

Allee Dynamics and the Spread of Invading Organisms

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We examine how an Allee effect in local population dynamics (reduced reproductive success at low densities) influences the spatio-temporal dynamics of ecological invasions. Our approach is to use a partial differential equation model of dispersal and population growth, and then ask whether we can identify "rates of spread" for an invading organism subject to an Allee effect. Results indicate that an Allee effect may substantially reduce the rate at which the invader moves into a new environment. Analysis of spread in two spatial dimensions entails application of a singular perturbation theory approach. Here the two-dimensional spread velocity is given in terms of the one-dimensional asymptotic spread rate and the curvature of a boundary between invaded and non-invaded regions. Using this result, we show that invasions cannot propagate unless they initially exceed a critical area. This prediction is verified by numerically solving the original model. Numerical solutions are used throughout in demonstrating the nature of the two-dimensional spread.

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1. INTRODUCTION

The ecology of invasions has received much attention in recent years (e.g., Mooney and Drake, 1986; Drake *et al.*, 1989; Hengeveld, 1989), largely because virtually every ecosystem has been invaded by exotic organisms with potentially drastic consequences for the native fauna or flora. In addition, agricultural scientists often try to sponsor beneficial invasions to control selected pest problems (see Baker and Dunn, 1990). Parallel with this empirical interest in invasions has been an explosion of mathematical models that attempt to describe or predict the fate of particular invasions (Williamson, 1989). One especially common way of mathematically analyzing invasions is to investigate the form and rate of a population's spread in a new environment. This approach can be traced back to R. A. Fisher, who was interested in the spatial spread of new genes that appeared in a population (Fisher, 1937).

A large portion of the mathematical literature on invasions is couched in

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terms of deterministic partial differential equations, which often yield appealingly tractable and compact models of invasion (Skellam, 1951). The simplest possible model of this form is

$$\frac{\partial u}{\partial t} = D\nabla^2 u + f(u), \quad (1)$$

where the operator ∇ denotes the spatial gradient, t is time, $u(x, y, t)$ is the local population density, D is the coefficient of diffusion, and $f(u)$ describes the net population change from birth and death. Clearly such models do not describe the exact ecological situation. For example, simple diffusion models such as (1) neglect stochastic aspects and assume a continually reproducing population, a spatially homogeneous environment, and an absence of strong interactions with other species. The usefulness of diffusion models arises, however, from the fact that they provide testable analytical predictions about the asymptotic rate of spread (ARS) of a population. For example, if $f(u)$ describes logistic population growth, analysis in one dimension indicates a travelling wave solution with the minimum wave speed of $2\sqrt{rD}$, where r is the intrinsic rate of increase of population growth (see Andow *et al.*, 1990, for tests of this model).

To date, estimates for ARS have ignored the Allee effect (Allee, 1938), which was originally proposed as a phenomenon associated with a paucity of reproductive opportunities at low population densities. The key feature of the Allee effect is that populations shrink at very low densities because, on average, individuals cannot replace themselves. For populations subject to an Allee effect, $f(u)$ has the form shown in Fig. 1. We now know that populations may exhibit Allee effects for a wide variety of reasons: less efficient feeding at low densities (Way and Banks, 1967; Way and Cammell, 1970), reduced effectiveness of vigilance and antipredator defenses (Kruuk,

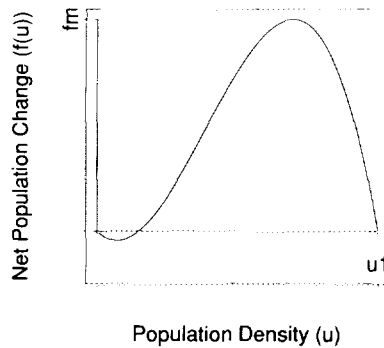


FIG. 1. Growth dynamics exhibiting the Allee effect. Very low population densities do not survive due to a paucity of reproductive opportunity. Growth dynamics for large u exhibit density-dependent mortality.

1964; Kenward, 1978), inbreeding depression (Ralls *et al.*, 1986; Gilpin and Soule, 1986), and several other factors (Folt, 1987; Foster and Trehern, 1981; Turchin and Kareiva, 1989; Pulliam and Caraco, 1984).

In this paper we extend classical analyses of invasion models and asymptotic rates of spread to include an Allee effect. We also extend the theory by adding convection to the dispersal mechanism. Convection might be important if organisms move with wind or water currents or purposely migrate in some particular direction (Pedgley, 1982; Banks *et al.*, 1988). Finally we consider spread in two spatial dimensions and investigate how the spatial arrangement of a founding population influences patterns of spread.

2. THE ALLEE EFFECT AND ASYMPTOTIC RATES OF SPREAD

We begin by showing how including the Allee effect in the reaction dynamics for (1) yields a substantially reduced travelling wave speed and thus a slower ARS. Our analysis in this section draws entirely upon classical results for travelling waves in reaction-diffusion theory (Fife and McLeod, 1975; Hadeler and Rothe, 1975; Aronson and Weinberger, 1975, 1978; Fife, 1979; Rothe, 1981). However, this application to ecological systems is new, and the mathematical results form the basis for further analysis in Section 4.

