

Species spreading due to environmental hostility, dispersal adaptation and Allee effects

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Abstract—A phenomenological model for species spreading which incorporates the Allee effect, a species' maximum attainable growth rate, collective dispersal rate and dispersal adaptability is presented. This builds on a well-established reaction-diffusion model for spatial spreading of invading organisms. The model is phrased in terms of the "hostility" (which quantifies the Allee threshold in relation to environmental sustainability) and dispersal adaptability (which measures how a species is able to adapt its migratory response to environmental conditions). The species' invading/retreating speed and the sharpness of the invading boundary are explicitly characterised in terms of the fundamental parameters, and analysed in detail.

Keywords—Allee effect, dispersal, migration speed, diffusion, invasion

I. INTRODUCTION

THE speed and the structure of population dispersal is an important area of study, in particular in the protection of native fauna and flora from invasive species. Factors influencing this include the species' range, density-dependence in its growth, dispersal rate, dependence of the dispersal rate on environmental conditions and density, habitat variation, and collective behaviour. Many types of mathematical models have been used to understand the ecology of spatial spreading, including partial differential equations [1]–[7], discrete models [4], [8], integro-differential equations [9], and neural nets [10]. Different models offer successes in different situations.

One factor influencing population spreading is whether the population is growing at a sufficient rate. The standard measure of this is the per capita growth rate (pgr), which is the rate of increase of the population per individual. The pgr is density-dependent in many relevant situations. The most common density-dependence expresses pgr as a linear decreasing function of the density, modelling the fact that an environment has limited resources. This simple pgr curve does not take into account an important phenomenon postulated by Warder Allee [11], in which the pgr curve increases at small densities [11]–[14]. Among many explanations for this phenomenon are the inability to find mates successfully, diminished anti-predator vigilance and reduction of genetic diversity [13]. If the pgr is actually negative at small densities, this is called the strong Allee effect, which has been demonstrated in gypsy moths [15], bighorn sheep [16], African wild dogs [17] and annual plants [18], [19]. The weak Allee effect (the pgr does not become negative) has been exhibited in flour beetles [11], the California channel island fox [20] and smooth cordgrass [21].

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Assuming that a population is increasing sufficiently, its spatial spreading is measured by a dispersal rate. This relates to how individuals move around: their typical range, the shape of the probability distribution of the range, the speed at which they move, etc. The density profile of the population as a whole moves according to how *all* the individuals move. For plants, the spatial probability distribution of the progeny of a plant and the frequency of seeds (and seasonality) contribute to the dispersal rate. Commonly used models for dispersal are neural-net simulations which populate a spatial grid based on a probabilistic dispersal [10], [21], or diffusion equations which incorporate the randomised individual motions into a deterministic model for the collective density [1]–[3], [5], [6], [22].

In this article, an extension to a well-established model [3], [4] which includes both Allee dynamics and diffusive spread is examined. The goal is to determine the spreading rate and the shape of the density profile, in terms of parameters fundamental to the species and the environment. As a first step, this is done in terms of the species' maximum attainable per capita growth rate, natural dispersal rate, and the *hostility* (a newly defined parameter which incorporates the Allee threshold and the environmental carrying capacity). As a second step, the fact that a species will change its dispersal rate depending on environmental conditions is considered, as suggested by Fretwell in his ideal free distribution hypothesis [23]. This can be incorporated in different ways, most of them mathematically difficult: density-dependent diffusion [6], [7], [22], [24], [25], discrete resource-dependent dispersal models [8], [9], and a host of habitat selection models (see the introduction of [26] for a review). Here, a simpler implementation of Fretwell's hypothesis through the definition of a new parameter, the species' *dispersal adaptability*, is formulated. This measures a species' ability to change its dispersal rate depending on resources and intra-species competition. The dependence of the spreading rate and density profile on these fundamental parameters is examined in detail, and ecological implications discussed.

