



The importance of being atomic: 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, dimension, and discreteness persist in the literature.

The standard mathematical approach to invasions is based on Fisher's analysis of traveling wave solutions for the spread of an advantageous allele. In this paper, we exploit 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, we show 4 key properties of Ellner's invasions previously suggested by simulation analysis: (1) greater spatial dispersal stochasticity quickens invasions, (2) greater demographic stochasticity slows invasions, (3) negative density-dependence slows invasions, and (4) greater temporal dispersal stochasticity quickens invasions. We prove the first three results by using generating functions and stochastic-dominance methods to rank furthest-forward dispersal distributions. The fourth result is proven in the special case of atomless theory, but remains an open conjecture in atomic theory. In addition, we explain why, unlike atomless invasions, 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.

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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 composite of discrete particles (atoms), and theories that treat nature as a smooth continuum (atomless). 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). And there was heated debate between Darwinians and Mendelians over whether

evolution occurred through selection on distributions of continuous variation or through selection on large discrete jumps in character (Provine, 2001). 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 two decades, 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 its birth in the 1930s until the 1990s, invasion theory was dominated by atomless models which are easy to analyze 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, and the advance of an invasion can often be described in terms of a traveling-wave solution. However, in the last two

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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.

The diversity of models has led to fingering of consensus, with a variety of model-specific results. The story begins when Mollison (1972) discovered that epidemics that dispersed according to fourth-order power-law kernels had a habit of leaping forward in large steps, in contrast to exponentially-tailed kernels where the waves of advance were more sedate. Two decades later, Kot et al. (1996) showed that heavy-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 spreading speed of an invasion must be bounded. Clark et al. (2001) subsequently argued that natural stochasticity stops this acceleration and only allows finite-speed invasions. Snyder (2003) performed analyses on two light-tailed dispersal kernels and found density-dependent stochastic simulations were significantly slower than integral-difference equation theory predicted (Kot, 1992) and concluded that “demographic stochasticity slows invasions”. But Kot et al. (2004) countered that density-independent stochastic models show that same spreading speeds as their density-independent deterministic counterparts, while Kawasaki et al. (2006) provide an example of how stochasticity increases the spreading speed of an invasion, relative to a deterministic process with the same expectations. More recently, Brockmann and Hufnagel (2007) showed that wave fronts generated by a density-dependent particle system where particles dispersed according to Lévy flights could move with constant velocity, rather than accelerating, and Pachepsky and Levine (2011) observe that it is likely discreteness and density dependence that are important. Hallatschek and Fisher (2015) provide a scaling-law approach to the analysis of long-range dispersal. Jacobs and Sluckin (2015) provide an extensive simulation analysis of lattice theories, and conclude that while finite-population stochasticity slows invasions and can stop acceleration in many heavy-tailed kernels, the heaviest-tailed power-law kernels can still exhibit accelerations.

It is 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 cannot be easily compared across models. And the differences between one and two dimensional models are not obvious. These obstacles have slowed our synthesis.

Yet, after digesting the menagerie of models and vague terminology, the collective mathematical research on invasions has actually led to a relatively simple general theory. In this paper, we will lay out this proposed synthesis, using a random-walk metaphor for invasions. We will construct a nonlinear atomic stochastic process, where individuals are represented discretely. The comparison of special cases of this process shows that demographic stochasticity and negative density-dependence slow invasions, while dispersal stochasticity hastens invasions. These results are mathematically proven using stochastic ordering (Shaked, 1994), the Weierstrass’s product inequality (Bromwich,

1908), and the Heyde–Schuh inequality (Heyde and Schuh, 1978), thus avoiding complications associated with simulations. Analysis of incrementally-shifted extreme-value statistics of different dispersal kernels under density-dependence reveals four 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 Lévy 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 spatial model

Let us construct a hierarchical invasion model (Jerde et al., 2009) in one spatial dimension with discrete non-overlapping generations and density-dependent mortality following settlement. The model will be atomic, in the sense that the population’s state is represented by a set of points on a line rather than a continuous distribution. Each point represents the location of one individual. We will consider only the case of a homogeneous population and homogeneous space. Readers interested in heterogeneous populations should investigate matrix and integral projection extensions (Rees et al., 2014; Neubert and Caswell, 2000).

In each generation, the dispersal of offspring is described by a kernel k that is independent of the parent’s location, and let

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

be the cumulative probability distribution for this dispersal kernel. The dispersal variables $y_{t,i,j}$ are the independent identically distributed (IID) dispersal distances of the j th offspring of parent i in generation t ($y_{t,i,j} \triangleleft k$, which reads “ $y_{t,i,j}$ is sampled from distribution k ”). We will adopt this uncommon notation to avoid confusion with our subsequent use of \sim to represent asymptotic equivalence).

Let the IID random variables $B_{t,i}$ be the number of offspring produced by parent i in generation t . Each $B_{t,i}$ is sampled from progeny density r ($B_{t,i} \triangleleft r$). This progeny density has probability generating function (PGF)

$$\mathcal{R}(s) := \sum_{\ell=0}^{\infty} r_{\ell} s^{\ell} = \langle s^{\ell} \rangle \quad \text{when } \ell \triangleleft r, \quad (2.2)$$

with $\langle \cdot \rangle$ denoting the expected value of a random variable. 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 $\mathcal{R}_0 := \mathcal{R}'(1)$ is the expected number of progeny. Readers interested in the use of generating functions for the study of branching processes may consult any of numerous sources, including the review article by Dorman et al. (2004) and books by Matis and Kiffe (2000), Athreya and Ney (1972), Harris (1963), and Ulam (1990).

In nature, individuals often fail to reproduce, and this can lead to extinctions (Lande, 1993). 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:

$$\mathcal{R}(0) = r_0 = \text{Prob}(B_{t,i} = 0) = 0, \quad (2.3)$$

implying that $\mathcal{R}_0 \geq 1$.

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