Modeling the dispersal-reproduction trade-off in an expanding population

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Abstract

Trade-offs between dispersal and reproduction are known to be important drivers of population dynamics, but their direct influence on the spreading speed of a population is not well understood. Using integrodifference equations, we develop a model that incorporates a dispersal-reproduction trade-off which allows for a variety of different shaped trade-off curves. We show there is a unique reproductive-dispersal allocation that gives the largest value for the spreading speed and calculate the sensitivities of the reproduction, dispersal, and trade-off shape parameters. Uncertainty in the model parameters affects the expected spread of the population and we calculate the optimal allocation of resources to dispersal that maximizes the expected spreading speed. Higher allocation to dispersal arises from uncertainty in the reproduction parameter or the shape of the reproduction trade-off curve. Lower allocation to dispersal arises from uncertainty in the shape of the dispersal trade-off curve, but does not come from uncertainty in the dispersal parameter. Our findings give insight into how parameter sensitivity and uncertainty influence the spreading speed of a population with a dispersal-reproduction trade-off.

Keywords: integrodifference equations, trade-offs, reproduction, dispersal, spreading speed

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1. Introduction

The principle of allocation states that if an organism has limited resources, then energy allocation to one function reduces the amount of energy available to all other functions (Cody, 1966). Under resource limitation, it can be assumed that an inherent trade-off will usually occur between different functions. There are a variety of trade-off effects that occur in populations such as behavioral trade-offs (Cressler et al., 2010; Verdolin, 2006), evolutionary trade-offs (Burton et al., 2010; Hughes et al., 2003; Yoshida et al., 2004), and life history trade-offs (Hanski et al., 2006; Zera and Harshman, 2001). In this work, we are interested in the life history trade-off between dispersal and reproduction. That is, by the principle of allocation we will consider the case in our study in which the further an individual disperses the fewer resources it will have for reproduction and vice versa.

The empirical evidence for the dispersal-reproduction trade-off effect in natural ecosystems occurs in a variety of insect species (Stevens et al., 2000; Zhao and Zera, 2002; Hughes et al., 2003; Hanski et al., 2006; Elliott and Evenden, 2012; Duthie et al., 2014; Tigreros and Davidowitz, 2019). In extreme cases, some female insects completely lose the ability to fly (Harrison, 1980; Roff, 1984, 1990; Zera and Denno, 1997). This response is commonly interpreted as an evolutionary adaptation to increase fecundity in a specific location. To elaborate on one example of this trade-off, we briefly discuss the results from Elliott and Evenden (2012) on the effect of flight and reproduction in an outbreaking forest lepidopteran, *Choristoneura conflictana*. Here, the population density of the insects limits the post-flight reproductive investment by females. High density levels reduce the amount of resources available to the individuals within the population and an adaptive response would be to disperse in order to access more food. Flight, however, reduces the stores available and in response individuals that disperse further also produce fewer eggs.

The dispersal-reproduction trade-off is not limited to insects. This trade-off has also been examined in diaspores (a seed with additional tissues that assist dispersal). There is a relationship between seed mass and dispersal capacity in wind-dispersed diaspores (Siggins, 1933; Greene and Johnson, 1993; Thompson et al., 2002). This is directly related to reproduction because increases seed mass is proportional to maternal provisioning. Assuming there is only passive wind-dispersal, the trade-off occurs because diaspores with larger seed mass will not spread as far as those with a lighter mass by wind due to the force of gravity causing the larger mass diaspores to settle earlier. There is also evidence for a trade-off between dispersal and reproduction for migrating birds (Gill, 2006; Proctor and Lynch, 1993; Prop et al., 2003; Récapet et al., 2017; Schmidt-Wellenburg et al., 2008). For migratory birds, the reproductive success of an individual correlates with the migration timing, which is determined by the pre-migration body fat stores. A similar trade-off has also been documented in a wild population of lizards (Cotto et al., 2015).

Incorporation of trade-offs into models has produced rich dynamics that are not present without such effects (Chuang and Peterson, 2016). By incorporating a trade-off between reproduction and dispersal ability in a population of non-pollinating fig wasps Duthie et al. (2014) constructed a model to explain the coexistence of these different strategies. At first glance, this result appears to be paradoxical to the competitive exclusion principle because non-pollinating fig wasps share similar life histories and compete for similar resources. However, the trade-off in the model influences individuals to specialize to different degrees on dispersal and reproductive abilities and create individual niches.

Models can also be used to study the evolution of dispersal in populations with multiple phenotypes in a spatially heterogeneous habitat. A primary finding from these studies is that the phenotype with the lowest diffusion rate is selected in a competitive environment (Hastings, 1983; Dockery et al., 1998). However, in our work, we are interested not in what is happening in a competitive environment but during colonization. During colonization, the spreading speed of the population is the primary driving force, not high level density-dependence or intraspecific competition, unlike in stationary competitive systems. Thus, our analysis aims to address a complementary area that evolution of dispersal models do not consider. That is, we are interested in understanding how dispersal is chosen in a colonizing population under range expansion.

In this work, we construct a mathematical model for population spread that incorporates a dispersal-reproduction trade-off. For our mathematical model, we use an integrodifference equation for reproduction and dispersal. We chose this particular model type because of its wide applicability in ecological modeling of populations with non-overlapping generations (Kot, 1992). The shape of trade-off curves are critical for predicting population dynamics (Hoyle et al., 2008). Therefore, in our model, we aim to incorporate a general trade-off effect that can encompass many different scenarios.

Throughout our analysis, we focus on the formula for the spreading speed because we are interested in how the dispersal-reproduction trade-off influences the colonizing population dynamics. Our goal is to understand how the dispersal-reproduction trade-off affects the spreading speed. In particular, we perform a sensitivity analysis to determine parameter sensitivity to the formula. This allows us to understand how the spreading speed would change with parameter variation. We then consider how parameter uncertainty in the trade-off affects the spreading speed formula. To achieve this, we assume that the uncertain parameters in the model are random variables with an underlying probability distribution, and then analyze the impact on optimal resource allocation.

In Section 2, we provide a general background for integrodifference equations, describe our assumptions on how the dispersal-reproduction trade-off is incorporated into the model, and present the trade-off model. We begin Section 3 with determining the condition for population persistence and calculating the formula for the spreading speed. The remainder of Section 3 is broken down into two primary parts; the first concerning the sensitivity of model parameters (Section 3.1), and the second for the uncertainty in the model parameters (Section 3.2). In Section 3.1, our results are divided into two pieces; in the first part we perform a sensitivity analysis on the trade-off parameters (Section 3.1.1), and in the second part we perform a sensitivity analysis on the reproduction and dispersal parameters (Section 3.1.2). In a similar manner for Section 3.2, we partition the results into two parts; the first concerning how the trade-off parameters affect the expected spreading speed (Section 3.2.1), and the second understanding how the reproduction and dispersal parameters affect the expected spreading speed (Section 3.2.2). To conclude the results, we provide a discussion of our model, techniques, and analyses in Section 4. For those interested in the technical details of our results, we present the proofs of the theorems in the Appendix.

2. Mathematical model

Integrodifference equations are a popular tool used in theoretical ecology to model spreading populations (Kot and Schaffer, 1986). Traditionally, the integrodifference equation is written in the following form

$$u_{t+1}(x) = \int_{-\infty}^{\infty} k(x-y) f(u_t(y))\, dy, \qquad t > 0,\, x \in \mathbb{R} \tag{1}$$

where u is the population density, f is the density-dependent local population growth function, and $k(x-y)\, dy$ is a probability density function, commonly called the dispersal kernel, describing the movement of individuals from the interval $(y, y+dy]$ to location x.

To incorporate a dispersal-reproduction trade-off into (1) we assume that the dispersal capability of an individual and the population growth rate are each given by a single parameter, and that the proportion of resources allocated to dispersal is given by p and the proportion of resources allocated to reproduction is given by $1-p$. Under resource limitation, we assume power functions for the change in reproductive and dispersal ability, so they are proportional to $(1-p)^{\alpha}$ and p^{β}, respectively where $\alpha, \beta > 0$.

For simplicity, we consider a population that spreads by diffusion (Kot et al., 1996) and reproduces according to a Beverton-Holt type growth function (Beverton and Holt, 2012). That is, the dispersal kernel k is a Gaussian probability density function with zero mean and variance σ^2,

$$k(x-y) = \frac{1}{\sqrt{2\pi p^{\beta}\sigma^2}} e^{-\frac{(x-y)^2}{2p^{\beta}\sigma^2}}, \tag{2}$$

and the growth function f is given by the Beverton-Holt dynamics

$$f(u_t(y)) = \frac{(1-p)^{\alpha} R u_t(y)}{1 + \frac{(1-p)^{\alpha}R-1}{K} u_t(y)} \tag{3}$$

where K is the carrying capacity and R is the growth rate per generation. By incorporating the dispersal-reproduction trade-off into the model as described above, the population density is then governed by

$$u_{t+1}(x) = \int_{-\infty}^{\infty} \frac{1}{\sqrt{2\pi p^{\beta}\sigma^2}} e^{-\frac{(x-y)^2}{2p^{\beta}\sigma^2}} \frac{(1-p)^{\alpha} R u_t(y)}{1 + \frac{(1-p)^{\alpha}R-1}{K} u_t(y)}\, dy. \tag{4}$$

When $\alpha, \beta = 0$ there is no trade-off in the model. Note that since we are modeling the trade-off in terms of resources allocated we obtain two different curves, one for the reproductive value against the allocation of resources, and the second for the dispersal value against the allocation of resources. We can see from Figure 1 that if the shape parameter is equal to one, then the corresponding resource allocation curve is linear. This means that the change in reproductive or dispersal ability is directly proportional to the proportion of resources invested. If the shape parameter is less than one, then the corresponding curve is concave, suggesting that the growth rate per generation (variation in dispersal distance) has an increasing (decreasing) rate of decrease (increase) with the proportion of resources allocated to dispersal. If the shape parameter is greater than one, then the corresponding allocation curve is convex, suggesting that the growth rate per generation (variation in dispersal distance) has a decreasing (increasing) rate of decrease (increase) with the proportion of resources allocated to dispersal. Note that the value of α and β can be chosen independently allowing for the curves to have different shapes. Previous studies have also incorporated trade-off effects using these same types of power functions (Cressler et al., 2010; Jones and Ellner, 2004).

