Stochasticity and Invasions

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ABSTRACT

In this paper, we relate the behavior of some simple, deterministic models for invasions to stochastic, individual-based simulations by means of the theory of branching random walks. We formulate some simple branching random walks, determine rates of spread of expected values of cumulative density, and determine rates of spread for probabilities of occurrence. For our density-independent branching random walks, stochastic variation in dispersal and reproduction does not lower the overall asymptotic speed of invasion. Demographic stochasticity may, however, lower the asymptotic probability of occurrence.

Keywords: branching random walks, integrodifference equations,
             fat-tailed kernels, dispersal, biological invasions

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Introduction

Spatial models are extraordinarily varied (Kareiva, 1990; Keeling, 1999). Ecologists have long used simple deterministic models, such as reaction-diffusion equations, to study persistence, spread, and other spatial phenomena (Skellam, 1951; Kierstead and Slobodkin, 1953; Okubo and Levin, 2001). More recently, ecologists have used individual-based, spatially explicit, computer-based models with stochastic births and displacements (Grimm, 1999; Berec, 2002) to study these same matters. There is keen interest in bridging this divide (Dieckmann et al., 2000). In this paper, we tie the behavior of some simple, deterministic invasion models, integrodifference equations, to stochastic, individual-based simulations by means of the theory of branching random walks.

Integrodifference equations are discrete-time, continuous-space models for the growth and spread of populations (Kot and Schaffer, 1986; Kot et al., 1996). These equations accommodate the varied dispersal mechanisms (Neubert et al., 1995) and the long-distance dispersal events (Shigesada and Kawasaki, 2002) that create the leptokurtic distributions of displacements found in nature (Bateman, 1950). Integrodifference equations have been used to study age and stage structure (Caswell et al., 2003; Neubert and Caswell, 2000), Allee effects (Veit and Lewis, 1996; Wang et al., 2002), chaos (Kot and Schaffer, 1986; Andersen, 1991; Kot, 1992; Sherratt et al., 1997), competition (Allen et al., 1996; Hart and Gardner, 1997), epidemics (Allen and Ernest, 2002), fluctuating environments (Neubert et al., 2000), long-term transients (Hastings and Higgins, 1994), pattern formation (Kot, 1989; Neubert et al., 1995; Sherratt et al., 1997; Allen et al., 2001), persistence (Kot and Schaffer, 1986; Van Kirk and Lewis, 1997; Latore et al., 1998, 1999; Lockwood et al., 2002), pest and weed control (Allen et al., 1996; Brewster and Allen, 1997; Legaspi et al., 1998), and many other phenomena.

Integrodifference equations are especially popular as models for invading organisms. They can, like reaction-diffusion equations, generate constant-speed traveling waves (Weinberger, 1978, 1982; Lui, 1983; Kot, 1992; Hart and Gardner, 1997). In addition, integrodifference equations can generate accelerating solutions with asymptotically infinite speeds (Kot et al., 1996; Lewis, 1997; Clark, 1998). They can, in other words, account for invasions in which spread rates increase with time.

Integrodifference equations are deterministic models that predict a continuous distribution of individuals. Real populations, in contrast, consist of finite numbers of discrete individuals that experience chance events. It is prudent, therefore, to ask if deterministic rates of spread are affected by stochasticity and by the discreteness of individuals. Several investigators (Lewis and Pacala, 2000; Lewis, 2000; Clark et al., 2001; Snyder, 2003) have addressed this question. These investigators have incorporated stochastic variation in dispersal and in reproduction into density-dependent models. Snyder (2003) has concluded that demographic stochasticity slows invasions, but that the effect is minor. Clark et al. (2001), in contrast, have argued that stochastic effects can turn accelerating invasions into constant-speed invasions.

Missing from this recent work is a clear and complete outline of the linear, density-independent theory. A linear theory provides us with a useful basis for judging nonlinear effects. It may help us distinguish the effects of stochasticity from the complicated effects of nonlinearity. In this paper, we use branching random walks as the stochastic analogs of linear integrodifference equations (Dekking, 1995). Branching random walks have the same relationship to linear integrodifference equations that the Galton-Watson branching process has to a simple linear difference equation. Branching random walks incorporate variation in dispersal and in reproduction, but they do not, typically, include density dependence.

The first branching random walk was proposed by Harris (1963). Vatutin and Zubkov (1993) summarize much of the early work on these models. Please see Biggins (1996) and Radcliffe and Rass (1997) for more recent references and results. Also, please see Mollison (1977) for a closely related discussion of continuous-time contact processes. Branching random walks handle stochasticity in a simple, elegant, and powerful way. They have much to offer ecologists. Unfortunately, the literature on branching random walks can be opaque.

In this paper, we offer a brief introduction to branching random walks, highlighting their relationship to integrodifference equations. In the section *Integrodifference Equations*, we remind the reader of the formulation of integrodifference equations and briefly summarize some standard results for these models. We formulate and analyze simple branching random walks in the next section, *Branching Random Walks*. In *Examples*, we analyze two examples previously discussed by Snyder (2003). It is here that we show how branching random walks can act as a bridge between integrodifference equations and individual-based simulations. We save our concluding remarks for the *Discussion*.

