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Consequences of dispersal heterogeneity for population spread and persistence

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Abstract

Dispersal heterogeneity is increasingly being observed in ecological populations and has long been suspected as an explanation for observations of non-Gaussian dispersal. Recent empirical and theoretical studies have begun to confirm this. Using an integro-difference model, we allow an individual's diffusivity to be drawn from a trait distribution and derive a general relationship between the dispersal kernel's moments and those of the underlying heterogeneous trait distribution. We show that dispersal heterogeneity causes dispersal kernels to appear leptokurtic, increases the population's spread rate, and lowers the critical reproductive rate required for persistence in the face of advection. Wavespeed has been shown previously to be determined largely by the form of the dispersal kernel tail. We qualify this by showing that when reproduction is low, the precise shape of the tail is less important than the first few dispersal moments such as variance and kurtosis. If the reproductive rate is large, a dispersal kernel's asymptotic tail has a greater influence over wavespeed, implying that estimating the prevalence of traits which correlate with long-range dispersal is critical. The presence of multiple dispersal behaviors has previously been characterized in terms of long-range vs short-range dispersal, and it has been found that rare long-range dispersal essentially determines wavespeed. We discuss this finding and place it within a general context of dispersal heterogeneity showing that the dispersal behavior with the highest average dispersal distance does not always determine wavespeed.

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1 Introduction

Intraspecific heterogeneity in individual traits, such as survival and reproduction, is common in ecological populations and can result from habitat heterogeneity (e.g., Gates and Gysel, 1978; Boulding and Van Alstyne, 1993; Menge et al, 1994; Winter et al, 2000; Franklin et al, 2000; Manolis et al, 2002; Bollinger and Gavin, 2004; Landis et al, 2005), early life conditions such as birth order effects (e.g., Lindström, 1999), unequal allocation of parental care (e.g., Manser and Avey, 2000; Johnstone, 2004), maternal family effect (e.g., Fox et al, 2006), persistent social rank (e.g., von Holst et al, 2002), or genetics (e.g., Yashin et al, 1999; Ducrocq et al, 2000; Gerdes et al, 2000; Casellas et al, 2004; Isberg et al, 2006).

In spite of this widespread occurrence, intraspecific heterogeneity has only recently begun to receive considerable theoretical treatment. It has been shown to affect demographic stochasticity (Fox and Kendall, 2002; Kendall and Fox, 2002; Kendall and Fox, 2003; Vindenes et al, 2008), extinction risk of both density-independent populations (Conner and White, 1999; Fox, 2005; Lloyd-Smith et al, 2005) and density-dependent populations (Robert et al, 2003), population growth rate (Kendall et al, 2011), and equilibrium population size (Stover et al, 2012). We aim to expand this literature to include dispersal heterogeneity's effect on spread rate and persistence in advective environments.

Studies of dispersal have usually assumed identical dispersal behavior among individuals although heterogeneity in dispersal ability or behavior is ubiquitous (c.f. Zera and Denno, 1997; Table 1 in Clobert et al, 2009), and is important for understanding biological phenomena such as invasions (Shigesada and Kawasaki, 1997) and the spread of alleles through a population (Fisher, 1937). Dispersal heterogeneity has been observed across a variety of taxa including cane toads (Phillips et al, 2006), rodent-dispersed trees (Xiao et al, 2005), flowering plants (e.g. Venable et al, 1995), dragonflies (McCauley, 2010), and freshwater killifish (Fraser et al, 2001) to name a few examples. Understanding dispersal presents a particular challenge due to the variety of dispersal mechanisms and the difficulty in accounting for rare dispersal events which have been shown to have a strong influence on spread rate (Shigesada and Kawasaki, 1997; Clark et al, 1998; Okubo and Levin, 2001).

Dispersal is especially important for populations living in advective environments (i.e. subject to unidirectional flow) due to the risk of being washed away. This may include species that are subject to long-shore drift currents (Byers and Pringle, 2006), flow in a river or stream (Speirs and Gurney, 2001), or facing pressures due to climate change (Potapov and Lewis, 2004). Persistence in an advective environment depends in part on the population's ability to disperse individuals upstream (Lutscher et al, 2010). The minimum reproductive rate needed for persistence also depends on the population's upstream dispersal ability. Understanding the impact heterogeneity has on dispersal is important to understanding

how populations persist in the face of advection.

The effect of dispersal heterogeneity on spatial spread has been explored only in a few special cases. Clark et al (1998) showed that when a small part of the population disperses according to a fatter-tailed kernel, a significantly higher wavespeed results. Neubert and Caswell (2000) considered a neotropical plant which is dispersed by four ant species, and the plant population's spread rate was essentially determined by one of the ant species due to its much greater dispersal distances. Okubo and Levin (2001) showed that a composite two-Gaussian kernel is leptokurtic (having positive excess kurtosis), and that when one variance is held fixed, and the other increases, then the kurtosis of the composite kernel increases and approaches that of the Laplace (double-sided exponential) distribution. Murray (2002) analyzed a Fisher-Kolmogorov equation model, where one phenotype is a disperser and the other is a non-disperser, and showed that the wavespeed increases when a greater proportion of individuals are dispersers. Shigesada and Kawasaki (2002) showed that increasing the proportion of long-range dispersers or their dispersal variance increases wavespeed in an integro-difference model. However, dispersal variance has a strong influence on wavespeed, and of these five studies, only Clark et al (1998) held the variance of the population dispersal kernel constant while changing the long-range dispersal component of the population.

Individual dispersal is often modeled as diffusion, where the location of the dispersing individual after some specified time is given by a Gaussian distribution (Okubo and Levin, 2001; Murray, 2002). However, empirical observations often show that long-range dispersal events occur more frequently and at greater extremes than would be expected if dispersal was truly Gaussian (e.g. Nathan, 2001; Delgado and Penteriani, 2008) — these dispersal patterns are commonly referred to as ‘fat-tailed’, ‘heavy-tailed’, or ‘leptokurtic’.

Heterogeneity has long been postulated as a cause for this preponderance of long-range dispersal (e.g. Dobzhansky and Wright, 1943). Skellam (1951) showed that having each individual's dispersal variance chosen from some probability distribution results in a leptokurtic dispersal kernel. The hypothesis that heterogeneity might explain the prevalence of long-range dispersal observed in ecological populations has more recently been confirmed mathematically in several studies (Skalski and Gilliam, 2000, 2003; Petrovskii et al, 2008; Petrovskii and Morozov, 2009). Petrovskii et al (2008) and Petrovskii and Morozov (2009) constructed model populations of dispersers in which each individual's diffusion coefficient is drawn from a continuous distribution and showed that the tail of the resulting population dispersal function decays slower than a Gaussian. However, these studies did not examine how a population's rate of spread is affected by heterogeneity in dispersal.

Wavespeed has been found to be highly dependent on the dispersal kernel tail (Kot et al, 1996) and to be determined by rare long-range dispersers (Neubert and Caswell, 2000; Okubo and Levin, 2001). We qualify this finding by discussing how

wavespeed depends on the moments of the dispersal kernel and reproduction and how to understand these findings within the general framework of dispersal heterogeneity. We use the term ‘diffusivity’ to refer to an individual’s diffusion coefficient and show how heterogeneity in diffusivity affects the shape of the population dispersal kernel. A general relationship between the dispersal kernel moments and the moments of the underlying trait distribution is derived. We describe scenarios where different dispersal behaviors have varying influence on wavespeed and also on the critical reproductive rate required for persistence in an advective environment. Using these results, we show how dispersal heterogeneity affects spread rate both in advective and non-advective environments and how heterogeneity impacts the critical reproductive rate needed for persistence under advective flow.

2 Model framework

The basic linear one-dimensional integro-difference model, which arises by linearizing many non-linear, spatially homogeneous, non-stage-structured integro-difference models around $n = 0$ (Kot et al, 1996), is given as

$$n(x, t + 1) = R \int_{-\infty}^{\infty} K(x - y)n(y, t)dy \quad (1)$$

where $n(x, t)$ is the population density at location x and time t , and R is the net reproductive rate. Given mean dispersal location μ , the *dispersal kernel* K is given as $K(u) = f(u - \mu)$, where f is called the *displacement kernel*. The displacement kernel is assumed to be a symmetric mean-zero distribution that describes an offspring’s displacement from the mean dispersal location μ . The system is called advective when the mean is nonzero such as in the presence of a unidirectional wind or flow of water. In each time step, the population reproduces at net rate R and then dies. The new offspring then disperse according to the kernel K . A semelparous aquatic insect living in a flowing stream is the example we keep in mind during the analysis of this model.

This model exhibits convergence to traveling wave solutions with a constant asymptotic speed c^* for dispersal kernels with exponentially bounded tails and compactly supported initial conditions (Kot et al, 1996). When advection is present (μ is non-zero) there is a critical net reproductive rate R^* such that the population only persists when $R > R^*$ (Lutscher et al, 2010). Under advection, there are constant wavespeeds for both upstream (possibly negative speed) and downstream movement of the population. When we discuss advection, by convention we consider the current drifting from right to left, hence a negative drift speed ($\mu < 0$).

The dispersal kernel K is assumed to have exponentially bounded tails so that

the moment generating function exists and is defined as

$$M_K(s) = \int_{-\infty}^{\infty} K(x)e^{xs} dx, \quad (2)$$

which can be written as the power series

$$M_K(s) = 1 + m_{K,1}s + m_{K,2}\frac{s^2}{2!} + m_{K,3}\frac{s^3}{3!} + \dots \quad (3)$$

The coefficients in (3) depend on the raw moments of dispersal: $m_{K,k} = E^K(x^k)$ (the expectation, according to the probability distribution K , of the dispersal distance raised to the k^{th} power) for $k \geq 1$. The central moments of K will be denoted by $\mu_{K,k} = E^K((x - \mu)^k)$. The moments of f are equivalent to the central moments of K . Because we assume symmetry about the mean, all odd moments of f are zero: $E^f(x^{2k-1}) = 0$ for $k \geq 1$ (i.e. all odd central moments of K are zero).

The second moment of f is the dispersal variance $\mu_{f,2} = \sigma^2$, which describes the ‘width’ of the distribution. The normalized fourth central moment is the kurtosis, or peakedness: $\mu_{f,4}/\sigma^4$ and describes how much weight is in the tail of the distribution as opposed to the shoulders (Balanda and Macgillivray, 1988; DeCarlo, 1997). The *excess kurtosis* $\gamma_{f,2}$ is often referred to instead which is the kurtosis minus three (since the kurtosis of a Gaussian is three). A distribution with positive excess kurtosis is called ‘leptokurtic’. The skewness is the normalized third central moment: $\gamma_{f,1} = \mu_{f,3}/\sigma^{3/2}$, which is zero for the dispersal kernels under current consideration.

