The Importance of Being Indivisible: Ecological Invasions as Random Walks Instead of Waves

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Abstract

Invasions are one of the most easily identified spatial phenomena in ecology, and have inspired a rich variety of theories for ecologists and naturalists consideration. However, a number of arguments over the sensitivities of invasion rates to stochasticity, density-dependence, localization, and discreteness persist in the literature.

The standard mathematical approach to invasions is based on Fisher’s analysis of travelling waves solutions for spread of an advantageous allele. In this paper, I present an alternative theory based on Ellner’s premise that species invasions are best interpreted not as waves, but as random walks, and that the discreteness of living organisms is fundamentally important. Using a density-dependent invasion model in a stationary environment with indivisible (atomic) individuals where reproduction and dispersal are stochastic and independent, I will prove 3 key properties of Ellner’s invasions previously suggested by simulation analysis: (1) greater dispersal stochasticity quickens invasions; (2) greater demographic stochasticity slows invasions, and (3) negative density-dependence slows invasions. The proofs are done using stochastic-dominance methods for ranking probability distributions, although one important result is left as a conjecture. We also explain why, in contradiction with continuous theory, an infinitely wide atomic invasion in two-dimensions can travel faster than a finite-width invasion and a one-dimensional invasion. The paper concludes with a classification of invasion dynamics based on dispersal kernel tails, providing proofs for atomic invasions with demographic stochasticity and negative density dependence that exponentially bounded kernels have speeds that can be bounded independent of carrying capacity, cubic-tailed and heavier kernels always accelerate, and the speeds for intermediate kernels depend on the carrying capacity.

Keywords: stochastic demography, species invasion, long-range dispersal, wave of advance, extreme events
1 Introduction

Since ancient Greek natural philosophers Democritus and Leucippus originated the concept of an atom [Curd, 2011], there has been a tension between theories that treat nature as a smooth continuum, and theories that treat nature as a composite of discrete particles (atoms). During the scientific revolution, this tension took center stage in the competition between particle and wave theories of light [Inwood, 2005]. At the turn of the twentieth century, the issue reappeared as physicists speculated on the cause of the “ultraviolet catastrophe” in empirical observations of black body radiation, eventually leading to quantum theory [Kuhn, 1987]. Around the same time, Einstein and Smoluchowski were demonstrating how Fourier’s continuous theory of heat propagation could be alternatively understood in terms of the Brownian motion of particles and atoms [Frey and Kroy, 2005]. Ninety years later, in a much less famous but ecologically important discussion, Durrett and Levin [1994] emphasized how the mistaken replacement of discrete spatial structure with continuum diffusion can lead to erroneous predictions in evolutionary games. Now again, over the last decade, controversies between continuum and discrete models have arisen in population ecologists’ theories of invasions.

Invasion theory is a rich field, with a wide variety of models. Neubert and Parker [2004], Hastings et al. [2005], and Hui et al. [2011] review the general theories, while Kot et al. [2004] present a supplementary list of important theoretical results. From it’s birth in the 1930’s until the 1990’s, invasion theory was dominated by non-atomic models which are easy to study and provide elegant results [Fisher, 1937, Skellam, 1951, Barton, 1979, Okubo et al., 1989, Hosono, 1998]. In these invasion models, the population is represented as a continuous density that can be infinitely subdivided. However, in the last two decades, alternative agent-based and particle models have been put forward [Ellner et al., 1998, Tang and Bennett, 2010]. In these “atomic” models, the populations are represented by sets of discrete and indivisible individuals. Ecologists are attracted to atomic models because of their flexibility and innate
parallels with nature. Atomic models have also been studied mathematically in some contexts -- notably in reference to *tribolium* population dynamics [Henson et al., 2001, Scheuring and Domokos, 2005]. But overall, atomic models have received relatively less mathematical analysis, perhaps because of the different approaches they require.

The diversity of models has lead to fingering of consensus, with a variety of model-specific results. The story begins when Mollison [1972] discovered that epidemics that dispersed according to kernels that decayed like the fourth power of distance had a habit of leaping forward in large steps, in contrast to exponentially-tailed kernels which advanced more sedately. Two decades later, Kot et al. [1996] showed that fat-tailed dispersal kernels in mean-field models could lead to invasions that progress as accelerating waves rather than waves with a constant speed. This was an exciting result with the potential to resolve Reid’s paradox [Clark et al., 1998], but the result also clashed with human intuition that the speed of an invasion must be bounded. Clark et al. [2001] argued that the stochastic nature of ecological invasions stops this acceleration and only allows finite-speed invasions. Snyder [2003] performed simulation analyses on two light-tailed dispersal kernels which were predicted to have finite-speed invasions under Kot’s model [Kot, 1992], and found density-dependent stochastic invasions were significantly slower than predicted. But Kot et al. [2004] countered that density-independent stochastic models show that same front speeds as their density-independent deterministic counterparts. Pachepsky and Levine [2011] counter that it is discreteness and density dependence that are important. Contrary to the prevailing trend, Kawasaki et al. [2006] provide an example of how stochasticity increases the speed of an invasion, relative to a deterministic process with the same expectations. More recently, Brockmann and Hufnagel [2007] concluded that wave fronts generated by a density-dependent particle system where particles dispersed according to Levy flights could move with constant velocity, rather than accelerating. Jacobs and Sluckin [2015] provide an extensive simulation analysis on a lattice model, and conclude that finite-population stochasticity slows invasions and can stop
acceleration in all but the heaviest-tailed power-law kernels.

It’s quite difficult to make sense of this thick body of results paper-by-paper. Different groups have adopted different models and terminologies to explain their ideas, and these differences can be challenging to reconcile. “Discrete models”, for example, may refer to models that describe spread on a lattice in continuous time, spread in continuous space with difference equations, or individual-based models. “Stochasticity” may appear in confounding forms which can not be easily compared across models. And the differences between one and two dimensional models is not obvious. These obstacles have made the general theory of invasions seem complicated and have blocked convergent synthesis.

It is my belief that once we see through the diversity models and vague terminology, the collective mathematical research on invasions has actually lead to a relatively simple general theory, that is so natural as to seem almost trivial in hindsight. In this paper, I lay out this proposed synthesis, using a random-walk metaphor for invasions as an alternative to the classical traveling-wave metaphor. We’ll construct a nonlinear atomic stochastic process model for invasion, where individuals are represented discretely. By comparing special cases of the general model, we show that demographic stochasticity and negative density-dependence slow invasions, while dispersal stochasticity hastens invasions. These results are mathematically proven using stochastic ordering, the Weierstrass’s product inequality, and the Heyde–Schuh inequality, thus avoiding complications associated with simulations. Analysis of incrementally-shifted extreme-value statistics of different dispersal kernels under density-dependence reveals 4 separate possible regimes of behavior for an ecological invasion’s random walk: (1) a regime where there is a finite upper bound on the speed of advancement, independent of density effects; (2) a regime where upper bounds on the advancement speed are determined by the strength of density-dependence behind the wave-front, but progresses like a Brownian random walk; (3) a regime where upper bounds on the advancement speed are determined by the strength of
density-dependence behind the wave-front, but progresses like a Levy flight; and (4) a regime where invasions eventually accelerate past all constant upper bounds on their speed of advancement. Formal arguments supporting this classification are provided in appendices.

2 An Atomic Invasion Model

Our analysis begins by constructing a hierarchical invasion model [Jerde et al., 2009] over a continuous linear space with discrete non-overlapping generations and density-dependent mortality following settlement. Our model will be atomic, in the sense that the population’s state is represented by a set up points on a line rather than a continuous distribution. I will consider only the case of a homogeneous population for simplicity. Readers interested in heterogeneous populations should investigate matrix and integral projection extensions of this analysis [Rees et al., 2014, Neubert and Caswell, 2000].

