let $\mathcal{S}'$ be any open set which contains $\mathcal{S}$. Then*

$$\limsup_{n\to\infty} \left[\sup_{\mathbf{x}\notin n\mathcal{S}'} \{u_n(\mathbf{x}) - \pi_0(\mathbf{x})\}\right] \le 0. \tag{2.13}$$

Note that the statements of Theorem 2.2 become stronger when $\pi_0 \equiv 0$.

Theorem 2.2 states that an observer moving in the direction $\boldsymbol{\eta}$ sees the values of the function above π_0 spread at a speed which is no faster than $C(\boldsymbol{\eta})$. The next theorem shows that, if $\mathcal{S}$ has interior points, these values do not spread at a slower speed either.

Theorem 2.3 *Suppose that the set $\mathcal{S}$ has nonempty interior, and let $\mathcal{S}''$ be any closed bounded subset of the interior of $\mathcal{S}$. For every positive constant σ there exists a radius R_σ with the property that if u_n is a solution of the recursion (2.1), if $0 \le u_0 \le \pi_1$, and if $u_0 \ge \pi_0 + \sigma$ on the ball $|\mathbf{x}| \le R_\sigma$, then*

$$\lim_{n\to\infty} \left[\sup_{\mathbf{x}\in n\mathcal{S}''} \{\pi_1(\mathbf{x}) - u_n(\mathbf{x})\}\right] = 0. \tag{2.14}$$

In particular, if $C(\boldsymbol{\eta})$ is defined and if $-C(-\boldsymbol{\eta}) < c < C(\boldsymbol{\eta})$, then

$$\lim_{N\to\infty} [\pi_1(nc\boldsymbol{\eta}) - u_n(nc\boldsymbol{\eta})] = 0.$$

Remark. A simple continuity argument shows that when $Q[u](y) := (1/2)\int_{y-1}^{y+1} u(x)$ $\{1+(u(x)-1)(3+\sin x - u(x))\}dx$, there is an initial function which lies above $\pi_0 \equiv 1$ somewhere and for which the sequence u_b approaches zero uniformly. Thus the requirement of this Theorem that u_0 lie above π_0 on a sufficiently large set is needed. [CORRECTION AFTER PUBLICATION: In order to satisfy the Hypotheses 2.1, the operator in this Remark should be changed to $Q[u](y) := \frac{1}{2\pi}\int_{y-\pi}^{y+\pi} u(x)\{1 + \frac{1}{12}(u(x)-1)(3+\sin x - u(x))\}dx$, which is order-preserving for $0 \leq u \leq \pi_1 \equiv 3$ and takes all 2π-periodic functions into constant functions.]

It is computationally difficult to calculate the spreading speed $c^*(\boldsymbol{\xi})$ from the definition in Section 3. As in the case of the Fisher equation, one can often obtain bounds for, and sometimes the value of, $c^*(\boldsymbol{\xi})$ in terms of a linear problem. Let L be a linear operator on nonnegative functions which are continuous on $\mathcal{H}$. Suppose that L is **strongly order preserving** in the sense that if $u \geq 0$ and $u \not\equiv 0$, then $L[u] > 0$. Also suppose that L is periodic with respect to $\mathcal{L}$. That is, $T_{\mathbf{a}}L = LT_{\mathbf{a}}$ for all $\mathbf{a} \in \mathcal{L}$. Finally, we assume that, for each μ, $L[e^{\mu|\mathbf{x}|}]$ exists in the following sense: The nondecreasing sequence $L[\min\{n, e^{\mu|\mathbf{x}|}\}](\mathbf{y})$ converges to a function, which we call $L[e^{\mu|\mathbf{x}|}](\mathbf{y})$. (We use the convention that L acts on a function of $\mathbf{x}$ to produce a function of $\mathbf{y}$.) If $L[e^{\mu|\mathbf{x}|}]$ exists, $L[e^{-\boldsymbol{\xi}\cdot\mathbf{x}}\psi(\mathbf{x})](\mathbf{y})$ with ψ is bounded and continuous can also be defined by a limiting process. In particular, one can seek traveling waves of the recursion $u_{n+1} = L[u_n]$ of the form

$$u_n(\mathbf{x}) = e^{-\mu(\boldsymbol{\xi}\cdot\mathbf{x}-nc)}\psi(\mathbf{x})$$

where the function ψ is continuous and periodic with respect to $\mathcal{L}$. If we insert this form into the recursion, we find that ψ has to satisfy the equation

$$e^{\mu\boldsymbol{\xi}\cdot\mathbf{y}}L[e^{-\mu\xi\cdot\mathbf{x}}\psi(\mathbf{x})](\mathbf{y}) = e^{\mu c}\psi(\mathbf{y}).$$

That is, $e^{\mu c}$ is a positive eigenvalue of the operator

$$L_{\mu\boldsymbol{\xi}}[\psi](\mathbf{y}) := e^{\mu\boldsymbol{\xi}\cdot\mathbf{y}}L[e^{-\mu\xi\cdot\mathbf{x}}\psi(\mathbf{x})](\mathbf{y}), \tag{2.15}$$

and ψ is the corresponding eigenfunction. By applying a translation $T_{\mathbf{a}}$ with $\mathbf{a} \in \mathcal{L}$ to this definition, it is easily verified that the linear operator $L_{\mu\boldsymbol{\xi}}$ is again periodic with respect to $\mathcal{L}$ and strongly order preserving. Consequently, $L_{\mu\boldsymbol{\xi}}$ takes nonnegative periodic functions into positive periodic functions, and we shall only consider the restriction of $L_{\mu\boldsymbol{\xi}}$ to such functions. Such an order preserving operator has a positive eigenvalue $\lambda(\mu\boldsymbol{\xi})$ with a positive eigenfunction, and with the property that the absolute values of all the eigenvalues of $L_{\mu\boldsymbol{\xi}}$ are below $\lambda(\mu\boldsymbol{\xi})$. $\lambda(\mu\boldsymbol{\xi})$ is called the **principal eigenvalue** of $L_{\mu\boldsymbol{\xi}}$. We note that the speed of the above wave satisfies $e^{\mu c} = \lambda(\mu\boldsymbol{\xi})$, so that $c = (1/\mu)\ln\lambda(\mu\boldsymbol{\xi})$.

Theorem 2.4 *Suppose that there is a linear operator L with the properties*

1. *there is a positive number η such that*

$$Q[u] \geq L[u] \text{ for every } u \text{ such that } 0 \leq u \leq \eta; \tag{2.16}$$

2. *L is $\mathcal{L}$-periodic and strongly order-preserving, and $L[e^{\mu|\mathbf{x}|}]$ is defined for all μ.*

3. *There is a positive $\mathcal{L}$-periodic function r such that $L[r] > r$, and the truncated operator*

$$Q^{[L,r]}[u] := \min\{L[u], r\}$$

satisfies the hypotheses 2.1;

Let $\lambda(\mu\boldsymbol{\xi})$ be the principal eigenvalue of the operator $L_{\mu\boldsymbol{\xi}}$ defined by (2.15). Then

$$c^*(\boldsymbol{\xi}) \geq \inf_{\mu>0}[(1/\mu)\ln\lambda(\mu\boldsymbol{\xi})], \tag{2.17}$$

and the ray speed in the direction $\boldsymbol{\eta}$ has the lower bound

$$C(\boldsymbol{\eta}) \geq \inf_{\substack{\boldsymbol{\zeta}\in R^d \\ \boldsymbol{\eta}\cdot\boldsymbol{\zeta}>0}} [\{\ln\lambda(\boldsymbol{\zeta})\}/\boldsymbol{\eta}\cdot\boldsymbol{\zeta}]. \tag{2.18}$$

We can also find an upper bound for $c^*(\boldsymbol{\xi})$ in terms of a linear problem.

Theorem 2.5 *Suppose that there is a linear operator L such that*

1. $$Q[u] \leq L[u] \text{ for all } u \text{ with } 0 \leq u \leq \pi_1; \tag{2.19}$$
2. *L is $\mathcal{L}$-periodic and strongly order-preserving, and $L[e^{\mu|\mathbf{x}|}]$ is defined for all μ.*
3. *there is a positive $\mathcal{L}$-periodic function r such that $L[r] > r$, and the truncated operator*

   $$Q^{[L,r]}[u] := \min\{L[u], r\}$$

   satisfies the hypotheses 2.1;

Let $\lambda(\mu\boldsymbol{\xi})$ be the principal eigenvalue of the operator $L_{\mu\boldsymbol{\xi}}[u]$ defined by (2.15). Then

$$c^*(\boldsymbol{\xi}) \leq \inf_{\mu>0}[(1/\mu)\ln\lambda(\mu\boldsymbol{\xi})], \tag{2.20}$$

and the ray speed in the direction $\boldsymbol{\eta}$ has the upper bound

$$C(\boldsymbol{\eta}) \leq \inf_{\substack{\boldsymbol{\zeta}\in R^d \\ \boldsymbol{\eta}\cdot\boldsymbol{\zeta}>0}} [\{\ln\lambda(\boldsymbol{\zeta})\}/\boldsymbol{\eta}\cdot\boldsymbol{\zeta}]. \tag{2.21}$$

We remark that if, instead of taking the infimum, we take a particular value of μ in (2.20) or a particular value of $\boldsymbol{\zeta}$ in (2.21), we still obtain an upper bound.

The linear operator M is said to be the **linearization** (or Fréchet derivative) of the operator Q at 0 if for every positive number σ there is a positive number η_σ such that $0 \leq u(\mathbf{x}) \leq \eta_\sigma$ implies that $|Q[u] - M[u]| \leq \sigma \sup_{\mathbf{x}} u(\mathbf{x})$. For most models which have been studied it is true that for every positive number δ there is an η such that the operator $(1-\delta)M$ satisfies the conditions on L in Theorem 2.4. By letting δ approach zero, one finds the lower bounds (2.17) and (2.18) with $\lambda(\boldsymbol{\zeta})$ replaced by the principal eigenvalue $\tilde{\lambda}(\boldsymbol{\zeta})$ of $M_{\boldsymbol{\zeta}}$. It many problems $Q[u] \leq M[u]$ for all u in $\mathcal{M}$. This can be interpreted as the lack of an Allee effect in the growth law. The following obvious corollary of Theorems 2.4 and 2.5 shows that when this is the case, one can determine $c^*(\boldsymbol{\xi})$ exactly in terms of the eigenvalues of a linear problem. When this happens, we say that the recursion (2.1) is **linearly determinate** in the direction $\boldsymbol{\xi}$.

Corollary 2.1 *If the linearization M of Q at $u = 0$ satisfies the conditions on L in Theorem 2.5 and if for each small positive δ the operator $(1-\delta)M$ satisfies the conditions on L in Theorem 2.4, then*

$$c^*(\boldsymbol{\xi}) = \inf_{\mu>0}[(1/\mu)\ln\tilde{\lambda}(\mu\boldsymbol{\xi})], \tag{2.22}$$

and

$$C(\boldsymbol{\eta}) = \inf_{\substack{\boldsymbol{\zeta}\in R^d \\ \boldsymbol{\eta}\cdot\boldsymbol{\zeta}>0}}[\{\ln\tilde{\lambda}(\boldsymbol{\zeta})\}/\boldsymbol{\eta}\cdot\boldsymbol{\zeta}]. \tag{2.23}$$

where $\tilde{\lambda}(\mu\boldsymbol{\xi})$ is the principal eigenvalue of $M_{\mu\boldsymbol{\xi}}$. Thus, the spreading speed is linearly determinate in all directions under these conditions.

The formula (2.23) was found by Gärtner and Freidlin [GF79]

Under the additional condition $\pi_0 \equiv 0$ we shall show that the spreading speed $c^*(\boldsymbol{\xi})$ can be characterized as a slowest speed of what Shigesada, Kawasaki, and Teramoto [SKT86] call a traveling periodic wave, and Berestycki and Hamel [BH02] call a pulsating wave, which is defined as follows:

Definition 2.1 *A solution u_n of the recursion (2.1) is called a* **periodic traveling wave** *of speed c in the direction of the unit vector $\boldsymbol{\xi}$ if it has the form $u_n(\mathbf{x}) = W(\boldsymbol{\xi}\cdot\mathbf{x} - nc, \mathbf{x})$, where the function $W(s, \mathbf{x})$ has the properties*

a. For each s the function $W(\boldsymbol{\xi}\cdot\mathbf{x} + s, \mathbf{x})$ is continuous in $\mathbf{x} \in \mathcal{H}$.

b. For each s, $W(s, \mathbf{x})$ is $\mathcal{L}$-periodic in $\mathbf{x}$;

c. For each $\mathbf{x} \in \mathcal{H}$, $W(s, \mathbf{x})$ is nonincreasing in s;

d. $W(-\infty, \mathbf{x}) = \pi_1(\mathbf{x})$;

e. $W(\infty, \mathbf{x}) = 0$.

Theorem 2.6 *Suppose that $\pi_0 \equiv 0$. Then there is a periodic traveling wave of speed c in the direction $\boldsymbol{\xi}$ if and only if $c \geq c^*(\boldsymbol{\xi})$.*

We remark that if Q is the time-one map of a continuous-time process such as (1.3), then $u_n(\mathbf{x}) = u(n, \mathbf{x})$. In this case, it it is easily seen that all our theorems have continuous-time analogs. For example, we may replace (2.7) and (2.8) by

$$\limsup_{t\to\infty}\left[\sup_{\boldsymbol{\xi}\cdot\mathbf{x}\geq ct}[u(t,\mathbf{x}) - \pi_0(\mathbf{x})]\right] \leq 0 \text{ when } c > c^*(\boldsymbol{\xi}),$$

and

$$\lim_{t\to\infty}\left[\sup_{\boldsymbol{\xi}\cdot\mathbf{x}\le ct}\,[\pi_1(\mathbf{x})-u(t,\mathbf{x})]\right]=0 \text{ when } c<c^*(\boldsymbol{\xi}),$$

(2.13) by

$$\limsup_{t\to\infty}\left[\sup_{\mathbf{x}\notin t\mathcal{S}'}\{u(t,\mathbf{x})-\pi_0(\mathbf{x})\}\right]\le 0,$$

and (2.14) by

$$\lim_{t\to\infty}\left[\sup_{\mathbf{x}\in t\mathcal{S}''}\{\pi_1(\mathbf{x})-u(t,\mathbf{x})\}\right]=0.$$

Moreover, we can see from the methods used in [LWL02] that there is a periodic traveling wave of the form $W(\boldsymbol{\xi}\cdot\mathbf{x}-ct,\mathbf{x})$ for the continuous-time problem if and only if $c\ge c^*(\boldsymbol{\xi})$.

We are unable to show the existence of traveling waves without assuming that $\pi_0\equiv 0$. In fact, simple phase plane analysis shows that the translation-invariant problem

$$u_{,t}=\Delta u+u\left(u-\tfrac{1}{3}\right)\left(u-\tfrac{2}{3}\right)(1-u), \tag{2.24}$$

whose time-one map satisfies the Hypotheses 2.1, does not have any traveling wave which connects $u\equiv 1$ with $u\equiv 0$.