The terms ‘fat-tailed’ and ‘heavy-tailed’ have been loosely used to describe distributions with a positive excess kurtosis, signifying that long-distance dispersal events occur more frequently than would be expected if Gaussian diffusion alone were operating. Confusingly, these terms have also been used to refer to distributions whose asymptotic tails are not exponentially bounded; they may have some (or all) undefined moments and thus no moment generating function (c.f. Kot et al, 1996, Clark et al, 1998). Leptokurtic kernels may still exhibit Gaussian tail decay (c.f. Okubo and Levin, 2001; Petrovskii and Morozov, 2009). This conflation is unfortunate because only exponentially bounded kernels (those whose tails decay at least exponentially fast) produce constant spread rates (Kot et al, 1996). The term ‘heavy tailed’ is the preferred technical term used to refer to distributions whose tails are not exponentially bounded (Foss et al, 2011).

The asymptotic upstream (which is to the right by convention here) wavespeed is given by

$$c^* = \min_{s>0} \left\{ \frac{1}{s} \ln RM(s) \right\}. \quad (4)$$

Equation (4) is attributed originally to Weinberger (1978, 1982) and further developed by Lui (1989) and others; for more straightforward derivations, see Kot

et al (1996) for an unstructured population and Neubert and Caswell (2000) for a structured population. The critical reproductive rate in a system with finite advection ($\mu < 0$) is given by

$$R^* = \frac{1}{\min_{s>0}\{M_K(s)\}} = \max_{s>0} \left\{ \frac{1}{M_K(s)} \right\} \quad (5)$$

(Lutscher et al, 2010). The values of s where the minima in (4) and (5) occur, s_c^* and s_R^* respectively, are shape parameters that give the exponential rate of decay of the upstream wavefront. Usually, $s_c^* \neq s_R^*$; equality between the two shape parameters holds when $R = R^*$ and the upstream wavespeed is zero.

To solve for wavespeed, the following parametric representation is often used:

$$R = \frac{e^{sM'_K(s)/M_K(s)}}{M_K(s)}, \quad c = \frac{M'_K(s)}{M'_K(s)}. \quad (6)$$

For a given R , one would solve the left equation for the shape parameter s_c^* and then plug it in to the right equation so get c^* .

When the dispersal kernel has mean zero (no advection), the critical reproductive rate is $R^* = 1$ (Kot et al, 1996). In the presence of advection, $R^* > 1$. In either case, the population persists everywhere in the domain when $R > R^*$ (Lutscher et al, 2010). In the presence of advection, a critical population ($R = R^* > 1$) has an exponentially shaped, stationary wavefront ($c^* = 0$), in which case the shape parameters from (4) and (5) are equivalent ($s_c^* = s_R^*$). When $1 < R < R^*$, the population still has an exponential shape given by s_c^* , but is washed downstream (negative wavespeed) while its total size still grows (assuming a suitable initial population and infinite downstream habitat). If $R < 1$, the population simply dies out.

3 Dispersal heterogeneity

We assume that offspring disperse in a one-dimensional environment (such as wind or stream flow) with a fixed drift velocity v ($v < 0$ by convention). The position at time τ of an offspring with dispersal diffusivity D (diffusion coefficient) is given by a Gaussian distribution with mean $\mu = v\tau$ and variance $\sigma^2 = 2D\tau$. These expressions may be derived from a random walk where dispersing individuals takes steps of length L with inter-step time T in either direction equally likely while drifting with constant velocity v . It is assumed that the ratio $L^2/(2T)$ converges as L and T go to zero, thusly, the ratio converges to the diffusivity constant D (see Okubo and Levin, 2001; Murray, 2002). Since heterogeneity in either L or T is expressed through differences among individuals in their diffusivity, we focus on heterogeneity in D . We assume that all dispersing individuals are subject to

the same drift velocity v and settle after a fixed time τ so that the displacement kernel is Gaussian.

We now derive a relationship between the distribution of offspring diffusivities and the population dispersal kernel. Let $\phi(D)$ be the probability distribution of offspring diffusivities which we call the *trait distribution*. We require that $\phi(D)$ be exponentially bounded as D goes to infinity. Zero parent-offspring correlation in diffusivity is assumed, so each individual offspring's diffusivity is an independent draw from $\phi(D)$. This assumption is appropriate in some ecological scenarios, such as the ant-mediated dispersal in [Neubert and Caswell \(2000\)](#). We denote the mean zero Gaussian with variance σ^2 as $G(x; \sigma^2)$. The displacement kernel f is then given by integrating over the distribution of offspring diffusivities:

$$f(x) = \int_0^\infty \phi(D)G(x; 2D\tau)dD. \quad (7)$$

We first wish to understand how dispersal heterogeneity affects the shape of the kernel. The $2k^{\text{th}}$ central moment of the population dispersal kernel is

$$m_{f,2k} = \int x^{2k} \int \phi(D)G(x; 2D\tau)dDdx \quad (8)$$

Changing the order of integration and noting that the $2k^{\text{th}}$ central moment of the Gaussian is $(2k - 1)!!\sigma^{2k}$ (where $k!!$ denotes the double factorial, which is the product of all odd numbers from k to 1 when k is odd), the right side of (8) becomes $(2k - 1)!!(2\tau)^k \int D^k \phi(D)dD$ which simplifies to $(2k - 1)!!(2\tau)^k m_{\phi,k}$. Thus we find that the k^{th} moment of the trait distribution gives the $2k^{\text{th}}$ moment of the population's displacement kernel:

$$m_{f,2k} = (2k - 1)!!(2\tau)^k m_{\phi,k}. \quad (9)$$

This has been shown previously by [Skellam \(1951\)](#) who examined heterogeneity in dispersal variance (which is proportional to diffusivity). The moment generating functions for f and ϕ are related by $M_f(s) = M_\phi(s^2)$ ([Skellam, 1951](#)).

The variance of the displacement kernel depends only on the mean of the trait distribution:

$$\sigma_f^2 = 2\bar{D}\tau, \quad (10)$$

where the expected diffusivity is $E^\phi(D) = \bar{D}$.

The excess kurtosis of the displacement kernel is given by

$$\gamma_{f,2} = \frac{m_{f,4}}{m_{f,2}^2} - 3 = 3 \frac{m_{\phi,2}}{m_{\phi,1}^2} - 3 = 3 \frac{\text{Var}(D)}{\bar{D}^2}, \quad (11)$$

and only depends on the mean and variance of the trait distribution.

Since the raw moments of the displacement kernel f are equivalent to the central moments of the dispersal kernel K , the dispersal variance is given by (10)

and the dispersal kurtosis is given by (11). This is a consequence of the assumption that all dispersers are subject to the same advection velocity and disperse for the same length of time τ . For the remainder of the paper, we assume $\tau = 1$ so that the mean dispersal location is equivalent in magnitude to the advection velocity, $\mu = v$.

From (11), it is evident that increasing the variance of the trait distribution (while holding the mean trait constant) increases the kurtosis of the population dispersal kernel. Thus heterogeneity in diffusivity naturally results in a leptokurtic dispersal kernel, a result also shown previously by Skellam (1951).

For concreteness, we illustrate this result and its consequences with two trait distributions, which we will use throughout the rest of the paper. The first is the gamma trait distribution studied by Petrovskii and Morozov (2009):

$$\phi_{\Gamma}(D) = \frac{D^B}{\alpha^{B+1}\Gamma(B+1)} \exp\left(-\frac{D}{\alpha}\right), \quad (12)$$

where $\Gamma(\cdot)$ is the gamma function, α and B are a fixed positive numbers, and D is the diffusivity. The dispersal kernel which arises from the gamma trait distribution will also arise if instead of heterogeneity in D , offspring have gamma-distributed settling times (Yasuda, 1975; Yamamura, 2002). The second trait distribution, $\phi_{\delta}(D)$, includes only two dispersal phenotypes with diffusivities $D_1 = \bar{D}(1 - h_1)$ and $D_2 = \bar{D}(1 + h_2)$ for $0 \leq h_1 \leq 1$ and $h_2 \geq 0$. With probability $1 - p$ an offspring has diffusivity D_1 and with probability p diffusivity D_2 , where $p = h_1/(h_1 + h_2)$ so that \bar{D} is the average diffusivity between the two types of offspring. This second trait distribution takes the form

$$\phi_{\delta}(D) = (1 - p)\delta_{D_1}(D) + p\delta_{D_2}(D) \quad (13)$$

where δ_{D_i} is the delta distribution with mass one at D_i . When $h_1 = 1$, phenotype one is non-dispersing (a case studied by Murray (2002) in the context of Fisher-Kolmogoroff diffusion equations).

The displacement kernel resulting from (12), $f_{\Gamma}(x)$, cannot be written down in a simple form, but its moment generating function is easily calculated (see next section). Petrovskii and Morozov (2009) showed that the decay rate in the tail of $f_{\Gamma}(x)$ is slower than Gaussian but still exponentially bounded. If a maximum diffusivity is imposed (i.e. no disperser has diffusivity larger than some maximum D_{max}), the displacement kernel tail is asymptotically Gaussian irrespective of the shape of the trait distribution (Petrovskii and Morozov, 2009). A distribution $K(x)$ is called asymptotically Gaussian if $K(x) \sim Ce^{-ax^2}$ for some positive C and a when x is large. Since the two-type trait distribution ϕ_{δ} has a maximum diffusivity, the corresponding displacement kernel has a tail which is asymptotically Gaussian, and in fact is exactly a linear combination of two Gaussian kernels.

The k^{th} raw moment for ϕ_δ is

$$m_{\phi_\delta, k} = \bar{D}^k \left(\frac{h_2(1-h_1)^k + h_1(1+h_2)^k}{h_1+h_2} \right), \quad (14)$$

and for ϕ_Γ is

$$\begin{aligned} m_{\phi_\Gamma, k} &= \alpha^k \frac{\Gamma(B+1+k)}{\Gamma(B+1)} \\ &= \alpha^k (B+k)(B+k-1) \cdots (B+2). \end{aligned} \quad (15)$$

Simplified formulas for the first few central moments of the trait distributions are given in Table 1.

central moments	trait distribution	
	two-type, ϕ_δ	gamma, ϕ_Γ
$E[D]$	\bar{D}	$\alpha(B+1)$
σ_D^2	$\bar{D}^2 h_1 h_2$	$\alpha^2(B+1)$
$\mu_{\phi, 3}$	$\bar{D}^3 h_1 h_2 (h_2 - h_1)$	$2\alpha^3(B+1)$
$\mu_{\phi, 4}$	$\bar{D}^4 h_1 h_2 (h_2^2 - h_1 h_2 + h_1^2)$	$3\alpha^4(B+1)(B+3)$

Table 1: Central moments are given for two trait distributions ϕ_Γ (12) and ϕ_δ (13).