In the trade-off model, the growth rate per generation is given by $(1-p)^{\alpha}R$. Thus, was have that R is the scaling parameter and α is the shape parameter.

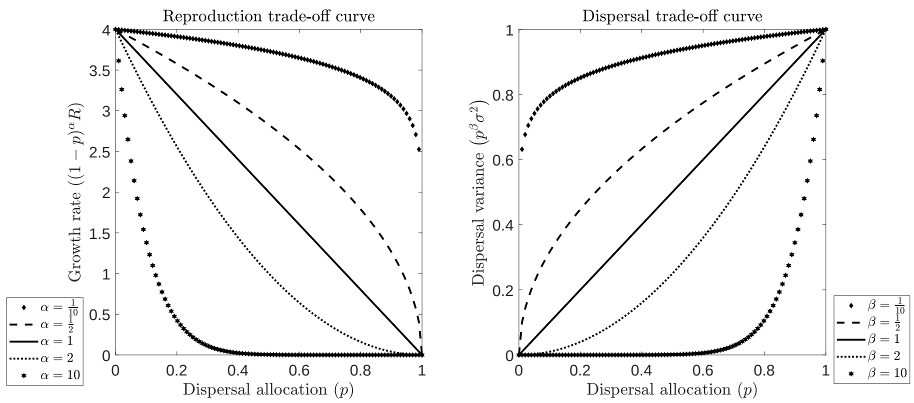

Figure 1: Allocation for dispersal and reproduction for different values of α and β with parameter values $R = 4$ and $\sigma^2 = 1$ chosen arbitrarily.

The variation in dispersal distance is given by $p^{\beta}\sigma^2$. In a similar manner, we see that σ^2 is the scaling parameter and β is the shape parameter. One interesting consequence of our model is the scaling of how we incorporate the trade-off in the model. For example, if $\beta = 1$, then we are assuming that the variance in dispersal distance is proportional to the proportion of resources invested. When $\beta = 2$, we are assuming that the standard deviation in dispersal distance is proportional to the proportion of resources invested.

3. Results

In this section, we provide the theoretical results for our model with the trade-off presented in (4). We begin with a brief description of fundamental results related to the existence, persistence, and spread of populations governed by (4). Once this preliminary material is established, we move into our primary analyses that are composed of two parts. We begin with performing a sensitivity analysis on the parameters of the model in Section 3.1. This section is split into two parts, a sensitivity analysis on the trade-off parameters (Section 3.1.1), and a sensitivity analysis on the reproduction and dispersal parameters (Section 3.1.2). Then, we move onto the second part where we explore the effects of parameter uncertainty in Section 3.2, which is also split into two parts.

First, we calculate the expected spreading speed and optimal resource allocation to dispersal when the trade-off parameters are uncertain (Section 3.2.1), and second we perform the same kinds of calculations when the reproduction and dispersal parameters are uncertain (Section 3.2.2).

We first deduce when the study population is persistent. When we say the population is persistent, we mean that there exists a traveling wave solution to (4) that spreads at some positive speed. This idea is consistent with the concept of weak uniform persistence (Freedman and Moson, 1990; Vasilyeva et al., 2016). The condition for persistence can be calculated directly by applying the seminal work from Weinberger (1982) see Property 3.1, and is provided in Proposition 1.

Proposition 1. *The population modeled by* (4) *is persistent if*

$$(1-p)^{\alpha}R > 1. \tag{5}$$

Note that this condition does not depend on the dispersal parameter, σ^2, or its shape parameter, β, but it does depend on the proportion of resources allocated to dispersal, p. In Figure 2, we can see that there are two areas of interest; above each curve is when $(1-p)^{\alpha}R > 1$ and hence we have population persistence, and the area equal to or below each curve is when $(1-p)^{\alpha}R \leq 1$ and the population becomes extinct. Note that when $(1-p)^{\alpha}R = 1$ our model becomes a purely diffusive process and hence the population cannot persist. Notice that as α increases the (p, R) parameter space where we have population persistence decreases, which is evident from the different curves plotted in Figure 2. As α approaches 0, we see that our persistence requirement becomes the standard persistence requirement in absence of the trade-off; that is, $R > 1$.

When the population is persistent, (4) emits traveling wave solutions (Weinberger, 1982, Theorem 6.6) and we can determine the spreading speed associated with the traveling wave solutions. That is, the population density spreads with fixed spatial profile that is translated by a fixed distance per generation. This translation is called the spreading speed. For a newly introduced population, the asymptotic spreading speed can be thought of in the following way. The

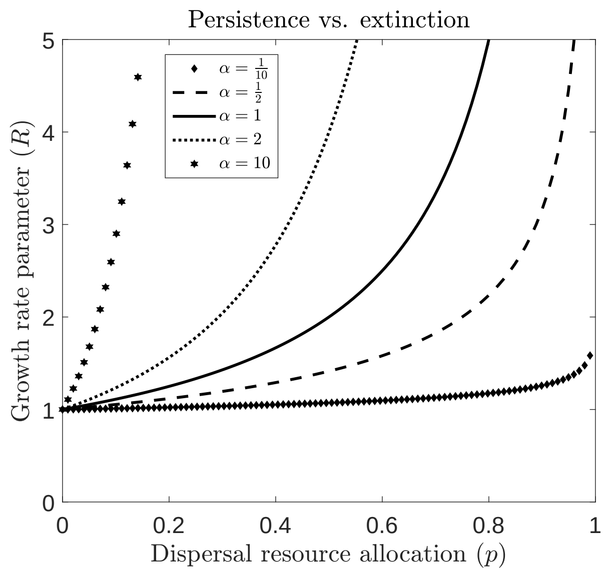

Figure 2: The stability regions for the parameters p and R are shown. For each value of α, the area above each respective curve corresponds to population persistence whereas the area below the curve results in population extinction.

population is said to spread with asymptotic speed c^* if an observer who travels at some speed $c > c^*$ will eventually be ahead of the population and see a density of zero whereas an observer who travels at speed $c < c^*$ will eventually see the population at this carrying capacity.

Proposition 2. *Assume that the population in* (4) *is persistent, then the spreading speed of the population is given by*

$$c^* = \sqrt{2p^\beta \sigma^2 \ln[(1-p)^\alpha R]}. \tag{6}$$

Throughout our analysis we use (6) frequently. The first thing we notice from the formula for the spreading speed is that it depends on the dispersal and reproduction parameters, the shape of the trade-off curves, and the allocation of resources. Thus, as we continue our analysis, we break down our results in terms of these individual pieces.

3.1. Sensitivity analysis

The technique of parameter sensitivity analysis is used to understand how the model response is altered by perturbations in the parameter values. The sensitivity is defined by the incremental rate of proportional change in the response (output) λ related to an incremental rate of proportional change in parameter values (input) θ (Haefner, 2005). In this paper we use proportional sensitivity

$$\text{Sensitivity}(\lambda, \theta) := \frac{\theta}{\lambda}\frac{\partial \lambda}{\partial \theta}, \tag{7}$$

henceforth referred to as simply as sensitivity. In some contexts this is called elasticity (Neubert and Caswell, 2000). The proportionality in (7) allows us to compare parameters with different scales (Link and Doherty Jr, 2002).

3.1.1. Sensitivity of trade-off parameters

In this section, we aim to understand how the trade-off parameters in our model affect the value for the spreading speed of the population. Using (7), we compute the sensitivity of c^* with respect to α, β, and p and find that

$$\text{Sensitivity}(c^*, \alpha) = \frac{\alpha \ln(1-p)}{2\ln\left((1-p)^\alpha R\right)}, \tag{8}$$

$$\text{Sensitivity}(c^*, \beta) = \frac{\beta \ln(p)}{2}, \text{ and} \tag{9}$$

$$\text{Sensitivity}(c^*, p) = \frac{1}{2}\left(\beta - \frac{\alpha p}{(1-p)\ln\left((1-p)^\alpha R\right)}\right). \tag{10}$$

Since $0 < p < 1$, we can immediately conclude that Sensitivity$(c^*, \alpha) < 0$ and Sensitivity$(c^*, \beta) < 0$. Thus, we find that any increase in α or β will cause the spreading speed of the population to decrease. We also see that when Sensitivity$(c^*, p) = 0$, we obtain an interesting result that we outline in Theorem 1. In particular, we can determine the fastest speed at which a species can spread and how it should allocate its resources to do so.

