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Families of discrete kernels for modeling dispersal

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Abstract

Integer lattices are important theoretical landscapes for studying the consequences of dispersal and spatial population structure, but convenient dispersal kernels able to represent important features of dispersal in nature have been lacking for lattices. Because leptokurtic (centrally peaked and long-tailed) kernels are common in nature and have important effects in models, of particular interest are families of dispersal kernels in which the degree of leptokurtosis can be varied parametrically. Here we develop families of kernels on integer lattices with several important properties. The degree of leptokurtosis can be varied parametrically from near 0 (the Gaussian value) to infinity. These kernels are all asymptotically radially symmetric. (Exact radial symmetry is impossible on lattices except in one dimension.) They have separate parameters for shape and scale, and their lower order moments and Fourier transforms are given by simple formulae. In most cases, the kernel families that we develop are closed under convolution so that multiple steps of a kernel remain within the same family. Included in these families are kernels with asymptotic power function tails, which have provided good fits to some observations from nature. These kernel families are constructed by randomizing convolutions of stepping-stone kernels and have interpretations in terms of population heterogeneity and heterogeneous physical processes.

Keywords: Dispersal kernel; Leptokurtosis; Discrete lattice; Negative binomial; Sichel distribution; Stable distribution

1. Introduction

Spatially explicit models are of increasing importance in population biology, especially in ecology where such models are relatively recent (Dieckmann et al., 2000). Key questions concern the patterning of organisms in space (Levin, 1992), the relationship of the patterning of organisms to patterns in the environment (Roughgarden, 1978), and the rate and pattern of spread of a species or allele across a landscape (Kinezaki et al., 2003; Lewis and Pacala, 2000). How organisms become patterned in space is of intrinsic interest (Klausmeier, 1999; Levin, 1992), but such patterns may also be used to draw conclusions about underlying processes. For example, spatial patterns may help distinguish different mechanisms of species coexistence (Bolker et al., 2003), or indicate dispersal distances (Ouborg et al., 1999). Spatial patterns potentially affect other processes. They may change the nature and outcomes of species interactions (Kareiva and Wennergren, 1995), potentially promoting coexistence of competitors (Bolker and Pacala, 1999; Hassell et al., 1994; Murrell and Law, 2003; Snyder and Chesson, 2003) or stabilizing host–parasitoid and predator–prey relationships (Briggs and Hoopes, 2004; Comins et al., 1992; De Roos et al., 1998).

Spatially explicit models inevitably require the use of functions called kernels, which describe dispersal in space (Snyder and Chesson, 2003) or represent interactions between individuals as functions of their distance apart (Bolker and Pacala, 1999; Snyder and Chesson, 2004). Our concern here is with dispersal kernels. In discrete time, a dispersal kernel defines for each spatial

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location the probability distribution of places dispersed from that location in one unit of time. The variance of this distribution defines the spatial scale of dispersal, but also important is kurtosis, which reflects the shape of the distribution. In nature, leptokurtosis is common, that is, dispersal kernels are often observed to have a sharp peak at the point of origin and a long tail. They are thus far from the Gaussian (normal) distributions often used in modeling. Of most importance, leptokurtosis has been shown to greatly increase the rate of spread of an invading organism or allele, and has been hypothesized to explain the faster than expected rates of spread sometimes found in nature (Cain et al., 1998; Kot et al., 1996; Lewis and Pacala, 2000). Moreover, recent modeling studies show that dispersal kurtosis may have important repercussions for the dynamics of spatial host–parasitoid interactions (Wilson et al., 1999) and disease (Brown and Bolker, 2004). Finally, leptokurtic models are of value in estimating dispersal characteristics from field data, giving greater precision when kurtosis is appropriately modeled (Clark et al., 1999). It is only recently, however, that suitable families of dispersal kernels, allowing broad ranges of kurtosis, have been in use. Hence, investigations of the full realistic range of kurtosis, including the extremes sometimes observed, are just beginning. This article facilitates this endeavor by providing new families of dispersal kernels for discrete space and time that allow exploration of the effects of kurtosis ranging from the Gaussian value to infinity.

In spatially explicit models, space can be represented as discrete or continuous, but integer lattices in one or two dimensions have advantages for many problems (Snyder and Chesson, 2003; Thomson and Ellner, 2003). However, models of dispersal on integer lattices are not well developed. The earliest integer-lattice models use stepping-stone dispersal: in one unit of time, only nearest neighbors of a lattice point are accessible (Kimura and Weiss, 1964; Malécot, 1969). Such models are useful for qualitative assessment of the effects of localized dispersal (Barton et al., 2002). Quantitative effects, and especially questions about the shape of the dispersal kernel, as discussed above, demand more sophisticated treatments. However, there has been very little development in the statistical literature of suitable probability distributions on integer lattices. Indeed, there is a need for parametric families of probability distributions on integer lattices in which the degree of kurtosis is a parameter so that the effects of leptokurtic dispersal can be studied in models.

Most discrete probability distributions of concern to statisticians are restricted to the nonnegative integers (Johnson et al., 1992). As a consequence, dispersal is often modeled by discretizing distributions on continuous Euclidean space for use on a lattice (e.g. Higgins and Richardson, 1999; Ibrahim et al., 1996). However, theory for the original continuous distributions does not apply to discretizations. Indeed, such features as convolutions, moments, and the relationships between them, transfer at best approximately to discretizations, and may be especially misleading for cases where the median dispersal distance is only a few lattice points. Similar difficulties arise with the common approach of using a probability distribution for distance dispersed to define the probabilities of dispersing to multidimensional lattice points regardless of direction (e.g. Levin and Kerster, 1975; Rousset, 2000).

We develop here a class of integer lattice distributions with a special focus on their applications to modeling dispersal. These distributions are designed to be simulated readily, with properties that are easy to define and control. We provide several families of such distributions defining dispersal kernels in any number of dimensions, although serious applications in population biology rarely go beyond two. These families are defined by time randomizations of convolutions of stepping stone kernels. A counterpart of this technique was recently applied by Yamamura (2002) to create a class of leptokurtic distributions for modeling dispersal in continuous space. For the most part, the families that we derive preserve convolutions, and so multiple dispersal steps of a kernel remain in the same family. The moments of these kernels have an elegant simplicity of interpretation, and their Fourier transforms have compact forms. Calculation of the probabilities for these distributions, i.e. calculation of the kernel itself, is often more complex, but robust numerical techniques are available in general. We build these distributions from stepping-stone distributions as the basic elements. In general, however, they have infinite tails and their properties vary from discrete approximation of multivariate normality to strong leptokurtosis suitable for representing rare long-distance dispersal.

To facilitate understanding, a list of notation is provided as Table 1.

2. Foundations

Given a probability mass function $K(\mathbf{x}) = P(\mathbf{X} = \mathbf{x})$, for some random variable $\mathbf{X} = (X_1, X_2, \ldots, X_d)$ on the d-dimensional integer lattice $(Z^d, \mathbf{x} \in Z^d)$, a dispersal kernel can be defined as the function of two variables $K(\mathbf{y} - \mathbf{x})$. This function gives the probability of dispersing in one unit of time from lattice point $\mathbf{x}$ to lattice point $\mathbf{y}$. Such kernels are translationally invariant because the dispersal probabilities depend only on the displacement $\mathbf{y} - \mathbf{x}$, not separately on the point of origin $\mathbf{x}$. Because of the direct relationship between $K(\mathbf{x})$ and the kernel $K(\mathbf{y} - \mathbf{x})$ derived from it, we refer to $K(\mathbf{x})$ as the kernel. Kernels are commonly chosen with further symmetry properties. In continuous space, radially