The displacement kernels f_Γ and f_δ have identical variances when their underlying trait distributions have the same mean (i.e. when $E^{\phi_\delta}(D) = \bar{D} = \alpha(B+1) = E^{\phi_\Gamma}(D)$). However, if one trait distribution has a larger variance than the other, its corresponding kernel will have a greater excess kurtosis (11). Since the two-type trait distribution can have a higher variance than the gamma trait distribution and the kurtosis of the dispersal kernel is proportional to trait variance (11), f_δ can have a larger kurtosis than f_Γ . This reveals that a larger kurtosis is not necessarily associated with a slower tail decay rate.

When the trait variance is small and identical among the two different trait distributions, the corresponding dispersal kernels appear nearly identical. A large trait variance can cause dispersal kernels arising from the different trait distributions to have clearly different shapes (Fig. 1). The gamma trait distribution results in a slower dispersal kernel tail decay rate than that of the two-type model (Fig. 1, inset panel). When the two-type trait distribution matches the skew of the gamma trait distribution, the corresponding displacement kernel appears nearly Gaussian due to high diffusivity being rare.

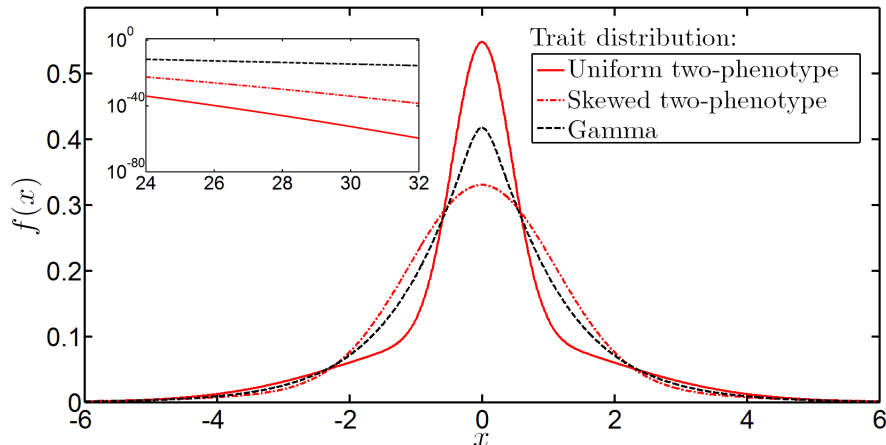


Figure 1: The displacement kernels are shown for three trait distributions with $\bar{D} = \tau = 1$ and $\text{Var}(D) = 0.81$. The kernels appear quite different although they share the same variance ($\text{Var}(x) = 2$) and kurtosis ($\gamma_{f,2} = 2.43$), and additionally the kernels from the skewed two-type and gamma trait distributions have the same sixth dispersal moment ($m_{\Gamma,6} \approx 170.36$; $m_{f,6} \approx 87.48$ for the uniform two-type trait distribution). The subpanel shows the tails of the dispersal kernels for large x .

4 How dispersal kernel shape impacts c^* and R^*

In this section, we discuss generally how wavespeed and the critical reproductive rate are impacted by dispersal kernel shape. The individual moments of the dispersal kernel are shown to have differing degrees of importance depending on the magnitude of the reproductive rate. We show that a single low-order dispersal moment is sometimes sufficient enough to determine whether or not one dispersal kernel imparts a larger wavespeed or a smaller critical reproductive rate when compared to another kernel.

Consider two symmetric, exponentially-bounded displacement kernels f_1 and f_2 such that $f_2(x) > f_1(x)$ for x sufficiently large. For our purposes, we say that f_2 has slower tail decay. Slower tail decay of f_2 guarantees that all sufficiently high-order dispersal moments are larger, $m_{f_2,2n} > m_{f_1,2n}$ for all n large enough (Appendix A.1). However, a displacement kernel with faster tail decay may still have one or more lower-order moments which are larger, such as variance or kurtosis. If there are N_1 and N_2 such that $m_{f_1,2n} \geq m_{f_2,2n}$ for $n \leq N_1$, but at least one $n \leq N_1$ such that $m_{f_1,2n} > m_{f_2,2n}$, and $m_{f_1,2n} < m_{f_2,2n}$ for $n \geq N_2$, we say that f_1 has *low-order dominance* over f_2 and equivalently say that f_2 is *high-order dominant*. Note that the low-order dominant kernel f_1 must have at least one moment which is strictly larger than that of f_2 . The concepts of high- and low-order

dominance transfer to dispersal kernels in the obvious way since we only compare dispersal kernels with the same mean.

We now show that a low-order dominant dispersal kernel can produce a larger wavespeed and a smaller critical reproductive rate than a kernel that has slower tail decay and is high-order dominant. If a single dispersal kernel is referred to as being low-order dominant, it is to be assumed that it is in comparison to another dispersal kernel which is high-order dominant, and vice versa.

4.1 Wavespeed in absence of advection

Consider kernels f_1 and f_2 where f_2 has slower tail decay, but kernel f_1 is low-order dominant and f_2 is high-order dominant. The corresponding moment-generating functions satisfy $M_1(s) > M_2(s)$ for s small enough (see Appendix A for detailed mathematical justification; Figure 2 illustrates this). To understand this fact, recall that the moment generating functions can be written as power series in s centered about $s = 0$. Hence, for s small enough, higher order terms are small in magnitude due to large powers of s .

Also, note that $M_1(s) < M_2(s)$ for s large enough since f_2 has larger high-order moments. Since the moment generating functions are continuous, they must cross paths at least once. Define \hat{s} to be the smallest value of s such that $M_1(\hat{s}) = M_2(\hat{s})$. Above \hat{s} , the graphs of M_1 and M_2 may intersect again, but for all s large enough $M_2(s) > M_1(s)$.

We now show that a population dispersing according to the low-order dominant kernel f_1 is guaranteed to have a larger wavespeed than a population dispersing by f_2 if the net reproductive rate is fixed close enough to one, even if f_2 has much more weight in its tail than f_1 . Appendix A shows this in a more rigorous, analytical way.

Define the wavespeed function, which is the function we minimize in (4) to find the asymptotic wavespeed, for kernel i by

$$c_i(s) = \frac{1}{s} \ln(RM_i(s)). \quad (16)$$

Since $M_1(s) > M_2(s)$ for $s < \hat{s}$, this also implies that $c_1(s) > c_2(s)$ for $s < \hat{s}$ as well due to monotonicity of the logarithm function. As R approaches one from above, the critical shape parameter s^* and wavespeed c^* approach zero (see Appendix A.2). Thus we can choose R close enough to one to ensure that the critical shape parameters for both f_1 and f_2 ($s_{c_1}^*$ and $s_{c_2}^*$, respectively) fall in the region where $M_1(s) > M_2(s)$ (see Figure 2). Standard mathematical analysis ensures that if both $c_1(s)$ and $c_2(s)$ have a local minimum in the interval $0 < s < \hat{s}$, where $c_1(s) > c_2(s)$, then $\min c_1(s) > \min c_2(s)$. When using (4) to calculate the wavespeeds, we have

$$c_1^* = c_1(s_{c_1}^*) = \min_{s>0} c_1(s) > \min_{s>0} c_2(s) = c_2(s_{c_2}^*) = c_2^*. \quad (17)$$

Hence slower tail decay alone does not automatically result in higher wavespeed, even if comparing kernels that have a number of identical low-order moments.

It is important to note that $s_{c_1}^*$ and $s_{c_2}^*$ can be distinct (and likely will be). Note that in practice R need not be extremely close to one for our results to hold; $R = 4.6$ in Figure 2 for two example kernels. This argument only declares existence of such an R value. The parameters are deliberately chosen in Figure 2 to make the differences in the graphs more apparent. In order for $c_\delta^* < c_\Gamma^*$ with the parameters as in Figure 2, $R = 537$ is required, hence quite a large R may be necessary for a high-order dominant kernel to give larger wavespeeds.

4.2 Critical reproduction and wavespeed under advection

When advection is present with dispersal mean $\mu < 0$, the moment generating functions for dispersal kernels $K_1(x) = f_1(x - \mu)$ and $K_2(x) = f_2(x - \mu)$ are simply $M_1(s)e^{\mu s}$ and $M_2(s)e^{\mu s}$ respectively. Following a similar argument as above with wavespeed, define the reproductive rate function $R_i(s)$, whose maximum (5) is the critical reproductive rate, and satisfies for $s < \hat{s}$:

$$R_1(s) = \frac{1}{M_1(s)e^{\mu s}} < \frac{1}{M_2(s)e^{\mu s}} = R_2(s) \quad (18)$$

since $M_1(s) > M_2(s)$. As long as the advective current is weak enough (μ close enough to zero) both critical shape parameters, $s_{R_1}^*$ and $s_{R_2}^*$, which give the critical reproductive rates using (5) are less than \hat{s} so that the critical reproductive rates satisfy

$$R_1^* = R_1(s_{R_1}^*) = \max_{s>0} R_1(s) < \max_{s>0} R_2(s) = R_2(s_{R_2}^*) = R_2^*. \quad (19)$$

Hence a low-order dominant dispersal kernel with faster tail decay can give a lower critical reproductive rate than a high-order dominant kernel with slower tail decay in sufficiently weak advective currents. It is not necessary that μ be extremely close to zero; for example, $\mu = -5.5$ in Figure 2, again for a somewhat extreme example. An advection velocity of $\mu = -8.9$ is required to make $R_\delta^* > R_\Gamma^*$ for the remaining parameters chosen in Figure 2.

Now that we have established that a weak enough advective current allows for $R_1^* < R_2^*$, even though f_2 has more weight in its tail than f_1 , we can show that under advection, $c_1^* > c_2^*$ is also possible.

Recall that the moment generating function with advection is identical to that without advection but multiplied by $e^{\mu s}$. The $c_i(s)$ (16) become

$$c_i(s) = \frac{1}{s} \ln(RM_i(s)e^{\mu s}) = \frac{1}{s} \ln(RM_i(s)) + \mu. \quad (20)$$

Hence the wavespeed under advection is just that without advection plus the advection speed μ . This alone however is not enough to show the result. We need

R to be small enough in order for $c_1^* > c_2^*$ (17) to hold, but R_1^* and R_2^* are greater than one and may be unequal. Thus we can not simply let R be close to one as done above in the case without advection.