Theorem 1. *Consider* (4) *with the persistence condition* $(1-p)^\alpha R > 1$. *Then, the optimal allocation of resources to dispersal* (p^*) *for the fastest spread of the population is given by the unique solution to the transcendental equation*

$$\frac{\beta \ln\left((1-p^*)^\alpha R\right)}{p^*} = \frac{\alpha}{(1-p^*)}. \tag{11}$$

The proof of Theorem 1 is provided in the Appendix (Section 5.1). It is interesting to note that the optimal allocation of resources does not depend on the diffusivity parameter σ^2. This is because the formula for the asymptotic spreading speed scales linearly with σ. We also see that the optimal resource allocation to dispersal is obtained when Sensitivity$(c^*, p) = 0$. To illustrate the results of Theorem 1, a plot of the spreading speed for different value of p and R with fixed values for α, β, and σ^2 is provided in Figure 3. Here the solid lines are a contour plot for the spreading speed where we vary the values of proportion of resources allocated to dispersal (p), and the growth rate per generation (R). The dashed line in Figure 3 is the optimal resource allocation to dispersal as calculated by Theorem 1. Notice that for each value of $R > 1$, there is a unique value for p that maximizes the spreading speed as predicted by Theorem 1.

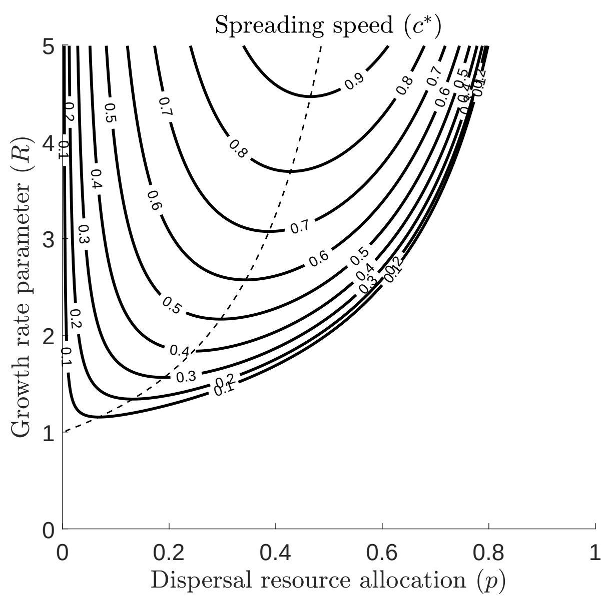

Figure 3: A contour plot for the spreading speed, c^*, for $\alpha = 1$, $\beta = 1$, and $\sigma^2 = 1$. In the plot above we vary the values of p and R. The dashed line is the optimal resource allocation to dispersal (p^*) as calculated by Theorem 1.

In Figure 4 we plot the spreading speed (c^*) against the proportion of resources allocated to dispersal (p), for various values of α and β. The optimal resource allocation to dispersal can be determined from the peak of each curve. From these plots, we can see that, as we increase β, the value for the optimal resource allocation to dispersal increases. As we increase the value of α, the value for the optimal resource allocation to dispersal decreases. This intuitively makes sense since p is the proportion of resources allocated to dispersal. Next, we determine whether α or β is more sensitive when the population is at its optimal resource allocation to dispersal.

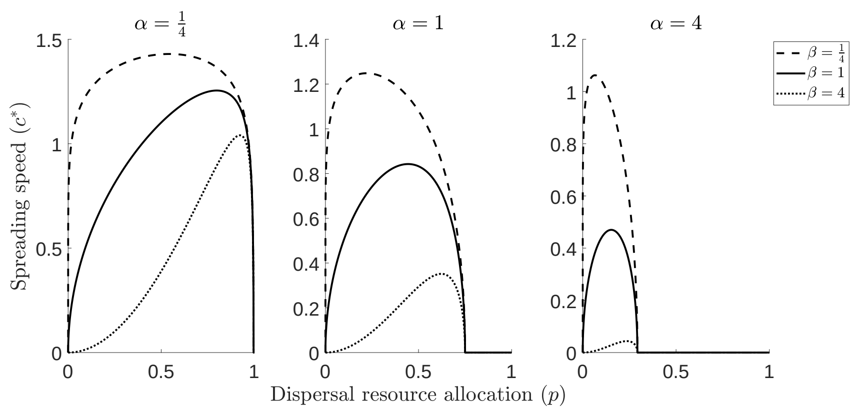

Figure 4: Three plots for the spreading speed, c^*, where $R = 4$ and $\sigma^2 = 1$. In the left, center, and right plots the values for α are $\frac{1}{4}$, 1, and 4, respectively. In each plot we vary β as indicated by the legend.

Theorem 2. *Let the optimal resource allocation to dispersal be denoted by p^*. Then, for the spreading speed (c^*)*

- *If $p^* < \frac{1}{2}$, then α is less sensitive than β.*
- *If $p^* = \frac{1}{2}$, then α and β are equally sensitive.*
- *If $p^* > \frac{1}{2}$, then α is more sensitive than β.*

The proof of Theorem 2 is provided in the Appendix (Section 5.1). The first result of Theorem 2 states that if more resources are allocated to reproduction than dispersal, then the shape parameter for the dispersal trade-off curve is more sensitive than the shape parameter for the reproduction trade-off curve. The second result of Theorem 2 states that if the resources are split equally between dispersal and reproduction, then the shape parameters for the dispersal and reproduction trade-off curves are equally sensitive. The third result of Theorem 2 states that if more resources are allocated to dispersal than reproduction, then the shape parameter for the reproduction trade-off curve is more sensitive than the shape parameter for the dispersal trade-off curve. Intuitively, allowing a majority of the resources to be allocated to one function decreases the amount available for the other function, thus increasing the sensitivity of the shape parameter for the function with the lower resource allocation.

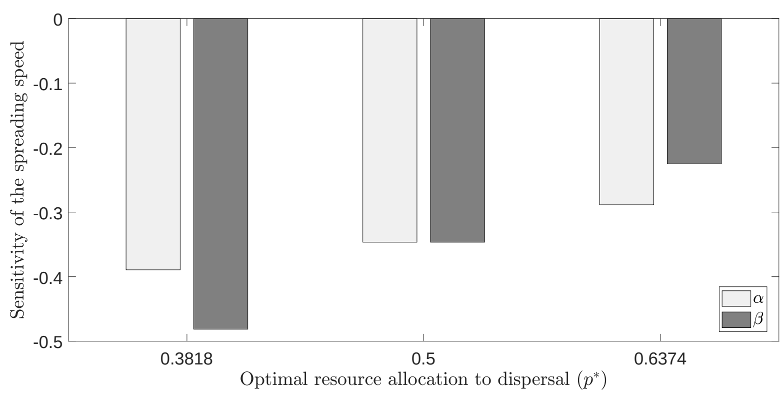

Figure 5: In this figure we plot the sensitivity of the spreading speed with respect to the parameter values α and β against different values for the optimal resource allocation to dispersal (p^*). In all three simulations we used the parameter values $\sigma^2 = 1$, $\alpha = 1$, $\beta = 1$ and vary $R = 3, 2e$, and 16, for the left, center, and right bar plots, respectively where e is Euler's constant.

Theorem 2 is illustrated in Figure 5. Recall that the optimal resource allocation to dispersal can be determined by calculating where Sensitivity$(c^*, p) = 0$ or by solving (11). In the left bar plot of Figure 5 the optimal resource allocation to dispersal is approximately 0.3818, in the center plot the optimal resource allocation to dispersal is 0.5, and in the right plot the optimal resource allocation to dispersal is 0.6374. In the left bar plot of Figure 5, we can see that since the optimal resource allocation is less than one half, that β is more sensitive than

α. In the center bar plot of Figure 5 since the optimal resource allocation is exactly one half, then α and β are both equally sensitive. In the right bar plot of Figure 5 since the optimal resource allocation is greater than one half, then α is more sensitive than β.

3.1.2. Sensitivity of reproduction and dispersal parameters

In this section, we aim to understand how the growth rate and standard deviation in dispersal distance affect the value for the spreading speed of the population. This idea is not novel; previous studies have used sensitivity analysis to understand the effect that dispersal and demographic parameters have on the spreading speed (Neubert and Caswell, 2000; Gharouni et al., 2015; Bateman et al., 2017). A commonality between all these studies is that the model used was a structured integrodifference equation. We are able to apply a simplified version to the theoretical results from Neubert and Caswell (2000) to perform a sensitivity analysis because we are studying a scalar model.

In our analysis, we consider the sensitivity of the spreading speed with respect to the population growth rate per generation (R) and the standard deviation in dispersal distance (σ). Using (7), we calculate

$$\text{Sensitivity}(c^*, R) = \frac{1}{2\ln\left((1-p)^\alpha R\right)}, \text{ and} \tag{12}$$

$$\text{Sensitivity}(c^*, \sigma) = 1. \tag{13}$$

The first thing to notice from these sensitivity calculations is that Sensitivity$(c^*, \sigma) = 1$. Since Sensitivity$(c^*, \sigma) = 1$, we can conclude that σ is a scaling parameter in the formula for the spreading speed. This is also evident from looking directly at the formula for the spreading speed in (6).