II. PER CAPITA GROWTH RATE

The model for the pgr, ignoring dispersal, is first presented. The important parameters which are used in the model are summarised in Table I, for quick reference. If u is the population density (population per unit habitat length) of a species, the pgr in the presence of Allee effects could be modelled by [4], [14]

$$\text{pgr} = L \left(1 - \frac{u}{K} \right) \left(\frac{u}{\alpha} - 1 \right), \quad (1)$$

TABLE I
LIST OF PARAMETERS AND VARIABLES USED IN THIS ARTICLE.

Quantity	Name	Dimensions
α	Allee threshold	Individuals
c	Spreading rate	Length/Time
h	Environmental hostility, $h = \alpha/K$	Dimensionless
K	Carrying capacity	Individuals
n	Dispersal adaptability	Dimensionless
Φ	Natural dispersal rate	Length ² / Time
r	Maximum per capita growth rate	Time ⁻¹
u	Population density	Individuals/Length

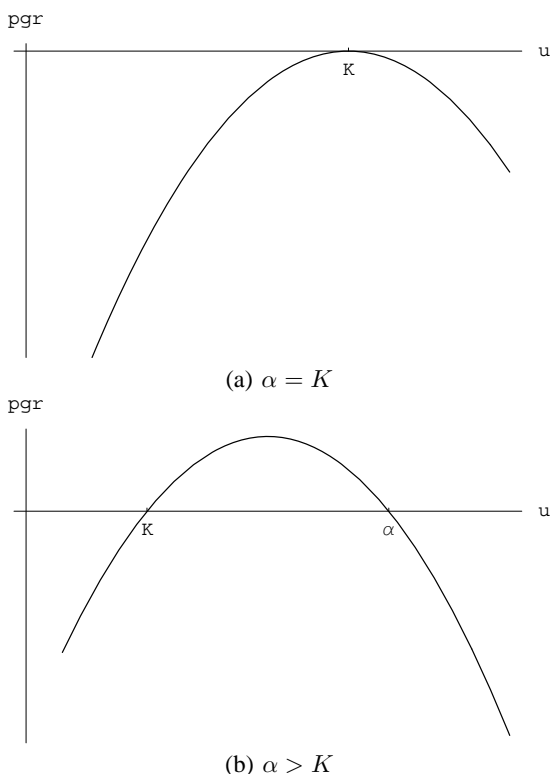


Fig. 1. Ecologically meaningless choices for pgr: (a) $\alpha = K$, and (b) $\alpha > K$.

is used, in which L is a positive normalizing constant, K is the carrying capacity, and α is the Allee threshold. While K needs to be non-negative to be ecologically meaningful, it is first argued that α needs to be less than K . Firstly, $\alpha = K$ is not a legitimate choice, since pgr is negative even for any $u < K$, any population below the carrying capacity will decay to zero (see Figure 1(a)). Secondly, $\alpha > K$ would result in Figure 1(b), in which α would be a stable equilibrium, while K would be unstable. The population density would therefore approach a value *greater* than the environmental carrying capacity K . Thus, $\alpha < K$.

The normalizing factor L in (1) modifies the height of the curve, and can be chosen in many ways (see [5] for a discussion). Following Lewis and Kareiva [5], it shall be chosen

to relate to a parameter of potential ecological significance: the species' maximum attainable per capita growth rate r . Elementary calculus reveals that the maximum value is seen to occur at $u = (\alpha + K)/2$, and hence

$$L = \frac{4 K \alpha}{(K - \alpha)^2} r. \tag{2}$$

By replacing L with the above, the pgr can be expressed by

$$\begin{aligned} \text{pgr} &= \frac{4 K \alpha}{(K - \alpha)^2} r \left(1 - \frac{u}{K}\right) \left(\frac{u}{\alpha} - 1\right) \\ &= \frac{4 r}{(K - \alpha)^2} (K - u)(u - \alpha), \end{aligned} \tag{3}$$

The graph of the pgr in (3) is shown in Figure 2. There are two qualitatively different possibilities for α which model ecological situations: $-K < \alpha \leq 0$ and $0 < \alpha < K$. As a special case of the former, suppose $\alpha = 0$, meaning that the organism does not encounter negative pgr. This is the weak Allee effect, whose graph is shown in Figure 2(a). This same qualitative increase in pgr at small densities occurs if $-K < \alpha < 0$, whose graph can be obtained by shifting the zero at $u = 0$ in Figure 2(a) to the left by the appropriate amount. As long as $-K < \alpha$, the peak of the graph occurs at positive u , leaving a region at small densities in which pgr initially increases with u . (If $\alpha \leq -K$, pgr is strictly decreasing for positive u , and hence qualitatively similar to standard logistic growth.) Weak Allee effects have been shown to exist in nature in both animals [11], [20] and plants [10], [21]. The strong Allee effect relates to $0 < \alpha < K$, and is shown in Figure 2(b). The strong Allee effect has been exhibited in animals [15]–[17], and in plants [18], [19].