Instead, we first assume that μ is close enough to zero so that $R_1^* < R_2^*$ (19). Now, decreasing R down towards R_2^* (the larger of the two critical reproductive rates) results in c_2^* decreasing to zero while c_1^* remains positive. This shows that under sufficiently weak advection, a low-order dominant dispersal kernel can produce higher wavespeeds in addition to producing a lower critical reproductive rate.

As the advection strength is increased, both R^* and s_R^* increase. In order to see that s_R^* increases, one must recognize that the moment generating function $M_f(s)$ for the displacement kernel has its minimum at $s = 0$, and it is a strictly increasing function. The moment generating function for the dispersal kernel with advection is $M_K(s) = M_f(s)e^{\mu s}$ (multiplication by an exponential decay factor since $\mu < 0$). The maximum of $e^{\mu s}$ is one and occurs at $s = 0$. This shifts to the right the location on the s -axis where the minimum of $M_K(s)$ occurs, and thus s_R^* increases.

Under sufficiently strong advection, a high-order dominant kernel gives a smaller critical reproductive rate and a larger wavespeed for any value of R . This occurs because there exists some \bar{s} such that $M_1(s) < M_2(s)$ for $s > \bar{s}$ since f_2 has larger high-order moments. As the magnitude of μ increases (stronger negative advection velocity), both $s_{R_1}^*$ and $s_{R_2}^*$ increase. Since $R_1(s) > R_2(s)$ for $s > \bar{s}$ and the maxima of both functions occur on $s > \bar{s}$, we have $R_1^* > R_2^*$. As R gets close to R_1^* , c_1^* approaches zero while c_2^* stays positive. For any $R > R_1^*$, s_c^* is larger than s_R^* and hence stays above \bar{s} resulting in $c_1^* < c_2^*$.

Any increase in the shape parameter s_R^* makes higher-order moments become more important in determining the value of $M_K(s_R^*)$ due to higher-order terms in the power series (3) having a greater contribution.

5 Heterogeneity's effects on wavespeed and persistence

In the preceding section, we saw how wavespeed and persistence may be more sensitive to low-order moments as opposed to the specific shape or tail decay rate of the dispersal kernel. In Section 3, we saw how the dispersal kernel's moments depend on those of the heterogeneous trait distribution. From (4), we know that wavespeed depends directly on the net reproductive rate and the moment generating function and from (5), that the critical reproductive rate depends only on the moment generating function (hence only on the moments of the dispersal kernel). Dispersal heterogeneity impacts wavespeed through changing a species' dispersal moments.

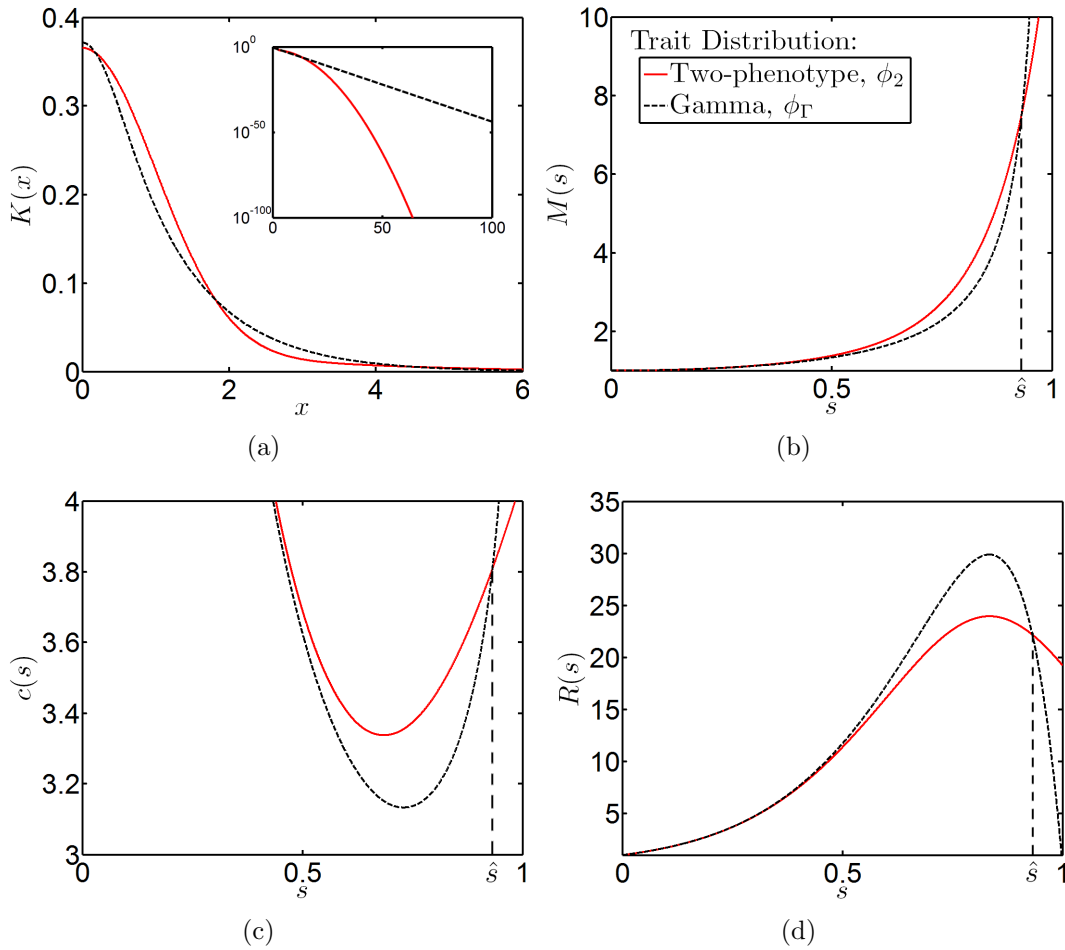


Figure 2: Graphs corresponding to trait distributions ϕ_Γ (12) are black, dashed lines and for ϕ_δ (13) in red, solid lines. (a) Dispersal kernels K_Γ and K_δ are shown with parameters $\mu = 0$, $\bar{D} = 1$, $B = 0$, $\alpha = 1$, $h_1 = 0.5$, and $h_2 = 3.5$. Both trait distributions have the same mean, but ϕ_δ has a larger variance than ϕ_Γ ($\sigma_{\phi_\delta}^2 = 1.75$, $\sigma_{\phi_\Gamma}^2 = 1$). The dispersal kernels have identical variance, but $m_{\delta,2n} > m_{\Gamma,2n}$ for $n = 2, 3, 4, 5, 6$; all higher-order raw moments are larger for K_Γ (first seven even moments listed in Table 2). K_Γ has slower tail decay, however K_2 is low-order dominant. (b) The corresponding moment generating functions $M(s)$ are shown. When $s < \hat{s}$, $M_\delta(s) > M_\Gamma(s)$. (c) Wavespeed functions $c_\delta(s)$ and $c_\Gamma(s)$ (defined in (16)) are shown. $R = 4.6$ is small enough so that $s_c^* < \hat{s}$ for both models, hence $c_\delta^* > c_\Gamma^*$ (minima of the graphs). (d) Reproductive rate functions $R(s)$ (defined in (18)) are shown for mean dispersal location $\mu = -5.5$ which is weak enough so that $R_\delta^* < R_\Gamma^*$ (maxima of the graphs).

raw moments	dispersal kernel	
	K_δ	K_Γ
$m_{K,2}$	2	2
$m_{K,4}$	33	24
$m_{K,6}$	1380	720
$m_{K,8}$	86,205	40,320
$m_{K,10}$	6,975,990	3,628,800
$m_{K,12}$	690,550,245	479,001,600
$m_{K,14}$	80,793,432,720	87,178,291,200

Table 2: The first seven nonzero raw dispersal moments are given for two dispersal kernels K_Γ and K_2 (using trait distributions ϕ_Γ (12) and ϕ_δ (13)) with parameters $R = 4.6$, $\bar{D} = 1$, $B = 0$, $\alpha = 1$, $h_1 = 0.5$, $h_2 = 3.5$, and $\mu = 0$ (hence odd moments are zero).

In this section, we examine how heterogeneity in dispersal behavior impacts wavespeed and persistence for the two-type (13) and gamma trait distributions (12). The two-type dispersal kernel K_δ has Gaussian tail decay, but the dispersal kernel K_Γ has slower tail decay and hence much larger high-order moments. We show that at low reproductive rates, the two-type model has a wavespeed which is very close to that of the gamma trait model. However, at high reproductive rates, the disparity between wavespeeds becomes more apparent.

We also explore the contribution to wavespeed made by individual heterogeneous dispersal types (e.g. long vs short range dispersers). This leads to insight on the question of what drives wavespeed. It has been shown in many studies that rare long-range dispersers or the shape or decay rate of the dispersal kernel tail has the strongest influence over wavespeed (Kot et al, 1996). We qualify these findings by examining them in a more general context of heterogeneous dispersal where the dispersal types may range from only slightly different in behavior to having orders of magnitude different mean dispersal distances.

5.1 Heterogeneity increases wavespeed

We now explore in more detail the asymptotic wavespeeds for the two example trait distributions ϕ_δ (13) and ϕ_Γ (12). The gamma trait distribution results in a displacement kernel which is not easily written down, but the displacement kernel's moment generating function is given by

$$M_\Gamma(s) = \left(\frac{1}{1 - s^2\alpha} \right)^{B+1}. \quad (21)$$

The moment generating function for the two-type displacement kernel is

$$M_\delta(s) = (1 - p) \exp(s^2 \bar{D}(1 - h_1)) + p \exp(s^2 \bar{D}(1 + h_2)). \quad (22)$$

The gamma distribution has only two parameters, so for a given mean \bar{D} and variance σ_D^2 , the parameters must satisfy

$$\alpha = \frac{\sigma_D^2}{\bar{D}} \quad \text{and} \quad B = \frac{\bar{D}^2}{\sigma_D^2} - 1. \quad (23)$$

This determines all of its higher order moments; the third central moment is

$$\mu_{\phi_\Gamma,3} = 2 \frac{\sigma_D^4}{\bar{D}}. \quad (24)$$

In contrast, the two-type trait distribution has an additional degree of freedom, so for a given mean and variance, the skewness can be large or small. If both trait distributions have the same mean and variance, we can set

$$h_2 = \frac{\mu_{\phi_\delta,3}}{2\sigma_D^2 \bar{D}^2} \left(1 + \sqrt{1 + \frac{\sigma_D^6}{\mu_{\phi_\delta,3}^2}} \right) \quad \text{and} \quad h_1 = \frac{\sigma_D^2}{\bar{D}^2 h_2} \quad (25)$$

so that they have the same skewness. Consequently, their respective dispersal kernels have the same variance, kurtosis, and sixth central moment. To maintain this relationship, the proportion of longer range dispersers in the two-type model, p , decreases as trait variance is increased (additionally, both h_1 and h_2 increase).