Integrodifference Equations

A simple, single-species integrodifference equation,

$$n_{t+1}(x) \ = \ \int_{-\infty}^{+\infty} k(x - y) \, f(n_t(y)) \, dy \, , \tag{1}$$

maps the density of a population in generation t, $n_t(x)$, to a new density, $n_{t+1}(x)$, in two stages. During the first or sedentary stage, individuals grow, reproduce, and die. At each point x, the local population, $n_t(x)$, produces $f(n_t(x))$ propagules. The function f is, typically, nonlinear. Well known choices of the function f include the Beverton–Holt stock-recruitment curve (Beverton and Holt, 1957; Pielou, 1977), the right-hand side of the logistic difference equation (Maynard Smith, 1968; May, 1972; May and Oster, 1976), and the Ricker spawner-recruit curve (Ricker, 1954).

During the second stage, the propagules disseminate. The dispersal kernel, $k(x)$, is the probability density function for the displacement of the propagules. A convolution

integral tallies the contributions from all potential sources y to each destination x. Well known examples of the kernel $k(x)$ include the Gaussian, Laplace, and Cauchy distributions.

We typically start equation (1) with an initial condition on a finite domain. For $f'(0) > 1$, solutions grow and spread and, for many kernels, converge to traveling waves (Weinberger, 1978; Lui, 1982, 1983; Kot, 1992). If a simple, nonlinear integrodifference equation has no Allee effect ($f(n) \leq f'(0)\, n$ for all $n > 0$), the asymptotic rate of spread is the same as that of the *linear* integrodifference equation

$$n_{t+1}(x) \; = \; R_0 \int_{-\infty}^{+\infty} k(x - y)\, n_t(y)\, dy \qquad (2)$$

(Weinberger, 1978, 1982; Mollison, 1991; Kot et al., 1996; Hart and Gardner, 1997), where $R_0 \equiv f'(0)$. For a discussion of the behavior in the presence of an Allee effect, see Wang et al. (2002).

The simplification that results from using linear integrodifference equation (2) for the asymptotic rate of spread is tremendous. Even so, integrodifference equations may display many different rates of spread, depending on the exact dispersal kernel. Detailed analyses (Kot et al., 1996) revealed a fundamental distinction between kernels that have exponentially bounded tails and those that are fat-tailed. Exponentially bounded kernels typically give rise to constant-speed traveling waves while fat-tailed kernels produce accelerating invasions. Further details, including formulas for speeds and examples, can be found in Kot et al. (1996), Lewis (1997), and Kot (2003).

In this paper, we wish to study the effects of adding stochasticity to equation (2). It is helpful, before doing so, to tally individuals to the left of x and to rewrite linear integrodifference equation (2) in terms of the cumulative density

$$N_t(x) \; \equiv \; \int_{-\infty}^{x} n_t(u)\, du \; . \qquad (3)$$

In Appendix A, we show that equation (2) implies that

$$N_{t+1}(x) \; = \; R_0 \int_{-\infty}^{+\infty} k(x - y)\, N_t(y)\, dy \; . \qquad (4)$$

In other words, the density and the cumulative density obey the same linear integrodifference equation. We are now ready to proceed to branching random walks.

Branching Random Walks

We will start with one individual at the origin. This individual will reproduce, leaving a discrete number of offspring Y, and then die. We will assume that Y is a

random variable with a well defined probability distribution,

$$\text{Prob } \{Y = i\} \;=\; p_i \,, \quad i = 0,\, 1,\, 2,\, \ldots. \tag{5}$$

The probability generating function (PGF) for the number of offspring is simply

$$F(s) \;\equiv\; E[s^Y] \;=\; \sum_i p_i \, s^i \,, \tag{6}$$

where E signifies expected value. The index i runs from zero to the maximum possible litter, clutch, or brood size. In using the probability generating function, we are, in effect, hanging the probabilities of the number of offspring as coefficients on a polynomial in s. The variable s has no special significance. Probability generating functions have many useful properties (Chiang, 1980; Grimmett and Stirzaker, 1992; Allen, 2003). Chief among these is the fact that the generating function for the sum of a random number of independent and identically distributed random variables can be written as the composition of two probability generating functions.

We assume that the population has discrete, nonoverlapping generations and synchronized reproduction. We will let each of the offspring of the founder disperse, with redistribution kernel $k(x)$, reproduce, with PGF $F(s)$, and die, continuing the process. Subsequent generations behave the same way. There is no density dependence.

Let $Z_t(x)$ be the number of living individuals in the interval $(-\infty, x]$ at time t. $Z_t(x)$ is the stochastic analog of the cumulative density, $N_t(x)$, that we introduced in equations (3) and (4). In particular, $Z_t(x)$ is an integer-valued random variable for all t and x. Consider the generating function

$$G_t(s;\, x) \;=\; E[s^{Z_t(x)}] \,, \tag{7}$$

where s is the variable of the generating function and x, position, is to be thought of as a parameter.

