

Discrete-Time Growth-Dispersal Models

MARK KOT AND WILLIAM M. SCHAFFER

*Department of Ecology and Evolutionary Biology,
The University of Arizona, Tucson, Arizona 85721*

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ABSTRACT

Integrodifference equations are discrete-time models that share many of the attributes of scalar reaction-diffusion equations. At the same time, they readily exhibit period doubling and chaos. We examine the properties of some simple integrodifference equations.

1. INTRODUCTION

To a greater or lesser extent all organisms disperse. Dispersal may be a response to temporal heterogeneity and deteriorating local conditions [12, 13] or, as argued by Hamilton and May [17], an effective strategy in constant and homogeneous environments. Any attempt at understanding the stability and persistence of entire populations and communities must take dispersal into account. Dispersal, in fact, is of significance in much of biology, and a great many authors have, since the pioneering work of Fisher and of Kolmogorov in population genetics, of Turing in developmental biology, and of Skellam and of Kierstead and Slobodkin in ecology [10, 26, 28, 61, 65], incorporated dispersal into their models.

In modeling dispersal, there has been an emphasis on reaction-diffusion equations, continuous-time growth models with within-habitat dispersal [50]. For such models, diffusion is generally thought of as a stabilizing influence [37], one that homogenizes populations and moderates temporal fluctuations. At the same time, it is well known [33, 60] that diffusion may combine with intra- and interspecific interactions to yield a Turing effect [65], instability, and spatial patterns. Other mechanisms may also yield spatial patterns; the study of these mechanisms is an exciting endeavor that has been carried quite far [36].

There is no comparable work for discrete-time systems. Recent work on cellular automata [14, 75, 76] has sparked some interest, but population

biologists have, by and large, been reluctant to consider discrete-time models that account for both growth and dispersal. This is particularly surprising given the large body of literature on discrete-time systems with no spatial component [15, 19, 29, 35, 42–46, 51, 53, 54, 68, 69].

In this paper we examine discrete-time growth-dispersal models. We emphasize those systems which can be represented as integrodifference equations. Our goal is simple. We wish to interest the reader in this class of problems. To meet this goal, we will, to some extent, sacrifice depth for breadth. Readers who feel that we have not fully developed interesting themes are encouraged to do so.

In Sections 2 and 3, we provide a general framework for study and illuminate this framework with examples. Section 4 is an abiotic section that outlines relevant mathematical theory. This section may prove difficult for some. Sections 5 and 6 examine, in detail, two continuous-habitat examples. Sections 7 and 8 contain a discussion of two of the mechanisms by which truly complex spatial patterns may arise. Finally, section 9 contains our concluding remarks.

2. FORMULATION OF THE PROBLEM

Consider an organism with synchronous, nonoverlapping generations. Let us assume that dispersal occurs during a distinct phase of the life cycle and that individuals are relatively sedentary for the remainder of the life cycle. This is a reasonable approximation for a great many organisms [6, 21]. Moreover, with this assumption, we may take the composition of a linear operator (good for the dispersal stage) and a nonlinear operator (for the sedentary stage) as our descriptor of growth.

For the sedentary stage, we begin with a nonlinear map

$$N_{t+1} = f(N_t) \quad (1)$$

such as the logistic difference equation [41, 47]

$$N_{t+1} = (1 + r) N_t - \frac{r}{K} N_t^2 \quad (2)$$

or the Ricker curve [52]

$$N_{t+1} = N_t \exp \left[r \left(1 - \frac{N_t}{K} \right) \right]. \quad (3)$$

K represents the carrying capacity of the environment. r is the intrinsic rate of growth. N_t is the population level at time t . Growth curves such as (2) and (3) appear quite extensively in the literature. Despite their simple appearance, they are capable of exhibiting a wide range of interesting dynamics [42–44, 46].

As it stands, Equation (1) makes no allowance for the dispersion of a population. If there is clustering, imagine that there are n discrete patches with coordinates x_i , $i = 1, \dots, n$, and that our population is distributed among these n patches. Let $N_i(x_i)$ represent the population in patch i at the start of the i th sedentary stage. Population growth occurs in two steps. During the sedentary stage, the population in each patch, $N_i(x_i)$, is mapped into $f(x_i, N_i(x_i))$. Explicit x_i dependence (from here on dropped) reflects clinal (spatially varying, time-independent) variation in the parameters. During the second stage, the dispersal stage, the $f(N_i(x_i))$ individuals at each site are, to varying degrees, shuffled about. The net result is a mapping of the form

$$N_{i+1}(x_i) = \sum_{j=1}^n k(x_i, x_j) f(N_i(x_j)), \quad (4)$$

where $k(x_i, x_j)$ is the probability that an individual will move, during the dispersal stage, from patch j to patch i .

When the population is continuously distributed, we instead take x as a continuous variable on some closed, finite interval $[a, b]$. Now $N_i(x)$ is the population at coordinate x at the start of the i th sedentary stage, and population growth, once again, occurs in two stages. Summation yields to integration and, in lieu of (4), we have the integrodifference equation

$$N_{i+1}(x) = \int_a^b k(x, y) f(N_i(y)) dy. \quad (5)$$

Here, $k(x, y) dy$ is the probability that an individual will move, during the dispersal stage, from the interval $(y, y + dy]$ to the point x . A similar model (for the spread of an advantageous gene) has been proposed by Weinberger [70, 71].

If the environment is isotropic, one may hope that the kernels $k(x_i, x_j)$ and $k(x, y)$ are symmetric in x and y , $k(x, y) = k(y, x)$, and that they depend only upon the distance between source and destination. In this case, (4) and (5) reduce to

$$N_{i+1}(x_i) = \sum_{j=1}^n k(|x_i - x_j|) f(N_i(x_j)) \quad (6)$$

and

$$N_{i+1}(x) = \int_a^b k(|x - y|) f(N_i(y)) dy. \quad (7)$$

We emphasize that the coupling in (4), (5), (6), and (7) is fundamentally nonlinear. It is the nonlinear $f(N_i(x_i))$'s and $f(N_i(x))$'s that are shuffled

about. This is in marked contrast to the linear coupling found in a great many continuous-time models (see also [24, 66, 67]). Discrete-time population models with linear coupling in effect mix generations and, as a result, may yield counterintuitive results.

3. EXAMPLES

The system (6) subsumes a wide assortment of models. Difference equations and partial difference equations both fall out as special cases.

Example 1. A particularly simple scenario involves a population, found throughout two identical patches, in which individuals have a probability $1 - p$ of staying home and a probability p of moving to the neighboring patch. For this scenario, the system (6) takes on the form

$$N_{t+1}(x_1) = (1 - p)f(N_t(x_1)) + pf(N_t(x_2)), \quad (8a)$$

$$N_{t+1}(x_2) = pf(N_t(x_1)) + (1 - p)f(N_t(x_2)), \quad (8b)$$

a system of two first-order difference equations.