Differentiating the k^{th} moment (15) of the gamma trait distribution with respect to σ_D^2 gives

$$\frac{\partial}{\partial \sigma_D^2} m_{\phi_\Gamma, k} = (\bar{D}^2 + (k-1)\sigma_D^2) (\bar{D}^2 + (k-2)\sigma_D^2) \cdots \bar{D}^2 \quad (26)$$

which can be algebraically manipulated into a polynomial of degree k with positive coefficients. This shows that each trait moment is an increasing function of trait variance.

For the uniform two-type trait distribution, set $h_1 = h_2 = \sqrt{\sigma_D^2}/\bar{D}$. Differentiating the k^{th} trait moment (14) with respect to σ_D^2 yields

$$\frac{\partial}{\partial \sigma_D^2} m_{\phi_\delta, k} = \frac{k \bar{D}^{k-1}}{4 \sqrt{\sigma_D^2}} \left[\left(1 + \frac{\sqrt{\sigma_D^2}}{\bar{D}} \right)^{k-1} - \left(1 - \frac{\sqrt{\sigma_D^2}}{\bar{D}} \right)^{k-1} \right]. \quad (27)$$

Because $(1 + h_2)^{k-1} > (1 - h_1)^{k-1}$, the right side of (27) is positive. Hence the trait moments increase as σ_D^2 is increased.

Since the moments of the dispersal kernels corresponding to both example trait distributions are proportional to the trait moments by (9), all dispersal moments are increasing functions of variance in diffusivity. Any increase in dispersal moments results in an increase in wavespeed, hence increasing variance in diffusivity while holding the mean trait constant increases the wavespeed (illustrated by Figure 3(a)).

Matching the first two dispersal moments of K_δ to those of K_Γ results in wavespeeds which are close, especially at low reproduction and low levels of heterogeneity. As the variance in diffusivity is increased, the disparity in wavespeeds grows (Figures 3(a)–(b)).

Setting $\mu_{\phi_\delta,3} = \mu_{\phi_\Gamma,3}$ as defined by (24) for fixed \bar{D} and σ_D^2 matches the skewness of the two-type trait distribution to that of gamma trait distribution. This brings wavespeeds for the two models even closer (Figure 3(a)). Analytically showing that all moments of the skew-matched two-type model are increasing functions of trait variance proves difficult, however, the results of Section 4 show that wavespeed is still increased for sufficiently low reproductive rates since the kurtosis and the sixth moment of the dispersal kernel both increase.

We are free to treat $\mu_{\phi_\delta,3}$ in (25) as a parameter for the two-type model. This allows the skewness of ϕ_δ to be set lower or higher than that of ϕ_Γ . Increasing the skewness of the two-type trait distribution results in the higher-diffusivity dispersal phenotype becoming more rare but dispersing much further. If the two-type trait distribution has a skewness which is larger than that of the gamma trait distribution allows the two-type model to give larger wavespeeds than the gamma trait model as long as reproductive rates are low enough (shown in Section 4). The mean and variance are identical among the two dispersal kernels, however, the gamma trait distribution always results in a dispersal kernel with a more slowly decaying tail (Fig. 1, inset panel).

5.2 Long vs. short range dispersal impacts on wavespeed

Past studies of dispersal heterogeneity have often focussed on populations with distinct long and short range dispersal behaviors. The difference between the mean dispersal distances of the two behaviors has often been orders of magnitude as well. For example, the ant-mediated dispersal in Neubert and Caswell (2000) had an average long-range dispersal distance which was seventeen times that of the average short-range dispersal distance. This is comparable to one dispersal morph having a diffusivity which is 289 times that of the low-diffusivity morph. Wavespeed is essentially determined by this extreme long-range dispersal alone, even when quite rare. In models with both long and short range dispersers, this is sometimes shown by calculating the wavespeed with only the (rare) long-range dispersers while the short-range dispersers are assumed to not disperse (e.g. Neubert and Caswell, 2000). Here we explore how ignoring one or the other dispersal

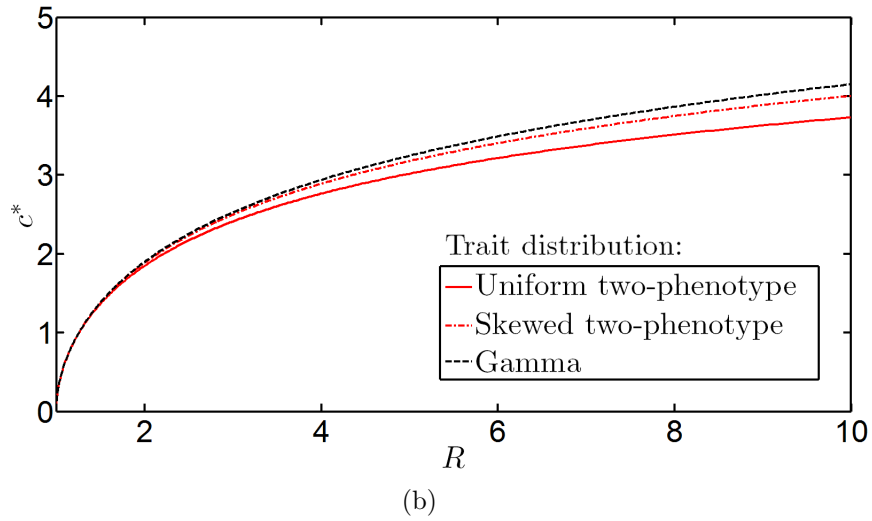
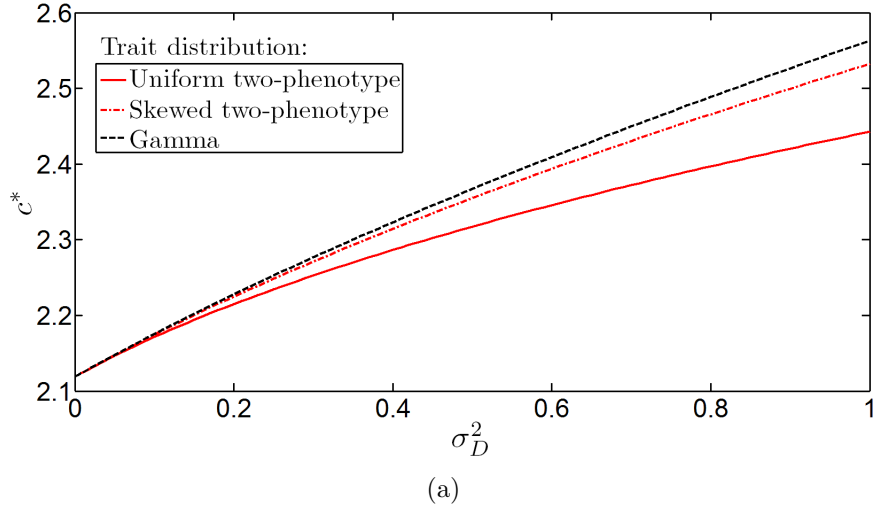


Figure 3: (a) The wavespeed increases with the variance of three trait distributions (diffusivity is the individual dispersal trait): gamma, uniform two-type, and skewed two-type (with the skew matched to that of the gamma trait distribution). $R = 3.07$, $\bar{D} = \tau = 1$. (b) The wavespeed increases with reproductive rate R ($\bar{D} = \tau = 1$, $\sigma_D^2 = 0.81$). The difference between the wavespeeds given by the dispersal kernels corresponding to the two-type and gamma trait distributions is made smaller by matching their skew.

behaviors in our two-type model might impact the approximation of the wavespeed for the non-advective case.

The mean absolute distance traveled by a dispersing offspring with diffusivity D is given by

$$\bar{x}_D = E(|x|) = 2 \int_0^\infty \frac{x}{\sqrt{4\pi D}} e^{-\frac{x^2}{4D}} dx = \sqrt{\frac{4D}{\pi}}. \quad (28)$$

Diffusivity and mean absolute dispersal distance are thus related to each other through dispersal variance by

$$\text{Var}(x) = 2D = \frac{\pi}{2} \bar{x}_D^2. \quad (29)$$

If mean absolute dispersal distances differ by a factor of ten, then diffusivities must differ by a factor of one hundred. Hence diffusivities differ by twice as many orders of magnitude as mean dispersal distances.

Consider our two-type model (13). If we assume that only a proportion p of offspring disperse with diffusivity D , and that the rest of the offspring do not disperse (remain at the origin as if having a diffusivity of zero), then the resulting dispersal variance for the entire population is

$$\text{Var}(x) = 2pD. \quad (30)$$

Now let p be the fraction of high-diffusivity offspring (the fraction of low-diffusivity offspring is $1 - p$) and D_1 and D_2 be the diffusivities of the two types of offspring with low and high diffusivities, respectively.

We now compare wavespeeds for four different populations:

- 1) Population \mathbf{P}_1 , where fraction $1 - p$ of offspring are low-diffusivity dispersers and fraction p are non-dispersers,
- 2) Population \mathbf{P}_2 , where fraction $1 - p$ of offspring are non-dispersers and fraction p are high-diffusivity dispersers,
- 3) Population \mathbf{P}_B , where both kinds of dispersers are present in their respective fractions, and
- 4) Population $\mathbf{P}_{\bar{D}}$, homogeneous with the mean diffusivity $\bar{D} = (1 - p)D_1 + pD_2$.

For a given net reproductive rate R , denote the wavespeeds of the above listed populations as c_1^* , c_2^* , c_B^* , and $c_{\bar{D}}^*$, respectively. The dispersal variances corresponding to each of the above populations are $\sigma_1^2 = 2(1 - p)D_1$, $\sigma_2^2 = 2pD_2$, $\sigma_B^2 = 2(1 - p)D_1 + 2pD_2$, and $\sigma_{\bar{D}}^2 = 2p\bar{D}$.