The *environmental hostility* parameter h is now defined by

$$h = \frac{\alpha}{K}. \tag{4}$$

For a particular species, the carrying capacity K is highly susceptible to the environment, for example through habitat destruction or resource depletion. The Allee threshold α is less influenced by environmental conditions. Thus, if a given species is considered in different environments, those which are most conducive to the species' survival have a higher K value, and therefore an h closer to zero. In contrast, in harsh environments with limited resources, K will be small, and in the worst case will approach α , meaning that h will be close to one. Thus, h represents the hostility of the environment in relation to the species, with h nearing 1 implying an environment highly hostile to the species, in which growth can occur only in a tiny density range $\alpha < u < K$. Since $-K < \alpha < K$, h satisfies $-1 < h < 1$, with $-1 < h \leq 0$ representing the weak Allee effect. If $h = 0$, the environment is friendly enough so that no negative growth occurs, with more negative h implying that the species has a better growth rate at small densities.

III. SPATIAL DISPERSAL

Let Φ be the natural dispersal rate constant; species which have greater speeds of motion, or which typically move over longer distances, have a larger value of Φ . For animal species,

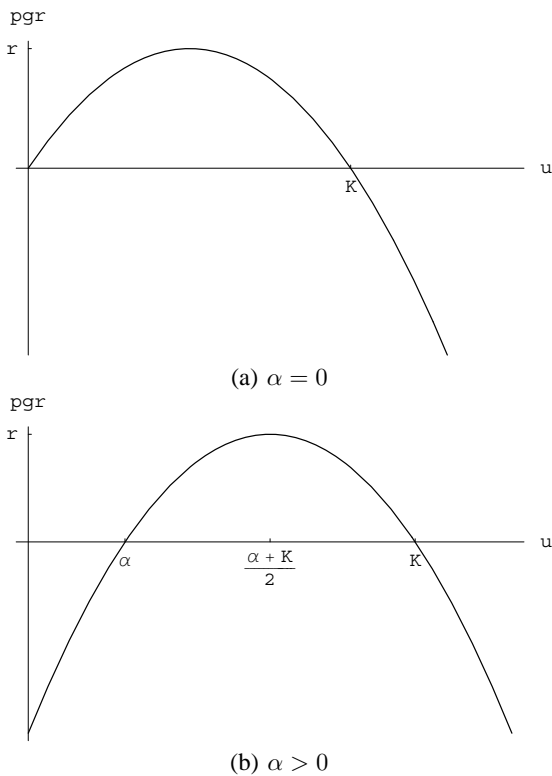


Fig. 2. Graph of the pgr in (3) illustrating the two possible Allee effects: (a) $\alpha = 0$ (a weak Allee effect scenario), and (b) $\alpha > 0$ (strong Allee effect). The normalisation chosen is such that r is the maximum value of the pgr.