By way of an example, we consider growth dynamics given by the cubic

$$f(u) = ku(1-u)(u-a), \quad (2)$$

on the range $u \in [0, 1]$. In other words, population densities have been rescaled so that they vary between 0 and 1. Note that the Allee effect is present when $0 < a < 1$, and that when $a = -1$, the model corresponds qualitatively with Fisher's original equation. When $0 < a < 1$ (i.e., an Allee effect), the magnitude of a represents the fraction of carrying capacity below which the ill-effects of a low density produce negative population growth.

So as to readily compare shapes of the $f(u)$ and the effects of varying population growth rate, we choose $k = k(a)$ as a normalization constant which is determined by a maximum growth rate. This yields a family of models which can be compared for various a . For example, if the growth rate ($f(u)$) is constrained to attain a maximum value of 1 then

$$k = 27 / (2(((1+a)^2 - 9a/2)(1+a) + ((1+a)^2 - 3a)^{3/2})) \quad (3)$$

(Fig. 2a). Alternatively, a more relevant biological constraint may be the maximum *per capita* growth rate ($\max_{0 \leq u \leq 1} f(u)/u$). If this attains a value of 1 then

$$k = 4/(1 - a)^2 \tag{4}$$

(Fig. 2b). In this section we will show that our qualitative results regarding the Allee effect and asymptotic rates of spread are independent from our choice of the normalization constant ((3) or (4)).

We consider travelling wave solutions to (1)–(2) of the form $u = U(z)$, with $z = x - ct$, and where c is the wave velocity. Substituting $u(x, t) = U(z)$ into (1)–(2) yields the ordinary differential equation

$$DU'' + cU' + kU(1 - U)(U - a) = 0. \tag{5}$$

Appropriate boundary conditions for an ecological invasion are given by

$$U(-\infty) = 1, \quad U(\infty) = 0. \tag{6}$$

It can be shown that there exists a unique (modulo translation in z) solution to (5)–(6) with a unique wave velocity (c) provided that $0 < a < 1$ (Fife, 1979). When $a \leq 0$ there is a minimum wave velocity, $c^* > 0$ such that for each $c \geq c^*$ there exists a corresponding travelling wave solution (Haderl and Rothe, 1975; Aronson and Weinberger, 1975; Fife, 1979).

Although the the initial conditions for (1)–(2), which describe the distribution of the founder population at $t = 0$, will not, in general, satisfy the travelling wave solution to (5)–(6) ($u(x, 0) \neq U(x)$), one can show uniform convergence (modulo translation) to the travelling wave solution for a wide

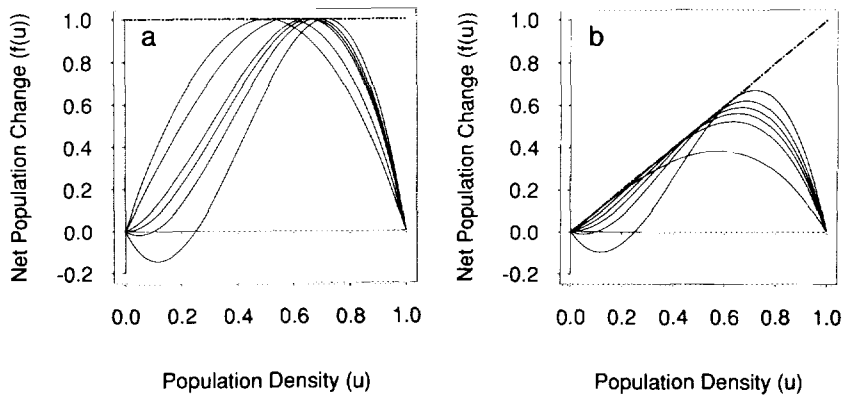


FIG. 2. Cubic growth dynamics. Shown are cubic growth dynamics, defined by (2) for $a = -1, -0.25, -0.1, 0.0, 0.1,$ and 0.25 (from left to right). The normalization constant (k) is given by (3) in (a) and by (4) in (b).

class of initial data. Therefore, after a very long period of time ($t \rightarrow \infty$), the solution to (1)–(2) may converge asymptotically to a travelling wave solution that satisfies (5)–(6). It is thus evident that, if an invasion converges to a travelling wave solution (i.e., is successful), the ARS of the invading population is given by velocity of the travelling wave (c).

Details of conditions for the convergence of initial data to a travelling wave solution are given in Fife and McLeod (1975) and Fife (1979) (for the case $0 < a < 1$) and in Aronson and Weinberger (1975) (for the case $a \leq 0$). Recall that when $0 < a < 1$ the magnitude of a is a threshold density which must be exceeded for growth of the population. In this case, a sufficient condition on initial data for convergence to the travelling wave solution is

$$\lim_{x \rightarrow -\infty} \inf u(x, 0) > a, \quad \lim_{x \rightarrow \infty} \sup u(x, 0) < a \quad (7)$$

(Fife, 1979). When $a \leq 0$, asymptotic travelling wave solutions achieve the minimum wave velocity ($c \rightarrow c^*$) provided that the initial conditions have bounded spatial support (Aronson and Weinberger, 1975, 1978); this is always the case for founder populations.