If $\pi_0\not\equiv 0$, we are also unable to show that the part below π_0 of the solution does not travel faster than the speed given by c^*. It may well be that there is a faster speed $c_+^*(\boldsymbol{\xi})>c^*(\boldsymbol{\xi})$ at which this smaller part travels. In fact, it is not difficult to show that for the equation (2.24) $c^*(\boldsymbol{\xi})$ is equal to the speed of a traveling wave which connects $u\equiv 1$ to $u\equiv\frac{1}{3}$. This speed is less than the speed $(2/3)^{2/3}$ of the slowest wave which connects $u\equiv 1$ to $u\equiv\frac{2}{3}$. On the other hand, the fact that the equation is of Fisher type for $0\le u\le\frac{1}{3}$ shows that for any initial data other than 0 the part of the solution below $\frac{1}{3}$ increases to $\frac{1}{3}$ at the faster speed $c_+^*(\boldsymbol{\xi})=\sqrt{3}(2/3)^{2/3}$. In this case the solution approaches not a traveling wave, but what Fife and McLeod [FM77] call a stacked combination of fronts.

3 Construction of the spreading speeds

The principal tool of this work is the following Comparison Principle, which is easily proved by induction.

Lemma 3.1 (Comparison Principle) *Let R be an order-preserving operator. If the sequences of functions v_n and w_n satisfy the recursive inequalities $v_{n+1}\le R[v_n]$ and $w_{n+1}\ge R[w_n]$, and if $v_0\le w_0$, then $v_n\le w_n$ for all n.*

One of the principal ideas in both [Wei82] and [Lui89] is to reduce the spreading speed problem from dimension d to dimension 1 by looking at propagation in one direction at a time. The analogous process here is to choose a fixed d-dimensional unit direction vector $\boldsymbol{\xi}$ and to look at functions of the form $v(\boldsymbol{\xi}\cdot\mathbf{x},\mathbf{x})$. We first need to define a suitable space of functions.

Definition 3.1 *For any unit vector $\boldsymbol{\xi}$ the space $\tilde{\mathcal{M}}_{\boldsymbol{\xi}}$ is the set of functions $v(s,\mathbf{x})$ such that*

a. $v(s,\mathbf{x})$ is $\mathcal{L}$-periodic in $\mathbf{x}$ for each fixed s;

b. $0\le v(s,\mathbf{x})\le \pi_1(\mathbf{x})$ for all s and $\mathbf{x}$;

c. the function $v(\boldsymbol{\xi}\cdot\mathbf{x}+s,\mathbf{x})$ is continuous in $\mathbf{x}$ for each s.

Note that periodic functions such as π_0 and π_1 can be considered as members of $\tilde{\mathcal{M}}_{\boldsymbol{\xi}}$ which do not depend upon s. We remark that the condition (c) does not imply that $v(s,\mathbf{x})$ is continuous in either s or $\mathbf{x}$. For instance, if $d=1$, $\boldsymbol{\xi}=(1)$, and $[x]$ denotes the largest integer which does not exceed x, the function

$$v(s,x):=\begin{cases}1 & \text{when } s\le x-[x]-1\\ 1-x+[x] & \text{when } x-[x]-1<s\le x-[x]\\ 0 & \text{when } s>x-[x]\end{cases}$$

is discontinuous in s and in x, but $v(x+s,x)$ is continuous in x, so that v is in $\tilde{M}_1$.

We observe that the transformation

$$H_{\boldsymbol{\xi}}[v](\mathbf{x}):=v(\boldsymbol{\xi}\cdot\mathbf{x},\mathbf{x})$$

takes the functions of $\tilde{\mathcal{M}}_{\boldsymbol{\xi}}$ into functions in $\mathcal{M}$. We define the operator [2]

$$\tilde{Q}_{\boldsymbol{\xi}}[v](s,\mathbf{y}):=Q[v(\boldsymbol{\xi}\cdot\{\mathbf{x}-\mathbf{y}\}+s,\mathbf{x})](\mathbf{y}). \tag{3.1}$$

We note that if $\mathbf{y}$ is replaced by $\mathbf{y}-\mathbf{a}$ where $\mathbf{a}$ is any element of $\mathcal{L}$, the $\mathcal{L}$-periodicity of Q and that of v show that the right-hand side of (3.1) remains unchanged. Therefore the function $\tilde{Q}_{\boldsymbol{\xi}}[v]$ has the property (a) in the definition of $\tilde{\mathcal{M}}_{\boldsymbol{\xi}}$. Since the other two properties follow from the properties of Q, we find that $\tilde{Q}_{\boldsymbol{\xi}}$ takes $\tilde{\mathcal{M}}_{\boldsymbol{\xi}}$ into itself. Moreover, the operator $\tilde{Q}_{\boldsymbol{\xi}}$ is translation invariant in the variable s and order preserving.

[2] Here and in what follows we use the convention that if ϕ is a functions of $\mathbf{x}$ and some other variables possibly including $\mathbf{y}$, then $Q[\phi](\mathbf{y})$ means the value at $\mathbf{y}$ of the result of letting Q act on the function of $\mathbf{x}$ which is obtained from ϕ by fixing the values of all its variables other than $\mathbf{x}$. The resulting function is independent of the dummy variable $\mathbf{x}$.

Setting $s = \boldsymbol{\xi} \cdot \mathbf{y}$ in (3.1) gives the intertwining property

$$H_{\boldsymbol{\xi}}[\tilde{Q}_{\boldsymbol{\xi}}[v]] = Q[H_{\boldsymbol{\xi}}[v]]. \tag{3.2}$$

We shall obtain comparison functions for solutions of the recursion (2.1) by observing that if $v_n(s, \mathbf{x})$ satisfies the recursion

$$v_{n+1} = \tilde{Q}_{\boldsymbol{\xi}}[v_n],$$

then, by the intertwining property (3.2), $H_{\boldsymbol{\xi}}[v_n]$ satisfies the recursion (2.1).

We now choose a continuous initial function $\phi(s, \mathbf{x})$ with the properties

$$\begin{aligned}
&\text{a. } \phi(s,\mathbf{x}) \text{ is uniformly continuous in } s \text{ and } \mathbf{x}, \text{ and } \mathcal{L}\text{-periodic in } \mathbf{x};\\
&\text{b. } \phi(s,\mathbf{x}) \text{ is nonincreasing in } s \text{ for each fixed } \mathbf{x};\\
&\text{c. } \phi(s,\mathbf{x}) \equiv 0 \text{ for } s \geq 0;\\
&\text{d. } \pi_0(\mathbf{x}) < \phi(-\infty,\mathbf{x}) < \pi_1(\mathbf{x}).
\end{aligned} \tag{3.3}$$

As in [Wei82] and [Lui89], we define for any real c the sequence $a_n(c, \boldsymbol{\xi}; s, \mathbf{x})$ by the recursion

$$\begin{aligned}
a_{n+1}(c, \boldsymbol{\xi}; s, \mathbf{x}) &= \max\{\phi(s, \mathbf{x}), \tilde{Q}_{\boldsymbol{\xi}}[a_n](s + c, \mathbf{x})\}\\
a_0(c, \boldsymbol{\xi}; s, \mathbf{x}) &= \phi(s, \mathbf{x}).
\end{aligned} \tag{3.4}$$

(The maximum is the larger of the two numbers for each s and $\mathbf{x}$.) Replacing s by $s + \boldsymbol{\xi} \cdot \mathbf{y}$ in the definition of $H_{\boldsymbol{\xi}}$ shows that the recursion equation in (3.4) can be written in the form

$$a_{n+1}(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{y} + s, \mathbf{y}) = \max\{\phi(\boldsymbol{\xi} \cdot \mathbf{y} + s, \mathbf{y}), Q[a_n(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{x} + s + c, \mathbf{x})](\mathbf{y}). \tag{3.5}$$

Clearly, $a_1 \geq a_0$. Because Q is order-preserving, an induction argument shows that $a_{n+1}(c, \boldsymbol{\xi}; s, \mathbf{x}) \geq a_n(c, \boldsymbol{\xi}; s, \mathbf{x})$. Because $\tilde{Q}_{\boldsymbol{\xi}}$ is also translation invariant in the variable s, it takes functions which are nonincreasing in s into functions which are nonincreasing in s. Therefore a_n is nonincreasing in s for all n. The translation $s \to s + c$ applied to a nonincreasing function is nonincreasing in c, and it follows that $a_n(c, \boldsymbol{\xi}; s, \mathbf{x})$ is also nonincreasing in c for all n. Because $a_n(c, \boldsymbol{\xi}; s, \mathbf{x}) \leq \pi_1(\mathbf{x})$, the nondecreasing sequence a_n has a limit

$$\lim_{n\to\infty} a_n(c, \boldsymbol{\xi}; s, \mathbf{x}) = a(c, \boldsymbol{\xi}; s, \mathbf{x}),$$

which is again nonincreasing in s and c. It follows, in particular, that the limits $a_n(c, \boldsymbol{\xi}; \pm\infty, \mathbf{x})$ and $a(c, \boldsymbol{\xi}, \pm\infty, \mathbf{x})$ all exist.

If $\{s_k\}$ is a sequence which goes to $-\infty$, then by Hypothesis 2.1.vi there is a subsequence $\{s'_k\}$ such that $Q[a_n(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{x} + s'_k, \mathbf{x})](\mathbf{y})$ converges uniformly on bounded sets. Because a is monotone in s, the same is true when s'_k is replaced by s and s approaches

$-\infty$. Thus we see from Hypothesis 2.1.v that we may let s in (3.5) approach $-\infty$ to find that

$$\begin{aligned} a_{n+1}(c, \boldsymbol{\xi}; -\infty, \mathbf{y}) &= \max\{\phi(-\infty, \mathbf{y}), Q[a_n(c, \boldsymbol{\xi}; -\infty, \mathbf{x}))](\mathbf{y})\} \\ &\geq Q[a_n(c, \boldsymbol{\xi}; -\infty, \mathbf{x})](\mathbf{y}). \end{aligned}$$

Since $a_0(c, \boldsymbol{\xi}; -\infty, \mathbf{x}) = \phi(-\infty, \mathbf{x}) > \pi_0(\mathbf{x})$, the Comparison Principle and Hypothesis 2.1.iv show that $a_n(c, \boldsymbol{\xi}; -\infty, \mathbf{x})$ increases to $\pi_1(\mathbf{x})$. Because $a_n \leq a \leq \pi_1$, it follows that

$$a(c, \boldsymbol{\xi}; -\infty, \mathbf{x}) = \pi_1(\mathbf{x}).$$

By Hypotheses 2.1.v and 2.1.vi we may let n go to infinity in (3.5) to obtain the equation

$$a(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{y} + s, \mathbf{y}) = \max\{\phi(\boldsymbol{\xi} \cdot \mathbf{y} + s, \mathbf{y}), Q[a(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{x} + s + c, \mathbf{x})](\mathbf{y})\}. \tag{3.6}$$

We now use Hypothesis 2.1.vi and the monotonicity in s to see that we can let s increase to infinity on both sides of this equation to find that

$$a(c, \boldsymbol{\xi}; \infty, \mathbf{y}) = Q[a(c, \boldsymbol{\xi}; \infty, \mathbf{x}))](\mathbf{y}).$$

That is, the continuous periodic function $a(c, \boldsymbol{\xi}; \infty, \mathbf{x})$ is an equilibrium of Q.

The last part of Hypothesis 2.1.iv now shows that there are two possibilities:

Case (i): $a(c, \boldsymbol{\xi}; \infty, \mathbf{x}) = \pi_1(\mathbf{x})$; or

Case (ii): $a(c, \boldsymbol{\xi}; \infty, \mathbf{x}) \leq \pi_0(\mathbf{x})$.

Because $a(c, \boldsymbol{\xi}; \infty, \mathbf{x})$ is the limit of functions which are nonincreasing in c, it has the same property. This means that if Case (i) holds for some c, it also holds for all smaller c, and that if Case (ii) is valid for one c, it is also valid for all larger c. We define $c^*(\boldsymbol{\xi})$ to be the unique number such $c < c^*(\boldsymbol{\xi})$ implies Case (i), and $c > c^*(\boldsymbol{\xi})$ implies Case (ii). If Case (i) is valid for all c, we define $c^*(\boldsymbol{\xi}) = \infty$. Proposition 3.1 will show that case (i) holds when c is sufficiently negative. The following Lemma states that $c = c^*(\boldsymbol{\xi})$ implies Case (ii), and also gives a way of characterizing the number $c^*(\boldsymbol{\xi})$.

Lemma 3.2 *The number $c^*(\boldsymbol{\xi})$ has the property that*

$$a(c, \boldsymbol{\xi}; \infty, \mathbf{x}) \begin{cases} = \pi_1(\mathbf{x}) & \text{if } c < c^*(\boldsymbol{\xi}) \\ \leq \pi_0(\mathbf{x}) & \text{if } c \geq c^*(\boldsymbol{\xi}). \end{cases} \tag{3.7}$$

Moreover, $c < c^*(\boldsymbol{\xi})$ if and only if there is an integer N such that

$$a_N(c, \boldsymbol{\xi}; 1, \mathbf{x}) > \phi(-\infty, \mathbf{x}). \tag{3.8}$$

Proof. We prove the second part first. Suppose that $a(c, \boldsymbol{\xi}; \infty) = \pi_1$. Because a is nonincreasing in s, $a(c, \boldsymbol{\xi}; s, \mathbf{x}) = \pi_1(\mathbf{x})$ for all s. Let the bounded set P be contained in the closed ball B_ρ of radius ρ centered at the origin. Since the function $a_n(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{x} + 1 + \rho, \mathbf{x})$ approaches $\pi_1(\mathbf{x})$ uniformly on the bounded set P, there is an N such that

$$a_N(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{x} + 1 + \rho, \mathbf{x}) > \phi(-\infty, \mathbf{x}) \text{ on } \bar{P}, \tag{3.9}$$

where $\bar{P}$ is the closure of P. Because $\boldsymbol{\xi} \cdot \mathbf{x} \geq -\rho$ on $\bar{P}$ and a is nonincreasing in s, we conclude that (3.8) is satisfied.

Conversely, suppose that (3.8) is valid. Then $a_N(c, \boldsymbol{\xi}; s+1, \mathbf{x}) \geq \phi(s, \mathbf{x}) = a_0(c, \boldsymbol{\xi}; s, \mathbf{x})$ for all s and $\mathbf{x}$. The Comparison Principle shows that $a_{N+n}(c, \boldsymbol{\xi}; s+1, \mathbf{x}) \geq a_n(c, \boldsymbol{\xi}; s, \mathbf{x})$ for all n. Let n approach infinity to see that $a(c, \boldsymbol{\xi}; s+1, \mathbf{x}) \geq a(c, \boldsymbol{\xi}; s, \mathbf{x})$. Since a is nonincreasing in s, this shows that a is independent of s, so that $a(c, \boldsymbol{\xi}; \infty, \mathbf{x}) = \pi_1(\mathbf{x})$.