Assuming that the population is persistent, we can conclude that the Sensitivity(c^*, R) is always positive. Since the natural logarithm is a monotone increasing function, we can conclude that when $(1-p)^\alpha R$ is small (but still greater than one) then Sensitivity(c^*, R) is high, but when $(1-p)^\alpha R$ becomes large then Sensitivity(c^*, R) becomes smaller. By a direct comparison between (12) and (13) we can conclude that if $(1-p)^\alpha R < (>) e^{\frac{1}{2}}$, then R is more (less) sensitive than σ, and if $(1-p)^\alpha R = e^{\frac{1}{2}}$, then R and σ are equally sensitive. This is seen in Figure 6. Recall that if population is persistent when $(1-p)^\alpha R > 1$, and notice that $e^{\frac{1}{2}} \approx 1.6487$. Therefore, the region where R is more sensitive than σ is quite small and only occurs when the growth rate per generation of the population is small.

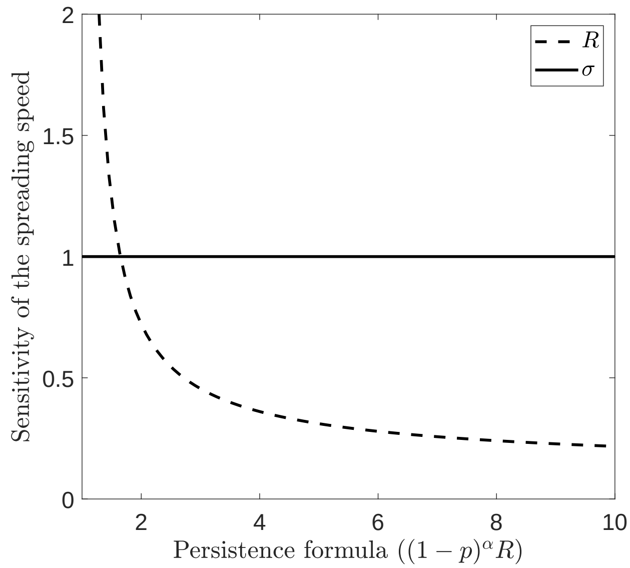

Figure 6: In this figure we plot the sensitivity of the spreading speed with respect to the parameter values R and σ against the persistence formula $(1-p)^\alpha R$.

3.2. Parameter uncertainty

In this section, we attempt to understand how the spreading speed changes when there is parameter uncertainty in the trade-off shape and scale parameters. To achieve this, we assume throughout that the parameter of interest is a random variable with some underlying probability distribution and then compute the expected value for the spreading speed. We break the results into two sections; the first section covers the case when there is uncertainty in the shape of the trade-off curves (Section 3.2.1), and the second section covers the case when there is uncertainty in the reproduction and dispersal parameters or as mentioned earlier the scaling parameters for the trade-off curves (Section 3.2.2).

3.2.1. Uncertainty in the shape of the trade-off curves

In this section, we study the uncertainty in the shape parameters for the trade-off curves α and β. To model the uncertainty in the parameters for α and β, we assume that these parameters are random variables. Since β can be any nonnegative real number, the probability density function for β must also cover the nonnegative real numbers. For α, we need to place a restriction on the upper bound because we require that the population is persistent. Returning to (5) we can see that the upper bound for α should be $-\frac{\ln(R)}{\ln(1-p)}$. Thus, the probability density function for α needs to be defined on $\left(0, -\frac{\ln(R)}{\ln(1-p)}\right)$. With this given uncertainty about the shape parameters for our trade-off curves, we wish to find the expected value for the spreading speed.

We begin with the case where the reproduction trade-off shape, α, is known and the dispersal trade-off shape, β, is uncertain. In this scenario, the parameter of interest is defined on $(0, \infty)$, and we use the gamma distribution with shape parameter $a > 0$ and scale parameter $b > 0$. This distribution is

$$f_1(\beta) = \frac{1}{\Gamma(a) b^a} \beta^{a-1} e^{-\frac{\beta}{b}} \tag{14}$$

with mean ab and variance ab^2. For shorthand notation we denote that β is a gamma distribution with shape parameter a and scale parameter b by $\beta \sim \text{Gamma}(a, b)$. We choose to use this distribution because of its generality due to the fact that special cases of this distribution are the exponential distribution, chi-squared distribution, and Dirac-delta distribution. We calculate the expected spreading speed in Theorem 3.

Theorem 3. *Let us assume that β is a random variable distributed on $(0, \infty)$. Then, the expected value for the spreading speed is*

$$E\left[c^*\right] = \sqrt{2\sigma^2 \ln[(1-p)^\alpha R]} M_\beta \left(\frac{\ln(p)}{2}\right) \tag{15}$$

where M_β is the moment generating function of β. Moreover, if $\beta \sim Gamma(a, b)$, *then*

$$E\left[c^*\right] = \frac{\sqrt{2\sigma^2 \ln[(1-p)^\alpha R]}}{\left(1 - b\frac{\ln(p)}{2}\right)^a} \tag{16}$$

and the optimal resource allocation to dispersal (p^*) is given by the transcendental equation

$$\frac{E[\beta]}{\alpha} \ln\left[(1-p^*)^\alpha R\right](1-p^*) = p^*\left(1 - \frac{1}{2}\frac{Var[\beta]}{E[\beta]}\ln(p^*)\right). \tag{17}$$

The proof of Theorem 3 is provided in the Appendix (Section 5.1). The results from Theorem 3 can be applied to understand how a population would expect to spread if the shape of the dispersal trade-off curve is uncertain. Here we provide a general formula for the expected spreading speed for a random variable β defined on $(0, \infty)$ in terms of its moment generating function in (15). In the special case when $\beta \sim \text{Gamma}(a, b)$, we calculate the formula for the expected spreading speed in (16) and calculate the optimal resource allocation to dispersal by the implicit equation (17). When $\text{Var}[\beta] = 0$, we have that $E[\beta] = \beta$ and (17) is equivalent to (11) in Theorem 1.

To understand the effects of the variation in the dispersal trade-off shape parameter, β, we provide plots of the optimal resource allocation to dispersal in Figure 7. In both plots, we see that as the expected dispersal trade-off shape increases, the optimal resource allocation to dispersal also increases. We also see that as the variation in the shape of the dispersal trade-off increases, the optimal resource allocation to dispersal decreases. That is, if there is a lot of uncertainty in the shape of the dispersal trade-off curve, then the best choice for the population is to invest more resources into reproduction.

Next, we consider the case when the reproduction trade-off shape, α, is uncertain and the dispersal trade-off shape, β, is known. To be able to discuss the spreading speed for the population here, we need to guarantee that the population is persistent. That is $(1-p)^\alpha R > 1$. Recall that this is satisfied when $\alpha < -\frac{\ln(R)}{\ln(1-p)}$. This provides us with an upper bound on the potential values for α. Hence, our distribution for α must be defined on the bounded interval $\left(0, -\frac{\ln(R)}{\ln(1-p)}\right)$ to guarantee persistence. In our case we will use a scaled

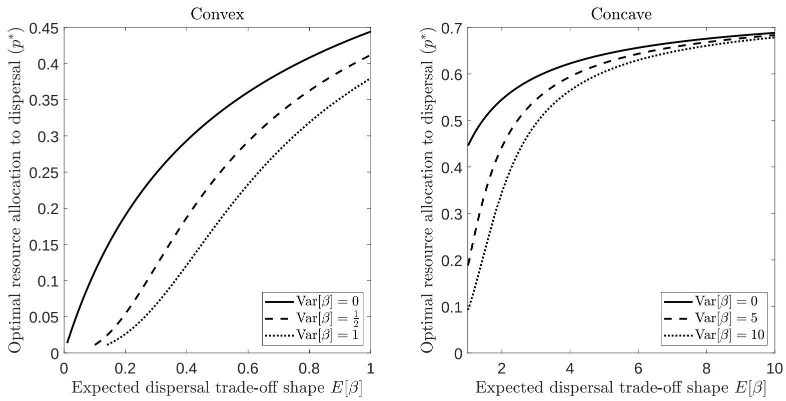

Figure 7: The plot in this figure shows the dispersal resource allocation versus the $E[\beta]$ for different values of $\mathrm{Var}[\beta]$ for the parameter values $\alpha = 1$ and $R = 4$.

beta distribution given by

$$f_2(\alpha) = \frac{\alpha^{a-1}\left(-\frac{\ln(R)}{\ln(1-p)} - \alpha\right)^{b-1}}{B(a,b)\left(-\frac{\ln(R)}{\ln(1-p)}\right)^{a+b-1}} \tag{18}$$

with shape parameter $a \geq 1$ and scale parameter $b \geq 1$ where B is the beta function. For our shorthand notation we say that $\alpha \sim \mathrm{Beta}(a,b)$ on $\left(0, -\frac{\ln(R)}{\ln(1-p)}\right)$. We choose this distribution because it is a well-known continuous distribution defined on a finite interval with two shape parameters which allows for a variety of distribution shapes. It is interesting to note that when the shape and scale parameters are both equal to one, then the scaled beta distribution becomes the uniform distribution on $\left(0, -\frac{\ln(R)}{\ln(1-p)}\right)$.

