Invasions with density-dependent ecological parameters

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ABSTRACT

The speed and the minimum carrying capacity needed for a successful population expansion into new territory are addressed using a reaction-diffusion model. The model is able to encapsulate a rich collection of ecological behaviours, including the Allee effect, resource depletion due to consumption, dispersal adaptation due to population pressure, biological control agents, and a range of breeding suppression mechanisms such as embryonic diapause, delayed development and sperm storage. It is shown how many of these phenomena can be characterised as density-dependence in a few fundamental ecological parameters. With the help of a powerful mathematical technique recently developed by Balasuriya and Gottwald (J. Math. Biol. 61, pp. 377–399, 2010), explicit formulae for the effect on the speed and minimum carrying capacity are obtained.

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1. 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 (Fisher, 1937; Kolmogorov et al., 1937; Skellam, 1951; Gurney and Nisbet, 1998; Murray, 1993; Lewis and Kareiva, 1993; Petrovskii and Li, 2003; Almeida et al., 2006; Lubina and Levin, 1988), discrete models (Murray, 1993; Morris and Dwyer, 1997; Kot et al., 1996; Leung et al., 2004; Keitt et al., 2001), integro-differential (Kot et al., 1996; Dwyer and Morris, 2006; Fagan et al., 2005), and neural nets (Taylor et al., 2004). Different models offer successes in different situations. Including a large variety of biological phenomena within one model, and determining explicit characterisations of how an ecological phenomenon affects the invasion speed, remain significant challenges.

Two main aspects influence the modelling of population spread. The first is the growth rate of the population in the local environment. The most common density-dependence expresses the per capita growth rate (pgr) as a linear decreasing function of

the density, which leads to logistic growth: a sigmoidal curve which has the population approaching the carrying capacity as time progresses (Fisher, 1937; Kolmogorov et al., 1937; Skellam, 1951). As a next correction, the Allee (1938) effect incorporates an increase in the pgr curve at small densities (Stephens et al., 1999; Stephens and Sutherland, 1999; Courchamp et al., 1999; Amarasekare, 1998). A common explanation for this is that when the density is too small, individuals are spread too thinly to be able to find mates successfully. Stephens and Sutherland (1999) and Keitt et al. (2001) summarise other reasons which can lead to the Allee effect, such as diminished anti-predator vigilance and reduced genetic diversity. The Allee effect has been demonstrated in gypsy moths (Johnson et al., 2006), bighorn sheep (Berger, 1990), African wild dogs (Courchamp and MacDonald, 2001), annual plants (Groom, 1998; Lamont et al., 1993), flour beetles (Allee, 1938), zebra mussels (Leung et al., 2004), the California channel island fox (Angulo et al., 2007) and smooth cordgrass (Davis et al., 2004).

The second aspect which influences how population spread is modelled is how dispersal is included. Dispersal relates to how individuals or propagules 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 (Taylor et al., 2004; Davis et al., 2004; Leung et al., 2004), continuous-time branching processes

(Schreiber and Lloyd-Smith, 2009), diffusion equations which incorporate the randomised individual motions into a deterministic model for the collective density (Fisher, 1937; Kolmogorov et al., 1937; Skellam, 1951; Gurney and Nisbet, 1998; Lewis and Kareiva, 1993; Petrovskii and Li, 2003; Lubina and Levin, 1988; Balasuriya and Gottwald, 2010), or integro-differential models with non-uniform dispersal (Kot et al., 1996; Dwyer and Morris, 2006).

An important aspect of biological invasions is the interaction between the invading species and the already existing species in the environment. This article, however, focusses on the more limited situation of a single species populating new territories, ignoring such interactions. The term "invasion" when used in this context represents a population successfully expanding its range. There is a well-established partial differential equation model (Gurney and Nisbet, 1998; Murray, 1993) which builds on classical models of diffusive spread (Fisher, 1937; Kolmogorov et al., 1937; Skellam, 1951) to include Allee dynamics. By suitably dimensionalising this model, it is possible to quantify the roles of important ecological parameters such as the carrying capacity, Allee threshold, maximum fertility and dispersal rate on speed of expansion of the population. (This shall be presented in Section 2.1.) However, there is strong evidence that each of these ecological parameters is not constant, implying that the above model is too simplistic. Firstly, the carrying capacity of an environment does not remain static; the presence of a large number of individuals reduces the local carrying capacity through resource depletion. Methods of incorporating this into models include discrete resource-dependent dispersal models (Morris and Dwyer, 1997; Fagan et al., 2005), and a host of habitat selection models (see the introduction of Morris and Diffendorfer, 2004 for a review).

Secondly, some species suppress their fertility rate in situations in which a large number of individuals is present in comparison to the resource availability. Embryonic diapause (delayed implantation of the embryo until favourable environmental conditions are available) is one such strategy, regularly used across seven orders of animals, including over 100 mammals (Renfree and Shaw, 2000). Delayed fertilisation (sperm storage) (Birkhead and Møller, 1993; Neubaum and Wolfner, 1999) is another, and is widespread in insects, reptiles and birds, and unusual in mammals except for bats (Wang et al., 2008). A diminished proportion of females coming into œstrus (Williams and Newsome, 1991) is another tactic. Permitting a large proportion of eggs to remain ephippial (dormant) in limited food situations is yet another approach (Slusarczyk, 2001). The concept of delayed development (MacArthur and Wilson, 1967; Szewczyk et al., 2006), in which a species forgoes short-time population growth in favour of a longer reproductive cycle in order to best utilise available resources, is yet another form of breeding suppression, which in fact encapsulates some of the strategies described above. While the methods described above has very different biological characteristics, they all have a common mathematical response: the difference between the birth and death rates diminishes at higher densities. This density-dependent fertility rate shall be called "breeding suppression", a scenario which can also be argued to occur in the presence of biological control agents (Louda et al., 1997; Fagan et al., 2002). Hence, rationalising the fertility rate as density-dependent is one method of conceptualising both breeding suppression and biological control.

Thirdly, a species is also likely to adapt its dispersal rate depending on environmental conditions. A natural method of utilising available resources best would be for there to be increased dispersal away from highly dense regions of population (a notable exception to this being humans). This implies that the dispersal (diffusion) rate changes with local population density,

examined in various ways in Gurney and Nisbet (1975), Shigesada et al. (1979), Petrovskii and Li (2003), Almeida et al. (2006), Balasuriya and Gottwald (2010), Dwyer and Morris (2006), and Amarasekare (2004). Given the mathematical difficulty of this situation, investigators are usually confined to using numerical methods to calculate the resulting speed of population expansion.

The above examples show that the principal ecological parameters (carrying capacity, maximum fertility, dispersal rate) must in reality be treated as density-dependent. If so, there are *no* currently existing methods of incorporating their effects on invasion speeds. This study remedies this situation, by determining such explicit formulae under the understanding that the density-independent effects are small in comparison to the main effects. The perturbative method used in based on a recent mathematical development by Balasuriya and Gottwald (2010). Surprisingly straightforward expressions for the role of density-dependence is obtained in each of the situations corresponding to resource depletion, breeding suppression and population pressure, in spite of the fact that the governing equations are formidably nonlinear. Therefore, this article is probably the first to explicitly enable incorporation of effects such as embryonic diapause, delayed development, resource depletion and population pressure into the invasion speed. The derived formulae are expected to form a new benchmark for quantifying invasion speeds in population spreading models, and suggest new avenues for experimentalists to investigate the role of biological phenomena on species spreading.

