

C. Carrillo · P. Fife

Spatial effects in discrete generation population models

Dedicated to the memory of Art Winfree

Received: 19 November 2003 / Revised version: 19 April 2004

Published online: 7 October 2004 – © Springer-Verlag 2004

Abstract. A framework is developed for constructing a large class of discrete generation, continuous space models of evolving single species populations and finding their bifurcating patterned spatial distributions. Our models involve, in separate stages, the spatial redistribution (through movement laws) and local regulation of the population; and the fundamental properties of these events in a homogeneous environment are found. Emphasis is placed on the interaction of migrating individuals with the existing population through conspecific attraction (or repulsion), as well as on random dispersion. The nature of the competition of these two effects in a linearized scenario is clarified. The bifurcation of stationary spatially patterned population distributions is studied, with special attention given to the role played by that competition.

1. Introduction

We consider discrete time, continuous one-dimensional space models of the form

$$u' = f[u]. \quad (1.1)$$

Here u , a function of space, represents a population density at some generation, and u' is the resulting density at the next generation. Then (1.1) simply says that u' is determined uniquely by u . Trivial linear examples are $u' = 0$ (total extinction), $u' = u$ (nothing happens) and $u'(x) = \int_{-\infty}^{\infty} k(x-y)u(y)dy$. In this paper we consider u to be a scalar function, although practically all of the concepts, methods, and conclusions have analogs for multiple species; see Section 5. The environment is taken to be homogeneous, so that f is translation-invariant.

Some of our analyses will involve bifurcation phenomena; then we introduce a bifurcation parameter μ , converting (1.1) into $u' = \mu f[u]$.

Evolution laws of the form (1.1) have been the subject of many investigations into single-species populations with discrete nonoverlapping generations, in particular those involving demographic processes such as growth and dispersal (special cases of the regulation and redistribution processes considered in this paper). In these studies, growth occurs at a sedentary stage in the life history of the population. Nonlinear maps F such as the Ricker curve [23], the Beverton-Holt stock-recruitment curve [3] and discrete forms of the logistic equation, e.g. [21], are still used

C. Carrillo: Centre for Mathematical Biology, University of Oxford, Oxford, UK.
e-mail: carrillo@maths.ox.ac.uk

P. Fife: Dept. of Mathematics, University of Utah, USA. e-mail: fife@math.utah.edu

by mathematical biologists, and the behaviour of these growth models has been extensively investigated [18–20]. A second stage in the life history of the population, clearly differentiated from the growth stage — the reason why these models are particularly suitable for annual species or those showing strong seasonality and synchronicity — is described by the action of a linear integral operator. Thus the models take the form

$$u'(x) = \int_{\Omega} k(x, y)F(u(y))dy, \quad (1.2)$$

where the dispersal kernel $k(x, y)$, central to this formulation, provides the probability that an individual in an interval of length dx about a location x in the spatial domain originates from an interval of length dy about y in the same spatial domain. Examples of this growth-dispersal framework can be found (beginning with Weinberger [28]) in [1, 7–16, 22, 29, 28].

The kernel k in (1.2), tied to a probability, is non-negative and represents random dispersal. Congregation effects do not fit into the described framework; moreover (as we show) spatial patterning cannot arise through bifurcation from a constant state. In part to remedy these deficiencies, we construct a framework for population redistribution beginning with movement laws which may represent not only random dispersion but also conspecific attraction. The result is a class of models for population redistribution which are conceptually more complex than would result from mere dispersion with a probability kernel. This redistribution is followed by a sedentary regulation stage, examples of which are the nonlinear mappings F of the types mentioned above. (Thus the order of the sedentary and migration phases are reversed from those studied in the above works; this has no real effect.) Each of these stages is population dependent.

A number of authors have highlighted the importance of intraspecific interactions for the study of population spread [24, 25, 27]. Indeed, conspecific aggregation can build a critical mass to locally sustain the population by e.g. providing availability of mates or avoidance of predators. At a later stage, interspecific repulsion may be the necessary cue to initiate longer-range dispersal and global spread of the species. A studied example of congregation effects on the dynamics of a population is the southern pine beetle. The work of Turchin and others (described in [27]) with this beetle is of particular relevance to our discussion. The beetle *Dendroctonus frontalis* is the most destructive insect pest of the pine forest in the southern United States. Individuals initiating the attack on a pine tree emit a congregation pheromone, frontalin, that attracts other conspecific beetles. These in turn secrete more frontalin. The result of this positive feedback mechanism of intraspecific attraction is a *mass attack*: some 2,000 to 4,000 beetles overcome the resin defenses of the tree. Larvae are deposited in the inner bark of the tree and feed on it. As this resource starts to be depleted by the high concentration of beetles present, they release a repelling pheromone to halt aggregation at the tree and shift the attack to adjacent trees. See [27, Sec. 6.7] for a description of efforts to quantitatively observe and model the movements of this pest.

Another, among many biological examples of movement quantification cited in that same book, involves a certain species of congregating male butterflies

[27, Sec. 4.5.2]. It is thought that these insects generally move in a straight line until they encounter “chasable” objects, conspecific butterflies of either gender. Then they begin frequently to change their direction, effectively localizing their position, until their time of flight is over, and they land. The attraction mechanism of either the pine beetles or the butterflies can, with some reinterpretation, be fit into the framework of our Section 3.2 below.

Many more biological examples involving migration and interaction can be observed in systems with several species (or genders or types) than in the present single species scenario. The models and bifurcation results in the present paper can be extended, with appropriate changes, to that more general situation; see Section 5.

It should be mentioned that explanations for biological patterning have very commonly been sought through bifurcation analyses of continuous-time models, contrary to our procedure. An interesting recent example is [6], in which a two-species PDE model for vegetation patchiness is constructed and analyzed.

It is intuitively clear that congregative movement of individuals, induced by conspecific attraction, will play a role in the existence of stable spatially patterned distributions. However, the details of this connection, as well as even the proper way to model such attraction in the context of discrete generation models, is far from being obvious. The difficulty is clear in the diffusion approach used by Turchin, and also in the relatively new integrodifference setting used here. We present a scenario wherein these things may be clarified.

Our main aims, therefore, are (1) to construct a basic framework, based on a balance law and movement laws, for modeling and analyzing discrete generation population processes, (2) to elucidate, in a linearized scenario, the nature of, and competition between, dispersion and congregation, and (3) to give conditions under which spatially patterned stationary population distributions bifurcate from spatially constant states. Especially revealing is the way the competition in (2) may provide the conditions for bifurcation in (3). Also regarding (2), we note that congregation comes from conspecific attraction; but by changing the sign of the coefficient of attraction, we can also treat corresponding repulsion mechanisms.

The basic redistribution-regulation framework is presented in Section 2. Section 3 is devoted to fundamental ideas appropriate to the study of redistribution-regulation laws for nearly constant populations. It is here that a careful study is made of dispersive and congregative migratory behavior (see Section 3.2). Under certain natural assumptions, the effects of these two modes of behavior on the redistribution operator are explored in detail, and the spectrum of the resulting derivative operator is given.

Specifically, the derivative $f'[c]$ at a constant population density c is found typically to have the following form, involving convolutions with a probability distribution $\phi_1(x)$ and a function $\phi_2(x)$, a real parameter A measuring the strength of the conspecific attraction, and a positive constant C :

$$f'[c]v = C[\phi_1 * v + A\phi_2 * v].$$

The prototypical form for ϕ_2 , which must satisfy $\int \phi_2(x)dx = 0$, will be seen to be $\phi_2 = \delta - \phi_3$ with ϕ_3 a probability distribution whose origin will be explained

in terms of the attraction mechanism. Although the actual distributions ϕ_i and the parameter A may be difficult to ascertain in concrete cases, examples are worked out in sections 3.3.1 and 3.3.2. Moreover they can be given generic interpretations in terms of dispersal and congregative mechanisms, and they figure in conditions under which bifurcation can occur. The bifurcation analysis for stationary patterns is presented in Sec. 4. Bifurcations are always of pitchfork type when the movement law is isotropic; whether they are subcritical and unstable or supercritical and stable is difficult to tell without detailed knowledge of the migration kinetics.

2. Balance laws

2.1. Movement laws

We speak of a population $u(x)$ distributed on the real line, although the same considerations carry over to higher dimensions. For mathematical reasons, we shall later restrict attention to densities $u(x)$ which are spatially periodic with fixed period Λ ; the patterned solutions which we find will then have wavelength Λ/m for some integer m . In reality, habitats are bounded and inhomogeneous. The periodicity assumption here, especially when Λ is large, is an attempt to model effects which are independent of boundaries and inhomogeneities.

Suppose there is a function $g(x, y, [u])$, depending on the entire function u (the density at the present generation) as well as on x and y , such that between the present time and the next generation, the number of individuals moving from the interval $(y, y + dy)$ to the interval $(x, x + dx)$ is given by $g(x, y, [u])dx dy$. Such a function g will be called a **movement law**, as in the book by Turchin [27]. Individuals may also die or reproduce, but we suppose that population changes due to those events take place after the movement phase considered here. They constitute the “regulation” phase, and will be considered later in section 2.3. Notice that by using this definition, we are implying that $g \geq 0$. There is no loss of generality in thus defining g so that individuals which move the opposite way, from x to y , can be accounted for by assigning them to the action $g(y, x, [u])$ with x and y interchanged. Of course there are intrinsic restrictions on possible movement laws. For one thing, they should not produce negative distributions at the next generation. Individuals which do not actually change positions in a generation will still be considered to migrate; just that their destination is the same as their starting point. With this understanding, the law g may contain a δ -function singularity to account for a possible fraction of the population which is sedentary. Moreover, the total number migrating from $(y, y + dy)$ must be $u(y)dy$, which implies the a priori restriction

$$\int_{-\infty}^{\infty} g(x, y, [u])dx = u(y). \quad (2.1)$$

(Although we work with Λ -periodic densities, the function g is not periodic; the integral in (2.1) exists.)