Example 2. One may imagine a linear array consisting of a large number of equally spaced, identical patches. If subpopulations interact only with their nearest neighbors,

$$k(x_i, x_j) = \begin{cases} 0, & i < j - 1, \\ \frac{1}{2}p, & i = j - 1, \\ 1 - p, & i = j, \\ \frac{1}{2}p, & i = j + 1, \\ 0, & i > j + 1, \end{cases} \quad (9)$$

one is led to consider the partial difference equation

$$N_{t+1}(x_i) = (1 + \frac{1}{2}p\delta^2)f(N_t(x_i)), \quad (10)$$

where δ^2 , the square of the central-difference operator, is defined by

$$\delta^2 f(x_i) = f(x_{i+1}) - 2f(x_i) + f(x_{i-1}). \quad (11)$$

Our primary interest in this paper is in discrete-time models for organisms with continuous distributions. That is, we are particularly interested in integrodifference equations, models of the form (7). For such models, choosing an appropriate kernel is difficult. The dispersal of real organisms is a well-studied phenomenon [4, 5, 50, 61, 71–73], but, as might be expected, realistic kernels often lead to intractable mathematics. For the purposes of

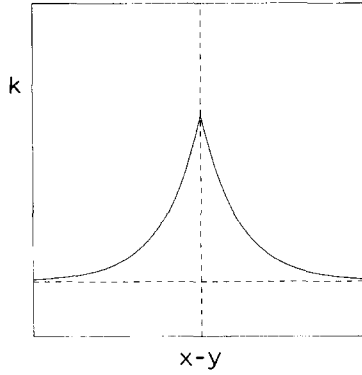


FIG. 1. Graphical representation of the kernel $k(x, y) = \frac{1}{2} \alpha \exp(-\alpha|x-y|)$.

this paper, we introduce two mathematically simple, biologically reasonable kernels.

Example 3. Let the viable habitat be the closed interval $[-L/2, L/2]$ of length L , and let us take as our kernel the function (Figure 1)

$$k(x, y) = \frac{1}{2} \alpha \exp(-\alpha|x-y|). \quad (12)$$

Equation (12) approximates many of the leptokurtic distributions found in nature [1, 4]. With this kernel, Equation (7) takes on the form

$$N_{t+1}(x) = \frac{1}{2} \alpha \int_{-L/2}^{L/2} \exp(-\alpha|x-y|) f(N_t(y)) dy. \quad (13)$$

Example 4. Once again, let the viable habitat be the closed interval $[-L/2, L/2]$. For organisms with a finite radius of dispersal R , we consider the kernel (Figure 2)

$$k(x, y) = \begin{cases} 0, & x \leq y - R, \\ \frac{\pi}{4R} \cos\left[\frac{\pi}{2R}(x-y)\right], & y - R \leq x \leq y + R, \\ 0, & x \geq y + R. \end{cases} \quad (14)$$

If the radius of dispersal is less than the length of the viable habitat ($R < L$), Equation (7) appears as

$$N_{t+1}(x) = \frac{\pi}{4R} \int_{\max(x-R, -L/2)}^{\min(x+R, L/2)} \cos\left[\frac{\pi}{2R}(x-y)\right] f(N_t(y)) dy. \quad (15)$$

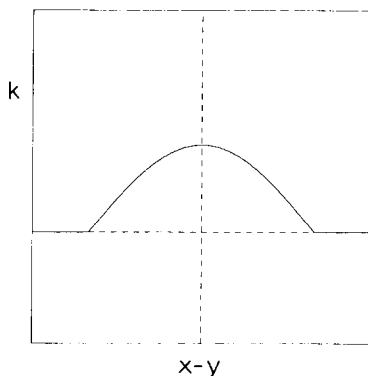


FIG. 2. Graphical representation of the kernel (14) of Example 4.

For a large radius of dispersal ($R \geq L$), we consider the substantially more tractable

$$N_{t+1}(x) = \frac{\pi}{4R} \int_{-L/2}^{L/2} \cos\left[\frac{\pi}{2R}(x-y)\right] f(N_t(y)) dy. \quad (16)$$

4. INTEGRODIFFERENCE EQUATIONS

In the remainder of this paper, we concentrate on nonlinear integrodifference equations of the form

$$N_{t+1}(x) = \int_{-L/2}^{L/2} k(x, y) f(N_t(y)) dy. \quad (17)$$

The study of these equations is, in many ways, reminiscent of the study of difference equations with no spatial component. The similarity may be made most striking by introducing the nonlinear Hammerstein [18] operator F :

$$FN(x) = \int_{-L/2}^{L/2} k(x, y) f(N(y)) dy. \quad (18)$$

Equation (17) then takes on the simple form

$$N_{t+1}(x) = FN_t(x). \quad (19)$$

Our first interest is in finding time-invariant [$N_{t+1}(x) = N_t(x) = N^*(x)$] equilibria. These are just the fixed points of (19):

$$N^*(x) = FN^*(x). \quad (20)$$

That is to say, our equilibria satisfy a Hammerstein integral equation

$$N^*(x) = \int_{-L/2}^{L/2} k(x, y) f(N^*(y)) dy. \quad (21)$$

For the f 's that we consider, $N^*(x) = 0$ is always a trivial solution of this equation. Oftentimes, we also have nontrivial solutions, and hence, nontrivial equilibria. Finding these nontrivial equilibria may be no small matter.

When is a given equilibrium stable? To answer this, we consider small perturbations $\xi_i(x)$ off of the equilibrium, $N_i(x) = N^*(x) + \xi_i(x)$. For sufficiently small $\xi_i(x)$, this is equivalent to studying the linearization of (19) (its Fréchet differential [30, 31]) at $N^*(x)$,

$$\xi_{i+1}(x) = F'(N^*) \xi_i(x) \quad (22)$$

or

$$\xi_{i+1}(x) = \int_{-L/2}^{L/2} k(x, y) \left[\frac{df(N(y))}{dN(y)} \right]_{N=N^*(y)} \xi_i(y) dy. \quad (23)$$

The asymptotic rate of convergence near $N^*(x)$ is determined by the Fréchet derivative $F'(N^*)$ [20]. If the Fréchet derivative is a strict contraction

$$\|F'(N^*)\| < 1, \quad (24)$$

$N^*(x)$ is certainly asymptotically stable. Equation (24) is, however, by no means necessary. One may easily construct operators which are not contractions but which nevertheless generate convergent sequences.