For a given species to successfully invade new territory, a minimum carrying capacity would seem to be necessary. The expressions obtained in this article also enable a determination of this minimum carrying capacity for species which have adaptive strategies such as breeding suppression and density-driven dispersal. As such, this study provides a comprehensive analysis of population spreading based on continuous (partial differential equation) models, with a detailed investigation of the relevant ecological parameters. A rich range of different behaviours is captured, thereby allowing the model to be used across fauna, flora, and many genera with judiciously chosen parameter values. The mathematical methods introduced in this article have enabled this detailed investigation, and provide a new technique potentially adaptable to diverse ecological models.

2. Model and methods

2.1. Base model

Let u be the population density (population per unit habitat length) of a species, modelled by Courchamp et al. (1999), Murray (1993), and Lewis and Kareiva (1993)

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

in which L is a positive normalising constant and K is the carrying capacity. The situation $\alpha \geq K$ is prohibited, since then K becomes unstable and loses its ecological meaning. The Allee (1938) effect, in which the pgr has a positive relationship to the density at small densities, is exhibited when $-K < \alpha < K$. If $0 < \alpha < K$, the species exhibits the strong Allee effect, with α representing the Allee threshold below which pgr is negative. Such has been observed in animals (Johnson et al., 2006; Berger, 1990; Courchamp and MacDonald, 2001) and in plants (Groom, 1998; Lamont et al., 1993). Choosing α in the range $-K < \alpha \leq 0$ leads to a model of the weak Allee effect, in which pgr increases with u at small densities

but is not negative. Both fauna (Allee, 1938; Angulo et al., 2007) and flora (Davis et al., 2004; Taylor et al., 2004) examples of this effect have been observed. If $\alpha \leq -K$, pgr is a strictly decreasing function of density for all (positive) densities: this models the classical "non-Allee" situation. The normalising factor L in (1) can be chosen in many ways; see Lewis and Kareiva (1993) for a discussion. Here, it shall be chosen to relate to a parameter of potential ecological significance: the species' maximum attainable per capita growth rate r, henceforth called the "maximum fertility". This choice for L was also made by Lewis and Kareiva (1993). Differentiating (1) with respect to u and setting to zero indicates that the maximum pgr occurs at $u = (K+\alpha)/2$, and setting pgr at this value equal to r gives the condition $L = 4K\alpha r/(K-\alpha)^2$. Hence

$$\text{pgr} = \frac{4K\alpha}{(K-\alpha)^2} r \left(1 - \frac{u}{K}\right)\left(\frac{u}{\alpha} - 1\right) = \frac{4r}{(K-\alpha)^2}(K-u)(u-\alpha). \qquad (2)$$

Define h as

$$h = \frac{\alpha}{K}. \qquad (3)$$

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. Then, growth can occur only in a tiny density range $\alpha < u < K$, and thus the environment is not very suitable for the species. Observe that $0 < h < 1$ represents the strong Allee effect, $-1 < h \leq 0$ the weak Allee effect, and if $h \leq -1$, the Allee effect is absent for that environment. Thus, h represents the lack of suitability, or *hostility*, of the environment to that particular species.

Next, spatial dispersal is included. 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, 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. A statistical averaging of the motions of all individuals leads to a standard diffusive term in the dynamics (Fisher, 1937; Kolmogorov et al., 1937; Skellam, 1951; Gurney and Nisbet, 1998, 1975; Murray, 1993; Lubina and Levin, 1988), and hence the density obeys

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

Incorporating diffusion in this way along with a growth rate is also a standard approach in cell proliferation in growing tissues (e.g. Binder and Landman, 2009; Trewenack and Landman, 2009), to which the current analysis is also potentially applicable. Eq. (4) is a *dimensional* equation for the population density $u(x,t)$, in which all ecological parameters are maintained. Utilising a well-known solution (Murray, 1993) to a standard non-dimensional version of this equation, the Fisher-KPP equation with Nagumo's bistable reaction term, an exact solution can be found. The population density evolves according to

$$u_0(x,t) = \frac{K}{1 + \exp\left[\frac{K}{K-\alpha}\sqrt{\frac{2r}{\Phi}}(x - c_0 t)\right]} \qquad (5)$$

in which the new parameter c_0 is given by

$$c_0 = \frac{K-2\alpha}{K-\alpha}\sqrt{2\Phi r}. \qquad (6)$$

The spatial variable x and the time t appear together in (5) in the combination $\xi = x - c_0 t$, enabling $u_0(x,t)$ to be written as a function of one variable $u_0(\xi)$. 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_0. Thus, c_0 is the migration speed of the population as a whole, due to the averaged motions of individuals coupled with population growth. The structure of this solution, together with its limitations, will be presented in more detail under the results section (Section 3). At this point, all the ecological parameters (K, α, r and Φ) are *constants* in this base model—they are density-independent.

2.2. Density-dependent parameters

This section will argue why conceptualising the fundamental parameters as density-dependent is an interesting method of extending the model to include the variety of effects such as resource depletion, embryonic diapause, delayed development and population pressure that have been discussed in Section 1.

First, resource depletion due to consumption will be addressed. The available resources at a given location will depreciate with more individuals present. Therefore, the carrying capacity needs to be a decreasing function of the population density. In other words, the value of pgr which is calculated for a larger value of u needs to be sampled from a pgr curve in Eq. (2), in which K is *smaller* than what would be used for a smaller u value. Therefore, a *family* of values of K need to be used in (2). To a first approximation, the carrying capacity will be modelled by a linearly decreasing function of the density, leading to the pgr

$$\text{pgr} = \frac{4r}{([K-\varepsilon_k u]-\alpha)^2}([K-\varepsilon_k u]-u)(u-\alpha) \qquad (7)$$

in which the replacement

$$K \to K\left[1 - \varepsilon_k \frac{u}{K}\right] = K - \varepsilon_k u$$

has been made to (2). The new carrying capacity, $K - \varepsilon_k u$, possesses a small positive parameter ε_k which incorporates the effect of the density on the carrying capacity. Therefore, $-\varepsilon_k$ represents the rate of change (elasticity) of the carrying capacity with respect to the density. Species which strip their habitat bare will have a larger value of ε_k, while those with more circumspect consumption patterns will have an ε_k near 0. The constant K retains its previous constant role, and is the carrying capacity in the absence of a density-dependent effect.

