Dispersal and Pattern Formation in a Discrete-Time Predator–Prey Model

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We investigate the dispersal-driven instabilities that arise in a discrete-time predator–prey model formulated as a system of *integrodifference equations*. Integrodifference equations contain two components: (1) difference equations, which model growth and interactions during a sedentary stage, and (2) redistribution kernels, which characterize the distribution of dispersal distances that arise during a vagile stage. Redistribution kernels have been measured for a tremendous number of organisms. We derive a number of redistribution kernels from first principles. Integrodifference equations generate pattern under a far broader set of ecological conditions than do reaction-diffusion models. We delineate the necessary conditions for dispersal-driven instability for two-species systems and follow this with a detailed analysis of a particular predator–prey model. © 1995 Academic Press, Inc.

1. INTRODUCTION

There is nothing surprising in the observation that organisms track spatial and environmental variation. Indeed, there is an extensive literature on habitat selection (Fretwell and Lucas, 1969; Morse, 1980; Cody, 1985; Bazzaz, 1991; Morrison *et al.*, 1992; Block and Brennan, 1993) and on the role of habitat selection in determining the dispersion of organisms. There

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is also an older literature on autecological components of niche (Grinell, 1917, 1924, 1928; James *et al.*, 1984), species-specific responses to gradients (Gleason, 1926), and populations (Andrewartha and Birch, 1954, 1984) that argues that environmental heterogeneity is frequently the principal determinant of distribution and abundance.

Despite the ubiquity of environmental heterogeneity, patterned spatial distributions may also arise in *homogeneous* environments (Steele, 1974, 1976, 1978; Mackas and Boyd, 1979; Levin, 1992). Thus it is essential that we ask whether patterns can arise solely as the result of trophic interactions and dispersal. A number of scientists have investigated this question using continuous-time growth models with simple (Fickian) diffusion. The diffusion in these reaction-diffusion models is generally thought of as a stabilizing influence (McMurtrie, 1978), one that homogenizes populations and moderates temporal fluctuations. However, Turing (1952) demonstrated that diffusion may also combine with intra- and interspecific interactions to yield instability and spatial patterns. Turing's concerns were largely developmental. However, his ideas regarding diffusive instability were soon transferred to ecology by Segel and Jackson (1972), Levin and Segel (1976), and Segel and Levin (1976). There is now an extensive literature on diffusive instability and pattern formation in ecology (Okubo, 1980; Conway, 1984; Murray, 1989).

The conditions for diffusive instability are surprisingly severe —at least by ecological standards. There are a number of predator–prey reaction-diffusion models that exhibit diffusive instability, but they invariably invoke tenuous biological assumptions such as the coupling of prey autocatalysis (Levin and Segel, 1976) or of an Allee effect (Mimura and Murray, 1978; Mimura, 1979; Mimura *et al.*, 1979) with a density dependent death rate for the predator. In effect, the assumption of Fickian diffusion in both predator and prey is sufficiently restrictive that it may place an undue burden on the interaction terms. A further difficulty with reaction-diffusion equations is that they are inappropriate for the innumerable species with discrete, nonoverlapping generations.

To circumvent these difficulties, we will consider discrete-time models built around *contact distributions* (Mollison, 1977)—probability distributions for the distance that an organism moves. Discrete-time spatial contact models have a surprisingly long history. They are at the heart of the *problem of random flights* (Markoff, 1912; Chandrasekhar, 1943) wherein a particle undergoes a sequence of independent and random displacements of given distribution. Later Slatkin (1973), Weinberger (1978, 1984), and Lui (1982a, 1982b, 1983, 1985, 1986, 1989a, 1989b) used them to describe changes in gene frequency. And recently, they have appeared in population ecology as integrodifference equations (Kot and Schaffer, 1986; Hardin *et al.* 1988a, 1988b, 1990; Kot, 1989, 1992; Andersen, 1991; Hastings and

Higgins, 1994) for populations with discrete nonoverlapping generations and well-defined growth and dispersal stages.

Our principal claim is that discrete-time spatial contact models—alias integrodifference equations—exhibit dispersal-driven instability under a broader set of ecological conditions than do reaction-diffusion models. Our purpose in this paper is to provide a general foundation for systems of integrodifference equations and to analyze and demonstrate the circumstances that lead to discrete-time dispersal-driven instability.

In Section 2, we briefly formulate a system of integrodifference equations for a predator and its prey. Each equation is built around a redistribution kernel (or contact distribution). There are a variety of possible redistribution kernels (Section 3); this multiplicity facilitates the occurrence of dispersal-driven instability. We derive necessary conditions for dispersal-driven bifurcations in Section 4. A detailed example is presented in Section 5. Concluding remarks are relegated to Section 6.

2. INTEGRODIFFERENCE EQUATIONS

We wish to consider some simple models for interacting populations—predator and prey or host and parasitoid—that grow, interact, and disperse, in synchrony, on a continuous one-dimensional habitat. Each model will be built on top of a system of first-order difference equations,

$$N_{t+1} = f(N_t, P_t), \tag{1a}$$

$$P_{t+1} = g(N_t, P_t), \tag{1b}$$

for the levels of the two populations, N_t and P_t, at time t. There is a long history of such difference equations (Nicholson, 1933; Nicholson and Bailey, 1935; Hassell, 1978). Some of the better-studied systems are known to exhibit complicated and/or chaotic dynamics (Beddington *et al.*, 1975; Gumowski and Mira, 1980; Lauwerier and Metz, 1986; Hadeler and Gerstmann, 1990; Neubert and Kot, 1992).

System (1) makes no allowance for the dispersion of our organisms. To amend this situation, let $N_t(x)$ and $P_t(x)$ represent each population's density in space at the start of the tth generation. We imagine that change occurs as the composition of two distinct stages. Growth, predation, and reproduction occur during a density-dependent sedentary stage. During this stage, $N_t(x)$ is mapped to $f(x, N_t(x), P_t(x))$ while $P_t(x)$ is mapped to $g(x, N_t(x), P_t(x))$. Explicit spatial dependences in f and g (from here on dropped) reflect clinal (spatially varying, time-independent) variation in the parameters. Movement occurs during the second stage. We describe the details of this movement with a pair of linear integral operators that tally

the movement from all y to x. The composition of these two stages yields a coupled system of integrodifference equations,

$$N_{t+1}(x) = \int_\Omega k_1(x, y) f(N_t(y), P_t(y))\, dy, \tag{2a}$$

$$P_{t+1}(x) = \int_\Omega k_2(x, y) g(N_t(y), P_t(y))\, dy, \tag{2b}$$

for the growth and dispersal of N and P in their one-dimensional domain Ω.

The two functions $k_1(x, y)$ and $k_2(x, y)$ are redistribution kernels. Each kernel describes the dispersal of one of the populations. The product $k_1(x, y)\, dy$ is the probability that an N individual at x originated from an interval of length dy about y. The product $k_2(x, y)\, dy$ provides the same information for P propagules. The two kernels are constrained to be non-negative. Each kernel may depend on absolute location or on relative distance. If both kernels depend on relative distance, we may rewrite system (2) in terms of convolution integrals:

$$N_{t+1}(x) = \int_\Omega k_1(x - y) f(N_t(y), P_t(y))\, dy, \tag{3a}$$

$$P_{t+1}(x) = \int_\Omega k_2(x - y) g(N_t(y), P_t(y))\, dy. \tag{3b}$$

All of the examples in this paper will involve convolution integrals.

3. REDISTRIBUTION IN SPACE AND TIME

There are a number of methods for estimating redistribution kernels from observed data (Southwood, 1978; Silverman, 1986). In point of fact, redistribution kernels have been measured for a tremendous number of organisms (see Fig. 1), ranging from plant spores to small animals (Dobzhansky and Wright, 1943; Wolfenbarger, 1946, 1959, 1975; Cremer, 1966; Platt and Weiss, 1977; Stapanian and Smith, 1978; Taylor, 1978; Westelaken and Maun, 1985; Okubo and Levin, 1989; Tang, 1989; Willson, 1993). Observed dispersal curves are frequently characterized as being leptokuric (Bateman, 1950; Okubo, 1980; Howe and Smallwood, 1982; Howe and Westley, 1986; Willson, 1992).

Our purpose in this section is not, however, to dwell on empirical distributions. Rather, we wish to derive, as parsimoniously as possible, theoretical distributions that highlight the inherent diversity of redistribution kernels. We begin by modelling dispersal as the diffusion or advection of volant propagules that settle with some prescribed failure rate. We
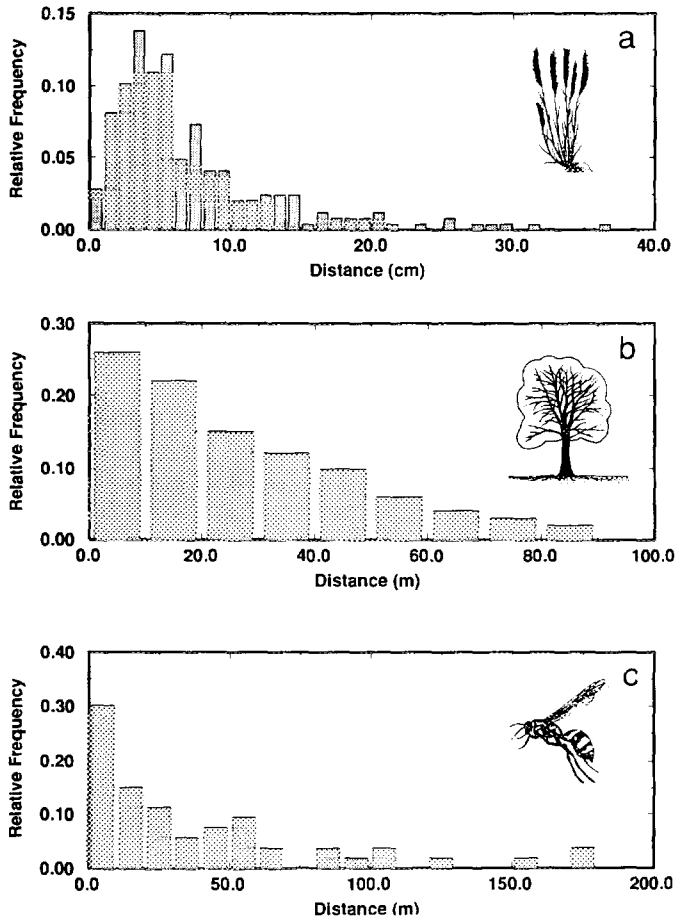
FIG. 1. Frequency distributions of distances (a) for the dispersal of diaspores of the annual grass *Vulpia fasciculata* ($n = 246$) (Carey and Watkinson, 1993), (b) for the dispersal of seeds of the European ash *Fraxinus excelsior* ($n = 127,070$) (Geiger, 1971), and (c) between natal sites and nests of the queens of the paper wasp *Polistes riparius* ($n = 53$) (Makino *et al.*, 1987).

follow this with a more mechanical approach, one that generates a redistribution kernel as the solution to a ballistics problem. We will use various of the derived probability density functions in our examples of dispersal-driven pattern formation in Section 5.