We have shown that Case (i) implies (3.9) which implies (3.8) which implies Case (i). Thus if $c > c^*(\boldsymbol{\xi})$ so that Case (ii) holds, then (3.9) cannot be satisfied for any N. In particular, for each pair of positive integers (N, ν) there is a point $\mathbf{x}_{N,\nu}$ in $\bar{P}$ such that

$$a_N(c^*(\boldsymbol{\xi}) + \nu^{-1}, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{x}_{N,\nu} + 1 + \rho, \mathbf{x}_{N,\nu}) \leq \phi(-\infty, \mathbf{x}_{N,\nu}). \tag{3.10}$$

Because $\bar{P}$ is closed and bounded, there is, for any fixed N, a sequence ν_i such that $\mathbf{x}_{N,\nu_i}$ converges to a point $\mathbf{x}_N$ in $\bar{P}$. Because both sides of (3.9) are continuous functions of c and $\mathbf{x}$, we conclude that

$$a_N(c^*(\boldsymbol{\xi}), \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{x}_N + 1 + \rho, \mathbf{x}_N) \leq \phi(-\infty, \mathbf{x}_N).$$

Thus, the inequality (3.9) cannot hold for any N, and we conclude that Case (ii) holds at $c = c^*(\boldsymbol{\xi})$. This is the statement (3.7).

This statement, in turn, shows that $c < c^*(\boldsymbol{\xi})$ if and only if Case (i) holds, and we have already shown that this is true if and only if there is an integer N for which the inequality (3.8) is satisfied. Thus we have proved the second statement of the lemma, so that the Lemma has been established.

Because of Theorem 2.1 we call $c^*(\boldsymbol{\xi})$ the **spreading speed in the direction $\boldsymbol{\xi}$** of the recursion (2.1). The following lemma shows that $c^*(\boldsymbol{\xi})$ does not depend on the choice of the initial function ϕ.

Lemma 3.3 *Let $\hat{a}_n(c, \boldsymbol{\xi}; s, \mathbf{x})$ be the sequence obtained from the recursion (3.4) when $\phi(s)$ is replaced by another nonincreasing function $\hat{\phi}$ with the properties (3.3). Then the limit $\hat{a}$ of $\hat{a}_n$ as $n \to \infty$ satisfies the equation $\hat{a}(c, \boldsymbol{\xi}; \infty) = a(c, \boldsymbol{\xi}; \infty)$. In particular, the property (3.7) holds when a is replaced by $\hat{a}$.*

Proof. Since $\hat{a}_n(c, \boldsymbol{\xi}; -\infty, \mathbf{x})$ satisfies the inequality $\hat{a}_{n+1} \geq Q_{\boldsymbol{\xi}}[\hat{a}_n]$, Hypotheses 2.1.iv and 2.1.vi show that $\hat{a}_n(c, \boldsymbol{\xi}; -\infty, \mathbf{x})$ converges to π_1, uniformly on P. Hence there exists an n_0 such that $\hat{a}_{n_0}(c, \boldsymbol{\xi}; -\infty, \mathbf{x}) > \phi(-\infty)$. Therefore there is an L such that $a_0(c, \boldsymbol{\xi}; s, \mathbf{x}) = \phi(s) \leq \hat{a}_{n_0}(c, \boldsymbol{\xi}; s - L, \mathbf{x})]$. By the Comparison Principle $a_\ell(c, \boldsymbol{\xi}; s, \mathbf{x}) \leq \hat{a}_{n_0+\ell}(c, \boldsymbol{\xi}; s - L, \mathbf{x})$ for all nonnegative integers ℓ. We now let ℓ and then s approach infinity to see that $a(c, \boldsymbol{\xi}; \infty, \mathbf{x}) \leq \hat{a}(c, \boldsymbol{\xi}; \infty, \mathbf{x})$. By reversing the roles of a_n and $\hat{a}_n$ in the above argument, we obtain the opposite inequality, and this establishes the statement of the Lemma.

We note that if we replace s by $s - (n+1)c$ in (3.5), we obtain the recursion

$$\begin{aligned} a_{n+1}(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{y} + s - &(n+1)c, \mathbf{y}) \\ &= \max\{\phi(\boldsymbol{\xi} \cdot \mathbf{y} + s - (n+1)c, \mathbf{y}), Q[a_n(\boldsymbol{\xi} \cdot \mathbf{x} + s - nc, \mathbf{x})](\mathbf{y})\} \\ &\geq Q[a_n(\boldsymbol{\xi} \cdot \mathbf{x} + s - nc, \mathbf{x})](\mathbf{y}). \end{aligned} \tag{3.11}$$

Thus the sequence $a_n(\boldsymbol{\xi} \cdot \mathbf{x} + s - nc, \mathbf{x})$ is a supersolution of the recursion (2.1).

We can use this fact to obtain a lower bound for $c^*(\xi)$. Let $b_n(s, \mathbf{x})$ be the solution of the recursion $b_{n+1}(s, \mathbf{y}) = \tilde{Q}_{\boldsymbol{\xi}}[b_n](s, \mathbf{y})$ with $b_0 = \phi$. We see from Hypothesis 2.1.iv that $b_n(-\infty, \mathbf{x}))$ approaches $\pi_1(\mathbf{x})$. Therefore for every sufficiently large n, $b_n(-\infty, \mathbf{x}) > \phi(-\infty, \mathbf{x})$, and hence there is a translation L such that $b_n(s, \mathbf{x}) \geq \phi(s - L, \mathbf{x})$.

Proposition 3.1 *Let $b_n(s, \mathbf{x})$ satisfy the recursion $b_{n+1} = Q_{\boldsymbol{\xi}}[b_n]$ with $b_0 = \phi$, where ϕ has the properties (3.3). If*

$$b_n(s, \mathbf{x}) \geq \phi(s - L, \mathbf{x}),$$

then

$$c^*(\boldsymbol{\xi}) \geq L/n. \tag{3.12}$$

Proof. Let δ be any small positive number. The Comparison Principle and (3.11) show that $a_n(L/n - \delta, \boldsymbol{\xi}; s - n(L/n - \delta), \mathbf{x}) \geq b_n(s, \mathbf{x}) \geq \phi(s - L, \mathbf{x}) = a_0(L/n - \delta, \boldsymbol{\xi}; s - L, \mathbf{x})$. As in the proof of lemma 3.2, this inequality implies that $a(L/n - \delta, \boldsymbol{\xi}; s, \mathbf{x}) \equiv \pi_1(\mathbf{x})$, so that $L/n - \delta < c^*(\boldsymbol{\xi})$. Since δ is arbitrary, this gives the lower bound (3.12).

In addition to showing that $c^*(\boldsymbol{\xi})$ is always bounded below, this inequality gives a numerical method for finding a lower bound for it from a simulation.

4 The speed limit: proof of Theorem 2.2

We begin with a simple lemma, which is the first statement of Theorem 2.1.

Lemma 4.1 *Suppose that $u_0(\mathbf{x})$ has the properties*

a. *u_0 is continuous and nonnegative;*

b. *$\sup_{\mathbf{x}}[\pi_1(\mathbf{x}) - u_0(\mathbf{x})] > 0$;*

c. There is a constant L such that $u_0(\mathbf{x}) = 0$ when $\boldsymbol{\xi} \cdot x \geq L$.

Then the solution u_n of the recursion (2.1) has the property that for any $c > c^*(\boldsymbol{\xi})$

$$\limsup_{n\to\infty}\left[\sup_{\boldsymbol{\xi}\cdot\mathbf{x}\geq nc}[u_n - \pi_0]\right] \leq 0.$$

Proof. Because of the properties (b) and (c) there is a nonincreasing function $\phi(s, \mathbf{x})$ with the properties (3.3) such that $\phi(\boldsymbol{\xi}\cdot\mathbf{x} - L - 1, \mathbf{x}) \geq u_0(\mathbf{x})$. Let $a_n(c, \boldsymbol{\xi}; s, \mathbf{x})$ be defined by the recursion (3.4). The Comparison Principle and (3.11) show that

$$u_n(\mathbf{x}) \leq a_n(c^*(\boldsymbol{\xi}), \boldsymbol{\xi}; \boldsymbol{\xi}\cdot\mathbf{x} - L - 1 - nc^*(\boldsymbol{\xi}), \mathbf{x}).$$

Because $a_n(s, \mathbf{x})$ is nonincreasing in s,

$$u_n(\mathbf{x}) \leq a_n(c^*(\boldsymbol{\xi}), \boldsymbol{\xi}; n[c - c^*(\boldsymbol{\xi})] - L - 1, \mathbf{x}) \text{ when } \boldsymbol{\xi}\cdot\mathbf{x} \geq nc.$$

We now recall that $c > c^*(\boldsymbol{\xi})$, let n approach infinity, and use the property (3.7) to obtain the statement of the Lemma.

We shall now use this Lemma to prove Theorem 2.2. To prove the first statement, we note that the definition (2.10) implies that if $c > C(\boldsymbol{\eta})$, then there is a unit vector $\boldsymbol{\xi}_0$ such that $\boldsymbol{\xi}_0 \cdot \boldsymbol{\eta} > 0$ and $c^*(\boldsymbol{\xi}_0)/\boldsymbol{\xi}_0 \cdot \boldsymbol{\eta} < c$. We write this as

$$c_0 := c\boldsymbol{\eta}\cdot\boldsymbol{\xi}_0 > c^*(\boldsymbol{\xi}_0),$$

and observe that for $\beta \geq c$ the point $n\beta\boldsymbol{\eta}$ satisfies the inequality $\boldsymbol{\xi}_0 \cdot (n\beta\boldsymbol{\eta}) \geq nc_0$. Thus Lemma 4.1 with $\boldsymbol{\xi} = \boldsymbol{\xi}_0$ and $c = c_0$ gives the inequality (2.11). $C(\boldsymbol{\eta})$ is undefined if and only if there is a $\boldsymbol{\xi}_0$ such that $c^*(\boldsymbol{\xi}_0) < 0$ and $\boldsymbol{\xi}_0 \cdot \boldsymbol{\eta} = 0$. We then obtain (2.12) by noting that $\boldsymbol{\xi}_0 \cdot (\beta\boldsymbol{\eta}) = 0 > c^*(\boldsymbol{\xi}_0)$ and applying Lemma 4.1) with $\boldsymbol{\xi} = \boldsymbol{\xi}_0$ and $c = 0$.

Suppose now that $\mathcal{S}$ is bounded and nonempty. If there were a vector $\mathbf{y} \neq \mathbf{0}$ such that $\boldsymbol{\xi}\cdot\mathbf{y} \leq 0$ for all $\boldsymbol{\xi}$ for which $c^*(\boldsymbol{\xi})$ is finite, then for every point $\mathbf{x}$ of $\mathcal{S}$ the half-line $\mathbf{x} + \alpha\mathbf{y}$ with $\alpha \geq 0$ would also be in $\mathcal{S}$. This would contradict the fact that $\mathcal{S}$ is nonempty and bounded. Consequently, the intersection of the closed bounded sets $\{\mathbf{x} : |\mathbf{x}| = 1, \boldsymbol{\xi}\cdot\mathbf{x} \leq 0\}$ over all $\boldsymbol{\xi}$ with $c^*(\boldsymbol{\xi})$ finite is empty. By Helly's Theorem (the finite intersection property; see, e. g., page 3 of [BF48]) there is a finite set $\boldsymbol{\xi}_1, \cdots, \boldsymbol{\xi}_K$ of unit vectors such that $c^*(\boldsymbol{\xi}_j) < \infty$ and $\max_{1\leq j\leq K} \boldsymbol{\xi}_j \cdot \mathbf{x} > 0$ when $|\mathbf{x}| = 1$. Since $\max_{1\leq j\leq K} \boldsymbol{\xi}_j \cdot \mathbf{x}$ is continuous, it has a positive minimum α on the unit sphere. Thus for all $\mathbf{x}$

$$\max_{1\leq j\leq K}[\boldsymbol{\xi}_j \cdot \mathbf{x}] \geq \alpha|\mathbf{x}|.$$

Therefore for all $\mathbf{x}$ on the closed set

$$A := \{\mathbf{x} : \boldsymbol{\xi}_j \cdot \mathbf{x} \leq c^*(\boldsymbol{\xi}_j) + 1 \text{ for } j = 1, \cdots K\} \tag{4.1}$$

$|\mathbf{x}| \leq \max_{1\leq j\leq K}[c^*(\boldsymbol{\xi}_j)+1]/\alpha$, so that A is bounded. By definition, the complement $c[\mathcal{S}']$ is closed, and its intersection with $\mathcal{S}$ is empty. Hence the intersection of the closed subsets $A \cap c[\mathcal{S}'] \cap \{\mathbf{x} : \boldsymbol{\xi}\cdot\mathbf{x} \leq c^*(\boldsymbol{\xi})+\delta\}$ of A over all $0<\delta<1$ and all unit vectors $\boldsymbol{\xi}$ is empty. Helly's Theorem shows that there are a $\delta \in (0,1)$ and a finite collection of unit vectors $\boldsymbol{\xi}_{K+1}, \boldsymbol{\xi}_{K+2}, \cdots \boldsymbol{\xi}_L$, such that the intersection of the sets $c[\mathcal{S}'] \cap \{\mathbf{x} : \boldsymbol{\xi}_j \cdot \mathbf{x} \leq c^*(\boldsymbol{\xi}_j)+\delta,\ j = 1, \cdots, L\}$ is already empty. (Note that this intersection is automatically a subset of A.) If $\mathbf{x} \notin n\mathcal{S}'$, then $n^{-1}\mathbf{x} \in c[\mathcal{S}']$, and hence one of these inequalities must be violated by $n^{-1}\mathbf{x}$. That is, $\mathbf{x} \notin n\mathcal{S}'$ implies that

$$\boldsymbol{\xi}_j \cdot \mathbf{x} > n[c^*(\boldsymbol{\xi}_j)+\delta] \text{ for some } j \leq L. \tag{4.2}$$

Lemma 4.1 with $c = c^*(\boldsymbol{\xi}_j)+\delta$ shows that for any positive ϵ there is an integer $n_{j,\epsilon}$ such that (4.2) implies that $u_n - \pi_0 \leq \epsilon$ when $n \geq n_{j,\epsilon}$. If we define $n_\epsilon := \max_{1\leq j\leq K} n_{j,\epsilon}$, we see that for $n \geq n_\epsilon$, $u_n - \pi_0 \leq \epsilon$ on the complement of $n\mathcal{S}'$. Since ϵ is arbitrary, this is the second statement (2.13) of Theorem 2.2, and the Theorem is proved.

5 Upward convergence: Proof of Theorem 2.3

In order to introduce some of the ideas in the proof of Theorem 2.3, we start with a lemma which is the second statement of Theorem 2.1.