Note that $K - \varepsilon_k u$ has been replaced for K in two places in (2), one of which is part of the "normalising factor" which ensures that r is the highest pgr attainable by the species. If only the second K were replaced (as would occur if care is not taken to elucidate the role of the multiplicative normalising factor in the pgr), r would no longer be the maximum fertility for the species. In order to isolate the roles of the fundamental parameters r, Φ and h, it is thus important to preserve the ecological meanings of the unaltered parameters. The new pgr in (7) is no longer quadratic, and loses ecological meaning at high densities; however, within and near the range $0 < u < K$, the pgr has the appropriate profile, and hence the approximation is valid near the wavefront solution. A comparison of the pgr in this situation (dashed curve) with the standard form (solid curve) is given in Fig. 1, with the choice $\varepsilon_k = 0.2$. For small values of ε_k (that is, when considering consumption-driven resource depletion as a smaller effect in
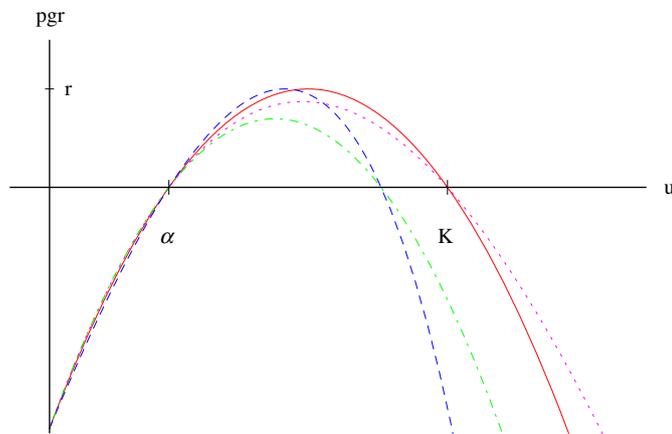
Fig. 1. The per capita growth rate (pgr) as a function of density: the standard situation ((2), solid), density-dependent carrying capacity ((7), dashed), and density-dependent maximum fertility ((8), dotted). The dot-dashed curve indicates an incorrect formulation, as described in the text. (Produced using $K = 1$, $\alpha = 0.3$, $r = 1$ and all ε values equalling 0.2.)

comparison to the effects in the base model), the pgr curve retains the qualitative form for the pgr in (7) to be ecologically sensible.

Note that the other ecological parameters r (maximum fertility) and α (Allee threshold) retain their original values correct to order ε_k by replacing K in both places in (2), as is also clear from Fig. 1. If the replacement was not done in the normalising factor, the maximum fertility would lose its leading-order meaning; this is illustrated with the dot-dashed curve in Fig. 1. This curve has a considerably smaller maximum fertility than r, which has therefore lost its original meaning, while the (correct) dashed curve has a maximum fertility which is still near r. Retaining the meanings is an essential part of this model, since examining the effects of density-dependence on each of the parameters *in isolation* is important in determining the role of each on the invasion speed.

Next, consider mechanisms such as embryonic diapause (Renfree and Shaw, 2000), delayed fertilisation (Neubaum and Wolfner, 1999) and delayed development (MacArthur and Wilson, 1967), all of which lead to the breeding rate being suppressed. Such suppression occurs in situations in which the available resources are deemed insufficient for the current population; in effect, a greater suppression occurs when u/K is large. Notice that this approach is equally applicable to modelling the presence of a biological control agent (Louda et al., 1997; Fagan et al., 2002), whose diminishing effect might be considered to be proportional to the density. This diminished fertility can be modelled though the replacement

$$r \to r\left(1 - \varepsilon_r \frac{u}{K}\right)$$

in (4), for a small non-dimensional positive parameter ε_r. Here, $-\varepsilon_r$ now represents the (scaled) elasticity of the maximum fertility with respect to density. Depending on the species and the specific biological phenomenon being examined, ε_r will take on different values; species which exhibit a large rate of embryonic diapause, for example, will have a relatively larger value of ε_r, while those with no embryonic diapause will have $\varepsilon_r = 0$. The resulting pgr function is now

$$\text{pgr} = \frac{4r}{K(K-\alpha)^2}(K-u)(u-\alpha)(K-\varepsilon_r u). \tag{8}$$

The change in the pgr curve is indicated in Fig. 1, by the dotted curve, which again possesses the correct qualitative structure for

small ε_r. Note that the maximum fertility, occurring near the density value $(\alpha + K)/2$, has now been diminished by an order-ε_r. The ecological meanings of K and α remain valid, even to order ε_r, as can be seen from where the pgr curve intersects the u-axis.

Population pressure, in which individuals tend to be driven away from regions of large population densities, is the next effect that will be considered. This can be thought of as modelling a resource-dependent dispersal rate (Dwyer and Morris, 2006; Kot et al., 1996), since it is the lower resources in the highly populated regions which causes this exodus. This behaviour implies that the dispersal rate is an increasing function of the density. In implementing this density-dependence, care needs to be taken to consider instead of (4) the model

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left[\Phi \frac{\partial u}{\partial x}\right] + \frac{4r}{(K-\alpha)^2}u(K-u)(u-\alpha) \tag{9}$$

in which Φ is u-dependent (Murray, 1993; Gurney and Nisbet, 1998; Gilding and Kersner, 2004; Malaguti et al., 2004). To model population pressure, the replacement

$$\Phi \to \Phi\left[1 + \varepsilon_\phi \frac{u}{K}\right], \tag{10}$$

needs to be made in (9). Having the dispersal rate as a linearly increasing function of u is a first-approximation which is common to many models (Gurney and Nisbet, 1975; Shigesada et al., 1979; Petrovskii and Li, 2003; Almeida et al., 2006; Balasuriya and Gottwald, 2010), but is nevertheless mathematically difficult. (This corresponds to the $s = 0$ scenario of Amarasekare (2004), who describes more general dependence in an ordinary differential equations setting with competition.) The small positive parameter ε_ϕ represents the sensitivity of the given species to population pressure, and the scaling by u/K has been chosen to ensure that ε_ϕ, in keeping with the other ε−values, is non-dimensional. Thus, Φ retains its meaning as the "natural" dispersal rate (which is constant), and the other ecological parameters are not affected by this replacement.

The final ecological parameter whose density-dependence has not been conceptualised above is α. There is little ecological motivation for doing this. As will be argued later, it is also mathematically irrelevant, since the resulting effects can be imputed from the density-dependent K situation.

The above density-dependent ecological parameters result in (4) becoming highly nonlinear, and mathematically difficult. Therefore, it is not possible to determine explicit solutions, and thereby the invasion speed, as a result of including these effects. Nevertheless, the above effects are to be thought of as *small* in comparison to the base model; that is, all the ε s are small positive parameters—the modifications to (4) are *perturbative* in nature. Hence, a perturbative method for determining the invasion speed is in order. The theory associated with such a technique is outlined in Appendix A, and is based on the theoretical development in Balasuriya and Gottwald (2010). Remarkably simple and informative results emerge from this complicated process, and are described in Section 3.