We assume the environment is spatially homogeneous, which implies that when $u \equiv c$ is constant, then g is a function only of the difference $x - y$:

$$g(x, y, [c]) = g_0^c(x - y), \quad (2.2)$$

where $g_0^c(r)$ is a nonnegative function (not necessarily even).

2.2. Redistributions

Since movement according to g does not entail births or deaths, knowing g now gives us, by simple accounting, an explicit expression for the population distribution $R[u]$ after the movement is completed:

$$R[u](x) = u(x) + \int_{-\infty}^{\infty} g(x, y, [u])dy - \int_{-\infty}^{\infty} g(y, x, [u])dy. \quad (2.3)$$

The first integral represents the change in the density at x due to individuals arriving from all other locations. The second integral, with its minus sign, is the change due to individuals leaving location x for any other location. We shall see that if u is periodic in x , these integrals may be replaced by integrals over the period interval $(0, \Lambda)$, g being replaced by a function \hat{g} dependent only on u and values of x and y in $[0, \Lambda]$.

Equation (2.3), then, is a **balance law**: it accounts for all changes in population in one generation due merely to the movement of individuals. The result is a redistribution of individuals. (Balance laws are fundamental in the study of continuum mechanics; they express conservation of such physical quantities as energy, momentum, and mass. They are generally supplemented by **constitutive relations** expressing perhaps the fluxes in terms of more basic physical quantities. In the present case, the specification of the function g would be such a constitutive relation.)

Although movement laws give rise to redistributions (2.3), a given redistribution R does not uniquely define a movement law. The movement of individuals can, in fact, be described on several different levels of detail. The least detailed is a redistribution law R . A movement law g provides more detail. The most detailed description would give individual trajectories (positions as functions of time) during the passage of a generation. We will not be indulging in this complete level of specificity, but nevertheless later in Section 3.3.1 will speak of certain statistics involving these trajectories. These statistics represent intermediate levels of detail between movement laws and individual trajectories.

Note that from (2.2) and (2.3),

$$R[c] = c \quad \text{for any constant } c. \quad (2.4)$$

The property (2.4) does not mean that movement does not occur when $u \equiv c$; just that its overall effect is nil.

2.3. Redistribution–regulation models

Redistribution–regulation models will be the primary focus of attention in this paper.

They are laws of the form (1.1), where

$$f[u] = F(R[u]) \quad (2.5)$$

with R a (generally nonlocal) redistribution process and F an ordinary local function. The nonlinear “regulation” function F reflects population changes due to births and deaths following the spatial movement. In the following it will be taken to be a nonnegative concave function for values of its argument in some interval $[0, U]$.

3. Linearization about constant population densities

Most of our analysis will be concerned with small deviations of the population around a positive constant value c . This provides a setting in which it is easier to grasp the competitive ideas of dispersion and congregation. Moreover, such a linearization is the starting point for our discussion of bifurcation of patterned stationary solutions in Sec. 4.

In preparation for this, we now examine certain basic properties of the movement law when the population is either constant or deviates by a small amount from a constant, so that the movement law can be approximated by a linear law.

3.1. Basic concepts for a constant density population

Suppose the density is constant, $u(x) \equiv c$. For any r , let

$g_0(r)dx dy$ = the number of individuals moving, in one generation, from the interval $(y, y + dy)$ to $(y + r, y + r + dx)$.

Here $g_0 \geq 0$ is the function already defined in (2.2) with the superscript c suppressed. Then

$$c = \int_{-\infty}^{\infty} g_0(r)dr, \quad (3.1)$$

which is a special case of (2.1). Here it should be explained again that not every individual is assumed to migrate; some fraction of the population may “stay put”. The sedentary individuals contribute a δ -function singularity at $r = 0$ to the function g_0 . Thus if the sedentary fraction is θ_s , then possibly $g_0(r) = c\theta_s\delta(r) + g_{01}(r)$, where g_{01} is regular and $\int_{-\infty}^{\infty} g_{01}(r)dr = (1 - \theta_s)c$.

The basic “ground state” movement law g_0 may incorporate any number of effects, linear or nonlinear, such as those described below in Section 3.2. We are not at the moment concerned with the identity of those effects, but rather wish to concentrate on small changes to the basic law due to variations in the density. In Section 3.2, we show how those changes might be generated by certain properties of the migration kinetics of individuals in the homogeneous background.

Because of (3.1), the function $\frac{g_0(r)}{c}$ has the properties of a probability distribution, and in fact can be interpreted on the level of single individuals:

Important observation: $\frac{g_0(r)}{c}dr$ is the probability that a given individual will migrate a distance in the interval $(r, r + dr)$ in the course of a generation. Since $u \equiv c$, the individual moves in a homogeneous background environment.

We use the notation $\phi_1(r) = \frac{g_0(r)}{c}$.

3.2. Some specific migration effects

Identifying the correct, or even a feasible, movement law g in specific cases may be difficult; particularly finding its dependence on $[u]$. We present a scenario in which the population distribution is almost constant:

$$u(x) = c + v(x), \quad |v| \ll c, \quad (3.2)$$

and examine some general dispersive and congregative influences that the deviation from constancy may have on g . It is based in part on the concept of residence times. Our objective is to identify the possible origin of changes in the movement law $g(x, y, [c + v])$ due to the increment v , which we will term the excess population (even though it may be negative). Using the notation Dg for the derivative of g with respect to u , we make the linearized approximation (see below) $g(x, y, [c + v]) \approx g(x, y, [c]) + Dg(x, y, [c])v$. We shall find some possible forms that $Dg(x, y, [c])v$ may take, in terms of (1) the basic unperturbed kinetics of individuals when $v = 0$, and (2) a linear mechanism of attraction/repulsion to/from other members of the population (this may give rise to a congregative effect.)

To justify the linear approximation under the simple assumption $|v| \ll c$, we normalize the population density and rate of movement by the constant c , defining $\tilde{u} = \frac{u}{c} = 1 + \frac{v}{c}$, and

$$\tilde{g}(x, y, [\tilde{u}]) \equiv \frac{1}{c}g(x, y, c[\tilde{u}]),$$

and make the basic assumption that

$\tilde{g}(x, y, [\tilde{u}]) = (\tilde{g}(x, y, [1]) + D\tilde{g}(x, y, [1])\frac{v}{c})(1 + o(\frac{v}{c}))$. Neglecting the error term, we obtain the given linear approximation.

We will find that it is natural to split the linear operator Dg into three parts: $D_1g + D_2g + D_3g$, each associated with a different mechanism. The three mechanisms are characterized by dispersion, congregation, and depletion. The last two parts, D_2g and D_3g , rely on conspecific attraction (or repulsion, which is negative attraction). Later we combine these two into a single effect.

Because we are operating on a linearized level, the interactions of the effects producing the D_i may be neglected, and they can be studied independently of one another.

This decomposition of Dg induces a corresponding decomposition of the differential DR (2.3). One of our main goals will be to display, in (3.34), the convolution representation

$$(DR[c]v)(x) = \phi_1 * v(x) - A\phi_2 * v(x), \quad (3.3)$$

where the two convolution terms come, in an explicit way, from dispersion and congregation, respectively. The function $\phi_1 \geq 0$ is a probability distribution, A is a constant measuring the strength of conspecific attraction, and $\int \phi_2(x)dx = 0$. The prototypical expression for ϕ_2 is $\phi_3 - \delta$, where ϕ_3 is a probability distribution.

From this representation, the spectrum of the linear operator DR can be written (Section 3.5).

3.2.1. Dispersion

First, we introduce the dispersive property of an individual moving in the background environment of a uniform population distribution, $u \equiv c$.

For simplicity, consider individuals beginning their intergenerational migration from the origin, $y = 0$. There will be a dispersion kernel $\phi_1(r)$, which is a probability distribution for the signed distance (since r could be negative) an individual

migrates in one generation. According to Section 3.1, we may identify ϕ_1 with a scaled version of g_0 :

$$\phi_1(r) = \frac{g_0(r)}{c}, \quad (3.4)$$

so that ϕ_1 may have a δ -function singularity at $r = 0$.

To obtain the corresponding increment in the movement law due to v and this one effect, we multiply by the excess population $v(0)$ at the originating point 0. We express the resulting increment in g as

$$D_1g(x, 0, [c])v(x) \equiv \phi_1(x)v(0). \quad (3.5)$$

More generally,

$$D_1g(x, y, [c])v(x) \equiv \phi_1(x - y)v(y). \quad (3.6)$$

We next look at the influence exerted by other members of the population in the course of the migrant's journey. Again, consider movements of individuals in the environment $u \equiv c$. The ultimate destinations of the migrants are described approximately by the probability distribution $\phi_1(x)$; but we now also consider certain properties of the trajectories enroute to those destinations, related to residence times.

3.3. Congregative effects

We have found in (3.6) the effect due to the excess population v at the point of departure y ; we now consider the possible effects of v at other locations. We shall postulate a linear attraction/repulsion mechanism that the migrant may have to/from existing individuals. When $u \equiv c$ is constant, this effect (and possibly many others) has already been incorporated into the basic flow. But when $v \neq 0$ in (3.2), it can be formulated with the aid of a postulate of conspecific attraction, to be given below (3.28), plus the concept of residence times. The postulate essentially says that a migrant is induced to terminate its journey at a given location with a probability proportional to how much time it spends near that location (residence time) times the excess population density there.