Lemma 5.1 *If $0 \leq u_0(\mathbf{x}) \leq \pi_1(\mathbf{x})$ and $u_0(\mathbf{x})$ is continuous, and if there is a positive constant K such that*

$$\inf_{\boldsymbol{\xi}\cdot\mathbf{x}\leq -K}[u_0(\mathbf{x}) - \pi_0(\mathbf{x})] > 0,$$

then for any $c < c^*(\boldsymbol{\xi})$ the solution u_n of the recursion (2.1) has the property

$$\lim_{n\to\infty}\left\{\sup_{\boldsymbol{\xi}\cdot\mathbf{x}\leq nc}[\pi_1(\mathbf{x}) - u_n(\mathbf{x})]\right\} = 0. \tag{5.1}$$

Proof. By the above assumption, there is a continuous $\mathcal{L}$-periodic function $\alpha_0(\mathbf{x})$ such that

$$u_0(\mathbf{x}) \geq \alpha_0(\mathbf{x}) > \pi_0(\mathbf{x}) \text{ when } \boldsymbol{\xi}\cdot\mathbf{x} \leq -K.$$

We choose a $\phi(s,\mathbf{x})$ with the properties (3.3) and the additional properties

$$\begin{aligned} &\phi(s,\mathbf{x}) = \alpha_0(\mathbf{x}) \text{ when } s \leq -K, \text{ and} \\ &\phi(\boldsymbol{\xi}\cdot\mathbf{x},\mathbf{x}) \leq u_0(\mathbf{x}). \end{aligned} \tag{5.2}$$

We define the sequence $a_n(c,\boldsymbol{\xi}; s,\mathbf{x})$ by the recursion (3.4) with this ϕ. Because $c < c^*(\boldsymbol{\xi})$, Lemma 3.2 shows that there is an integer n_0 such that

$$a_{n_0}(c,\boldsymbol{\xi}; 1,\mathbf{x}) > \alpha_0(\mathbf{x}). \tag{5.3}$$

Moreover, since α_n increases to π_1 uniformly, there is for any positive number δ an integer n_δ such that

$$\pi_1(\mathbf{x}) - \alpha_{n_\delta}(\mathbf{x}) < \delta. \tag{5.4}$$

We suppose for the moment that Q has the additional property

$$u < \pi_1 \text{ implies that } Q[u] < \pi_1. \tag{5.5}$$

Since $\alpha_0 < \pi_1$, this property implies that

$$\alpha_{n_0}(\mathbf{x}) < \pi_1(\mathbf{x}). \tag{5.6}$$

We define the sequence of $\mathcal{L}$-periodic functions $\beta_n(\mathbf{x})$ by the recursion

$$\beta_{n+1}(\mathbf{y}) = Q[\beta_n(\cdot)](\mathbf{y})$$

with $\beta_0(\mathbf{x}) = \alpha_0(\mathbf{x})$. Hypotheses 2.1.iv, 2.1.v, and 2.1.vi show that $\beta_n(\mathbf{x})$ converges to $\pi_1(\mathbf{x})$ uniformly. Then there is an integer $n_1 > n_0$ such that

$$\beta_{n_1}(\mathbf{x}) > \alpha_{n_0}(\mathbf{x}). \tag{5.7}$$

We shall assume without loss of generality that

$$n_\delta > n_1.$$

In order to prove the Lemma, we need to obtain a lower bound for u_n. We first choose a real-valued continuous nonincreasing cutoff function $\zeta(s)$ with the properties

$$\zeta(s) = \begin{cases} 1 & \text{for } s \leq \frac{1}{2} \\ 0 & \text{for } s \geq 1. \end{cases} \tag{5.8}$$

For each positive integer k, we define the approximating operator

$$Q_k[u](\mathbf{y}) := Q[\zeta(|\mathbf{x}-\mathbf{y}|/k)u(\mathbf{x})](\mathbf{y}). \tag{5.9}$$

(Recall the convention in Footnote 2.) This operator is again order preserving and periodic with respect to $\mathcal{L}$. It has the advantage that the value of $Q_k[u]$ at $\mathbf{y}$ only depends on the values of $u(\mathbf{x})$ on the ball $|\mathbf{x}-\mathbf{y}| \leq k$. We also define the new operator $\tilde{Q}_{k,\boldsymbol{\xi}}$ by replacing Q by Q_k in the definition (3.1) of $\tilde{Q}_{\boldsymbol{\xi}}$:

$$\tilde{Q}_{k,\boldsymbol{\xi}}[v](s,\mathbf{y}) := Q[\zeta(|\mathbf{x}-\mathbf{y}|/k)v(\boldsymbol{\xi}\cdot(\mathbf{x}-\mathbf{y})+s,\mathbf{x})](\mathbf{y}).$$

We define the sequence $\alpha_n^{(k)}$ by the recursion

$$\alpha_{n+1}^{(k)}(\mathbf{y}) = \max\{\alpha_0(\mathbf{y}), Q_k[\alpha_n^{(k)}(\cdot)](\mathbf{y})$$

with $\alpha_0^{(k)} = \alpha_0$. We also define the sequence $a_n^{(k)}(c, \boldsymbol{\xi}; s, \mathbf{x})$ by the recursion (3.4) with the operator $\tilde{Q}_{\boldsymbol{\xi}}$ replaced by $\tilde{Q}_{k,\boldsymbol{\xi}}$, and $a_0^{(k)}(c, \boldsymbol{\xi}; s, \mathbf{x}) = \phi(s, \mathbf{x})$. Because $\tilde{Q}_{k,\boldsymbol{\xi}}[w](s, \mathbf{x})$ depends only on the values of $w(\sigma, \mathbf{x})$ with $|\sigma - s| \leq k$, we find from (5.2) that

$$a_n^{(k)}(c, \boldsymbol{\xi}; s, \mathbf{x}) = \begin{cases} \alpha_n^{(k)}(\mathbf{x}) & \text{for } s \leq -K - n(k+c) \\ 0 & \text{for } s \geq n(k-c). \end{cases} \tag{5.10}$$

Finally, we define the sequence $b_n^{(k)}(s, \mathbf{x})$ as the solution of the recursion

$$b_{n+1}^{(k)}(\boldsymbol{\xi} \cdot \mathbf{y} + s, \mathbf{y}) = Q_k[b_n^{(k)}(\boldsymbol{\xi} \cdot \mathbf{x} + s, \mathbf{x})](\mathbf{y})$$

with $b_0^{(k)} = \phi$. (Note the absence of a translation by $-c$ on the right.) By Hypothesis 2.1.v $Q_k[u]$ increases to $Q[u]$ for any u in $\mathcal{M}$. By using this fact repeatedly and using the inequalities (5.3), (5.4), and (5.7), we choose a k_0 such that

$$a_{n_0}^{(k_0)}(c, \boldsymbol{\xi}; 1, \mathbf{x}) > \alpha_0(\mathbf{x}), \tag{5.11}$$

$$\pi_1 - \alpha_n^{(k_0)}(-\infty, \mathbf{x}) < \delta \text{ for } n \geq n_\delta, \tag{5.12}$$

and

$$b_{n_1}^{(k_0)}(-\infty, \mathbf{x}) > \alpha_{n_0}(\mathbf{x}) \geq \alpha_{n_0}^{(k_0)}(\mathbf{x}). \tag{5.13}$$

The inequality (5.13) and the fact that $a_n(c, \boldsymbol{\xi}; s, \mathbf{x})$ vanishes for sufficiently large s by (5.10) show that there is a constant L_1 such that

$$b_{n_1}^{(k_0)}(\boldsymbol{\xi} \cdot \mathbf{x} + s, \mathbf{x}) \geq a_{n_0}^{(k_0}(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{x} + s - n_0 c + L_1, \mathbf{x}).$$

Because (5.11) implies that $a_n^{(k_0)}(c, \boldsymbol{\xi}; s, \mathbf{x}) > \phi(s, \mathbf{x})$ when $n \geq n_0$, the maximization can be dropped from the recursion for $a_n^{(k_0)}$. The Comparison Principle and (3.11) with Q replaced by Q_{k_0} then show that

$$b_n(\boldsymbol{\xi} \cdot \mathbf{x} + s, \mathbf{x}) \geq a_{n-n_1+n_0}^{(k_0)}(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{x} + s - nc + L_1, \mathbf{x}) \text{ when } n \geq n_1.$$

In particular,

$$b_n(nc, \mathbf{x}) \geq a_{n-n_1+n_0}^{(k_0)}(c, \boldsymbol{\xi}; L_1, \mathbf{x}) \geq a_{n-n_1+n_0}^{(k_0)}(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot \mathbf{x} + \rho + L_1, \mathbf{x}).$$

We see from Lemma 3.2, (5.11), and Hypothesis 2.1.vi that the last function on the right approaches the limit of the sequence $\alpha_n^{(k_0)}(\mathbf{x})$, uniformly on $\bar{P}$. By (5.12) this limit is larger than $\pi_1(\mathbf{x}) - \delta$. Thus we conclude from (5.14) that for all sufficiently large n

$$\pi_1(\mathbf{x}) - b_n(nc, \mathbf{x}) < \delta.$$

We recall that ϕ was chosen so that $u_0(\mathbf{x}) \geq \phi(\boldsymbol{\xi} \cdot \mathbf{x}, \mathbf{x}) = b_0(\boldsymbol{\xi} \cdot \mathbf{x}, \mathbf{x})$. Since $u_{n+1} = Q[u_n] \geq Q_{k_0}[u_n]$, the Comparison Principle shows that

$$u_n(\mathbf{x}) \geq b_n(\boldsymbol{\xi} \cdot \mathbf{x}, \mathbf{x})$$

for all n. Because $b_n(s, \mathbf{x})$ is nonincreasing in s, we see that

$$\sup_{\boldsymbol{\xi}\cdot\mathbf{x}\leq nc} \pi_1(\mathbf{x}) - u_n(\mathbf{x})] \leq \pi_1(\mathbf{x}) - b_n(nc, \mathbf{x}) < \delta \tag{5.14}$$

for all sufficiently large n. Since δ can be taken arbitrarily small, this proves the statement (5.1) of the Lemma under the additional assumption (5.5).

If Q does not have the property (5.5), we replace it by the operator

$$\hat{Q}[u](\mathbf{x}) := \min\{Q[u](\mathbf{x}), (1-\gamma)Q[u](\mathbf{x}) + \gamma u(\mathbf{x})\}, \tag{5.15}$$

where γ is a small positive constant to be determined. This operator is order preserving and periodic. It is easily verified that $\hat{Q}$ has the property (5.5), and that it has exactly the same equilibria as Q. Moreover, $\hat{Q}[u]$ approaches $Q[u]$ from below as γ goes to zero. In particular, we can and shall choose γ so small that if the sequence $\hat{a}_n$ is defined by the recursion (3.4) with Q replaced by $\hat{Q}$ and $\hat{a}_0 = \phi$, then $\hat{a}_{n_0}(c, \boldsymbol{\xi}; 1, \mathbf{x}) > \alpha_0(\mathbf{x})$. The above proof then shows that the solution $\hat{u}_n$ of the recursion (2.1) with Q replaced by $\hat{Q}$ and $\hat{u}_0 = u_0$ has the property (5.1). The Comparison Principle and the inequality $u_{n+1} = Q[u_n] \geq \hat{Q}[u_n]$, imply that $u_n \geq \hat{u}_n$. Since $u_n \leq \pi_1$, the property (5.1) for $\hat{u}_n$ implies the same property for u_n, and this establishes the Lemma.

We remark that Lemmas 4.1 and 5.1 prove Theorem 2.1.

Proof of Theorem 2.3. The above proof needs considerable adaptation to produce a spreading result in all directions $\boldsymbol{\xi}$. We begin by examining the geometric properties of the sets $\mathcal{S}$ and $\mathcal{S}''$. Let $\mathbf{x}_0$ be a point of $\mathcal{S}''$. If we introduce the new coordinates $\mathbf{x}' := \mathbf{x} - \mathbf{x}_0$, we find that the habitat $\mathcal{H}$ is replaced by $T_{\mathbf{x}_0}[\mathcal{H}]$ and the set P is replaced by $T_{\mathbf{x}_0}[P]$. Moreover, the operator Q is replaced by $T_{\mathbf{x}_0}QT_{-\mathbf{x}_0}$. It is easily seen that the Hypotheses 2.1 are satisfied by this new operator, and that $c^*(\boldsymbol{\xi})$ is replaced by $c^*(\boldsymbol{\xi})+\boldsymbol{\xi}\cdot\mathbf{x}_0$. That is, the coordinates $\mathbf{x}'$ move with the velocity $-\mathbf{x}_0$. Thus we shall assume without loss of generality that the origin $\mathbf{0}$ is in $\mathcal{S}''$, and hence that it is an interior point of $\mathcal{S}$. Then $c^*(\boldsymbol{\xi}) > 0$ for all $\boldsymbol{\xi}$.

We observe that the Theorem is strengthened if $\mathcal{S}''$ is replaced by a larger set. A result in §27 of [BF48] shows that $\mathcal{S}''$ is contained in a closed bounded subset of the interior of $\mathcal{S}$, of which the origin is an interior point, and which has a smooth boundary with a uniformly positive curvature tensor. We shall replace $\mathcal{S}''$ by this larger set, which we again call $\mathcal{S}''$. If $\mathbf{x}$ is any point other than the origin, let $[1/D(\mathbf{x})]\mathbf{x}$ be the unique point of the ray from the origin through $\mathbf{x}$ which lies on the boundary of $\mathcal{S}''$. Then the set $\mathcal{S}''$ is characterized by the fact that $D(\mathbf{x}) \leq 1$ there. In particular, the unit outward normal vector $\boldsymbol{\tau}(\mathbf{x})$ to the boundary at $[1/D(\mathbf{x})]\mathbf{x}$ is given by

$$\boldsymbol{\tau}(\mathbf{x}) = |\nabla D(\mathbf{x})|^{-1}\nabla D(\mathbf{x}). \tag{5.16}$$

Because the origin is interior to $\mathcal{S}''$, this set contains a ball of some positive radius r centered at the origin. Because $\mathcal{S}''$ is bounded, it is contained in a ball of some radius R

centered at the origin. The support function of $\mathcal{S}''$ is defined as

$$S(\boldsymbol{\xi}) = \max_{\mathbf{x}\in\mathcal{S}''} \boldsymbol{\xi}\cdot\mathbf{x}. \tag{5.17}$$

It satisfies the inequalities

$$r \le S(\boldsymbol{\xi}) \le R. \tag{5.18}$$

Because the closed set with smooth boundary $\mathcal{S}''$ lies in the interior of $\mathcal{S}$, there is a positive ϵ such that

$$\max_{|\boldsymbol{\xi}|=1}[(1+\epsilon)S(\boldsymbol{\xi})/c^*(\boldsymbol{\xi})] < 1. \tag{5.19}$$

It is easily seen that the maximum in (5.17) is attained when $\mathbf{x}$ is a boundary point and $\boldsymbol{\tau}(\mathbf{x}) = \boldsymbol{\xi}$. Since D is homogeneous of degree 1, we have the equation $\mathbf{x}\cdot\nabla D(\mathbf{x}) = D(\mathbf{x}) = 1$ at a boundary point. Thus we see from (5.16) that $S(\boldsymbol{\tau}(\mathbf{x})) = |\nabla D(\mathbf{x})|^{-1}$, so that

$$\boldsymbol{\tau}(\mathbf{x}) = S(\boldsymbol{\tau}(\mathbf{x}))\nabla D(\mathbf{x}). \tag{5.20}$$

As in the proof of Lemma 5.1, we choose a continuous $\mathcal{L}$-periodic function $\alpha_0(\mathbf{x})$ with $\pi_0 < \alpha_0 < \pi_1$, and a continuous function $\phi(s,\mathbf{x})$ with the properties (3.3) and the additional property

$$\phi(s,\mathbf{x}) = \alpha_0(\mathbf{x}) \text{ for } s \le -1. \tag{5.21}$$

For each unit vector $\boldsymbol{\xi}$ define the sequence $a_n((1+\epsilon)S(\boldsymbol{\xi}), \boldsymbol{\xi}; s, \mathbf{x})$ by the recursion (3.4) with $c = (1+\epsilon)S(\boldsymbol{\xi})$ and $a_0 = \phi$. As before, this sequence is nondecreasing in n. Because $c < c^*(\boldsymbol{\xi})$, a_n converges to π_1. In particular, we see that for each $\boldsymbol{\xi}$ there is an integer n_0 such that

$$a_{n_0}((1+\epsilon)S(\boldsymbol{\xi}), \boldsymbol{\xi}; 1, \mathbf{x}) > \alpha_0(\mathbf{x}). \tag{5.22}$$

Because the left-hand side is continuous for $\boldsymbol{\xi}$ on the unit sphere, the n_0 required for this inequality is bounded, and we choose a fixed n_0 so that the inequality holds for all $\boldsymbol{\xi}$.