Since we start with one individual at the origin,

$$Z_0(x) \;=\; \begin{cases} 0\,, & x < 0\,, \\ 1\,, & x \geq 0\,, \end{cases} \tag{8}$$

so that

$$G_0(s;\, x) \;=\; \begin{cases} 1\,, & x < 0\,, \\ s\,, & x \geq 0\,. \end{cases} \tag{9}$$

In the next generation,

$$G_1(s;\, x) \;=\; F\left(\int_{-\infty}^{+\infty} k(x - y)\, G_0(s;\, y)\, dy \right). \tag{10}$$

Here is how to interpret this equation. The expression within the large parentheses is the probability generating function for the cumulative density, after dispersal, of any one of the founder's offspring. The founder has a random number of offspring; we use F to add a random number of cumulative densities. For subsequent generations,

$$G_{t+1}(s;\, x) \;=\; F\left(\int_{-\infty}^{+\infty} k(x-y)\, G_t(s;\, y)\, dy \right). \tag{11}$$

It is tempting to write the related equation

$$G_{t+1}(s;\, x) \;=\; \int_{-\infty}^{+\infty} k(x-y)\, F(G_t(s;\, y))\, dy\,, \tag{12}$$

but this is *not* what we want. In this case, reproduction occurs at the parent's location and the entire clutch or litter of offspring moves as a unit.

Many useful statistics can be derived from equation (11). One useful way to measure the growth and spread of a population is to track the average cumulative density (Mollison, 1977). In Appendix B, we show that the expected value of $Z_t(x)$,

$$a_t(x) \;=\; E[Z_t(x)]\,, \tag{13}$$

satisfies

$$a_{t+1}(x) \;=\; R_0 \int_{-\infty}^{+\infty} k(x-y)\, a_t(y)\, dy \tag{14}$$

with the initial condition

$$a_0(x) \;=\; \begin{cases} 0\,, & x < 0\,, \\ 1\,, & x \geq 0\,. \end{cases} \tag{15}$$

$R_0 \equiv F'(1)$ is the expected number of offspring. Equation (14) implies that the expected value of the cumulative density moves at the same rate for the stochastic process as for the deterministic process.

Higher moments can be derived in a straightforward manner. In Appendix B, we show that the second moment of $Z_t(x)$,

$$b_t(x) \;=\; E[Z_t^2(x)]\,, \tag{16}$$

satisfies the recurrence equation

$$b_{t+1}(x) \;=\; R_0 \int_{-\infty}^{+\infty} k(x-y)\, b_t(y)\, dy + \beta \left(\int_{-\infty}^{+\infty} k(x-y)\, a_t(y)\, dy \right)^2 \tag{17}$$

with the initial condition

$$b_0(x) = \begin{cases} 0, & x < 0, \\ 1, & x \geq 0. \end{cases} \tag{18}$$

Here, $\beta \equiv F''(1)$.

A second useful way to track an invasion is to look for the presence or absence of individuals. We can determine the probability that the cumulative density is zero, $G_t(0; x)$, by setting s equal to zero in equations (9) and (11)

$$G_{t+1}(0; x) = F\left(\int_{-\infty}^{+\infty} k(x - y) \, G_t(0; y) \, dy \right), \tag{19}$$

$$G_0(0; x) = \begin{cases} 1, & x < 0, \\ 0, & x \geq 0. \end{cases} \tag{20}$$

The family-size generating function $F(s)$ is a convex function on the interval $[0, 1]$. This makes equation (19) hard to work with analytically. If we instead let

$$q_t(x) \equiv 1 - G_t(0; x) \tag{21}$$

represent the probability of occurrence (up through x at time t), matters proceed smoothly. Indeed, the right-hand side of the recurrence relation

$$q_{t+1}(x) = 1 - F\left(1 - \int_{-\infty}^{+\infty} k(x - y) \, q_t(y) \, dy \right) \tag{22}$$

is a concave function of the convolution integral and one can easily show that

$$q_{t+1}(x) \leq R_0 \int_{-\infty}^{+\infty} k(x - y) \, q_t(y) \, dy . \tag{23}$$

Thus, the asymptotic rate of spread of the probability of occurrence is bounded above by the asymptotic speed of the cumulative density. (Please compare equation (23) to equations (4) and (14).) Numerical iterations of equation (22) with the initial condition

$$q_0(x) = \begin{cases} 0, & x < 0, \\ 1, & x \geq 0, \end{cases} \tag{24}$$

(see next section) suggest that the asymptotic rate of spread of $q_t(x)$ is, in fact, the same as that of the cumulative density. For a more formal proof, please see Biggins (1977).

Examples

We consider two examples. The first example is a binary-fission model in which each individual leaves two offspring whose dispersal distances are drawn from a given distribution. Snyder (2003) refers to this as a "stochastic dispersal" model since there is no variation in reproduction. We then consider a "fully stochastic" model in which dispersal is random and the number of offspring is drawn from a Poisson distribution with mean $\mu = 2$.