In each generation, the dispersal of offspring is described by a dispersal kernel \( k() \) that is independent of the parent’s location, so the independent identically distributed (IID) dispersal variables \( y_{t,i,j} \) become the dispersal distances of the \( j \)th offspring of parent \( i \) in generation \( t \) (\( \forall y_{t,i,j} \in y, y_{t,i,j} \sim k \), where \( a \sim b \) reads “\( a \) is sampled from distribution \( b \)”\(^1\)). The cumulative probability distribution for the dispersal kernel

\[
K(z) := \text{Prob}(x < z) = \int_{-\infty}^{z} k(x)dx.
\] (2.1)

Let the IID variables \( B_{t,i} \) be the number of offspring produced by parent \( i \) in generation \( t \), drawn from the progeny density \( r \), so \( \forall B_{t,i} \in B, B_{t,i} \sim r \). The progeny

\(^1\)We will adopt this uncommon notation to avoid confusion with our subsequent use of \( \sim \) to represent asymptotic equivalence.
probability generating function (PGF)

\[ \mathcal{R}(s) := \sum_{i=0}^{\infty} r(i)s^i. \]  

As with all PGF’s, \( \mathcal{R}(s) \) is increasing, convex and \( s \in [0,1] \rightarrow \mathcal{R}(s) \in [0,1] \). The basic reproduction number \( R_0 := \mathcal{R}'(1) \) is the expected number of progeny.

In nature, individuals often fail to reproduce, and this can lead to extinctions. But all of our simulation experiments suggest that this complicates our invasion analysis without changing the core results. So to avoid the complications, we only consider populations where each adult produces at least one offspring:

\[ \mathcal{R}(0) = r(0) = \text{Prob}(B_{t,i} = 0) = 0, \]  

which also implies \( R_0 \geq 1 \).

To incorporate density dependence, we abstractly define a sieve \( \mathcal{F}(A) \) which for every set of individual locations, returns the subset which survive to produce the next generation \( (\mathcal{F}(A) \subseteq A) \). We want our sieve to be invariant under translation, so

\[ \mathcal{F}(A + c) = \mathcal{F}(A) + c \]  

where the additions are performed element-wise over the sets. We also expect the sieve to be local in the sense that there exists \( c > 0 \) such that for any two finite nonempty sets \( A_1 \) and \( A_2 \) with \( \max(A_1) = \min(A_2) \),

\[ \mathcal{F}(A_1 \cup (A_2 + c)) = \mathcal{F}(A_1) \cup [\mathcal{F}(A_2 + c)]. \]  

The smaller the value of \( c \), the weaker the density-dependent mortality.

It is not yet clear how to deal with general density-dependent mortality phenomena behind an invasion front, particularly when attempting to construct lower bounds on
range expansion rate. Some sieves may remove dispersers expanding the range limits or even cause population extinction. To avoid these issues and greatly simplify our mathematical analysis, we assume density-dependence is strictly right-sided in the sense that

\[ \forall (A : \exists \min A), \min A \in \mathcal{F}(A). \quad (2.6) \]

This one-sided density dependence is certainly not true in general in nature, but would be challenging to empirically refute. One-sided density-dependence will allow us to cleanly develop a richer set of results, and we expect our results to continue to hold under the most natural relaxations. I will also propose that the sieve should be linearly bounded i.e. there exists a density-dependence length-scale \( \gamma > 0 \), such that for all finite \( A \),

\[ |\mathcal{F}(A)| \leq \gamma \times (\max A - \min A). \]

This linear bound is similar to Lipschitz continuity condition employed in analysis and rules out un-realistically dense populations, including all multi-set scenarios where 2 or more individuals occupy the exact same location. The existence of a finite length scale \( \gamma \) is reasonable in all real-world settings, but does rule out fronts invading in two or three dimensions. A finite \( \gamma \) rules out planar fronts because if we sum over the extra space dimensions, we may find an infinite number of individuals in a finite interval. We comment on this further in the Discussion section.

Having dealt with the preliminaries, we now construct our model. Let \( \mathcal{M}_t \) be the configuration of dispersed offspring from generation \( t \). Without losing any generality, assume the left-most individual in the current generation is located at the origin (\( \min \mathcal{M}_t = 0 \)). Density-dependent mortality is applied during mortality until individuals become reproductively mature adults. Then the stochastic process (see Figure 1) for the configuration of dispersed offspring from one generation to the next
Figure 1: From the 4th to 5th generations, triangle-shaped plants invade to the left under Eq. (2.8) with Laplace-kernel ($\langle |x| \rangle = 1$) dispersal when $R_0 = 4$ without demographic stochasticity. The right side of the population has been truncated, and the location scale has been shifted so the FFD in generation 4 is at $x = 0$. The width of each lopsided plant (0.2) represents the domain where settlement is excluded by density dependence.

is

$$
\mathcal{N}_{t+1} := \bigcup_{x_i \in \mathcal{F}(\mathcal{N}_t)} \{x_i + y_{i,j,t} : j = 1 \ldots B_{t,i}\},
$$

(2.7)

or in the language of multi-type non-commuting random variables [Reluga, 2009],

$$
\mathcal{N}_{t+1} := \mathcal{F}(\mathcal{N}_t) \cdot r \cdot k.
$$

(2.8)

Within the model space of Eq. (2.8) (see Figure 2), there are several ways to arrive at distinguished limits. One is to reduce the distributions dispersal processes comb functions and to make reproduction constant so that dynamics match deterministic lattice theories where invasion occurs in fixed increments each generation. If, on the other hand, the length-scale of density dependence $\gamma$ is taken to zero, with everything else constant, then the population densities behind the invasion front will be large, and the law of large numbers implies that to those of spatial branching processes (which can be analyzed using deterministic probability generating functions) or nor nonlinear non-atomic deterministic integral-difference equations.
Figure 2: A Venn diagram of a topological classification of the kinds of invasion models that have been studied in stationary environments. The yellow bullseye marks the class of models considered here, with the halo extending to asymptotic limiting cases. Non-atomic populations impose a second layer on the diagram -- deterministic density-independent models can be both atomic and non-atomic.

3 Invasion random walks

Having constructed our atomic invasion model, we now need a method for characterizing the invasion process. Invasion theory has often been approached from the perspective of travelling-wave analysis based on continuous representations of population density [Fisher, 1937, Komogorov et al., 1937, Weinberger et al., 2002]. But we may imagine an alternative metaphor: species invasion is like a random walk [Ellner et al., 1998] -- while there is a general expectation about the rate of advancement of species-occupancy boundaries, particular invasions may randomly progress faster or slower than this expectation. Specifically, in each generation the species invades with a random step size $z_t$ beyond it’s previous limits, so the range boundary $\omega_t$ over time $t$ progresses according to

$$\omega_{t+1} = \omega_t + z_t.$$  \hspace{1cm} (3.1)
We’ll call $z_t$ the invasion step. The probability distribution of the location of the invasion front, after many steps, is approximately described by the convection-diffusion equation

$$\dot{p} + cp' = Dp''$$

where $D := [\langle z_t^2 \rangle - \langle z_t \rangle^2] / 2$, $c := \langle z_t \rangle$, $\langle \cdot \rangle$ represents the expected value, and time is scaled appropriately [Weiss, 1994]. So there is a deterministic component $cp'$ to the invasion process which convects the invasion forward at speed $c$. There is also a diffusive component $Dp''$ which accounts for the accumulation of random variation in the advancement of the invasion. The randomness may lead to ranges that are ahead of or behind the expected point of advance at any given time. In fact, this is the very pattern of invasion observed by Melbourne and Hastings [2009] in their marvelous Tribolium experiments. However, if the variance of the invasion step is infinitely large, the invasion will progress like a Levy flight rather than a Brownian random walk. And if the expectation of the invasion step is infinitely large, the invasion process will have infinite asymptotic speed, rather than a finite speed. So, the distribution of the invasion step determines the basic properties of a single-species ecological invasion.