Theorem 4. *Let us assume that α is a random variable distributed on $\left(0, -\frac{\ln(R)}{\ln(1-p)}\right)$. Then, the expected value for the spreading speed is*

$$E\left[c^*\right] = \sqrt{2\sigma^2 p^\beta \ln(R)} \sum_{n=0}^{\infty} \binom{\frac{1}{2}}{n} \left(\frac{\ln(1-p)}{\ln(R)}\right)^n E\left[\alpha^n\right]. \tag{19}$$

Moreover, if $\alpha \sim \mathrm{Beta}(a,b)$ on $\left(0, -\frac{\ln(R)}{\ln(1-p)}\right)$, then

$$E\left[c^*\right] = \sqrt{2\sigma^2 p^\beta \ln(R)} \frac{\Gamma(a+b)\Gamma\left(b+\frac{1}{2}\right)}{\Gamma(b)\Gamma\left(a+b+\frac{1}{2}\right)} \tag{20}$$

and the optimal resource allocation to dispersal (p^*) is the largest value of p that satisfies

$$p < 1 - \frac{1}{\sqrt[\alpha]{R}}. \tag{21}$$

The proof of Theorem 4 is provided in the Appendix (Section 5.1). A plot of the optimal resource allocation to dispersal is provided in Figure 8. Figure 8 is split into two parts for the shape of the reproduction trade-off curve. That is, in the left plot when $0 < \alpha < 1$ the reproduction trade-off curve is convex and in the right plot when $1 < \alpha < 10$ the reproduction trade-off curve is concave. It is clear from the left plot in Figure 8 that when α and R are small, the optimal resource allocation to dispersal is highly volatile. We also see that by increasing the growth rate parameter, R, increases the optimal resource allocation to dispersal. This is interesting because it suggests that by increasing the growth rate parameter an individual should invest more resources into dispersal to maximize their spreading speed. We also can conclude from Figure 8 that by increasing the reproduction trade-off shape parameter, α, decreases the optimal resource allocation to dispersal.

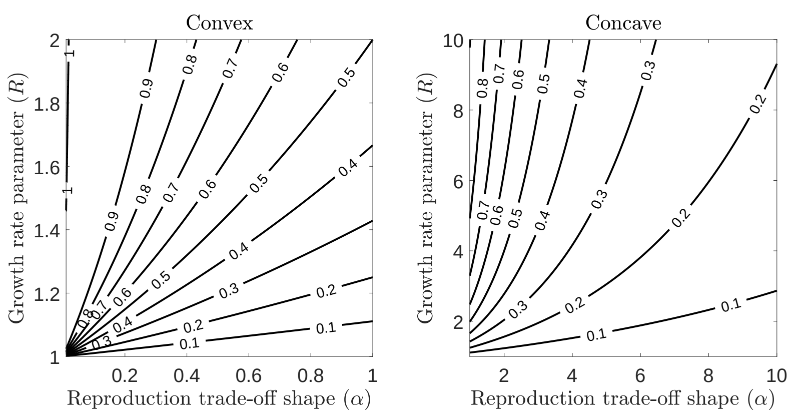

Figure 8: The contour plots in this figure show the optimal resource allocation to dispersal for different values of α and R. In the left plot, we have $0 < \alpha < 1$ that means the shape of the reproduction trade-off curve is convex. In the right plot, we have $1 < \alpha < 10$ that means the shape of the reproduction trade-off curve is concave.

3.2.2. Uncertainty in the reproduction and dispersal parameters

In this section we will study the uncertainty in the reproduction and dispersal parameters R and σ. To model the uncertainty in the parameters for R and σ, we assume that these parameters are random variables. First, we will consider when R is known and σ is uncertain. Since σ is the standard deviation in dispersal distance, this value can be any real valued number so our distribution for σ should be defined over the nonnegative real line. We begin with calculating the expected spreading speed and the optimal resource allocation to dispersal in Theorem 5.

Theorem 5. *Let us assume that σ is a random variable distributed on $[0, \infty)$. Then, the expected value for the spreading speed is*

$$E\left[c^*\right] = \sqrt{2p^\beta \ln[(1-p)^\alpha R]}E\left[\sigma\right]. \tag{22}$$

Moreover, the optimal resource allocation to dispersal (p^*) is given by

$$\frac{\beta \ln\left((1-p^*)^\alpha R\right)}{p^*} = \frac{\alpha}{(1-p^*)}. \tag{23}$$

The proof of Theorem 5 is provided in the Appendix (Section 5.1). Since σ is a scaling parameter in the formula for the spreading speed, we see that the by simply replacing σ by $E[\sigma]$ in (6), we obtain the formula for the expected spreading speed. Notice that (23) is the same as (11) in Theorem 1. This means that the optimal resource allocation to dispersal when all parameter values are known is the same for when σ is uncertain. Therefore, the uncertainty in σ does not affect the optimal resource allocation to dispersal.

Next, we will consider when R is uncertain and σ is known. Since R is the population growth rate parameter, this value must be greater than $\frac{1}{(1-p)^\alpha}$ to guarantee population persistence. For simplicity in our calculations, we look at the distribution of $\ln(R)$ on $(-\alpha \ln(1-p), \infty)$. Thus, we look at a translated random variable that is shifted by $-\alpha \ln(1-p)$. In this scenario, we assume that $\ln(R)$ is a shifted gamma distribution on $(-\alpha \ln(1-p), \infty)$ with shape parameter $a > 0$ and scale parameter $b > 0$. For shorthand notation, we say that $\ln(R) \sim \text{Gamma}(a, b)$ on $(-\alpha \ln(1-p), \infty)$. This distribution is given by

$$f_4(\ln(R)) = \frac{1}{\Gamma(a) b^a} \left(\ln(R) + \alpha \ln(1-p)\right)^{a-1} e^{-\frac{(\ln(R)+\alpha \ln(1-p))}{b}} \tag{24}$$

for $\ln(R) \in (-\alpha \ln(1-p), \infty)$.

Theorem 6. *Let us assume that* $\ln(R)$ *is a shifted random variable distributed on* $(-\alpha \ln(1-p), \infty)$. *Then, the expected value for the spreading speed is*

$$E[c^*] = \sqrt{2p^\beta \sigma^2} E\left[(\ln(R) + \alpha \ln(1-p))^{\frac{1}{2}} \right]. \tag{25}$$

Moreover, if $\ln(R) \sim$ *Gamma*(a, b) *on* $(-\alpha \ln(1-p), \infty)$, *then*

$$E[c^*] = \sqrt{2p^\beta \sigma^2 b} \frac{\Gamma\left(a + \frac{1}{2}\right)}{\Gamma(a)}, \tag{26}$$

and the optimal resource allocation to dispersal (p^*) *is the largest value of* p *that satisfies*

$$p < 1 - \frac{1}{\sqrt[\alpha]{R}}. \tag{27}$$

The proof of Theorem 6 is provided in the Appendix (Section 5.1). In Theorem 6, we compute the expected spreading speed for the population for a shifted random variable distributed on $(-\alpha(1-p), \infty)$ in (25). Notice that the expected spreading speed is written in terms of the one halfth moment. In (26) we provide an example for when $\ln(R) \sim \text{Gamma}(a, b)$ on $(-\alpha \ln(1-p), \infty)$ where the expected spreading speed now depends on the shape and scale parameters of the distribution. After computing the spreading speed, we also determine the optimal resource allocation to dispersal in (27). Note that the optimal resource allocation to dispersal in this theorem is the same as when we assumed that α was uncertain in Theorem 4. Therefore, a plot of the optimal resource allocation when R is uncertain is also given in Figure 8.

4. Discussion

The model presented in (4) provides a framework to understand the effects of dispersal-reproduction trade-offs on population persistence and the spreading speed of a population. From our analysis, it is evident that resource allocation is an important feature that impacts both the persistence and spread of a population. The influence of the trade-off shows that if an organism allocates too many resources to dispersal there may not be enough resources left for successful reproduction. Alternatively, if an individual spends too many resources on reproduction then it will not be able to spread quickly. We also determined how sensitive the spreading speed is to small changes in the model parameters, and studied how parameter uncertainty impacts the population spread.

To understand how trade-off parameter values affect the spreading speed of the population we performed a sensitivity analysis in Section 3.1 (Haefner, 2005). In Theorem 1, we were able to prove that there is a unique value for the optimal allocation of resources to dispersal that maximizes the spreading speed for the population. However, this unique value is not always observed in practice for other trade-offs. For a trade-off between seed size and number, Geritz (1995) showed that by assuming asymmetric intraspecific competition in favor of larger seeds that any unique seed size can be unstable and the evolutionary stable strategy becomes polymorphic. In another study, intraspecific competition, determined by a trade-off between egg load and dispersal ability, leads to coexistence of non-pollinating fig wasps that specialize to different degrees on dispersal ability and fecundity (Duthie et al., 2014).

By calculating the sensitivity of the spreading speed with respect to the trade-off shape parameters α and β, we first deduce that these quantities are always negative. This means that the spreading speed always decreases when the trade-off shape parameters increase. We were able to prove in Theorem 2 that if the population is at its optimal resource allocation and the resources are split equally between dispersal and reproduction, then α and β are equally sensitive. The results from Theorem 2 also show that if the population is at its optimal resource allocation and more (less) resources are allocated to dispersal than reproduction, then α is more (less) sensitive than β. An example of this result is seen in Figure 5. This result is somewhat counter intuitive because α is the shape parameter for the reproduction trade-off curve and β is the shape parameter for the dispersal trade-off curve. This means that if more (less) resources are allocated to dispersal than reproduction, then the shape of the reproduction (dispersal) trade-off curve is more sensitive than the shape of the dispersal (reproduction) trade-off curve.