We define the sequence of $\mathcal{L}$-periodic functions $\alpha_n(\mathbf{x})$ by the recursion $\alpha_{n+1}(\mathbf{x}) = \max\{\alpha_0(\mathbf{x}), Q[\alpha_n](\mathbf{x})\}$, so that $a_n((1+\epsilon)S(\boldsymbol{\xi}), \boldsymbol{\xi}; -\infty, \mathbf{x}) = \alpha_n(\mathbf{x})$. We choose an arbitrary positive constant δ, and again see that there is an integer n_δ for which the inequality (5.4) is satisfied for all unit vectors $\boldsymbol{\xi}$.

As before, we suppose for the moment that Q has the property (5.5). Then $\alpha_{n_0}(\mathbf{x}) < \pi_1(\mathbf{x})$, and the fact that each $a_n((1+\epsilon)S(\boldsymbol{\xi}), \boldsymbol{\xi}; s, \mathbf{x})$ increases to π_1 implies that there is an index m, again independent of $\boldsymbol{\xi}$, such that

$$a_m((1+\epsilon)S(\boldsymbol{\xi}), \boldsymbol{\xi}; 1, \mathbf{x}) > \alpha_{n_0}(\mathbf{x}). \tag{5.23}$$

As above, we choose a real-valued continuous nonincreasing cutoff function $\zeta(s)$ with the properties (5.8), and define the operators Q_k by (5.9). We define the sequence $\alpha_n^{(k)}$ by the recursion

$$\alpha_{n+1}^{(k)}(\mathbf{y}) = \max\{\alpha_0(\mathbf{y}), Q[\zeta(|\mathbf{x}-\mathbf{y}|/k)\alpha_n^{(k)}(\mathbf{x})](\mathbf{y})\}$$

with $\alpha_0^{(k)} = \alpha_0$. (Recall th convention of Footnote 2.) We also define the sequence $a_n^{(k)}(c,\boldsymbol{\xi};s,\mathbf{x})$ by the recursion (3.4) with the operator $\tilde{Q}_{\boldsymbol{\xi}}$ replaced by $\tilde{Q}_{k,\boldsymbol{\xi}}$, and $a_0^{(k)}(c,\boldsymbol{\xi};s,\mathbf{x}) = \phi(s,\mathbf{x})$. Because $\tilde{Q}_{k,\boldsymbol{\xi}}[v](s,\mathbf{x})$ depends only on the values of $v(\sigma,\mathbf{x})$ with $|\sigma - s| \le k$, we find the properties (5.10) with $K = 1$.

By Hypothesis 2.1.iv and Dini's theorem $a_n^{(k)}((1+\epsilon)S(\boldsymbol{\xi}),\boldsymbol{\xi};1,\mathbf{x})$ increases to $a_n((1+\epsilon)S(\boldsymbol{\xi}),\boldsymbol{\xi};1,\mathbf{x})$ as k goes to infinity, uniformly in $\mathbf{x}$ and $\boldsymbol{\xi}$. We see from (5.22), (5.23), and (5.4) that we can choose a k_0 independent of $\boldsymbol{\xi}$ so that

$$a_{n_0}^{(k_0)}((1+\epsilon)S(\boldsymbol{\xi}),\boldsymbol{\xi};1,\mathbf{x}) > \alpha_0(\mathbf{x}),$$

$$a_m^{(k_0)}((1+\epsilon)S(\boldsymbol{\xi}),\boldsymbol{\xi};1,\mathbf{x}) > \alpha_{n_0}^{(k_0)}(\mathbf{x}),$$

and the inequality (5.12) is satisfied. The first of these states that for $n \ge n_0$, $a_n^{(k_0)} > \phi$, so that

$$a_{n+1}^{(k_0)}((1+\epsilon)S(\boldsymbol{\xi}),\boldsymbol{\xi};s,\mathbf{x}) = \tilde{Q}_{k_0,\boldsymbol{\xi}}[a_n^{(k_0)}](s+(1+\epsilon)S(\boldsymbol{\xi}),\mathbf{x})) \text{ for } n \ge n_0. \tag{5.24}$$

Lemma 3.2 shows that $a_n^{(k_0)}$ converges to $\lim_{n\to\infty} \alpha_n^{(k_0)}$. The second inequality shows that this limit is larger than $\alpha_{n_0}^{(k_0)}$. Hence, there is an $n_1 > n_0$, independent of $\boldsymbol{\xi}$, so that

$$a_{n_1}^{(k_0)}((1+\epsilon)S(\boldsymbol{\xi}),\boldsymbol{\xi};(R/r)n_0k_0,\mathbf{x})) \ge \alpha_{n_0}^{(k_0)}(\mathbf{x}). \tag{5.25}$$

We now combine the functions $a^{(k_0)}((1+\epsilon)S(\boldsymbol{\xi});s,\mathbf{x})$ into a function of $\mathbf{x}$ by setting $\boldsymbol{\xi} = \boldsymbol{\tau}(\mathbf{x})$ and letting s depend on $\mathbf{x}$. More specifically, we form the function

$$\begin{aligned} e_\ell(\mathbf{x}) := a_{n_1}^{(k_0)}((1+\epsilon)&S(\boldsymbol{\tau}(\mathbf{x})),\boldsymbol{\tau}(\mathbf{x}); \\ &\boldsymbol{\tau}(\mathbf{x})\cdot\mathbf{x} - [A + \ell(1+\tfrac{1}{2}\epsilon)(n_1-n_0)]S(\boldsymbol{\tau}(\mathbf{x})),\mathbf{x}), \end{aligned} \tag{5.26}$$

where A is a constant. We shall make use of the following Lemma, whose proof will be given in the Appendix.

Lemma 5.2 *Let μ be a bound for the square root of the sum of the squares of the third partial derivatives of $D(\mathbf{x})$ for $\mathbf{x}$ on the unit sphere. Then if*

$$A \ge r^{-1}\left\{2k_0(n_1-n_0) - (R/r)k_0n_0 + \frac{\mu k_0^2(n_1-n_0)^2}{\epsilon(n_1-n_0)+2(1+\epsilon)n_0}\right\}, \tag{5.27}$$

the sequence e_ℓ satisfies the inequality

$$e_{\ell+1} \le Q[e_\ell]. \tag{5.28}$$

In order to apply this Lemma, we first choose any small positive constant σ. By Hypothesis 2.1.iv, the solution u_n of the recursion $u_{n+1} = Q[u_n]$ with $u_0 = \pi_0 + \sigma$ converges to π_1. In particular, there is an integer M_σ such that $u_{M_\sigma} > \alpha_{n_1}^{(k_0)}$. If $\zeta(s)$ is again a scalar-valued cut-off function with the properties (5.8), the family of functions $\zeta(|\mathbf{x}|/\gamma)[\pi_0+\sigma]$ converges to $\pi_0+\sigma$ uniformly on every bounded set as γ approaches infinity. (5.10) shows that e_0 vanishes outside a bounded set. By applying Hypothesis 2.1.v repeatedly, we see that if $w_n^{(\gamma)}$ is the solution of (2.1) with $w_0^{(\gamma)}(\mathbf{x}) = \zeta(|\mathbf{x}|/\gamma)[\pi_0+\sigma]$, there is a constant R_σ such that

$$w_{M_\sigma}^{(R_\sigma)} \geq \alpha_{n_1}^{(k_0)} \text{ on the bounded set where } e_0 > 0.$$

Since $e_0 \leq \alpha_{n_1}^{(k_0)}$, this implies that $w_{M_\sigma}^{(R_\sigma)} \geq e_0$. Because $w_0^{(R_\sigma)} \leq \pi_0 + \sigma$ and vanishes for $|\mathbf{x}| \geq R_\sigma$, the Comparison Principle shows that if u_n is a solution of the recursion (2.1) and $u_0 \geq \pi_0 + \sigma$ for $|\mathbf{x}| \leq R_\sigma$, then $u_{M_\sigma} \geq e_0$. Because of (5.28), another application of the Comparison Principle shows that

$$u_{M_\sigma+\ell(n_1-n_0)} \geq e_\ell$$

for all ℓ.

We see from (5.10) with $K=1$ that

$$a_{n_1}^{(k_0)}(s,\mathbf{x}) = \alpha_{n_1}^{(k_0)}(\mathbf{x}) \text{ for } s \leq -1 - n_1[k_0 + (1+\epsilon)S(\boldsymbol{\tau}(\mathbf{x})).$$

The definition (5.26) of e_ℓ then shows that

$$e_\ell(\mathbf{x}) = \alpha_{n_1}^{(k_0)} \text{ when } \boldsymbol{\tau}(\mathbf{x})\cdot\mathbf{x} - [A+\ell(1+\tfrac{1}{2}\epsilon)(n_1-n_0)]S(\boldsymbol{\tau}(\mathbf{x})) \leq -1-n_1[k_0+(1+\epsilon)S(\boldsymbol{\tau}(\mathbf{x}))].$$

The identity (5.20) and the homogeneity of D show that $\boldsymbol{\tau}(\mathbf{x})\cdot\mathbf{x} = D(\mathbf{x})\mathcal{S}(\boldsymbol{\tau}(\mathbf{x}))$. Because $\mathcal{S}(\boldsymbol{\xi}) \geq r$, we obtain the weaker statement

$$e_\ell(\mathbf{x}) = \alpha_{n_1}^{(k_0)} \text{ when } D(\mathbf{x}) \leq A + \ell(1+\tfrac{1}{2}\epsilon)(n_1-n_0) - r^{-1}(1+n_1k_0) - n_1(1+\epsilon). \quad (5.29)$$

Division shows that for any $n \geq M_\sigma + n_\delta - n_1$ there is a unique integer ℓ such that

$$0 < n - (M_\sigma + n_\delta - n_1) - \ell(n_1-n_0) \leq n_1 - n_0 \quad (5.30)$$

The Comparison Principle shows that $Q_{k^0}^{n-M_\sigma-\ell(n_1-n_0)}[e_\ell]$ is a lower bound for u_n. If $\mathbf{y}$ is a point with the property that $e_\ell = \alpha_{n_1}^{(k_0)}$ throughout the ball of radius $k_0(n_\delta - n_0)$ centered at $\mathbf{y}$, then $u_n(\mathbf{y}) \geq \alpha_{n_\delta} > \pi_1(\mathbf{y}) - \delta$. Suppose that $\mathbf{y}$ lies in the set $n\mathcal{S}''$. The set of points at distance at most $k_0(n_\delta - n_0)$ from a point of $n\mathcal{S}''$ is a convex set with the support function $nS(\boldsymbol{\xi}) + k_0(n_\delta - n_0)$. Because $S(\boldsymbol{\xi}) \geq r$, this set is contained in the set with the support function $[n + r^{-1}k_0(n_\delta - n_0)]S(\boldsymbol{\xi})$. Therefore if $e_\ell = \alpha_{n_1}^{(k_0)}$ on this set, then $u_n > \pi_1 - \delta$ on $n\mathcal{S}''$. The inequality (5.30) shows that this set is contained in the set $[\ell(n_1-n_0) + M_\sigma + n_\delta - n_0 + r^{-1}k_0(n_\delta - n_0)]\mathcal{S}''$.

We have shown that if $e_\ell = \alpha_{n_1}^{(k_0)}$ for every point with

$$D(x) \leq \ell(n_1-n_0) + M_\sigma + n_\delta - n_0 + r^{-1}k_0(n_\delta - n_0),$$

then $u_n > \pi_1 - \delta$ on $n\mathcal{S}''$. Because the coefficient of ℓ in this inequality is smaller than that in the statement (5.29), we see that the conclusion holds for all sufficiently large ℓ. Since the definition (5.30) of ℓ shows that large n implies large ℓ, we have shown that $\inf_{\mathbf{x}\in n\mathcal{S}''}[\pi_1(\mathbf{x}) - u_n(\mathbf{x})] < \delta$ for all sufficiently large n. Since δ is arbitrary, this proves the first statement (2.14) of Theorem 2.3 under the additional hypothesis (5.5).

If this hypothesis is not valid, we proceed exactly as in the last paragraph of the proof of Lemma 5.1 by defining the auxiliary operator $\hat{Q}$ by (5.15) with a sufficiently small γ and first proving (2.14) for the sequence $\hat{u}_n$ obtained from the recursion (2.1) with Q replaced by $\hat{Q}$ and $\hat{u}_0 = u_0$. Since $\hat{u}_n \le u_n \le \pi_1$, (2.14) follows, so that the first statement of the Theorem is proved in all cases.

We observe that if $-C(-\boldsymbol{\eta}) < c < C(\boldsymbol{\eta})$, then $c\boldsymbol{\eta}$ is an interior point of $\mathcal{S}$. If we choose $\mathcal{S}''$ so that it contains this point, then $nc\boldsymbol{\eta}$ lies in $n\mathcal{S}''$, so that (2.14) implies the last statement of the Theorem. This finishes the proof of Theorem 2.3.

6 Bounds for the spreading speed from linear problems

In this section we shall show how to obtain bounds for the spreading speed $c^*(\boldsymbol{\xi})$ in terms of the properties of some linear operators, and, in some cases, to obtain the exact value of the spreading speed. We shall also give some examples to show what is involved in finding these bounds.

The proofs of Theorems 2.4 and 2.5 will be based on two lemmas.

