A spatial model for the spread of invading organisms subject to competition

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Abstract. A spatially explicit integrodifference equation model is studied for the spread of an invading organism against an established competitor. Provided the invader is initially confined to a bounded region, the invasion spreads asymptotically as a travelling wave whose speed depends on the strength of the competitive interaction and on the dispersal characteristics of the invader. Even an inferior, but established, competitor can significantly reduce the invasion speed. The invasion speed is also influenced by the exact shape of the dispersal kernel (especially the thickness of the tail) as well as the mean dispersal distance for each generation.

Key words: Biological invasions – Integrodifference equations – Competition – Travelling waves – Dispersal

1 Introduction

The study of invading populations has long been of interest from many points of view (Elton 1958; Mooney and Drake 1986; Hengeveld 1989; Andow et al. 1991). Whether introduced purposely, accidentally or by natural means, the invasion of new species can have serious economic and ecological consequences. The prospect of global climate change, which may cause broad scale shifts in species distributions including invasions of species into new ranges (Baker et al. 1991; Richardson and Bond 1991; Neilson 1993) makes the understanding of biological invasions even more important. Other phenomena, such as the spread of an epidemic (Diekmann 1978, 1979; Mollison 1986, 1991), can be treated in a similar way to invasions. For these reasons, the understanding of the spread of biological invasions is of great importance.

Skellam (1951) gave the first mathematical model of biological invasions. His model (with logistic growth) satisfied a partial differential equation first

introduced by Fisher (1937) and analyzed further by Komogorov et al. (1937), in the context of the related question of the spread of an advantageous allele. Fisher's equation admits non-negative traveling wave solutions of speeds greater or equal to a minimal speed c_0. If the invader is restricted initially to a bounded region, the asymptotic speed of invasion will be this minimal wave speed c_0. Until recently, most subsequent models of invasion were reaction-diffusion partial differential equation models, of which Fisher's equation is a prototypical example (see e.g., Fife 1979 or Murray 1989). These models typically assume that dispersal can be approximated by Brownian processes, although this assumption is not always realistic (see e.g., Harper 1977).

A more flexible approach to modeling invasions uses integrodifferential or integrodifference equations; this approach is becoming increasingly popular in recent years (Weinberger 1978, 1982; Diekmann 1978, 1979; Kot and Schaffer 1986; Lui 1989a, b; Hardin et al. 1990; van den Bosch et al. 1990; Mollison 1986, 1991; Anderson 1991; Kot 1992; Neubert et al. 1995; Allen et al. 1996; Kot et al. 1996). This approach can allow for almost any type of dispersal and can naturally handle discrete time models. Integrodifference and integrodifferential equations exhibit traveling wave solutions of a similar nature as reaction-diffusion equations.

Although invading species typically must compete with established competitors, there have been only a few models of invasion under competition. Okubo et al. (1989) discussed the invasion of the American gray squirrel in England, which is apparently a superior competitor to the native Eurasian red squirrel; their model was a system of two reaction-diffusion equations with Lotka-Volterra competition. They were in some cases able to calculate the invasion speed, which depends in part on the strength of the competitive interaction. Recently, Allen et al. (1996) gave a quite general integrodifference equation formulation of invasion under competition. They could however give only numerical solutions to their model.

The purpose of this article is to study a simple integrodifference equation model of invasion under competition for which analytical formulas for the speed of invasion can be obtained. We will use these results to study the relationship between the speed of invasion to the strength of competition and the mode of dispersal.

2 Discrete growth and dispersal models using integrodifference equations

Most plants and some animals have a life cycle consisting of two distinct phases: a mobile immature stage, where the seeds or larvae disperse away from their parent, and a sessile growth and reproduction stage. The model presented here is for organisms with such a two phase life cycle. We will assume that the organisms complete their life cycle synchronously in exactly one time period (e.g., annually); for simplicity of exposition the organisms will be taken to be annual plants that reproduce once a year. This type of two stage growth

and dispersal process can be modeled mathematically as follows. Let $p_n(x)$ be the (adult) population density at position x of a species at year n, and let $s_n(x)$ be the density of seeds that land at x which were produced in year n; it will be assumed that there are no seed banks in which seeds can lie dormant (see Allen et al. 1996 for models which include perennials or seed banks). The seed density is related to the density of their parent plants by the linear integral operator:

$$s_n(x) = a \int_R K(x, y) p_n(y)\, dy\,, \tag{2.1}$$

where the integration is taken over the entire region R in which the plants live; it will be assumed for the moment that this region is the real numbers. The extension of this analysis to two dimensions will be discussed in Sect. 4. In equation (2.1), the constant a is the number of seeds produced by a parent plant (which is assumed to be the same for all plants of the same species), and $K(x, y)$ (the dispersal kernel) represents the probability density that a seed whose parent is at y lands at the point x. It will be further assumed that the dispersal kernel density $K(x, y)$ depends only on the distance between x and y, and not explicitly on the absolute positions of these two places. In other words, seed dispersal is homogeneous and isotropic, and there is a probability density function k such that $K(x, y) = k(x - y) = k(y - x)$.