Rothe (1981) distinguishes between “pulled” fronts and “pushed” fronts for travelling waves. The minimum velocity of a “pulled” front is determined by the leading edge of the wave (near $U = 0$) and is given by

$$c^{*2} = 4f'(0).$$

On the other hand, the minimum velocity of a “pushed” front is not determined by the leading edge of the wave, but by the whole travelling wave front. This terminology is useful when considering solutions to (5)–(6); the wave is “pulled” when $a \leq -1/2$ and is “pushed” when $-1/2 < a \leq 0$. The resulting minimum velocity of the travelling wave front is:

$$c^* = \begin{cases} 2\sqrt{-akD} & \text{for } a \leq -1/2 \\ \sqrt{2kD}(1/2 - a) & \text{for } -1/2 \leq a \leq 0 \end{cases} \quad (8)$$

(Haderler and Rothe, 1975; Rothe, 1981). The case $0 < a < 1$ has the unique wave speed

$$c = \sqrt{2kD}(1/2 - a). \quad (9)$$

This last result can be seen easily by choosing V to be the (unique modulo translation) solution of

$$V'(z) = AV(1 - V), \quad V(-\infty) = 1, \quad V(\infty) = 0.$$

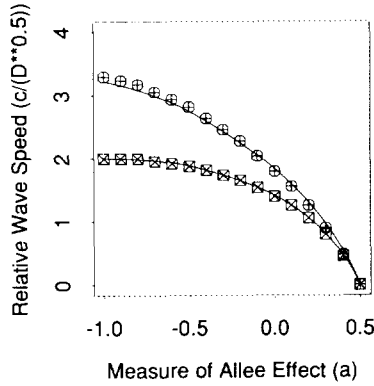


FIG. 3. Theoretical and numerically simulated wave speeds. Theoretical one-dimensional travelling wave speeds for (1)–(2) are shown. These are given (8) for $-1 \leq a \leq 0$ and by (9) for $0 < a \leq 0$. The normalization constant (k) is given by (3) for the upper curve and by (4) for the lower curve. Numerically simulated wave speeds (crosses) are calculated from the movement of the $u = 0.5$ point on the wave front solution to (1) with $D = 0.0001$. The numerical solution algorithm employs the method of lines and Gear's method.

Then V also satisfies (5)–(6) provided we choose

$$A = -\sqrt{\frac{k}{2D}} \quad \text{and} \quad c = \sqrt{2kD}(1/2 - a).$$

Equation (9) tells us that for a successful invasion ($c > 0$) we require $a < 1/2$. In other words, the magnitude of the threshold density for the Allee effect must be less than half the value of the carrying capacity.

The theoretical wave speeds, given by (8) and (9) and the numerically calculated wave speeds are shown in Fig. 3 for $-1 \leq a \leq 1/2$. The upper and lower curves correspond to normalization constants (k) given by (3) and (4). The Allee effect causes a considerable reduction in the rate of spread of an invading population. For example, if k is chosen so $\max_{0 < u < 1} f(u) = 1$ (upper curve) then the wave speed for $a = 0.3$ is less than one third that for $a = -1.0$, and if k is chosen so $\max_{0 < u < 1} f(u)/u = 1$ (lower curve) then the wave speed for $a = 0.3$ is less than one half that for $a = -1.0$.

3. INCLUDING CONVECTION

Theory from the previous section can be easily extended to include convection from bulk flows of the external medium. The appropriate model is

$$\frac{\partial u}{\partial t} + (\mathbf{w} \cdot \nabla)u = D\nabla^2 u + f(u), \tag{10}$$

where the only new parameter is $\mathbf{w} = (w_1, w_2)'$, which represents the velocity of convection (in units distance/time). Employing the change of variables

$$t^* = t, \quad x^* = x - w_1 t, \quad y^* = y - w_2 t,$$

and dropping the asterisks for notational simplicity we transform (10) to the reaction-diffusion equation (1). In other words, the convection term merely shifts the entire travelling wave solution with a velocity \mathbf{w} .

4. TWO-DIMENSIONAL SPREAD OF INVADING POPULATIONS SUBJECT TO THE ALLEE EFFECT

Although the issue of spread in two dimensions is not difficult conceptually, actual analytical predictions become challenging when we move from a one-dimensional environment to two spatial dimensions. Planar travelling waves do exist (Aronson and Weinberger, 1978) and this planar form may be asymptotically achieved by an invading population. However, the most important stage of an invasion may occur before the asymptotic form of plane wave propagation is achieved; this is also the stage at which the eventual success or failure of an invasion may be determined. We will show that, when a newly established founder population is subject to Allee dynamics, it may fail to establish itself, even when it is initially present at levels which exceed the threshold density described for growth of the population. This is because the growth in population density through reproduction may not be sufficient to counteract the decline in population density through dispersal of individuals. The net result may be the decline and eventual extinction of the invading population. Critical factors in determining the success of an invasion thus include the shape and size of the region which the founder population occupies because these affect the extent to which dispersal reduces population density. We will show how the shape and size factors can be conveniently summarized mathematically by the curvature of the interface that exists between the region which is invaded and that which is as yet unoccupied (Fig. 4f).