One can simulate these two models, keeping track of the positions of all individuals, using random number generators for the number and displacement of offspring. Snyder (2003) estimated the rates of spread for the Laplace kernel,

$$k(x) \; = \; \frac{\alpha}{2} \, e^{-\alpha|x|} \, , \tag{25}$$

with $\alpha = 0.5$, in just this way. She ran each stochastic model 2000 times, determined the slope of the linear regression of the furthest-forward location against time for each run, and averaged the resulting speeds. As an alternative, we plotted the cumulative distribution of the leftmost location from each of the 2000 runs for each time step (Figure 1a) and then kept track of the movement of the resulting wave. Computational constraints prevented Snyder from continuing her runs for more than 17 or 18 times steps. Our equations for branching random walks eliminate this problem, as shown below.

For binary fission, the PGF for the number of offspring is simply

$$F(s) \; = \; s^2 \, . \tag{26}$$

Since $R_0 \equiv F'(1) = 2$, equation (14), for the expected value of $Z_t(x)$, reduces to

$$a_{t+1}(x) \; = \; 2 \int_{-\infty}^{+\infty} k(x-y) \, a_t(y) \, dy \, . \tag{27}$$

The asymptotic rate of spread c for this equation, with a Laplace kernel, equation (25), can be written parametrically as

$$c \; = \; \frac{2\,u}{\alpha^2 - u^2} \, , \quad R_0 \; = \; \left(1 - \frac{u^2}{\alpha^2}\right) e^{2\,u^2/(\alpha^2 - u^2)} \tag{28}$$

(Kot et al., 1996). For $R_0 = 2$ and $\alpha = 0.5$, we find that $u = 0.302$. It now follows that the asymptotic rate of spread, c, is 3.8.

For binary fission, the recurrence relation for the probability of occurrence, equation (22), reduces to

$$q_{t+1}(x) \; = \; 2 \int_{-\infty}^{+\infty} k(x-y) \, q_t(y) \, dy \; - \; \left(\int_{-\infty}^{+\infty} k(x-y) \, q_t(y) \, dy \right)^2 \, . \tag{29}$$

If we iterate this equation, with initial condition (24), we obtain the cumulative distribution of the leftmost location of individuals at each time step (Figure 1b). These theoretical curves are the infinite-sample-size limits of the empirical cumulative distributions that we previously obtained by simulation (Figure 1a). We illustrate the similarity between the simulations and the theoretical curves with a quantile-quantile plot for $t = 5$ (Figure 2).

Equation (29) has the advantage that it can be iterated for arbitrarily large times. It would be impossible to keep track of the $2^{50} \approx 10^{15}$ positions required for stochastic simulations of 50 time steps. In contrast, the speeds for each of the first 50 iterates of equation (29) (Figure 3a) were computed quickly and with little demand on computer memory. The speeds in this figure slowly approach the theoretic traveling-wave speed $c = 3.8$. Snyder (2003) correctly points out that her speeds (3.37 ± 0.11 for the above example) for her density-independent simulations fall short of the predicted asymptote. Our results suggest that Snyder would have had to continue her stochastic runs for another 8 or more generations to obtain speed estimates within 5% of the predicted asymptote.

The behavior of the binary-fission model differs for a fat-tailed kernel. Consider the exponential square root distribution,

$$k(x) = \frac{\alpha^2}{4} e^{-\alpha\sqrt{|x|}} .$$
(30)

This distribution has finite moments of all orders, but no moment-generating function. We now set $\alpha = \sqrt{3}$ so that the mean absolute dispersal distance is 2, as in our previous example with the Laplace distribution. For kernel (30), the spread rate for the probability of occurrence (Figure 3b) does *not* approach a horizontal asymptote. After a short transient, the spread rate increases linearly. This matches the prediction of a linear increase in speed for the corresponding deterministic model (Kot et al., 1996). For this fat-tailed kernel, discrete individuals and stochastic dispersal alone are not enough to turn an accelerating invasion into a constant-speed invasion.

Similar results occur if we add stochasticity to reproduction. For a "fully stochastic" model in which dispersal is random and the number of offspring is drawn from a Poisson distribution with mean $\mu = 2$, the PGF for the number of offspring is

$$F(s) = e^{2(s-1)} .$$
(31)

The asymptotic probability of extinction for the corresponding non-spatial (Galton–Watson) branching process is the unique nonnegative root of $F(s) = s$ that is less than one (Harris, 1963; Caswell, 2001). For function (31), this asymptotic probability of extinction is approximately 0.2. Thus, the asymptotic probability of occurrence is approximately 0.8.

The expected value of $Z_t(x)$ is, once again, given by equation (27) and the asymptotic rate of spread for the Laplace kernel with $\alpha = 0.5$ is, again, $c = 3.8$. Equation (22), for the probability of occurrence, now reduces to

$$q_{t+1}(x) \;=\; 1 - \exp\left(-2 \int\limits_{-\infty}^{+\infty} k(x-y)\, q_t(y)\, dy \right). \tag{32}$$

The iterates of equation (32) for the Laplace distribution (Figure 4) are waves that rise from $q_t = 0$ to $q_t \approx 0.8$. The value $q_t \approx 0.8$, the asymptotic probability of occurrence after the wave has passed, matches the prediction of the Galton-Watson process. The speeds for the first 50 iterates of equation (32) for the Laplace kernel (Figure 3c) are similar to the corresponding speeds for binary fission (Figure 3a). Demographic stochasticity lowers the asymptotic probability of occurrence, but does not have any obvious effect on the speed of invasion. The speeds for the first 50 iterates of equation (32) for the exponential square root distribution (Figure 3d) are also similar to their binary-fission counterparts (Figure 3b). In our previous example, with binary fission, discreteness of individuals and stochastic dispersal were not enough to turn an accelerating invasion into a constant-speed invasion. The addition of demographic stochasticity does not change this outcome.