In Section 3.2, we explored how parameter uncertainty influences the expected spreading speed of the population and the optimal resource allocation to dispersal. This problem has been studied before for linear models with an emphasis on how stochasticity can influence the spreading speed (Mollison, 1991) and more complicated nonlinear models (Lewis and Pacala, 2000). We split our results into two parts: Section 3.2.1 considers the case when the trade-off shape parameters are uncertain, and Section 3.2.2 considers when the reproduction and dispersal parameters are uncertain. To include the parameter uncertainty, we assume the parameter of interest is a random variable distributed on a suitable interval. In all cases, we determine two things; the expected spreading speed for the population and the optimal resource allocation to dispersal.

Throughout our analyses, we find that the expected spreading speed is slower than if there was no uncertainty. Previous studies have also found slower spreading speeds when there is individual variation in dispersal rates or demographic stochasiticty (Clark et al., 2001; Snyder, 2003). While this type of variation is not the same as the parametric uncertainty we consider it suggests in general that uncertainty can slow the speed of a spreading population. For a population with uncertainty about the nature of the trade-off between dispersal and reproduction, the maximization process calculates the resource allocation strategy that would maximize its expected rate of spatial spread, given the nature of uncertainty in the trade-off. Uncertainty in the trade-off can be in terms of uncertainty in the shapes of the trade-off curve for the reproduction (as given by parameter α) or dispersal (as given by the parameter β) or uncertainty in the reproduction parameter (R) or dispersal parameter (σ). In the case when the growth rate or the shape parameter for α is uncertain, we find that the strategy to maximize the expected spreading speed is to allocate as many resources as possible to dispersal, while still maintaining the persistence criterion. However, when there is variation in the shape of the dispersal trade-off curve, β, then the optimal strategy involves investing more resources into reproduction. Due to the fact that σ is simply a scaling variable in the formula for the spreading speed, we see that when there is uncertainty in σ the formula for the spreading speed is altered by replacing σ in (6) with the expected value of σ. In Theorem 5, we calculate the optimal resource allocation to dispersal in (23), where we find that the formula in (23) is the same as (11) in Theorem 1.

While dispersal-reproduction trade-offs have been widely accepted in the literature, it should be mentioned that there are numerous examples for which this trade-off does not occur, or if it does, the degree of the trade-off varies greatly (Mole and Zera, 1994; Tigreros and Davidowitz, 2019; Therry et al., 2015; Guerra, 2011; Roff, 1995; Sappington and Showers, 1992). These studies argue for a lack of a trade-off between dispersal and reproduction in some insect species, or even a positive association between dispersal and reproduction. A recent meta-analysis indicates that although trade-offs between dispersal and reproduction likely occur in many insects, the strength and correlation of the trade-off vary significantly across insect orders (Guerra, 2011). Our model suggests that the trade-off occurs due to resource limitation, which is supported by another meta-analysis showing that in 76% of the studies, conditions of resource restriction result in a negative association between dispersal and reproduction (Tigreros and Davidowitz, 2019). Moreover, negative associations between dispersal and reproduction do not necessarily indicate a resource allocation trade-off.

Our results are based on Gaussian dispersal kernels and Beverton-Holt growth functions. We chose these functions because they allow us to express the formula for the spreading speed explicitly, as given in (6). For non-Gaussian, thin-tailed dispersal kernels, we would still have an abstract formula for the spreading speed (Weinberger, 1982), but we would not be able to perform many of the explicit calculations done in our work. If one were interested in fat-tailed dispersal kernels, then we would no longer have a traveling wave solution, but an accelerating wave where the speed of the wave increases over time. The choice of the growth function also does not consider an Allee effect or overcompensatory population dynamics. For the Allee effect, there is only one function where an explicit form of the spreading speed is known (Wang and Kot, 2001). By considering a function with overcompensation and Gaussian dispersal one could still obtain an explicit formula for the spreading speed (Li et al., 2009).

The results presented in Theorems 3-6 assume that the underlying parameter values are unknown and follow a given distribution. In these scenarios, we calculate the expected rate of spatial spread, but we neglect to compute any results regarding the uncertainty in the distribution for the rate of spatial spread. From a theoretical standpoint, one way to quantify the uncertainty in the distribution for the rate of spatial spread is to calculate the variance of the spreading speed. While this is possible, it is quite complicated to achieve an analytical result for these calculations and hence would be best done via numerics. Alternatively, confidence intervals could also be computed.

A shortcoming in the model is the assumption that the life history strategies do not evolve over time. This assumption is only biologically reasonable if the time scale of the model is much shorter than the time it takes for the life history to change. In many cases this is not feasible. It has been empirically shown that resource allocation can have seasonal fluctuations (Barbour et al., 1999) or evolve due to genetic mutations in offspring (Burton et al., 2010). Typical annual plants, a plant that completes its life cycle within one year and then dies, devote most resources to growth in the early part of the growing season with a small amount of resources for maintenance, and late in the growing season nearly all the resources are devoted to reproduction. Whereas stress-tolerant plants such as shrubs in subarctic or dessert regions must allocate most resources to maintenance, and a small amount to growth. Only during good years, when resources are plentiful, can they devote resources to reproduction (Barbour et al., 1999). Thus, the type of resource allocation is highly dependent on the particular population of interest. Time-dependent variation in reproduction and dispersal can accelerate the spread of invading species (Ellner and Schreiber, 2012). In our study, we find variation in reproduction slows the spread, whereas variation in dispersal does not alter the expected spreading speed. This provides motivation to extend the model to include time-dependent trade-offs.

Another drawback of the modeling techniques presented is that there is no spatial heterogeneity in the resource allocation. In other systems, resource allocation is highly dependent on the location of the individuals in the population (Burton et al., 2010). Individuals in the core of the population were found to allocate more resources on reproduction than dispersal while individuals at the front of the population allocated more resources to dispersal than reproduction. Understanding the consequences of populations colonizing new habitats can also be explored by incorporating spatial heterogeneity in the resource allocation. One way to incorporate this into the model would be to consider density-dependent trade-offs.

Habitat fragmentation can affect the dispersal-reproduction trade-off (Ziv and Davidowitz, 2019). Using a common garden experiment, Gibbs and Van Dyck (2010) studied the effects of increased dispersal on the reproduction of speckled wood butterflies from closed continuous woodland populations to open highly fragmented agricultural landscapes. Gibbs and Van Dyck (2010) concluded that butterflies from fragmented landscapes were better able to cope with the increased dispersal demands relative to those from non-fragmented landscapes suggesting a difference in the strength of trade-off due to the energetic cost of dispersal. Theoretical studies using integrodifference equations have previously investigated the role that landscape heterogeneity plays in predicting population dynamics (Dewhirst and Lutscher, 2009; Kawasaki and Shigesada, 2007; Latore et al., 1999; Van Kirk and Lewis, 1997), but have yet to incorporate dispersal-reproduction trade-offs into the models. A natural extension would be to fuse these two approaches together.

While our model is aimed to be applied to populations with nonoverlapping generations that have distinct dispersal and reproduction phases in their life cycle, these kinds of dispersal-reproduction trade-offs have also been documented in smaller scales of daily dispersal and foraging patterns (Bonte et al., 2012; Van Dyck and Baguette, 2005). Empirical evidence for these small scale dispersal-reproduction trade-offs have been documented in insects (Harrison, 1980), guppies (Ghalambor et al., 2004), lizards (Cox and Calsbeek, 2010; Miles et al., 2000), and snakes (Seigel et al., 1987). Thus, extending this modeling approach beyond integrodifference equations would allow for these types of trade-offs to be considered in a theoretical framework.

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5. Appendix

5.1. Proofs of the theorems

Proof of Theorem 1.

Proof. To begin, it should be noted that we treat α, β, R, and σ^2 as constants since we are interested in how p affects the asymptotic spreading speed c^*. To find the optimal allocation of resources for a species to spread we first find the first derivative of $(c^*)^2/2\sigma^2$ with respect to p. Using Equation (6), we calculate

$$\frac{d(c^*)^2/2\sigma^2}{dp} = \beta p^{\beta-1}\ln\left((1-p)^\alpha R\right) + p^\beta \frac{-\alpha(1-p)^{\alpha-1}}{(1-p)^\alpha} \tag{28}$$

$$= p^\beta\left(\frac{\beta\ln\left((1-p)^\alpha R\right)}{p} - \frac{\alpha}{(1-p)}\right). \tag{29}$$

Hence, we have a critical point when

$$\frac{\beta\ln\left((1-p)^\alpha R\right)}{p} = \frac{\alpha}{(1-p)}. \tag{30}$$

Next, we show that Equation (30) has a unique solution. Define

$$l(p) := \frac{\ln\left((1-p)^{\alpha} R\right)}{p} \quad \text{and} \tag{31}$$

$$r(p) := \frac{1}{1-p}. \tag{32}$$

Both $l(p)$ and $r(p)$ are continuous functions on $(0, 1)$. Also, $l(p)$ is a monotone decreasing function for $p \in (0, 1)$ where $\lim_{p\to 0} l(p) = \infty$ and $\lim_{p\to 1} l(p) = -\infty$. We also have that $r(p)$ is a monotone increasing function for $p \in (0, 1)$ where $r(0) = 1$ and $\lim_{p\to 1} r(p) = \infty$. Therefore, for each α, β, and R there exists a unique value $p^* \in (0, 1)$ such that p^* solves Equation (30). □

Proof of Theorem 2.