Initially, we shall assume that the attraction depends on the excess population $v(x)$ only at the beginning of the generation. Later, building on this analysis, we shall indicate extensions that can be made to account for the intergenerational variation in v .

First, we explain the concept of residence time.

3.3.1. Residence times

Although we will not assume known all the statistical properties of the movement of individuals in the interval between generations, we refer symbolically to their unknown paths of migration in order to define the properties we shall need. So consider the possible dynamics of individuals from time $t = 0$ to $t = 1$. We suppose they move in two stages: (1) a migratory phase lasting a generally random period

of time $t_\ell \leq 1$, followed by (2) a quiescent phase during which their position x_ℓ does not change. By homogeneity, there is no loss of generality in assuming the migrant begins its journey (at $t = 0$) at the origin. Let $X(t)$ be the migration path. The time of landing t_ℓ and the location x_ℓ of the landing are random quantities. Since no one moves after landing, $x_\ell = X(t_\ell) = X(1)$ is also the location of the individual at time $t = 1$.

Let $K(x, t)$, $0 < t < 1$, be the distribution of locations $X(t)$ of those individuals with $X(0) = 0$ that are still migrating at time t . More specifically, for fixed t , $\int_{a_1}^{a_2} K(x, t) dx$ is the probability that an individual will be still migrating at time t (i.e. $t < t_\ell$), and moreover is located then in the interval $[a_1, a_2]$. Also we set

$$T_r(a_1, a_2) = \int_0^1 \int_{a_1}^{a_2} K(x, s) dx ds; \tag{3.7}$$

it is the *total expected residence time* in (a_1, a_2) , i.e. the total expected time that an individual will spend in that interval during the migratory phase. The residence time counts only the time the individual is in that interval while still moving; when the migrant “lands”, its clock stops.

The *specific expected residence time* is

$$\bar{\tau}(x) = \frac{d}{dx} T_r(-\infty, x) = \int_0^1 K(x, s) ds. \tag{3.8}$$

Summing, we find that

$$\int_{-\infty}^{\infty} \bar{\tau}(x) dx \doteq \theta \tag{3.9}$$

is the total expected migration time. Being a fraction of the unit generation time, $\theta \in [0, 1]$.

We now calculate $\bar{\tau}$ and θ for two special movement laws.

Example 1: Movement at constant speed and direction. As a first canonical example, suppose that for some constant speed $|q| > 0$, every individual in the migratory stage moves with constant velocity $q = |q|$ or $-|q|$ with equal probability (unequal probability could be handled with a slight extension of the following). It will always move away from the origin, either right or left. The location x_ℓ where the movement stops is random, with probability distribution $\frac{g_0(x_\ell)}{c} = \phi_1(x_\ell)$. In this example, no migrant can travel further than the distance $|q|$ in one generation, so that $\phi_1(x) = 0$ for $|x| > |q|$.

First, suppose $q = |q| > 0$ (Case 1). The probability that a migrant has not stopped ($t < t_\ell$) and lies in $(-\infty, x)$ at time t is 0 if $qt > x$, because during this time it will have remained in the migratory stage, so it would have moved a distance $qt \notin (-\infty, x)$. On the other hand if $qt < x$, this probability is simply the probability of not stopping (still moving) while it travels to the location qt , i.e.

the probability that $x_\ell \geq qt$. This probability is $\int_{|q|t}^{\infty} \phi_1(\xi) d\xi$. Thus for Case 1 we have, in terms of the Heaviside function H ,

$$Pr(t < t_\ell, X(t) < x \mid q > 0) = 2 \int_{|q|t}^{\infty} \phi_1(\xi) d\xi H(x - |q|t). \quad (3.10)$$

By similar reasoning, we know that if $q = -|q| < 0$ (Case 2), then this same probability is

$$Pr(t < t_\ell, X(t) < x \mid q < 0) = 2 \int_{-\infty}^{-|q|t} \phi_1(\xi) d\xi H(x + |q|t). \quad (3.11)$$

Since the two cases occur with equal probability, we have

$$\begin{aligned} Pr(t < t_\ell, X(t) < x) &= \int_{|q|t}^{\infty} \phi_1(\xi) d\xi H(x - |q|t) \\ &\quad + \int_{-\infty}^{|q|t} \phi_1(\xi) d\xi H(x + |q|t). \end{aligned} \quad (3.12)$$

Differentiating with respect to x , we get

$$\begin{aligned} K(x, t) &= \frac{d}{dx} Pr(t < t_\ell, X(t) < x) \\ &= \int_{|q|t}^{\infty} \phi_1(\xi) d\xi \delta(x - |q|t) + \int_{-\infty}^{-|q|t} \phi_1(\xi) d\xi \delta(x + |q|t); \end{aligned} \quad (3.13)$$

$$\begin{aligned} \bar{\tau}(x) &= \int_0^1 K(x, s) ds = \int_0^1 \int_{|q|t}^{\infty} \phi_1(y) dy \delta(x - |q|t) dt \\ &\quad + \int_0^1 \int_{-\infty}^{-|q|t} \phi_1(\xi) d\xi \delta(x + |q|t) dt \\ &= \int_0^{|q|} \frac{1}{|q|} \int_{t'}^{\infty} \phi_1(\xi) d\xi \delta(x - t') dt' - \int_0^{-|q|} \frac{1}{|q|} \int_{-\infty}^{t'} \phi_1(\xi) d\xi \delta(x - t') dt' \\ &= \frac{1}{|q|} \int_x^{\infty} \chi_{[0, |q|]}(x) \phi_1(\xi) d\xi + \frac{1}{|q|} \int_{-\infty}^x \chi_{[-|q|, 0]}(x) \phi_1(\xi) d\xi \\ &= \frac{1}{|q|} \chi_{[0, |q|]}(x) \int_x^{\infty} \phi_1(\xi) d\xi + \frac{1}{|q|} \chi_{[-|q|, 0]}(x) \int_{-\infty}^x \phi_1(\xi) d\xi, \end{aligned} \quad (3.14)$$

where χ_A denotes the characteristic function of a set A .

Finally, by (3.9), (3.14) and the fact that $\phi_1 = 0$ for $|x| > |q|$,

$$\begin{aligned} \theta &= \frac{1}{|q|} \left[\int_0^{|q|} |\xi| \phi_1(\xi) d\xi + \int_{-|q|}^0 |\xi| \phi_1(\xi) d\xi \right] \\ &= \frac{1}{|q|} \int_{-|q|}^{|q|} \phi_1(\xi) |\xi| d\xi < \int_{-|q|}^{|q|} \phi_1(\xi) d\xi = 1. \end{aligned} \quad (3.15)$$

Example 2: Brownian motion. This is a limit of random walk migration patterns. Assume that the random walk proceeds without stopping, until $t = 1$. Thus $t_\ell = 1$. We have

$$K(x, t) = \frac{1}{\sqrt{4\sigma t\pi}} \exp\left(-\frac{x^2}{4\sigma t}\right), \tag{3.16}$$

where σ is the Brownian parameter. Also by (3.8),

$$\bar{\tau}(x) = \int_0^1 \frac{1}{\sqrt{4\sigma t\pi}} \exp\left(\frac{-x^2}{4\sigma t}\right) dt.$$

By first treating the case $x > 0$, changing to the integration variable $y = x/\sqrt{4\sigma t}$, and then observing that $\bar{\tau}(x)$ is even in x , we obtain

$$\bar{\tau}(x) = \frac{\zeta}{\sqrt{\sigma\pi}} \int_\zeta^\infty y^{-2} \exp(-y^2) dy, \tag{3.17}$$

where $\zeta = \frac{|x|}{2\sqrt{\sigma}}$.

Of course since $t_\ell = 1$, we also have $\theta = 1$.

3.3.2. Conditional residence times

We go one step further. Let $\tilde{K}(\xi, x, t)$ be the distribution in ξ , at time t , of positions $\xi = X(t)$ of migrants with $X(0) = 0$ and $X(1) = x$, i.e., $x_\ell = x$.

Analogous to (3.7), the conditional expected residence time for (a_1, a_2) under the condition $x_\ell = x$ is

$$T_r(a_1, a_2; x) = \int_0^1 \int_{a_1}^{a_2} \tilde{K}(\xi, x, s) d\xi ds,$$

and the specific conditional expected residence time at ξ is

$$\hat{\tau}(\xi, x) = \frac{d}{d\xi} T_r(-\infty, \xi; x) = \int_0^1 \tilde{K}(\xi, x, s) ds. \tag{3.18}$$

Also

$$\tilde{K}(\xi, x, t) = \frac{d}{d\xi} Pr(t < t_\ell, X(t) < \xi \mid x_\ell = x). \tag{3.19}$$

Using the definition of conditional distribution function as in [5], we have

$$\begin{aligned} Pr(t < t_\ell, X(t) < \xi \mid x_\ell = x) &= \frac{\frac{d}{dx} Pr(t < t_\ell, X(t) < \xi, x_\ell < x)}{\frac{d}{dx} Pr(x_\ell < x)} \\ &= \frac{\frac{d}{dx} Pr(t < t_\ell, X(t) < \xi, x_\ell < x)}{\phi_1(x)}. \end{aligned} \tag{3.20}$$

Example 1 revisited. Referring again to the constant speed example given above, we find the following probability relations. First, assume $x \geq 0$. Under this condition $q = |q|$. Also notice that from (3.20), $t < t_\ell$ is equivalent with $X(t) = |q|t < x_\ell$. Thus

$$\begin{aligned} Pr(t < t_\ell, X(t) < \xi \mid x_\ell = x) &= \frac{\frac{d}{dx} Pr(|q|t < x_\ell < x, |q|t < \xi)}{\phi_1(x)} \\ &= \frac{\frac{d}{dx} \left(\int_{|q|t}^x \phi_1(y) dy H(x - |q|t) \right) H(\xi - |q|t)}{\phi_1(x)} \\ &= H(x - |q|t)H(\xi - |q|t). \end{aligned} \tag{3.21}$$

To see this more clearly, consider for example the case that $x > |q|t$ and $\xi > |q|t$. The right side of (3.21) is 1. We verify independently that the left side is also 1. In this case, $x_\ell = x$ implies that $x_\ell > |q|t$, so that the migrant hasn't stopped, and $t < t_\ell$. Hence $X(t) = |q|t$, so that $X(t) < \xi$. Therefore the probability on the left of (3.21) is indeed 1.