For finite limits of integration and continuous kernels, the Fréchet derivative $F'(N^*)$ is a compact operator. As such, its spectrum consists of, at most, the point zero and a countable number of nonzero eigenvalues. We take our lead from the study of ordinary difference equations and determine the stability of the equilibrium $N^*(x)$ by examining the magnitude of the eigenvalues associated with $F'(N^*)$. For (22), setting

$$\xi_i(x) = \lambda^i \mu(x) \quad (25)$$

leads us to consider

$$\lambda \mu(x) = F'(N^*) \mu(x) \quad (26)$$

or

$$\lambda \mu(x) = \int_{-L/2}^{L/2} k(x, y) f'(N^*(y)) \mu(y) dy. \quad (27)$$

If all the eigenvalues λ of (27) lie within the unit circle of the complex plane

$$|\lambda| < 1, \quad (28)$$

$N^*(x)$ is asymptotically stable.

There are several instances in which the analysis of (26) may be streamlined. Many of the greatest simplifications arise from a combination of symmetry and nonnegativity in the kernel $k(x, y)f'(N^*(y))$ [77]. Let us assume that the kernel is nontrivial. For a kernel symmetric in x and y , the Fréchet derivative is self-adjoint. Nontrivial, self-adjoint, compact, linear operators always possess at least one nonzero eigenvalue. All eigenvalues of such an operator are real, and the norm of the operator is just the total radius of its eigenvalues. If the kernel is, in addition, nonnegative (nonpositive), we are guaranteed that the eigenvalue that controls stability (the dominant eigenvalue or eigenvalue of greatest modulus) is positive (negative).

Consider, for example, for f , the logistic function [Equation (2)]. In considering the stability of the trivial solution $N^* = 0$, we analyse

$$\lambda \mu(x) = F'(0) \mu(x) \quad (29)$$

or

$$\lambda \mu(x) = (1 + r) \int_{-L/2}^{L/2} k(x, y) \mu(y) dy \quad (30)$$

$k(x, y)$ is, typically, continuous, symmetric in x and y , and nonnegative. All eigenvalues are real. Loss of stability can occur only through $\lambda = +1$.

For an arbitrary equilibrium $N^*(x)$, the eigenvalue problem

$$\lambda \mu(x) = \int_{-L/2}^{L/2} k(x, y) f'(N^*(y)) \mu(y) dy \quad (31)$$

is built about an operator that lacks symmetry. If, however, $f'(N^*)$ is strictly positive, one may introduce the transformation

$$\mu(x) = \frac{\phi(x)}{\sqrt{f'(N^*(x))}}, \quad (32)$$

yielding

$$\lambda \phi(x) = \int_{-L/2}^{L/2} k(x, y) \sqrt{f'(N^*(x)) f'(N^*(y))} \phi(y) dy. \quad (33)$$

We have, again, a self-adjoint operator. For $k(x, y)$ continuous, symmetric, and nonnegative, and $f'(N^*)$ continuous and positive, all eigenvalues are real and loss of stability may occur only through $\lambda = +1$.

Similarly, for $f'(N^*)$ strictly negative, we introduce the transformation

$$\mu(x) = \frac{\phi(x)}{\sqrt{-f'(N^*(x))}}, \quad (34)$$

yielding

$$\lambda \phi(x) = - \int_{-L/2}^{L/2} k(x, y) \sqrt{f'(N^*(x))f'(N^*(y))} \phi(y) dy. \quad (35)$$

If $k(x, y)$ is continuous, symmetric, and nonnegative, and $f'(N^*)$ is continuous and negative, all eigenvalues are, once again, real, but now $\lambda = -1$ is the route for loss of stability. This route often leads to period doubling and chaos.

One other simplification is worth mentioning. Often the kernel of the Fréchet derivative is separable (degenerate) [49]:

$$k(x, y) f'(N^*(y)) = \sum_{i=1}^n p_i(x) q_i(y). \quad (36)$$

Separable kernels yield finite-dimensional problems. Well-behaved, compact linear operators may be approximated, to an arbitrary degree, by separable kernels. That is, all such operators may be represented as the sum of a finite-rank operator (integral operator with degenerate kernel) and an operator of arbitrarily small norm.

After equilibria, it is natural to consider periodic solutions (but see [2]). Solutions of period two, for example, often appear with the ($\lambda = -1$) loss of stability of an equilibrium. In considering two-cycles, it is useful to think of (17) as a two-step iterative process

$$M_{t+1}(x) = FN_t(x), \quad (37a)$$

$$N_{t+1}(x) = FM_t(x). \quad (37b)$$

$M^*(x)$ and $N^*(x)$ constitute a two-cycle if they map into each other under this two-step process:

$$M^*(x) = FN^*(x), \quad (38a)$$

$$N^*(x) = FM^*(x). \quad (38b)$$

Equivalently, $M^*(x)$ and $N^*(x)$ are elements of a two-cycle if each is a fixed point of the composition of F with itself:

$$M^*(x) = F^2 M^*(x) \quad (39a)$$

$$= FFM^*(x),$$

$$N^*(x) = F^2 N^*(x) \quad (39b)$$

$$= FFN^*(x).$$

Equilibria automatically satisfy all these conditions, but our real interest is in functions, other than equilibria, for which (38) and (39) hold true.

The stability of a two-cycle may be analysed by considering slight perturbations off of the two-cycle,

$$M_t(x) = M^*(x) + \xi_t(x), \quad (40a)$$

$$N_t(x) = N^*(x) + \eta_t(x). \quad (40b)$$

As with equilibria, the stability of a two-cycle is determined by the linearization of (37) near the two cycle:

$$\xi_{t+1}(x) = F'(N^*) \eta_t(x), \quad (41a)$$

$$\eta_{t+1}(x) = F'(M^*) \xi_t(x) \quad (41b)$$

or

$$\xi_{t+2}(x) = F'(N^*) F'(M^*) \xi_t(x), \quad (42a)$$

$$\eta_{t+2}(x) = F'(M^*) F'(N^*) \eta_t(x). \quad (42b)$$

Use of (25) once again yields an eigenvalue problem, and if all the eigenvalues lie within the unit circle, the two-cycle is asymptotically stable. Higher-order cycles can be handled in a comparable manner.

Finally, as with scalar difference equations, integrodifference equations may be chaotic. Kloeden [27] considers a sufficient condition for chaos that is a generalization, to Banach space, of Marotto's [38] snapback repeller. This condition may be applied quite fruitfully to integrodifference equations.