Diffusion and Settling

Consider a propagule, at the origin of an infinite one-dimensional domain. If the propagule performs an unbiased random walk, the probability density

function for the propagule's location at time t, $u(x, t)$, satisfies the diffusion equation

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2},$$ (4)

subject to the Dirac delta-function initial condition

$$u(x, 0) = \delta(x)$$ (5)

(Berg, 1983). The solution to this initial value problem is just

$$u(x, t) = \frac{1}{2\sqrt{\pi Dt}} e^{-x^2/4Dt}$$ (6)

(e.g., Kevorkian, 1990) and the position of the propagule is seen to be a normally distributed random variable.

We now extrapolate to an entire population of propagules that disperse in synchrony and that settle simultaneously at $t = t_s$. From Eq. (6), the redistribution kernel is just

$$k(x) = \frac{1}{2\sqrt{\pi Dt_s}} e^{-x^2/4Dt_s}$$ (7)
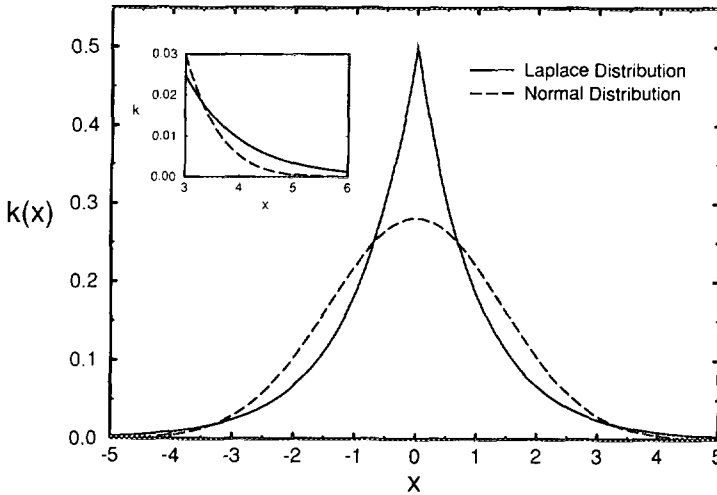
(see Fig. 2).

FIG. 2. Redistribution kernels for simple diffusive dispersal with settling. Synchronous settling gives a normal distribution; settling at a constant rate gives a leptokurtic Laplace distribution. Leptokurtic distributions—frequently observed in field studies—are more peaked and have fatter tails than normal distributions (see inset). In this figure, $Dt_s = 1$ (see Eq. (7)) while $a = D$ (see Eq. (11)).

It seems contrived, however, to assume that each individual settles at the exact same instant of time. We may instead assign a probability of settling, $h(t)\,dt$, to each time interval dt. The function $h(t)$ is commonly referred to as a *failure rate* or *hazard function* (Fox, 1993). If we let $v(x, t)$ represent the normalized density of settled propagules, u and v must satisfy

$$\frac{\partial u}{\partial t} = D\,\frac{\partial^2 u}{\partial x^2} - h(t)\,u, \tag{8a}$$

$$\frac{\partial v}{\partial t} = h(t)\,u, \tag{8b}$$

subject to the initial conditions

$$u(x, 0) = \delta(x), \tag{9a}$$

$$v(x, 0) = 0. \tag{9b}$$

Let us begin with the simplest interesting failure rate: $h(t) = a$, a a constant. If the dispersal period is long enough for all propagules to settle, we may take the redistribution kernel as the limit as t goes to infinity of $v(x, t)$. Integrating Eq. (8a) from $t = 0$ to $t = \infty$, we derive a modified Helmholtz equation for the redistribution kernel $k(x)$:

$$\frac{D}{a}\frac{\partial^2 k}{\partial x^2} - k = -\delta(x). \tag{10}$$

The solution to this equation is the leptokurtic Laplace or double-exponential distribution

$$k(x) = \tfrac{1}{2}\sqrt{a/D}\;e^{-\sqrt{a/D}\,|x|} \tag{11}$$

(see Fig. 2).

Broadbent and Kendall (1953), in their examination of the dispersal of larvae of the helminth *Trichostrongylus retortaeformis*, and Williams (1961), in a discussion of the infestation of fruit by the larvae of the codling moth, give a more general derivation of the Laplace distribution as the marginal distribution of a random walk in *two* spatial dimensions with constant failure rate (see also Turchin and Thoeny, 1993). Other failure rates may be used in system (8), resulting in redistribution kernels qualitatively similar to the Laplace distribution.

A simple extension of this dispersal process is a multi-stage process such as

$$\frac{\partial u}{\partial t} = D_1 \frac{\partial^2 u}{\partial x^2} - au,$$ (12a)

$$\frac{\partial v}{\partial t} = D_2 \frac{\partial^2 v}{\partial x^2} + au - bv,$$ (12b)

$$\frac{\partial w}{\partial t} = bv,$$ (12c)

where v is now a secondary dispersal stage and w is the density of settled individuals. For example, seeds that initially diffuse in the air may be redistributed on the ground by ants and rodents (Beattie and Lyons, 1975; Brown et al., 1979; Price and Jenkins, 1986; Vander Wall, 1992; Moore, 1992). This example results in the redistribution kernel

$$k(x) = \begin{cases} \dfrac{1}{2} \dfrac{\delta \varepsilon}{\delta - \varepsilon} \left(\dfrac{1}{\sqrt{\varepsilon}} e^{-\sqrt{\varepsilon}\,|x|} - \dfrac{1}{\sqrt{\delta}} e^{-\sqrt{\delta}\,|x|} \right), & \delta \neq \varepsilon \\ \dfrac{1}{4} \sqrt{\varepsilon}\,(1 + \sqrt{\varepsilon}\,|x|)\, e^{-\sqrt{\varepsilon}\,|x|}, & \delta = \varepsilon \end{cases}$$ (13)

with $\delta = a/D_1$ and $\varepsilon = b/D_2$ (see Fig. 3). The extension to even more dispersal stages is straightforward.
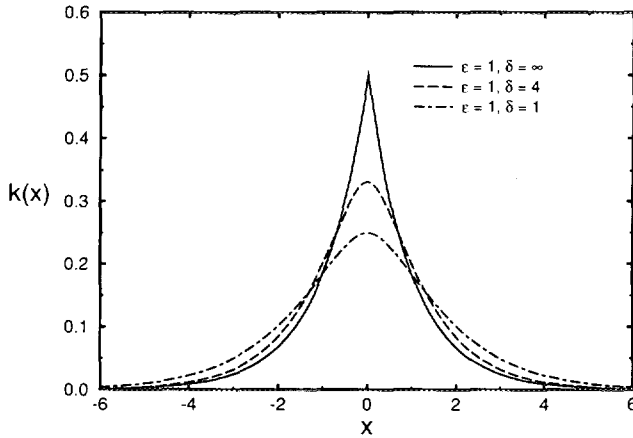

FIG. 3. Two-stage dispersal. Two diffusive dispersal stages coupled by a constant failure rate generate a redistribution kernel that is a combination of two Laplace distributions (see Eq. (13)). This process might describe seeds initially dispersed through the air that are subsequently redistributed on the ground by ants or rodents. In the limit as δ approaches infinity, we recover the Laplace distribution for a single dispersal stage (solid line).

Advection and Settling

Many dispersal curves have their maxima at some intermediate distance from the parent (Cremer, 1966; Platt and Weiss, 1977; Stapanian and Smith, 1978; Howe *et al.*, 1985). This may reflect an increase in propagule mortality close to the parent, as proposed by Janzen (1970) and Connell (1971). Or, it may simply indicate advection (Okubo and Levin, 1989).

Consider propagules that move outward with constant speed c and that fall or settle with failure rate $h(t)$. Let $u(x, t)$ be the (normalized) density of volant propagules and $v(x, t)$ the density of settled propagules. This new dispersal process is governed by the partial differential equations

$$\frac{\partial u}{\partial t} = -c \operatorname{sgn}(x) \frac{\partial u}{\partial x} - h(t) u, \tag{14a}$$

$$\frac{\partial v}{\partial t} = h(t) u, \tag{14b}$$

and the initial conditions

$$u(x, 0) = \delta(x), \tag{15a}$$

$$v(x, 0) = 0. \tag{15b}$$

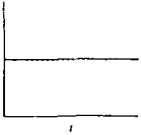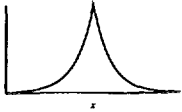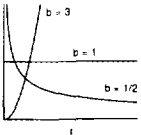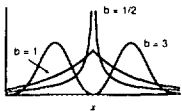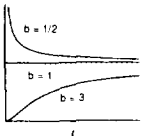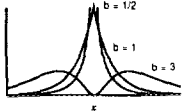We may solve Eq. (14a) by the method of characteristics (Zwillinger, 1992),

$$u(x, t) = \tfrac{1}{2} \delta(|x| - ct) \, e^{-\int_0^t h(s)\,ds}. \tag{16}$$

The redistribution kernel is just the final distribution of propagules on the ground. Integrating Eq. (14b) from $t = 0$ to $t = \infty$, we obtain

$$k(x) = \frac{1}{2c} h\left(\frac{|x|}{c}\right) e^{-\int_0^{|x|/c} h(s)\,ds}. \tag{17}$$

Remarkably different redistribution kernels may arise for different choices of the hazard function $h(t)$ (see Table I). A constant failure rate once again generates a Laplace or double-expontial distribution. If the failure rate increases or decreases as a power of time, we obtain the double-Weibull distribution of Andersen (1991). Finally, a carefully chosen failure rate that tends monotonically towards a constant yields a double-gamma distribution. The double-gamma distribution has a simple characteristic function (Fourier transform) and will be used extensively in Section 5.