The density of plants at x in the next generation is assumed to be a (typically increasing and non-linear) continuously differentiable function of the seed density at x:

$$p_{n+1}(x) = f(s_n(x)/a)\,. \tag{2.2}$$

Note that it is assumed that the function f does not explicitly depend on position; in other words the habitat is homogeneous for growth as well as dispersal. The following assumptions about the growth function f will be made throughout:

$$f(0) = 0, \qquad f(1) = 1 \quad \text{but } f(x) > x \text{ for all } x \in (0, 1)$$

and

$$f'(x) \geqq 0 \quad \text{and} \quad f(x) \leqq f'(0)\, x \quad \text{for all } x \in [0, 1]\,.$$

The assumption that $f(1) = 1$ means that there is a non-zero equilibrium density, which has been normalized for convenience to be the unit density; a constant (in space) density of 1 will remain at this value for all time. The inequality $f(x) > x$ says that at uniform densities less than the non-zero equilibrium, the population will grow, so that this equilibrium is at least stable from below. The last two conditions imply that the adult density will be a non-decreasing function of the seed density and that an increase of the seed density when it is near zero will have a bigger effect on the adult population than the average increase at a higher seed density. All these assumptions are biologically reasonable (a discussion of the situation when this last assumption is relaxed in order to incorporate Allee effects can be found in Kot et al., 1996).

Equations (2.1) and (2.2) can be combined to give single recursive formulas for the adult plant and seed densities:

$$p_{n+1}(x) = f\left(\int_{-\infty}^{\infty} k(x-y)p_n(y)\,dy\right) \tag{2.3}$$

and

$$s_{n+1}(x) = a\int_{-\infty}^{\infty} k(x-y)f(s_n(y)/a)\,dy. \tag{2.4}$$

It was shown by Weinberger (1982) that equations (2.3) and (2.4) exhibit traveling wave solutions $p_{n+1}(x) = p_n(x+c)$ and $s_{n+1}(x) = s_n(x+c)$, where c is the speed of the wave. As (2.3) and (2.4) are non-linear, these equations can have traveling wave solutions of many speeds. However, if the initial density is less than unit density everywhere and has compact support (i.e., the initial population is confined to a bounded region), and the kernel k has exponentially bounded tails, then the solution to (2.3) or (2.4) approaches a traveling wave as $n \to \infty$; this wave has velocity (Weinberger 1978, 1982):

$$c^* = \min_{\mu > 0}\left[\frac{1}{\mu}\ln\left(f'(0)\int_{-\infty}^{\infty} e^{\mu x}k(x)\,dx\right)\right]. \tag{2.5}$$

In other words, c^* is the asymptotic speed of invasion; it is also the minimum possible wave speed for which the wave will have all non-negative values. To put Eq. (2.5) in a bit more tractable form, let

$$M(\mu) = \int_{-\infty}^{\infty} e^{\mu x}k(x)\,dx \tag{2.6}$$

be the moment generating function of k, define

$$c(\mu) = \frac{1}{\mu}\ln(f'(0)M(\mu)) \tag{2.7}$$

and let μ^* be the value of μ for which $c(\mu^*) = c^*$. Then

$$e^{\mu c(\mu)} = f'(0)M(\mu). \tag{2.8}$$

Differentiating both sides of (2.8) with respect to μ gives

$$[c(\mu) + \mu c'(\mu)]\,e^{\mu c(\mu)} = f'(0)\,M'(\mu). \tag{2.9}$$

Since $c'(\mu^*) = 0$,

$$c^*e^{\mu^* c^*} = f'(0)M'(\mu^*) = f'(0)\int_{-\infty}^{\infty} x\,e^{\mu^* x}k(x)\,dx. \tag{2.10}$$

Combining Eq. (2.8) (evaluated at $\mu = \mu^*$) with equation (2.10) gives the system

$$c^* = \frac{M'(\mu^*)}{M(\mu^*)} = \frac{\int_{-\infty}^{\infty} xk(x)\,e^{\mu^* x}\,dx}{\int_{-\infty}^{\infty} k(x)\,e^{\mu^* x}\,dx} \tag{2.11}$$

and

$$\frac{1}{f'(0)} = e^{-\mu^* c^*} M(\mu^*) = e^{-\mu^* c^*} \int_{-\infty}^{\infty} k(x) e^{\mu^* x} dx .$$ (2.12)