3. Results

3.1. Density-independent parameters

The behaviour of the base model described in Section 2.1 is first established. This model represents a single established propagule, invading from left to right; for pre-established multi-propagule studies, see the numerical work of Schreiber and Lloyd-Smith (2009). The explicit solution appears in (5) and (6). Fig. 2 shows the density profile at four different values of h. The profiles

are sharper at larger hostilities; species boundaries are more pronounced in environments less conducive to the species in the presence of the Allee effect. Since c_0 is the speed that this profile moves to the *right*, (6) indicates that only those situations in which $\alpha < K/2$ (that is, $h < 1/2$) correspond to an *invading* species. If $\alpha = K/2$, the profile is stationary (the so-called Maxwell point), whereas for $\alpha < K/2$, the species retreats (the invasion fails, or the range contracts). Hence, the invasive (successfully colonising) situation is $\alpha < K/2$, or $h < 1/2$.

The solution can be rewritten in terms of the hostility as

$$\frac{u_0(x,t)}{K} = \frac{1}{1 + \exp\left[\frac{1}{1-h}\sqrt{\frac{2r}{\Phi}}(x-c_0 t)\right]}, \tag{11}$$

with the speed

$$c_0 = \frac{1-2h}{1-h}\sqrt{2\Phi r}. \tag{12}$$

Both u/K and c_0 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. In essence, there are only three fundamental ecological parameters in the problem: α/K, r and Φ. This is the mathematical reason why it is unnecessary to separately examine the effect of density-dependence in α once that of K has been studied.

A technical point regarding the weak Allee ($-K < \alpha \leq 0$) and the absence of Allee effect ($\alpha \leq -K$) situations are in order. While the solution in (5) and (6) does work in this situation, there also exist *other* solutions with slightly distorted density profiles, each moving at different speeds (Murray, 1993). Different initial conditions will evolve into each of the different solutions. As in the standard Fisher-KPP equation (Fisher, 1937; Kolmogorov et al., 1937; Skellam, 1951) with the last term in (4) being proportional to the logistic term $u(K-u)$, such a system possesses an *unstable* equilibrium at $u=0$. Having both the "front" and "back" of the travelling wave (the right and left, respectively, of Fig. 2) be associated with *stable* equilibria would seem to be necessary for profile-preserving invasion. A similar point in favour of the Beverton–Holt model for discrete systems, rather than Ricker or logistic, has been made by Dwyer and Morris (2006). Stability of both $u=0$ and K only occurs if $\alpha > 0$, that is, in the strong Allee situation. Thus, it is unreasonable to use (6) as an expression for

Fig. 2. Density profile u_0/K at time zero with $r=1$ and $\Phi=1$, at four different hostilities: $h=0.01$ (dashed), $h=0.2$ (solid), $h=0.49$ (dot-dash), and $h=0.8$ (dotted).

the spreading speed if $\alpha \leq 0$. The remainder of the analysis will therefore be confined to strong Allee effects in which $0 < \alpha < K$ ($0 < h < 1$).

3.2. Consumption-driven resource depletion

Under resource depletion due to consumption by the species, the pgr is given by (7). The corresponding dynamics are given by

$$\frac{\partial u}{\partial t} = \Phi\frac{\partial^2 u}{\partial x^2} + \frac{4r}{([K-\varepsilon_k u]-\alpha)^2}u([K-\varepsilon_k u]-u)(u-\alpha). \tag{13}$$

When $\varepsilon_k = 0$, (13) collapses to (4), but for non-zero ε_k (13) cannot be solved. Since ε_k is small, a perturbative expansion of the invasion speed, which shall be called c_k in this density-dependent carrying capacity situation, is in order. The speed can be written as

$$c_k = c_0 + \varepsilon_k c_{1k}. \tag{14}$$

Since $c_{1k} = (c_k - c_0)/(\varepsilon_k - 0)$ from (14), c_{ik} is the rate of change of the speed in relation to the consumption parameter ε_k. (More precisely, the reader familiar with Taylor series will notice that $c_{1k} = \partial c_k/\partial\varepsilon_k|_{\varepsilon_k = 0}$.) Since ε_k is positive, (14) indicates that another way of thinking of c_{1k} is as the addition (multiplied by the consumption parameter) to the speed due to the influence of consumption-driven resource depletion. Now, after considerable mathematical work as described in Appendix B, it is possible to obtain the fact that c_{1k} has the astonishingly simple form

$$c_{1k} = -\frac{\sqrt{2r\Phi}}{10}\frac{(K+\alpha)(K+2\alpha)}{(K-\alpha)^2} = -\frac{\sqrt{2r\Phi}}{10}\frac{(1+h)(1+2h)}{(1-h)^2}. \tag{15}$$

It is noted that c_{1k} can be expressed entirely in terms of the fundamental parameters r, Φ and $h = \alpha/K$, highlighting that K and α affect invasions not independently, but based on their ratio. Since c_{1k} is negative for all relevant parameters, the spreading acquires a leftwards component. Thus, invasions ($h < 1/2$) slow down due to the influence of consumption. If the species was retreating (if $h > 1/2$), the implication is that the retreating speed increases. In either case, the species suffers as a result of consumption-drive resource depletion diminishing the growth rate. Note from (15) that in highly hostile environments (h near to 1), a large leftwards speed results from this effect. Hence resource depletion has a much larger effect when the available resources are small anyway—a not surprising result.

Utilising (14), the full invasion speed c_k associated with (13) is given by

$$c_k = \sqrt{2r\Phi}\frac{K-2\alpha}{K-\alpha} - \varepsilon_k\frac{\sqrt{2r\Phi}}{10}\frac{(K+\alpha)(K+2\alpha)}{(K-\alpha)^2}$$

$$= \frac{\sqrt{2r\Phi}}{1-h}\left[1-2h-\frac{\varepsilon_r}{10}\frac{(1+h)(1+2h)}{1-h}\right]. \tag{16}$$

A graph of c_k as a function of h is presented in Fig. 3, in which r and Φ are set equal to 1, and several different ε_k values are used. Species which have a larger consumption parameter ε_k retreat faster than species whose influence on their environmental resources are less. Since the variation of c_k with respect to the maximum fertility and dispersal rate only occur in the straight-forward combination $\sqrt{2r\Phi}$, exactly as in the base model, an additional graph on their influence is unnecessary.