In field studies, it can be difficult to account for rare long-range dispersal behavior, yet spread may be largely driven by rare long-range dispersers (Neubert

and Caswell, 2000). We wish to understand under what conditions the wavespeed of a heterogeneous population is largely determined by only one of the dispersal types. Hence we examine when the wavespeed of population \mathbf{P}_B (containing both types of dispersers) is better approximated by that of population \mathbf{P}_2 as opposed to \mathbf{P}_1 . Using (30) to compare dispersal variances of \mathbf{P}_2 and \mathbf{P}_1 , we can see that if

$$\frac{1-p}{p} > \frac{D_2}{D_1}, \quad (31)$$

then population \mathbf{P}_1 has a larger dispersal variance than population \mathbf{P}_2 . Applying the results from Section 4, for R sufficiently close to one c_1^* is larger than c_2^* (again, Appendix A provides more rigorous mathematical justification). Since the population with both types of dispersers \mathbf{P}_B has the largest wavespeed, c_1^* is a better approximation to c_B^* than c_2^* . In order for c_2^* to be a better approximation to c_B^* than c_1^* , either there must be a sufficiently large difference between the two diffusivities (i.e. D_2/D_1 must be large enough), the fraction p of high-diffusivity dispersers must be large enough, or the reproductive rate R must be large enough. Each of these situations results in higher-order moments of the dispersal kernel having a greater contribution to the wavespeed.

Figure 4 shows the wavespeed divided by c_1^* for each of the four populations plotted against the ratio of the mean dispersal distances of the two dispersal types: $\bar{x}_{D_2}/\bar{x}_{D_1}$. Ratios are used so that the graph does not depend on the specific value of D_1 . As described in the preceding paragraph, we allow one type to disperse while the other remains at the origin. With $R = 1.01$ and $p = 0.01$, the offspring type that disperses further on average (higher diffusivity) must have a mean dispersal distance of more than 8.55 times that of the less diffusive type in order to better approximate the wavespeed of the population with both types. Since diffusivity is proportional to the square of the mean dispersal distance (29), the longer range dispersing type must possess a diffusivity of more than 73 times greater than that of the low-diffusivity type for c_2^* to better approximate c_B^* than c_1^* . In order to consider the long-range dispersal behavior as the primary driver of spread – i.e. that ignoring all but the long-range dispersers has little impact on wavespeed (e.g. Neubert and Caswell, 2000) – the higher of the two diffusivities should probably be well beyond two orders of magnitude greater than the lower.

When the long-range disperser only travels an order of magnitude further than the short range disperser, most of the increase in wavespeed could be explained by the increase in the mean diffusivity trait (and hence explained by dispersal variance, as shown by (9)). This is evident from Figure 4 since c_2^* becomes a better approximation to c_B^* than c_1^* only once \bar{x}_{D_2} is greater than 16.7 times \bar{x}_{D_1} . Even when the higher diffusivity is just over two orders of magnitude greater than the lower diffusivity, most of the increase in wavespeed could be explained as being due to the increase in the overall dispersal variance.

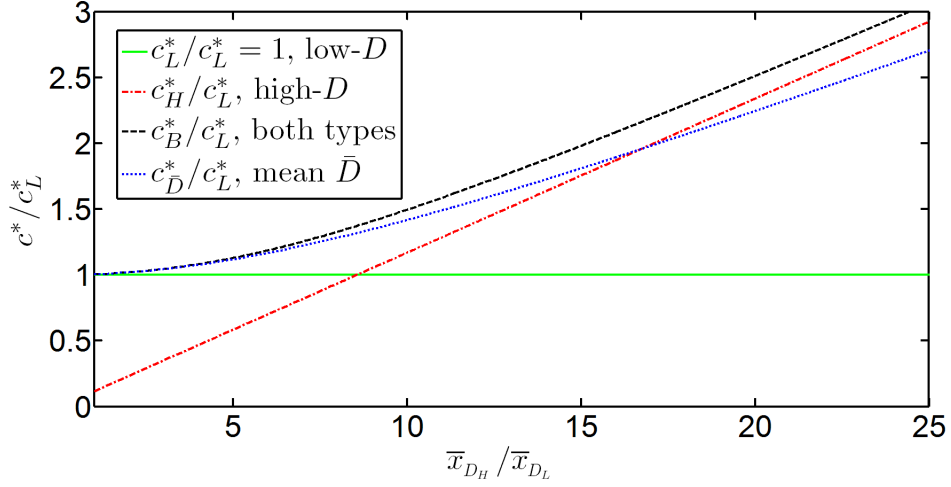


Figure 4: Wavespeed divided by c_1^* for each of the four models is shown as a function of the ratio of the mean dispersal distances of the two dispersal types. The probability of high-diffusivity is $p = 0.01$ and the net reproductive rate is $R = 1.01$; D_1 is fixed and D_2 varies from 1 to 625 times D_1 , which corresponds to a mean dispersal distance ranging from 1 to 25 times \bar{x}_{D_1} (see Equation (29)). Wavespeed c_B^* is shown for \mathbf{P}_B (the heterogeneous population with both types), c_1^* and c_2^* for \mathbf{P}_1 and \mathbf{P}_2 (the populations with only one type dispersing while the other type stays at the origin), and $c_{\bar{D}}^*$ for $\mathbf{P}_{\bar{D}}$ (the homogeneous population with the mean diffusivity trait). The overall mean dispersal distance of the heterogeneous population increases as $\bar{x}_{D_H}/\bar{x}_{D_L}$ increases. The high-diffusivity dispersal type must have a mean dispersal distance that is sufficiently higher (about 8.55 times higher with the given parameters) in order for its contribution to wavespeed to be greater than the low-diffusivity type. This gives the high diffusivity D_2 as being greater than 73 times D_1 , nearly two orders of magnitude.

5.2.1 Sensitivity to range and proportion of long-range dispersers

It has also been shown in a number of ecological examples that wavespeed is more sensitive to the range of the long-range dispersers than to the fraction of long-range dispersers (e.g. [Neubert and Caswell, 2000](#)). We now establish this more generally but also show when it does not hold. To understand this, consider the moment generating function of the model with both types of dispersers:

$$M(s) = (1 - p)e^{s^2 D_1} + pe^{s^2 D_2}.$$

The $2k^{\text{th}}$ central dispersal moment is given by

$$m_{2k} = (1 - p)(2k - 1)!!2^k D_1^k + p(2k - 1)!!2^k D_2^k$$

and is linear in p and a polynomial of degree k in diffusivity (a similar statement is true for Laplace dispersal kernels).

Instead of analyzing the sensitivity of wavespeed to p and D_2 directly, we derive the sensitivity and elasticity of the dispersal moments. Because an increase in any dispersal moment directly causes an increased wavespeed (so long as no other moment decreases), knowing the sensitivity of each moment is to p and D_2 gives important information about the sensitivity of c^* .

The sensitivities of m_{2k} to p and D_2 are

$$\frac{\partial}{\partial p} m_{2k} = (2k - 1)!!2^k D_2^k \left(1 - \frac{D_1^k}{D_2^k}\right), \quad (32)$$

$$\frac{\partial}{\partial D_2} m_{2k} = p(2k - 1)!!2^k k D_2^{k-1}. \quad (33)$$

Comparing (32) and (33) shows that m_{2k} is more sensitive to D_2 than to p if

$$1 - \frac{D_1^k}{D_2^k} < \frac{pk}{D_2}. \quad (34)$$

Recall that $D_2 > D_1$, thus the left side is less than one. For fixed p and D_2 , as long as k is large enough, (34) holds. However when p is extremely small or D_2 is large, only moments of very high order are more sensitive to D_2 than to p , hence moments of sufficiently low order can be more sensitive to changes in p than D_2 .

Multiplying (32) by p/m_{2k} and (33) by D_2/m_{2k} , gives the elasticities of m_{2k} to p and D_2 , respectively. Comparing these elasticities shows that m_{2k} is more elastic to changes in D_2 than to p if

$$1 - \frac{D_1^k}{D_2^k} < k \quad (35)$$

which holds for all $k \geq 1$. All moments are more elastic in D_2 than p .

Increasing either p or D_2 results in all dispersal moments increasing. However, we have shown that when R is close to one, low-order moments are important in determining wavespeed. Since low-order moments can be more sensitive to small changes in p than D_2 , wavespeed may be more sensitive to changes in the proportion of long-range dispersers than to their range of dispersal when reproductive rates are low. This conclusion is strengthened further when the proportion p is already extremely small or the range of dispersal is large (D_2 large). Considering elasticity and relative changes in p or D_2 , wavespeed is always more sensitive to the range of the long-range dispersers than to their proportion.

We can also understand the disparity of effects on wavespeed between increases in p as opposed to increases in D_2 at high reproduction by noting that the shape parameter s_c^* , which gives the shape of the invading wave-front, increases as R increases (the invasion wavefront becomes more ‘compressed’ with a steeper exponential shape). When R is close to one, the wave is more spread out with a less-steep exponential shape. Higher-order moments in the power series representation of moment-generating function (3) are multiplied by higher powers of s_c^* , and when R is close to one, s_c^* is close to zero thus making higher-order moments less important.

5.3 Heterogeneity in an advective environment

Now we study the effects of dispersal heterogeneity on wavespeed and on the critical reproductive rate in an advective environment. Dispersal heterogeneity is found to reduce the critical reproductive rate required to persist in the face of advection, and at high advection speeds the reduction is found to be large.

When advection is present, the moment generating function of the dispersal kernel is that of the displacement kernel multiplied by $e^{\mu s}$: $M_K(s) = M_f(s)e^{\mu s}$. Minimizing (20) in order to find the wavespeed shows that dispersal heterogeneity increases wavespeed in an advective environment for our two example trait distributions ϕ_δ (13) and ϕ_Γ (12) since it increases wavespeed when advection is absent (see Section 5.1).

In an advective environment, dispersal heterogeneity reduces the critical net reproductive rate for population persistence for our two example trait distributions (Figure 5) as could be anticipated with increasing the wavespeed (Figure 3(a)). At low advection speeds, heterogeneity has little impact on R^* (Figure 5(a): as σ_D^2 increases from 0 to 1, the quantity $R^* - 1$ decreases by about 7%). If the two-type trait distribution has the same skewness as the gamma trait distribution, then the critical reproductive rates resulting from each is quite close (Figure 5(a)). Thus at low advection speeds, knowing the first few moments of dispersal may allow a sufficient approximation of the critical reproductive rate. Higher-order moments have more influence on persistence at high advection speeds and heterogeneity can cause a dramatic reduction in R^* (Figure 5(b)).