These two equations give a parametric representation of the relationship between the speed of the invasion c^* and $f'(0)$. Intuitively, the invasion speed should depend in part on the net reproductive rate at the edge of the invasion front. At this edge, this rate is $f'(0)$ since the population density is near zero. Hence, the invasion speed is a function of $f'(0)$, as well as the form of the kernel k. Kot (1992) derived equations (2.7) and (2.10) in a somewhat different way and gave the following interpretation of them: at small speeds and densities, traveling wave solutions to (2.4) oscillate and take on negative and hence biologically unrealistic values. At low density, one can linearize equation (2.5) about $s_n(x) = 0$ and try solutions of the form $s_n(x) = e^{\mu x}$; the minimal invasion speed is the smallest c for which there exists a non-trivial solution for a real value of μ, since only such a solution would not oscillate.

3 Invasion of annual plants subject to competition

This section will study a model for an invasion of an annual plant that is subject to competition from an established competitor annual. It will be assumed that the habitat is homogeneous, so in absence of competition each of the species would have a equilibrium density constant in space. Let $p_n(x)$ and $q_n(x)$ be the respective (adult) population densities of these two species at year n, normalized so that they would have unit density at equilibrium in the absence of the other species. Let $s_n(x)$ and $r_n(x)$ be the seed density at x produced in year n after they have been dispersed. It will be assumed that both species have the same dispersal characteristics, with dispersal kernel k, but with different fecundities a and b, respectively. Hence, the seed densities in year n are:

$$s_n(x) = a \int_{-\infty}^{\infty} k(x-y) p_n(y) dy$$ (3.1)

and

$$r_n(x) = b \int_{-\infty}^{\infty} k(x-y) q_n(y) dy .$$ (3.2)

The seedlings then compete for space in a "seed lottery," so that the density of plants in the next generation is:

$$p_{n+1}(x) = \frac{s_n(x)}{s_n(x) + r_n(x)} \quad \text{and} \quad q_{n+1} = \frac{r_n(x)}{s_n(x) + r_n(x)}.$$ (3.3)

Note that it is assumed that individual seedlings of the two species compete equally for space, so the competitive advantage of one species over another is due only to differences in fecundity. However, it is easy to see that in lottery competition, an increase in the competitive capabilities of individuals of one

species is mathematically equivalent to a corresponding increase in fecundity (Chesson and Warner 1981). Thus the assumption that individuals of the two species compete equally is made for convenience only. It will be assumed that the invading (s) species is originally confined to a bounded region, and that outside this region, the established species (r) is at unit (equilibrium) density. It is further assumed the invading species is the stronger competitor, i.e., that $a > b$; if this were not the case, the introduced species would not spread.

Note that since $p_{n+1}(x) + q_{n+1}(x) = 1$, the adult density of one species totally specifies the density of the other. Moreover, the seed densities are related by $r_n(x) = b(1 - s_n(x)/a)$. The problem therefore can be reduced to a one species model, and can be dealt with using the methods discussed in the last section. Combining the last equality with equations (3.1) and (3.3) gives a recursion relation for the seed density of the invader:

$$s_{n+1}(x) = a \int_{-\infty}^{\infty} k(x - y) \frac{s_n(y)}{b + (1 - b/a)s_n(y)} \, dy \,. \tag{3.4}$$

Equation (3.4) can be analyzed further for specific choices of the dispersal kernel k. The simplest such kernel is the uniform density:

$$k(x) = \begin{cases} 1/(2L) & \text{if } -L \leqq x \leqq L \\ 0 & \text{otherwise} \end{cases}$$

This density represents the situation where each plant distributes its seeds uniformly throughout an interval of length $2L$ centered on the plant. In this case, equation (3.4) reduces to:

$$s_{n+1}(x) = a \int_{x-L}^{x+L} \frac{s_n(y)}{b + (1 - b/a)s_n(y)} \, dy \,, \tag{3.5}$$

and equations (2.11) and (2.12) become:

$$c^* = \frac{\int_{-L}^{L} x e^{\mu x} \, dx}{\int_{-L}^{L} e^{\mu x} \, dx} \tag{3.6}$$

and

$$\frac{b}{a} = \frac{1}{2L} e^{-\mu c^*} \int_{-L}^{L} e^{\mu x} \, dx \,. \tag{3.7}$$