Discussion

There are several conclusions that follow from our examples:

1) The general results of linear, deterministic invasion theory remain valid for linear, stochastic models. For our density-independent models, discreteness of individuals and stochastic variation in dispersal and reproduction are not enough, in general, to slow invasions. The asymptotic rate of spread for a a stochastic branching random walk is the same as that of a deterministic, density-independent integrodifference equation. This is most clearly seen, for the Laplace kernel, in Figures 3a and 3c, where the speeds of the waves of occurrence for two branching random walks approach the asymptotic speed c of a deterministic integrodifference equation. Also, stochasticity was not enough to turn the accelerating invasion for a fat-tailed kernel into a constant-speed invasion, as seen in Figures 3b and 3d. There are also striking parallels between stochastic, density-independent, branching random walks and deterministic, density-dependent, integrodifference equations: in both cases, the speeds of invasion are determined by a linear integrodifference equation. Many of our conclusions for discrete-time models parallel those of Mollison (1977) and Mollison and Daniels (1993) for continuous-time contact models.

The combined effect of stochasticity and density dependence can, nonetheless, slow an invasion, as previously demonstrated by Mollison (1972, 1977), Lewis and Pacala (2000), Lewis (2000), Clark et al. (2001) and Snyder (2003). Most stochastic, density-dependent models are difficult to analyze and our understanding of these models

is quite incomplete. Snyder (2003) has shown that population variance may interact with density dependence to slow population growth at the front of an invasion, but she concludes that the slowing due to stochasticity "is not large enough to be noticeable in most ecological time series." Clark et al. (2001), in contrast, argue that stochastic variation can turn an accelerating invasion into a constant-speed invasion. They propose a scenario in which the outermost or extreme members of a population set the rate of spread. Early work by Mollison (1972, 1977) and our own stochastic simulations suggest that the situation is complicated: Some fat-tailed kernels, e.g., the Cauchy distribution, will continue to give accelerating invasions in the presence of density dependence and stochasticity. Other fat-tailed kernels won't. In the latter instances, the speed of invasion may depend, rather strongly, on the carrying capacity and on the exact nature of the density dependence, as well as on traditional factors. There is further work needed here and branching random walks provide a useful baseline for new studies.

2) Stochastic, density-independent models may exhibit significant transient effects. At the same time, we have not seen evidence that transients are longer than for comparable deterministic models. In our examples with the Laplace kernel, it took a good 26 or 27 iterates for the speeds of the waves of occurrence (Figures 3a and 3c) to rise to within 5% of the predicted asymptotic speed. A stochastic, individual-based simulation would need to keep track of $2^{27} \approx 10^8$ positions in order to attain this speed. Branching random walks circumvent this problem.

3) Branching random walks provide an elegant and powerful means for dealing with discreteness of individuals and stochastic variation in dispersal and reproduction. The use of branching random walks as models for invasions complements renewed interest in other uses of branching processes in biology (Caswell et al., 1999; Caswell, 2001; Kimmel and Axelrod, 2002).

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Appendix A

In this appendix, we quickly derive a linear integrodifference equation for the cumulative density. We start with the usual linear integrodifference equation for density,

$$n_{t+1}(x) \;=\; R_0 \int_{-\infty}^{+\infty} k(x-y)\, n_t(y)\, dy \;,\tag{A.1}$$

and rewrite this equation as

$$n_{t+1}(u) \;=\; R_0 \int_{-\infty}^{+\infty} k(y)\, n_t(u-y)\, dy \;.\tag{A.2}$$

For a finite population, we may integrate each side of the last equation with respect to u, from $-\infty$ to x, to obtain

$$\int_{-\infty}^{x} n_{t+1}(u)\, du \;=\; R_0 \int_{-\infty}^{+\infty} k(y) \int_{-\infty}^{x} n_t(u-y)\, du\; dy \tag{A.3}$$

$$=\; R_0 \int_{-\infty}^{+\infty} k(y) \int_{-\infty}^{x-y} n_t(v)\, dv\; dy \;.\tag{A.4}$$

If we now let

$$N_t(x) \equiv \int_{-\infty}^{x} n_t(u)\, du \tag{A.5}$$

represent the cumulative density, we see that

$$N_{t+1}(x) \;=\; R_0 \int_{-\infty}^{+\infty} k(y)\, N_t(x-y)\, dy \tag{A.6}$$

$$=\; R_0 \int_{-\infty}^{+\infty} k(x-y)\, N_t(y)\, dy \;.\tag{A.7}$$

It is now clear that the cumulative density obeys the same linear integrodifference equation as the density.