TABLE 1

Advective Dispersal

Hazard Function $h(t)$	Graph of $h(t)$	Redistribution Kernel $k(x)$	Graph of $k(x)$
a		$\dfrac{1}{2}\dfrac{a}{c}\,e^{-a\|x\|/c}$ Laplace Distribution	
$b\,a^b\,t^{b-1}$		$\dfrac{1}{2}\dfrac{a}{c}\left(\dfrac{a\|x\|}{c}\right)^{b-1} b\,e^{-(a\|x\|/c)^b}$ Double – Weibull Distribution	
$\dfrac{1}{\displaystyle\int_0^\infty \left(1+\dfrac{u}{t}\right)^{b-1} e^{-au}\,du}$		$\dfrac{1}{2}\dfrac{a}{c}\left(\dfrac{a\|x\|}{c}\right)^{b-1}\dfrac{e^{-a\|x\|/c}}{\Gamma(b)}$ Double – Gamma Distribution	

Ballistics

Finally, consider a propagule that is launched from a fixed point on the ground, with fixed speed c, but at random angle θ. We imagine that only gravity acts upon this propagule and that we may describe the trajectory of this propagule with the differential equations

$$\frac{d^2x}{dt^2} = 0, \tag{18a}$$

$$\frac{d^2y}{dt^2} = -g, \tag{18b}$$

subject to the initial conditions

$$x(0) = 0, \qquad \frac{dx}{dt}(0) = c\cos\theta, \tag{19a}$$

$$y(0) = 0, \qquad \frac{dy}{dt}(0) = c\sin\theta, \tag{19b}$$

with $0 \leqslant \theta \leqslant \pi$.

Equations (18) are easy to solve. Each propagule returns to the ground with a horizontal displacement x determined by the launch angle θ,

$$x(\theta) = \frac{c^2}{g} \sin 2\theta. \tag{20}$$

We may also invert Eq. (20) to find the *two* launch angles corresponding to a given horizontal displacement. If we combine this information with the probability density function $f(\theta)$ of launch angles, we can derive the probability density function $k(x)$ for the distribution of displacements. In particular, let the launch angles be uniformly distributed over the interval $0 \leqslant \theta \leqslant \pi$, so that

$$f(\theta) = 1/\pi. \tag{21}$$

Then, a simple change of variables,

$$\int_0^\pi f(\theta) \, d\theta = \int_{-c^2/g}^{+c^2/g} 2f(\theta(x)) \left| \frac{d\theta}{dx} \right| dx, \tag{22}$$

leads us to the redistribution kernel

$$k(x) = 2f(\theta(x)) \left| \frac{d\theta}{dx} \right| \tag{23}$$

and to the distribution

$$k(x) = \frac{1}{\pi \sqrt{(c^2/g)^2 - x^2}}, \qquad |x| < \frac{c^2}{g} \tag{24}$$

(see Fig. 4). This kernel has singularities at $x = \pm c^2/g$. However, the area underneath the kernel, and hence the probability of landing in any interval, is finite.

Distribution (24) neglects factors such as air resistance and the height of the source. Buller (1909) included air resistance (proportional to the velocity) in his study of basidiospores discharged from a basidium. Each basidiospore follows a rather peculiar trajectory, a "sporabola," consisting of a horizontal leg, traversed very quickly, and a vertical leg wherein the spore falls slowly with a terminal velocity determined by Stokes' law. Similarly, Beer and Swaine (1977) included the effects of (1) the height of the source, (2) air resistance (proportional to the velocity squared), and (3) a limited range of launch angles in their study of explosively dispersed seeds. Finally, Stamp and Lucas (1983) have discussed the ecological correlates of ballistic dispersal.
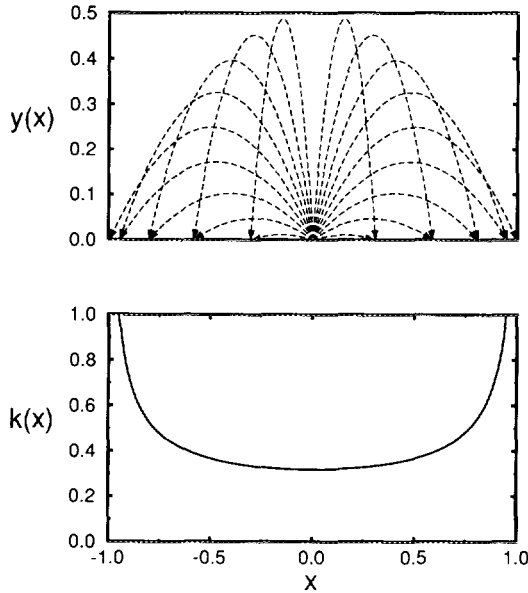
FIG. 4. Ballistic dispersal. The top graph shows the trajectories of propagules launched at various angles and moving under the influence of gravity. Although the angles are uniformly distributed, the landing sites cluster near the maximal dispersal distance. This produces a redistribution kernel (bottom, see also Eq. (24)) with singularities at $x = \pm c^2/g$. In this figure, $c^2 = g$.

4. DISPERSAL-DRIVEN INSTABILITIES

Turing (1952) was the first to appreciate that diffusion may *destabilize* a spatially uniform solution. Diffusive instability occurs when one species diffuses and decays so rapidly that it cannot exert its stabilizing influence upon a second species (Segel and Jackson, 1972). However, the conditions for diffusive instability are surprisingly stringent, at least from an ecological perspective. There are a number of predator–prey reaction-diffusion models that exhibit diffusive instability, but they invariably invoke tenuous biological assumptions such as the coupling of prey autocatalysis (Levin and Segel, 1976) or of an Allee effect (Mimura and Murray, 1978; Mimura, 1979; Mimura *et al.*, 1979) with a density-dependent death rate for the predator.

Are the conditions for dispersal-driven instability in discrete-time integrodifference equations any less stringent than those for diffusive instability in continuous-time reaction-diffusion models? The tremendous diversity of redistribution kernels and of difference-equation dynamics

suggest that this might be so. The preliminary results of Kot and Schaffer (1986) and of Kot (1989) also point in this direction. So as to go beyond suggestion, we study the effects of dispersal on an otherwise stable equilibrium.

We start with a pair of difference equations,

$$N_{t+1} = f(N_t, P_t), \tag{25a}$$

$$P_{t+1} = g(N_t, P_t), \tag{25b}$$

with an equilibrium point (N^*, P^*) in the interior of the first quadrant. The equilibrium point must satisfy

$$N^* = f(N^*, P^*), \tag{26a}$$

$$P^* = g(N^*, P^*). \tag{26b}$$

We assume that this equilibrium point is asymptotically stable, with all of the eigenvalues of the Jacobian or community matrix

$$\mathbf{J} = \begin{pmatrix} \dfrac{\partial f}{\partial N} & \dfrac{\partial f}{\partial P} \\ \dfrac{\partial g}{\partial N} & \dfrac{\partial g}{\partial P} \end{pmatrix}_{(N^*, P^*)} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \tag{27}$$

of magnitude less than one.

Next, we add dispersal and consider

$$N_{t+1}(x) = \int_{-\infty}^{+\infty} k_1(x - y) f(N_t(y), P_t(y)) \, dy, \tag{28a}$$

$$P_{t+1}(x) = \int_{-\infty}^{+\infty} k_2(x - y) g(N_t(y), P_t(y)) \, dy. \tag{28b}$$

The domain is infinite so that we may start with a spatially uniform steady state. We further limit ourselves to kernels $k_1(x - y)$ and $k_2(x - y)$ that are symmetric (or even) and nonnegative. Finally, as a matter of convenience, we assume that there is no mortality during dispersal,

$$\int_{-\infty}^{+\infty} k_i(x) \, dx = 1, \tag{29}$$

so that the equilibrium (N^*, P^*) is also a spatially uniform steady state of the full integrodifference system (28).

Can dispersal destabilize (N^*, P^*)? Consider perturbations of the steady state of the form

$$N_t(x) = N^* + n_t(x), \tag{30a}$$

$$P_t(x) = P^* + p_t(x). \tag{30b}$$

For sufficiently small perturbations, we may linearize about (N^*, P^*),

$$n_{t+1}(x) = \int_{-\infty}^{+\infty} k_1(x - y)[a_{11}n_t(y) + a_{12}p_t(y)] \, dy, \tag{31a}$$

$$p_{t+1}(x) = \int_{-\infty}^{+\infty} k_2(x - y)[a_{21}n_t(y) + a_{22}p_t(y)] \, dy. \tag{31b}$$

The a_{ij} are once again given by the Jacobian of the underlying system of difference equations evaluated at (N^*, P^*) (see Eq. (27)). If the perturbations n_t and p_t decay to zero, (N^*, P^*) is asymptotically stable.

