Long-range dispersal, stochasticity and the broken accelerating wave of advance

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HIGHLIGHTS

- We present deterministic and stochastic models of species invading new territory.
- Fat-tailed dispersal kernels lead to accelerating spread in the deterministic case.
- Only Lévy flight dispersal causes acceleration in our stochastic model.
- Stochastic and mean-field results can be very different given long-range dispersal.
- In such circumstances, mean-field results should be applied with caution.

ARTICLE INFO

ABSTRACT

Rare long distance dispersal events are thought to have a disproportionate impact on the spread of invasive species. Modelling using integrodifference equations suggests that, when long distance contacts are represented by a fat-tailed dispersal kernel, an accelerating wave of advance can ensue. Invasions spreading in this manner could have particularly dramatic effects. Recently, various authors have suggested that demographic stochasticity disrupts wave acceleration. Integrodifference models have been widely used in movement ecology, and as such a clearer understanding of stochastic effects is needed. Here, we present a stochastic non-linear one-dimensional lattice model in which demographic stochasticity and the dispersal regime can be systematically varied. Extensive simulations show that stochasticity has a profound effect on model behaviour, and usually breaks acceleration for fat-tailed kernels. Exceptions are seen for some power law kernels, $K(l) \propto |l|^{-\beta}$ with $\beta < 3$, for which acceleration persists despite stochasticity. Such kernels lack a second moment and are important in 'accelerating' phenomena such as Lévy flights. Furthermore, for long-range kernels the approach to the continuum limit behaviour as stochasticity is reduced is generally slow. Given that real-world populations are finite, stochastic models may give better predictive power when long-range dispersal is important. Insights from mean-field models such as integrodifference equations should be applied with caution in such circumstances.

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1. Introduction

The manner in which alleles, species and diseases spread over space is of fundamental interest to population biologists. These processes have an important impact on many evolutionary and ecological systems, and are particularly relevant in the modern world, where increasing global trade (Hulme, 2009) and highly interconnected transport systems (Guimerà et al., 2005) change the dynamics of disease and species dispersal. For example, international air travel has been suggested as a major driver of the spread of disease, including the 2009 H1N1 influenza A swine flu virus pandemic (Khan et al., 2009). Anticipating species invasions, and identifying how they might progress in such conditions, is an immediate and relevant problem.

Various models have been constructed in order to theoretically explore the dynamics of spreading populations. These guide our predictions about future genetic, demographic or disease prevalence trends, and our understanding of the history implied by current patterns. A core feature of models is whether they explicitly incorporate stochasticity. Traditional approaches tend to use deterministic approximations of the underlying stochastic process. Here, there is an assumption that over many repeats of an event with a random element the stochasticity will average out, and can be ignored without invalidating results. Such models can

often be analysed mathematically, but are sometimes sufficiently complex that a computational solution is necessary.

Stochastic models are usually more computationally intensive and less analytically transparent, but accept that explicitly including the randomness of events is important. It is often unclear which approach is preferable. In the specific case of species dispersal, a finite population of organisms that move and reproduce with a degree of independence implies a finite number of dispersal events. Stochasticity at small scales can have a significant impact on larger scale behaviour, and it is possible that averaging these events has a qualitative impact on model results.

One feature of population spread that is of particular practical interest is the expected rate of invasion. Deterministic equations predict that under many conditions population expansion occurs through a wave of advance travelling at constant velocity (Weinberger, 1982). In certain cases, however, where there is a relatively high frequency of long-distance dispersal events, this wave will accelerate indefinitely (Kot et al., 1996). The integrodifference model that retrieves this latter result has been widely applied in modelling species dispersal (Veit and Lewis, 1996; Neubert and Caswell, 2000; Takasu et al., 2000; Lockwood et al., 2002; Schofield, 2002; Krkošek et al., 2007; Dewhirst and Lutscher, 2009). However, the approach is deterministic, and it is not clear that the underlying stochasticity of dispersal can be ignored without causing inaccuracies. The impact of randomness on the accelerating wave of advance will therefore be the principal subject of this paper. We explore this by considering a range of stochastic models and their mean-field deterministic approximations, in which many dispersal events are described as a single average process.