For a population living in an environment with strong advection speeds and making a slow upstream advance or getting washed out due to a reproductive rate which is too low, heterogeneity could make all the difference needed to allow for persistence. When advection is strong, a small increase in dispersal heterogeneity causes a large reduction in the critical reproductive rate for our two example trait distributions (Figure 5(b): as σ_D^2 increases from 0 to 1, the quantity $R^* - 1$ decreases by about 80%).

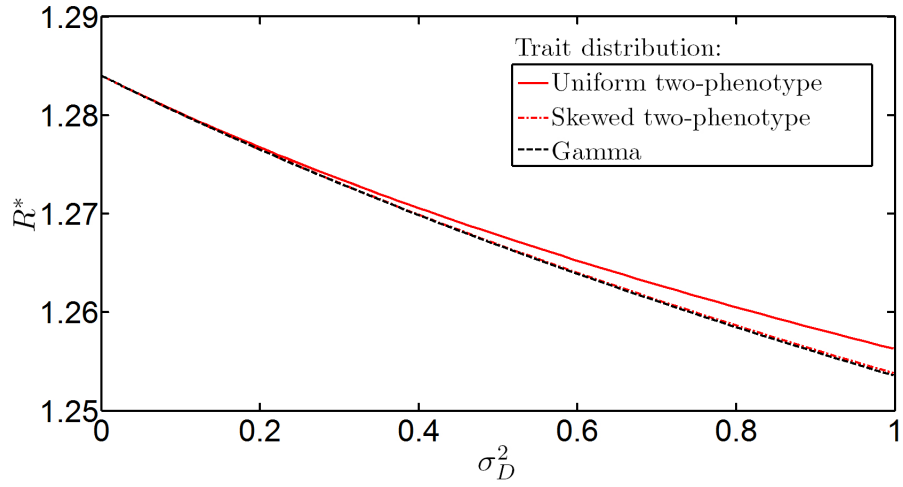
A strong advective current is needed to show a noticeable difference between the two-type and gamma trait cases when the skewness of the trait distributions is identical, as is evidenced by comparing Figures 5(a) and (b). This illustrates the importance of low-order moments as discussed in Section 4.

6 Discussion

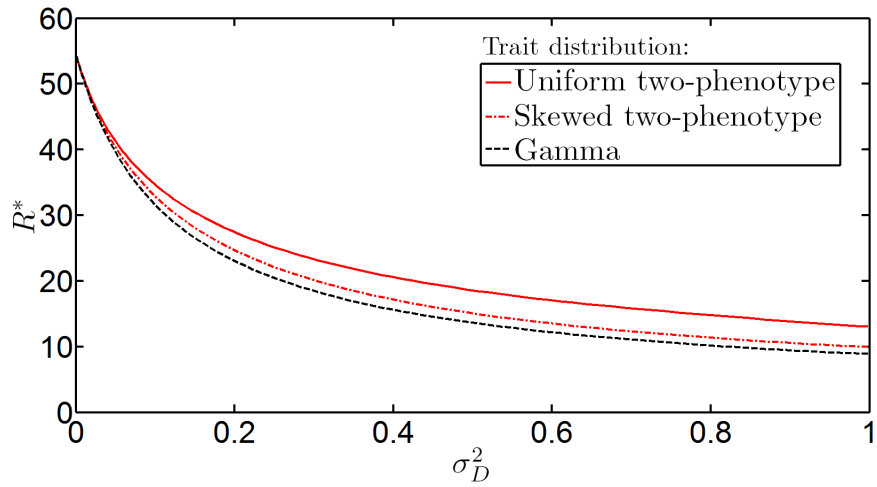
Using a one-dimensional integro-difference model, we investigated the effects of demographic heterogeneity on asymptotic wavespeed and on the critical (minimum) reproductive rate needed for persistence in the face of advection. We assumed that the diffusivity of individual organisms was determined by a trait distribution and derived a general relationship between the moments of the dispersal kernel and those of the trait distribution. We showed that dispersal heterogeneity causes dispersal kernels to appear leptokurtic, increases the population's spread rate, and lowers the critical reproductive rate required for persistence in the face of advection.

Our analysis also revealed some general insights into the determinants of the speed of population spread: (i) when the net reproductive rate is close to one, the first few moments of the dispersal kernel determine the wavespeed; (ii) with large reproductive rates, the shape of the tail of the dispersal kernel strongly influences wavespeed. In many previous studies, wavespeed has been described as being highly dependent on the dispersal kernel tail, an observation largely influenced by the fact that distributions with tails that are not exponentially bounded may lead to accelerating waves (e.g. Kot et al (1996)). In contrast, Lutscher (2007) showed that including kurtosis to a moment-based approximation improved accuracy. Our results show that neither kurtosis nor tail decay rate universally determine wavespeed in models with exponentially bounded kernels since a low-order dominant kernel can produce higher wavespeeds at low reproductive rates (see Section 4).

Reproduction and dispersal behavior both impact the shape of an invasion wavefront. For a more 'spread out' wave (small s^* shape parameter) as occurs with low net reproductive rates, low-order moments significantly influence wavespeed (see Appendix A). Increasing the level of heterogeneity in the population strongly influences wavespeed in this situation. Larger net reproductive rates typically lead



(a)



(b)

Figure 5: The critical reproductive rate is a decreasing function of diffusivity variance at (a) weak ($\mu = -1$), and (b) strong ($\mu = -4$) advection speeds.

to fast moving, ‘tightly packed’ invasions (large s^*) of highly fecund individuals, in which higher-order moments of dispersal are important in determining wavespeed, and thus slower tail decay of the dispersal kernel can become important.

Rigorous assessment of the importance of rare long-distance dispersers in determining invasion speed (e.g. [Neubert and Caswell, 2000](#)) is hampered by linguistic vagueness around the terms “rare” and “long-distance”. Even if “rare” means a frequency on the order of 0.01, then the long-distance dispersers need to disperse on average an order of magnitude further than the typical individual in order to be the primary source of population spread. Furthermore, we have shown that such results are only unequivocal when net reproductive rates (which include survival to adulthood) are high. High reproductive rates are not characteristic of all species; furthermore, fast growing populations would rapidly experience density dependence, which is absent from the present analysis.

Our current study is limited to trait distributions whose moments are all increasing functions of trait variance. Since heterogeneity increases all trait moments, it increases all dispersal moments (9). This increase in dispersal moments directly results in increased wavespeeds. However, selective pressure which changes the distribution of traits within an ecological population is not guaranteed to act in such a simple way. If trait variance increases and the mean trait remains unchanged, higher-order moments of the trait distribution may either increase or decrease. Even if heterogeneity decreases all higher-order moments, it is only transforming a high-order dominant kernel into a low-order dominant kernel. Our results in Section 4 show that for low reproductive rates, this still results in increased wavespeeds.

[Ellner and Schreiber \(2012\)](#) explored temporal variability (as opposed to the form of heterogeneity we study here) in dispersal in integro-difference models, but also included heterogeneity in individual dispersal in one of their models. Comparing both panels of Figure 1 in [Ellner and Schreiber \(2012\)](#) suggests that increasing heterogeneity increases wavespeed, but the authors do not discuss this. Indeed, their figure suggests that heterogeneity has a larger impact on wavespeed than temporal variability (the focus of their study), which we can understand by considering the underlying averaging processes. For simplicity, consider a population which alternates seasonally between long (L) and short (S) range Gaussian dispersal (with respectively high and low diffusivities). The wavespeed in this case is determined by using the geometric average of moment generating functions, $M_{TV} = \sqrt{M_L(s)M_S(s)}$ for $M(s)$ in Equation (4) where M_L and M_S are the moment generating functions corresponding to the long and short range dispersal years, respectively ([Ellner and Schreiber, 2012](#)). In contrast, a heterogenous population in which both diffusivities are present in each season results in an arithmetic average of moment generating functions: $M_H = \frac{1}{2}(M_L(s) + M_S(s))$. One can see that $M_{TV}(s) \leq M_H(s)$ for each s by the standard comparison of arithmetic and geometric means. Hence the minimum wavespeed corresponding

to M_{TV} will be less than that for M_H . This shows that dispersal heterogeneity where individuals with high and low diffusivity are present simultaneously results in a higher wavespeed than if the population were to seasonally alternate between high and low diffusivity. In particular, for mean-zero Gaussian dispersal, a quick calculation shows that temporally alternating between long and short range dispersal behaviors (high and low diffusivities) gives an asymptotic wavespeed which is identical to that using the average of the two diffusivities. However, as we have shown in this paper, if individuals of both diffusivities disperse in each time-step, then asymptotic wavespeed increases dramatically.

If heterogeneity in the time spent dispersing τ is included in our two-type model with advection, then a skewed displacement kernel results, and increasing the magnitude of heterogeneity in τ leads to the more diffusive phenotype drifting further downstream on average. Skewed kernels, such as the asymmetric Laplace (Lutscher et al, 2005; Lutscher et al, 2010), have dispersal moments of alternating sign and may make moment approximating methods of little value when the skewing is sufficiently strong. Further work is needed to understand the impact of heterogeneity when displacement is not symmetric about the mean dispersal location.

Dispersal ability might also be correlated with demographic rates. Heterogeneity in survival is known to cause ‘cohort selection’; irrespective of the initial composition of a cohort, as it ages it will become increasingly dominated by individuals with a higher propensity to survive (Vaupel and Yashin, 1985). This causes an increase in population growth rate for density-independent populations (Kendall et al, 2011) and an increase in equilibrium population size under density-dependence (Stover et al, 2012). Through its impact on growth rate, demographic heterogeneity will affect spread rates. A positive correlation between dispersal ability and survival – which might result from dispersing individuals reaching higher quality sites (Lowe, 2010) – may cause a further increase in wavespeed beyond that due to either type of heterogeneity acting alone. However, a trade-off between dispersal ability and survival could result in a decreased wavespeed such as might occur if individuals dispersing further were at increased predation risk. A trade-off between reproduction and dispersal ability may also exist (Simmons and Thomas, 2004). How this trade-off impacts wavespeed and persistence likely depends on its strength, but if it is strong enough, reduced fecundity may reverse any benefit of further dispersal. This provides an number of interesting topics for future work.