Eq. (16) also enables the determination of the Maxwell point corresponding to the species being stationary. In the base model (6), this occurs when $h = \frac{1}{2}$; the species' growth and dispersal rates conspire to ensure that the species collectively neither invades nor retreats. When including the effect of resource depletion due to consumption, this stationary situation now occurs at a
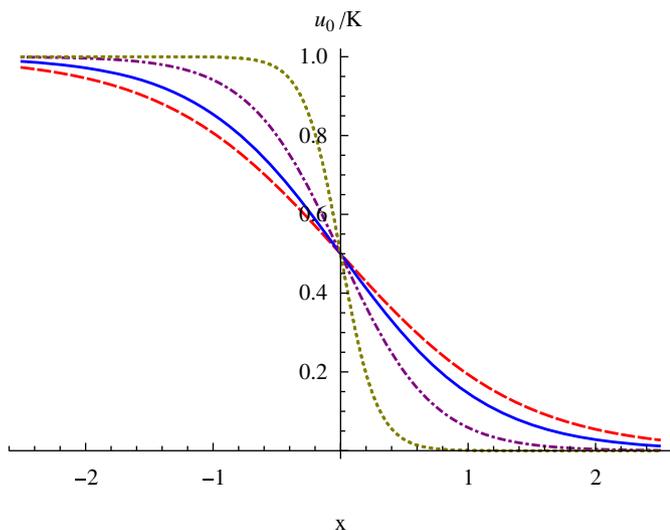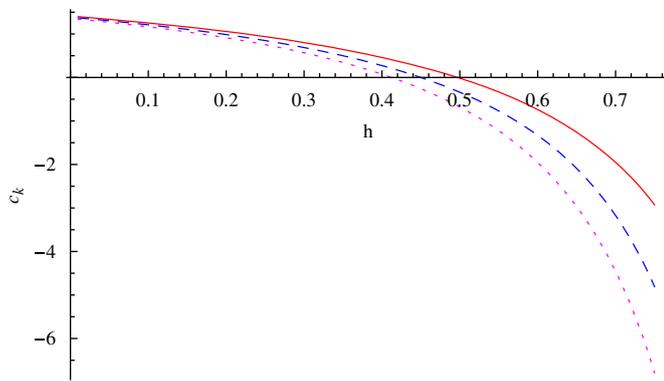
Fig. 3. Invasion speed under resource depletion, as given by (16), as a function of $h = \alpha/K$. Here, $r = 1$, $\Phi = 1$, and $\varepsilon_k = 0.01$ (solid), 0.2 (dashed) and 0.4 (dotted).
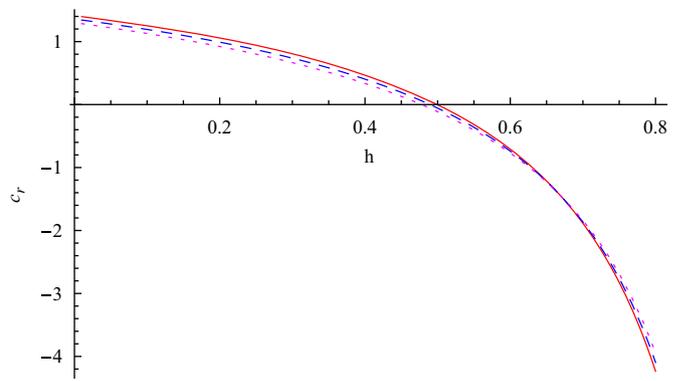

Fig. 4. Invasion speed c_r under breeding suppression, as given by (21), as a function of $h = \alpha/K$. Here, $r = 1$, $\Phi = 1$, and $\varepsilon_r = 0.01$ (solid), 0.2 (dashed) and 0.4 (dotted).

hostility slightly smaller than $\frac{1}{2}$. By setting (16) to zero, it can be shown that this corresponds to

$$\overline{h} = \tfrac{1}{2} - \tfrac{3}{10}\varepsilon_k.$$

The overbar is used to indicate the specialised value of h corresponding to the transition between a successfully invading and a retreating situation. This implies that the minimum carrying capacity, $\overline{K}$, needed for a successful invasion has now risen to

$$\overline{K} = 2\alpha + \tfrac{6}{5}\alpha\varepsilon_k, \tag{17}$$

and both these results are derived in Appendix E. This represents an additional carrying capacity of $1.2\alpha\varepsilon_k$ needed for a species to be able to invade new territory, which increases with both ε_k and α. Therefore, the inclusion of consumption-driven resource depletion represents an increase in this "minimal" carrying capacity, which is also influenced more for "delicate" species which have larger Allee thresholds.

3.3. Breeding suppression

Next, consider the wide variety of behaviours which have been given the term "breeding suppression" in this article. The pgr is therefore given by (8), and such a suppression of the maximum fertility can also be thought of as a method of incorporating the affect of certain types of biological control agents. The dynamics can be written in the form

$$\frac{\partial u}{\partial t} = \Phi\frac{\partial^2 u}{\partial x^2} + \frac{4r\left(1 - \varepsilon_r\frac{u}{K}\right)}{(K-\alpha)^2} u(K-u)(u-\alpha). \tag{18}$$

As before, think of expanding the corresponding invasion speed c_r in terms of the small parameter ε_r, which in this case would take the form

$$c_r = c_0 + \varepsilon_r c_{1r} \tag{19}$$

in which c_{1r} represents the rate of change of the speed with respect to the breeding suppression parameter ε_r. It is shown in Appendix D that

$$c_{1r} = \frac{\sqrt{2r\Phi}}{10}\frac{(K+2\alpha)(3\alpha-2K)}{K(K-\alpha)} = \frac{\sqrt{2r\Phi}}{10}\frac{(1+2h)(3h-2)}{(1-h)}. \tag{20}$$

In the invading situation $\alpha < K/2$, c_{1r} is negative, meaning that the inclusion of this effect slows down the invasion speed. The suppression of breeding in the higher-density regions decreases the numbers available to venture into new regions. If $K/2 < \alpha < 2K/3$, c_{1r} contributes to the negativity of c_0, and the populations retreats even faster. The interesting phenomenon is in the situation $\alpha > 2K/3$, in which c_{1r} is positive. Breeding suppression

slows down the retreat of the species in highly hostile environments. By producing fewer offspring the species reduces the probability of increasing the population beyond the carrying capacity, which would result in a rapid diminishing of the population. Effectively, it is possible to increase the collective lifespan of a species in a hostile environment by suppressing breeding. This implication from the model is in conformity with experiments on the nematode *Cænorhabditis elegans*, whose life history "maximises the efficiency of exploitation of the carrying capacity of the environment" (Szewczyk et al., 2006).

The full invasion speed is given by

$$\begin{aligned} c_r &= \sqrt{2r\Phi}\frac{K-2\alpha}{K-\alpha} + \varepsilon_r\frac{\sqrt{2r\Phi}}{10}\frac{(K+\alpha)(3\alpha-2K)}{K(K-\alpha)} \\ &= \frac{\sqrt{2r\Phi}}{1-h}\left[1-2h+\frac{\varepsilon_r}{10}(1+2h)(3h-2)\right]. \end{aligned} \tag{21}$$

A graph of this speed is given in Fig. 4, and illustrates the described features.

It must be emphasised that breeding suppression in the wild is strongly linked to seasonality, which is not per se included in the current model. If, however, the diffusive time-scale is large in comparison to a year, then the seasonality can be thought of as being present in the model, but "smeared out" at the time-scale of investigation. Hence the above results remain valid, though not for species with very long breeding suppression regimes, such as some reptiles who store sperm for years (Neubaum and Wolfner, 1999). The observation that domesticated animals, in contrast to wild animals of the same species, lose seasonally varying reproductive behaviour (Santiago-Moreno et al., 2006) is further evidence that understanding breeding suppression purely as a function of diminished resources is important. To truly incorporate seasonal effects in the present model, it would be necessary as a first step to have a time-dependent carrying capacity. Inclusion of such time-dependence destroys the possibility of a constant invasion speed; the front then invades in a pulsating fashion, with the pulsating time-scale being governed by the seasonality. This situation is mathematically difficult, and is a future area of investigation (in which the appropriate theoretical methods need to be developed).