When analysing the spread of an invading population it is useful to consider four stages:

1. Initial introduction of a founding population (Fig. 4b),
2. Convergence of the population density profile to a moving wave front which connects invaded regions (where the population density is near the carrying capacity) and non-invaded regions (where the population density is zero) (Fig. 4c),

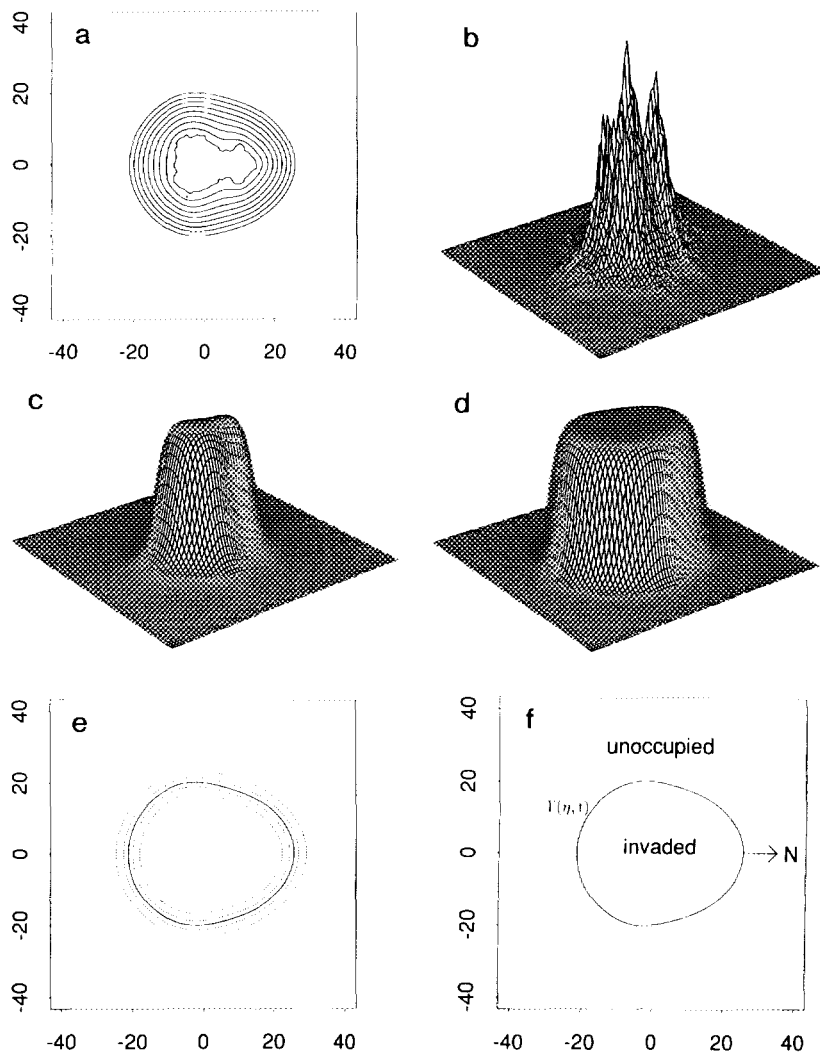


FIG. 4. Numerical solution showing the two-dimensional spread of an invading population. Shown is the finite difference numerical solution to (1)–(2) for $D=1$, $k=1$, and $a=0.05$. A founding population, which is initially introduced at $t=0$, converges to a moving wave front and spreads. The location of the spreading wave front is shown by the $u=0.5$ contour at successive equal time intervals of size 2, between $t=0$ (inner) and $t=16$ (outer) (a). The corresponding profiles for u are given at $t=0$ (b), $t=4$ (c), and $t=16$ (d). The profile for u at $t=16$ is also given a plot of $u=\text{constant}$ isoclines (e). These isoclines are taken as $u=0.9$ (inner), 0.7, 0.5, 0.3, and 0.1 (outer). The $u=0.5$ isocline (solid in (e)) denotes the location of the interface, $\Gamma(\eta, t)$ separating invaded and unoccupied regions (f). The normal velocity of Γ is given by N , and, for any fixed time, the dummy parameter η parameterizes the length of Γ .

3. Movement of this wave front as the invading population spreads (Fig. 4d),

4. Eventual spread of a successful invading population after a very long time.

In this section we will use some "initial asymptotics" to estimate the dynamics in the Stage 3: those of the early spread of an invading population. Our approach will entail the application of results from singular perturbation theory to derive an approximate formula for the two-dimensional rate of spread. These asymptotics lead us to suggest that the invading population may approach a planar travelling wave form in Stage 4.