Another important avenue for future research is to determine how the inclusion of heritability impacts our results. Our models were unstructured and only required a suitably constructed dispersal kernel for analysis, however introducing parent-offspring correlations results in a structured population. Analysis should be possible using the methods developed in Neubert and Caswell (2000). As long as offspring are not identical to the parent (in which case two non-interacting

invasion waves result), results in Neubert and Caswell (2000) suggest that asymptotically, the fraction of individuals in each dispersal phenotype will be the same throughout the invasion front. This contrasts with the biological intuition that the faster dispersers should occur at increasing frequency the further out one looks along the leading edge of the invasion. If a simple form of heritability is included in our example models, increasing the magnitude of dispersal heterogeneity still increases the wavespeed in the non-advective case and decreases the critical reproductive rate in the advective case. However, a general analysis of how dispersal heterogeneity impacts wavespeed and persistence when traits are heritable may require different analytical techniques and is left open for future exploration.

Population spread is a complex ecological process involving an interplay between a number of factors including heterogeneity, reproduction, and dispersal behavior. Our results have shown that a higher frequency of long-range dispersal events is not enough on its own to produce larger wavespeeds in all ecological scenarios – this is especially true at low reproductive rates. Our purpose is not to de-emphasize the role of long-range dispersal but to call for careful attention to the specifics of each situation. A greater wavespeed may simply be due a single low-order moment such as variance or kurtosis irrespective of long-range dispersal. The existence of heterogeneity in the dispersal behaviors of natural ecological populations and its ability to alter the shapes of dispersal kernels further reinforces this call for attention to detail when studying invasion speeds and persistence in the face of advection.

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A Appendix: moments and wavespeed

In this appendix, we will show that a dispersal kernel with faster tail decay can result in larger wavespeeds than a kernel with a more slowly decaying tail as long as the reproductive rate is sufficiently small.

Let $M_1(s)$ and $M_2(s)$ be two moment generating functions for mean-zero, exponentially bounded, symmetric dispersal kernels $f_1(x)$ and $f_2(x)$ respectively. We assume that $f_2(x) > f_1(x)$ for $x > y > 0$ and that $f_2(x) < f_1(x)$ for some $x < y$. Only a finite number of moments of f_2 can be less than those of f_1 (see A.1 below).

The $2n^{th}$ moment of a distribution f is defined as $m_{i,2n} = \int_{-\infty}^{\infty} x^{2n} f_i(x) dx$.

We further assume that the first $k - 1$ even moments of the distributions are the same (all odd moments are zero), but that the $2k^{\text{th}}$ moment of f_1 is larger than that for f_2 . We drop the first subscript on the first $k - 1$ moments since they are equivalent among the two kernels to get:

$$M_1(s) = 1 + m_2 \frac{s^2}{2!} + m_4 \frac{s^4}{4!} + \cdots + m_{2(k-1)} \frac{s^{2(k-1)}}{(2(k-1))!} + m_{1,2k} \frac{s^{2k}}{(2k)!} + \sum_{j=k+1}^{\infty} m_{1,2j} \frac{s^{2j}}{(2j)!} \quad (36)$$

$$M_2(s) = 1 + m_2 \frac{s^2}{2!} + m_4 \frac{s^4}{4!} + \cdots + m_{2(k-1)} \frac{s^{2(k-1)}}{(2(k-1))!} + m_{2,2k} \frac{s^{2k}}{(2k)!} + \sum_{j=k+1}^{\infty} m_{2,2j} \frac{s^{2j}}{(2j)!}. \quad (37)$$

We know that $m_{1,2k} > m_{2,2k}$, and the rest of the moments can have any arbitrary relationship as long as some K exists such that $m_{1,2j} < m_{2,2j}$ for all $j > K$.

$$M_1(s) - M_2(s) = \left((m_{1,2k} - m_{2,2k}) + \sum_{j=k+1}^{\infty} (m_{1,2j} - m_{2,2j})(2j)! \frac{s^{2j-2k}}{(2j)!} \right) \frac{s^{2k}}{(2k)!} \quad (38)$$

For s small enough, $M_1(s) - M_2(s) > 0$ because the dominant term becomes that with the $2k^{\text{th}}$ moment $m_{i,2k}$, which is larger for f_1 . However $M_1(s) < M_2(s)$ for s large enough, since the higher-order moments of f_2 are larger. Thus \hat{s} exists such that $M_1(\hat{s}) = M_2(\hat{s})$ and that $M_1(s) > M_2(s)$ for $0 < s < \hat{s}$ and that $M_1(s) < M_2(s)$ for $\hat{s} < s < \tilde{s}$ (for some \tilde{s} — depending on the precise relationship among the moments, it may be possible for the moment generating functions to cross at multiple points).

For any given reproductive rate, R :

$$c(\hat{s}; R) = c_1(\hat{s}; R) = \frac{1}{\hat{s}} \ln(RM_1(\hat{s})) = \frac{1}{\hat{s}} \ln(RM_2(\hat{s})) = c_2(\hat{s}; R), \quad (39)$$

and $c_1(s; R) > c_2(s; R)$ for $s < \hat{s}$. The wavespeed is defined as

$$c_i^* = c(s_i^*; R) = \min \left\{ \frac{1}{s} \ln(RM_i(s)) \right\}. \quad (40)$$

As R goes down to one, both s_1^* and s_2^* go to zero since $R = 1$ corresponds to a wavespeed of zero with a shape parameter $s^* = 0$. So for R sufficiently close to one, we can get s_1^* and s_2^* as close to zero as we like (see Appendix A.2) and hence both smaller than \hat{s} . Because both critical shape parameters are in the region where $c_1(s; R) > c_2(s; R)$, $c_1^* > c_2^*$. This shows that a dispersal kernel with a ‘thinner’ tail can give a larger wavespeed than a dispersal kernel with a ‘fatter

tail' as long as the former dominates the latter in lower-order moments and that the net reproductive rate is sufficiently close to one.

When the mean dispersal location is negative, the critical reproductive rate is greater than one and the above argument does not apply since s^* does not approach zero as R goes down to R^* . However as long as the mean dispersal location is close enough to zero, R^* is close to one, and for a fixed R close enough to R^* , f_1 gives larger wavespeeds than f_2 .

A.1 Miscellaneous moment calculations

High-order moments tend towards infinity Here we show that the magnitude of a probability distribution's moments grows unboundedly as we look at higher and higher order moments.

To see that the $2n^{\text{th}}$ moment goes to infinity as $n \rightarrow \infty$ for a symmetric kernel f which has support for $x > 1$, find $j > 1$ such that $f(x) > C_j$ on the interval $(j, j + 1)$. The $2n^{\text{th}}$ moment is $m_{2n} = 2 \int_0^\infty x^{2n} f(x) dx$. This integral is then bounded from below by $2j^{2n} C_j$. As $n \rightarrow \infty$, $m_{2n} > 2j^{2n} C_j \rightarrow \infty$ which proves the result.

High-order moments are larger for slower decaying tail In this section, we show that if one dispersal kernel is eventually above another $f_2(x) > f_1(x)$ for all x greater than some y , then the higher order moments of f_2 are all larger than those of f_1 (for sufficiently large order). This is a somewhat looser requirement than f_2 having a slower tail decay rate, which may involve showing that the ratio $f_1(x)/f_2(x)$ goes to zero as x goes to infinity.

Assume that symmetric, mean-zero, exponentially bounded kernels satisfy $f_2(x) > f_1(x)$ for all $x > y$. Also assume that the minimum of $f_2(x) - f_1(x) = -C < 0$ for $0 < x < y$. For the interval $0 < x < y$, $x^{2n}(f_2(x) - f_1(x)) > -Cy^{2n}$, and for $x > y$, $x^{2n}(f_2(x) - f_1(x)) > \tilde{C}z^{2n}$ assuming that $f_2(x) - f_1(x) > \tilde{C}$ for $z < x < z + 1$ given some $z > y$.

$$\begin{aligned} \frac{1}{2}(m_{2,2n} - m_{1,2n}) &= \int_0^y x^{2n}(f_2(x) - f_1(x))dx + \int_y^\infty x^{2n}(f_2(x) - f_1(x))dx \\ &> -Cy^{2n+1} + \tilde{C}z^{2n} \end{aligned}$$

Because z is greater than y , n being large enough ensures that $\tilde{C}z^{2n} - Cy^{2n+1}$ is positive, demonstrating that all higher-order moments of $f_2(x)$ are larger than those of $f_1(x)$.

A.2 As $R \searrow 1$, $c^* \rightarrow 0$ and $s^* \rightarrow 0$

As the net reproductive rate R goes down to one, we will show that the wavespeed

c^* goes to zero and the corresponding critical shape parameter s^* also goes to zero.

Let R_n be a decreasing sequence of reproductive rates which converges to one. The moment generating function for some mean-zero, symmetric, and exponentially bounded dispersal kernel is

$$M(s) = 1 + m_2 \frac{s^2}{2} + \dots$$

When s is near zero, the moment generating function is near one and is thus $M(s) = 1 + O(s^2)$. The power series expansion of the natural logarithm is $\ln(1+x) = x - \frac{1}{2}x^2 + \dots$, thus $\ln(M(s)) = O(s^2)$. Now we look at the sequence of functions

$$c_n(s) = \frac{1}{s} \ln(R_n M(s)).$$

It is clear that $c_n(s) > c_{n+1}(s)$ for any n and for any s because R_n is a decreasing sequence and the natural logarithm is a monotone function.

Following a standard analytical technique, for any $\epsilon > 0$, choose an s close enough to zero such that $\frac{1}{s} \ln(M(s)) = O(s) < \frac{\epsilon}{2}$. Because $R_n \rightarrow 1$ and for the fixed value of s we just chose, a natural number N can be chosen such that $\frac{1}{s} \ln(R_n) < \frac{\epsilon}{2}$ for any $n > N$ since $\ln(R_n)$ can be made as close to zero as we like.

Now we have established that, for the sequence of functions $c_n(s)$, we can choose an N and a fixed s such that for any $n > N$,

$$c_n(s) = \frac{1}{s} \ln(R_n) + \frac{1}{s} \ln(M(s)) < \frac{\epsilon}{2} + \frac{\epsilon}{2} = \epsilon.$$

Because $c_n(s) < \epsilon$ at some s , its minimum is also less than ϵ . Thus we can choose R close enough to one to make the wavespeed as close to zero as we like.

Using the parametric representation (6) and letting R go down to one:

$$c^* = \frac{M'(s^*)}{M(s^*)} \rightarrow 0.$$

Since the moment generating function $M(s)$ is positive and monotonically increasing in s (hence $M'(s) > 0$ for any $s > 0$), as R goes down to one, $M'(s^*)$ must go to zero. This happens only if $s^* \rightarrow 0$.

Now we have established that for any exponentially bounded, symmetric dispersal kernel with mean-zero, we can choose a R close enough to one to give s^* as close to zero as we like.

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