3.4. Population pressure

Finally, the modification in the invasion speed due to the presence of population pressure is investigated. Suppose the replacement (10) quantifying a dispersal rate which increases linearly with density is applied to (9). This leads to the

dynamics

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left[\left(\Phi + \Phi\varepsilon_\phi \frac{u}{K}\right)\frac{\partial u}{\partial x}\right] + \frac{4r}{(K-\alpha)^2}u(K-u)(u-\alpha),\qquad(22)$$

which is significantly a more difficult partial differential equation than the previous situations. Nevertheless, it is perturbative in nature, and the expansion

$$c_\phi = c_0 + \varepsilon_\phi c_{1\phi},\qquad(23)$$

for the speed c_ϕ is possible. Here, $c_{1\phi}$ is the rate of change (elasticity) of the speed with respect to the dispersal sensitivity parameter ε_ϕ. It is shown in Appendix F that

$$c_{1\phi} = \frac{\sqrt{2r\Phi}}{10}\frac{(K+2\alpha)(2K-3\alpha)}{K(K-\alpha)} = \frac{\sqrt{2r\Phi}}{10}\frac{(1+2h)(2-3h)}{(1-h)}.\qquad(24)$$

While coming from a quite different calculation, $c_{1\phi}$ above is exactly the negative of c_{1r} calculated for breeding suppression as given in (20). Thus, in the invading $(0 < h < 1/2)$ situation, population pressure increases the speed of invasion. This makes ecological sense, since the population in the higher density areas at the back end of the invasion will disperse more, leading to an increased population in previously lower density areas. This prediction from (24) agrees with results from a different mathematical models; the resource-dependent discrete dispersal model of Dwyer and Morris (2006) possesses exactly this behaviour as shown in their Fig. 2A, and the spatially heterogeneous probabilistic model of Schreiber and Lloyd-Smith (2009) numerically shows that less hostile environments have improved invasion success when the natural dispersal rate is increased. Eq. (24) also shows that in retreating populations with intermediate hostilities $(K/2 < \alpha < 3K/2)$, population pressure reduces the speed of retreat, whereas in retreating situations at high hostility $(3K/2 < \alpha < K)$, the retreat hastens. This last fact is particularly interesting, since population pressure might be expected to always cause motion from higher to lower densities (from left to right) on average. An explanation for this is that the large numbers of individuals who progress towards the right because of population pressure succumb quickly since the pgr is highly negative, whereas the smaller number of individuals who went to the left fared better since the pgr is positive within the range $\alpha < u < K$. Therefore, population pressure actually quickens the retreat of a prospective invasion if the hostility is sufficiently large.

The full invasion speed is given from (23) as

$$\begin{aligned}c_\phi &= \sqrt{2r\Phi}\frac{K-2\alpha}{K-\alpha} + \varepsilon_\phi\frac{\sqrt{2r\Phi}}{10}\frac{(K+\alpha)(2K-3\alpha)}{K(K-\alpha)}\\&= \frac{\sqrt{2r\Phi}}{1-h}\left[1-2h+\frac{\varepsilon_\phi}{10}(1+2h)(2-3h)\right].\end{aligned}\qquad(25)$$

In this case, it can be shown that the hostility at which the species is stationary is now slightly larger that $\frac{1}{2}$, and is

$$\bar{h} = \frac{1}{2} + \frac{1}{20}\varepsilon_\phi.$$

This implies that the minimum natural carrying capacity needed from an environment to sustain an invasion is

$$\bar{K} = 2\alpha - \frac{1}{5}\alpha\varepsilon_\phi.\qquad(26)$$

The calculations leading to these results are given in Appendix G. Thus, the minimum carrying capacity for an invasion to be successful has diminished from 2α by an amount $0.2\alpha\varepsilon_\phi$ due to the population pressure effect. The species' adaptation to population pressure, as measured by ε_ϕ, has enabled it to survive in a less resource-rich environment than before.

4. Concluding remarks

The role played by the density-dependence in ecological parameters (carrying capacity, maximum fertility and dispersal rate) in population spreading was investigated in this study. These correspond, respectively, to including resource/habitat depletion, breeding suppression and dispersal adaptability, as perturbations to a base situation which also includes the Allee effect. Remarkably, explicit (and simple) analytical expressions for the invasion speed in these highly non-linear situations were obtained. These results enabled a discussion on the parameter regimes which enable a species to successfully invade a region. Qualitatively, the results agreed well with ecological intuition, and in some cases provided additional insight into less obvious characteristics. For example, a species may using breeding suppression prolong its collective lifespan in a highly hostile environment.

An interesting connection of the current study is to "r and K selection" questions in evolution (MacArthur and Wilson, 1967). These models do not account for the motion of the species, but rather the evolution of genes in a spatially stationary population. The original model (MacArthur, 1962) concludes that density-independent evolution maximises the carrying capacity in a *constant* environment (MacArthur, 1962). In a recent article, Lande et al. (2009) extend these ideas to include the role of environmental stochastically in density-dependent evolution, and conclude that low stochasticity favours an increase in K, while high stochasticity an increase in r, as the species evolves (Lande et al., 2009). Within the context of a species that is additionally dispersing, the results of the current study may be connected to these ideas. Under low environmental stochasticity, since K increases, the appropriate variation would be given by replacing K with $K + \varepsilon_k u$, with $\varepsilon_k > 0$. This means that the new ε_k is negative the ε_k in this study, and by (14), the speed modification would be negative that predicted in Section 3.2. Thus, the spreading speed increases, leading to an expansion in the species' range. Under high stochasticity, the increase in r can once again be thought of as replacing ε_r in (8) with $-\varepsilon_r$, and thus from Section 3.3, the speed increases in this situation as well. Thus, environmental stochasticity relates to an increase in spreading speeds in either case, although different mechanisms contribute to this increase in the two limits of small and large randomness.

This study has the potential for incorporating a wide variety of ecological behaviours within one framework. Different phenomena can be captured by suitably tuning the parameter values K, α, r, Φ, ε_k, ε_r and ε_ϕ, with each parameter having a well-defined ecological meaning. For example, ε_k would represent the effect consumption has on the carrying capacity, and with knowledge of this parameter, the effect on population expansion can be quantified. Similarly, a quantification of how embryonic diapause effects the per capita growth rate (through the parameter ε_r) will lead to a computation of how embryonic diapause affects species colonisation speeds. The power of this model arises from the usage of a technique new to mathematical ecology (Balasuriya and Gottwald, 2010), in conjunction with a unified approach which is encapsulated through the density-dependence of three fundamental ecological parameters. Additionally, the final formulae arising from the model are refreshingly simple, providing benchmarks for determining invasion speeds, and initial guesses for numerical solutions to more refined models which include effects such as competition, predation and environmental heterogeneity.