After some simple calculations and manipulations they become:

$$c^* = [L\mu \coth(L\mu) - 1]/\mu \tag{3.7}$$

and

$$\frac{b}{a} = \frac{e^{-\mu c^*}}{\mu L} \sinh(\mu L) \,. \tag{3.8}$$

A change in variables can effect some simplification; let $z = \mu L$ and $v = c^*/L$. Substituting into (3.7) and (3.8) gives:
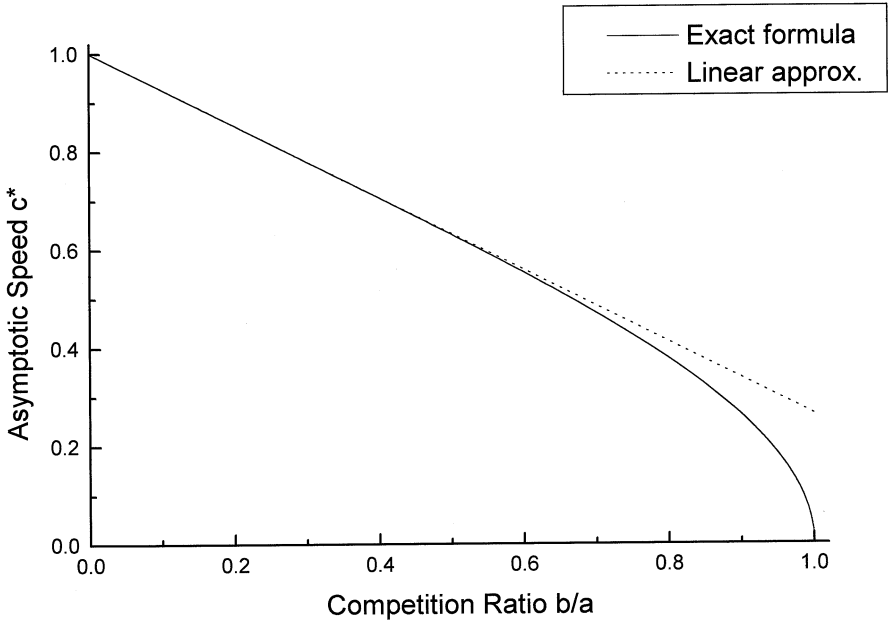
$$v = \coth z - \frac{1}{z} \tag{3.9}$$

Fig. 1. Invasion speed with one-dimensional uniform dispersal as a function of competition strength, with linear approximation

and

$$\frac{b}{a} = \frac{e^{-vz} \sinh z}{z}. \tag{3.10}$$

These equations implicitly define v as a function of b/a. The ratio b/a represents the competitive ability of the established species over that of the invader. Since in the absence of competition it is clear that the invasion speed would be L, the non-dimensional variable v represents the fraction of the maximal speed L at which the invasion will spread under competition. For large values of the parameter z (and hence small values of b/a), it is possible to express the velocity v explicitly as a function of the competition ratio b/a. For such values of z, $\coth z \approx 1$ and hence $v \approx 1 - 1/z$. On the other hand, by eq. (3.10), for these values of z, $b/a \approx e^{-vz+z}/(2z) \approx e^{z(1-(1-1/z))}/(2z) = e/(2z) = e(1-v)/2$. Therefore,

$$v \approx 1 - \frac{2b}{ae}. \tag{3.11}$$

The parametric relationship (3.9) and (3.10) between v and b/a can easily be calculated for various values of z using a spreadsheet and then plotted; Fig. 1 shows this graph together with the approximate relationship (3.11); the approximation is quite good when the competition ratio b/a is less than 0.5.
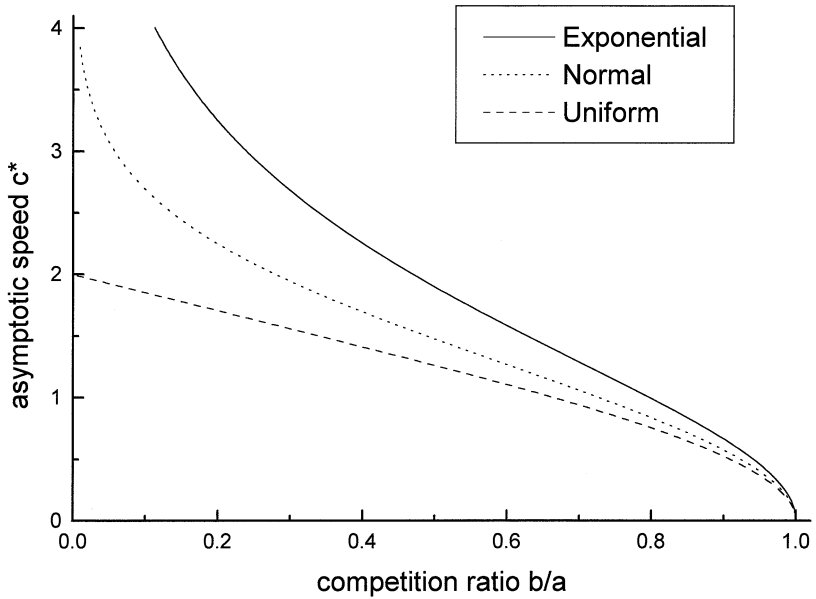
Fig. 2. Invasion speeds with one-dimensional uniform, exponential and normal dispersal, as a function of competition strength