5. EXEMPLUM

Let us return to the kernel

$$k(x, y) = \frac{1}{2} \alpha \exp(-\alpha|x - y|) \quad (43)$$

and to the integrodifference equation

$$N_{t+1}(x) = \frac{1}{2} \alpha \int_{-L/2}^{L/2} \exp(-\alpha|x - y|) f(N_t(y)) dy \quad (44)$$

that it engenders. As we have seen, the equilibria of Equation (44) appear as solutions to the Hammerstein integral equation

$$N^*(x) = \int_{-L/2}^{L/2} k(x, y) f(N^*(y)) dy. \quad (45)$$

More explicitly,

$$N^*(x) = \frac{1}{2}\alpha \int_x^{L/2} \exp[\alpha(x-y)] f(N^*(y)) dy + \frac{1}{2}\alpha \int_{-L/2}^x \exp[-\alpha(x-y)] f(N^*(y)) dy. \quad (46)$$

In the study of boundary-value problems [64], it is often useful to reformulate a differential equation and associated boundary conditions as an integral equation. We may profitably reverse the direction of this flow. Let us identify $N(x)$ with $N^*(x)$. With repeated differentiation (46) yields the differential equation

$$N'' + \alpha^2 [f(N) - N] = 0 \quad (47)$$

and the boundary conditions

$$N' = \alpha N \quad \text{at } x = -L/2, \quad (48a)$$

$$N' = -\alpha N \quad \text{at } x = L/2. \quad (48b)$$

For f the logistic function [Equation (2)], and setting $K=1$, we have

$$N'' + \alpha^2 r N(1-N) = 0 \quad (49)$$

with

$$N' = \alpha N \quad \text{at } x = -L/2, \quad (50a)$$

$$N' = -\alpha N \quad \text{at } x = L/2. \quad (50b)$$

As expected, $N(x) = N^*(x) = 0$ is a solution to this problem for all L . Are there any other solutions?

We consider two approaches to this problem. First of all, (49) may be attacked directly. Multiplying (49) by $N'(x)$ and integrating, we obtain, as a first integral,

$$\frac{1}{2}(N')^2 + \alpha^2 r \left(\frac{N^2}{2} - \frac{N^3}{3} \right) = c. \quad (51)$$

Along each solution curve, the “total energy” on the left-hand side of (51) is a conserved quantity. Equation (51), in turn, is integrable by quadratures.

A more instructive approach is to set

$$u(x) = N(x), \quad (52a)$$

$$v(x) = N'(x) \quad (52b)$$

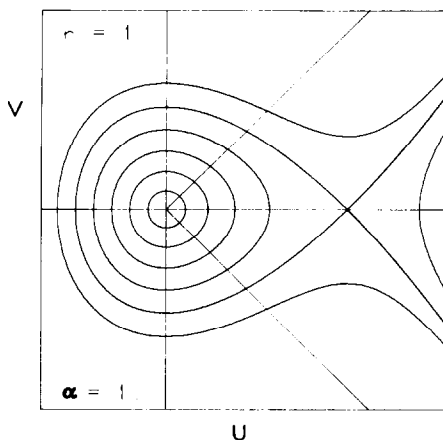


FIG. 3. Phase portrait for the system (53). The boundary conditions (50) appear as rays of slope α and $-\alpha$.

and to consider (49) as a first-order system

$$u' = v, \quad (53a)$$

$$v' = -\alpha^2 r u(1 - u). \quad (53b)$$

A typical phase portrait for this system is shown in Figure 3. The boundary conditions (50) appear as rays of slope α and $-\alpha$. Solutions correspond to those orbits which begin on $v = \alpha u$ (at $x = -L/2$) and pass through $v = 0$ (at $x = 0$) in such a way as to end on $v = -\alpha u$ (at $x = L/2$). These orbits are bounded by singular solutions, $(u, v) = (0, 0)$ on the left and $(u, v) = (1, 0)$ on the right. For fixed α and r , specifying a length L corresponds to choosing one from among the sector of possible orbits.

Let us consider in greater detail the role that the viable-habitat size L plays. A large viable habitat leads, in effect, to a "slow-moving" solution close to the saddle point $(1, 0)$. The resulting equilibria—flat over most of their domain—fall off quite rapidly toward the edge of the habitat. As one decreases the habitat size, a greater proportion of each year's offspring disperse to disadvantageous, unfavorable, feral habitat. $N^*(x)$ decreases, (49) tends toward linearity, and the equilibria begin to resemble cosine functions. There is, in fact, a habitat threshold size L^* at which reproduction just keeps even with the cost of dispersal. For $L < L^*$, populations experience extinction. The influence of L , gleaned from Figure 3, is shown quite clearly in Figure 4. Here, for fixed α and r , we have plotted equilibrium distributions for an assortment of L values.

Examining the stability of the trivial solution $N^*(x) = 0$ enables one to derive an expression for the threshold size L^* . $N^*(x) = 0$ is asymptotically

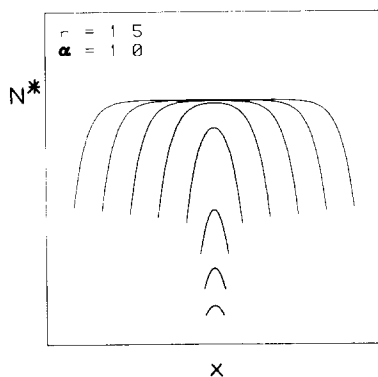


FIG. 4. Steady-state solutions for the system (46). Equilibria are plotted for an assortment of viable habitat sizes L .

stable if all eigenvalues λ of

$$\lambda \mu(x) = (1+r) \int_{-L/2}^{L/2} k(x, y) \mu(y) dy \quad (54)$$

lie within the unit circle of the complex plane (see Section 4). For $k(x, y)$ continuous, symmetric, and nonnegative, all eigenvalues are real, and stability may be lost only through $\lambda = +1$. For the kernel we have posited, (54) may be recast as a linear differential equation

$$\mu''(x) + \alpha^2 \frac{(1+r) - \lambda}{\lambda} \mu(x) = 0 \quad (55)$$

with boundary conditions

$$\mu'(x) = \alpha \mu(x) \quad \text{at } x = -L/2, \quad (56a)$$

$$\mu'(x) = -\alpha \mu(x) \quad \text{at } x = L/2. \quad (56b)$$

Let

$$\beta^2 = \frac{(1+r) - \lambda}{\lambda}. \quad (57)$$

The eigenvalues λ satisfy the transcendental equation

$$\tan \frac{\alpha \beta L}{2} = \frac{1}{\beta}. \quad (58)$$

There are an infinite number of roots to this equation and hence an infinite number of eigenvalues. $\lambda = 0$, however, is the only point of accumulation for

the eigenvalues. And indeed, it is only the root β of smallest magnitude that we need concern ourselves with. When the eigenvalue associated with this root hits the unit circle (at $\lambda = +1$), $\beta = \sqrt{r}$, and the critical threshold L^* must satisfy

$$\tan\left(\frac{\alpha\sqrt{r}L^*}{2}\right) = \frac{1}{\sqrt{r}}. \quad (59)$$