Acknowledgments

Appendix A. Invasion speed change due to a perturbation

A newly developed analytical technique will be used to quantify the change in the invasion speed due to including density-dependence in each of the parameters. The results below were derived by Balasuriya and Gottwald (2010) using specialised mathematical techniques from dynamical systems theory, which are well beyond the scope of the present article. The main result will be explained in this section, and the interested reader is referred to Appendix A in Balasuriya and Gottwald (2010) for a mathematical development. Suppose a partial differential equation

$$\frac{\partial u}{\partial t} = \Phi \frac{\partial^2 u}{\partial x^2} + f(u) \tag{A.1}$$

has a known solution $u(x,t) = u_0(x - c_0 t)$, in which x and t appear together in the combination $\xi = x - c_0 t$. It is assumed that the constant c_0 is well-defined (unique), which occurs for example when f is bistable (Malaguti et al., 2004; Gilding and Kersner, 2004), but not in the KPP-situation where f is a logistic quadratic (Murray, 1993). (While this latter situation possesses a maximum attainable speed (Kolmogorov et al., 1937; Skellam, 1951), a range of speeds is possible.) The profile $u_0(\xi)$ is assumed to possess well-defined limits as $\xi \to \pm\infty$—that is, at the "front" and "back" of the profile. For example, u_0 approaching 1 as $\xi \to -\infty$, and approaching 0 as $\xi \to +\infty$, as happens in fact in the base model (5). This profile simply moves to the right at speed c_0 while retaining its shape, and is therefore called a travelling wave. Now, suppose the perturbed dynamics

$$\frac{\partial u}{\partial t} = \Phi \frac{\partial^2 u}{\partial x^2} + f(u) + \varepsilon g\left(u, \frac{\partial u}{\partial x}, \frac{\partial^2 u}{\partial x^2}\right), \tag{A.2}$$

in which $|\varepsilon|$ is small, and g is an arbitrary function potentially depending on u and its first two spatial derivatives, is considered. If this system continues to support a travelling wave which is "close" to that of (A.1), then its wavespeed c can be expanded in ε as

$$c = c_0 + \varepsilon c_1 + \mathcal{O}(\varepsilon^2) \tag{A.3}$$

in which $\mathcal{O}(\varepsilon^2)$ means terms of order ε^2 or higher (such as ε^3, etc). This means that if ε is small, say 10^{-2}, then the higher-order terms are of size 10^{-4}, which can therefore be neglected in comparison to the first-order term c_1. The reader familiar with Taylor series would recognise c_1 as representing the rate of change of c with respect to ε; alternatively, it is the leading-order modification to the speed. Balasuriya and Gottwald (2010) show that

$$c_1 = \frac{-\int_{-\infty}^{\infty} \exp\left(\frac{c_0 \xi}{\Phi}\right) u_0'(\xi) g(u_0(\xi), u_0'(\xi), u_0''(\xi)) \, d\xi}{\int_{-\infty}^{\infty} \exp\left(\frac{c_0 \xi}{\Phi}\right) [u_0'(\xi)]^2 \, d\xi}. \tag{A.4}$$

The primes appearing above are the derivatives with respect to the argument. Eq. (A.4) enables the quantification of the leading-order effect on the speed purely in terms of information from the unperturbed system (A.1). Comparison of $c_0 + \varepsilon c_1$ with numerical solutions by Balasuriya and Gottwald (2010) indicate that the method is remarkably accurate in quantifying the speed, even when ε is fairly large (say, $\varepsilon = 0.3$). Many sorts of perturbations can be considered in (A.2) by choosing g appropriately. Formula (A.4)

can therefore be used in instances when the inclusion of density-dependence can be expressed as a perturbation on (4), in fact, for all instances outlined in Section 2.2.

Appendix B. Derivation of speed for density-dependent carrying capacity

The first step in the analysis is to write (13) in the perturbed form of (A.2). This is accomplished using binomial expansions, as described in Appendix C, leading to

$$\frac{\partial u}{\partial t} = \Phi \frac{\partial^2 u}{\partial x^2} + \frac{4r}{(K-\alpha)^2} u(K-u)(u-\alpha) + \varepsilon_k \frac{4ru^2(u-\alpha)(K+\alpha-2u)}{(K-\alpha)^3}. \tag{B.1}$$

By comparison with (A.2) and (A.3), it is possible to take $\varepsilon = \varepsilon_k$, $c_1 = c_{1k}$ and

$$g(u) = \frac{4ru^2(u-\alpha)(K+\alpha-2u)}{(K-\alpha)^3}.$$

Now, formulae for the unperturbed profile u_0 and wavespeed c_0 are available in (5) and (6) for this system. Reiterating these in the current notation,

$$u_0(\xi) = \frac{K}{1 + \exp\left[\frac{K}{K-\alpha}\sqrt{\frac{2r}{\Phi}}\xi\right]}, \quad c_0 = \frac{K-2\alpha}{K-\alpha}\sqrt{2\Phi r}. \tag{B.2}$$

Substituting these into (A.4) to compute c_{1k} leads to many complicated integrals. Now, employ the change of variable

$$\tau = \frac{K}{K-\alpha}\sqrt{\frac{2r}{\Phi}}\xi, \tag{B.3}$$

and define the new parameter

$$p := \frac{3K-2\alpha}{K} = 3 - 2h. \tag{B.4}$$

Upon additionally defining the family of integrals

$$I_n^m := \int_{-\infty}^{\infty} \frac{e^{m\tau}}{(1+e^\tau)^n} \, d\tau,$$

it is possible to write c_{1k} as

$$c_{1k} = -\frac{2\sqrt{2r\Phi}}{(K-\alpha)^2} \frac{(K-\alpha)^2 I_6^{p-1} - (K-\alpha)(K+2\alpha)I_6^p + \alpha(K+\alpha)I_6^{p+1}}{I_4^p} \tag{B.5}$$

after some algebra. Now, with the help of the computational algebra package Mathematica (Wolfram Research Inc., 2005), it can be shown that

$$I_n^m = \int_{-\infty}^{\infty} \frac{e^{m\tau}}{(1+e^\tau)^n} \, d\tau = \frac{(-1)^{n-1}\pi \csc(m\pi)}{(n-1)!} \prod_{j=1}^{n-1} (m-j), \tag{B.6}$$

for integer n satisfying $n > m > 0$, in which $\prod$ is the product. The validity of formula (B.6) was further verified by numerically investigating its left and right hand sides. Since $0 < \alpha < K$, p satisfies $1 < p < 3$, and hence (B.6) is relevant for all the four occurrences of I_n^m in (B.5). Noting also that $\csc[(p \pm 1)\pi] = -\csc[p\pi]$, significant cancellations in (B.5) occur, enabling it to be written as

$$c_{1k} = \frac{2\sqrt{2r\Phi}}{(K-\alpha)^2} \frac{p-4}{20(p-1)}$$
$$[(K-\alpha)^2(p-5)(p-6) + (K-\alpha)(K+2\alpha)(p-1)(p-5) + \alpha(K+\alpha)p(p-1)].$$

The remainder of the calculation simply amounts to replacing p with (B.4) and simplifying, which leads to (15).