The integrals in Eqs. (31) are convolutions. Since convolution integrals simplify under Fourier transformation, we may use the Fourier transform pair

$$\hat{f}(\omega) = \int_{-\infty}^{+\infty} e^{i\omega x} f(x) \, dx, \tag{32a}$$

$$f(x) = \frac{1}{2\pi} \int_{-\infty}^{+\infty} e^{-i\omega x} \hat{f}(\omega) \, d\omega, \tag{32b}$$

and the transformed perturbations

$$\hat{n}_t(\omega) = \int_{-\infty}^{+\infty} e^{i\omega x} n_t(x) \, dx, \tag{33a}$$

$$\hat{p}_t(\omega) = \int_{-\infty}^{+\infty} e^{i\omega x} p_t(x) \, dx, \tag{33b}$$

to simplify our analysis. Indeed, upon taking the Fourier transform of system (31), we get

$$\begin{pmatrix} \hat{n}_{t+1} \\ \hat{p}_{t+1} \end{pmatrix} = \mathbf{KJ} \begin{pmatrix} \hat{n}_t \\ \hat{p}_t \end{pmatrix}, \tag{34}$$

where $\mathbf{J}$ is the Jacobian or community matrix

$$\mathbf{J} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \tag{35}$$

and $\mathbf{K}$ is given by

$$\mathbf{K} = \begin{pmatrix} \hat{k}_1(\omega) & 0 \\ 0 & \hat{k}_2(\omega) \end{pmatrix}. \tag{36}$$

Decay of the $\hat{n}_t(\omega)$ and $\hat{p}_t(\omega)$ for all ω guarantees the decay of $n_t(x)$ and $p_t(x)$ in $L_2(\mathbf{R})$.

In the absence of dispersal,

$$\begin{pmatrix} n_{t+1} \\ p_{t+1} \end{pmatrix} = \mathbf{J} \begin{pmatrix} n_t \\ p_t \end{pmatrix}. \tag{37}$$

With dispersal,

$$\begin{pmatrix} \hat{n}_{t+1} \\ \hat{p}_{t+1} \end{pmatrix} = \mathbf{KJ} \begin{pmatrix} \hat{n}_t \\ \hat{p}_t \end{pmatrix}. \tag{38}$$

By assumption, (N^*, P^*) is asymptotically stable in the absence of dispersal, with all of the eigenvalues of $\mathbf{J}$ of modulus less than one. Dispersal-driven instability arises if the matrix $\mathbf{KJ}$, in turn, has one or more eigenvalues of modulus greater than one.

One can say more. All of the eigenvalues of $\mathbf{J}$ have modulus less than one if the trace and determinant of $\mathbf{J}$ satisfy the Jury test (Jury, 1964, 1974)

$$1 - \operatorname{tr} \mathbf{J} + \det \mathbf{J} > 0, \tag{39a}$$

$$1 + \operatorname{tr} \mathbf{J} + \det \mathbf{J} > 0, \tag{39b}$$

$$1 - \det \mathbf{J} > 0. \tag{39c}$$

For dispersal-driven instability, conditions (39) must still hold. In addition, one of the corresponding conditions on $\mathbf{KJ}$,

$$1 - \operatorname{tr}(\mathbf{KJ}) + \det(\mathbf{KJ}) > 0, \tag{40a}$$

$$1 + \operatorname{tr}(\mathbf{KJ}) + \det(\mathbf{KJ}) > 0, \tag{40b}$$

$$1 - \det(\mathbf{KJ}) > 0, \tag{40c}$$

must be violated. The matrix $\mathbf{K}$ depends on the wave number ω; dispersal-driven instability will occur (if it occurs at all) for limited ranges of ω.

Inequality (40a) guarantees that all real eigenvalues of $\mathbf{KJ}$ are less than $+1$. If we reverse this inequality, the uniform steady state will lose its stability to a spatially structured solution. We refer to this as a *plus-one bifurcation*. If we reverse inequality (40b), so that an eigenvalue passes below -1, stability is lost to a spatially structured, time-periodic solution

of period two (a two-cycle); we have a *minus-one bifurcation*. The reversal of (40c) would lead to a Hopf bifurcation (with a complex conjugate pair of eigenvalues passing through the unit circle), would that it could occur. However, two-species dispersal-driven Hopf bifurcations are impossible on an infinite domain, as we prove in the Appendix (see also Kot, 1986, 1989).

Inequalities (39) and (40) impose restrictions on the elements a_{ij} of the community matrix and on the transformed kernels (or characteristic functions) $\hat{k}_1(\omega)$ and $\hat{k}_2(\omega)$. If dispersal-driven bifurcations are to arise, certain necessary conditions must be satisfied by the elements of the of the community matrix. These necessary conditions are summarized in Table II. We prove these conditions in the Appendix. Despite the fact that these conditions are rather varied, it is immediately clear that one must have a $(+, -)$ interaction $(a_{12}a_{21} < 0)$ between, for example, a predator and its prey or a parasitoid and its host, for dispersal-driven instability.

If both characteristic functions are of the same sign, we also require an activator $(|a_{ii}| > 1)$ and an inhibitor $(|a_{jj}| < 1)$. If, for example, a plus-one bifurcation is to occur at a wave number where both characteristic functions are positive, we require

$$(a_{11} - 1)(a_{22} - 1) < 0. \tag{41}$$

As with reaction-diffusion equations (Segel and Jackson, 1972; Levin and Segel, 1976; Mimura and Murray, 1978; Mimura, 1979; Mimura *et al.*, 1979; Okubo,

TABLE II

Necessary Conditions for Dispersal-Driven Bifurcations for System (3)
on an Infinite Domain

	Characteristic Functions		
Bifurcation Type	$0 \leq \hat{k}_1(\omega) \leq 1$ $0 \leq \hat{k}_2(\omega) \leq 1$	$-1 \leq \hat{k}_1(\omega) \leq 0$ $-1 \leq \hat{k}_2(\omega) \leq 0$	$0 < \hat{k}_1(\omega) \leq 1$ $-1 \leq \hat{k}_2(\omega) < 0$
+1	$(a_{11} - 1)(a_{22} - 1) < 0$ $a_{12}a_{21} < 0$	$(a_{11} + 1)(a_{22} + 1) < 0$ $a_{12}a_{21} < 0$	$a_{ii} > 1 \ or \ a_{jj} < 1$ $a_{12}a_{21} < 0$
-1	$(a_{11} + 1)(a_{22} + 1) < 0$ $a_{12}a_{21} < 0$	$(a_{11} - 1)(a_{22} - 1) < 0$ $a_{12}a_{21} < 0$	$a_{ii} < 1 \ or \ a_{jj} > 1$ $a_{12}a_{21} < 0$
Hopf	Impossible		

1980), this condition may be satisfied by coupling prey autocatalysis or an Allee effect with a density-dependent death rate for the predator.

Similarly, if a minus-one bifurcation is to occur at a wave number where both characteristic functions are positive, we require

$$(a_{11} + 1)(a_{22} + 1) < 0. \tag{42}$$

In this instance, a predator that stabilizes a cyclic or chaotic prey $(a_{11} < -1)$ in the absence of dispersal may fail to do so in the presence of dispersal (Kot, 1989).

These necessary conditions are relatively severe. Surprisingly, the replacement for conditions (41) or (42) when $\hat{k}_i(\omega) > 0$ and $\hat{k}_j(\omega) < 0$,

$$a_{ii} > 1 \qquad \text{or} \qquad a_{jj} < 1, \tag{43}$$

is rather undemanding. An activator may no longer be essential! Many realistic kernels are bimodal, have characteristic functions that go negative, and would appear to facilitate the occurrence of dispersal-driven instability. We explore this possibility further, by way of example, in Section 5.

5. An Extended Example

A simple system of two reaction-diffusion equations with logistic growth of the prey and mass-action functional and numerical responses is *incapable* of exhibiting diffusive instability (Conway, 1984). Can a similar system of integrodifference equations exhibit dispersal-driven instability? To answer this question, we started with the (rescaled) set of difference equations

$$N_{t+1} = (1 + r) N_t - rN_t^2 - cN_t P_t, \tag{44a}$$

$$P_{t+1} = cN_t P_t \tag{44b}$$

(Maynard Smith, 1968; Neubert and Kot, 1992).

System (44) possesses one computationally undesirable property: predator and prey numbers may become negative. To circumvent this problem, we replaced system (44) with the system

$$N_{t+1} = N_t e^{r(1 - N_t - P_t)}, \tag{45a}$$

$$P_{t+1} = cN_t P_t. \tag{45b}$$

The linearizations of systems (44) and (45) yield identical eigenvalues for equilibria with prey. The full nonlinear systems exhibit qualitatively similar behavior except for the aforementioned lack of first-quadrant invariance in system (44).

In the absence of the predator, system (45) reduces to the Ricker curve (Ricker, 1954); a prey species with a high intrinsic rate of growth ($r > 2$), bereft of its predator, may thus exhibit oscillatory or chaotic behavior (May, 1975; May and Oster, 1976). System (45) also possesses a unique equilibrium,

$$N^* = 1/c, \tag{46a}$$

$$P^* = 1 - 1/c, \tag{46b}$$

where predator and prey coexist. The stability of this equilibrium is determined by the Jacobian or community matrix $\mathbf{J}$ evaluated at equilibrium point (46):

$$\mathbf{J} = \begin{pmatrix} 1 - \dfrac{r}{c} & -\dfrac{r}{c} \\ c - 1 & 1 \end{pmatrix}. \tag{47}$$

The jury conditions (39) guarantee that this equilibrium is stable for

$$1 < c < 2, \tag{48a}$$

$$0 < r < \frac{4c}{3 - c} \tag{48b}$$

(see Fig. 5). For $c < 1$, the predator is inadequate and is unable to persist, leaving the prey to its natural tendencies. For $c > 2$, equilibrium (46) is unstable because of a Hopf bifurcation; predator and prey exhibit sustained oscillations. Finally, as we tune r so that $r > 4c/(3 - c)$, we observe a subcritical flip bifurcation (Neubert and Kot, 1992): the predator population undergoes a catastrophic collapse to extinction and the prey population is, once again, left to its natural tendencies.