The key problem with this analogy is that the invasion steps $z_t$ are not independent -- the invasion steps depend on the population configurations $N_t$ which depend on the preceding generation’s configurations $N_{t-1}$. This interdependence is what makes the analysis of invasion processes challenging. We will have to work around this dependence by comparing spreads conditional on given population configurations, and by constructing bounds rather than exact results.
3.1 Furthest-forward dispersers

One of the most useful ways to formalizing the dependence population range on dispersal and demography has been the tracking of the “furthest-forward disperser” (FFD) [Kot et al., 2004, Clark et al., 2001, Ellner et al., 1998, Bramson, 1978]. This individual, by definition, provides a concrete representation of the boundary of species range. The position of this individual in each generation defines the trajectory of species advancement. By deriving a distribution for the change in position of the FFD generation-to-generation, we get a step-size distribution sufficient to complete our random-walk analogy of the invasion process.

Let \( \mathcal{N} = \{x_0, x_1, \ldots, x_n\} \) be a non-empty population configuration where for convenience we assume the entries are sorted \((x_0 < x_1 < x_2 \ldots)\). If, without loss of generality, the location of the preceding furthest forward disperser \( x_0 = 0 \), then for the invasion step \( z := \min(\mathcal{F}(\mathcal{N}) \cdot r \cdot k) \), and the cumulative probability distribution of the current FFD \( P(z|\mathcal{N}) := \text{Prob}(\min(\mathcal{F}(\mathcal{N}) \cdot r \cdot k < z) \) is increasing. Since we have assumed density-dependence is right-sided, density-dependence does not directly affect the location of the FFD. Clark et al. [2001] construct a formula for \( P(z|\mathcal{N}) \) based on knowledge of the reproduction probability generating function \( \mathcal{R}(s) \) and the dispersal CDF \( K(x) \):

\[
P(z|\mathcal{N}) = 1 - \prod_{x_i \in \mathcal{F}(\mathcal{N})} \mathcal{R}(1 - K(z - x_i)). \tag{3.3}
\]

A closely related formula was obtained by Pachepsky and Levine [2011]. As long as \( \mathcal{N} \) is a finite set, we must have

\[
\lim_{z \to -\infty} P(z|\mathcal{N}) = 0. \tag{3.4}
\]
And since we have assumed the sieve can not cause extinction, Eq. (2.3) implies

\[
\lim_{z \to \infty} P(z|\mathcal{N}) = 1 - R(0)^{|\mathcal{N}|} = 1 - r(0)^{|\mathcal{N}|} = 1.
\] (3.5)

A more complete analysis allowing for potential population extinction will not differ significantly from what follows, in terms of invasion rates.

Throughout the subsequent conversation, we will at times refer to situations where one random variable is greater than or less than another. In these cases, the inequalities should be interpreted as an ordering in the sense of stochastic dominance [Shaked, 1994]. For example, if \(x\) and \(y\) are scalar random variables, then \(x \preceq y\) in a stochastic sense if and only if for every real number \(u\), \(\text{Prob}(x < u) > \text{Prob}(y < u)\). Note that for particular realizations of \(x\) and \(y\), we may have \(x < y\) or \(x > y\), despite \(x \preceq y\).

4 Dispersal stochasticity quickens an invasion

Stochasticity in dispersal events quickens the pace of an invasion. Why? The pace is set by the expectation of the FFD, which is an extreme event. Increasing the variation among individual dispersal events (while keeping the expectation constant) enhances the range of the extremes.

A proof comparing the deterministic and stochastic cases is not hard to outline. It’s an elementary though less commonly stated result of statistics related to Fatou’s Lemma and Jensen’s inequality that (as long as all the needed expectations exist) the expectation of a minimum is less than the minimum of the expectations; i.e., given a set of random variables \(\mathcal{N}\),

\[
\langle \min_{x \in \mathcal{N}} x \rangle \leq \min_{x \in \mathcal{N}} \langle x \rangle.
\]

The invasion step is constructed as such a minimum of independent dispersal events. If dispersal is always a constant distance \(u\), then the invasion step must be \(\langle z \rangle = u\). But
if dispersal occurs with the same expectation $u$ and sufficient stochasticity, then the expectation of the invasion step must be less than the expectation of each individual dispersal event ($\langle z \rangle < u$). Since we have adopted the convention of tracking waves moving from right to left, the stochasticity is hastening the invasion.

A more general statement can be made using majorization or second-order stochasticity [Hardy et al., 1934, Rothschild and Stiglitz, 1970, Machina and Pratt, 1997, Marshall and Olkin, 1979] (see Appendix A for details).

**Proposition 1.** Increases in dispersal stochasticity that do not change the expected dispersal distance increase the expected rate of invasion.

A similar effect is seen in time-varying dispersal processes [Ellner and Schreiber, 2012].

The effect of dispersal stochasticity is captured within density-independent branching-process theories of invasion, and consequently, within density-independent deterministic theory. Consider an invasion process with density-independent proliferation ($F(A) = A$) and a dispersal kernel that is a shifted Gauss distribution

$$k(x) = \frac{1}{\sqrt{2\sigma^2\pi}} e^{\frac{(x-u)^2}{2\sigma^2}}. \quad (4.1)$$

This kernel converges to a delta-function representing deterministic dispersal as the standard deviation $\sigma$ vanishes. Using standard methods [Kot, 1992], we can show the speed

$$c^* = \sigma \sqrt{2 \log (R_0)} + u \quad (4.2)$$

So, all else being equal, increased dispersal stochasticity accelerates the waves compared to deterministic dispersal (which is the $\sigma \to 0$ delta-function limit).

Variation-in-space is not the only form of stochasticity present in natural dispersal processes. Variation can also occur in the timing of dispersal, with some dispersal
events occurring soon than others. Equation (2.8) is poorly suited to addressing such variation, but density-dependent semi-Markov and age-dependent branching process models can account for such variation in timing [Metz et al., 2000]. It’s been suggested that this form of variation also accelerates invasions (G. Jacobs, personal communications). Indeed, the kind of analysis used for Eq. (4.2) also shows that for some separable kernels, increased variation in delay accelerates invasions (see Appendix E).

**Conjecture 1** (Jacobs’ conjecture). *Increases in the stochasticity of dispersal timing that do not change the expected dispersal time increase the expected rate of invasion.*

This would, if it holds, seem to explain the results of Kawasaki et al. [2006], whose continuous-time model comparisons emphasize stochasticity that occurs primarily in the timing dispersal phase.

## 5 Demographic stochasticity slows invasions

To show that demographic stochasticity slows the invasion, as Snyder [2003] argues, we compare the progression when reproduction is governed by the random variable $r$ with PGF $R(s)$ to the most deterministic reproduction allowed with the same expectation. For a given $R_0$, the most deterministic reproduction PGF is

$$R^*(s) = (1 - \psi)s^{n-1} + \psi s^n$$

where $n$ is an integer with $n - 1 < R_0 \leq n$ and $\psi$ is chosen so $R_0 = (1 - \psi)(n - 1) + \psi n$. Heyde and Schuh [1978] show that for all $s \in [0, 1]$, $R^*(s) \leq R(s)$. Then

$$P(z|N) = 1 - \prod_{x_i \in F(N)} R(1 - K(z - x_i)) \leq 1 - \prod_{x_i \in F(N)} R^*(1 - K(z - x_i)).$$

Thus, the randomness in reproduction always reduces the invasion step, compared to the most deterministic possibility, and hence, slows the invasion. A more general
Theorem can be established again using comparative risk [Machina and Pratt, 1997] in combination with Heyde and Schuh [1978]’s result (see Appendix B).