To examine invasions with an Allee effect in two dimensions we use (1) where the population growth function ($f(u)$) is given by a curve that satisfies

$$f'(0) < 0, \quad f'(u_1) < 0,$$

but is not given explicitly (see, for example, Fig. 1). Thus the model retains a degree of robustness by not stating $f(u)$ exactly. The carrying capacity for the population is u_1 and the maximum value of $f(u)$ on $0 \leq u \leq u_1$ is given by f_m (Fig. 1). To facilitate analysis of the relevant processes we nondimensionalize (1) by choosing

$$\begin{aligned} \mathbf{x}^* &= -f'(0) \sqrt{\frac{u_1}{Df_m}} \mathbf{x}, & t^* &= -f'(0)t, & u^* &= \frac{u}{u_1}, \\ f^* &= \frac{f}{f_m}, & \varepsilon &= \frac{-f'(0)u_1}{f_m}. \end{aligned}$$

The new carrying capacity is $u^* = 1$ and f^* now attains a maximum value of 1. Dropping asterisks for notational simplicity we obtain

$$\varepsilon \frac{\partial u}{\partial t} = \varepsilon^2 \nabla^2 u + f(u). \quad (11)$$

To further simplify matters we consider the case where the reaction dynamics are fast and exhibit a slight Allee effect, and thus ε is a small positive parameter, $0 < \varepsilon \ll 1$.

We now assume that the spread of the invading population has reached Stage 3 (above). In other words, the initial invasion by a founding population has converged to moving wave form which joins the $u = 1$ (invaded) steady state solution to the $u = 0$ (non-invaded) steady state solution of the nondimensionalized system (11). We are unaware of rigorous mathematical conditions for this convergence in higher dimen-

sions. However, two-dimensional numerical solutions, such as those shown in Fig. 4, do indicate convergence for a wide class of initial data.

Using results from singular perturbation theory, we employ an approximate formula for the normal velocity, N , of an interface marking the spatial separation of invaded and non-invaded regions (Fig. 4f). In mathematical terms, this interface shows the location of a moving transition layer joining the $u=0$ and the $u=1$ steady states. The width of the transition layer is $\mathcal{O}(\varepsilon)$ and thus the location of the interface becomes exact as $\varepsilon \rightarrow 0$.

If the interface is planar then the wave front has constant velocity at all points in the forward, normal direction (N is constant). However, if the plane geometry of the interface is distorted, the normal velocity may now vary locally along the wave front. Similar kinds of interfacial systems are commonplace in physics, chemistry, and biology (for a discussion, see Fife, 1988). The system (11) arises in the theory of excitable reaction-diffusion systems. For this system it has been established that the normal velocity of the interface obeys the "eikonal equation for reaction-diffusion systems," namely,

$$N = \gamma - \varepsilon\kappa, \quad (12)$$

where γ is the unique planar travelling wave speed for (11) and κ is the curvature of the interface (Keener, 1986; Keener and Tyson, 1986; Gomatam and Grindrod, 1987; Grindrod *et al.*, 1991). When applied to Eq. (11), this equation is valid to $\mathcal{O}(\varepsilon^2)$ (Lewis and Grindrod, 1991).

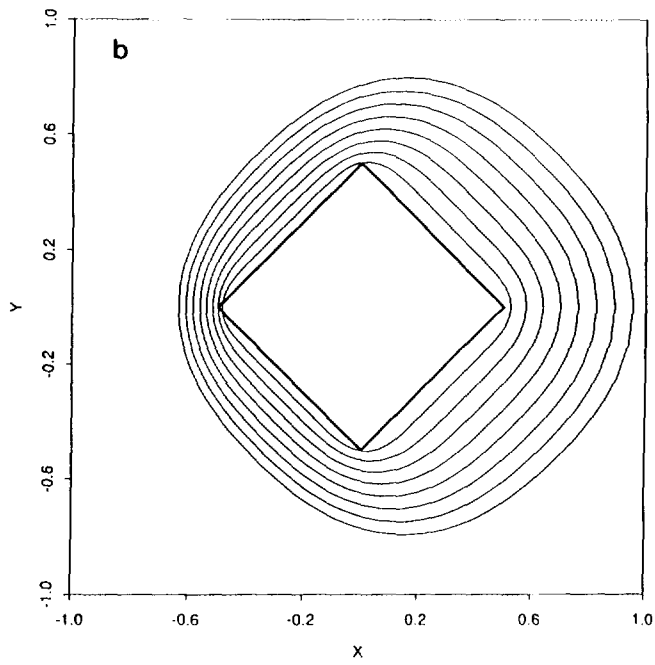
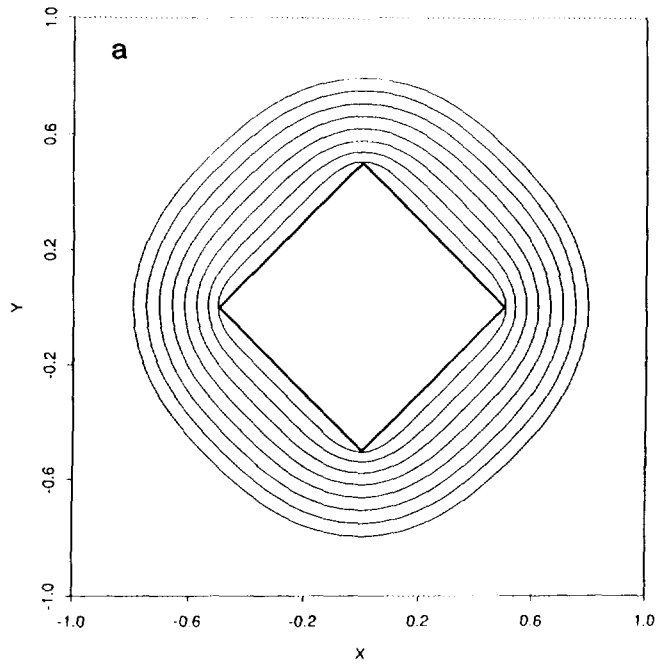
We denote the time-dependent location of the interface by $F(\eta, t)$, where η is a dummy variable used to parameterize the length of the interface (Fig. 4f). If we represent a point on the interface by Cartesian coordinates $(x(\eta, t), y(\eta, t))$ then the movement, given by (12), satisfies