From (3.21) and (3.19) we have

$$\tilde{K}(\xi, x, t) = \delta(\xi - |q|t)H(x - |q|t). \tag{3.22}$$

In the opposite case, when $x < 0$ and thus $q = -|q| < 0$, we similarly obtain

$$\tilde{K}(\xi, x, t) = \delta(\xi + |q|t)H(-|q|t - x). \tag{3.23}$$

These two expressions characterise the desired probability for any landing point $x_\ell = x$ and

$$\begin{aligned} \hat{\tau}(\xi, x) &= \int_0^1 \tilde{K}(\xi, x, s) ds \\ &= \frac{1}{|q|} [H(x - \xi)\chi_{[0, |q|]}(\xi) + H(-x + \xi)\chi_{[-|q|, 0]}(\xi)]. \end{aligned} \tag{3.24}$$

Example 2 revisited. These quantities can be worked out explicitly also in the case of Brownian motion. Specifically, since $t_\ell = 1$, we have $K(x, 1) = \phi_1(x)$, so that with K given by (3.16),

$$\begin{aligned} Pr(t < t_\ell, X(t) < \xi, x_\ell < x) &= \int_{-\infty}^x dz \int_{-\infty}^\xi dy K(y, 1)K(z - y, 1 - t), \\ \tilde{K}(\xi, x, t) &= \frac{\frac{\partial^2}{\partial x \partial \xi} \int_{-\infty}^x dz \int_{-\infty}^\xi dy K(y, 1)K(z - y, 1 - t)}{K(x, 1)} \\ &= \frac{K(\xi, 1)K(x - \xi, 1 - t)}{K(x, 1)}, \end{aligned} \tag{3.25}$$

$$\hat{\tau}(\xi, x) = \int_0^1 \tilde{K}(\xi, x, s) ds. \tag{3.26}$$

So in the examples, the functions $\bar{\tau}$ and $\hat{\tau}$ can be readily found.

Remark In all cases, the conditional and unconditional probabilities are related as follows:

$$\bar{\tau}(\xi) = \int_{-\infty}^{\infty} \hat{\tau}(\xi, x) \phi_1(x) dx. \quad (3.27)$$

The reason is that $\phi_1(x)dx$ is the probability that x_ℓ lies in $(x, x + dx)$. This relation could be verified in the examples.

These quantities are always simply a matter of kinetics. We assume that they do not depend on the population distribution, except through the removal and addition of individuals to the group of migrants, which will be our main concern. Among other things, this means that the attraction or repulsion that an individual may feel in the presence of the extra population v does not make the migration speed decrease or increase, so that the residence times are not changed. We allow that an individual may terminate its journey more readily, for example, where the population is denser, but the termination must be done instantaneously.

3.3.3. Interactions with existing excess population

This postulate refers only to individuals which are induced to terminate their journey (land) near the location x due to attraction to the excess population. It is responsible for two other increments in g , analogous to the one in (3.6).

Postulate of conspecific attraction:

$$Pr [\text{landing in } (x, x + dx)] = \alpha \bar{\tau}(x) v(x) dx, \quad (3.28)$$

which we now explain. Of course the probability should be proportional to the interval size dx . The other factor $\alpha \bar{\tau}(x) v(x)$, representing the influence of others, is of the form $B v(x)$, since that influence should be proportional to how many others there are, when there are few. The factor B , representing the intensity of the attraction effects, depends on how long the individual, while migrating, stays in that neighborhood. If its residence time $T_r(x, x + dx) = \tau(x) dx$ (3.7) were known, then $B = \alpha \tau(x)$, where α (which has dimensions of inverse time) is the rate of attraction (in the following we denote repulsion by negative attraction). But since we only know a probability distribution for τ , we must set $B = \alpha \bar{\tau}(x)$. Thus τ is replaced by its expected value. This is the rationale for postulate (3.28), except that we have neglected any dependence of the function v , hence the left side of (3.28), on t . That will be considered in Sec. 3.4. .

Now the number of individuals originating in the interval $(0, dy)$ which land in $(x, x + dx)$ due to attraction is this probability (3.28) times the total number of potential migrants leaving from the interval $(0, dy)$. This latter number (except for higher order terms, which we neglect) is given by $c dy$. Therefore the number of individuals landing in that interval due to attraction is

$$c \alpha \bar{\tau}(x) v(x) dx dy \quad (3.29)$$

This effect, attraction to other individuals at the final location x , thus gives rise to an additional increment, besides D_1 (3.5), namely

$$(D_2g(x, 0, [c])v)(x) = c\alpha\bar{\tau}(x)v(x), \quad (3.30)$$

where higher order terms have also been neglected.

We pass on to a third effect. The number migrating from $(0, dy)$ to $(x_\ell, x_\ell + dx)$, namely $g_0(x_\ell)dx dy$ (once again neglecting higher order terms), has to be modified by the action of depletion enroute to the destination. That is, it may be reduced since some of the migrants will be attracted to other excess individuals during the course of the migration. The probability of a migrant being removed from the migrating population this way is given by

$$\alpha \int_{-\infty}^{\infty} \hat{\tau}(\xi, x_\ell)v(\xi)d\xi. \quad (3.31)$$

This integral (3.31) samples all possible locations ξ where the migrant may be induced to leave its normal trajectory due to attraction by the excess population $v(\xi)$. The strength of this attraction is proportional to the conditional residence time $\hat{\tau}(\xi, x)$ as well as to $v(\xi)$.

The arriving population size is therefore reduced from $g_0(x_\ell)dx dy$ to

$$[1 - \alpha \int \hat{\tau}(\xi, x_\ell)v(\xi)d\xi]g_0(x_\ell)dx dy.$$

The effect of this depletion is to introduce a third increment in g :

$$(D_3g(x, 0, [c])v)(x) = -\alpha \int_{-\infty}^{\infty} \hat{\tau}(\xi, x)v(\xi)d\xi g_0(x). \quad (3.32)$$

3.3.4. Summing up

In all, we have the total change in g ((3.5), (3.30), (3.32)) given by

$$\begin{aligned} (Dg(x, 0, [c])v)(x) &= ((D_1 + D_2 + D_3)g(x, 0, [c])v)(x) \\ &= \phi_1(x)v(0) + c\alpha\bar{\tau}(x)v(x) - \alpha \int_{-\infty}^{\infty} \hat{\tau}(\xi, x)v(\xi)d\xi g_0(x) \end{aligned} \quad (3.33)$$

Theorem 3.1. *The expression (3.33) implies the validity of the representation*

$$(DR[c]v)(x) = \phi_1 * v(x) - \alpha c\theta(\phi_3 * v(x) - v(x)). \quad (3.34)$$

for DR in terms of certain probability distributions $\phi_1(x)$ and $\phi_3(x)$ (defined below).

Proof. From (3.33), we have

$$(Dg(x, 0, [c])v)(x) = \int_{-\infty}^{\infty} G(x, 0, \xi)v(\xi)d\xi, \quad (3.35)$$

where

$$G(x, 0, \xi) = \phi_1(x)\delta(\xi) + \alpha c \bar{\tau}(x)\delta(x - \xi) - \alpha c \phi_1(x)\hat{\tau}(\xi, x).$$

We have thus far looked only at the flow originating near $y = 0$. But the same holds for any value of y . We obtain, in place of (3.35),

$$(Dg(x, y, [c])v)(x) = \int_{-\infty}^{\infty} G(x, y, \xi)v(\xi)d\xi, \tag{3.36}$$

where

$$G(x, y, \xi) = \phi_1(x - y)\delta(\xi - y) + \alpha c \bar{\tau}(x - y)\delta(x - \xi) - \alpha c \phi_1(x - y)\hat{\tau}(\xi - y, x - y). \tag{3.37}$$

As a side comment, using expression (3.37), we may check that g satisfies the condition in (2.1), i.e.,

$$\int_{-\infty}^{\infty} dx \int_{-\infty}^{\infty} G(x, y, \xi)v(\xi) d\xi = v(y). \tag{3.38}$$

For this, note by (3.27) that

$$\int_{-\infty}^{\infty} \phi_1(x - y)\hat{\tau}(\xi - y, x - y)dx = \bar{\tau}(\xi - y).$$

And from (3.37),

$$\int_{-\infty}^{\infty} G(x, y, \xi)dx = \delta(\xi - y) + \alpha c \bar{\tau}(\xi - y) - \alpha c \bar{\tau}(\xi - y) = \delta(\xi - y).$$

Hence (3.38) follows.