We have as our critical threshold, therefore,

$$L^* = \frac{2}{\alpha\sqrt{r}} \tan^{-1}\left(\frac{1}{\sqrt{r}}\right). \quad (60)$$

In addition to the bifurcation that gives rise to the nontrivial equilibrium, one may also observe, for increasing r , a cascade of period-doubling ($\lambda = -1$) bifurcations (Fig. 5). The simplest elements in this cascade, the

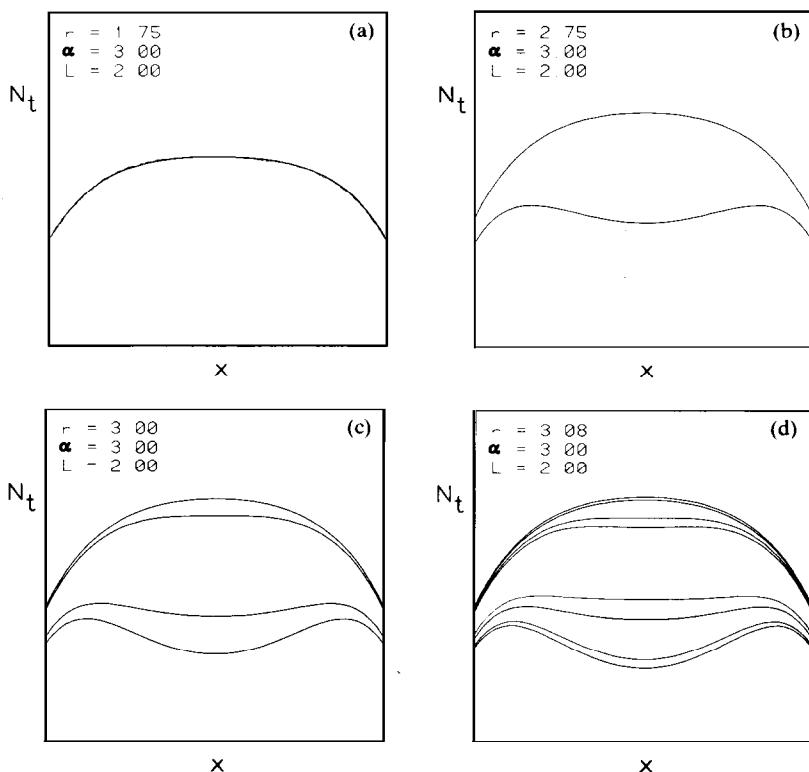


FIG. 5. Period-doubling bifurcations in system (46): (a) an equilibrium, (b) a two-cycle, (c) a four-cycle, (d) an eight-cycle.

functions $M(x)$ and $N(x)$ that make up a two-cycle, satisfy the integral system

$$M(x) = \int_{-L/2}^{L/2} k(x, y) f(N(y)) dy, \quad (61a)$$

$$N(x) = \int_{-L/2}^{L/2} k(x, y) f(M(y)) dy. \quad (61b)$$

With $k(x, y)$ as in (43), Equation (61) may be recast as the system of differential equations

$$M'' + \alpha^2 [f(N) - M] = 0, \quad (62a)$$

$$N'' + \alpha^2 [f(M) - N] = 0 \quad (62b)$$

with

$$M' = \alpha M \quad \text{at } x = -L/2, \quad (63a)$$

$$M' = -\alpha M \quad \text{at } x = +L/2, \quad (63b)$$

$$N' = \alpha N \quad \text{at } x = -L/2, \quad (63c)$$

$$N' = -\alpha N \quad \text{at } x = +L/2. \quad (63d)$$

This system, however, does not lend itself to straightforward analysis.

6. DEGENERATE KERNELS

One problem that does allow easy analysis of higher-order cycles is the integrodifference equation

$$N_{t+1}(x) = \frac{\pi}{4R} \int_{-L/2}^{L/2} \cos\left[\frac{\pi}{2R}(x-y)\right] f(N_t(y)) dy \quad (64)$$

first encountered in Section 3 as a model for organisms with large dispersal radii ($R \geq L$). What facilitates analysis in this case is the presence of a separable kernel

$$\begin{aligned} \cos\left[\frac{\pi}{2R}(x-y)\right] &= \cos\left(\frac{\pi}{2R}x\right) \cos\left(\frac{\pi}{2R}y\right) \\ &\quad + \sin\left(\frac{\pi}{2R}x\right) \sin\left(\frac{\pi}{2R}y\right) \end{aligned} \quad (65)$$

With (65), Equation (64) may be written

$$\begin{aligned} N_{t+1}(x) &= \cos\left(\frac{\pi}{2R}x\right) \left[\frac{\pi}{4R} \int_{-L/2}^{L/2} \cos\left(\frac{\pi}{2R}y\right) f(N_t(y)) dy \right] \\ &\quad + \sin\left(\frac{\pi}{2R}x\right) \left[\frac{\pi}{4R} \int_{-L/2}^{L/2} \sin\left(\frac{\pi}{2R}y\right) f(N_t(y)) dy \right]. \end{aligned} \quad (66)$$

In other words, within one iteration, any initial distribution is cast onto the invariant subspace spanned by $\cos(\pi x/2R)$ and $\sin(\pi x/2R)$. With no loss of generality, then, let us imagine that *all* the action occurs on this subspace:

$$N_t(x) = a_t \cos\left(\frac{\pi}{2R}x\right) + b_t \sin\left(\frac{\pi}{2R}x\right). \quad (67)$$

We concentrate our effort on a_t and on b_t . In understanding the dynamics of these two amplitudes

$$a_{t+1} = \frac{\pi}{4R} \int_{-L/2}^{L/2} \left(\cos \frac{\pi}{2R} y \right) f\left(a_t \cos \frac{\pi}{2R} y + b_t \sin \frac{\pi}{2R} y \right) dy, \quad (68a)$$

$$b_{t+1} = \frac{\pi}{4R} \int_{-L/2}^{L/2} \left(\sin \frac{\pi}{2R} y \right) f\left(a_t \cos \frac{\pi}{2R} y + b_t \sin \frac{\pi}{2R} y \right) dy, \quad (68b)$$

we capture all that is of interest in (64).