$$\frac{\partial x}{\partial t} = \left(\gamma + \varepsilon \frac{x_{\eta\eta} y_{\eta} - y_{\eta\eta} x_{\eta}}{(x_{\eta}^2 + y_{\eta}^2)^{3/2}} \right) \frac{y_{\eta}}{(x_{\eta}^2 + y_{\eta}^2)^{1/2}} \quad (13)$$

$$\frac{\partial y}{\partial t} = \left(\gamma + \varepsilon \frac{x_{\eta\eta} y_{\eta} - y_{\eta\eta} x_{\eta}}{(x_{\eta}^2 + y_{\eta}^2)^{3/2}} \right) \frac{-x_{\eta}}{(x_{\eta}^2 + y_{\eta}^2)^{1/2}}, \quad (14)$$

(Keener, 1986). This system can be conveniently solved by finite difference methods (Grindrod *et al.*, 1991).

FIG. 5. Finite difference solution for movement of the wave boundary. Initial wave boundary configurations are shown by dark lines. Equations (13)–(14) are solved numerically, using the method outlined in Grindrod *et al.* (1991) and the location of the wave boundary is plotted at equal 0.1 time increments (a). Parameter values are $\gamma=0.5$ and $\varepsilon=0.025$. In (b) a modification of (13)–(14) incorporating the convection velocity $\mathbf{w} = (0.2, 0)$ is solved numerically.



We numerically solved (13)–(14) with a square initial boundary between invaded and non-invaded areas, using the method of Grindrod *et al.* (1991) (Figure 5a). Note how the curvature term in (12) serves to round out corners which were initially sharp. Convection was added in the numerical solutions shown in Fig. 5b. As discussed in Section 3, this merely shifts the entire solution with a velocity given by \mathbf{w} .

If we consider radially symmetric solutions to (12), denoting the location of the interface by $r(\eta, t) = r(t)$, we have

$$\frac{\partial r}{\partial t} = \gamma - \frac{\varepsilon}{r}. \quad (15)$$

Hence we obtain a spherical wave which exhibits threshold behavior; the region occupied by the invading population in Stage 3 (above) must exceed a certain radius, $r(0) > \varepsilon/\gamma$, in order to initiate a radially expanding wave, while regions of subcritical radius collapse in on themselves (Fig. 6). The dimensional version of (15) is

$$\frac{\partial r}{\partial t} = c - \frac{D}{r}, \quad (16)$$

where c is the dimensional travelling wave speed. If we choose the reaction dynamics as (2), with $0 < a < 1/2$, we obtain c from (9) and calculate the minimum initial radius in dimensional terms as

$$r_{\min} = \left(\frac{D}{2k}\right)^{1/2} \frac{1}{1/2 - a}. \quad (17)$$

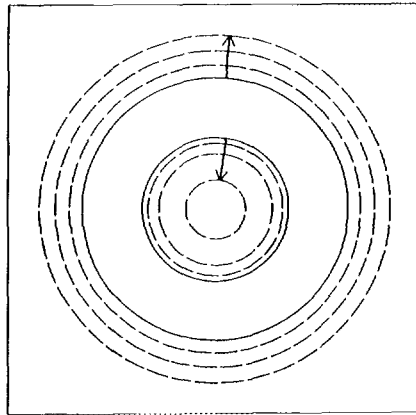


FIG. 6. Threshold behaviour for radially expanding waves. Disturbances must exceed the critical radius, $r_c = \varepsilon/\gamma$, in order to initiate a radially expanding wave. Numerical solutions of (13)–(14), with $\varepsilon/\gamma = 0.5$, show how subthreshold disturbances ($r(0) = 0.44$) collapse while suprathreshold disturbances ($r(0) = 0.8$) initiate a radially expanding wave.

Thus, an increase in the diffusion coefficient (D) or an increase in the Allee effect will have the same effect of requiring a larger initial "beachhead" if an invading population is to take hold and expand (i.e., for $\partial r/\partial t > 0$). The effect of the minimum radius (17) is illustrated in Fig. 7, where the radially symmetric version of (1)–(2) is solved numerically for subcritical and supercritical initial radii.