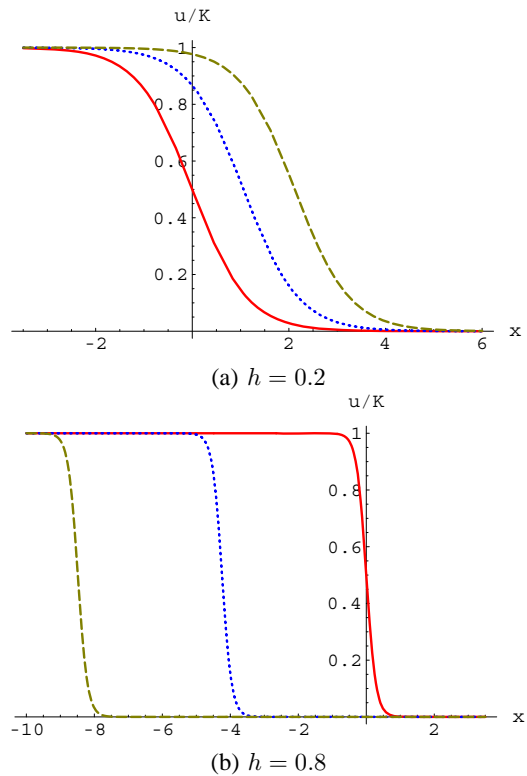


Fig. 3. The density profile in (7) at times $t = 0$ (solid), $t = 1$ (dotted) and $t = 2$ (dashed). Both figures use $r = 1$ and $\Phi = 1$. A spreading population is shown in (a), with $h = 0.2$, while a shrinking (retreating) one is shown in (b), with $h = 0.8$.

Φ can be thought of as the typical speed of an individual, multiplied by the typical distance the individual travels during a typical excursion. For plant species, Φ can be the typical inter-generational time multiplied by the square of the distance away from a plant that its seedling hatches. This situation is analogous to Brownian motion, in which particles (say, perfume particles in air) move randomly at a typical speed, over a typical distance. A statistical averaging of the motions of all particles leads to the fact that the particle concentration at a position x at time t would be given by the standard (Fickian) diffusion equation [3], [4]

$$\frac{\partial u}{\partial t} = \Phi \frac{\partial^2 u}{\partial x^2} \tag{5}$$

If population motion is viewed in this same way, equation (5) can be used to model how a population spreads spatially, by averaging random motions of individuals [24].

Including growth as in (3) and spatial motion as in (5), the governing equations become

$$\frac{\partial u}{\partial t} = \Phi \frac{\partial^2 u}{\partial x^2} + \frac{4r}{(K - \alpha)^2} u (K - u) (u - \alpha) \tag{6}$$

The last term takes this form since the pgr is defined by $(1/u)(\partial u/\partial t)$. Equation (6) is a dimensional equation for the population density $u(x, t)$, in which all ecological parameters are maintained. This is advantageous since, for example, by non-dimensionalising the density by the carrying capacity K ,

the direct influence of K on assorted properties of interest remains hidden. A solution to a standard non-dimensional version of this equation, the Fisher-KPP equation with Nagumo's bistable reaction term, is well-known [4]. An exact solution to (6) was determined by scaling arguments, and verified using the symbolic computational software package Mathematica [27]. The population density evolves according to

$$u(x, t) = \frac{K}{1 + \exp \left[\frac{K}{K - \alpha} \sqrt{\frac{2r}{\Phi}} (x - ct) \right]} \tag{7}$$

in which $\exp[z]$ is used for e^z for improved readability, and the new parameter c is given by

$$c = \frac{K - 2\alpha}{K - \alpha} \sqrt{2\Phi r} \tag{8}$$

The spatial variable x and the time t appear together in (7) in the combination $\xi = x - ct$, enabling $u(x, t)$ to be written as a function of one variable $u(\xi)$. This special feature represents a density profile which remains fixed (with ξ being the variable along the profile), but which moves to the right at speed c . Thus, c is the migration speed of the population as a whole. It is important to observe the distinction between the dispersal rate constant Φ (which is the product of a typical speed and distance travelled by an individual) and the migration speed c (which is the end result of how fast the species as

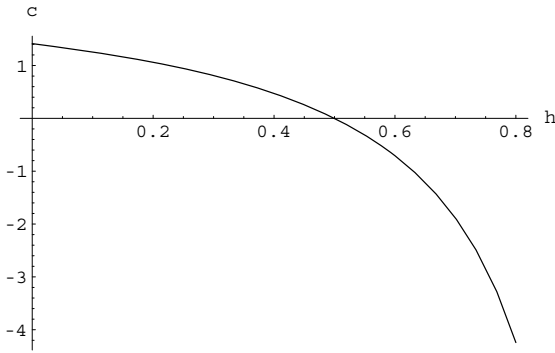


Fig. 4. The speed (10) at which the profile moves, as a function of h . The values $r = 1$ and $\Phi = 1$ are used in this graph.

a whole spreads, having averaged over the random motions of individuals).