Taking for f the logistic function [Equation (2)], we get

$$a_{t+1} = (\alpha - \beta a_t) a_t - \gamma b_t^2, \quad (69a)$$

$$b_{t+1} = (\delta - \epsilon a_t) b_t \quad (69b)$$

with

$$\alpha = (1+r) \left[\frac{\pi L}{8R} + \frac{1}{4} \sin\left(\frac{\pi L}{2R}\right) \right], \quad (70a)$$

$$\beta = r \sin\left(\frac{\pi L}{4R}\right) \left[1 - \frac{1}{3} \sin^2\left(\frac{\pi L}{4R}\right) \right], \quad (70b)$$

$$\gamma = \frac{1}{3} r \sin^3\left(\frac{\pi L}{4R}\right), \quad (70c)$$

$$\delta = (1+r) \left[\frac{\pi L}{8R} - \frac{1}{4} \sin\left(\frac{\pi L}{2R}\right) \right], \quad (70d)$$

$$\epsilon = \frac{2}{3} r \sin^3\left(\frac{\pi L}{4R}\right). \quad (70e)$$

$b_t = 0$ is an invariant manifold for this system. Moreover, for

$$-1 < \delta - \epsilon a_t < 1 \quad (71)$$

$b_t = 0$ is an attracting, stable manifold. Once on this manifold, (69) collapses down to

$$a_{t+1} = \alpha a_t - \beta a_t^2, \quad (72)$$

a slightly rescaled version of the logistic difference equation. The various equilibria and periodic solutions of (64), then, are just cosine functions with amplitudes as given by the equilibria and periodic solutions of (72). This is one of those rare instances (but see [32]) in which a reasonable problem which looks to be of infinite dimension collapses down to a dimension of one.

All problems with separable kernels may be reduced to problems of finite dimension. Moreover (see Section 4) the presence of a continuous kernel on a finite interval of integration is often enough to allow approximation by a separable kernel (e.g., by a multiple Fourier series).

7. MULTIPLE STABLE STATES

By their very nature, integrodifference equations often exhibit spatially nonuniform steady states. This nonuniformity is an artifact of the boundary conditions that are, in effect, built into integrodifference equations. There are, however, several mechanisms by which truly complex spatial patterns may arise [36]. We have yet to discuss any of these mechanisms. In this section we make a first attempt at redress by considering several systems with multiple stable states in their underlying dynamics. In Section 8 we discuss diffusive instability.

In studying systems with multiple stable states one is struck by the strong contrast in behavior that discrete environments and continua engender. One quickly observes (see [34] for continuous-time systems) that discrete-space models, by and large, appear to support a greater number and diversity of stable states than do continuous-space models.

Consider, for example, the difference equation

$$N_{t+1} = g(N_t) \quad (73)$$

given by

$$N_{t+1} = N_t + N_t(N_t - b)(1 - N_t) \quad (74)$$

(with $0 < b < 1$). Equation (74) is intended as a simple caricature of a population with a threshold, $N = b$, and two stable equilibria, $N^* = 0$ and $N^* = 1$ (see also [39]). If the population has a patchy distribution, one might, as a first approximation, consider the partial difference equation

$$N_{t+1}(x_i) = (1 + \tfrac{1}{2}p\delta^2)g(N_t(x_i)) \quad (75)$$

(Section 3). For a population with a continuous distribution, we consider, in addition, the integrodifference equation

$$N_{t+1}(x) = \int_{-L/2}^{L/2} k(x, y)g(N_t(y))dy \quad (76)$$

with kernel

$$k(x, y) = \frac{1}{2} \alpha \exp(-\alpha |x - y|) \quad (77)$$

(Section 5).

With no migration ($p = 0$), the discrete-space model (75) collapses down to a set of n independent populations. Each population tends to zero or one solely on the basis of the initial level in that patch. If, at equilibrium, one surveys the whole metapopulation, one observes a series of ones and zeros. There are 2^n possible equilibrial configurations. All are equally stable.

For sufficiently small p , this basic scenario is modified only slightly [25]. Only as we increase p does migration diminish the number of stable

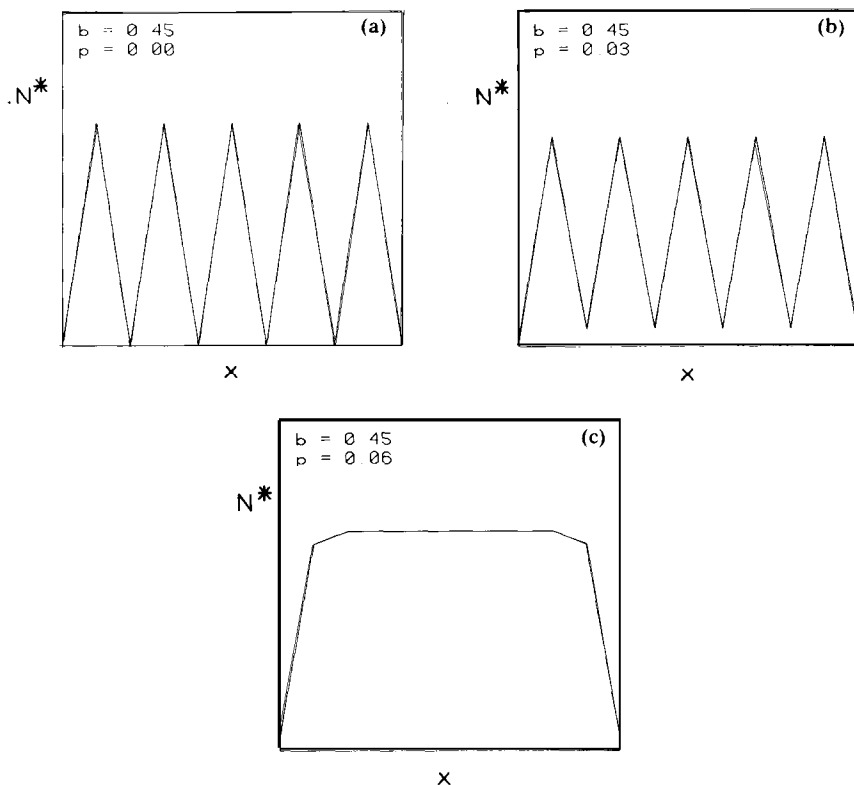


FIG. 6. Effect of diffusivity on equilibria of (75). (a) For a system with alternative stable states and no migration between patches ($p = 0.00$), spatially heterogeneous equilibria easily arise. (b) Small amounts of migration ($p = 0.03$) decrease spatial heterogeneity only slightly. (c) A further increase in migration ($p = 0.06$) greatly reduces heterogeneity. Each simulation involved 11 patches and identical initial conditions.

equilibria and impose a trend toward uniformity (Figure 6). To quote Levin [34],

This phenomenon is ecologically very important, because it means that in a patchy environment, a complex and spatially heterogeneous pattern of species abundance can result either due to micro-variation in parameters, or due to multiple steady states, and small amounts of migration will not destabilize such patterns.