A second possible dispersal density function is the bilateral exponential density $k(x) = (\lambda/2)e^{-\lambda|x|}$. This is a fairly realistic dispersal kernel for wind dispersed seeds (Harper 1977). The mean dispersal distance is then $1/\lambda$. After some calculations, applying (2.11) and (2.12) to this density gives the parametric system:

$$c^* = \frac{2\mu}{\lambda^2 - \mu^2} \tag{3.12}$$

and

$$\frac{b}{a} = \frac{\lambda^2}{\lambda^2 - \mu^2} \, e^{-\mu c^*} . \tag{3.13}$$

The solid line in Fig. 2 gives the plot of this parametric relationship for $\lambda = 1$. The invader spreads very rapidly when it has a large competitive advantage. This result is due to the long and heavy "tail" of the exponential density, which causes a significant number of seeds to be thrown large distances. Note that the model predicts that for exponential dispersal, the invader would spread everywhere in a single time step to a unit density if there was no competition. Realistically, the seed density a large distance from the adult plants would not be large enough for this to happen; thus the high predicted invasion speed for a large competitive advantage is spurious. Still, the model is reasonable so long as the competitive advantage of the invader is not completely overwhelming.

A third possible dispersal kernel is the normal density function with mean 0 and standard deviation σ:

$$k(x) = \frac{1}{\sqrt{2\pi}\sigma}\, \mathrm{e}^{-x^2/(2\sigma^2)} . \tag{3.14}$$

This type of dispersal is more typical for seeds dispersed by animals or by other multiple chance events. Putting this into equations (2.11) and (2.12) gives, after some calculations,

$$c^* = \mu\sigma^2 \tag{3.15}$$

and

$$\frac{b}{a} = \mathrm{e}^{-\mu c^*}\mathrm{e}^{\mu^2\sigma^2/2} . \tag{3.16}$$

An explicit relationship between b/a and c^* can be obtained from these equations. By (3.15), $\mu = c^*/\sigma^2$. Putting this into (3.16) and simplifying gives:

$$\frac{b}{a} = \mathrm{e}^{-c^{*2}/(2\sigma^2)} . \tag{3.17}$$

Solving this equation for the non-dimensional quantity c^*/σ gives the explicit formula

$$\frac{c^*}{\sigma} = \sqrt{2\ln(a/b)} . \tag{3.18}$$

The dotted line in Fig. 2 gives a plot of equation (3.18) for $\sigma = \sqrt{\pi/2}$. There is the same spurious rapid spread of the invading species when its competitive advantage is very large. Since the normal density drops off much more rapidly than the bilateral exponential, this problem is evident only for very small values of b/a.

4 Extension to two dimensions

The results of the last two sections can be extended to two dimensional invasions. It will be assumed here again that the dispersal kernel $K(\mathbf{x}, \mathbf{y})$, where $\mathbf{x}, \mathbf{y} \in \mathbf{R}^2$, depends only on the distance between $\mathbf{x}$ and $\mathbf{y}$, i.e., $K(\mathbf{x}, \mathbf{y}) = k(\|\mathbf{y} - \mathbf{x}\|) = k(r)$ for some piecewise continuous function $k: \mathbf{R}_+ \to \mathbf{R}_+$ with exponentially bounded tail. Weinberger (1982) showed that if the initial density is less than unity everywhere and has compact support, then the solution of the vector version of (2.3) or (2.4) has asymptotic speed:

$$c^* = \min_{\mu > 0}\left[\frac{1}{\mu}\ln\left(f'(0)\iint_{\mathbf{R}^2} \mathrm{e}^{\mu \mathbf{r}\cdot\mathbf{u}}k(r)\,dA\right)\right], \tag{4.1}$$

where **u** is any unit vector. The analogs to the parametric equations (2.11) and (2.12) are:

$$c^* = \frac{\iint_{\mathbf{R}^2} \mathbf{r} \cdot \mathbf{u}\, k(r) e^{\mu \mathbf{r} \cdot \mathbf{u}}\, dA}{\iint_{\mathbf{R}^2} k(r) e^{\mu \mathbf{r} \cdot \mathbf{u}}\, dA} \tag{4.2}$$

and

$$\frac{b}{a} = e^{-\mu c^*} \iint_{\mathbf{R}^2} k(r) e^{\mu \mathbf{r} \cdot \mathbf{u}}\, dA . \tag{4.3}$$