Now applying (3.36) to the derivative of (2.3) at $u = c$, we find

$$\begin{aligned} (DR[c]v)(x) &= v(x) + \int_{-\infty}^{\infty} (Dg(x, y, [c])v)(y)dy - \int_{-\infty}^{\infty} (Dg(y, x, [c])v)(y)dy \\ &= v(x) + \int_{-\infty}^{\infty} dy \left(\int_{-\infty}^{\infty} d\xi v(\xi)[G(x, y, \xi) - G(y, x, \xi)] \right). \end{aligned} \tag{3.39}$$

We calculate from (3.37) and (3.9)

$$\begin{aligned} G(x, y, \xi) - G(y, x, \xi) &= \phi_1(x - y)\delta(\xi - y) \\ &\quad - \phi_1(y - x)\delta(\xi - x) + \alpha c \bar{\tau}(x - y)\delta(\xi - x) - \alpha c \bar{\tau}(y - x)\delta(\xi - y) \\ &\quad - \alpha c \phi_1(x - y)\hat{\tau}(\xi - y, x - y) + \alpha c \phi_1(y - x)\hat{\tau}(\xi - x, y - x); \end{aligned}$$

$$\begin{aligned}
 \int_{-\infty}^{\infty} dy [G(x, y, \xi) - G(y, x, \xi)] &= \phi_1(x - \xi) - \delta(\xi - x) \\
 &+ \alpha c \theta \delta(x - \xi) - \alpha c \bar{\tau}(\xi - x) - \alpha c \int_{-\infty}^{\infty} \phi_1(x - y) \hat{\tau}(\xi - y, x - y) dy \\
 &+ \alpha c \int_{-\infty}^{\infty} \phi_1(y - x) \hat{\tau}(\xi - x, y - x) dy \\
 &= \phi_1(x - \xi) - \delta(\xi - x) + \alpha c \theta \delta(x - \xi) - \alpha c \bar{\tau}(\xi - x) \\
 &- \alpha c \int_{-\infty}^{\infty} \phi_1(x - y) \hat{\tau}(\xi - y, x - y) dy + \alpha c \bar{\tau}(\xi - x) \\
 &= \phi_1(x - \xi) - \delta(\xi - x) + \alpha c \theta \delta(x - \xi) \\
 &- \alpha c \int_{-\infty}^{\infty} \phi_1(x - y) \hat{\tau}(\xi - y, x - y) dy.
 \end{aligned}$$

Finally

$$\begin{aligned}
 \int_{-\infty}^{\infty} dy \int_{-\infty}^{\infty} d\xi v(\xi) [G(x, y, \xi) - G(y, x, \xi)] \\
 = \phi_1 * v(x) - v(x) + \alpha c \theta v(x) - \alpha c \psi * v(x),
 \end{aligned} \tag{3.40}$$

where

$$\psi(x - \xi) = \int_{-\infty}^{\infty} \phi_1(x - y) \hat{\tau}(\xi - y, x - y) dy. \tag{3.41}$$

To see that this integral is a function only of the combination $(x - \xi)$, change the variable of integration from y to $\omega = x - y$ to convert the integral to

$$\int_{-\infty}^{\infty} \phi_1(\omega) \hat{\tau}(\omega - (x - \xi), \omega) d\omega \equiv \psi(x - \xi). \tag{3.42}$$

Clearly $\psi(x) \geq 0$. We calculate, by (3.9), (3.27),

$$\begin{aligned}
 \int_{-\infty}^{\infty} \psi(x) dx &= \int_{-\infty}^{\infty} dy \int_{-\infty}^{\infty} \phi_1(x) \hat{\tau}(\xi - y, x) dx \\
 &= \int_{-\infty}^{\infty} \bar{\tau}(\xi - y) dy = \int_{-\infty}^{\infty} \bar{\tau}(\eta) d\eta = \theta.
 \end{aligned} \tag{3.43}$$

The function

$$\phi_3(x) = \frac{\psi(x)}{\theta} \tag{3.44}$$

is therefore a probability density and (3.40), (3.39) imply (3.34), which completes the proof.

This is where, partly for mathematical reasons, we assume that u and v are periodic functions of x . Space may be rescaled, so there is no loss of generality in

taking the period to be 2π . In place of (3.34), it may be natural to seek a representation of $DR[c]$ involving only integrals over the interval $[0, 2\pi]$. This can be done by expressing the convolutions in the form

$$\begin{aligned}\phi * v(x) &= \int_{-\infty}^{\infty} \phi(x-y)v(y)dy = \sum_m \int_0^{2\pi} \phi(x-y+2m\pi)v(y)dy \\ &= \int_0^{2\pi} \phi^P(x-y)v(y)dy,\end{aligned}\tag{3.45}$$

where

$$\phi^P(x) = \sum_m \phi(x+2m\pi), \quad x \in [0, 2\pi].$$

It can be checked directly that

$$\int_0^{2\pi} (DR[c]v)(x)dx = \int_0^{2\pi} v(x)dx,\tag{3.46}$$

which is consistent with (2.3) being a balance law.

3.4. Accounting for the time variation of v

In the previous subsection, the basic postulate (3.28) was used to construct an expression (3.34) for the differential DR involving two probability distributions ϕ_1 and ϕ_3 , the latter fashioned in an explicit but involved way in terms of residence times. However, a simplified interpretation of (3.28) was used: the function $v(x)$ there was meant to signify the population distribution at the beginning of the generation rather than at the time we are computing the probability of landing. This section is devoted to showing how this possible modeling inadequacy can largely be overcome.

Consider the duration of the generation to be divided into m equal time intervals, each of length $1/m$. The total change during the generation will then be the sum of changes during each interval. If the time interval $1/m$ is small, we may use the expression (3.34) to account approximately for the change $D_i R$ in R during the i -th subinterval. Note that the convolution functions in (3.34) depend on i ; we write this version of (3.34) as

$$(D_i R[c]v)(x, i/m) = \phi_1^i * v(x, i/m) - A(\phi_2^i * v(x, i/m))\tag{3.47}$$

where $A = \alpha c\theta$. Here we have written $\phi_2^i = \phi_3^i - \delta$, and the superscript i denotes the subinterval. The total change during the generation is then the composition of these m linear differential operators $D_i R$. This composition can be taken as our model. We show that the new dR remains of the form (3.3). Note that each ϕ_2^i satisfies

$$\int \phi_2^i(x)dx = 0;\tag{3.48}$$

this will be the crucial property of those functions, which of course were derived from consideration of residence times.

Note also that the composition of linear operators of the form (3.47), (3.48), is an operator of the same type.

Finally, observe that the composition of the random dispersal operators $\phi_1^i *$ is a random dispersal operator over the combined time interval. Thus $(\phi_1^2 *) (\phi_1^1 *)$ describes dispersion over the time interval $[0, 1/m]$ with the original kernel ϕ_1 , and so on. Therefore the composition of all m operators produces

$$DR[c]v(x) = \prod_{i=0}^{m-1} (D_i R[c])v(x) = \phi_1 * v(x) - A\phi_2(x, A), \tag{3.49}$$

for some function ϕ_2 satisfying (3.48). It will depend on A in a polynomial fashion. The function ϕ_1 here is the given dispersion kernel over one generation.

3.5. The spectrum of $DR[c]$

For a 2π -periodic function $g(\xi)$ we denote its scaled Fourier Transform by

$$\hat{g}(k) = \int_0^{2\pi} e^{ik\xi} g(\xi) d\xi, \tag{3.50}$$

for every integer k . Similarly, although our probability kernels ϕ_i are not periodic, their transforms are defined the same way, integrating over all space. Set $e_k(x) = e^{ikx}$. Note that $\int_0^{2\pi} e^{ikx} (\phi_i^p * v)(x) dx = \hat{\phi}_i^p(k) \hat{v}(k)$ and $(\phi_i^p * e_k)(x) = \hat{\phi}_i^p(k) e^{ikx}$. Also $\hat{\phi}_i(k) = \hat{\phi}_i^p(k)$.

Applying the operator $DR[c]$ to $e_k = e^{ikx}$, we find from (3.49) that

$$DR[c]e_k(x) = \hat{\phi}_1(k)e^{ikx} - A\hat{\phi}_2(k, A)e^{ikx} \equiv \hat{R}(k)e_k(x), \tag{3.51}$$

$$\hat{R}(k) = \hat{\phi}_1(k) - A\hat{\phi}_2(k, A), \tag{3.52}$$

where $A = \alpha c \theta$ can be considered a dimensionless parameter measuring the strength of the conspecific attraction. Thus e_k are the eigenfunctions of the operator $DR[c]$, with eigenvalues $\hat{R}(k)$.

Recall that ϕ_1 is a probability distribution which governs random dispersion, and ϕ_2 governs congregation. These kernels may be difficult to measure precisely in any example existing in nature; nevertheless it is important to know the typical form (3.49) that $DR[c]$ takes, and the interpretation of the parameter $A = \alpha c \theta$ as measuring the strength of the attraction mechanism, whatever that may be. It is also important to recall the prototypical form (3.33): $\phi_2 = \phi_3 - \delta$ where ϕ_3 is a probability distribution. As regards the appearance of patterned solutions, the most important property concerns the value k^* of k at which $|\hat{R}(k)|$ has a maximum. For bifurcation, we need

$$k^* \neq 0, \quad |\hat{R}(k^*)| > 1.$$

As we shall see in Sec. 5, sufficient conditions, in terms of the variances of the ϕ_i and A , for this to happen in the prototypical case can be given. Necessary conditions will also be given.