To these dynamics, we added combinations of two redistribution kernels, the double-gamma distribution and the Laplace distribution (see Table I). we thus considered four different models (two species, each with one of two kernels). For a high-r prey and fixed prey dispersal, sufficiently high

FIG. 5. Solutions of system (45), a simple predator–prey model without dispersal: (a) Solutions in the (N, P) phase plane superimposed upon the (c, r) parameter plane. For different values of c and r, solutions tend to a stable equilibrium point (inset I), an invariant circle (inset II), a chaotic strange attractor (inset III), a periodic two-cycle bereft of predators (inset IV), or a variety of other attractors. The equilibrium point is stable for parameter values falling within the tooth-shaped region defined by inequalities (48). (b) Time series corresponding to the phase-plane trajectories (I–IV).

a

b
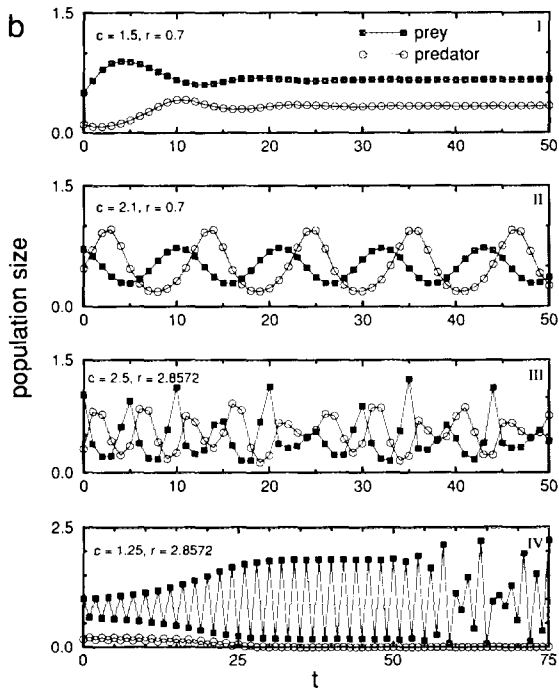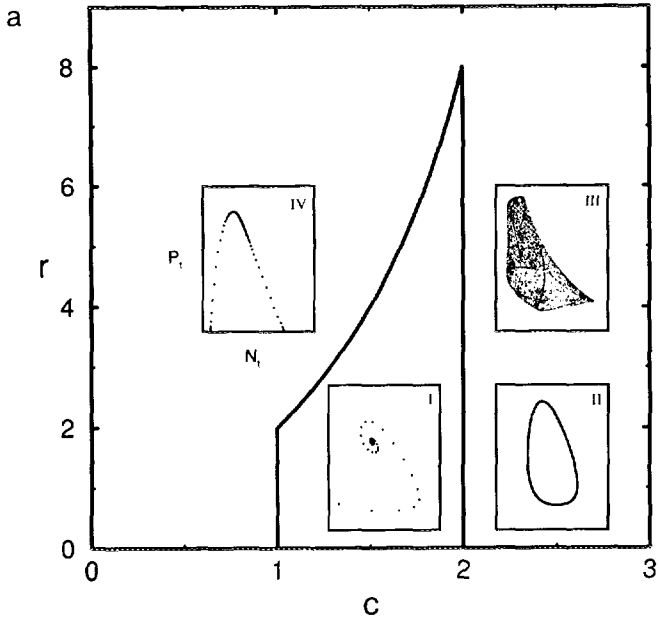
predator dispersal invariably set off a minus-one bifurcation with pattern formation. In three of the four models (the exception involved two Laplace distributions), sufficiently high *prey* overdispersal led to a plus-one bifurcation, again with pattern formation. Plus one bifurcations did not require high prey intrinsic rates of growth; they occurred throughout region (48).

Figure 6 shows the outcome of a typical numerical simulation. The parameters r and c were chosen so as to lie in region (48). We added
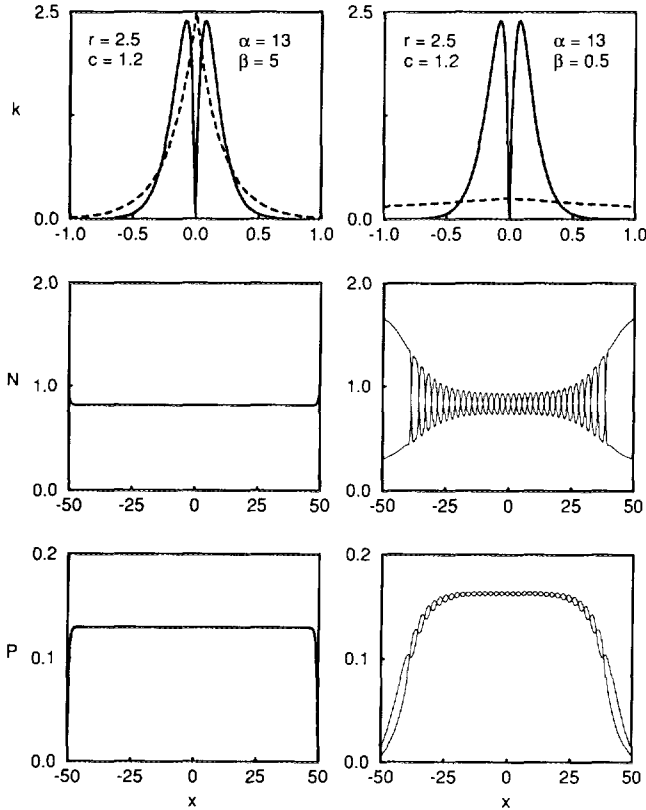

FIG. 6. A minus-one bifurcation. For the indicated values of r, c, and α, increasing predator dispersal from $\beta = 5$ to $\beta = 0.5$ destabilizes a spatially homogeneous solution. The resulting instability grows until a stable, spatially-patterned, two-cycle is reached. We iterated system (49) 5000 times on a domain of length 100 using the initial conditions $N(x) = 0.833$, $P(x) = 0.167$, and 4096 grid points prior to plotting the two-cycle. The top panel illustrates the redistribution kernels for the predator (dashed line) and for the prey (solid line) before (left) and after (right) the bifurcation. The middle and bottom panels show the prey and predator distributions for succeeding iterations, after convergence, before (left) and after (right) the bifurcation.

double-gamma-distribution dispersal to the prey and Laplace-distribution dispersal to the predator so as to give us

$$N_{t+1}(x) = \int_\Omega k_1(x-y)\, N_t(y)\, e^{r[1-N_t(y)-P_t(y)]}\, dy, \tag{49a}$$

$$P_{t+1}(x) = \int_\Omega k_2(x-y)[cN_t(y)\, P_t(y)]\, dy, \tag{49b}$$

with

$$k_1(x-y) = \frac{\alpha^2}{2}\, |x-y|\, e^{-\alpha |x-y|}, \tag{50a}$$

$$k_2(x-y) = \frac{\beta}{2}\, e^{-\beta |x-y|}. \tag{50b}$$

Mathematical analyses were performed on an infinite domain. Numerical simulations were, in contrast, performed on a large finite domain Ω using a fast FFT algorithm (Andersen, 1991). In particular, we iterated system (49) until we obtained a stable solution. Figure 6 shows the resulting steady state for $\alpha = 13$ and, $\beta = 5$. The interior of this solution is flat. There is variation toward the ends, but this is an edge effect stemming from the finiteness of the domain. As we increased the variance of the predator's redistribution kernel (by decreasing β), the "homogeneous" solution eventually became unstable. In its place, we obtained a spatially structured two-cycle. This period doubling is characteristic of a minus-one bifurcation.

In contrast, when we increased the variance of the prey's redistribution kernel (by decreasing α), we obtained a plus-one bifurcation: the spatially homogeneous solution was replaced by a time-independent, but spatially structured, steady state (see Fig. 7).

A Detailed Analysis

How much predator or prey overdispersal is necessary in order to destabilize the spatially homogeneous solution? What is the wavelength of the spatially structured solution? We can predict these quantities using inequalities (39) and (40).

Let us consider the plus-one bifurcation of Fig. 7. This bifurcation arises when inequality (40a) (alone) is reversed. The characteristic functions for the double-gamma distribution

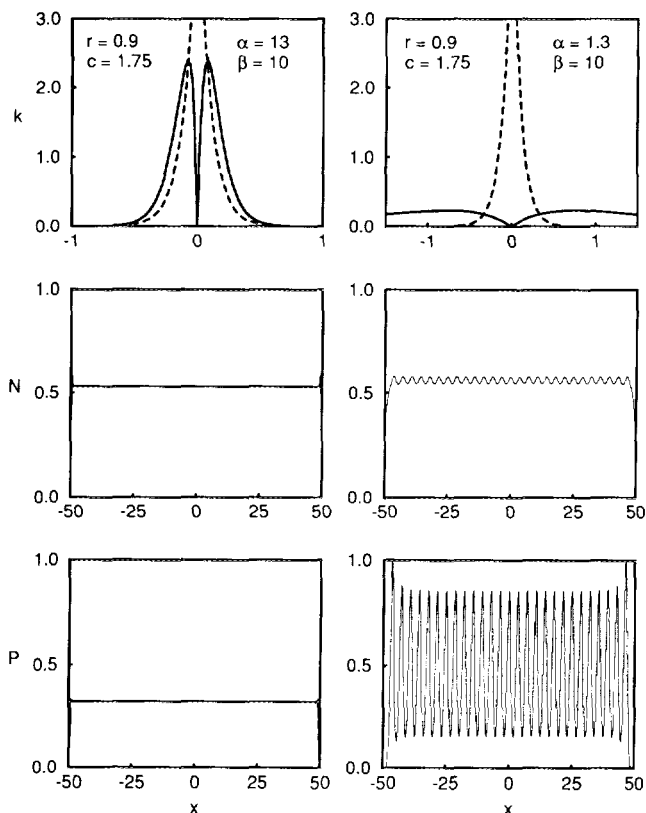$$\hat{k}_1(\omega) = \frac{\alpha^2(\alpha^2 - \omega^2)}{(\alpha^2 + \omega^2)^2}, \tag{51}$$