**Proposition 2.** *Increases in demographic stochasticity that do not change $R_0$ slow the rate of invasion.*

Intuitively, this appears to be because of the diminishing returns of extreme-value operations -- the increases in the invasion step from higher-than-expected reproduction events are outweighed by the decreases in the invasion step from lower-than-expected reproduction events.

This result seems to apply equally in density-dependent and density-independent scenarios, suggesting a contradiction with other results established for branching processes [Kot et al., 2004, Biggins, 1996]; if demographic stochasticity slows invasions, shouldn’t branching processes move more slowly than their deterministic counterparts? One possible explanation that I like is that an invasion is not a standard random-walk, where the invasion step is independent and identically distributed each generation. Rather, the invasion step depends on the current population configuration $N_t$ which in-turn depends on the configuration in the previous generation $N_{t-1}$. In density-independent scenarios, $z_t$ becomes negatively correlated over successive generations -- small steps forward are offset by subsequent larger steps forward because of built-up dispersal potential in the population’s configuration (see Fig. 3). An analysis conditional on a single population configuration can not capture this negative correlation.

### 6 Negative density-dependence slows an invasion

As Snyder [2003] and Pachepsky and Levine [2011] argue, negative density-dependence slows an invasion. This is almost a trivial observation under our model. Since the density-dependent mortality imposed by our sieve leaves a subset of individuals to reproduce the next generation ($F(N_t) \subseteq N_t$), compared to the density-
Figure 3: In an invasion, successive step sizes are not independent when density-dependence is weak -- successive steps are negatively correlated (left, kernel-smoothed scatter plot). As density-dependence strengthens, the likelihood that the furthest-forward disperser comes from a parent behind the front diminishes, diminishing the negative correlation (right). Demographic randomness also appears to weaken the correlation (right). Parameters (left) Laplace dispersal kernel with expected dispersal distance 1, and density-dependence width 0.004, with 1 or 4 offspring randomly such that $R_0 = 2$. Estimates based on $10^4$ simulation runs of 20 generations, discarding the first 10 as burn-in.

So, density-dependence always reduces the probability that the FFD disperses $z$ or more to the left compared to the density-independent case. Note that this depends intimately on the population state being atomic. Atomic density-independent populations [Kot et al., 2004] and continuum populations with negative density-dependence [Weinberger, 1982] can all invade with the same asymptotic speeds as density-independent continuum models. It’s invasions in atomic populations with negative density dependence that proceed more slowly than deterministic density-independent invasions.

The full importance of atomic density-dependence is best seen by considering common classes of dispersal kernels using bounding arguments in Appendix C. Generally, tail properties of dispersal kernels can be classified hierarchically based on the
existence of moments and the MGF’s.

**Bounded kernels** - The MGF is finite for all arguments \( s \) and there are absolute finite limits on dispersal distance. (Ex. Top-hat distribution)

**Sub-Exponential tails** - The MGF is finite for all arguments \( s \), but there is no strict upper bound on dispersal distance. (Ex. Gauss distribution).

**Exponential tails** - All moments are finite but the MGF is finite only for some arguments \( s \). (Ex. Laplace distribution).

**Super-exponential tails** - All moments are finite but the moment generating function is only defined at \( s = 0 \) (Ex. Square-root exponentials like \( c \exp(-\sqrt{|x|}) \)).

**Power-law tails** - Most moments are infinite, and the MGF is only defined at \( s = 0 \). (Ex. Cauchy distributions).

For simplicity, we have only considered kernels with symmetric left and right tails, but this classification can be easily generalized to handle asymmetric kernels. Collectively, bounded kernels, sub-exponentially tailed, and exponential tailed kernels are referred to as “light-tailed kernels”, while kernels with super-exponential and power-law tails are referred to as “heavy-tailed kernels”. Méndez et al. [2010] takes an approach to kernel tails based on a random-velocities theory using Hamilton–Jacobi equations and obtains a rather complete set of results. Here, we use an alternative approach based on elementary probability results from Appendix C to show related results.

### 6.1 Light tails

If the dispersal kernel is bounded in the sense that dispersal never exceeds a finite distance from the source, then there will be an absolute upper bound on expected distance of the FFD \( \langle z \rangle \), independent of the population distribution \( \mu(x) \) describing the wave-front. So, bounded kernels always lead to finite invasion speeds. A formal justification is provided by Theorem 5.
For sub-exponential and exponential-tailed kernels, we know from Eq. (6.1) that the density-independent special case always provides an upper bound. Based on the known results for spatial branching processes [Kot et al., 2004, Biggins, 1996], we can make use of the minimizing wave shape calculated from the deterministic speed formula [Kot, 1992, Mollison, 1972] and conclude that exponentially-tailed and sub-exponentially-tailed kernels also lead to finite-speed waves with speed-bounds that are independent of the strength of density-dependence.

6.2 Super-exponential tails

Kernels with super-exponential tails have no moment-generating function, by definition. It follows from the definitions of the moment-generating function and the CDF that integrals of the form

$$\mathcal{R}_0 \int_0^\infty C e^{s^* x} K(z - x) dx$$

will diverge for all $s^* > 0$. Thus, our upper bounds on $P(z|\mu)$ from Thm. 8 and Eq. (C.1) can not be applied to populations with density-independent proliferation behind the wave-front. Under density-independent proliferation, super-exponential tails lead to accelerating waves and the speed of these waves can sometimes be characterized using the inverted dispersal kernel CDF [Kot, 1992, Mollison, 1972]. Kot et al. [1996] shows that a square-root stretched exponential kernel has a front position that progresses quadratically over time (linear acceleration).

But for an atomic population with sufficiently strong density-dependence, invasion will have a finite speed. We can show this by constructing an alternative upper bound invoking carrying-capacity limits on population size from our Lipsitch conditions on our density-dependent sieve (see Appendix C, Theorem 9).

$$P(z|\mu) \lesssim \mathcal{R}_0 K(z) + \mathcal{R}_0 \gamma \int_0^\infty K(z - x) dx.$$
As long as the kernel tails decay faster than all power-law tails, Eq. (6.3) can always be calculated and all moments for the FFD will exist, including the first and second moments of the FFD (determined by Eqs. (D.1) and (D.2), Appendix D).

### 6.3 Power-law tails

When the dispersal kernel has heavier tails, our upper bounds behave differently. Specifically, if the kernel is an asymptotic power law \( k(x) \sim A|x|^{-\beta} \), then the cumulative distribution has asymptotic tail shape

\[
K(x) \sim A|x|^{1-\beta}/(\beta - 1).
\] (6.4)

Our upper bound now depends on the population’s configuration behind the wave front. For the case of density-independent proliferation, invasions accelerate faster than geometrically [Kot et al., 1996]. Méndez et al. [2010] predicted and Jacobs and Sluckin [2015] observed numerically that invasions with carrying capacities exhibited finite speeds as long as \( \beta > 3 \), but that infinite speeds appeared when \( \beta < 3 \), even in systems with hard carrying capacities. The subsequent analysis provides further explanation.

For any exponential population distribution \( \mu(x) \propto \exp(sx) \), Eq. (6.4) implies the integral in Eq. (C.1) diverges, so we obtain the useless bound that \( P(z|\mu) \leq 1 \). This suggests that when proliferation is density-independent, the invasion will accelerate without bound, and analyses have born this out [Kot et al., 1996, Mancinelli et al., 2002, del Castillo-Negrete et al., 2003]. Mundt et al. [2009] actually observe such exponential rates of invasion in some continent-scale pathogen data sets.