Proof. Recall that the optimal resource allocation is given by (11). That is,

$$\beta = \frac{\alpha p}{(1-p)\ln\left((1-p)^{\alpha} R\right)}. \tag{33}$$

To determine which parameter is more sensitive we compare Sensitivity(c^*, α) and Sensitivity(c^*, β). Recall that from (8) and (9) we know that Sensitivity(c^*, α) and Sensitivity(c^*, β) are both negative. When Sensitivity(c^*, α) = Sensitivity(c^*, β), this means that α and β are equally sensitive, when Sensitivity(c^*, α) > Sensitivity(c^*, β) this means that α is less sensitive than β, and finally when Sensitivity(c^*, α) < Sensitivity(c^*, β), this means that α is more sensitive than β. We will first compute when α and β are equally sensitive. That is,

$$\text{Sensitivity}(c^*, \alpha) = \text{Sensitivity}(c^*, \beta) \tag{34}$$

gives

$$\frac{\alpha \ln(1-p)}{2\ln\left((1-p)^{\alpha} R\right)} = \frac{\beta \ln(p)}{2}. \tag{35}$$

Since we are assuming we are at the optimal resource allocation, substituting (33) into the previous equation we have

$$\frac{\alpha \ln(1-p)}{2\ln\left((1-p)^{\alpha} R\right)} = \frac{\alpha p \ln(p)}{2(1-p)\ln\left((1-p)^{\alpha} R\right)}. \tag{36}$$

Simplifying, we find that

$$(1-p)\ln(1-p) = p\ln(p). \tag{37}$$

The only solution to this equation is given by $1-p=p$. Solving for p we find that $p=\frac{1}{2}$. Thus, if the optimal resource allocation is $p=\frac{1}{2}$, then α and β are both equally sensitive parameters. Repeating these same calculations but with Sensitivity$(c^*,\alpha) >$ Sensitivity(c^*,β), we find that $0<p<\frac{1}{2}$. Thus, if the optimal resource allocation is less than $\frac{1}{2}$, then β is more sensitive than α. By repeating these same calculations but with Sensitivity$(c^*,\alpha) <$ Sensitivity(c^*,β), we find that $\frac{1}{2}<p<1$. Thus, if the optimal resource allocation is greater than $\frac{1}{2}$, then α is more sensitive than β. □

Proof of Theorem 3.

Proof. Assuming that β is a random variable defined on $(0,\infty)$ with probability density function $f_1(\beta)$, the expected spreading speed is given by

$$\begin{aligned}
E\left[c^*\right] &= \int_0^\infty \sqrt{2p^\beta\sigma^2\ln[(1-p)^\alpha R]}\,f_1(\beta)\,d\beta && (38)\\
&= \sqrt{2\sigma^2\ln[(1-p)^\alpha R]}\int_0^\infty p^{\frac{\beta}{2}}f_1(\beta)\,d\beta && (39)\\
&= \sqrt{2\sigma^2\ln[(1-p)^\alpha R]}\int_0^\infty e^{\beta\frac{\ln(p)}{2}}f_1(\beta)\,d\beta && (40)\\
&= \sqrt{2\sigma^2\ln[(1-p)^\alpha R]}M_\beta\left(\frac{\ln(p)}{2}\right). && (41)
\end{aligned}$$

Note that the above integral becomes the moment generating function of $f_2(\beta)$, with parameter $\frac{\ln(p)}{2}$. If $f_1(\beta)$ is a gamma distribution, then

$$\begin{aligned}
M_\beta\left(\frac{\ln(p)}{2}\right) &= \int_0^\infty e^{\beta\frac{\ln(p)}{2}}\frac{1}{\Gamma(a)b^a}\beta^{a-1}e^{-\frac{\beta}{b}}\,d\beta && (42)\\
&= \frac{1}{\Gamma(a)b^a}\int_0^\infty \beta^{a-1}e^{-\frac{\beta}{b}\left(1-b\frac{\ln(p)}{2}\right)}\,d\beta && (43)\\
&= \frac{1}{\Gamma(a)b^a}\Gamma(a)\left(\frac{b}{\left(1-b\frac{\ln(p)}{2}\right)}\right)^a && (44)\\
&= \frac{1}{\left(1-b\frac{\ln(p)}{2}\right)^a} && (45)
\end{aligned}$$

for $\frac{\ln(p)}{2} < \frac{1}{b}$. Since $0 < p < 1$ and $b > 0$, this condition is always satisfied. Therefore,

$$E\left[c^*\right] = \frac{\sqrt{2\sigma^2 \ln[(1-p)^\alpha R]}}{\left(1 - b\frac{\ln(p)}{2}\right)^a}. \tag{46}$$

We can next determine what the optimal resource allocation to dispersal should be in order to maximize the expected value of the spreading speed. To do this, we determine when

$$\frac{d}{dp} E\left[c^*\right] = 0. \tag{47}$$

We find that the implicit equation that satisfies this is given by

$$\frac{a}{\alpha} \ln\left[(1-p)^\alpha R\right](1-p) = \frac{p}{b}\left(1 - \frac{1}{2} b \ln(p)\right). \tag{48}$$

Recall that the $E[\beta] = ab$ and $\mathrm{Var}[\beta] = ab^2$. We can rewrite our previous condition as

$$\frac{E[\beta]}{\alpha} \ln\left[(1-p^*)^\alpha R\right](1-p^*) = p^*\left(1 - \frac{1}{2}\frac{\mathrm{Var}[\beta]}{E[\beta]} \ln(p^*)\right). \tag{49}$$

Therefore, the optimal resource allocation for dispersal is given implicitly by (49). □

Proof of Theorem 4.

Proof. Assuming that α is a random variable defined on $\left(0, -\frac{\ln(R)}{\ln(1-p)}\right)$ with probability density function $f_2(\alpha)$, the expected spreading speed is given by

$$E\left[c^*\right] = \int_0^{-\frac{\ln(R)}{\ln(1-p)}} \sqrt{2p^\beta \sigma^2 \ln[(1-p)^\alpha R]} f_2(\alpha)\, d\alpha \tag{50}$$

$$= \sqrt{2p^\beta\sigma^2} \int_0^{-\frac{\ln(R)}{\ln(1-p)}} \sqrt{\ln[(1-p)^\alpha R]} f_2(\alpha)\, d\alpha \tag{51}$$

$$= \sqrt{2p^\beta\sigma^2} \int_0^{-\frac{\ln(R)}{\ln(1-p)}} \sqrt{\alpha \ln(1-p) + \ln(R)} f_2(\alpha)\, d\alpha. \tag{52}$$

Using Newton's Generalized binomial theorem, we have that

$$\sqrt{\alpha \ln(1-p) + \ln(R)} = \sum_{n=0}^{\infty} \binom{\frac{1}{2}}{n} (\ln(R))^{\frac{1}{2}-n} (\alpha \ln(1-p))^n \tag{53}$$

$$= \sqrt{\ln(R)} \sum_{n=0}^{\infty} \binom{\frac{1}{2}}{n} \left(\frac{\ln(1-p)}{\ln(R)}\right)^n \alpha^n. \tag{54}$$

This series converges when $\ln(R) > |\alpha \ln(1-p)|$ which is equivalent to our persistence criterion $R(1-p)^{\alpha} > 1$. Using Fubini's theorem,

$$\int_0^{-\frac{\ln(R)}{\ln(1-p)}} \sum_{n=0}^{\infty} \binom{\frac{1}{2}}{n} \left(\frac{\ln(1-p)}{\ln(R)}\right)^n \alpha^n f_2(\alpha)\, d\alpha = \sum_{n=0}^{\infty} \binom{\frac{1}{2}}{n} \left(\frac{\ln(1-p)}{\ln(R)}\right)^n \int_0^{-\frac{\ln(R)}{\ln(1-p)}} \alpha^n f_2(\alpha)\, d\alpha \tag{55}$$

$$= \sum_{n=0}^{\infty} \binom{\frac{1}{2}}{n} \left(\frac{\ln(1-p)}{\ln(R)}\right)^n E\left[\alpha^n\right]. \tag{56}$$

From (52), (54), and (56) we can see that when α is uncertain the expected value for the spreading speed is given by

$$E\left[c^*\right] = \sqrt{2\sigma^2 p^{\beta} \ln(R)} \sum_{n=0}^{\infty} \binom{\frac{1}{2}}{n} \left(\frac{\ln(1-p)}{\ln(R)}\right)^n E\left[\alpha^n\right]. \tag{57}$$