The role of the parameters Φ and r will not be extensively analysed, since their effects in (8) and (7) are straightforward. The population density can be rewritten in terms of h as

$$\frac{u(x, t)}{K} = \frac{1}{1 + \exp \left[\frac{1}{1-h} \sqrt{\frac{2r}{\Phi}} (x - ct) \right]} \quad (9)$$

with the speed

$$c = \frac{1 - 2h}{1 - h} \sqrt{2\Phi r}. \quad (10)$$

Both u/K and c can be written in terms of only three fundamental parameters r , Φ and h . The carrying capacity K only plays the role of stretching the density profile vertically. A graph of the normalised density u/K at several different times with $r = 1$, $\Phi = 1$ and $h = 0.2$ appears in Figure 3(a). The front maintains its shape, while moving to the right. Therefore, the population spreads to uninhabited regions, gradually approaching carrying capacity everywhere in the domain. Figure 3(b) also shows u/K , but now with $h = 0.8$. This front moves to the left, resulting in a *shrinking* population which fails to colonise the region. By examining (10), the transition from a spreading to a shrinking population occurs when h drops below $1/2$. If the hostility is exactly $1/2$, the so-called Maxwell point [4], the profile remains stationary, with diffusive dispersal exactly counteracting population growth. While h is 0.3 away from the Maxwell point in either direction in Figure 3, the shrinking population profile moves much faster, as can be obtained by analysing (10) and Figure 4. The fastest spreading rate of $\sqrt{2\Phi r}$ occurs when the hostility is least, as can be seen from (10). For hostilities approaching 1 in (10), c becomes increasingly negative, indicating a population shrinking so rapidly to be almost instantaneously disappearing. The limit $h \rightarrow 1$ applied to (10) verifies that $c \rightarrow -\infty$ in this situation. The ecological implication is that for highly hostile environments, a tiny increase in hostility (through habitat destruction, say) has an inordinate effect on the population shrinking rate. Such situations are particularly vulnerable to rapid extinctions. In contrast, small modifications in hostility for less hostile environments have only marginal effects on population spreading.

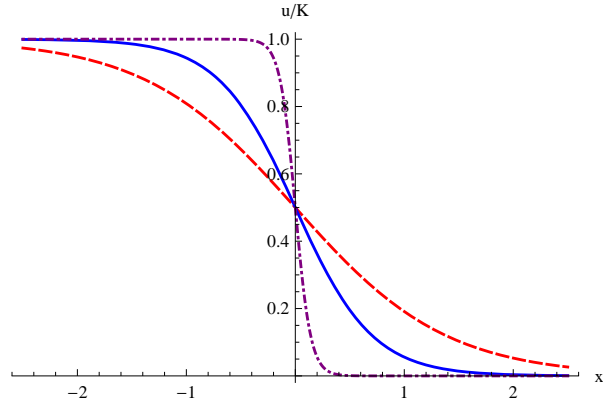


Fig. 5. Density profile u/K at time zero with $r = 1$ and $\Phi = 1$, at different hostilities: $h = 0.02$ (dashed), $h = 0.5$ (solid), and $h = 0.9$ (dot-dash).

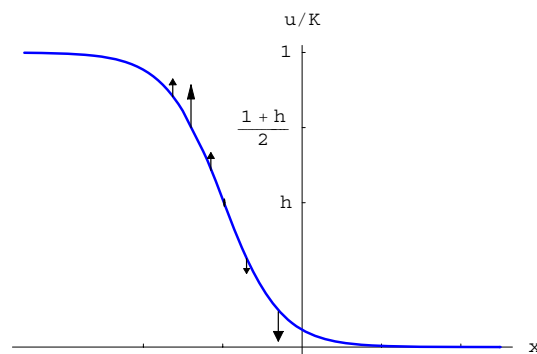


Fig. 6. A cartoon explaining the sharpness of the density profile in relation to hostility. The arrows indicate the direction and size of population growth at that location, due to the Allee effect.