Under our probabilistic model, the Weak Upper-Bound Theorem and Eq. (6.4) imply

\[
P(z) \approx \min \left\{ 1, \frac{\mathcal{R}_0 \gamma A|z|^{2-\beta}}{\beta - 1} + \frac{\mathcal{R}_0 A|z|^{1-\beta}}{\beta - 1} \right\} \approx \frac{\mathcal{R}_0 \gamma A|z|^{2-\beta}}{(\beta - 1)(\beta - 2)}. \] (6.5)
When we construct a lower bound, we find that the $P(z)$ exhibits the same power-law behavior. Two important observations can be made from Eq. (6.5). Our first observation is that only a finite number of moments of the invasion step distribution are known to exist, though the number increases linearly with $\beta$. Based on Eq. (D.4), dispersal kernels with tails thinner than cubic scaling ($3 < \beta$) will be certain to possess both 1st and 2nd moments sufficient for specification of our diffusion model. For dispersal kernels between quadratic and cubic tail-weights ($2 < \beta \leq 3$), the first-moment exists, but the second does not, giving rise to Levy-walk-like behavior. However, because of the natural directional asymmetry of invasion processes, these flights will appear as accelerating processes.

Our upper bound only has finite expectation when our dispersal kernels decay faster than the square of distance ($2 < \beta$). Based on our second lower bound, expressed by Theorem 5 in Appendix C, we can show that the expected value of invasion step can only be finite if for some $\zeta > 0$ and some $x_k$,

$$\lim_{z \to -\infty} \sum_{j=0}^{\infty} K(z - x_k - j\zeta) = 0.$$  

(6.6)

But for any kernel with a power law tail of $\beta \leq 2$, $K(z) \geq C/z$. Thus, Eq. (6.6) dominates partial sums of the harmonic series. Since Nicole Oresme showed the summation of a harmonic series diverges, so does Eq. (6.6) diverge for all $z$. This is analytic confirmation of the observations of Jacobs and Sluckin [2015] that Cauchy kernels lead to accelerating invasions, even in the presence of density-dependence.

The second observation is that our upper bound in Eq. (6.5) depends linearly on the population density $\gamma$. The lower bound would also have linear dependence on carrying capacity. While we can attempt to construct sharper bounds, the presence of a lower bound with linear density-dependence is good evidence that the first moment will also have linear density-dependence on the carrying capacity behind the invasion. For heavy-tailed dispersal kernels, the expected invasion step would
then increase without bound as the carrying capacity increases. Thus, a primary
difference between light and heavy-tailed dispersal kernels in atomic models seems
to be that for light-tailed kernels, invasion speeds can be bounded independent of
carrying capacities, while for heavy-tailed kernels, invasion speeds depend on the
carrying capacity.

For the heaviest-tailed dispersal kernels, we can not construct finite moments,
and expect Levy-walk invasions no matter how strong the density dependence. If
\( K(z) \sim 1/z \), then the integral blows up under a uniform carrying capacity assumption,
and so we can not get a bound on the mean or second moment of the invasion step.
This is the case when the dispersal kernel resembles a Cauchy distribution, for the
which the CDF is an arctangent having \( 1/z \)-scaling tails.

7 Discussion

In conclusion, we re-iterate the smoldering idea that invasion processes in ecology
can be interpreted as random walks with positive drift. In spread models with
discrete generations where the dispersal process is independent of demographic
processes, negative density-dependence slows down these walks, as does demographic
stochasticity, but dispersal stochasticity accelerates the invasion. For light-tailed
dispersal kernels, the asymptotic speed will be approximately independent of the
carrying capacity, but for heavy-tailed dispersal kernels, the asymptotic speed may
depend strongly on the carrying capacity. For power-law kernels with tails heavier
than \( |x|^{-3} \), even strong density-dependence will not suppress the acceleration of the
invasions, and all finite speeds will be exceeded.

In continuous theory, simple invasion with concave density dependence in 2,
3, and \( n \)-dimensional spaces all advance asymptotically at the same speed as the
1-dimensional system linear system. But the behavior is different in atomic invasion
theory. When the spatial dimension of our atomic theory is expanded from a one-
dimensional environment to a two-dimensional strip of finite width, we will still be able to derive upper and lower bounds on the invasion step, although with a correspondingly increased value for the maximum density at and behind the invasion front. However, our results will fail for an infinitely wide invasion front in two dimensions because we will not be able to construct an upper bound on the number of individuals per unit distance in the 1-dimensional profile of the invasion wave. Instead, the invasion step will be infinite for any dispersal kernel that does not have absolute bounds on it’s distance. But, for any population that is initially finite in two dimensions, deterministic density-independent models should still provide valid upper limits on the invasion speeds for exponentially bounded dispersal kernels, since two-dimensional models will still possess some negative density-dependence which can only slow the invasion process compared to density-independent spread. In two dimensions, we also often see front-roughening [Kawasaki et al., 2006], a phenomena impossible in one-dimensional theories that might be explained by the Tracy–Widom distribution and KPZ equation [O’Malley et al., 2009].

Our results have implications for some areas of network analysis. In a recent manuscript, Marvel et al. [2013] argue that the “small-world effect” commonly observed in today’s interaction networks is a modern phenomena. As evidence of this, they use past studies of the Black Plague’s spread across Asia and Europe in the 14th century. Based on a deterministic distributed-contacts model [Kendall, 1965, Medlock and Kot, 2003], they argue that the dispersal kernel must have been exponentially bounded to generate the constant-speed invasion observed historically, and that such a dispersal kernel could number be generated if the contact network exhibited the small-world property. While the over-all conclusion seems almost trivial, being an artifact of the dramatic increase in ease and speed of human dispersal, the argument itself is flawed. As we have shown, heavy-tailed kernels do not necessarily generate accelerating waves of spread.

If we were to extend our model to allow for the possibility that an adult fails
to reproduce, in all cases with a finite initial population and a density-dependent sieve meeting our conditions, the population will certainly go extinct, at which point $P(z|\mathcal{K})$ can no longer be defined. But we conjecture that our results should be recoverable by conditioning the invasion process on non-extinction. We must also note that our formulation using one-sided density-dependent mortality after settling is mathematically convenient, but not general; a general model would allow arbitrary local density-dependence. In addition, density-dependent mortality effects may appear in reproduction, dispersal, and settling phases of the life cycle. In cases where density-dependent mortality is order-preserving and monotone [Weinberger, 1982], our results should still hold, but in cases of strong or weak Allee effects, these density-dependent processes may lead to further slowing of invasion waves. In fact, many have speculated that the discreteness of individuals is analogous to the introduction of a strong Allee effect in a deterministic model. Such an analogy can not be complete, since deterministic models will not exhibit random walks, but it may still be useful.

On the other hand, one can certainly find theoretical examples, and perhaps even natural examples, where dispersal and demographic stochasticity can not be separated as we have assumed. For example, in any situation where increasing the number of dispersing propagules decreases the average dispersal distance, the effect of demographic stochasticity can not be as simple as we have modelled here. We cannot say at this time what theory modifications the coupling of reproduction and dispersal will necessitate. But the assumption of independence between demography and dispersal seems like it will be satisfactory for many applications.

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A Dispersal stochasticity

In order to make Proposition 1 precise, we must define “greater variation in dispersal”. One very powerful way to do this is with “comparative risk” [Machina and Pratt, 1997], which is closely related to second-order stochastic dominance Rothschild and Stiglitz [1970], as well as majorization [Hardy et al., 1934, Marshall et al., 2011]. Comparative risk was designed to recognize situations where probability densities have the same expectation, but one has greater variation in the tails than another (hence generating greater variation around the mean). It has been previously considered in population biology [Nayak and Christman, 1992, Tong, 1997], though does not seem to have been employed in invasion theory yet.