To reiterate, the basic random dispersion mechanism in spectral form $\hat{\phi}_1(k)$, associated with (3.5), is tempered with a term $-c\alpha\theta\hat{\phi}_2(k)$ due to congregation. If $\alpha < 0$, so that repulsion replaces attraction, then both terms appear dispersive, but in fact the sum is not. In this case, the movement law is such that when $v(x) > 0$, the number of individuals migrating away from a neighborhood of x due to the presence of that excess is greater than that excess itself.

If only linear dispersion occurs, then the spectrum $|\hat{R}(k)| \leq 1$; and < 1 when $k \neq 0$.

The isotropic case. If $\phi_1(x)$ and $\bar{\tau}(x)$ are even (see (3.4), (3.8)), so that in this sense the movement law is isotropic, it can be shown that the ϕ_i functions are also even. It then follows from (3.34) that $DR[c]$ is given by convolutions with even functions, and therefore that $\hat{R}(k)$ is real and even in k . Therefore the relation (3.51) reduces to

$$DR(\cos kx) = \hat{R}(k) \cos kx, \tag{3.53}$$

and the set of eigenfunctions in this case consists of cosines.

3.6. Spectrum of the linearization

3.6.1. The anisotropic case

We take our basic space \mathcal{S} to consist of periodic functions in x with period (wavelength) 2π , which are L_2 within a period.

We have

$$Df[c]v = F'(c)DR[c]v, \tag{3.54}$$

where the derivative $DR[c]$ is given by (3.34).

The eigenvalues and eigenfunctions can be enumerated by integers k . The eigenfunctions

$$\psi_k \equiv \sqrt{\frac{1}{2\pi}} e^{ikx}, \quad k = 0, \pm 1, \pm 2, \dots \tag{3.55}$$

lie in the class of functions \mathcal{S} we are considering for u . Moreover, they form a complete orthonormal basis for \mathcal{S} , in terms of the L_2 norm.

It is seen from (3.51) that the eigenvalues of $Df[c]$ are

$$\hat{L}(k) = F'(c)\hat{R}(k), \tag{3.56}$$

where $\hat{R}(k)$, the eigenvalues of R , are given by (3.52).

Thus the infinite discrete set of functions ψ_k , for all integers $k \geq 0$, form a complete set of eigenfunctions with associated eigenvalues $\hat{L}(k)$.

3.6.2. The isotropic case

Isotropy implies, among other things, that the function $g_0(r) = g_0^c(r)$ (2.2), hence $\phi_1(r)$ (3.4), is even in r . The same is true of $\bar{\tau}(x)$, and finally we have $\hat{\tau}(x, \xi) = \hat{\tau}(-x, -\xi)$.

It follows that $\phi_i(x)$ are even, and hence $\hat{\phi}_i(k)$ in (3.51) and (3.52) are even. Since now $\hat{R}(-k) = \hat{R}(k)$, each eigenvalue $\hat{R}(k)$ of $DR([c])$ is double: e^{ikx} and e^{-ikx} are both eigenfunctions of the same eigenvalue. This is normally disallowed by assumption 4.3 to be given below. However, reconciliation may be effected by redefining \mathcal{S} . In the case of isotropy, we take our basic space \mathcal{S} to be a subspace of the one before, namely the subspace of even functions.

With this difference, the assumptions below will be seen to be reasonable in both the isotropic and anisotropic cases.

4. Bifurcation of patterned solutions from constants

We shall now revert to the original expression (1.1), with a bifurcation parameter μ adjoined.

$$u' = \mu f[u] = \mu F(R[u]), \quad (4.1)$$

where $u(x)$ is a population distribution lying in \mathcal{S} and f is a redistribution-regulation function from \mathcal{S} to itself with certain properties to be given below in the following section.

Our object will be to find a value μ^* of μ , such that when μ is near μ^* (perhaps restricted to one side of it), there is a constant population level c_μ , such that small amplitude spatially patterned stationary solutions, which are perturbations of c_μ , appear. They arise through a bifurcation process.

Our principal assumption, leading to the possibility of such a bifurcation, is about the spectral function $\hat{R}(k)$. We will assume that $|\hat{R}(k)|$ attains its maximum at some single value of $k = k^* \neq 0$ (hence this maximum is larger than 1, since (3.52) together with $\hat{\phi}_1(0) = 1$, $\hat{\phi}_2(0) = 0$ imply $\hat{R}(0) = 1$). We will then discuss conditions that guarantee bifurcation. The spectral function $\hat{R}(k)$ was found already (3.52) within the scenario of the movement laws considered in Sec. 3.2. We continue in that scenario, and merely specify the properties that we need. These really are assumptions about the functions f and $\hat{R}(k)$.

4.1. The main assumptions on our redistribution-regulation models

Assumption 4.1. f is three times continuously differentiable.

Assumption 4.2. $F(0) = 0$, $F'(0) = 1$, and $F''(u) < 0$ for $u \geq 0$.

As a consequence of Assumption 4.2, we have

Proposition 4.1. For any $\mu > 1$, the equation

$$c = \mu F(c) \quad (4.2)$$

has exactly one positive solution c_μ , which is therefore a stationary solution of (4.1).

The proof is trivial.

We introduce the operators L_μ and H by

$$L_\mu = \mu Df[c_\mu] = \mu F'(c_\mu)DR[c_\mu], \quad H = \mu D^2 f[c_\mu]. \tag{4.3}$$

The operator $H(v, w)$, which also depends on μ , is a bounded bilinear function from $\mathcal{S} \times \mathcal{S}$ to \mathcal{S} . There is no loss of generality in assuming H to be symmetric.

The following is a restatement of our conclusion in Section 3.6.

Proposition 4.2. *The operator L_μ has, for each $\mu > 1$, a complete countable set of orthonormal eigenfunctions $\{\psi_k\}$ (independent of μ), with eigenvalues $\hat{L}(\mu, k)$. Here the index k ranges over the integers (in the isotropic case, only the nonnegative ones). The eigenfunction with $k = 0$ is constant, and the others are not constant.*

Thus

$$L_\mu \psi_k = \hat{L}(\mu, k) \psi_k. \tag{4.4}$$

In the context of Section 3.2, these eigenvalues are given via (4.3) by (3.51) and (3.52): $\hat{L}(\mu, k) = \mu F'(c_\mu) \hat{R}(k)$.

Since $\lim_{k \rightarrow \infty} \hat{L}(\mu, k) = 0$, for each $\mu > 1$ there is an integer $k^*(\mu)$ such that

$$\max_k |\hat{L}(\mu, k)| = |\hat{L}(\mu, k^*(\mu))|. \tag{4.5}$$

Assumption 4.3. *There is a value μ^* such that for μ in a neighborhood of μ^* , $k^*(\mu)$ is positive, unique, and constant, so that $k^*(\mu) = k^*(\mu^*)$ (we denote this constant integer simply by k^*), $b_\mu \equiv \hat{L}(\mu, k^*)$ is real, and*

$$b_{\mu^*} = 1, \quad \frac{d}{d\mu} b_\mu < 0. \tag{4.6}$$

Note: $b_\mu = \mu F'(c_\mu) \hat{R}(k^*)$. If $\hat{R}(k^*) > 0$, which is implied here, this assumption means that $\frac{d}{d\mu} (\mu F'(c_\mu)) < 0$, which is a natural condition to require for the concave function F .

Let $\psi^* = \psi_{k^*}$. Note that in the isotropic case,

$$\psi^*(x) = \frac{1}{\sqrt{\pi}} \cos k^* x. \tag{4.7}$$

4.2. The existence of bifurcating branches

The problem for stationary solutions can be written

$$Z(\mu, u) \equiv u - \mu F(R[u]) = 0, \tag{4.8}$$

where we consider Z as a mapping from $I \times \mathcal{S}$ to \mathcal{S} . Here I is a small enough interval on the real μ -axis containing μ^* (Assn. 4.3), and \mathcal{S} is the L_2 space of 2π -periodic functions, further restricted in the isotropic case to be even. There is a given branch of constant solutions $u = c_\mu$. The well known results of Crandall and Rabinowitz [4, Thm. 1] give conditions under which there is another branch of

solutions intersecting the given one. Our assumptions ensure that those conditions are fulfilled, and we conclude the existence of that other branch. Moreover, the cited paper provides an approximate form for the new solutions near the bifurcation point, and in the present case it takes the form $c + \epsilon\psi^*$, where $\psi^* = \frac{1}{\sqrt{\pi}}e^{ik^*x}$ (or $\frac{1}{\sqrt{\pi}}\cos(k^*x)$ in the isotropic case), which we call $\psi^*(x)$ below. Denote by Q the orthogonal projection onto the complement of $\text{span}\{\psi^*\}$.

Theorem 4.3. *Let (4.7) hold. For some positive ϵ_0 and all $0 < \epsilon < \epsilon_0$, there exist regular functions $\hat{B}(\epsilon)$ and $\overline{W} : I = (0, \epsilon_0) \rightarrow QS$, such that $u_\epsilon = c_{\mu(\epsilon)} + \epsilon(\psi^* + \epsilon\overline{W}(\epsilon))$ satisfies (4.8) with $\mu = \mu^* + \epsilon^2\hat{B}(\epsilon)$ and $\psi^*(x) = \frac{1}{\sqrt{\pi}}\cos(k^*x)$.*

Moreover, the stability of the bifurcating solutions can be calculated, and we address that issue below. For this and other later studies, we shall need details about the bifurcation, and so record them in the following sections for that purpose. This will provide an independent proof of Theorem 4.3. Only the isotropic case will be considered.