Lemma 6.1 *Suppose that the operator Q satisfies the hypotheses 2.1, and that the operator $\hat{Q}$ satisfies the same hypotheses with π_0 and π_1 replaced by the $\mathcal{L}$-periodic functions $\hat{\pi}_0$ and $\hat{\pi}_1$. Assume that*

$$0 \le \hat{\pi}_0 \le \pi_0 < \hat{\pi}_1 \le \pi_1,$$

and that

$$\hat{Q}[u] \le Q[u] \text{ for all } u \text{ with } 0 \le u \le \hat{\pi}_1.$$

Then for each unit vector $\boldsymbol{\xi}$ the spreading speed $\hat{c}^*(\boldsymbol{\xi})$ of the recursion (2.1) with Q replaced by $\hat{Q}$ satisfies the inequality

$$\hat{c}^*(\boldsymbol{\xi}) \le c^*(\boldsymbol{\xi}).$$

Proof. Choose a function $\phi(s, \mathbf{x})$ which is uniformly continuous in both variables, $\mathcal{L}$-periodic in $\mathbf{x}$, and nonincreasing in s, and for which $\pi_0(\mathbf{x}) < \phi(-\infty, \mathbf{x}) < \hat{\pi}_1(\mathbf{x})$. Construct the sequence a_n defined by the recursion (3.4) and the sequence $\hat{a}_n$ defined by replacing Q by $\hat{Q}$ in this recursion, with $a_0 = \hat{a}_0 = \phi$. Then $\hat{a}_n(c, \boldsymbol{\xi}; s, \mathbf{x}) \le \hat{\pi}_1(\mathbf{x})$. If $\hat{a}_n(c, \boldsymbol{\xi}; s, \mathbf{x}) \le a_n(c, \boldsymbol{\xi}; s, \mathbf{x})$, then

$$\begin{aligned} \hat{a}_{n+1}(s, \mathbf{y}) = \max\{\phi(s, \mathbf{y}), \{\tilde{\hat{Q}}\}_{\boldsymbol{\xi}}[\hat{a}_n](s + c, \mathbf{y}\} \le \max\{\phi(s, \mathbf{y}), \tilde{Q}_{\boldsymbol{\xi}}[\hat{a}_n](s + c, \mathbf{y})\} \\ \le \max\{\phi(s, \mathbf{y}), \tilde{Q}_{\boldsymbol{\xi}}[a_n](s + c, \mathbf{y})\} = a_{n+1}(s, \mathbf{y}). \end{aligned}$$

Since $\hat{a}_0 = a_0$, induction shows that $\hat{a}_n \le a_n$ for all n, and hence that the limit functions satisfy $\hat{a}(c, \boldsymbol{\xi}; s, \mathbf{x}) \le a(c, \boldsymbol{\xi}; s, \mathbf{x})$. Since by definition $a(c^*(\boldsymbol{\xi}), \boldsymbol{\xi}; \infty) \le \pi_0$, it follows that $\hat{a}(c^*(\boldsymbol{\xi}), \boldsymbol{\xi}; \infty) \le \pi_0 < \hat{\pi}_1$. Thus the property (3.7) of $\hat{c}^*$ implies the statement of the Lemma.

Lemma 6.2 *Let L be a linear operator on the continuous functions on $\mathcal{H}$ with the following properties:*

1. *L is periodic with respect to $\mathcal{L}$, and $L[e^{\mu|\mathbf{x}|}]$ is defined for all real μ.*
2. *L is strongly order preserving in the sense that if u is nonnegative and not identically zero, then $L[u]$ is strictly positive;*
3. *There is a strictly positive $\mathcal{L}$-periodic function $r(\mathbf{x})$ with the property that $L[r] > r$, and the truncated operator*

$$Q^{[L,r]}[u](\mathbf{x}) := \min\{L[u](\mathbf{x}), r(\mathbf{x})\}$$

satisfies the hypotheses 2.1.

Let $\lambda(\mu\boldsymbol{\xi})$ be the principal eigenvalue of the operator $L_{\mu\boldsymbol{\xi}}$ defined in (2.15) and restricted to $\mathcal{L}$-periodic functions.

Then the spreading speed $\bar{c}(\boldsymbol{\xi})$ of $Q^{[L,r]}$ in the direction $\boldsymbol{\xi}$ is given by the formula

$$\bar{c}(\boldsymbol{\xi}) = \inf_{\mu > 0} \left\{ \frac{1}{\mu} \ln \lambda(\mu\boldsymbol{\xi}) \right\}. \tag{6.1}$$

Moreover, the ray speed $C(\boldsymbol{\eta})$ of $Q^{L,r}$ in the direction of the unit vector $\boldsymbol{\eta}$ is given by the formula

$$C(\boldsymbol{\eta}) = \inf_{\substack{\boldsymbol{\zeta} \in R^d \\ \boldsymbol{\eta} \cdot \boldsymbol{\zeta} > 0}} \left\{ \frac{\ln \lambda(\boldsymbol{\zeta})}{\boldsymbol{\eta} \cdot \boldsymbol{\zeta}} \right\}. \tag{6.2}$$

Proof. Because for each fixed $\mathbf{y}$ the number $L[u](\mathbf{y})$ is a nonnegative bounded linear functional on the bounded continuous functions, $L[u]$ can be written in the form

$$L[u](\mathbf{y})) = \int_{\mathcal{H}} u(\mathbf{x}) m(\mathbf{y}; \mathbf{x}, d\mathbf{x}),$$

where, for each $\mathbf{y} \in \mathcal{H}$, $m(\mathbf{y}; \mathbf{x}, d\mathbf{x})$ is a bounded nonnegative measure in $\mathbf{x}$. (See, e.g., Theorem 2 of Section IV.6.2 of [DS58].) Because L takes continuous functions into continuous functions, m varies continuously in $\mathbf{y}$ in the sense of total variations of measures. The $\mathcal{L}$-periodicity of L is equivalent to the condition

$$m(\mathbf{y} - \mathbf{z}; \mathbf{x}, d\mathbf{x}) = m(\mathbf{y}; \mathbf{x} + \mathbf{z}, d\mathbf{x}) \text{ for all } \mathbf{z} \in \mathcal{L}.$$

The operator $L_{\mu\boldsymbol{\xi}}$ defined by (2.15) is then given by

$$L_{\mu\boldsymbol{\xi}}[\psi_0](\mathbf{y})) = \int_{\mathcal{H}} \psi_0(\mathbf{x}) e^{\mu\boldsymbol{\xi}\cdot[\mathbf{y}-\mathbf{x}]} m(\mathbf{y}; \mathbf{x}, d\mathbf{x})$$

for any $\mathcal{L}$-periodic function ψ_0. This linear operator is just the extension from the finite-dimensional vector space to the infinite-dimensional space of $\mathcal{L}$-periodic functions of the matrix operator B_μ which was introduced by Lui [Lui89] . We shall prove the Lemma by extending the proof of Lemma 6.3 in [Lui89].

In order to prove the convexity of the function $\ln \lambda(\mu\boldsymbol{\xi})$ not only in μ, but in the vector variable $\mu\boldsymbol{\xi}$, we adapt the proof of Lemma 6.4 in [Lui89]. The Perron-Frobenius theorem is now replaced by the Krein-Rutman theorem [KR50], which states that if $\rho(\mathbf{x})$ is any positive $\mathcal{L}$-periodic function, then

$$\min_{\mathbf{x}\in P} \frac{L_{\mu\boldsymbol{\xi}}[\rho](\mathbf{x})}{\rho(\mathbf{x})} \leq \lambda(\mu\boldsymbol{\xi}) \leq \max_{\mathbf{x}\in P} \frac{L_{\mu\boldsymbol{\xi}}[\rho](\mathbf{x})}{\rho(\mathbf{x})} \tag{6.3}$$

with equality on both sides when ρ is the eigenfunction $\psi(\mu\boldsymbol{\xi}; \mathbf{x})$ corresponding to $\lambda(\mu\boldsymbol{\xi})$. To obtain the convexity, choose any vectors $\mu_1\boldsymbol{\xi}_1$ and $\mu_2\boldsymbol{\xi}_2$, and set $\mu\boldsymbol{\xi} = \frac{1}{2}(\mu_1\boldsymbol{\xi}_1 + \mu_2\boldsymbol{\xi}_2)$ and $\rho = \sqrt{\psi(\mu_1\boldsymbol{\xi}; \mathbf{x})\psi(\mu_2\boldsymbol{\xi}; \mathbf{x})}$. Then by (6.3) and Schwarz's inequality,

$$\begin{aligned}
\lambda(\tfrac{1}{2}[\mu_1\boldsymbol{\xi}_1 + \mu_2\boldsymbol{\xi}_2]) &\leq \max_{\mathbf{y}\in P} \frac{\int_{\mathcal{H}}\{\psi(\mu_1\boldsymbol{\xi}_1; \mathbf{x}) e^{\mu_1\boldsymbol{\xi}_1\cdot[\mathbf{y}-\mathbf{x}]}\psi(\mu_2\boldsymbol{\xi}_2; \mathbf{x}) e^{\mu_2\boldsymbol{\xi}_2\cdot[\mathbf{y}-\mathbf{x}]}\}^{1/2} m(\mathbf{y}; \mathbf{x}, d\mathbf{x})}{\{\psi(\mu_1\boldsymbol{\xi}_1; \mathbf{y})\psi(\mu_2\boldsymbol{\xi}_2; \mathbf{y})\}^{1/2}} \\
&\leq \max_{\mathbf{y}\in P} \frac{\{L_{\mu_1\boldsymbol{\xi}_1}[\psi(\mu_1\boldsymbol{\xi}_1)](\mathbf{y}) L_{\mu_2\boldsymbol{\xi}_2}[\psi(\mu_2\boldsymbol{\xi}_2)](\mathbf{y})\}^{1/2}}{\{\psi(\mu_1\boldsymbol{\xi}_1; \mathbf{y})\psi(\mu_2\boldsymbol{\xi}_2; \mathbf{y})\}^{1/2}} \\
&= \{\lambda(\mu_1\boldsymbol{\xi}_1)\lambda(\mu_2\boldsymbol{\xi}_2)\}^{1/2}.
\end{aligned}$$

Taking the logarithms of both sides shows that $\ln \lambda(\mu\boldsymbol{\xi})$ is convex in $\mu\boldsymbol{\xi}$..

Once we have this convexity, we can follow the proof of Lemma 6.3 in [Lui89]. For a fixed unit vector $\boldsymbol{\xi}$ define the functions

$$\Phi(\mu) := (1/\mu) \ln \lambda(\mu\boldsymbol{\xi})$$

and

$$\Psi(\mu) = \frac{\partial}{\partial\mu} \ln \lambda(\mu\boldsymbol{\xi}).$$

The convexity of $\ln \lambda$ shows that Ψ is nondecreasing. The fact that $\mu\Phi' = \Psi - \Phi$ shows that the graph of Ψ lies below that of Φ when μ is below the value μ^* at which the infimum of Φ is attained. If μ^* is finite, the graph of Ψ crosses that of Φ at μ^*, and then stays above it. Lui's arguments show that

$$\Psi(\mu) \le \bar{c}(\boldsymbol{\xi}) \le \Phi(\mu) \text{ for all } \mu < \mu^*. \tag{6.4}$$

If μ^* is finite, both Φ and Ψ approach the infimum $\Phi(\mu^*)$ of Φ as μ increases to μ^*. If $\mu^* = \infty$, then L'Hôpital's rule shows that Φ and Ψ have the same limit at infinity, and this limit is the infimum of Φ. In either case, letting μ increase to μ^* in (6.4) yields the statement (6.1) of the Lemma.

The formula (6.2) is obtained by combining (6.1) with the formula (2.10) for the ray speed, noting that both formulas involve infima, and setting $\boldsymbol{\zeta} = \mu\boldsymbol{\xi}$.

Remark It is easily seen that the first two conditions of Lemma 6.2 and the existence of r imply all but the last of the hypotheses 2.1. Thus the last part of the third condition is just the assumption that Hypothesis 2.1.vi is also valid.

Proof of Theorem 2.4 If γ is any positive constant, then because L is linear, $L[\gamma r] > \gamma r$. Thus we may assume without loss of generality that $r \le \eta$. Then the operators Q and $Q^{[L,r]}$ defined by $Q^{[L,r]}[u](\mathbf{x}) := \min\{r(\mathbf{x}),\ L[u](\mathbf{x})\}$ satisfy the conditions of Lemma 6.1. Therefore, $c^*(\boldsymbol{\xi}) \le \bar{c}(\boldsymbol{\xi})$. By combining this with Lemma 6.2 we obtain the inequality (2.17) of Theorem 2.4. The inequality (2.18) follows from this and the formula (2.10).

Proof of Theorem 2.5 By the same argument as in the proof of the preceding lemma, we may assume without loss of generality that $r \ge \pi_1$. Then Lemmas 6.1 and 6.2 yield the inequality (2.20), and (2.21) follows from this and (2.10).

The use of either Theorem 2.4 or Theorem 2.5 depends on finding the principal eigenvalues $\lambda(\mu\boldsymbol{\xi})$ of a linear operator. For problems with a discrete habitat $\mathcal{H}$ this is a matrix eigenvalue problem.

Example 6.1 *Recall the stepping stone model (2.3) with the growth function (2.4) of Example 2.1. We take the periods $N_1 > 1$ and $N_2 = 1$, so that the parameters are periodic of period N_1 in i and independent of j. The linearization M of Q is given by replacing $g(i,u)$ by its linearization $e^{r(i)}u$, where $r(i)$, like $d(i)$, is periodic of period N_1 in i.*

Let $\psi(i)$ be N_1-periodic and independent of j. Then $M_{\boldsymbol{\zeta}}[\psi](\mathbf{y}) = e^{\boldsymbol{\zeta}\cdot\mathbf{y}}M[e^{-\boldsymbol{\zeta}\cdot\mathbf{x}}\psi(\mathbf{x})](\mathbf{y})$ is again N_1 periodic and independent of j. Thus the eigenvalue problem $M_{\boldsymbol{\zeta}}[\psi] = \lambda\psi$ consists of N_1 equations in the N_1 independent values $\psi(1),\ \psi(2), \cdots, \psi(N_1)$. By taking account of the fact that the quantities at 0 which occur in the first equation can be replaced by the values at N_1 and that the values at $N_1 + 1$ which appear in the last equation can be replaced by the values at 1, we find that the operator $M_{\boldsymbol{\zeta}}$ is a matrix operator with a simple pattern, which is best conveyed by writing the matrix for $N_1 = 4$:

$$\begin{pmatrix} [1+\{2\cosh\zeta_2 - 4\}d(1)]e^{r(1)} & d(2)e^{r(2)-\zeta_1} & 0 & d(4)e^{r(4)+\zeta_1} \\ d(1)e^{r(1)+\zeta_1} & [1+\{2\cosh\zeta_2 - 4\}d(2)]e^{r(2)} & d(3)e^{r(3)-\zeta_1} & 0 \\ 0 & d(2)e^{r(2)+\zeta_1} & [1+\{2\cosh\zeta_2 - 4\}d(3)]e^{r(3)} & d(4)e^{r(4)-\zeta_1} \\ d(1)e^{r(1)-\zeta_1} & 0 & d(3)e^{r(3)+\zeta_1} & [1+\{2\cosh\zeta_2 - 4\}d(4)]e^{r(4)} \end{pmatrix}. \tag{6.5}$$

The principal eigenvalue of this matrix with nonnegative entries, that is, the eigenvalue with a positive eigenvector, is $\tilde{\lambda}(\boldsymbol{\zeta})$*, which can be used in the formulas (2.22) and (2.23). We recall that the model (2.3) has a positive* N_1*-periodic equilibrium* π_1 *such the Hypotheses 2.1 are satisfied with this* π_1 *and* $\pi_0 \equiv 0$ *if and only if the equilibrium 0 is unstable. The condition for this is simply that* $\lambda(\mathbf{0}) > 1$*.*

Rough bounds for an eigenvalue can be found by using the finite dimensional case of the bound (6.3), which is called the Perron-Frobenius bounds. For example, if one sets $\psi(i) = e^{-r(i)}/d(i)$*, one finds that*

$$\min_i [1 + 2(\cosh\zeta_2 + \cosh\zeta_1 - 2)d(i)]e^{r(i)} \le \lambda(\boldsymbol{\zeta}) \le \max_i [1 + 2(\cosh\zeta_2 + \cosh\zeta_1 - 2)d(i)]e^{r(i)}.$$