FIG. 7. A plus-one bifurcation. For the indicated values of r, c, and β, increasing prey dispersal from $\alpha = 13$ to $\alpha = 1.3$ destabilizes a spatially homogeneous solution. The resulting instability grows until a stable, spatially-patterned, equilibrium is reached. We iterated system (49) 5000 times on a domain of length 100 using the initial conditions $N(x) = 0.571$, $P(x) = 0.429$, and 4096 grid points prior to plotting the new equilibrium. The layout of this figure mirrors that of Fig. 6.

and for the Laplace distribution

$$\hat{k}_2(\omega) = \frac{\beta^2}{\beta^2 + \omega^2}, \tag{52}$$

coupled with the left-hand side of inequality (40a), give us the "dispersion relation"

$$Q(\omega) \equiv 1 - \hat{k}_1(\omega)\left(1 - \frac{r}{c}\right) - \hat{k}_2(\omega) + \hat{k}_1(\omega)\hat{k}_2(\omega)\left(1 + r - \frac{2r}{c}\right). \tag{53}$$

A plot of $Q(\omega)$, for the parameter values of Fig. 7, is shown in Fig. 8. Increasing prey dispersal (by decreasing x) causes $Q(\omega)$ to cross the ω-axis at ω^*. This ω^* predicts the wavelength of the spatially structured solution sufficiently close to the bifurcation. In our example, $\omega^* \approx 1.8$; there are $(1.8)(25)/2\pi \approx 7$ troughs between $x = 0$ and $x = 25$ in Fig. 7. Note that $\hat{k}_1(\omega^*) < 0$, $\hat{k}_2(\omega^*) > 0$; this plus-one bifurcation satisfies the necessary conditions in column 3 of Table II.

To determine the degree of prey overdispersal required for bifurcation, we calculated β/x at the point of contact of $Q(\omega)$ with the ω-axis. We set our dispersion relation equal to zero, multiplied by $(x^2 + \omega^2)^2 (\beta^2 + \omega^2)$, and made the change of variables

$$z = \frac{\omega^2}{x^2}, \qquad A = \frac{r}{c}, \qquad B = \frac{\beta^2}{x^2}, \qquad C = c - 1. \tag{54}$$

This gave us

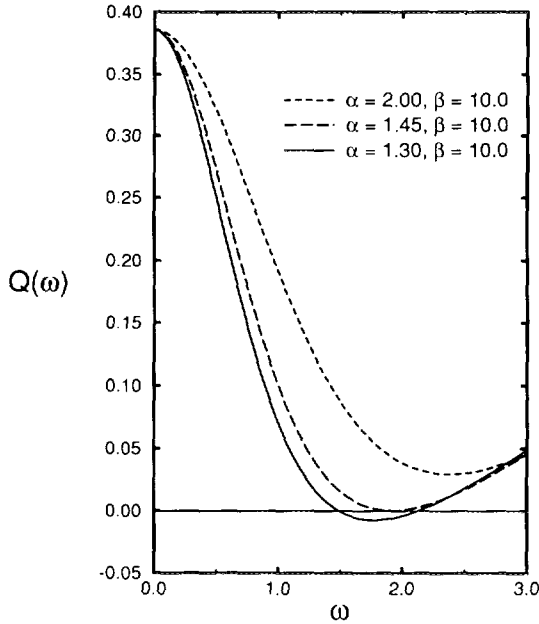$$R(z) \equiv z^3 + (3 - A) z^2 + A(1 - BC) z + ABC = 0. \tag{55}$$

FIG. 8. Dispersion relation (53). When $Q(\omega)$ crosses the ω-axis (at $\omega^* \approx 1.8$), a plus-one bifurcation occurs. The critical wave number ω^* is an accurate predictor of the spatial frequency of the resulting spatially-structured equilibrium, as evidenced by Fig. 7.

The critical wavelength z^* is determined by simultaneously solving

$$R(z^*) = z^{*3} + (3 - A)\, z^{*2} + A(1 - BC)\, z^* + ABC = 0, \qquad (56a)$$

$$\frac{dR}{dz}(z^*) = 3z^{*2} + 2(3 - A)\, z^* + A(1 - BC) = 0. \qquad (56b)$$

Alternatively, one can solve for A and C. Reversing the change of variables then gives us c and r parametrically as

$$c = 1 + \frac{\alpha^2}{\beta^2} \frac{z^*(z^* + 1)(3 - z^*)}{2(z^{*2} - 3)}, \qquad (57a)$$

$$r = \frac{2cz^*(z^{*2} - 3)}{(z^* - 1)^2}. \qquad (57b)$$

By fixing β/α and varying z^*, we may thus determine the locus of points in the (c, r) parameter plane where that fixed β/α is just enough to set off a plus-one bifurcation. If we fix z^* and vary β/α, we may also draw the curves in the (c, r) parameter plane corresponding to fixed values of ω^*/α at bifurcation. These two sets of level curves are illustrated in Fig. 9. Increasing r decreases the amount of prey overdispersal needed to initiate a plus-one bifurcation and shortens the wavelength of the corresponding spatially structured solution.

An equivalent procedure can be used to analyze the minus-one bifurcation that follows from predator overdispersal. Level curves of β/α and ω^*/α
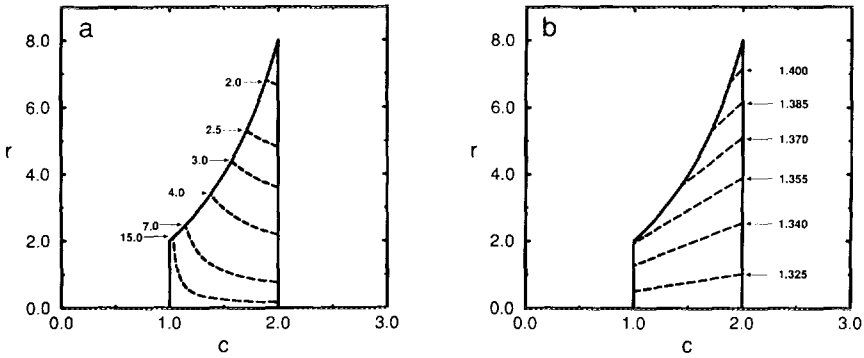

FIG. 9. Level curves of critical dispersal ratios and of critical wave numbers for the plus-one bifurcation: (a) For different values of the parameters c and r, differing levels of prey overdispersal are required to initiate a plus-one bifurcation. We plot level curves of the ratio β/α at bifurcation. High-r prey are most susceptible to plus-one bifurcations. (b) Here we plot level curves of the ratio ω^*/α. This critical wave number ω^* increases with r for fixed α.
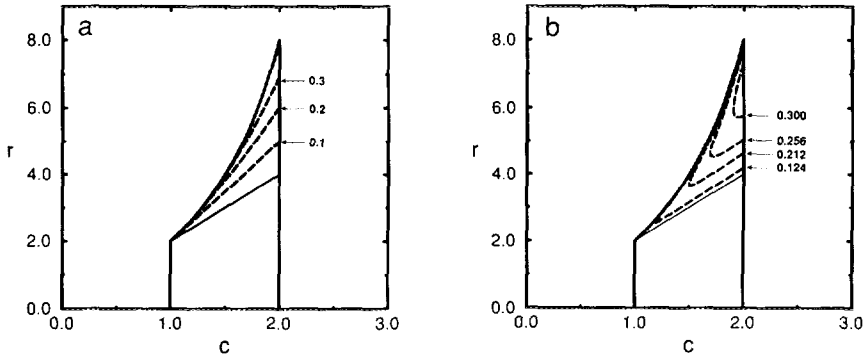
FIG. 10. Critical dispersal ratios and wave numbers for the minus-one bifurcation. Minus-one bifurcations are restricted to that subset of the stability region above the line $r = 2c$: (a) For different values of the parameters c and r, differing levels of predator overdispersal are required to initiate a minus-one bifurcation. We plot level curves of the ratio β/α at bifurcation. High-r prey are more susceptible to minus-one bifurcations. (b) Here we plot level curves of the ratio ω^*/α. These curves exhibit a complicated dependence on r and c.

are displayed in Fig. 10. Minus-one bifurcations are restricted to that subset of the stability region above the line $r = 2c$. This stands in marked contrast to the situation with plus-one bifurcations and follows directly from the necessary condition $(a_{11} + 1)(a_{22} + 1) < 0$. As one might expect, high-r prey require less predator overdispersal for dispersal-driven minus-one bifurcations than do low-r prey.

We have just begun analyzing dispersal-driven bifurcations in a higher number of spatial dimensions. Nevertheless, the patterns that arise in two dimensions are, if anything, more dramatic than those that arise in one.

6. DISCUSSION

The wide variety of dispersal mechanisms in nature produces an equally wide variety of redistribution kernels. This diversity, coupled with the complicated dynamics inherent in discrete-time systems, predisposes systems of integrodifference equations to produce striking spatial patterns—under a more generous set of ecological circumstances than for reaction-diffusion models. How do dispersal and predation interact to produce these patterns? Equivalently, what is it that causes the instability of the spatially uniform steady state?

The growth of our model's prey is limited by two factors: predation and intraspecific competition. Predation will typically keep the prey population depressed below its carrying capacity. If prey are able to escape predation, at least locally, an instability may arise. Small, local perturbations to the

prey population will then grow until the prey is once again kept in check by intraspecific competition and predation. There are, as we have seen, two scenarios. Prey may escape predation *in situ* because of predator over-dispersal, leading to a minus-one bifurcation. As this is a large-r bifurcation, strong density-dependence then causes the prey to oscillate. For sufficiently large r, further increases in predator overdispersal can set off a sequence of period-doubling bifurcations leading to chaos, à la the logistic difference equation (May, 1975; May and Oster, 1976).