Appendix B

We now use standard properties of probability generating functions to determine equations for the first and second moments of $Z_t(x)$. The expected value of $Z_t(x)$ is simply

$$a_t(x) \;=\; E[Z_t(x)] \;=\; \left. \frac{dG_t(s; x)}{ds} \right|_{s = 1} . \qquad (A.8)$$

After differentiating equation (11), using the chain rule, and setting $s = 1$, we obtain

$$a_{t+1}(x) \;=\; F'\left(\int_{-\infty}^{+\infty} k(x - y)\, G_t(1; y)\, dy \right) \times \qquad (A.9)$$

$$\int_{-\infty}^{+\infty} k(x - y)\, G_t'(1; y)\, dy .$$

We now invoke the identity

$$G_t(1, x) \;=\; 1 , \qquad (A.10)$$

the fact that

$$\int_{-\infty}^{+\infty} k(u)\, du \;=\; 1 , \qquad (A.11)$$

and the fact that

$$F'(1) \;=\; \sum_i i\, p_i \;=\; R_0 \qquad (A.12)$$

to conclude that

$$a_{t+1}(x) \;=\; R_0 \int_{-\infty}^{+\infty} k(x - y)\, a_t(y)\, dy . \qquad (A.13)$$

The initial condition for integrodifference equation (A.13) is simply

$$a_0(x) \;=\; \begin{cases} 0, & x < 0, \\ 1, & x \geq 0, \end{cases} \qquad (A.14)$$

since we start with one individual at the origin.

In a similar way, let

$$b_t(x) \;=\; E[Z_t^2(x)] . \qquad (A.15)$$

be the second moment of the $Z_t(x)$. By usual generating-function arguments,

$$\left[\frac{d^2 G_t(s; x)}{ds^2} \right]_{s = 1} \;=\; b_t(x) - a_t(x) . \qquad (A.16)$$

Let us derive an expression for the left-hand side. Differentiating equation (11) once

gives

$$G'_{t+1}(s; x) = F'\left(\int_{-\infty}^{+\infty} k(x-y)\, G_t(s; y)\, dy\right) \times \qquad (A.17)$$

$$\int_{-\infty}^{+\infty} k(x-y)\, G'_t(s; y)\, dy \;.$$

Differentiating again gives us

$$G''_{t+1}(s; x) = F'\left(\int_{-\infty}^{+\infty} k(x-y)\, G_t(s; y)\, dy\right) \times \qquad (A.18)$$

$$\int_{-\infty}^{+\infty} k(x-y)\, G''_t(s; y)\, dy \;+$$

$$F''\left(\int_{-\infty}^{+\infty} k(x-y)\, G_t(s; y)\, dy\right) \times$$

$$\left(\int_{-\infty}^{+\infty} k(x-y)\, G'_t(s; y)\, dy\right)^2 \;.$$

Let us designate

$$\beta = F''(1)\;. \qquad (A.19)$$

If we now let $s = 1$, equation (A.18) simplifies to

$$b_{t+1}(x) - a_{t+1}(x) = R_0 \int_{-\infty}^{+\infty} k(x-y)\, [b_t(y) - a_t(y)]\, dy \;+ \qquad (A.20)$$

$$\beta\left(\int_{-\infty}^{+\infty} k(x-y)\, a_t(y)\, dy\right)^2 \;.$$

In light of equation (A.13), equation (A.20) reduces to

$$b_{t+1}(x) = R_0 \int_{-\infty}^{+\infty} k(x-y)\, b_t(y)\, dy \;+ \qquad (A.21)$$

$$\beta \left(\int_{-\infty}^{+\infty} k(x-y)\, a_t(y)\, dy \right)^2 .$$

This equation has the initial condition

$$b_0(x) = \begin{cases} 0, & x < 0, \\ 1, & x \geq 0, \end{cases} \qquad \text{(A.22)}$$

since we start with one individual at the origin.

Equations for higher moments may be derived in a similar way. The equations for the moments of $Z_t(x)$ may also be derived using moment generating functionals rather than probability generating functions. Equations (A.13) and (A.21), for the first and second moments, were first stated by Harris (1963), who used moment generating functionals.

FIGURE LEGENDS

Figure 1   Cumulative distributions for the positions of the leftmost individuals for each of 15 time steps of a simple binary-fission model in which each individual leaves two offspring whose dispersal distances are drawn from the Laplace kernel with $\alpha = 0.5$. In (a), these curves were obtained empirically by simulating the stochastic process 2000 times. For each time step, we selected the leftmost individual for each run, ordered the selected individuals, and determined the fraction of the individuals below x for each x. In (b), the curves were obtained by numerically iterating equation (29) for the probability of occurrence. Integrations were performed with the extended trapezoidal rule on a domain of length 1000 with 20,000 grid points. Note the similarity between the top and bottom curves.

Figure 2   Quantile-quantile plot comparing the empirical distribution function for $t = 5$ from Figure 1a with the corresponding distribution for the probability of occurrence from Figure 1b. The points all lie on or close to a line of slope one, suggesting that the distributions are identical.