4.3. Taylor expansion and stability of the constant solutions in the isotropic case

We now consider functions u near c_μ for some fixed μ . We look for solutions of (4.1) in the form

$$u = c_\mu + \epsilon v, \quad u' = c_\mu + \epsilon v', \tag{4.9}$$

where ϵ is a small real parameter to be characterized later, and v is a new function, bounded independently of ϵ . Our construction will seek $v \neq \text{const}$. Thus $u \neq \text{const}$ and the functions (4.9) will be “patterned”. The equation (4.1) becomes

$$\begin{aligned} c_\mu + \epsilon v' &= \mu f[c_\mu + \epsilon v] \\ &= \mu F(c_\mu) + \epsilon L_\mu v + \epsilon^2 H(v, v) + O(\epsilon^3), \end{aligned} \tag{4.10}$$

By (4.2), (4.10),

$$v' = L_\mu v + \epsilon H(v, v) + O(\epsilon^2) \equiv L_\mu v + \epsilon z. \tag{4.11}$$

Consider first the linearized equation obtained from this by setting $\epsilon = 0$:

$$v' = L_\mu v. \tag{4.12}$$

Because of the completeness of the eigenfunctions $\{\psi_k\}$, it suffices to seek the solutions with $v = \psi_k$. With this choice of v we obtain $L_\mu v = \hat{L}(\mu, k)v$, so that

$$v' = \hat{L}(\mu, k)v. \tag{4.13}$$

Iterating (4.13) and calling the iterates $v^{(n)}$, we have

$$v^{(n)} = (\hat{L}(\mu, k))^n v^{(0)}. \tag{4.14}$$

This leads to the **criterion of linearized instability**: *The constant solution c_μ is unstable if there is a k such that*

$$|\hat{L}(\mu, k)| > 1. \tag{4.15}$$

Remark. If $|\hat{L}(\mu, k)| > 1$ for some $k \neq 0$, the growth in time of the iterates (4.14) of $v = \psi_k$ can be regarded as a clumping phenomenon. As we shall see, it leads to the emergence of spatially patterned stationary solutions of the original nonlinear problem.

4.4. Properties of the bifurcating stationary patterns

4.4.1. Reformulation

We now return to the nonlinear problem (4.11), and reformulate it in terms of the patterned function ψ^* .

We can define the orthogonal projection P onto the one-dimensional subspace spanned by ψ^* , and the complementary projection $Q = I - P$. In terms of these projections, we set

$$Pv = a\psi^*, \quad Qv = \epsilon W, \quad Pv' = a'\psi^*, \quad Qv' = \epsilon W'. \tag{4.16}$$

We have $PW = PL_\mu W = 0$, $P\psi^* = \psi^*$ and

$$v(x) = a\psi^*(x) + \epsilon W(x), \quad v'(x) = a'\psi^*(x) + \epsilon W'(x). \tag{4.17}$$

Thus (from (4.9)) ϵa and $\epsilon a'$ are amplitudes of the projections of $u - c_\mu$ and $u' - c_\mu$ onto the span of ψ^* . The orthogonal projections ϵW and $\epsilon W'$ are written with a coefficient ϵ because according to our construction, it will turn out that they are indeed $O(\epsilon)$ as $\epsilon \rightarrow 0$.

The real parameter a' and function W' are to be determined in terms of a , W , ϵ and μ . Also note $L_\mu \psi^* = \hat{L}(\mu, k^*(\mu))\psi^*$, so that according to Assumption 4.3 $L_\mu \psi^* = b_\mu \psi^*$ (see the definition of b_μ in that assumption).

Substituting (4.17) into (4.11), we find

$$a'\psi^* + \epsilon W' = ab_\mu \psi^* + \epsilon L_\mu W + \epsilon z. \tag{4.18}$$

Thus we have

$$(a' - a)\psi^* + \epsilon(W' - L_\mu W) = a(b_\mu - 1)\psi^* + \epsilon z. \tag{4.19}$$

We shall work with values of μ which are near μ^* ; hence by (4.6) b_μ is close to 1.

4.4.2. Stationary patterns

Suppose that the function f is quadratic (this can be relaxed with a few more details); then

$$f[c_\mu + \epsilon v] = F(c_\mu) + \epsilon L_\mu v + \epsilon^2 H(v, v). \quad (4.20)$$

Thus in (4.11),

$$z = H(v, v) \quad (4.21)$$

and (recall (4.17))

$$z = H(v, v) = a^2 H(\psi^*, \psi^*) + 2\epsilon a H(\psi^*, W) + \epsilon^2 H(W, W). \quad (4.22)$$

First, we consider stationary solutions of (4.19). We set $a = a' = 1$, and thereby identify ϵ for the first time as the magnitude of the projection of the stationary solution $u - c_\mu$ onto the span of ψ^* . This magnitude turns out to be related to μ . Setting $a' = a = 1$, $W' = W$, we have

$$(1 - L_\mu)W = \frac{(b_\mu - 1)}{\epsilon} \psi^* + z. \quad (4.23)$$

Therefore applying P to (4.23), we conclude that $P[(b_\mu - 1)\psi^* + \epsilon z] = 0$, which implies the orthogonality condition (recall the ψ_k are orthonormal)

$$(b_\mu - 1) + \epsilon \langle z, \psi^* \rangle = 0, \quad (4.24)$$

where z is given by (4.11), (4.22). This is an equation relating μ to ϵ . We will show that for small ϵ it can be expressed as

$$\mu = \mu(\epsilon) \equiv \mu^* - \eta(\epsilon). \quad (4.25)$$

One of our objectives will be to characterize the function $\eta(\epsilon)$. **From this point on, we consider only the isotropic case.**

Lemma 4.4. *In the isotropic case,*

$$\langle H(\psi^*, \psi^*), \psi^* \rangle = 0. \quad (4.26)$$

Proof. Let σ_a denote the shift operator: $\sigma_a \psi(x) = \psi(x + a)$. Spatial homogeneity for f implies that for any function u , we have $f[\sigma_a u] = \sigma_a f[u]$. Setting $u = c + \epsilon v$ for a fixed constant c , function v and variable ϵ , and differentiating twice with respect to ϵ , we get $D^2 f[c](\sigma_a v, \sigma_a v) = \sigma_a D^2 f[c](v, v)$. We now set $a = \frac{\pi}{k^*}$, $v = \psi^*$, and observe that $\sigma_a \psi^* = -\psi^*$ and that the scalar product is invariant under $\sigma = \sigma_{\pi/k^*}$. We obtain that $\langle H(\psi^*, \psi^*), \psi^* \rangle = \langle D^2 f[c](\psi^*, \psi^*), \psi^* \rangle = \langle \sigma D^2 f[c](\psi^*, \psi^*), -\psi^* \rangle = \langle H(-\psi^*, -\psi^*), -\psi^* \rangle$. Thus defining $\beta(v) = \langle H(v, v), v \rangle$, we know that $\beta(-\psi^*) = \beta\psi^*$. On the other hand, $\beta(-\psi^*) = -\beta(\psi^*)$ since β is cubic, therefore odd. It follows that $\beta(\psi^*) = 0$, which completes the proof.

Thus from (4.26) we see that the term involving a^2 in the scalar product in (4.24) (considering (4.22)) vanishes.

We now use (4.22) ($a = 1$) to write (4.24) as

$$(b_\mu - 1) + \epsilon^2 \langle (2H(\psi^*, W) + \epsilon H(W, W)), \psi^* \rangle = 0. \tag{4.27}$$

Applying Q to (4.23), we obtain

$$(1 - L_\mu)W = Qz. \tag{4.28}$$

Recall from (4.6) that $\frac{d}{d\mu}b_\mu < 0$, $b_{\mu^*} = 1$. Thus by the implicit function theorem, recalling (4.25), we may solve (4.27) for

$$\eta = \epsilon^2 q(W, \epsilon). \tag{4.29}$$

Or more directly,

$$b_\mu - 1 = \epsilon^2 B(W, \epsilon), \tag{4.30}$$

where

$$B(W, 0) = -2 \langle H(\psi^*, W), \psi^* \rangle.$$

Our next task is to solve (4.28). Using (4.22) ($a = 1$), we obtain

$$W = (I - L_\mu)^{-1} QH(\psi^*, \psi^*) + O(\epsilon). \tag{4.31}$$

We have recognized that the operator $(I - L_\mu)$ restricted to QS is invertible. The implicit function theorem now yields a solution $W = \bar{W}(\epsilon)$ as a function of ϵ , for small ϵ . Note that

$$\bar{W}(0) = (I - L_\mu)^{-1} QH(\psi^*, \psi^*). \tag{4.32}$$

Referring to (4.30), we let

$$\hat{B}(\epsilon) = B(\bar{W}(\epsilon), \epsilon). \tag{4.33}$$

The equation (from (4.30))

$$b_\mu - 1 = \epsilon^2 \hat{B}(\epsilon) \tag{4.34}$$

can be solved for μ :

$$\mu(\epsilon) = \mu^* - \epsilon^2 r(\epsilon) \equiv \mu^* - \eta(\epsilon). \tag{4.35}$$

We shall call the steady solution (using the notation in (4.9))

$$\bar{v}_\epsilon = \psi^* + \epsilon \bar{W}(\epsilon), \quad \bar{u}_\epsilon = c_{\mu(\epsilon)} + \epsilon \bar{v}_\epsilon. \tag{4.36}$$

This proves Theorem 4.3.

According to Assumption 4.3, the trivial solution c_μ loses stability as the bifurcation parameter μ **decreases** through the value μ^* . The stability of the resulting nontrivial solution (4.36) is determined according to whether the bifurcation is supercritical, i.e. occurs for $\mu < \mu^*$, or subcritical, $\mu > \mu^*$. This choice in turn is determined by the sign of $\hat{B}(0)$ in (4.34). If $\hat{B}(0) > 0$, the new solutions occur for

$b_\mu > 1$, i.e. $\mu < \mu^*$, so they are supercritical and stable. The opposite occurs if $\hat{B}(0) < 0$.