In contrast, there is no plethora of stable equilibria for the continuous-space system (76)–(77). For here, equilibria appear as solutions to the differential equation

$$N'' - \alpha^2 N(N - b)(1 - N) = 0 \quad (78)$$

and the boundary conditions

$$N' = \alpha N \quad \text{at } x = -L/2, \quad (79a)$$

$$N' = -\alpha N \quad \text{at } x = +L/2. \quad (79b)$$

Let

$$u = N(x), \quad (80a)$$

$$v = N'(x). \quad (80b)$$

In terms of these new variables, (78) may be expressed

$$u' = v, \quad (81a)$$

$$v' = \alpha^2 u(u - b)(1 - u). \quad (81b)$$

A typical phase portrait for this system is shown in Figure 7. The boundary

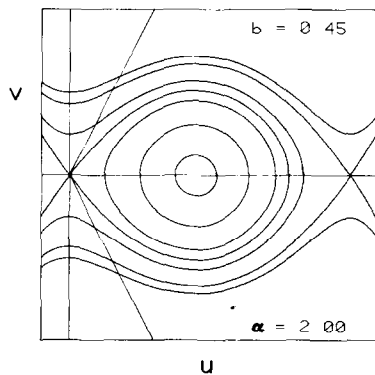


FIG. 7. Phase portrait for the system (81). The boundary conditions (79) appear, once again, as rays of slope α and $-\alpha$.

conditions appear as rays of slope α and $-\alpha$, and solutions appear as orbits which begin on $v = \alpha u$ (at $x = -L/2$), pass through $v = 0$ (at $x = 0$), and terminate on $v = -\alpha u$ (at $x = +L/2$). Solutions which pass close to a saddle point, either $(u, v) = (0, 0)$ or $(u, v) = (1, 0)$, are “slow-moving” solutions with large habitat sizes L . Between the two separatrices there is a single critical value L^* . For short intervals, $L < L^*$, the only solution is $N^*(x) = 0$; then for $L = L^*$, an additional nonconstant solution appears, while for $L > L^*$, this solution bifurcates into two nonconstant solutions. This argument, though heuristic, may be made rigorous in the manner of Smoller [62] and Smoller and Wasserman [63]. There are, in other words, at most three equilibria (and on *a priori* grounds, I expect that only two of these are stable). This is a marked contrast to the 2^n equilibria of the system (75).

As one makes the transition from discrete space to continuous space it appears, then, that the number of stable solutions decreases. This is probably a bit simplistic. The boundary conditions (79) most closely resemble, in their effect, Dirichlet boundary conditions. For continuous-time systems, much of the theory has developed around scalar reaction-diffusion equations with homogeneous Neumann (no-flux) boundary conditions. For such systems, Casten and Holland [3] have demonstrated that, on a convex domain, any nonconstant equilibrium is unstable. The number of stable equilibria is thus limited by the requirement of uniformity. Matano [40], however, has produced stable nonuniform equilibria by altering the geometry of the problem. In the simplest case [16, 34] one can introduce a nonconvex, barbell-shaped domain that, in effect, mimics a patchy environment. Similarly, Fife and Peletier [9] and Fusco and Hale [11] have introduced clines by allowing for spatial variation in migration rate. The limited number of continuous-space solutions we have seen may, in other words, simply reflect the idyllic geometry that we have imposed.

We have examined several systems with multiple stable equilibria in this underlying dynamics. The multiple stable states need not be equilibria. Out-of-phase periodic solutions yield many of the same effects. Figure 8 shows some of the truly beautiful two-cycles that arise upon simulating (10) with f as the logistic function [Equation (2)]. This plethora of two-cycles has not been seen for Equation (13) and is known to be absent for (64).

8. DIFFUSIVE INSTABILITY

Complex spatial patterns may also arise as the result of diffusive instability [48]. In continuous-time systems [59], diffusive instability appears when one species (e.g. a predator) diffuses and decays so rapidly that it cannot exert its stabilizing influence upon a second species (e.g. the prey). This may also happen in discrete-time systems.

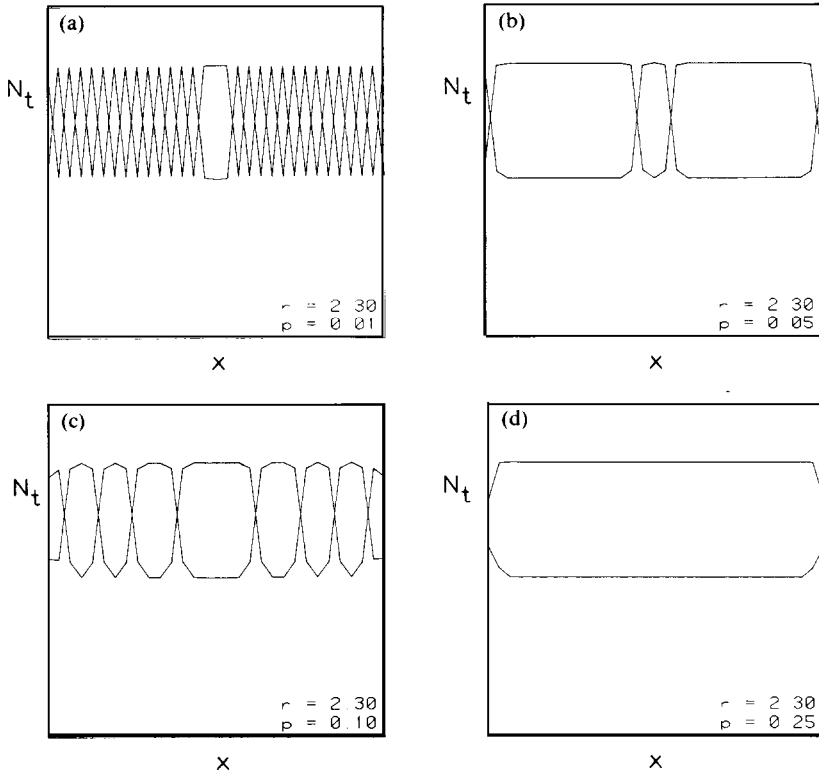


FIG. 8. Two-cycles that arise from simulating (10) with f as the logistic function. Thirty-one patches and identical initial conditions were used in each simulation.

Consider two species, $N^{(1)}$ and $N^{(2)}$, which grow and disperse, in synchrony, on an infinite, one-dimensional habitat:

$$N_{t+1}^{(1)}(x) = \int_{-\infty}^{\infty} k_1(x-y) f_1(N_t^{(1)}(y), N_t^{(2)}(y)) dy, \quad (82a)$$

$$N_{t+1}^{(2)}(x) = \int_{-\infty}^{\infty} k_2(x-y) f_2(N_t^{(1)}(y), N_t^{(2)}(y)) dy. \quad (82b)$$

The interval is infinite, so that we may begin with spatially uniform equilibria. $k_1(x-y)$ and $k_2(x-y)$ are symmetric, nonnegative, and satisfy

$$\int_{-\infty}^{\infty} k_i(x-y)(dx \text{ or } dy) = 1. \quad (83)$$

We assume the existence of a spatially uniform steady state $(N_t^{(1)}(x), N_t^{(2)}(x)) = (N^{(1)*}, N^{(2)*}) = \mathbf{N}^*$ such that

$$N^{(i)*} = f_i(\mathbf{N}^*), \quad (84)$$

and we take the steady state as stable in the absence of diffusion.