Figure 3   Rates of spread for some simple branching random walks. (a) Speeds for a simple binary-fission model in which each individual leaves two offspring whose dispersal distances are drawn from the Laplace kernel with $\alpha = 0.5$. To compute these rates, we first iterated equation (29), for the probability of occurrence, for 50 time steps. Integrations were performed using the extended trapezoidal rule on a domain of length 1000 with 20,000 grid points. We then tracked the position of the 0.5 quantile and took the (per-step) speed as the distance that the 0.5 quantile moved each time step. Speeds approach the constant $c = 3.8$. (b) Speeds for a simple binary-fission model in which dispersal distances are drawn from the exponential square root distribution with $\alpha = \sqrt{3}$. Integrations were now performed on a domain of length 1500 with 30,000 grid points. After a short transient, speeds increase linearly. (c) Speeds for a "fully stochastic" model in which dispersal distances are drawn from a Laplace distribution, with $\alpha = 0.5$, and the number of offspring is drawn from a Poisson distribution with mean $\mu = 2$. We iterated equation (32), with 20,000 grid points on a domain of length 1000, for 50 time steps and tracked the position of the 0.4 quantile. Speeds approach $c = 3.8$. (d) Speeds for a "fully stochastic" model in which dispersal distances are drawn from an exponential square root distribution with $\alpha = \sqrt{3}$ and the number of offspring is drawn from a Poisson distribution with mean $\mu = 2$. Integrations were on a domain of length 1500

with 30,000 grid points. After a short transient, speeds increase linearly.