The effect of the hostility on the shape of the population density front (9) is shown in Figure 5. The front gets steeper as the hostility increases, irrespective of whether it is an invading or a retreating front. That is, the boundary between highly populated and sparse regions gets sharper. As $h \rightarrow 1$, the profile approaches the abrupt situation in which the population is at the carrying capacity for $x < 0$, and at zero for $x > 0$. Friendly environments have a slow transition between high density regions to the left, and low density ones to the right, whereas hostile environments possess a stronger clumping of population.

The reason for this is the interaction between the Allee effect and dispersal rate. Figure 6 is a sketch of any one of the curves in Figure 5. The location on the vertical axis labelled as h corresponds to the value $u = \alpha$. If dispersal is ignored, the direction and size of population growth, as obtained from Figure 2(b), is indicated by the arrows in Figure 6. For example, the maximum per capita growth of r occurs at $(1 + h)/2$, which corresponds to the midpoint between α and K in Figure 2(b). There is negative growth when the density is below h . Thus densities to the right of the critical value h exhibit decay, with smaller densities decaying faster, leading to a sharpening of the drop. A similar

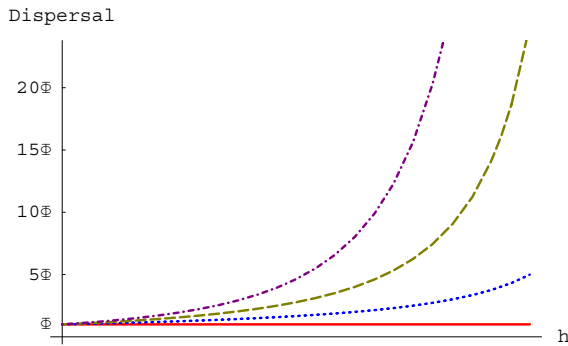


Fig. 7. Dispersal rate as a function of hostility, with the choice $r = 1$, and the axis labelled in factors of the natural dispersal rate Φ . The curves are $n = 0$ (solid), $n = 1$ (dotted), $n = 2$ (dashed) and $n = 3$ (dot-dash).

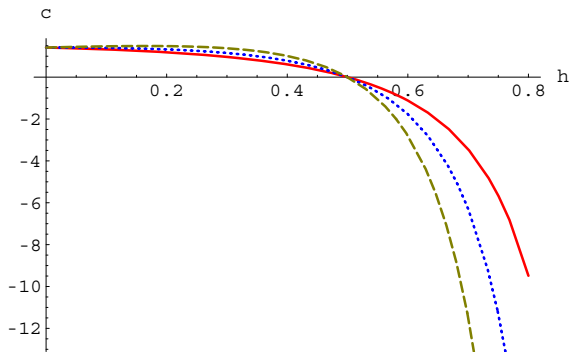


Fig. 8. Spreading speed in the presence of a hostility-influenced dispersal rate, as given in (12). The values $r = 1$ and $\Phi = 1$ are used, and the curves are drawn for $n = 1$ (solid), $n = 2$ (dotted), and $n = 3$ (dashed).

sharpening occurs near the maximum growth value $(1+h)/2$. Hence the profile continues to sharpen. If h is larger, this sharpening is more pronounced, since as h gets pushed up towards 1, the spatial region corresponding to positive growth gets smaller. Now dispersal causes the profile to disperse in the horizontal direction, lessening the sharpening. That is, the Allee effect stretches the profile vertically, while dispersal stretches it horizontally. In this particular solution is that these two effects balance such that the profile maintains its shape.

Recall also that the profile moves to the right (that is, the population spreads) if $h < 1/2$, but moves to the left (retreats) if $h > 1/2$. A plausible explanation for this is also obtainable from Figure 6. If $h < 1/2$, the region of negative growth is “small” in comparison to positive growth. Since dispersal occurs indiscriminately in either direction, more population would venture into regions of positive growth than negative. The profile would then “move up” because of this positive growth, which exhibits itself as the profile moving to the right. To see this, notice that the dotted curve in Figure 3(a) is higher than the solid curve; making the density larger is relatively the same as moving the curve to the right. The opposite occurs if $h > 1/2$.