Again, these equations can be analyzed further for specific dispersal kernels k. For the bivariate normal dispersal kernel $(1/2\pi\sigma^2) e^{-(x^2 + y^2)/2\sigma^2}$, there is the same explicit relationship between the asymptotic speed and the competition ratio as in the one dimensional case:

$$\frac{c^*}{\sigma} = \sqrt{2 \ln (a/b)}. \tag{4.4}$$

However, the two dimensional exponential dispersal kernel $k(r) = (\lambda^2/2\pi) e^{-\lambda r}$ gives different results than its one dimensional counterpart. Applying (4.2) and (4.3) to this kernel gives, after some computations,

$$c^* = \frac{3\mu}{\lambda^2 - \mu^2} \tag{4.5}$$

and

$$\frac{b}{a} = e^{-\mu c^*} \frac{\lambda^3}{(\lambda^2 - \mu^2)^{3/2}} . \tag{4.6}$$

Another related dispersal function, derived in Broadbent and Kendall (1953) and Williams (1961), is:

$$k(r) = \frac{\lambda^2}{2\pi} K_0 (\lambda r) , \tag{4.7}$$

where K_0 is the zeroth order modified Bessel function of the second kind. It has the property that its marginal density is the bilateral exponential (Williams 1961, or see Erdélyi et al., p. 54), i.e.,

$$\frac{\lambda^2}{2\pi} \int_{-\infty}^{\infty} K_0 (\lambda r)\, dy = \frac{\lambda^2}{2\pi} \int_{-\infty}^{\infty} K_0 (\lambda \sqrt{x^2 + y^2})\, dy = \frac{\lambda}{2} e^{-\lambda |x|} \tag{4.8}$$

From this, it is easy to see that dispersal following the Bessel density (4.7) has the same formulas for the asymptotic wave speed, Eqs. (3.12) and (3.13), as the one dimensional bilateral exponential density.

The case of the two dimensional uniform dispersal kernel $k(r) = (1/\pi R^2)$ if $r < R$ and $k(r) = 0$ otherwise, does not seem to yield to analytical methods.

5 Discussion

It is natural to now ask which of the dispersal strategies discussed here is best, i.e., for a fixed mean dispersal, which dispersal kernel has the fastest
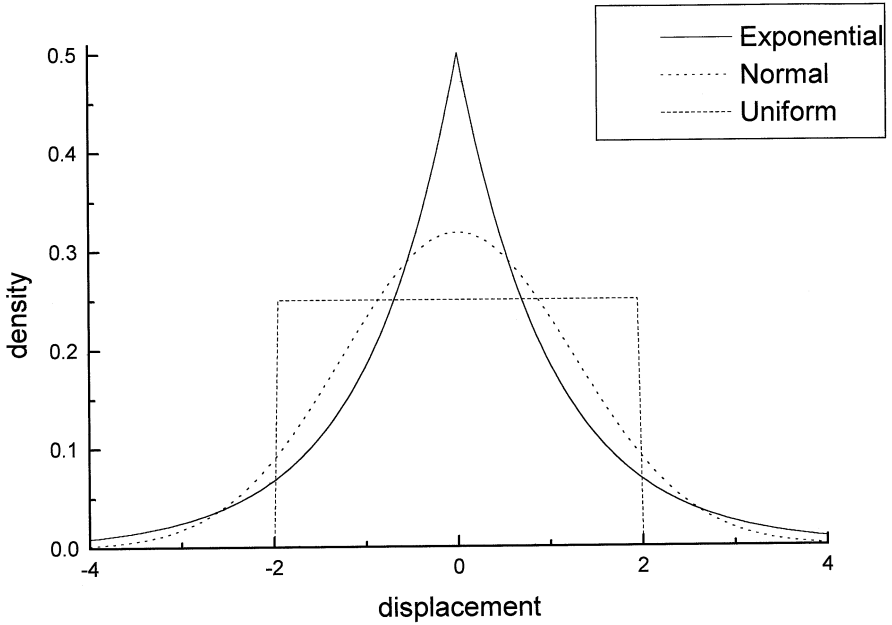
Fig. 3. Comparison of the one-dimensional uniform, exponential, and normal dispersal kernels

asymptotic speed c^*? Consider first the one dimensional case. Figure 2 is a graph of c^* as a function of the competition ratio b/a for the three dispersal strategies discussed here, each with a mean dispersal distance of 1 (so $L = 2$, $\lambda = 1$ and $\sigma = \sqrt{\pi/2}$). The bilateral exponential is clearly the best strategy, followed by the normal and then the uniform dispersal kernels. The shape of these density functions, shown in Fig. 3, gives some insight into this phenomena. One would expect intuitively that the farthest distance that a "significant" amount of seeds are dispersed would be a crucial factor in the invasion speed. Hence, the thick tail of the exponential density gives it an advantage over the other two density functions, while the normal density, with its thin tail, is better than the tailless uniform density. These advantages are especially evident when the invader's competitive advantage is great. Figure 4 compares invasion speeds for the two dimensional versions of exponential and normal dispersal together with the Bessel dispersal density (4.7), again normalized to have unit mean dispersal distance. The Bessel density, due to its slightly thicker tail than the two dimensional exponential, spreads the fastest, followed by the exponential and the thin-tailed bivariate normal densities.