Therefore, we can express the expected value for the spreading speed in terms of a series of the moments of the distribution. In particular, when $\alpha \sim \mathrm{Beta}(a,b)$ on $\left(0, -\frac{\ln(R)}{\ln(1-p)}\right)$,

$$E\left[\alpha^n\right] = \int_0^{-\frac{\ln(R)}{\ln(1-p)}} \alpha^n \frac{\alpha^{a-1}\left(-\frac{\ln(R)}{\ln(1-p)} - \alpha\right)^{b-1}}{B(a,b)\left(-\frac{\ln(R)}{\ln(1-p)}\right)^{a+b-1}}\, d\alpha \tag{58}$$

$$= \left(-\frac{\ln(R)}{\ln(1-p)}\right)^n \int_0^{-\frac{\ln(R)}{\ln(1-p)}} \frac{\alpha^{a+n-1}\left(-\frac{\ln(R)}{\ln(1-p)} - \alpha\right)^{b-1}}{B(a,b)\left(-\frac{\ln(R)}{\ln(1-p)}\right)^{a+n+b-1}}\, d\alpha \tag{59}$$

$$= \left(-\frac{\ln(R)}{\ln(1-p)}\right)^n \frac{B(a+n,b)}{B(a+b)} \tag{60}$$

$$= \left(-\frac{\ln(R)}{\ln(1-p)}\right)^n \frac{\Gamma(a+b)\Gamma(a+n)}{\Gamma(a)\Gamma(a+b+n)} \tag{61}$$

for $n \geq 0$, and the expected value for the spreading speed is

$$E\left[c^*\right] = \sqrt{2\sigma^2 p^{\beta} \ln(R)} \sum_{n=0}^{\infty} \binom{\frac{1}{2}}{n} \left(\frac{\ln(1-p)}{\ln(R)}\right)^n \left(-\frac{\ln(R)}{\ln(1-p)}\right)^n \frac{\Gamma(a+b)\Gamma(a+n)}{\Gamma(a)\Gamma(a+b+n)} \tag{62}$$

$$= \sqrt{2\sigma^2 p^{\beta} \ln(R)} \frac{\Gamma(a+b)}{\Gamma(a)} \sum_{n=0}^{\infty} \binom{\frac{1}{2}}{n} (-1)^n \frac{\Gamma(a+n)}{\Gamma(a+b+n)} \tag{63}$$

Using the fact that

$$\sum_{n=0}^{\infty} \binom{\frac{1}{2}}{n} (-1)^n \frac{\Gamma(a+n)}{\Gamma(a+b+n)} = \frac{\Gamma\left(b+\frac{1}{2}\right)\Gamma(a)}{\Gamma\left(a+b+\frac{1}{2}\right)\Gamma(b)}, \tag{64}$$

we can simplify (63) to

$$E\left[c^*\right] = \sqrt{2\sigma^2 p^\beta \ln(R)} \frac{\Gamma(a+b)\Gamma\left(b+\frac{1}{2}\right)}{\Gamma(b)\Gamma\left(a+b+\frac{1}{2}\right)}. \tag{65}$$

Attempting to determine the optimal resource allocation to dispersal, we find that there are no critical points for $0 < p < 1$ since

$$\frac{d}{dp} E\left[c^*\right] = \sqrt{2\sigma^2 \ln(R)} \frac{\Gamma(a+b)\Gamma\left(b+\frac{1}{2}\right)}{\Gamma(b)\Gamma\left(a+b+\frac{1}{2}\right)} \frac{d}{dp} p^{\frac{\beta}{2}} \tag{66}$$

$$= \sqrt{2\sigma^2 \ln(R)} \frac{\Gamma(a+b)\Gamma\left(b+\frac{1}{2}\right)}{\Gamma(b)\Gamma\left(a+b+\frac{1}{2}\right)} \frac{\beta}{2} p^{\frac{\beta}{2}-1} \tag{67}$$

$$> 0. \tag{68}$$

Therefore, we can conclude that the best resource allocation would be to allocate as many resources as possible to dispersal while still maintaining the persistence condition that $(1-p)^\alpha R > 1$. This would mean that

$$p < 1 - \frac{1}{\sqrt[\alpha]{R}}. \tag{69}$$

Therefore, we would want to choose p as close to $1 - \frac{1}{\sqrt[\alpha]{R}}$ as possible without reaching or going over this value. □

Proof of Theorem 5.

Proof. Assuming that σ is a random variable defined on the real line with probability density function $f_3(\sigma)$, the expected spreading speed is given by

$$E\left[c^*\right] = \int_0^\infty \sqrt{2p^\beta \sigma^2 \ln[(1-p)^\alpha R]} f_3(\sigma)\, d\sigma \tag{70}$$

$$= \sqrt{2p^\beta \ln[(1-p)^\alpha R]} \int_0^\infty \sigma f_3(\sigma)\, d\sigma \tag{71}$$

$$= \sqrt{2p^\beta \ln[(1-p)^\alpha R]} E\left[\sigma\right]. \tag{72}$$

Determining the optima resource allocation to dispersal, we find that

$$0 = \frac{d}{dp}E\left[c^*\right] \tag{73}$$

$$= E[\sigma]\frac{d}{dp}\sqrt{2p^\beta \ln[(1-p)^\alpha R]} \tag{74}$$

$$= E[\sigma]p^\beta \frac{\frac{\ln((1-p)^\alpha R)}{p} - \frac{\alpha}{1-p}}{\sqrt{2p^\beta \ln\left((1-p)^\alpha R\right)}}. \tag{75}$$

Hence, we have our critical point when

$$\frac{\ln\left((1-p)^\alpha R\right)}{p} = \frac{\alpha}{1-p}. \tag{76}$$

□

Proof of Theorem 6.

Proof. Assuming that $\ln(R)$ is a random variable defined on $(-\alpha\ln(1-p), \infty)$ with probability density function $f_4(\ln(R))$, the expected spreading speed is given by

$$E\left[c^*\right] = \int_{-\alpha\ln(1-p)}^{\infty} \sqrt{2p^\beta\sigma^2 \ln[(1-p)^\alpha R]} f_4(\ln(R))\, d\ln(R) \tag{77}$$

$$= \sqrt{2p^\beta\sigma^2}\int_{-\alpha\ln(1-p)}^{\infty} \sqrt{\ln[(1-p)^\alpha R]} f_4(\ln(R))\, d\ln(R) \tag{78}$$

$$= \sqrt{2p^\beta\sigma^2}\int_{-\alpha\ln(1-p)}^{\infty} \sqrt{\alpha\ln(1-p)+\ln(R)} f_4(\ln(R))\, d\ln(R) \tag{79}$$

$$= \sqrt{2p^\beta\sigma^2} E\left[\left(\ln(R)+\alpha\ln(1-p)\right)^{\frac{1}{2}}\right]. \tag{80}$$

Assuming that $\ln(R) \sim \text{Gamma}(a,b)$ on $(-\alpha\ln(1-p), \infty)$, we define $r = \ln(R)+$

$\alpha(1-p)$ and calculate the one halfth moment to be

$$
\begin{aligned}
E\left[(\ln(R)+\alpha\ln(1-p))^{\frac{1}{2}}\right] &= E\left[r^{\frac{1}{2}}\right] && (81)\\
&= \int_{-\alpha\ln(1-p)}^{\infty} r^{\frac{1}{2}} f_4(\ln(R))\,d\ln(R) && (82)\\
&= \int_{-\alpha\ln(1-p)}^{\infty} r^{\frac{1}{2}} \frac{1}{\Gamma(a)b^a} r^{a-1} e^{-\frac{r}{b}}\,d\ln(R) && (83)\\
&= \frac{1}{\Gamma(a)b^a}\int_{-\alpha\ln(1-p)}^{\infty} r^{a+\frac{1}{2}-1} e^{-\frac{r}{b}}\,d\ln(R) && (84)\\
&= \frac{1}{\Gamma(a)b^a}\Gamma\left(a+\frac{1}{2}\right) b^{a+\frac{1}{2}} && (85)\\
&= \frac{\Gamma\left(a+\frac{1}{2}\right) b^{\frac{1}{2}}}{\Gamma(a)}. && (86)
\end{aligned}
$$

Then, using (86) the expected spreading speed becomes

$$
\begin{aligned}
E\left[c^*\right] &= \sqrt{2p^\beta\sigma^2}\,E\left[(\ln(R)+\alpha\ln(1-p))^{\frac{1}{2}}\right] && (87)\\
&= \sqrt{2p^\beta\sigma^2}\frac{\Gamma\left(a+\frac{1}{2}\right) b^{\frac{1}{2}}}{\Gamma(a)} && (88)\\
&= \sqrt{2p^\beta\sigma^2 b}\frac{\Gamma\left(a+\frac{1}{2}\right)}{\Gamma(a)}. && (89)
\end{aligned}
$$

Determining the optimal resource allocation to dispersal, we find that

$$
\begin{aligned}
\frac{d}{dp}E\left[c^*\right] &= \frac{d}{dp}\sqrt{2p^\beta\sigma^2 b}\frac{\Gamma\left(a+\frac{1}{2}\right)}{\Gamma(a)} && (90)\\
&= \sqrt{2\sigma^2 b}\frac{\Gamma\left(a+\frac{1}{2}\right)}{\Gamma(a)}\frac{\beta}{2}p^{\frac{\beta}{2}-1} && (91)\\
&> 0. && (92)
\end{aligned}
$$

Therefore, we can conclude that the best resource allocation would be to allocate as many resources as possible to dispersal while still maintaining the persistence condition that $(1-p)^\alpha R > 1$. This would mean that

$$
p < 1 - \frac{1}{\sqrt[\alpha]{R}}. \tag{93}
$$

Therefore, we would want to choose p as close to $1-\frac{1}{\sqrt[\alpha]{R}}$ as possible without reaching or going over this value. □

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