It is therefore important to know the sign of $\hat{B}(0)$, which according to (4.33) and (4.32), is

$$\hat{B}(0) = -2\langle H(\psi^*, \bar{W}(0)), \psi^* \rangle, \quad \bar{W}(0) = (I - L_\mu)^{-1}QH(\psi^*, \psi^*). \quad (4.37)$$

The sign of this expression, then, determines the stability of the bifurcating patterned solutions, except in degenerate cases.

5. Multispecies models; discussion

We have considered patterning through bifurcation in general single-species discrete-time population models of distribution-regulation type. It was mentioned in Section 1 that there are analogs, in the multispecies scenario, of the concepts, methods, and results expounded here. In (1.1), the symbol u would represent an n -component vector $u = (u_1, \dots, u_n)$, and f as well. Similarly for movement laws g , redistribution operators R (2.3), and regulation functions F (2.5). In Section 3.1, c and g_0 will have n components, and $f'[c]$ will be a matrix. In (3.34), there will be a dispersion kernel ϕ_{1i} and other kernel ϕ_{3i} for each $i = 1, \dots, n$, and the attraction parameter $A = \alpha d\theta$ will be an $n \times n$ matrix, the elements A_{ij} representing the force of attraction that species i undergoes toward species j . The equation (3.34) then will become

$$(DR[c]v)_i(x) = \phi_{1i} * v_i(x) - \sum_j A_{ij} [\phi_{3i} * v_j(x) - v_j(x)]. \quad (5.1)$$

The spectral and bifurcation analyses will proceed as before in a straightforward way.

Coming back to the single-species case, we have argued ((3.34) and (3.54)) that the linearization of the operator f about a constant solution typically assumes the form

$$Df[c]v = F'(c) (\phi_1 * v(x) - A\phi_2 * v(x)), \quad (5.2)$$

where in the prototypical case $\phi_2 = \phi_3 - \delta$ and ϕ_1 and ϕ_3 are probability kernels representing the competing actions of random dispersion and congregation; and the parameter A is a measure of the strength of conspecific attraction. We have developed, mainly in terms of the spectral function $\hat{R}(k)$ (3.52), conditions for the existence and for the stability of bifurcating stationary patterned solutions.

For the existence of a bifurcation, the most important criterion is Assumption 4.3 in Sec. 4. In the typical case (3.52) holds, and

$$\hat{L}(\mu, k) = \mu F'(c_\mu) \hat{R}(k) = \mu F'(c_\mu) (\hat{\phi}_1(k) - A\hat{\phi}_2(k)). \quad (5.3)$$

In the isotropic case when $\hat{R}(k)$ is real and even, if $\phi_2 = \phi_3 - \delta$ the assumption will typically be fulfilled if the spectral function

$$\hat{R}(k) = \hat{\phi}_1(k) + A(1 - \hat{\phi}_3(k))$$

has a global maximum occurring at a finite positive value $k = k^*$, and $\hat{R}(k^*) > 1$. This condition cannot happen when $A \leq 0$, so some attraction is necessary for patterning in the present context. Also if A is too large, $\sup \hat{R}(k)$ will only be attained at $k = \infty$.

It is useful to have a simpler sufficient condition for the existence of these patterns. Think of k as being a continuous variable. Then a sufficient condition for the criterion is that

$$\hat{R}''(0) > 0, \quad A < 1. \quad (5.4)$$

The reason is that $\hat{R}'(0) = 0$, $\hat{R}(0) = 1$, so that $\hat{R}(k)$ will assume values > 1 ; but $\hat{R}(\infty) = A < 1$, so that $0 < k^* < \infty$.

Letting V_i be the variance of ϕ_i , we have the relation

$$V_i = -\hat{\phi}_i''(0), \quad \text{so that } \hat{R}''(0) > 0 \text{ if } A > V_1/V_2. \quad (5.5)$$

In short, this sufficient condition is that A lie in the interval

$$\frac{V_1}{V_2} < A < 1. \quad (5.6)$$

For this to hold, it is of course required that $V_1 < V_2$, i.e. that the dispersion have a shorter range than the congregation. This condition is reminiscent of other biological models involving activation and inhibition, the activation having a shorter range than the inhibition.

One may model repulsion by setting $A < 0$; then various consequences of the model may be easily deduced.

The form (5.2) for the derivative was derived in the context of our postulate of conspecific attraction in Section 3.3.3; that postulate was general enough to provide justification for our claim that (5.2) is typical.

Acknowledgements. We gratefully received valuable help through discussions with Hiroshi Matano, Davar Khosnevisan, and Nacho Barradas. Khosnevisan provided us with the background information for Sections 3.3.1 and 3.3.2. Matano provided us with a proof of Lemma 4.4 similar to the one given here. Barradas drew our attention to the relation (2.1).

References

1. Allen, E.J., Allen, L.J.S., Gilliam, X.: Dispersal and competition models for plants. *J. Math. Biol.* **34**, 455–481 (1996)
2. Bascompte, J., Solé, R.V., eds.: *Modeling Spatiotemporal Dynamics in Ecology*. Springer-Verlag, 1997
3. Beverton, R.J.H., Holt, S.J.: On the dynamics of exploited fish populations. *Fish Invest. Minist. Agric. Fish. Food. (London) Ser.* **2**, 19 (1957)
4. Crandall, M.G., Rabinowitz, P.H.: Bifurcation from simple eigenvalues. *J. Funct. Anal.* **8**, 321–340 (1971)
5. Grimmett, G.R., Stirzaker, D.R.: *Probability and Random Processes*. Oxford: Oxford Science Publications, 1992
6. von Hardenberg, J., Meron, E., Shachak, M., Zarmi, Y.: Diversity of vegetation patterns and desertification. *Phys. Rev. Lett.* **87**, 1998101 (2001)

7. Hardin, D.P., Takác, P., Webb, G.F.: A comparison of dispersal strategies for survival of spatially heterogeneous populations. *SIAM J. Appl. Math.* **48**, 1396–1423 (1988)
8. Hardin, D.P., Takác, P., Webb, G.F.: Asymptotic properties of a continuous-space discrete-time population model in a random environment. *J. Math. Biol.* **26**, 361–374 (1988)
9. Hardin, D.P., Takác, P., Webb, G.F.: Dispersion population models discrete in time and continuous in space. *J. Math. Biol.* **28**, 1–20 (1990)
10. Hart, D.R., Gardner, R.H.: A spatial model for the spread of invading organisms subject to competition. *J. Math. Biol.* **35**, 935–948 (1997)
11. Kot, M.: Discrete-time travelling waves: ecological examples. *J. Math. Biol.* **30**, 413–436 (1992)
12. Kot, M., Schaffer, W.M.: Discrete-time growth-dispersal models. *Math. Biosci.* **80**, 109–136 (1986)
13. Kot, M., Lewis, M.A., van den Driessche, P.: Dispersal data and the spread of invading organisms. *Ecology* **77** (7), 2027–2042 (1996)
14. Lewis, M.A., Li, B., Weinberger, H.F.: Spreading speed and linear determinacy for two-species competition models. *J. Math. Biol.* **45** (3), 219–233 (2002)
15. Lui, R.: Biological growth and spread modeled by systems of recursions. I. Mathematical theory. *Math. Biosci.* **93**, 269–295 (1989)
16. Lui, R.: Biological growth and spread modeled by systems of recursions. II. Biological theory. *Math. Biosci.* **93**, 297–312 (1989)
17. Matano, H., Ogiwara, T.: Stability Analysis in order-preserving systems in the presence of symmetry. *Proc. Royal Soc. Edinburgh* **129**, 397–442 (1999)
18. May, R.M.: On relationships among various types of population models. *Am. Nat.* **107**, 45–57 (1972)
19. May, R.M.: Biological populations obeying difference equations: stable points, stable cycles and chaos. *J. Theor. Biol.* **49**, 511–524 (1975)
20. May, R.M., Oster, G.F.: Bifurcations and dynamic complexity in simple ecological models. *Am. Nat.* **110**, 573–599 (1976)
21. Maynard Smith, J.: *Mathematical Ideas in Biology*. Cambridge: Cambridge University Press, 1968
22. Neubert, M.G., Kot, M., Lewis, M.A.: Dispersal and pattern formation in a discrete-time predator-prey model. *Theor. Pop. Biol.* **48** (1), 7–43 (1995)
23. Ricker, W.E.: Stock and recruitment. *J. Fish. Res. Board Can.* **11**, 559–623 (1954)
24. Sanchez-Garduno, F., Maini, P.K.: A non-linear degenerate equation for direct aggregation. Unpublished manuscript
25. Shigesada, N., Kawasaki, K.: *Biological Invasions: Theory and Practice*. Oxford Series in Ecology and Evolution, Oxford: Oxford University Press, 1997
26. Tilman, D., Kareiva, P., eds.: *Spatial Ecology*. Princeton, NJ: Princeton University Press, 1997
27. Turchin, P.: *Quantitative Analysis of Movement*. Sunderland, MA: Sinauer Associates Inc., 1998
28. Weinberger, H.F.: Long-time behavior of a class of biological models. *SIAM J. Math. Anal.* **13**, 353–396 (1982)
29. Weinberger, H.F., Lewis, M.A., Li, B.: Analysis of linear determinacy for spread in cooperative models. *J. Math. Biol.* **45** (3), 183–218 (2002)