These results show clearly that it is not only fecundity and average dispersal distance, but also the specific shape of the dispersal density function that is important in determining the invasion speed. In particular, the probability of the rare event of a seed being dispersed a long distance is very significant in determining the invasion speed, and not just the distance that an
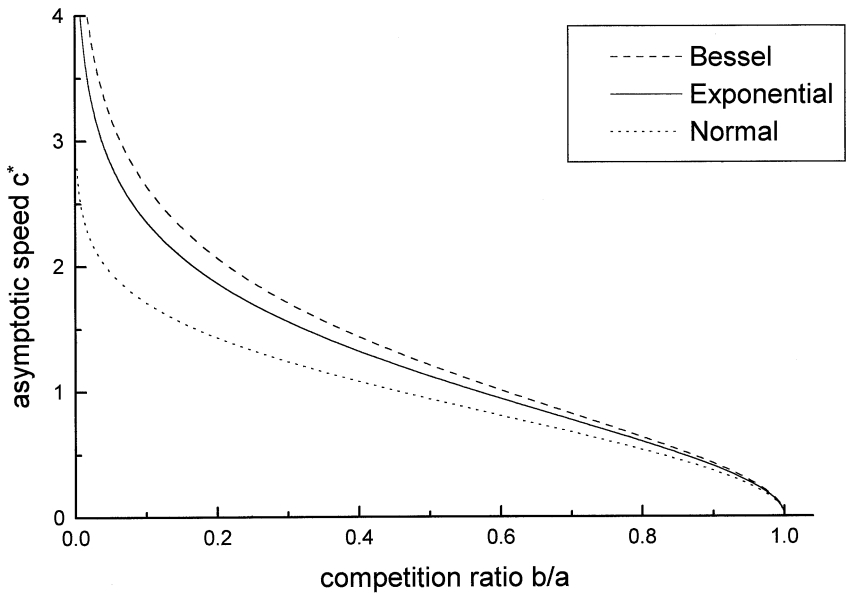
Fig. 4. Invasion speeds with two-dimensional Bessel, exponential and normal dispersal, as a function of competition strength

"average" seed would travel. This is consistent with the recent work of Kot et al. (1996), who show in considerable detail how important (in the single population case) the shape of the dispersal distribution, and in particular the thickness of the tail is to the speed of invasion.

The model studied here shows that even inferior established competitors can considerably slow the advance of an invading species. This agrees with the results of Okubo et al. (1989), despite the fact that their model differed from ours both in their reaction-diffusion approach and that they used Lotka-Volterra type competition.

One idiosyncrasy of our model is the "blow up" of the speed as the competition ratio b/a tends to zero in the case when the dispersal kernel has infinite tails. This is caused by the assumption of lottery competition, which in particular assumes that the adult populations are always limited by seedling competition. Intraspecific competition between invaders is always negligible on the edge of the wave front, so when interspecific competition is also not significant (i.e., when b/a is small), the lottery competition model breaks down. As competition in this case is negligible, such a situation is better modeled as a single invading population with a standard functional response in place of lottery competition. Alternatively, one could construct a more general two species model which reduces to lottery competition where there is an oversupply of seeds and to a single population model where there is little seed competition. For example, the first equation of (3.3) could be

replaced by

$$p_{n+1}(x) = \frac{\alpha_1 s_n(x)}{1 + \alpha_1 s_n(x) + \alpha_2 r_n(x)}, \qquad (5.1)$$

with the second equation modified similarly. This system would reduce to lottery competition where there is a large number of seeds and to a Beverton-Holt type functional response when interspecific competition is negligible.

The model given in this article assumes that there is a uniform, homogeneous and isotropic distribution of suitable habitat. Although these assumptions limit the realism of the model, they are necessary to obtain analytic results. However, the modeling approach used here can be easily adapted to cellular automata computer simulations, where these assumptions can be relaxed. Our results with such simulations show that spatial heterogeneity can slow the speed of invasion compared to the analytic results given here. A detailed discussion of these simulations will be given in a forthcoming article.