Suppose we are given two dispersal kernels \( k(x) \) and \( \ell(x) \) with the same expected value. From Eq. (D.1), equality in expected value implies

\[
\int_{-\infty}^{\infty} \int_{-\infty}^{v} k(u) - \ell(u) du dv = 0. \tag{A.1}
\]

Now, we say \( \ell \) majorizes \( k \) (\( \ell \succ k \)) if and only if

\[
\forall x, \int_{-\infty}^{x} \int_{-\infty}^{u} \ell(u) du dv \geq \int_{-\infty}^{x} \int_{-\infty}^{u} k(u) du dv, \tag{A.2}
\]

with strict inequality holding for some \( x \). This appears at first to be an odd definition, but as Rothschild and Stiglitz [1970] show, Equation (A.2) is equivalent to saying that the dispersal kernel \( \ell \) majorizes \( k \) if and only if \( \ell \) can be created from \( k \) by a secondary dispersal process with no bias i.e. \( \ell \sim k + \epsilon \) in random-variable notation,
where $\epsilon$ can depend on the value of $k$, but $E(\epsilon) = 0$ for all $k$. So $\ell \succ k$ when $\ell$ has greater variation, but the same expectation.

We can now establish that greater dispersal variation in the sense of Eq. (A.2) leads to greater invasion speeds. Our result probably appears in [Marshall et al., 2011], and elsewhere, but we present our own argument for completeness. First, we establish as a widely known lemma that conditional expectation preserves concavity.

**Lemma 1.** If $f(x, y)$ is concave, then $E(f(x, y)|x)$ is concave in $x$.

**Proof.** Given a concave function $f(x, y)$ and $p \geq 0, q \geq 0$ such that $p + q = 1$, then, by definition, for any $x_p, x_q$,

$$pf(x_p, y) + qf(x_q, y) \leq f(px_p + qx_q, y).$$

Integrating both sides over a given conditional probability distribution $p(y|x)$,

$$\int [pf(x_p, y) + qf(x_q, y)]p(y|x)dy \leq \int f(px_p + qx_q, y)p(y|x)dy$$

Using the definition of conditional expectation $E(f(x, y)|x) = \int f(x, y)p(y|x)dy$, it follows that

$$pE(f(x, y)|x = x_p) + qE(f(x, y)|x = x_q) \leq E(f(x, y)|x = px_p + qx_q)$$

Thus, by definition, $E(f(x, y)|x)$ must be concave in $x$. \qed

We now establish our main theorem.

**Theorem 2.** If $\ell$ and $k$ represent dispersal distributions where $\ell$ majorizes $k$ ($\ell \succ k$) then $\forall x \in \mathbb{R}^n$,

$$E(\min\{\ell_0 + x_0, .., \ell_n + x_n\}|x) < E(\min\{k_0 + x_0, .., k_n + x_n\}|x)$$

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Proof. Let $F_i := E(\min\{\ell_0 + x_0, \ell_1 + x_1, ... \ell_{i-1} + x_{i-1}, x_i, x_{i+1}, ... x_n\}|x)$. Let $G_i := E(\min\{k_0 + x_0, k_1 + x_1, ... k_{i-1} + x_{i-1}, x_i, x_{i+1}, ... x_n\}|x)$. By Lemma 1, $F_i$ and $G_i$ are concave functions of the parameter vector $x$. $F_i$ and $G_i$ are also weakly increasing in $x$, by inspection.

We now proceed by induction. First $F_0 = G_0$, since they are deterministically specified by $x$. Next, if $F_i \leq G_i$, then $F_{i+1} \leq G_{i+1}$. Using the laws of conditional expectation, $F_{i+1}$ can be rewritten so $F_{i+1} = E(E(\min\{\ell_0 + x_0, ..., \ell_i + x_i, x_{i+1}, ... x_n\}|x, \ell_i)|x)$

Since $\ell_i \succ k_i$,

$$E(E(\min\{\ell_0 + x_0, ... \ell_{i-1} + x_{i-1}, \ell_i + x_i, x_{i+1}, ... x_n\}|x, \ell_i)|x) < E(E(\min\{\ell_0 + x_0, ... \ell_{i-1} + x_{i-1}, k_i + x_i, x_{i+1}, ... x_n\}|x, k_i)|x) \quad (A.3)$$

according to Rothschild and Stiglitz [1970] because of the concavity and monotonicity of the interior conditional expectation. By assumption, $F_i \leq G_i$, so $\forall k_i$,

$$E(\min\{\ell_0 + x_0, ... \ell_{i-1} + x_{i-1}, k_i + x_i, x_{i+1}, ... x_n\}|x, k_i) < E(\min\{k_0 + x_0, ... k_{i-1} + x_{i-1}, k_i + x_i, x_{i+1}, ... x_n\}|x, k_i) \quad (A.4)$$

which implies

$$E(E(\min\{\ell_0 + x_0, ... \ell_{i-1} + x_{i-1}, k_i + x_i, x_{i+1}, ... x_n\}|x, k_i)|x) < E(E(\min\{k_0 + x_0, ... k_{i-1} + x_{i-1}, k_i + x_i, x_{i+1}, ... x_n\}|x, k_i)|x) \quad (A.5)$$

By transitivity, Eqs. (A.3) and (A.5) imply

$$E(E(\min\{\ell_0 + x_0, ... \ell_{i-1} + x_{i-1}, \ell_i + x_i, x_{i+1}, ... x_n\}|x, \ell_i)|x) < E(E(\min\{k_0 + x_0, ... k_{i-1} + x_{i-1}, k_i + x_i, x_{i+1}, ... x_n\}|x, k_i)|x). \quad (A.6)$$
Simplifying our nested conditional expectations,

\[
E(\min\{\ell_0 + x_0, \ldots, \ell_{i-1} + x_{i-1}, \ell_i + x_i, x_{i+1}, \ldots x_n\}|x) < E(\min\{k_0 + x_0, \ldots, k_{i-1} + x_{i-1}, k_i + x_i, x_{i+1}, \ldots x_n\}|x) \tag{A.7}
\]

which is equivalent to \( F_{i+1} \leq G_{i+1} \). Thus, by induction, \( \forall n \in \mathbb{N}, F_n \leq G_n \) \( \square \)

It follows directly from this that dispersal by a majorizing kernel leads to faster invasions.

## B Demographic stochasticity

As in our analysis of dispersal stochasticity (Appendix A), we can represent increases in demographic stochasticity using mean-preserving spreads. Suppose we say that a progeny probability generating function \( Q(s) \) is related to \( R(s) \) by mean preserving spreads if and only if

\[
Q(s) = R(s) + \sum_{n=1}^{\infty} \epsilon_n [H_n(s) - s^n] \tag{B.1}
\]

where \( H_n(s) \) is a PGF with mean \( n \) \( (H'_n(1) = n) \), where the parameters \( \epsilon_n \) are non-negative and sufficiently small that all the Taylor-series coefficients of \( Q(s) \) around \( s = 0 \) are non-negative. Such a transform is mean-preserving [Machina and Pratt, 1997] because

\[
Q'(1) = R'(1) + \sum_{n=1}^{\infty} \epsilon_n [H'_n(1) - n] = R'(1) \tag{B.2}
\]

and the variance associated with probability distributions for each \( H_n(s) \) is greater than that of a point-mass distribution. We can now restate Proposition 2 more precisely.