Appendix C. Binomial expansion leading from (13) to (B.1)

The binomial expansion is a standard technique which works in the situation when $|x|$ is small, and states that

$$(1+x)^n = 1 + nx + \frac{n(n-1)}{2}x^2 + \frac{n(n-1)(n-2)}{6}x^3 + \cdots, \qquad (C.1)$$

where n is any real number. For small $|x|$, the "higher-order" terms can be neglected, resulting in the approximation $(1+x)^n = 1 + nx$. Applying (C.1) to the pgr term in (13) with the understanding that ε_k is small:

$$
\begin{aligned}
\text{pgr} &= \frac{4r}{([K-\varepsilon_k u]-\alpha)^2} u([K-\varepsilon_k u]-u)(u-\alpha) \\
&= 4ru(u-\alpha)(K-u-\varepsilon_k u)(K-\alpha-\varepsilon_k u)^{-2} \\
&= 4ru(u-\alpha)(K-u)\left(1-\varepsilon_k \frac{u}{K-u}\right)(K-\alpha)^{-2}\left(1-\varepsilon_k \frac{u}{K-\alpha}\right)^{-2} \\
&= \frac{4ru(u-\alpha)(K-u)}{(K-\alpha)^2}\left(1-\varepsilon_k \frac{u}{K-u}\right)\left[1+(-2)\left(-\varepsilon_k \frac{u}{K-\alpha}\right)\right] + \mathcal{O}(\varepsilon_k^2) \\
&= \frac{4ru(u-\alpha)(K-u)}{(K-\alpha)^2}\left[1+\varepsilon_k u\left(-\frac{1}{K-u}+2\frac{1}{K-\alpha}\right)\right] + \mathcal{O}(\varepsilon_k^2) \\
&= \frac{4ru(u-\alpha)(K-u)}{(K-\alpha)^2}\left[1+\varepsilon_k u\frac{\alpha-K+2K-2u}{(K-u)(K-\alpha)}\right] + \mathcal{O}(\varepsilon_k^2) \\
&= \frac{4ru(u-\alpha)(K-u)}{(K-\alpha)^2} + \varepsilon_k \frac{4ru^2(u-\alpha)(K+\alpha-2u)}{(K-\alpha)^3} + \mathcal{O}(\varepsilon_k^2).
\end{aligned}
$$

Neglecting the higher-order term gives (B.1).

Appendix D. Derivation of speed for density-dependent maximum fertility

The procedure followed here is similar to that in Appendix B, and hence the descriptions will be brief. By comparing (18) with (A.2), and using the identification with $\varepsilon = \varepsilon_r$ and $c_1 = c_{1r}$, the function g is seen to take the form

$$g(u) = -\frac{4ru^2(u-\alpha)(K-u)}{K(K-\alpha)^2}.$$

An expression for c_{1r} involving integrals can be written by substituting into (A.4). Using the definitions for τ, p and I_n^m given, respectively, by (B.3), (B.4) and (B.6) in Appendix B, the value of c_{1r} is

$$c_{1r} = \frac{2\sqrt{2r\Phi}}{K-\alpha} \frac{\alpha I_5^p - KI_6^p}{I_4^p}.$$

Once again, using the formula (B.6) for each of the I_n^m's, this can be simplified to the expression (20).

Appendix E. Derivation of minimum carrying capacity (17) for resource depletion

Setting $c=0$ in (16) leads to the quadratic equation

$$2\left(1-\frac{\varepsilon_k}{10}\right)h^2 - 3\left(1+\frac{\varepsilon_k}{10}\right)h + \left(1-\frac{\varepsilon_k}{10}\right) = 0.$$

Using the standard quadratic formula, this has the solution

$$\overline{h} = \frac{3\left(1+\frac{\varepsilon_k}{10}\right) \pm \sqrt{9\left(1+\frac{\varepsilon_k}{10}\right)^2 - 8\left(1-\frac{\varepsilon_k}{10}\right)^2}}{4\left(1-\frac{\varepsilon_k}{10}\right)}.$$

Now, the negative sign corresponds to the solution near 1/2. Choosing this sign, and bearing in mind that ε_k is a perturbative parameter and hence small, binomial expansions (C.1) can be done for all the terms above. Keeping only terms up to first order in ε_k, this leads to

$$\overline{h} = \tfrac{1}{2} - \tfrac{3}{10}\varepsilon_k.$$

An alternative method for obtaining this is to follow the procedure outlined in Appendix G. Now, since $h = \alpha/K$,

$$\overline{K} = \frac{\alpha}{\overline{h}} = \frac{\alpha}{\frac{1}{2}\left(1-\frac{3}{5}\varepsilon_k\right)} = 2\alpha\left(1-\frac{3}{5}\varepsilon_k\right)^{-1} = 2\alpha\left(1+\frac{3}{5}\varepsilon_k\right)$$

by using binomial expansions (C.1) for small ε_k, as desired.

Appendix F. Derivation of speed for density-dependent dispersal rate

Examining (22) in comparison to (A.2), one can take $\varepsilon = \varepsilon_\phi$ and

$$g\left(u, \frac{\partial u}{\partial x}, \frac{\partial^2 u}{\partial x^2}\right) = \frac{\Phi}{K}\left(u\frac{\partial^2 u}{\partial x^2} + \left(\frac{\partial u}{\partial x}\right)^2\right). \qquad (F.1)$$

While this is fundamentally different from the previous cases in that g depends on higher derivatives of u, the calculations turn out to be similar. Substituting (F.1) into (A.4) and simplifying using exactly the change of variables (B.3) and the definitions (B.4) and (B.6), the expression

$$c_{1\phi} = \sqrt{2r\Phi}\frac{K}{K-\alpha}\frac{2I_6^{p+1}-I_6^p}{I_4^p}$$

is obtained. Proceeding as in Appendix B leads to (24) after some algebra.

Appendix G. Derivation of minimum carrying capacity (26) under population pressure

Setting c_ϕ in (25) to zero leads to the expression

$$1 - 2h + \frac{\varepsilon_\phi}{10}(2+h-6h^2) = 0.$$

This quadratic equation for h is "singular"; a small parameter ε_ϕ multiplies the highest-order term. Thus, rather than employing the quadratic formula to determine values of h satisfying the above, a simpler method is to set

$$h = \frac{1}{2} + a\frac{\varepsilon_\phi}{10},$$

substitute into the quadratic equation above, and retain only terms of $\mathcal{O}(\varepsilon_\phi^2)$. Here, a is a as-yet unknown quantity. This leads to

$$\frac{\varepsilon_\phi}{10}\left(-2a+\frac{5}{2}-\frac{3}{2}\right) = 0,$$

and hence a must equal $\frac{1}{2}$. Thus, the h value at which the species is stationary is

$$\overline{h} = \frac{1}{2} + \frac{1}{2}\frac{\varepsilon_\phi}{10} = \frac{1}{2}\left(1+\frac{\varepsilon_\phi}{10}\right),$$

which equals α/K. Hence the carrying capacity value, $\overline{K}$, corresponding to this is given by

$$\frac{\overline{K}}{\alpha} = 2\left(1+\frac{\varepsilon_\phi}{10}\right)^{-1} = 2\left(1-\frac{\varepsilon_\phi}{10}\right)$$

by using the binomial expansion (C.1) and neglecting higher-order terms in ε_ϕ. When rearranged, (26) results.

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