Following Grindrod *et al.* (1991) we now show that planar interfaces obeying the eikonal equation approximation (12) are linearly stable to perturbations. This is a necessary condition for the asymptotic approach towards a planar travelling wave form ($\kappa=0$, $N=\gamma$) in Stage 4 (above). Suppose that there is an interface, $\Gamma(\eta, t) = (x(\eta, t), y(\eta, t))$, propagating over the infinite plane and that for each t fixed, $y(\eta, t)$ is invertible with $y_\eta < 0$. Eliminating η , we write $x(\eta, t) = X(y, t)$ so Eqs. (13) and (14) yield

$$X_t = \varepsilon \frac{X_{yy}}{(1 + X_y^2)^{3/2}} + c(1 + X_y^2)^{1/2}. \quad (18)$$

The solution $X = ct$ represents a planar wave propagating over the (x, y) plane in the x -direction. Linearizing about this solution by setting $X = ct + w(y, t)$ and keeping leading order terms yields

$$w_t = \varepsilon w_{yy}.$$

These planar wave solutions are stable (modulo translation) because $w \rightarrow 0$ uniformly as $t \rightarrow \infty$ provided $\int w(0, y) dy$ is finite.

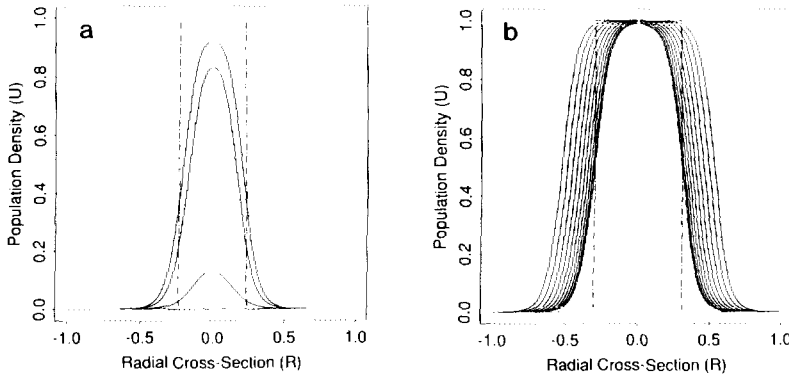


FIG. 7. Numerical solution of the radially symmetric version of (1), (2) indicates threshold behaviour. Parameter values, given by $D = 0.02$, $a = 0.4$, and $k = 15.25$, yield a critical radius of $r_{\min} = 0.256$ (17). Initial conditions are given by the dashed lines, and the wave front configuration is plotted at equal 1.0 time increments. Subcritical perturbations collapse (a) but superthreshold perturbations expand radially (b). The numerical algorithm employs the method of lines and Gear's method.

Equation (12) leads us to expect that highly corrugated initial wave boundary configurations may lead to a rapid invasion by the organism, particularly in the limit as ε is very small. Denoting the area of the invaded region by A , we observe that

$$\frac{\partial A}{\partial t} = \int_{\Gamma(\eta, t)} N(\eta, t) d\eta = \gamma l(t) - \varepsilon \int_{\Gamma(\eta, t)} \kappa(\eta, t) d\eta,$$

where $l(t)$ is the length of the interface $\Gamma(\eta, t)$. As $\varepsilon \rightarrow 0$, the area invaded increases at a rate proportional to the length of the interface ($l(t)$). We verified this by contrasting numerical simulations for an invasion with an initially sinusoidal wave boundary to numerical simulations for an invasion

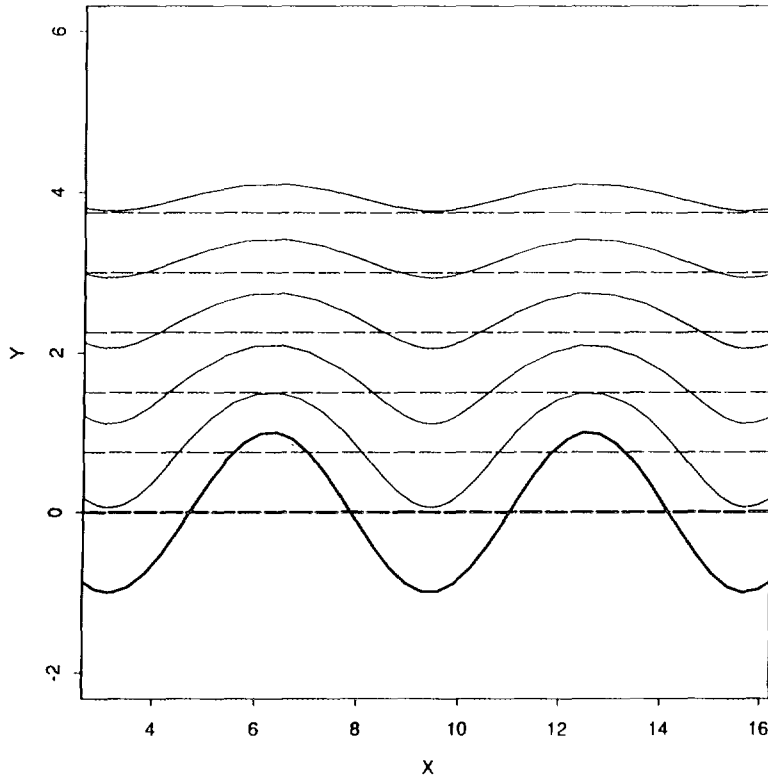


FIG. 8. Highly corrugated wave boundaries may lead to a rapid invasion. Initial wave boundary configurations are shown by dark lines. Equations (13)–(14) are solved numerically, using the method outlined in Grindrod *et al.* (1991), and the location of the wave boundary is plotted at equal 1.5 time increments. Parameter values are $\gamma = 0.5$ and $\varepsilon = 0.25$. By the time $t = 7.5$ (last position plotted) the sinusoidal wave boundary (solid lines) has progressed farther than the planar wave boundary (dashed lines) for all x .