The above arguments are based on the fact that the dispersal rate Φ is assumed constant. In reality, of course, a species will change its dispersal rate Φ depending on the environmental conditions, as will be examined in the next section.

IV. HOSTILITY-DEPENDENT DISPERSAL

Assuming that the dispersal rate Φ remains constant is an oversimplification, since species will move more when food is in short supply. The standard method of modelling this issue of population pressure is to have the dispersal be a linearly increasing function of u [6], [7], [22], [24], [25], but this leads to considerable mathematical difficulties. A more tractable scenario is presented in this article, in which the species moves more in highly hostile environments. As the hostility approaches 1 (that is, in environments in which the carrying capacity is approximately the same as the number of individuals needed to ensure a positive pgr), individuals are likely to venture far and wide in search of food and

mates, since remaining in one location is not sustainable. As a phenomenological model of this, the dispersal rate will be expressed by

$$\text{Dispersal rate} = \frac{\Phi}{(1-h)^n}, \quad (11)$$

in which n is a non-negative number. Thus, Φ is the dispersal rate the species will use as $h \rightarrow 0$, that is, in the absence of environmental pressure. This is the species' *natural dispersal rate*. The dispersal rate in (11) increases with h , but very slowly in good conditions. As h approaches 1, the dispersal rate increases without bound, as individuals desperately attempt to escape a hopeless environment. This mimics the behaviour suggested by Dwyer and Morris [9], who imputed its necessity having numerically analysed a complicated integro-difference model. Figure 7 shows graphs of the dispersal rate as a function of the hostility, for different values of n . Larger values of n have a dispersal rate which changes more rapidly with h . Putting $n = 0$ in (11) recovers a constant value Φ for the dispersal rate, as was previously studied. Thus, n can be thought of as quantifying the hostility's influence on the dispersal. Species which adapt their motion strongly to the environmental conditions have a larger n , which shall be called the *dispersal adaptability*.

Now, if the dispersal rate is as in (11), the spreading speed (10) becomes

$$c = \frac{1-2h}{(1-h)^{1+n/2}} \sqrt{2\Phi r}. \quad (12)$$

Graphs of the spreading speed c as a function of the hostility appears in Figure 8. Larger values of n produce a larger speed, which is consistent with the fact that individuals are moving more. This behaviour mimics density-dependent diffusion: Almeida et al [7] show in their numerically generated Figure 8 that larger dependence on density increases the wavespeed, and thus the current parameter n has qualitatively the same effect. However, this movement is in different directions depending on h . In the population spreading situation ($h < 1/2$), the population invades new territory more rapidly. In the shrinking situation ($h > 1/2$), the species withdraws from currently populated regions more quickly. In the latter situation, α is

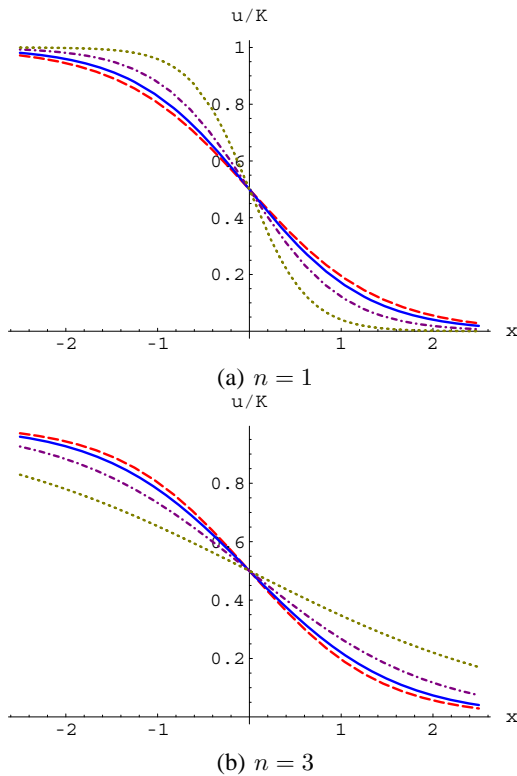


Fig. 9. Density profile u/K under hostility-influenced dispersal, at time zero with $r = 1$ and $\Phi = 1$. The four different hostilities shown are $h = 0.01$ (dashed), $h = 0.2$ (solid), $h = 0.49$ (dot-dash), and $h = 0.8$ (dotted). In (a), $n = 1$ is shown, in which higher hostilities sharpen the profile. In (b), $n = 3$ is shown, and here higher hostilities spread out the profile.

relatively large. Individuals who moved too far to the right encountered regions with population density below the Allee threshold and hence suffered from negative growth, whereas those who moved to the left fell into positive pgr territory. The end result is that the population profile as a whole moves to the left.