Can dispersal destabilize \mathbf{N}^* ? Consider perturbations off the steady state:

$$N_t^{(i)}(x) = N^{(i)*} + \xi_t^{(i)}(x). \quad (85)$$

If the perturbations $\xi_t^{(i)}$ are sufficiently small, we can linearize about \mathbf{N}^* :

$$\xi_{t+1}^{(1)}(x) = \int_{-\infty}^{\infty} k_1(x-y) [a_{11}\xi_t^{(1)}(y) + a_{12}\xi_t^{(2)}(y)] dy, \quad (86a)$$

$$\xi_{t+1}^{(2)}(x) = \int_{-\infty}^{\infty} k_2(x-y) [a_{21}\xi_t^{(1)}(y) + a_{22}\xi_t^{(2)}(y)] dy, \quad (86b)$$

where the a_{ij} are given by

$$a_{ij} = \left. \frac{\partial f_i}{\partial N_t^{(j)}} \right|_{\mathbf{N}^*}. \quad (87)$$

If the $\xi_t^{(i)}$ decay to zero, \mathbf{N}^* is asymptotically stable.

Rather than analyse the $\xi_t^{(i)}$ directly, we examine the Fourier-transformed perturbations

$$\hat{\xi}_t^{(1)}(\omega) = \int_{-\infty}^{\infty} \xi_t^{(1)}(x) e^{-i\omega x} dx, \quad (88a)$$

$$\hat{\xi}_t^{(2)}(\omega) = \int_{-\infty}^{\infty} \xi_t^{(2)}(x) e^{-i\omega x} dx. \quad (88b)$$

The mapping that describes the transformed perturbations has a simple form. Upon taking the Fourier transformation of (86), we see that it is just

$$\hat{\xi}_{t+1}(\omega) = KJ\hat{\xi}_t(\omega) \quad (89)$$

where J is just the Jacobian matrix

$$J = [a_{ij}]$$

and K is given by

$$K = \begin{bmatrix} \hat{k}_1(\omega) & 0 \\ 0 & \hat{k}_2(\omega) \end{bmatrix} \quad (90)$$

with

$$0 \leq \hat{k}_1(\omega), \hat{k}_2(\omega) \leq 1. \quad (91)$$

Decay of the $\hat{\xi}_i^{(i)}$ guarantees decay of the $\xi_i^{(i)}$.

In the absence of diffusion,

$$\hat{\xi}_{i+1}(\omega) = J\hat{\xi}_i(\omega). \quad (92)$$

With diffusion,

$$\hat{\xi}_{i+1}(\omega) = KJ\hat{\xi}_i(\omega). \quad (93)$$

If N^* is stable in the absence of diffusion, all eigenvalues of J have modulus less than one. Diffusive instability arises if, in contrast, the matrix KJ has one or more eigenvalues of modulus greater than one.

We can say more. All eigenvalues of J have modulus less than one if [22, 23]

$$1 - \text{Tr } J + \text{Det } J > 0, \quad (94a)$$

$$1 + \text{Tr } J + \text{Det } J > 0, \quad (94b)$$

$$\text{Det } J < 1, \quad (94c)$$

where $\text{Tr } J$ and $\text{Det } J$ are, respectively, the trace and the determinant of J . For diffusive instability, (94) must hold and, in addition, one of the corresponding conditions for KJ

$$1 - (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2 \text{Det } J > 0, \quad (95a)$$

$$1 + (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2 \text{Det } J > 0, \quad (95b)$$

$$\hat{k}_1 \hat{k}_2 \text{Det } J < 1 \quad (95c)$$

must be violated.

If (94) holds and only (95a) is violated, stability is lost through $+1$. If only (95b) is violated, -1 is the avenue of loss. Given (91) and (94c), (95c) always holds true; diffusive instability, in and of itself, cannot lead to a Hopf bifurcation. In a similar manner, we see that diffusive instability is impossible if the diffusivities are equal. For if $\hat{k}_1(\omega) = \hat{k}_2(\omega) = \hat{k}(\omega)$, (95) implies asymptotic stability if all eigenvalues of J are of modulus less than $1/\hat{k}$. Indeed, the eigenvalues of J satisfy a stronger condition: they are all of modulus less than one.

J has all its eigenvalues within the unit circle. Given that K is diagonal and that $\|K\| \leq 1$, it may seem odd that KJ may have eigenvalues outside the unit circle. Remember, however, that J is not, in general, symmetric.

Consider, as an example, the matrix

$$J = \begin{bmatrix} 2.0 & -1.25 \\ 3.0 & -2.0 \end{bmatrix} \quad (96)$$

with eigenvalues $\lambda = \pm 0.5$. For

$$K = \begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix} \quad (97)$$

$\lambda_{KJ} = 2.0, 0.0$. For

$$K = \begin{bmatrix} 0 & 0 \\ 0 & 1 \end{bmatrix} \quad (98)$$

$\lambda_{KJ} = -2.0, 0.0$. In both instances, differential diffusivity leads to diffusive instability.

We have, once again emphasized integrodifference equations. An analysis of diffusive instability in discrete patch models of the form (6) is also possible. (A comparison of continuous-space and discrete-space diffusive instability in continuous-time models is to be found in Segel and Levin [60].)

9. CONCLUSION

We have presented and discussed a number of simple discrete-time growth-dispersal models. In keeping with the nature of the topic, our presentation has an ending that is somewhat diffuse—there are simply too many avenues that need to be pursued.

To the extent that we have touched base with the literature, it has been the reaction-diffusion literature. Hence the emphasis on concept such as critical habitat size and diffusive instability. Just as easily, we could have emphasized dynamical systems theory. The integrodifference equations we have studied exhibit cascades of period-doubling bifurcations. Often, our models have one-dimensional unimodal maps embedded in them (Section 6). They must, therefore, exhibit certain ordering [55] and universality properties [7, 8].

One of the more important lessons of dynamical systems theory is that discrete-time systems often provide a great deal of insight into the behavior of continuous-time systems. Simple one-dimensional maps often appear, for example, upon taking the Poincaré section of higher-dimensional flows and semiflows [56–58]. It is particularly intriguing to wonder whether the same might not also be true for integrodifference equations.

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