**Theorem 3.** If a progeny probability distribution with PGF \( Q(s) \) is a mean-preserving
spread a second progeny probability distribution with PGF $R(s)$, then

$$1 - \prod_{x_i \in H(s)} Q(1 - K(z - x_i)) \leq 1 - \prod_{x_i \in H(s)} R(1 - K(z - x_i))$$

Proof. By definition,

$$Q(s) = R(s) + \sum_{n=1}^{\infty} \epsilon_n [H_n(s) - s^n]. \quad (B.3)$$

By Heyde and Schuh [1978], $H_n(s) - s^n$ is non-negative for $s \in [0, 1]$, so $Q(s) \geq R(s)$.

It is then a matter of simple algebra to show

$$1 - \prod_{x_i \in H(s)} Q(1 - K(z - x_i)) \leq 1 - \prod_{x_i \in H(s)} R(1 - K(z - x_i)).$$

\[\square\]

For establishing the converse, that if $Q(s) \geq R(s)$ and $Q'(1) = R'(1)$, then the probability distribution of $Q(s)$ can be reached by a mean-preserving spread of the probability distribution of $R(s)$, see Machina and Pratt [1997].

\section{Kernel-dependent speed bounds}

Our first theorem is a lower bound on the FFD CDF. General lower bounds are difficult to construct. This is not because the math is difficult, but because they often depend on the specific details of the invasion process. Finite-state processes often have certain extinction, while contact processes and spatial branching processes have parameter-dependent thresholds. By assuming that all adults have at least 1 child, we avoid these complications and can construct a general lower bound.

\textbf{Theorem 4} (Weak Lower-Bound). \textit{If} $|\mathcal{N}| \geq 1$ \textit{and} $\min \mathcal{N} = 0$, \textit{then}

$$K(z) \leq P(z|\mathcal{N})$$
Proof. To obtain the lower bound, we only need apply the approximation of Clark et al. [2001] based on the dispersals from the furthest-forward individual alone:

\[ P(z|\mathcal{N}) = 1 - \prod_{x_i \in \mathcal{F}(\mathcal{N})} \mathcal{R}(1 - K(z - x_i)) \]

Since the population is non-empty and \( \mathcal{R}(s) \in [0, 1] \) for any probability \( s \),

\[ P(z|\mathcal{N}) \geq 1 - \mathcal{R}(1 - K(z - x_0)) \]

Since \( \mathcal{R}(s) \) is convex, we can construct a linear upper bound.

\[ P(z|\mathcal{N}) \geq 1 - [\mathcal{R}(0) + (1 - \mathcal{R}(0))(1 - K(z - x_0))], \]

and with some algebra,

\[ P(z|\mathcal{N}) \geq [1 - \mathcal{R}(0)] K(z - x_0). \]

As we have already stated in Eq. (2.3), \( \mathcal{R}(0) = 0 \) and without loss of generality we assumed \( x_0 = 0 \), completing the proof. \( \square \)

An alternate lower bound can be constructed under the assumption that gaps between points are bounded behind the invasion front.

**Theorem 5** (Strong Lower-Bound). If \( |\mathcal{N}| \geq 1 \), \( \min \mathcal{N} = 0 \), and there exists \( \zeta \in (0, \infty) \) such that for all \( x \geq 0 \), \( [x, x + \zeta] \cap \mathcal{N} \neq \emptyset \), then

\[ 1 - \exp \left[ -\sum_{j=0}^{\infty} K(z - j\zeta) \right] \leq P(z|\mathcal{N}). \]

**Proof.** From Eq. (3.3),

\[ P(z|\mathcal{N}) = 1 - \prod_{x_i \in \mathcal{F}(\mathcal{N})} \mathcal{R}(1 - K(z - x_i)). \]

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By Eq. (2.2) and (2.3), \( R(s) \) is convex with \( R(0) = r(0) = 0 \) and \( R(1) = 1 \), so

\[
P(z|\mathcal{N}) \geq 1 - \prod_{x_i \in \mathcal{F}(\mathcal{N})} 1 - K(z - x_i).
\]

Since \( e^{-x} \geq 1 - x \), then

\[
P(z|\mathcal{N}) \geq 1 - \exp \left[ - \sum_{x_i \in \mathcal{F}(\mathcal{N})} K(z - x_i) \right].
\]

By hypothesis, the density of points must be greater than \( 1/\zeta \), so that since \( x_0 = 0 \),

\[
\sum_{x_i \in \mathcal{F}(\mathcal{N})} K(z - x_i) \geq \sum_{j=0}^{\infty} K(z - j\zeta).
\]

This implies

\[
\exp \left[ - \sum_{x_i \in \mathcal{F}(\mathcal{N})} K(z - x_i) \right] \leq \exp \left[ - \sum_{j=0}^{\infty} K(z - j\zeta) \right].
\]

So we conclude

\[
P(z|\mathcal{N}) \geq 1 - \exp \left[ - \sum_{j=0}^{\infty} K(z - j\zeta) \right].
\]

To derive an upper bound on the range-expansion step-size, we make use of one of many mild generalizations of the Weierstrass product inequality [Bromwich, 1908]:

**Lemma 6** (Generalized Weierstrass Product Inequality). For any finite set \( W = \{w_0, w_1, w_2 \ldots \} \) where \( \forall i, \ 0 \leq w_i \leq 1 \),

\[
\prod_i \max\{0, 1 - w_i\} \geq \max\{0, 1 - \sum_i w_i\}.
\]

**Proof.** We leave the proof as an exercise in induction methods for students. \qed
Lemma 7. For any PGF $\mathcal{R}(s)$ of a probability distribution with expected value $\mathcal{R}_0$, and any finite set $\{K_0, K_1, K_2 \ldots \}$ where $\forall i$, $0 \leq K_i \leq 1$,

$$\prod_i \mathcal{R}(1 - K_i) \geq \max\{0, 1 - \mathcal{R}_0 \sum_i K_i\}.$$ 

Proof. First, $\mathcal{R}_0 = \mathcal{R}'(1)$. Since probability generating functions are convex, positive, and monotone increasing, then for any $K \in [0, 1]$,

$$\mathcal{R}(1 - K) \geq \max\{0, 1 - \mathcal{R}_0 K\}$$

Extending this inequality to a product,

$$\prod_i \mathcal{R}(1 - K_i) \geq \prod_i \max\{0, 1 - \mathcal{R}_0 K_i\}$$

By the Generalized Weierstrass Product Inequality,

$$\prod_i \mathcal{R}(1 - K_i) \geq \max\{0, 1 - \mathcal{R}_0 \sum_i K_i\}.$$ 

Using Lemma 7, we can build our upper bound on the extreme-value distribution for range expansion.

Theorem 8 (Strong Upper-Bound).

$$P(z|\mathcal{N}) < \min \left\{ 1, \mathcal{R}_0 \sum_{x_i \in \mathcal{F}(\mathcal{N})} K(z - x_i) \right\}.$$ 

Proof. Applying Lemma 7 to Eq. (3.3),

$$P(z|\mathcal{N}) = 1 - \prod_{x_i \in \mathcal{F}(\mathcal{N})} \mathcal{R}(1 - K(z - x_i)) \leq 1 - \max\{0, 1 - \mathcal{R}_0 \sum_{x_i \in \mathcal{F}(\mathcal{N})} K(z - x_i)\}$$

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and with a little algebra,

\[ P(z|\mathcal{N}) \leq \min\{1, \mathcal{R}_0 \sum_{x_i \in \mathcal{F}^{(\mathcal{N})}} K(z - x_i)\}. \]

So we have an upper bound on the likelihood that the leftmost individual is to the right of \( z \).

The sum in our upper bound may be rewritten as

\[ P(z|\mathcal{N}) < \min \left\{ 1, \mathcal{R}_0 \int_0^\infty \mu(x) K(z - x) dx \right\} \quad (C.1) \]

where \( \mu(x) \) is a measure of the density of parent individuals. In exact calculations under a specific configuration, \( \mu(x) \) must be a set of \( \delta \)-functions corresponding to the positions of the elements of \( \mathcal{N} \). But for approximation purposes, it is useful to consider a mollified measure comparable to the average shape of the wave, based on the Euler–Maclaurin summation formula or a simpler Riemann-sum inequality.