The qualitative migration speeds obtained with this model agree with those of Dwyer and Morris [9], who formulated a discrete time resource-consumer Beverton-Holt model in which resources were density-dependent. While the numerical solutions from their model initially exhibited pulsing of the wavefront, it gradually settled (though never actually becoming constant). Their Figure 3 indicates that the wavespeed increases with the consumer growth rate, consistent with (12).

The density profile with hostility-dependent dispersal is given by

$$\frac{u(x, t)}{K} = \frac{1}{1 + \exp \left[\frac{1}{(1-h)^{1-n/2}} \sqrt{\frac{2r}{\Phi}} (x - ct) \right]} \quad (13)$$

If $n = 2$, the profile u/K no longer depends on the hostility. This is a marginal situation, in which the hostility's influence on the dispersal rate counteracts the hostility's direct effect on the shape of the density profile. If n is less than this marginal value of 2 (that is, if the influence of the hostility

on the dispersal rate is fairly small), then the property that smaller hostilities possess a more spread-out density profile is preserved. This is shown in Figure 9(a), where $n = 1$, whose qualitative structure is similar to Figure 5. On the other hand, if $n > 2$, then precisely the opposite occurs; *higher* hostilities imply a more spread out density profile. This is illustrated in Figure 9(b), where $n = 3$. The reason for this reversal is since the dispersal rate, which causes a horizontal stretching of the profile as shown in Figure 6, is now large enough to counteract the vertical stretching resulting from the Allee effect. Since the dispersal rate increases with h , higher hostilities spread the profile out more.

The ecological implication is that if a species is highly adaptable in its dispersal, it will spread out more in hostile environments. Its invasion pattern will possess a gradual transition between the highly populated region behind the "front boundary" and the sparser region in front of it. On the other hand, if the species is less able to adapt its dispersal rate, the more hostile the environment, the sharper the front boundary would be. This observation may be new to the literature on dispersal modelling.

V. CONCLUSIONS

The model that has been considered builds on standard reaction-diffusion models for population spread, but highlights the role of the Allee effect and dispersal rate. The initial results are obtained in terms of the species' maximum attainable per capita growth rate r , natural dispersal rate Φ , Allee threshold α and the environmental carrying capacity K . Most properties could be expressed in terms of three parameters only, by defining the hostility $h = \alpha/K$. Permitting the dispersal rate to be influenced by the environmental hostility leads to an additional fundamental parameter, n , which quantifies the species' ability to adapt its dispersal due to environmental conditions. If so, species invade faster than would have been predicted using a constant dispersal rate, and retreating populations also retreat substantially faster. The relation of the hostility to the sharpness of the density profile as also examined. The increasing of sharpness with hostility (with individuals banding closer together) is a property that reverses if the organism can disperse strongly enough in response to environmental hostility.

This is a simple phenomenological model, whose major advantage is the possibility of obtaining explicit expressions for both the spreading speed and the profile shape. The model does not take into account heterogeneous environmental conditions and habitat selection, or density-dependent diffusion. Nevertheless, some understanding of these issues can be obtained from the model. For example, an invading species spreading into a region whose resources diminish would be expected to slow down, since this is effectively a situation in which h increases, and Figure 4 predicts exactly that. Similarly, the density-dependent pressure faced by a species venturing into a resource-depleted region is related to a greater drive to leave, that is, a dispersal rate which increases with hostility. The model also captures this. The presence of an explicit solution also permits a detailed analysis of the sharpness of the invading

boundary, which is difficult to obtain in more complicated models.

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