In contrast, a plus-one bifurcation occurs when the *prey* overdisperse. In this instance, prey manage to escape not only predation, but over-compensation as well. The "excess" reproduction of one generation, which ordinarily would have produced a local population crash the following year, disperses to regions of lower density. Prey overdispersal is thus associated with static patterns.

Is there any indication of dispersal-driven pattern formation in nature? Janzen (1970) observed that adult individuals of lowland tropical tree species appear to be more regularly distributed then expected. He hypothesized that this regularity is generated by the combined effects of a seed shadow that declines with distance from the source and the dispropor-tionate depredation of seeds and seedlings close to the parent tree. He argued that the composition of these two processes would produce a population recruitment curve with a peak at some distance from the parent. We have shown that redistribution kernels with just this shape are those that are most likely to generate dispersal-driven instability and pattern formation, at least in one dimension. Janzen's observations may, in fact, be an indication of dispersal-driven pattern formation.

In this paper, we have emphasized the destabilizing effects of dispersal. However, dispersal can also stabilize the predator–prey interaction that we have studied. For $c = 1.1$ and $r = 2.32$, system (45) possesses a single inte-rior equilibrium point where predator and prey coexist. This equilibrium is unstable. Small perturbations about this equilibrium grow, leading to the extinction of the predator and to an oscillatory two-cycle for the prey. When we simulated this system on a finite domain with the same moderate dispersal for both the predator and the prey (using Laplace redistribution kernels with $\alpha = \beta = 10$ on a domain of length 20), we observed the same phenomena. However, as we increased the prey's dispersal ability, we passed through two qualitatively different regimes. In the first ($\alpha = 1$, $\beta = 10$), we found two attractors: a steady state where predator and prey coexist, and a prey two-cycle without the predator. With a further decrease in α ($\alpha = 0.2$) the two-cycle lost its stability, leaving the steady state of coexistence as the only attractor. This sequence mimics the subcritical flip bifurcation that occurs in model (45) as r is reduced below $4c/(3 - c)$ (Neubert and Kot, 1992). Increasing the prey's dispersal ability has the

same effect as lowering its intrinsic rate of growth because of the increased dispersal through the ends of the domain. The situation is reminiscent of the minimum patch-size problem studied by Kierstead and Slobodkin (1953) and Ludwig et al. (1979), wherein diffusion out through the domain boundary must be compensated for by increased reproduction within the domain if the organism is to survive. In the current model, moderate increases in prey dispersal allow the predator to persist.

We have described one of the mechanisms by which integrodifference equations can generate complex spatial patterns. This scenario depends upon the richness of redistribution kernels. Recent analyses (Kot et al., 1995) suggest an even greater role for this variety in predicting the speed of biological invasions. There are many other interesting questions regarding the behavior of integrodifference equations waiting to be answered. We encourage the reader to pursue these questions.

Appendix

In the absence of dispersal, a spatially homogeneous solution of system (28) is stable if

$$1 - (a_{11} + a_{22}) + (a_{11}a_{22} - a_{12}a_{21}) > 0, \tag{A1a}$$

$$1 + (a_{11} + a_{22}) + (a_{11}a_{22} - a_{12}a_{21}) > 0, \tag{A1b}$$

$$1 - (a_{11}a_{22} - a_{12}a_{21}) > 0. \tag{A1c}$$

This same solution is stable despite dispersal if

$$1 - (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2 (a_{11}a_{22} - a_{12}a_{21}) > 0, \tag{A2a}$$

$$1 + (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2 (a_{11}a_{22} - a_{12}a_{21}) > 0, \tag{A2b}$$

$$1 - \hat{k}_1 \hat{k}_2 (a_{11}a_{22} - a_{12}a_{21}) > 0, \tag{A2c}$$

for all positive wave numbers ω.

Inequalities (A1) and (A2) impose restrictions on the elements a_{ij} of the community matrix and on the Fourier-transformed kernels (characteristic functions) $\hat{k}_1(\omega)$ and $\hat{k}_2(\omega)$. In this appendix, we will derive certain necessary conditions that must be satisfied by the elements of the community matrix for dispersal-driven bifurcation (see Table II). The exact nature of these necessary conditions is determined by the signs of the characteristic functions and by the bifurcation type (i.e., which of inequalities (A2) is reversed). The results for the case of nonnegative characteristic functions were derived previously by Kot (1989); we include them below for completeness.

Plus-One Bifurcation

A dispersal-driven plus-one bifurcation occurs when inequalities (A1), (A2b), and (A2c) hold, but inequality (A2a) is reversed:

$$1 - (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2 (a_{11} a_{22} - a_{12} a_{21}) < 0. \tag{A3}$$

Equation (29) guarantees that $|\hat{k}_1| \leqslant 1$, $|\hat{k}_2| \leqslant 1$. First consider the case $0 \leqslant \hat{k}_1 \leqslant 1$ and $0 \leqslant \hat{k}_2 \leqslant 1$. If we use inequality (A1c) to eliminate $a_{11} a_{22} - a_{12} a_{21}$ from inequality (A1a), we obtain

$$a_{11} + a_{22} < 2. \tag{A4}$$

The a_{ii} can thus be arranged in one of two ways. Either

$$(a_{11} - 1)(a_{22} - 1) < 0, \tag{A5}$$

or

$$a_{11} \leqslant 1 \quad \text{and} \quad a_{22} \leqslant 1. \tag{A6}$$

We can also use inequality (A1a) to eliminate $a_{11} a_{22} - a_{12} a_{21}$ from inequality (A3):

$$\hat{k}_1 (1 - \hat{k}_2) a_{11} + \hat{k}_2 (1 - \hat{k}_1) a_{22} > 1 - \hat{k}_1 \hat{k}_2. \tag{A7}$$

But this inequality cannot be satisfied for any of the a_{ii} that satisfy condition (A6), for if it could, it would hold for the particular values $a_{11} = a_{22} = 1$. Inequality (A7) would then simplify to

$$\hat{k}_1 (1 - \hat{k}_2) > 1 - \hat{k}_2, \tag{A8}$$

which is clearly impossible, given our restrictions on $\hat{k}_1$ and $\hat{k}_2$. Instead, we must have that $(a_{11} - 1)(a_{22} - 1) < 0$.

Inequality (A5) may, in turn, be rewritten as

$$1 - (a_{11} + a_{22}) + (a_{11} a_{22} - a_{12} a_{21}) + a_{12} a_{21} < 0. \tag{A9}$$

Hence, by inequality (A1a), $a_{12} a_{21} < 0$.

For $-1 \leqslant \hat{k}_1 \leqslant 0$ and $-1 \leqslant \hat{k}_2 \leqslant 0$, we obtain different necessary conditions. Proceeding in analogy with the previous case, we use inequality (A1c) to eliminate $a_{11} a_{22} - a_{12} a_{21}$ from inequality (A1b) and obtain

$$a_{11} + a_{22} > -2. \tag{A10}$$

Thus either

$$(a_{11} + 1)(a_{22} + 1) < 0 \tag{A11}$$

or

$$a_{11} \geqslant -1 \qquad \text{and} \qquad a_{22} \geqslant -1. \tag{A12}$$

If we now use inequality (A1b) to eliminate $a_{11} a_{22} - a_{12} a_{21}$ from inequality (A3), we obtain, after some algebra,

$$\hat{k}_1 (1 + \hat{k}_2) a_{11} + \hat{k}_2 (1 + \hat{k}_1) a_{22} > 1 - \hat{k}_1 \hat{k}_2. \tag{A13}$$

If this last inequality were to hold under condition (A12), it would have to hold for the particular values $a_{11} = a_{22} = -1$. But the resulting inequality,

$$-\hat{k}_1 (1 + \hat{k}_2) > 1 + \hat{k}_2, \tag{A14}$$

is clearly impossible given our restriction that both $-1 \leqslant \hat{k}_1 \leqslant 0$ and $-1 \leqslant \hat{k}_2 \leqslant 0$. Since inequality (A13) must be true, condition (A12) must be false. The only alternative is that $(a_{11} + 1)(a_{22} + 1) < 0$.

Having obtained inequality (A11), we rewrite it as

$$1 + (a_{11} + a_{22}) + (a_{11} a_{22} - a_{12} a_{21}) + a_{12} a_{21} < 0, \tag{A15}$$

which, along with inequality (A1b), gives us $a_{12} a_{21} < 0$.

Finally, consider the case $0 < \hat{k}_1 \leqslant 1$ and $-1 \leqslant \hat{k}_2 < 0$ for some wave number ω. (For $0 < \hat{k}_2 \leqslant 1$ and $-1 \leqslant \hat{k}_1 < 0$, one can simply permute the indices in all that follows.) The necessary conditions that we derive for this case are far less stringent than the necessary conditions for the previous two cases.

Imagine that

$$\hat{k}_1 a_{11} + \hat{k}_2 a_{22} \leqslant \hat{k}_1 + \hat{k}_2. \tag{A16}$$

It would then follow, using inequalities (A1c) and (A3), that

$$(1 - \hat{k}_1)(1 - \hat{k}_2) = 1 - (\hat{k}_1 + \hat{k}_2) + \hat{k}_1 \hat{k}_2, \tag{A17a}$$

$$(1 - \hat{k}_1)(1 - \hat{k}_2) \leqslant 1 - (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2, \tag{A17b}$$

$$(1 - \hat{k}_1)(1 - \hat{k}_2) < 1 - (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2 (a_{11} a_{22} - a_{12} a_{21}), \tag{A17c}$$

$$(1 - \hat{k}_1)(1 - \hat{k}_2) < 0. \tag{A17d}$$

But this last inequality is impossible, given that $0 < \hat{k}_1 \leqslant 1$ and $-1 \leqslant \hat{k}_2 < 0$. Therefore, supposition (A16) is impossible; it must be that

$$\hat{k}_1 a_{11} + \hat{k}_2 a_{22} > \hat{k}_1 + \hat{k}_2, \tag{A18}$$

or

$$\hat{k}_1(a_{11} - 1) + \hat{k}_2(a_{22} - 1) > 0. \tag{A19}$$

Thus $a_{11} > 1$, or $a_{22} < 1$.