Figure 4   Distribution functions for the positions of the leftmost individuals for each of 15 steps of a "fully stochastic" model in which dispersal distances are drawn from a Laplace distribution, with $\alpha = 0.5$, and the number of offspring is drawn from a Poisson distribution with mean $\mu = 2$. The curves were computed by numerically iterating equation (32) for the probability of occurrence. Integrations were performed on a domain of length 1000 with 20,000 grid points using the extending trapezoidal rule. The asymptotic probability of occurrence after the wave has passed is 0.8 and matches the prediction of a Galton-Watson process.
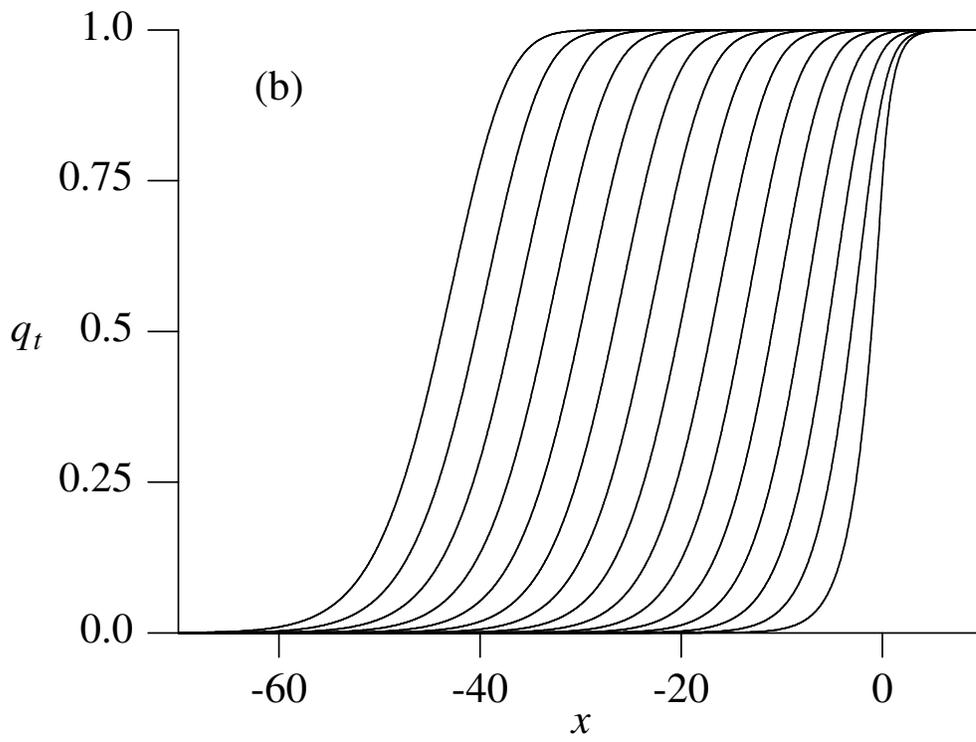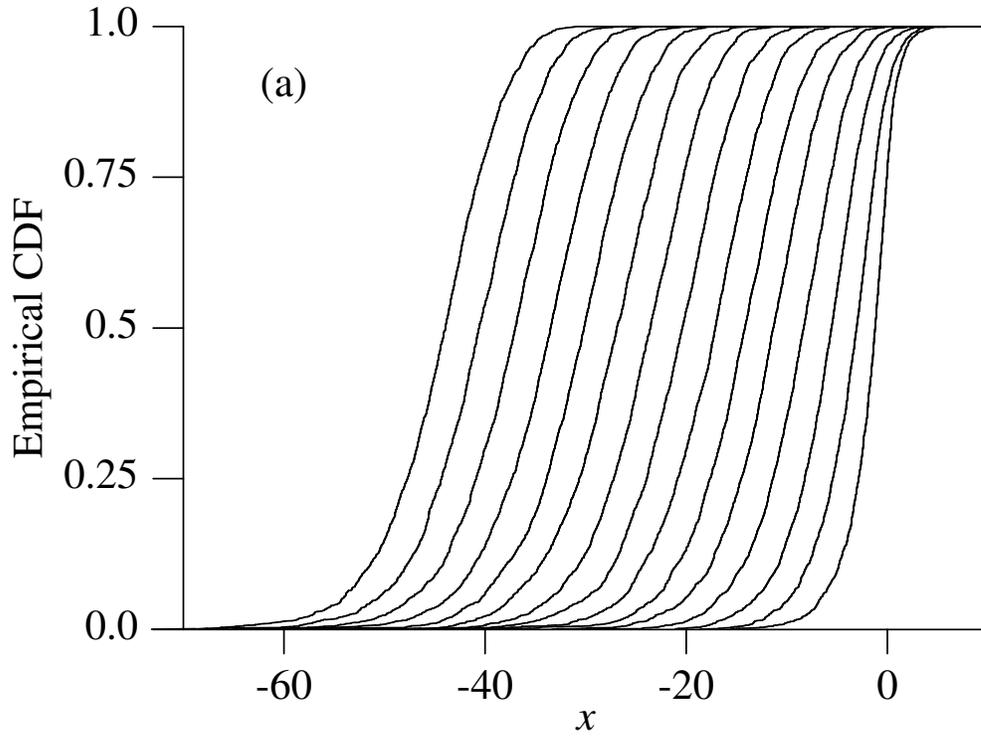
Figure 1
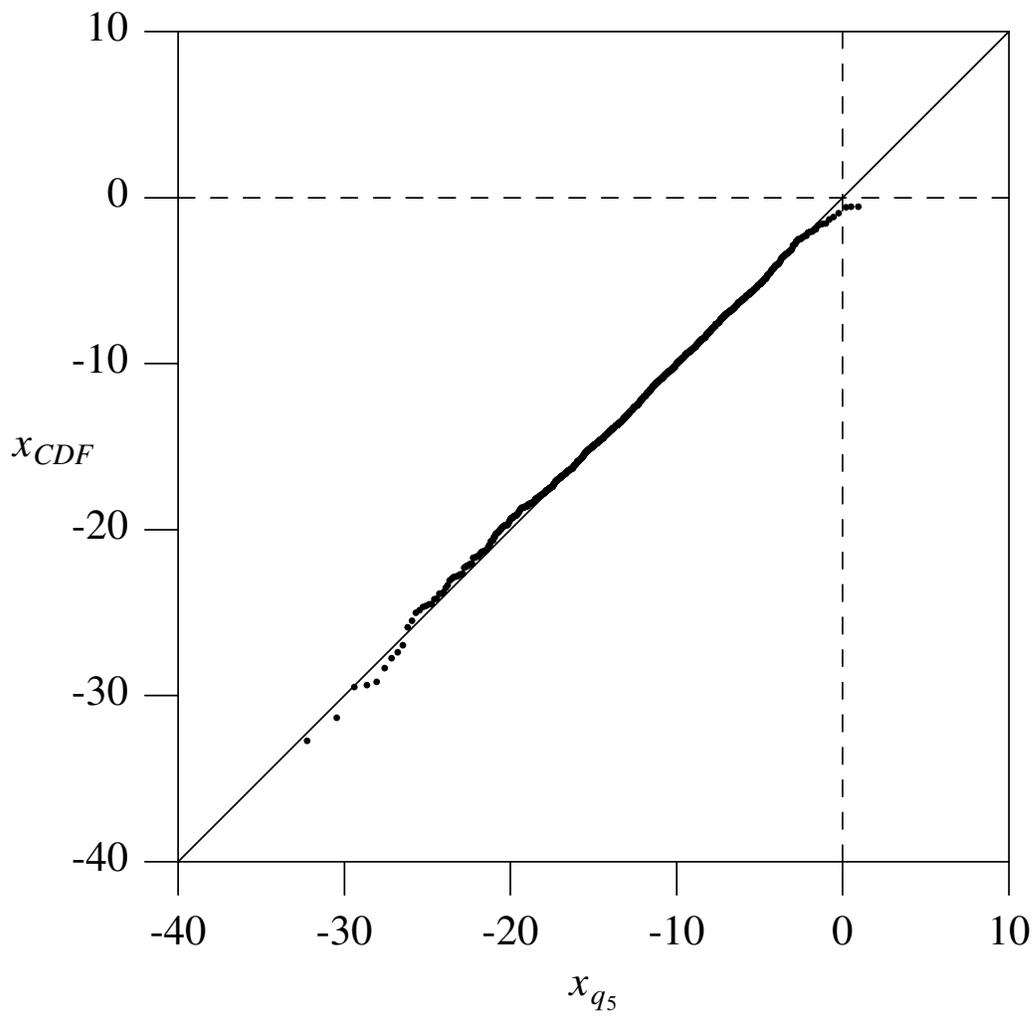
Figure 2

Figure 3

Figure 4