Fisher–Kolmogorov and its limitations

Classical modelling of population spread has taken the form of reaction–diffusion equations. Here, a diffusion approximation is used to model the underlying stochastic dispersal and reproduction processes, which occur concurrently and independently of one another. This is a macroscopic approximation, obtained from the stochastic description by truncating in space or time to some finite order (Méndez et al., 2014). The paradigm is the Fisher–Kolmogorov equation (Fisher, 1937; Kolmogorov et al., 1937; Skellam, 1951):

$$\frac{\partial n}{\partial t} = \alpha n \left(1 - \frac{n}{K}\right) + D\nabla^2 n, \tag{1}$$

where n is population density at time t, α is the maximum growth rate, K is the carrying capacity (in some suitable units) and D is the diffusion constant. The equation is continuous in space and time and expresses the combination of logistic growth and Fickian diffusion. The diffusion constant, or diffusivity, describes the mean square distance over which a particle diffuses per unit time given a gradient of one unit, and may be expressed in dimensions L^2T^{-1}. A higher diffusion constant implies that the flow of organisms from full to empty space is easier and thus more rapid.

The use of a single parameter D to represent many possible dispersal regimes follows from arguments based on the central limit theorem (Bouchaud and Georges, 1990). It is justified by the relationship between Fickian diffusion and the stochastic process underlying it, Brownian motion. We can describe this process mathematically as a random walk.

A basic random walk is a stochastic system in which the position, x, of a particle is iteratively updated by its jump distance, drawn from a given probability distribution. This probability distribution describes the probability of dispersal over a distance l in a time interval, and is known as the *dispersal kernel*, $K(l)$. If we run many random walks with a given starting position, the distribution of the particles will spread out over time. Supposing a symmetric dispersal process, the mean position remains close to zero, but the diffusivity can be captured by the deviations around

this mean. For Brownian motion, and indeed more general random walks,

$$\langle x(t)^2 \rangle = 2Dt, \tag{2}$$

with the constant of proportionality defining the diffusivity. The central limit theorem prescribes that the distribution function of long-time positions is Gaussian so long as the same kernel applies to all particles, there are no long-range correlations in jump-distance, and the kernel has a finite first and second moment. D is related to the variance of the kernel by

$$D = \frac{1}{2} \int_{-\infty}^{+\infty} l^2 K(l) \, dl. \tag{3}$$

When the variance is unbounded, D is similarly not well defined, a point we return to shortly.

An initially isolated population that behaves according to the Fisher–Kolmogorov equation spreads out over time, creating a 'wave of advance', while maintaining a logistically determined level of occupation behind the travelling front. The model has been subject to much mathematical investigation, and a range of velocities can be sustained. However, under suitable initial conditions (Kolmogorov et al., 1937), including those most relevant to biological invasions, the wave speed (after transient acceleration) asymptotically approaches

$$c = 2\sqrt{\alpha D}. \tag{4}$$

For c to be asymptotically constant both D and α must exist and be asymptotically constant.

Laying aside model-specific issues such as environmental heterogeneity, advection, and qualities of population growth such as Allee effects, there are two general concerns about the application of the Fisher–Kolmogorov equation. Firstly, long distance dispersal may complicate the diffusion term. Secondly, stochasticity may invalidate results obtained from averaged processes. We deal with these points in turn.

Long-distance dispersal through integrodifference models

Standard theory suggests the diffusivity D can capture a wide range of stochastic dispersal processes through the relationship in Eq. (2). In the context of population spread, a naïve assumption of a normally distributed dispersal kernel would seem reasonable. However, many species appear not to follow this dispersal pattern, with dispersal better represented by a 'fat-tailed' kernel. These kernels involve an excess probability of dispersal at longer distances; specifically, the tail of the dispersal kernel decays more slowly than an exponential distribution. Such dispersal regimes have been observed in fungal spores (Brown and Hovmøller, 2002), plant seeds (Bullock and Clark, 2000), and in mammals and birds (Sutherland et al., 2000). Under these conditions, it becomes less clear that D will capture the dispersal process faithfully, and there is a strong argument for explicitly incorporating the dispersal kernel itself into a model.

As we have noted, some fat-tailed kernels decay so slowly that the variance or other moments are not well defined. Specifically, when the tail of a kernel decays as a power law, $K(l) \propto l^{-\beta}$ as $l \to \infty$, the $(\beta - 1)^{\text{nth}}$ and greater moments are not finite. This phenomenon is due to the dominant role that rare large values have on the characteristics of the distribution, and is useful for incorporating a relatively high probability of extremely long-range events into the dispersal regime. If $\beta \leq 3$, we can predict dispersal behaviour by considering a particular class of random walks, known as Lévy flights, for which the second moment is undefined (Lévy, 1937; Hughes et al., 1981).

When the variance is unbounded the effective diffusivity increases with time, termed superdiffusion. Given the role of D in the Fisher–Kolmogorov equation, we might expect these kernels to