**Theorem 9 (Weak Upper-Bound).** Under our model hypotheses,

\[ P(z|\mathcal{N}) < \min \left\{ 1, \mathcal{R}_0 \gamma \int_0^\infty K(z - x) dx + \mathcal{R}_0 K(z) \right\}. \]

**Proof.** From Theorem 8,

\[ P(z|\mathcal{N}) < \min \left\{ 1, \mathcal{R}_0 \sum_{x_i \in \mathcal{F}^{(\mathcal{N})}} K(z - x_i) \right\}. \]

Under the Lipschitz condition we have placed on our sieve and the monotonicity of \( K(x) \),

\[ \sum_{x_i \in \mathcal{F}^{(\mathcal{N})}} K(z - x_i) \leq \sum_{i=0}^\infty K(z - i/\gamma). \]
By a Riemann sum inequality for decreasing functions,

\[ \sum_{i=1}^{\infty} K(z - i/\gamma) \leq \gamma \int_0^{\infty} K(z - x) dx, \]

so

\[ \sum_{i=0}^{\infty} K(z - i/\gamma) \leq \gamma \int_0^{\infty} K(z - x) dx + K(z) \]

Thus,

\[ P(z|\mathcal{N}) < \min \left\{ 1, \mathcal{R}_0 \gamma \int_0^{\infty} K(z - x) dx + \mathcal{R}_0 K(z) \right\}. \]

The bounds on \( P(z|\mathcal{N}) \) from Theorems 4, 5, 8, and 9 are summarized by the inequalities

\[ K(z) \leq 1 - \exp \left[ -\sum_{j=0}^{\infty} K(z - j\zeta) \right] \leq 1 - \exp \left[ -\sum_{x_i \in \mathcal{F}(\mathcal{N})} K(z - x_i) \right] \leq P(z|\mathcal{N}) \]

(C.2)

\[ P(z|\mathcal{N}) < \min \left\{ 1, \mathcal{R}_0 \sum_{x_i \in \mathcal{F}(\mathcal{N})} K(z - x_i) \right\} < \mathcal{R}_0 \left[ K(z) + \gamma \int_0^{\infty} K(z - x) dx \right]. \]

(C.3)

where the average density of \( \mathcal{N} \) on the right is between \( 1/\zeta \) and \( 1/\gamma \).

**D Calculation of moments by integration**

When working with cumulative distribution functions, it is sometimes useful to express the distribution moments as integrals. Here are the most useful formulas.

The expectation

\[ \langle z \rangle = \int_{-\infty}^{\infty} z P'(z) dz = \int_{-\infty}^{\infty} \frac{1}{2} - P(z|X) dz \]  

(D.1)
while the second moment
\[ \langle z^2 \rangle = \int_{-\infty}^{\infty} z^2 P(z) dz = \int_{-\infty}^{\infty} |z| - 2zP(z) dz. \quad (D.2) \]

and the variance
\[ \langle z^2 \rangle - \langle z \rangle^2 = \int_{-\infty}^{\infty} |z| - 2zP(z) dz - \left( \int_{-\infty}^{\infty} \frac{1}{2} - P(z|X) dz \right)^2 \quad (D.3) \]

where the cross-bar is used to denote principle-value integrals. The existence of the first and second moments depends on the tail-properties of \( P(z|X) \). In particular, if there exists \( z_0 \) such that for all \( z > z_0 \), \( P(z|X) = 1 \), then the second moment \( \langle z^2 \rangle \) exists if and only if
\[ \lim_{z \to -\infty} z^2 P(z) = 0. \quad (D.4) \]

**E Calculation of effect of dispersal-delays in deterministic models**

Let’s suppose our invasion process deterministic, non-atomic and age-structured so
\[ b(x, t) = \int_0^t \int_{-\infty}^{\infty} A(\tau, y)b(x - y, t - \tau) dy d\tau \]

where
\[ A(t, x; \epsilon, a, \sigma) = R_0 \left[ \frac{t^{1/\epsilon} - e^{-t/\epsilon}}{(\epsilon a)^{1/\epsilon}} \right] \left[ \frac{e^{-x^2/2\sigma^2}}{\sqrt{2\pi\sigma^2}} \right] \]

The second term in the kernel \( A(t, x) \) is a Gamma distribution with mean \( a \) and shape parameter \( \epsilon \), while the third term is a Gauss distribution with mean 0 and variance \( \sigma \). In the limit as \( \epsilon \to 0 \), all the reproduction and dispersal are concentrated exactly
at time $a$, so

$$A(t, x; 0, a, \sigma) = R_0 \delta(t - a) \left[ e^{-\frac{x^2}{2\sigma^2}} \right]$$

We analyze travelling-wave solutions using the method of Metz et al. [2000]. The travelling wave moment generating transform

$$\mathcal{M}[A](c, w) = \int_0^\infty \int_{-\infty}^{\infty} A(t, x) e^{-w(x+ct)} dx dt = \frac{R_0 e^{\frac{\sigma^2 w^2}{2}}}{(1 - \epsilon acw)^{1/\epsilon}}$$

and for all solutions $\exp(-w(x - ct))$, $\mathcal{M}[A](c, w) = 1$. The minimum wave speed $c^*$ solves

$$\frac{\partial \mathcal{M}[A](c^*, w^*)}{\partial w} = 0.$$

If we expand our travelling wave moment generating transform in powers of $\epsilon$,

$$\mathcal{M}[A](c, w) = R_0 e^{-acw + \sigma^2 w^2/2} (1 + \epsilon a^2 w^2 c^2/2 + \mathcal{O}(\epsilon^2))$$

and using regular perturbation theory, we find

$$c = \frac{\sigma \sqrt{2 \log(R_0)}}{a} \left[ 1 + \epsilon \log(R_0) + \mathcal{O}(\epsilon^2) \right]$$

Thus, the speed is increasing in $\epsilon$. Since the variance of our gamma distribution is $a^2 \epsilon$, this means increasing variance in our dispersal delay accelerates the invasion.

This is not particular to a Gauss kernel -- we can use an arbitrary spatial distribution kernel (as long as $A(t, x)$ remains separable) and show that to first order,

$$c(\epsilon) = c_0 \left[ 1 + \epsilon \frac{ac_0 w_0}{2} + \mathcal{O}(\epsilon^2) \right]$$

where $c_0$ and $w_0$ are the speed and wave number when $\epsilon = 0$. Since $c_0$ and $w_0$ have same sign, increasing the variance of our dispersal delay accelerates an invasion, at least in the limit of small $\epsilon$. 

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This can be expanded to a more general result for all $\epsilon$ and arbitrary spatial distributions with moment generating function transform $F(w)$. Solving $\mathcal{M}[A](c, w) = 1$ for $c(w, \epsilon)$,

$$
c(w; \epsilon) = \frac{R_0^\epsilon F^\epsilon(w) - 1}{\epsilon a w}.
$$

Since $x \ln x \geq x - 1$ for all $x > 0$, it follows that for all $\epsilon$,

$$
\frac{dc}{d\epsilon} = \frac{R_0^\epsilon F^\epsilon(w) \left[ \log (R_0^\epsilon F^\epsilon(w)) - 1 \right] + 1}{a \epsilon^2 w} \geq 0,
$$

the minimum speed $c^\ast(\epsilon)$ must also increase as $\epsilon$ increases when $w > 0$. Thus, more variation in delay always accelerates the invasion in this deterministic case.