References

1. Allen, E. J., Allen, L. J. S., Gilliam, X.: Dispersal and competition models for plants. J. Math. Biol. **34**, 455–481 (1996)
2. Anderson, M.: Properties of some density-dependent integrodifference equation population models. Math. Biosci. **104**, 135–157 (1991)
3. Andow, D, Kareiva, P., Levin, S., Okubo, A.: Spread of invading organisms. Land. Ecology **4**, 177–188 (1990)
4. Baker, W. L., Egbert, S. L., Frazier, G. F.: A spatial model for studying the effects of climatic change on the structure of landscapes subject to large disturbances. Ecological Modelling **56**, 109–125 (1991)
5. Broadbent, S. R., Kendall, K. G.: The random walk of Trichostrongylus retortaeformis. Biometrika **9**, 460–465 (1953)
6. Chesson, P. L., Warner, R. R.: Environmental variability promotes coexistence in lottery competitive systems. Am. Nat. **117**, 923–943 (1981)
7. Diekmann, O.: Thresholds and traveling waves for the geographical spread of infection. J. Math. Biol. **6**, 109–130 (1978)
8. Diekmann, O.: Run for your life. A note on the asymptotic speed of propagation of an epidemic. J. Diff. Eq. **33**, 58–73 (1979)
9. Elton, C.: The ecology of invasions by animals and plants. London: Methuen 1958
10. Erdélyi, A., Magnus, W., Oberhettinger, F. G., Tricomi, F. G.: Higher Trancendental Functions Vol. II. New York Toronto London: McGraw-Hill 1953
11. Fife, P.: Mathematical aspects of reacting and diffusing systems. Berlin Heidelberg New York: Springer-Verlag 1979
12. Fisher, R.: The wave of advance of advantageous genes. Ann. Eugenics **7**, 353–369 (1937)
13. Hardin, D., Takac, P., Webb, G.: Dispersion population models discrete in time and continuous in space. J. Math. Biol. **28**, 1–20 (1990)
14. Harper, J. R.: Population biology of plants. London New York San Francisco: Academic Press 1977

15. Hengeveld, R.: Dynamics of biological invasions. London: Chapman and Hall 1989
16. Kolmogorov, A., Petrovsky, I., Piscounov, N.: Étude de l'équation de la diffusion avec croissance de la quantité de matière et son application a un problème biologique. Moscow U. Bull. Math. **1**, 1–25 (1937)
17. Kot, M., Schaffer, W.: Discrete-time growth-dispersal models. Math. Biosci. **80**, 109–136 (1986)
18. Kot, M.: Discrete-time traveling waves: Ecological examples. J. Math. Biol. **30**, 413–436 (1992)
19. Kot, M., Lewis, M. A., van den Driessche, P.: Dispersal data and the spread of invading organisms. Ecology, **77**, 2027–2042 (1996)
20. Lui, R.: Biological growth and spread modeled by systems of recursions. I. Mathematical theory. Math. Biosci. **93**, 269–295 (1989)
21. Lui, R.: Biological growth and spread modeled by systems of recursions. II. Biological theory. Math. Biosci. **93**, 297–312 (1989)
22. Mollison, D.: Modeling biological invasions: chance, explanation, prediction. Phil. Trans. Roy. Soc. Lond. B **314**, 675–693 (1986)
23. Mollison, D.: Dependence of epidemic and population velocities on basic parameters. Math. Biosci. **10**, 255–287 (1991)
24. Mooney, H., Drake, J.: Ecology of biological invasions of North America and Hawaii. New York Heidelberg Berlin: Springer-Verlag 1991
25. Murray, J.: Mathematical biology. New York Heidelberg Berlin: Springer-Verlag 1989
26. Neilson, R. P.: Vegetation redistribution: A possible biosphere source of CO_2 during climatic change. Water, Air, and Soil Pollution **70**, 659–673 (1993)
27. Neubert, M. G., Kot, M., Lewis, M. A.: Dispersal and pattern formation in a discrete time predator-prey model. Theor. Pop. Bio. **48**, 7–43 (1995)
28. Okubo, A., Maini, P., Williamson, M., Murray, J.: On the spatial spread of the grey squirrel in Britain. Proc. Roy. Soc. Lond. B **238**, 113–125 (1989)
29. Richardson, D. M., Bond, W. J.: Determinants of plant distribution: Evidence from pine invasions. Am. Nat. **137**, 639–668 (1991)
30. van den Bosch, F., Metz, J. and Diekmann, O.: The velocity of spatial population expansion. J. Math. Biol. **28**, 529–565 (1990)
31. Weinberger, H. F.: Asymptotic behavior of a model in population genetics. In: J. Chadam (ed.) : Nonlinear partial differential equations and applications (Lect. Notes Math., vol. 648, pp. 47–98), New York Heidelberg Berlin: Springer-Verlag 1978
32. Weinberger, H. F.: Long-time behavior of a class of biological models, SIAM J. on Math. Anal. **13**, 353–396 (1982)
33. Williams, E. J.: The distribution of larvae of randomly moving insects. Austr. J. Bio. Sci. **14**, 598–604 (1961)