To show that we still require a "predator–prey" interaction, we prove that the left-hand side of inequality (A3) is negative only if the product $a_{12}a_{21}$ is negative. Let

$$f(a_{11}, a_{22}) \equiv 1 - (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2 (a_{11} a_{22} - a_{12} a_{21}). \tag{A20}$$

We find the local extrema of f with respect to a_{11} and a_{22} by setting the following partial derivatives equal to zero:

$$\frac{\partial f}{\partial a_{11}} = -\hat{k}_1 + \hat{k}_1 \hat{k}_2 a_{22} = 0, \tag{A21a}$$

$$\frac{\partial f}{\partial a_{22}} = -\hat{k}_2 + \hat{k}_1 \hat{k}_2 a_{11} = 0. \tag{A21b}$$

Solving these equations for a_{11} and a_{22} gives $(a_{11}^*, a_{22}^*) = (1/\hat{k}_1, 1/\hat{k}_2)$ as the only candidate for an extremum of f. This extremum is a global minimum of f since

$$(a_{11}^* \quad a_{22}^*) \, \mathbf{H} \begin{pmatrix} a_{11}^* \\ a_{22}^* \end{pmatrix} = 2 > 0, \tag{A22}$$

where $\mathbf{H}$ is the Hessian matrix

$$\mathbf{H} = \begin{pmatrix} \dfrac{\partial^2 f}{\partial a_{11}^2} & \dfrac{\partial^2 f}{\partial a_{11} \partial a_{22}} \\ \dfrac{\partial^2 f}{\partial a_{22} \partial a_{11}} & \dfrac{\partial^2 f}{\partial a_{22}^2} \end{pmatrix} = \begin{pmatrix} 0 & \hat{k}_1 \hat{k}_2 \\ \hat{k}_1 \hat{k}_2 & 0 \end{pmatrix}. \tag{A23}$$

But $f(a_{11}^*, a_{22}^*) = -\hat{k}_1 \hat{k}_2 a_{12} a_{21}$. So for inequality (A3) to be true, we must have $a_{12} a_{21} < 0$.

Minus-One Bifurcation

A dispersal-driven minus-one bifurcation occurs when inequalities (A1), (A2a), and (A2c) are in effect while inequality (A2b) is reversed:

$$1 + (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2 (a_{11} a_{22} - a_{12} a_{21}) < 0. \tag{A24}$$

As with the plus-one bifurcation, we will consider three cases corresponding to the various combinations of signs that the Fourier-transformed kernels may take for a given wave number. If we first consider the case

$0 \leqslant \hat{k}_1 \leqslant 1$ and $0 \leqslant \hat{k}_2 \leqslant 1$, we may use inequality (A1c) to eliminate the term $a_{11} a_{22} - a_{12} a_{21}$ from inequality (A1b). We thereby obtain

$$a_{11} + a_{22} > -2. \tag{A25}$$

Thus the a_{ii} must satisfy either

$$(a_{11} + 1)(a_{22} + 1) < 0 \tag{A26}$$

or

$$a_{11} \geqslant -1 \quad \text{and} \quad a_{22} \geqslant -1. \tag{A27}$$

Note, however that if we eliminate $a_{11} a_{22} - a_{12} a_{21}$ from inequality (A24), using inequality (A1b), we also have that

$$1 + (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) - \hat{k}_1 \hat{k}_2 (1 + a_{11} + a_{22}) < 0, \tag{A28}$$

which is equivalent to

$$\hat{k}_1 (1 - \hat{k}_2) a_{11} + \hat{k}_2 (1 - \hat{k}_1) a_{22} < -1 + \hat{k}_1 \hat{k}_2. \tag{A29}$$

This latter inequality cannot be satisfied for any of the a_{ii} that satisfy condition (A27), for if it could, it would hold for the particular values $a_{11} = a_{22} = -1$. Inequality (A29) could then be rewritten

$$\hat{k}_1 (1 - \hat{k}_2) > 1 - \hat{k}_2. \tag{A30}$$

However, this last inequality contradicts the assumption that both $\hat{k}_1$ and $\hat{k}_2$ are bounded between 0 and 1. We are left with inequality (A26). It was shown above that inequality (A26) implies $a_{12} a_{21} < 0$ (cf. inequality (A15)).

If $-1 \leqslant \hat{k}_1 \leqslant 0$ and $-1 \leqslant \hat{k}_2 \leqslant 0$, different necessary conditions once again arise. Inequality (A1c) may be used to eliminate $a_{11} a_{22} - a_{12} a_{21}$ from inequality (A1a). This yields

$$a_{11} + a_{22} < 2. \tag{A31}$$

Thus the a_{ii} must be arranged as either

$$(a_{11} - 1)(a_{22} - 1) < 0 \tag{A32}$$

or

$$a_{11} \leqslant 1 \quad \text{and} \quad a_{22} \leqslant 1. \tag{A33}$$

Inequalities (A33) lead to a contradiction. In particular, note that we may also use (A1a) to eliminate $a_{11}a_{22} - a_{12}a_{21}$ from (A24):

$$\hat{k}_1(1 + \hat{k}_2) a_{11} + \hat{k}_2(1 + \hat{k}_1) a_{22} < -1 + \hat{k}_1 \hat{k}_2. \tag{A34}$$

If condition (A33) were true, inequality (A34) would of necessity be true for $a_{11} = a_{22} = 1$, implying that

$$-\hat{k}_1(1 + \hat{k}_2) > 1 + \hat{k}_2. \tag{A35}$$

This last inequality is inconsistent with our assumption that $-1 \leqslant \hat{k}_1 \leqslant 0$ and $-1 \leqslant \hat{k}_2 \leqslant 0$. Hence $(a_{11} - 1)(a_{22} - 1) < 0$. From here it follows that $a_{12}a_{21} < 0$ (cf. inequality (A9)).

Finally, let $0 < \hat{k}_1 \leqslant 1$, $-1 \leqslant \hat{k}_2 < 0$. (For $0 < \hat{k}_2 \leqslant 1$ and $-1 \leqslant \hat{k}_1 < 0$, one may permute the indices in all that follows.) Imagine that

$$\hat{k}_1 a_{11} + \hat{k}_2 a_{22} \geqslant \hat{k}_1 + \hat{k}_2. \tag{A36}$$

It would then follow, by inequalities (A1c) and (A24), that

$$(1 + \hat{k}_1)(1 + \hat{k}_2) = 1 + (\hat{k}_1 + \hat{k}_2) + \hat{k}_1 \hat{k}_2, \tag{A37a}$$

$$(1 + \hat{k}_1)(1 + \hat{k}_2) \leqslant 1 + (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2, \tag{A37b}$$

$$(1 + \hat{k}_1)(1 + \hat{k}_2) < 1 + (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2(a_{11}a_{22} - a_{12}a_{21}), \tag{A37c}$$

$$(1 + \hat{k}_1)(1 + \hat{k}_2) < 0. \tag{A37d}$$

But $(1 + \hat{k}_1)(1 + \hat{k}_2) > 0$ by hypothesis. Therefore supposition (A36) is impossible; it must be that

$$\hat{k}_1(1 - a_{11}) + \hat{k}_2(1 - a_{22}) > 0. \tag{A38}$$

Now, since $\hat{k}_1$ is positive and $\hat{k}_2$ is negative, $a_{11} < 1$ or $a_{22} > 1$.

We must have a predator–prey interaction $(a_{12}a_{21} < 0)$ in this case as well. To show this, we prove that, at its minimum, the left-hand side of (A24) is negative only if $a_{12}a_{21} < 0$. Let

$$f(a_{11}, a_{22}) \equiv 1 + (\hat{k}_1 a_{11} + \hat{k}_2 a_{22}) + \hat{k}_1 \hat{k}_2(a_{11}a_{22} - a_{12}a_{21}). \tag{A39}$$

Setting the partial derivatives of f with respect to a_{11} and a_{22} equal to zero,

$$\frac{\partial f}{\partial a_{11}} = \hat{k}_1 + \hat{k}_1 \hat{k}_2 a_{22} = 0, \tag{A40a}$$

$$\frac{\partial f}{\partial a_{22}} = \hat{k}_2 + \hat{k}_1 \hat{k}_2 a_{11} = 0, \tag{A40b}$$

gives $(a_{11}^*, a_{22}^*) = (-1/\hat{k}_1, -1/\hat{k}_2)$ as the only candidate for an extremum of f. This extremum is a global minimum of f, since

$$(a_{11}^* a_{22}^*) \, \mathbf{H} \begin{pmatrix} a_{11}^* \\ a_{22}^* \end{pmatrix} = 2 > 0. \tag{A41}$$

Here $\mathbf{H}$ is the Hessian matrix (cf. Eq. (A23)). At this minimum $f(a_{11}^*, a_{22}^*) = -\hat{k}_1 \hat{k}_2 a_{12} a_{21}$. Thus, for inequality (A24) to be true, we must have $a_{12} a_{21} < 0$.

Hopf Bifurcation

A dispersal-driven Hopf bifurcation would occur if inequalities (A1), (A2a) and (A2b) applied, while (A2c) were reversed. This situation is impossible. Adding inequality (A1a) to (A1b) yields

$$a_{11} a_{22} - a_{12} a_{21} > -1. \tag{A42}$$

Along with inequality (A1c), this implies that

$$|a_{11} a_{22} - a_{12} a_{21}| < 1. \tag{A43}$$

Given that $|\hat{k}_1| \leqslant 1$ and $|\hat{k}_2| \leqslant 1$, it follows that

$$|\hat{k}_1 \hat{k}_2 (a_{11} a_{22} - a_{12} a_{21})| \leqslant |a_{11} a_{22} - a_{12} a_{21}| < 1. \tag{A44}$$

In other words, we cannot reverse inequality (A2c). For two species on an infinite domain, we cannot use dispersal to precipitate loss of stability via a Hopf bifurcation.

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