These bounds show that if $r(i) > 0$ *for all* i*, then* $\lambda(\mathbf{0}) > 1$ *so that 0 is linearly unstable and the Hypotheses 2.1 are valid with* $\pi_0 \equiv 0$*, and that when* $r(i) < 0$ *for all* i*,* $\lambda(\mathbf{0}) < 1$ *so that there is no positive equilibrium. More accurate bounds can be obtained by using a numerically approximated eigenvector in the Perron-Frobenius bounds.*

It remains to determine whether the conditions of Corollary 2.1 are satisfied. It is easily verified that for every positive δ *the function* $g(i, u)$ *is bounded below by* $(1-\delta)e^{r(i)}u$ *when* u *is positive and sufficiently small, and that* $g(i, u) \le e^{r(i)}u$ *for all positive* u *if and only if*

$$t(i) \le e^{r(i)}.$$

Thus, M *satisfies the conditions of Corollary 2.1 if and only if this additional inequality is valid for all* i*. Since* $t(i) < 1$*, this is automatically true when* $r(i) \ge 0$*, but may be false if* $r(i) < 0$*. If it is false, then the right-hand sides of (2.22) and (2.23) still serve as lower bounds for* $c^*(\boldsymbol{\xi})$ *and* $C(\boldsymbol{\eta})$*. However, one only obtains upper bounds by applying Theorem 2.5 with an* L *which is obtained from the right-hand side of (2.3) by replacing* g *by the linear function* $\max\{e^{r(i)}, t(i)\}u$*. The failure of the inequality* $Q[u] \le M[u]$ *does not imply that the equations (2.22) and (2.23) are not true. In fact, Theorem 3.1 of [WLLnt] indicates that there may be a weaker condition which suffices to establish these equations.*

Example 6.2 *We consider the growth-migration model of [KKTS03]*

$$u_{,t} = \{D(x)u_{,x}\}_{,x} + \{D(x)u_{,y}\}_{,y} + u(\epsilon(x) - u) \tag{6.6}$$

where D *is strictly positive, and* D *and* ϵ *are periodic of period 1 in* x *and independent of* y*. This problem was discussed in Example 2.2. The operator* Q *is the time-1 map of this differential equation. Because for every positive* δ*,* $u(\epsilon(x) - u) \ge (1-\delta)\epsilon(x)u$ *for all sufficiently small positive* u *and* $u(\epsilon(x) - u) \le \epsilon(x)u$ *for all positive* u*, the comparison theorem for parabolic equations shows that the time-one map* M *of the linearized equation in which* $u(\epsilon(x)-u)$ *is replaced by* $\epsilon(x)u$ *satisfies the conditions of Corollary 2.1. To find the principal eigenvalue of* $M_{\boldsymbol{\zeta}}$ *one looks at a separated solution of the form* $e^{\gamma t - \zeta_1 x - \zeta_2 y}\psi(x)$ *of the linearized equation, where* ψ *depends only on* x *and is periodic of period 1. This leads to the eigenvalue problem*

$$\begin{aligned} &D\psi'' + (D' - 2\zeta_1 D)\psi' + [(\zeta_1^2 + \zeta_2^2)D - \zeta_1 D' + \epsilon]\psi = \gamma\psi \\ &\psi(1) = \psi(0),\ \psi'(1) = \psi'(0). \end{aligned} \tag{6.7}$$

The principal eigenvalue $\tilde{\gamma}(\boldsymbol{\zeta})$ of this equation is that eigenvalue whose eigenfunction $\tilde{\psi}$ does not change sign. Because of the factor $e^{\gamma t}$ in the solution of the linearized equation, the principal eigenvalue $\tilde{\lambda}(\boldsymbol{\zeta})$ of the time-one map $M_{\boldsymbol{\zeta}}$ is equal to $e^{\tilde{\gamma}(\boldsymbol{\zeta})}$. Thus $\ln\tilde{\lambda}(\boldsymbol{\zeta})$ is to be replaced by $\tilde{\gamma}(\boldsymbol{\zeta})$ in the formulas (2.22) and (2.23).

While (6.7) is an eigenvalue problem for an ordinary differential equation, it is usually not possible to solve it exactly, and the eigenvalue must be approximated numerically. Kinezaki, Kawasaki, Takasu, and Shigesada [KKTS03] treated the special case in which the functions D and ϵ are piecewise constant, and showed how to find the ray speed $C(\boldsymbol{\eta})$ in this case.

Arguments like those in [PW66] show that if $N_{\boldsymbol{\zeta}}[\psi]$ denotes the left-hand side of (6.7) and ρ is any smooth positive $\boldsymbol{\mathcal{L}}$-periodic function, then

$$\min_{\mathbf{x}\in P}\frac{N_{\boldsymbol{\zeta}}[\rho]}{\rho}\le\bar{\gamma}(\boldsymbol{\zeta})\le\max_{\mathbf{x}\in P}\frac{N_{\boldsymbol{\zeta}}[\rho]}{\rho}.$$

By choosing $\rho\equiv 1$, one finds that

$$\min[(\zeta_1^2+\zeta_2^2)D-\zeta_1 D'+\epsilon]\le\bar{\gamma}(\boldsymbol{\zeta})\le\max[(\zeta_1^2+\zeta_2^2)D-\zeta_1 D'+\epsilon].$$

In particular, we find that $\min\epsilon(\mathbf{x})\le\bar{\gamma}(\mathbf{0})\le\max\epsilon(\mathbf{x})$. This shows that when the growth rate ϵ is positive everywhere, the equilibrium 0 is unstable, so that there is a positive equilibrium such that the hypotheses 2.1 are valid with $\pi_0\equiv 0$, and that if $\epsilon<0$ everywhere, then 0 is stable and there is no positive equilibrium. Better bounds can be obtained from the above inequalities by using a smooth numerical approximation to the eigenfunction for ρ.

The minimization processes in the formulas (6.1) and (6.2) of Lemma 6.2 may be facilitated by the fact that the function $(\boldsymbol{\eta}\cdot\boldsymbol{\zeta})^{-1}\ln\lambda(\boldsymbol{\zeta})$ is convex in the variable $\boldsymbol{\sigma}:=(\boldsymbol{\eta}\cdot\boldsymbol{\zeta})^{-1}[\boldsymbol{\zeta}+(1-\boldsymbol{\eta}\cdot\boldsymbol{\zeta})\boldsymbol{\eta}]$. In particular, the right-hand side of (6.1) is convex in $1/\mu$.

7 The existence of traveling waves: Proof of Theorem 2.6

To establish the existence of a periodic traveling wave when $\pi_0\equiv 0$ and $c\ge c^*(\boldsymbol{\xi})$, we recall the construction of the function $a(c,\boldsymbol{\xi};s,\mathbf{x})$ as the limit of the solution $a_n(c,\boldsymbol{\xi};s,\mathbf{x})$ of the recursion (3.4). Because of the presence of the maximization on the right, the formula (3.6) shows that a is not quite a traveling wave. To eliminate this maximization, we recall that, by Lemma 3.3, the spreading speed $c^*(\boldsymbol{\xi})$ is independent of the choice of the initial function $\phi=a_0$, as long as it has the properties (3.3). If ϕ has these properties and m is any positive integer, $m^{-1}\phi$ also has these properties.

We define the sequence $a_n(c, \boldsymbol{\xi}, m; s, \mathbf{x})$ as the solution of the problem (3.4) with ϕ replaced by $m^{-1}\phi$. This sequence is again nondecreasing in n, and converges to a function $a(c, \boldsymbol{\xi}, m; s)$ as n approaches infinity. Then (3.6) becomes

$$\begin{aligned} a(c, \boldsymbol{\xi}, m; \boldsymbol{\xi}\cdot\mathbf{y} + s, \mathbf{y}) = \max\{&m^{-1}\phi(\boldsymbol{\xi}\cdot\mathbf{y} + s, \mathbf{y}), \\ &Q[a(c, \boldsymbol{\xi}, m; \boldsymbol{\xi}\cdot\mathbf{x} + s + c, \mathbf{x})](\mathbf{y})\}. \end{aligned} \tag{7.1}$$

The obvious way to get a traveling wave is to let m approach infinity on both sides. However, it may happen that $a(c, \boldsymbol{\xi}, m; s, \mathbf{x})$ approaches zero as $m \to \infty$. We shall avoid this problem by letting s depend upon m before taking the limit.

Assume that $c \geq c^*(\boldsymbol{\xi})$, so that $a(c, \boldsymbol{\xi}, m; -\infty, \mathbf{x}) = \pi_1(\mathbf{x})$, and $a(c, \boldsymbol{\xi}, m; \infty, \mathbf{x})) = 0$. We wish to show that there are pairs of points (s_m, s'_m) whose distance $s'_m - s_m$ is bounded and such that, for a fixed value $\mathbf{x}_0$ of $\mathbf{x}$, $a(c, \boldsymbol{\xi}, m; s_m, \mathbf{x_0}) \leq \frac{3}{4}\pi_1(\mathbf{x}_0)$ and $a(c, \boldsymbol{\xi}, m; s'_m, \mathbf{x}_0)$ $\geq \frac{1}{4}\pi_1(\mathbf{x}_0)$. This fact with $s'_m = s_m$ clearly follows from the intermediate value theorem if $a(c, \boldsymbol{\xi}; s, \mathbf{x}))$ is continuous in s. However, the uniform convergence of $a_n(c, \boldsymbol{\xi}; \boldsymbol{\xi}\cdot\mathbf{x} + s, \mathbf{x}))$ to $a(c, \boldsymbol{\xi}; \boldsymbol{\xi}\cdot\mathbf{x} + s, \mathbf{x}))$ on bounded subsets of $\mathcal{H}$ does not imply continuity in s.

We shall overcome the possible lack of continuity by a trick found in [Wei82] and [Lui89]. Choose a $\mathbf{z}_0$ in $\mathcal{L}$ such that

$$\boldsymbol{\xi}\cdot\mathbf{z}_0 > 0$$

and an $\mathbf{x}_0$ in $\mathcal{H}$. For any positive integer m define the sequence

$$K_m(\ell) := \tfrac{1}{2}[a(c, \boldsymbol{\xi}, m; \boldsymbol{\xi}\cdot[\mathbf{x}_0 + \ell\mathbf{z}_0], \mathbf{x}_0) + a(c, \boldsymbol{\xi}, m; \boldsymbol{\xi}\cdot[\mathbf{x}_0 + (\ell+1)\mathbf{z}_0], \mathbf{x}_0)],$$

where ℓ ranges over all the integers. Then K_m is nonincreasing in ℓ, $K_m(-\infty) = \pi_1(\mathbf{x}_0)$, and $K_m(\infty) = 0$. Moreover,

$$\begin{aligned} &K_m(\ell) - K_m(\ell - 1) \\ &\quad = \tfrac{1}{2}[a(c, \boldsymbol{\xi}, m; \boldsymbol{\xi}\cdot[\mathbf{x}_0 + (\ell+1)\mathbf{z}_0], \mathbf{x}_0) - a(c, \boldsymbol{\xi}, m; \boldsymbol{\xi}\cdot[\mathbf{x}_0 + (\ell-1)\mathbf{z}_0], \mathbf{x}_0)] \leq \tfrac{1}{2}\pi_1(\mathbf{x}_0). \end{aligned}$$

Thus, $K_m(\ell)$ cannot decrease by more than half of its range at consecutive integers. It follows that there must be an integer ℓ_m such that $\frac{1}{4}\pi_1(\mathbf{x}_0) \leq K_m(\ell_m) \leq \frac{3}{4}\pi_1(\mathbf{x}_0)$. Because a is nonincreasing, these inequalities imply that

$$a(c, \boldsymbol{\xi}, m; \boldsymbol{\xi}\cdot[\mathbf{x}_0 + \ell_m\mathbf{z}_0], \mathbf{x}_0) \geq \tfrac{1}{4}\pi_1(\mathbf{x}_0) \text{ and } a(c, \boldsymbol{\xi}, m; \boldsymbol{\xi}\cdot[\mathbf{x}_0 + (\ell_m+1)\mathbf{z}_0], \mathbf{x}_0) \leq \tfrac{3}{4}\pi_1(\mathbf{x}_0). \tag{7.2}$$

By Hypothesis 2.1.vi there is, for any fixed s and positive integer N, a sequence $m_i^{(N)}$ which increases to ∞ with i, and such that the sequence $Q[a(c, \boldsymbol{\xi}, m_i^{(N)}; \boldsymbol{\xi}\cdot\mathbf{x} + s + \ell_{m_i^{(N)}}\boldsymbol{\xi}\cdot\mathbf{z}_0 - nc), \mathbf{x})](\mathbf{y})$ converges uniformly for $\mathbf{y}$ in any bounded subset of $\mathcal{H}$, and for all n with $|n| \leq N$. By induction we make $m_i^{(N+1)}$ a subsequence of $m_i^{(N)}$. Then by (7.1) and Hypothesis 2.1.v the diagonal sequence $a(c, \boldsymbol{\xi}, m_i^{(i)}; \boldsymbol{\xi}\cdot\mathbf{y} + s + \ell_{m_i^{(i)}}\boldsymbol{\xi}\cdot\mathbf{z}_0 - (n+1)c, \mathbf{x}))](\mathbf{y})$ converges to a function of $s - (n+1)c$ and $\mathbf{y}$ which we write in the form $W(\boldsymbol{\xi} \cdot \mathbf{y} + s - (n+1)c, \mathbf{y})$, uniformly in $\mathbf{y}$ on bounded subsets of $\mathcal{H}$ for every n. Thus the function $\tilde{W}(s, \mathbf{y})$ is defined for all $s \in \mathcal{R}$ and is nonincreasing in s. Hypothesis 2.1.v shows that we may take limits on both sides of (7.1) to see that the sequence $u_n = W(\boldsymbol{\xi} \cdot \mathbf{x} - nc + s, \mathbf{x})$ satisfies the recursion (2.1).

The fact that $a(c, \boldsymbol{\xi}; s, \mathbf{x})$ is $\mathcal{L}$-periodic in $\mathbf{x}$ is equivalent to saying that for any fixed i the function $\psi_i(s, \mathbf{x}) := a(c, \boldsymbol{\xi}; \boldsymbol{\xi} \cdot (\mathbf{x} + s + \ell_{m_i^{(i)}} \boldsymbol{\xi} \cdot \mathbf{z}_0, \mathbf{x})$ has the property $\psi_i(s + \boldsymbol{\xi} \cdot \mathbf{z}, \mathbf{x} - \mathbf{z}) = \psi_i(s, \mathbf{x})$ for all $\mathbf{z} \in \mathcal{L}$. By fixing $\mathbf{z}$ and s and letting i approach infinity, we see that the limit function $\psi(s, \mathbf{x}) := W(\boldsymbol{\xi} \cdot \mathbf{x} + s, \mathbf{x})$ has the same property, which implies that $W(s, \mathbf{x})$ is $\mathcal{L}$-periodic in $\mathbf{x}$. Thus W has the first three properties in the Definition 2.1 of a traveling wave.