with an initially planar boundary; numerical results showed that invasions outlined by corrugated boundaries increase their range more rapidly than invasions outlined with planar boundaries (Fig. 8). This result suggests that deliberate introductions of organisms may be most successful when the initial distribution leads to a highly corrugated boundary between invaded and non-invaded areas. The degree of corrugation can be measured as the ratio of the shortest distance between adjacent peaks to the length of the boundary that lies between them, a ratio which is independent of scale. Ultimately, when the time since initiation of the invasion goes to infinity, the importance of such a corrugation effect will diminish to zero. However, in the early stages of an invasion, corrugation could be quite important.

5. DISCUSSION

Returning to the general ecological issue of invasions, there are several potentially useful results that have emerged from our analyses. Notably, the idea of an asymptotic rate of spread for an invader can be extended beyond simple logistic population dynamics and beyond simple diffusive dispersal. In particular, we show how to calculate a rate of spread for Allee dynamics, and for diffusion plus convection. More interesting is what these calculations tell us biologically: even if a population is introduced at a density above its critical Allee threshold, its spread will still be substantially reduced by the presence of an Allee effect. This is easiest to summarize for invasions in one dimensional environments. For example, if we quantify the Allee effect by the fraction of the equilibrium density at which population growth becomes negative (because of inbreeding, mate-finding problems, and so forth), then the rate of spread decreases substantially as this fraction increases, in the manner shown in Fig. 3.

In two-dimensional environments, the implications of an Allee effect are more complex, but also more interesting. The major new feature that arises in analyzing rates of spread in two dimensions is the role that "curvature" plays in determining spread. Relevant curvature is defined by the boundary between the invader's occupied territory and unoccupied territory. The more sharply this boundary curves outward (i.e., into vacant space), the slower the spread will be; conversely, the more sharply this curvature bends inward (i.e., so that there are fingers of vacant space sticking into an invader's territory), the faster the spread will be. Taken together, these effects mean that details about the geometry of an invasion boundary can play a substantial role in exactly how, and at what speed, that invasion advances. For example, a critical area must be covered by an invader subject to Allee dynamics, if the invasion is to take hold. Even if a population is inoculated at densities well above its low-density Allee threshold, the

invasion will fail unless that inoculation covers a sufficiently large area. The reason behind such a failure is that for a small area, with a highly curved boundary between invaded and unoccupied regions, diffusion dissipates the local density faster than population growth supplies new individuals. Another result relates to the degree of corrugation of the initial boundary between occupied and unoccupied territories; the overall increase in an invader's area will proceed more rapidly the greater the degree of corrugation (see Fig. 8).

Our two-dimensional analysis of invasions with an Allee effect may also resolve a puzzle that has turned up in several field studies of real invasions. In particular, Okubo (1988) observes that often the rate of expansion of an invader's range is initially very slow, but gradually increases until a constant rate of radial expansion is achieved. This pattern is not predicted by the classical analysis for constant diffusion plus logistic growth (see Okubo, 1988), but can be explained for organisms with an Allee effect by using results from Section 4. Integrating Eq. (16) yields

$$t = \frac{1}{c} \left[r + \frac{D}{c} \log |cr - D| \right]_{r(0)}^{r(t)}. \quad (19)$$

Plotting the radius of expansion (r) versus the time elapsed (t) for various different initial conditions ($r(0)$) gives the curves shown in Fig. 9: radial expansion begins slowly (if at all) before attaining the asymptotic rate.

Our results, together with other recent extensions of the mathematical theory of invasions (Shigesada *et al.*, 1986; van den Bosch *et al.*, 1990), suggest that it may be possible to develop a theory which is sufficiently rich to describe a large portion of the invasion processes likely to arise in the natural world. The challenge now is to develop methods for testing or distinguishing among the many different models, and for anticipating which model is most likely to capture the essentials of any given invasion.

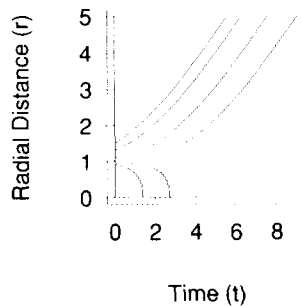


FIG. 9. Radial expansion rates are shown for different initial conditions. Solutions to (16), given by (19), are shown for $c = D = 1$ and various initial invasion radii ($r(0)$).

Because most invasions start with only a few individuals and Allee effects are likely to be common for small populations, we think that invasion models need to incorporate these effects. Although our efforts in this direction have involved totally deterministic models, there is currently a need to investigate the implications of Allee effects in stochastic models of invasion. We predict that stochastic versions of our model will not only produce a similar reduction in the rate of spread, but an even more pronounced threshold area effect.

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