It follows as before that the limits $W(\pm\infty, \mathbf{x})$ must be periodic equilibria. Hypothesis 2.1.iv shows that the only equilibria between 0 and π_1 are these equilibria. Since (7.2) shows that $W(0, \mathbf{x}_0) \geq \frac{1}{4}\pi_1(\mathbf{x}_0)$ and $W(\boldsymbol{\xi} \cdot \mathbf{z}_0, \mathbf{x}_0) \leq \frac{3}{4}\pi_1(\mathbf{x}_0)$, and since W is nonincreasing in s, we conclude that $W(-\infty, \mathbf{x}) = \pi_1(\mathbf{x})$ and $W(\infty, \mathbf{x}) = 0$. Thus W has all the properties of Definition 2.1, and is therefore a periodic traveling wave. We have established the existence of the periodic traveling wave of speed c in the direction $\boldsymbol{\xi}$ whenever $c \geq c^*(\boldsymbol{\xi})$.

To prove that there is no such wave when $c < c^*(\boldsymbol{\xi})$, we suppose that for some c there is a wave $W(\boldsymbol{\xi} \cdot \mathbf{x} - nc, \mathbf{x})$ with the desired properties. Because $W(-\infty, \mathbf{x}) = \pi_1(\mathbf{x})$, we can choose a nondecreasing function ϕ with the properties (3.3) such that $\phi \leq W$. The Comparison Principle shows that the solution a_n of (3.4) satisfies $a_n(c, \boldsymbol{\xi},\ s, \mathbf{x}) \leq W(s, \mathbf{x})$. Therefore $a(c, \boldsymbol{\xi}; s, \mathbf{x}) \leq W(s, \mathbf{x})$. Because $W(\infty, \mathbf{x}) = 0$, this shows that $a(c, \boldsymbol{\xi}; \infty, \mathbf{x}) = 0$. Therefore $c \geq c^*(\boldsymbol{\xi})$ by (3.7). Thus Theorem 2.6 is established.

Remark. By using the methods in [LWL02] we can show that if the time-one map of a continuous-time problem which is invariant under time translation satisfies the Hypotheses 2.1, then there is a periodic traveling wave of the form $W(\boldsymbol{\xi} \cdot \mathbf{x} - ct, \mathbf{x})$ with $W(\infty) = \pi_1$ and $W(\infty) = 0$ if and only if $c \geq c^*(\boldsymbol{\xi})$. When Q_τ is the time-τ map of a parabolic partial differential equation, the function W satisfies an elliptic or possibly degenerate parabolic equation. For the equation (2.6) in Example 2.2 with D and r independent of y, the equation for the wave $W(\xi_1 x + \xi_2 y - ct, x)$ is

$$-cW_{,s} = D(x)[W_{,ss} + 2\xi_1 W_{,sx} + W_{,xx}] - e_1(x)[\xi_1 W_{,s} + W_{,x}] - e_2(x)\xi_2 W_{,s} + r(x)W(1-W).$$

When $\xi_2 \neq 0$ so that $|\xi_1| < 1$, this equation is elliptic. When $\xi_2 = 0$, the equation is parabolic if $c \neq 0$, but degenerate elliptic if $c = 0$.

8 Partially bounded habitats.

Berestycki and Nirenberg [BH02] have shown how to obtain traveling waves for a partial differential equation on a region such as the strip $-\infty < x < \infty$, $-1 < y < 1$ when the coefficients and the boundary conditions are periodic in x. These results have been extended in a recent paper of Berestycki and Hamel [BH02] to boundary value problems on a very general class of domains which are bounded in some directions and periodic in others.

Example 8.1 *Consider the stepping stone model of Example 2.1 not in the whole Euclidean plane, but only on those unit squares (experimental fields) whose centers are of the form* $(i-1/2, j-1/2)$ *with* $j=1$ *or 2 and* i *arbitrary, or with* $j=3$ *and* i *even. All other squares will be assumed to have such hostile environments that the population* u_n *is always zero there. We shall assume that the parameters* $r(i,j),\ s(i,j),\ t(i,j)$ *in the growth law (2.4), and the mobility* $d(i,j)$ *depend only on the function* $(-1)^{i+j}$*, so that they form a checkerboard pattern. Then* $\mathcal{L}$ *is the one-dimensional lattice of horizontal integer translations* $\{(i,0)\}$*.*

We can extend all our results to such domains by removing the requirement that $\mathcal{L}$ be d-dimensional from Hypothesis 2.1.iii. If the dimension of $\mathcal{L}$ is less than d, there are direction vectors $\boldsymbol{\xi}$ which are orthogonal to all members of $\mathcal{L}$. These are just the directions in which the habitat is bounded. It is clear that neither spreading nor a traveling wave in such a direction makes sense. If, on the other hand, there is a member $\mathbf{z}$ of $\mathcal{L}$ such that $\boldsymbol{\xi}\cdot\mathbf{z}\neq 0$, then all our proofs go through.

In this way we recover all our results with the understanding that only those $\boldsymbol{\xi}$ which are not orthogonal to all members of $\mathcal{L}$ are to be used. In particular, the infima in such formulas as (2.10) are to be taken only over such $\boldsymbol{\xi}$ or $\boldsymbol{\zeta}$. For instance, in the above example, we omit the cases where $\xi_1=0$ or $\zeta_1=0$.

A Appendix: Proof of Lemma 5.2

We shall first prove the inequality (5.28) when $\ell=0$. We see from the definition (5.26) of e_ℓ and (5.24) that

$$\begin{aligned}
e_1(\mathbf{y}) &= a_{n_1}^{(k_0)}((1+\epsilon)S(\boldsymbol{\tau}(\mathbf{y})),\boldsymbol{\tau}(\mathbf{y});\\
&\qquad \boldsymbol{\tau}(\mathbf{y})\cdot\mathbf{y}-[A+(1+\tfrac{1}{2}\epsilon)(n_1-n_0)]S(\boldsymbol{\tau}(\mathbf{y})),\mathbf{y}))\\
&= Q_{k_0}^{n_1-n_0}[a_{n_0}^{(k_0)}((1+\epsilon)S(\boldsymbol{\tau}(\mathbf{y})),\boldsymbol{\tau}(\mathbf{y});\boldsymbol{\tau}(\mathbf{y})\cdot\mathbf{x}\\
&\quad -[A+(1+\tfrac{1}{2}\epsilon)(n_1-n_0)]S(\boldsymbol{\tau}(\mathbf{y}))+(n_1-n_0)(1+\epsilon)S((\boldsymbol{\tau}(\mathbf{y})),\mathbf{x})](\mathbf{y})\\
&= Q_{k_0}^{n_1-n_0}[a_{n_0}^{(k_0)}((1+\epsilon)S(\boldsymbol{\tau}(\mathbf{y})),\boldsymbol{\tau}(\mathbf{y});\boldsymbol{\tau}(\mathbf{y})\cdot\mathbf{x}-AS(\boldsymbol{\tau}(\mathbf{y}))\\
&\qquad +\tfrac{1}{2}\epsilon(n_1-n_0)S(\boldsymbol{\tau}(\mathbf{y})),\mathbf{x})](\mathbf{y}).
\end{aligned}$$

Because $Q_{k_0}^{n_1-n_2}[u](\mathbf{y})$ depends only on the values of $u(\mathbf{x})$ with $|\mathbf{x}-\mathbf{y}|\leq k_0(n_1-n_0)$

and because Q_{k_0} is order-preserving, we see from the definition (5.26) of e_0 that if

$$\begin{aligned} &a_{n_1}^{(k_0)}((1+\epsilon)S(\boldsymbol{\tau}(\mathbf{x})), \boldsymbol{\tau}(\mathbf{x}); \boldsymbol{\tau}(\mathbf{x})\cdot\mathbf{x} - AS(\boldsymbol{\tau}(\mathbf{x})), \mathbf{x}) \\ &\quad \geq a_{n_0}^{(k_0)}((1+\epsilon)S(\boldsymbol{\tau}(\mathbf{y})), \boldsymbol{\tau}(\mathbf{y}); \boldsymbol{\tau}(\mathbf{y})\cdot\mathbf{x} - AS(\boldsymbol{\tau}(\mathbf{y})) + \tfrac{1}{2}\epsilon(n_1-n_0)S(\boldsymbol{\tau}(\mathbf{y})), \mathbf{x}) \\ &\quad\ \text{when } |\mathbf{x}-\mathbf{y}| \leq k_0(n_1-n_0), \end{aligned} \tag{A.1}$$

then $Q_{k_0}^{n_1-n_0}[e_0](\mathbf{y}) \geq e_1(\mathbf{y})$. Thus if we can prove the inequality (A.1), we have proved the case $\ell = 0$ of Lemma 5.2.

The inequality (5.25) shows that if

$$\boldsymbol{\tau}(\mathbf{x})\cdot\mathbf{x} - AS(\boldsymbol{\tau}(\mathbf{x})) \leq (R/r)n_0k_0, \tag{A.2}$$

then the left-hand side of (A.1) is no smaller than $\alpha_{n_0}^{(k_0)}$, which is an upper bound for the right-hand side. Thus the inequality (A.1) is valid when (A.2) holds.

On the other hand, (5.10) shows that if

$$\boldsymbol{\tau}(\mathbf{y})\cdot\mathbf{x} - AS(\boldsymbol{\tau}(\mathbf{y})) + \tfrac{1}{2}\epsilon(n_1-n_0)S(\boldsymbol{\tau}(\mathbf{y})) \geq n_0[k_0 - (1+\epsilon)S(\boldsymbol{\tau}(\mathbf{y}))], \tag{A.3}$$

then the right-hand side of (A.1) is zero, so that the inequality is again valid. Thus if we can show that at least one of the inequalities (A.2) and (A.3) holds whenever $|\mathbf{x}-\mathbf{y}| \leq k_0(n_1-n_0)$, we will have proved (A.1). To do this, we suppose that the inequality (A.2) is violated, so that

$$\boldsymbol{\tau}(\mathbf{x})\cdot\mathbf{x} - AS(\boldsymbol{\tau}(\mathbf{x}) > (R/r)n_0k_0. \tag{A.4}$$

We recall the identity (5.20), which says that $\boldsymbol{\tau}(\mathbf{x}) = S(\boldsymbol{\tau}(\mathbf{x}))\nabla D(\mathbf{x})$. Thus we may write the inequality (A.4) in the form

$$[\nabla D(\mathbf{x})\cdot\mathbf{x} - A]S(\boldsymbol{\tau}(\mathbf{x})) > (R/r)n_0k_0. \tag{A.5}$$

Because $r \leq S(\boldsymbol{\xi}) \leq R$ for all $\boldsymbol{\xi}$, this inequality implies that

$$[\nabla D(\mathbf{x})\cdot\mathbf{x} - A]S(\boldsymbol{\tau}(\mathbf{y})) > n_0k_0. \tag{A.6}$$

The identity (5.20) also shows that the inequality (A.3) can be written in the form

$$[\nabla D(\mathbf{y})\cdot\mathbf{x} - A + \tfrac{1}{2}\epsilon(n_1-n_0) + n_0(1+\epsilon))]S(\boldsymbol{\tau}(\mathbf{y})) \geq n_0k_0. \tag{A.7}$$

The inequality (A.6) implies this if the coefficient of $S(\mathbf{x})$ on the left of (A.6) is no larger than the corresponding coefficient in (A.7); that is, if

$$\nabla D(\mathbf{x})\cdot\mathbf{x} - \nabla D(\mathbf{y})\cdot\mathbf{x} \leq \tfrac{1}{2}\epsilon(n_1-n_0) + n_0(1+\epsilon) \tag{A.8}$$

Thus the inequality (A.1) will follow if we can show that the inequality (A.4) and the inequality

$$|\mathbf{x}-\mathbf{y}| \leq k_0(n_1-n_0) \tag{A.9}$$

imply (A.8). To obtain a bound for the left-hand side of (A.8), we define the function

$$h(\theta) := \nabla D(\mathbf{y} + \theta(\mathbf{x} - \mathbf{y})) \cdot \mathbf{x},$$

so that $h(1) = \nabla D(\mathbf{x}) \cdot \mathbf{x}$ and $h(0) = \nabla D(\mathbf{y}) \cdot \mathbf{x}$. Because ∇D is homogeneous of degree zero, we see that $h'(1) = 0$. Thus Taylor's theorem with remainder shows that for some $\theta \in (0, 1)$

$$\nabla D(\mathbf{x}) \cdot \mathbf{x} - \nabla D(\mathbf{y}) \cdot \mathbf{x} = \tfrac{1}{2} h''(\theta) = \tfrac{1}{2} \sum_{\alpha,\beta,\gamma=1}^{d} D_{,x_\alpha x_\beta x_\gamma} x_\alpha (x_\beta - y_\beta)(x_\gamma - y_\gamma).$$

By Schwarz's inequality

$$\nabla D(\mathbf{x}) \cdot \mathbf{x} - \nabla D(\mathbf{y}) \cdot \mathbf{x} \le \tfrac{1}{2} |\mathbf{x}| |\mathbf{y} - \mathbf{x}|^2 \left\{ \sum_{\alpha,\beta,\gamma=1}^{d} D^2_{,x_\alpha x_\beta x_\gamma} \right\}^{1/2}. \tag{A.10}$$

Because $|\boldsymbol{\tau}(\mathbf{x})| = 1$, the inequality (A.4) implies that

$$|\mathbf{x}| \ge rA + (R/r) n_0 k_0. \tag{A.11}$$

The third derivatives of D are homogeneous of degree -2, and

$$|\mathbf{y} + \theta(\mathbf{x} - \mathbf{y})| \ge |\mathbf{x}| - |\mathbf{y} - \mathbf{x}| \ge |\mathbf{x}| - k_0(n_1 - n_0) \text{ for } 0 \le \theta \le 1.$$

By (A.11) and (5.27) the right-hand side is positive. Thus (A.10) implies the inequality

$$\nabla D(\mathbf{x}) \cdot \mathbf{x} - \nabla D(\mathbf{y}) \cdot \mathbf{x} \le \frac{\mu k_0^2 (n_1 - n_0)^2 |\mathbf{x}|}{2[|\mathbf{x}| - k_0(n_1 - n_0))]^2}, \tag{A.12}$$

where μ is a bound for the square root on the right of (A.10) when its argument is any unit vector. The right-hand side of (A.12) is nonincreasing in $|\mathbf{x}|$, so that it can be bounded by replacing $|\mathbf{x}|$ by the right-hand side of (A.11). Thus

$$\nabla D(\mathbf{x}) \cdot \mathbf{x} - \nabla D(\mathbf{y}) \cdot \mathbf{x} \le \frac{\mu k_0^2 (n_1 - n_0)^2 [rA + (R/r) n_0 k_0]}{2[rA + (R/r) n_0 k_0 - k_0(n_1 - n_0)]^2}.$$

It is easily verified that the inequality (5.27) implies that this right-hand side is no larger than the right-hand side of (A.8).

Thus we have proved the inequality (A.8), which shows that (A.1) is true whether or not (A.2) is satisfied. This, in turn, implies that $e_1 \le Q_{k_0}^{n_1 - n_0}[e_0] \le Q^{n_1 - n_0}[e_0]$. To obtain the statement of the the Lemma, we observe that replacing the constant A by $A + \ell(1 + \frac{1}{2}\epsilon)$ replaces e_0 by e_ℓ and e_1 by $e_{\ell+1}$. Since the constant $A + \ell(1 + \frac{1}{2}\epsilon)$ still satisfies the inequality (5.27), the same proof shows that $e_{\ell+1} \le Q[e_\ell]$ for any nonnegative ℓ, which proves Lemma 5.2.

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