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Increasing accuracy of dispersal kernels in grid-based population models

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ABSTRACT

Dispersal kernels in grid-based population models specify the proportion, distance and direction of movements within the model landscape. Spatial errors in dispersal kernels can have large compounding effects on model accuracy. Circular Gaussian and Laplacian dispersal kernels at a range of spatial resolutions were investigated, and methods for minimizing errors caused by the discretizing process were explored. Kernels of progressively smaller sizes relative to the landscape grid size were calculated using cell-integration and cell-center methods. These kernels were convolved repeatedly, and the final distribution was compared with a reference analytical solution. For large Gaussian kernels ($\sigma > 10$ cells), the total kernel error was $<10^{-11}$ compared to analytical results. Using an invasion model that tracked the time a population took to reach a defined goal, the discrete model results were comparable to the analytical reference. With Gaussian kernels that had $\sigma \leq 0.12$ using the cell integration method, or $\sigma \leq 0.22$ using the cell center method, the kernel error was greater than 10%, which resulted in invasion times that were orders of magnitude different than theoretical results. A goal-seeking routine was developed to adjust the kernels to minimize overall error. With this, corrections for small kernels were found that decreased overall kernel error to $<10^{-11}$ and invasion time error to <5%.

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1. Introduction

Spatially explicit population models are useful for forecasting spatial processes that cannot be solved with single-location analytical models. They combine temporal reproduction and mortality processes with spatial redistribution processes. The earliest spatial population models were analyzed with continuous time and space equations (e.g. Kolmogorov et al., 1937), and this form is still important and useful (e.g. Andow et al., 1990; Lutscher et al., 2007). Continuous systems allow for exact solutions to research questions such as density of organisms and speed of invasion wavefronts at a given time and place. They simulate populations that have free, or non-seasonal, reproduction throughout the time domain.

For modeling organisms that have a distinct breeding season, integro-difference models that are discrete in time, but continuous in space, are often used (e.g. Neubert and Caswell, 2000; Lutscher and Lewis, 2004). Because of increased complexity in the model system compared to all-continuous models, numeric fast-Fourier transformations or numerical solutions are commonly found in ecological applications of integro-difference dispersal models, rather than analytical solutions (e.g. Kot et al., 1996). Because of computational complexity, theoretical spatial processes are often developed first in continuous space, and then demonstrated with a grid-based discrete map lattice (e.g. Lutscher and Lewis, 2004).

1.1. Discrete-space models

If a continuous-space model is analytically intractable or if a fragmented, realistic map landscape is desired, the landscape of interest can be modeled directly in discrete space. Methods of discretizing space include nodal models that simulate the measured distances and directions among habitat nodes (spatially explicit population model; Dunning et al., 1995), or simulate the "movement cost" associated with movement between two nodes (Minor and Urban, 2007). These "graph models" are by definition unconcerned with the space between nodes of interest. Space can also be subdivided into grids that simulate all of the landscape of interest. Irregular grids, such as unstructured polygonal meshes or curvilinear grids, allow for different sized cells to concentrate computing power and resolution in those locations that are more complex. This approach has been used to model hydrodynamics (e.g. Bockelmann et al., 2004; Crowder and Diplas, 2000), but apparently not for animal or plant models due to the complexity of calculating dispersal in cells that have various sizes and spatial arrangements.

Subdividing the spatial domain into a map lattice of regular polygons (generally squares) simplifies dispersal modeling. Grid-based kernel redistribution models are useful for simulating spatial dispersal processes such as invasion in complex, natural landscapes with varying features and multiple types of irregular habitat

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patches. Dispersal routines in grid-based population models specify the proportion, distance and direction of movement within each cell of the model landscape. Dispersal methods in regular grid models include global redistribution (e.g. King and Hastings, 2003), and nearest-neighbor redistribution (e.g. cellular automata; Ellner et al., 1998). A flexible modeling paradigm that can be applied to both graphs and (with effort) grids is circuit theory (McRae et al., 2008).

To simulate local dispersal processes in a grid-based spatial system, a continuous dispersal kernel, or probability density function for redistribution, can be split into component cells to generate and apply a discrete kernel through spatial convolution (Allen et al., 2001) or similarly, to apply a displacement matrix (Sebert-Cuvillier et al., 2008; Westerberg and Wennergren, 2003).

1.2. Problems with discrete spatial models

Standard terminology for cartographic standards, modified for ecological use, will be used (Dungan et al., 2002). "Spatial extent" is the overall size of the spatial domain, and "grain size" is the size of the cells in the landscape grid relative to the spatial extent. As the grain size decreases, the number of cells within a given spatial extent (the resolution) increases, and the accuracy of spatial processes, such as dispersal, increases.

Kernel smoothing and accuracy measures for "binned" data, and the determination of what grain size is needed for a given level of accuracy has been well documented (Jones, 1989; González-Manteiga et al., 1996; Hall and Wand, 1996; Pielaat et al., 2006). With classical numerical simulation of a complicated system that cannot be solved analytically, the grain of the landscape can be dynamically adjusted to preserve a defined, low error rate. For theoretical applications in discrete systems with a small spatial extent, a small grain size can be implemented for good accuracy. However, if the landscape is large compared to the dispersal abilities of the organism, a fine grain size for detailed dispersal kernels would lead to a very large number of cells across the spatial domain, thus requiring large amounts of computer processor power, RAM and data storage. Depending on the complexity of non-dispersal operations, the amount of time needed to run grid-based models tends to increase to the fourth power of the number of cells in any linear dimension of the simulation, so the time to run a simulation quickly increases as the spatial resolution becomes finer.

For some applications, the resolution of the model is already set due to precedent models or available data resolution (e.g. satellite imagery), and the modeler must work within that framework. For example, there are several spatial population models that support decision-making in the greater Everglades restoration process (CERP; http://www.evergladesplan.org/). Many of these models are driven by hydrological state variables, such as water depth or salinity. Hydrological models that provide these variables are available for different regions and purposes in 2×2 mile squares (SFWMM; SFWMD, 2005), 500×500 m (ATLSS; DeAngelis et al., 1998), or 400×400 m (EDEN; Liu et al., 2009). Land managers generally expect ecological model output to be in the same grid system as the hydrological models for consistency and ease of interpretation. These pre-defined grid sizes can lead to very coarse-grained spatial processes and small dispersal kernels. Climate models often are calculated with grid sizes of several kilometers. Downscaling to a finer scale presents substantial challenges and effort (Araújo et al., 2005), so tools to use coarse-scale models directly would be useful.

When dispersal of organisms is introduced to a discrete spatial model, the square shape of the landscape cells introduces errors in distance and direction as compared to the analytical dispersal process. Simple discrete dispersal methods such as nearest-neighbor, where propagules are redistributed only to the nearest contiguous cells, limit dispersal patterns, and are inappropriate for wide-ranging organisms. Using a discrete form of the continuous integro-difference redistribution kernel may reduce spatial errors compared to a simple nearest-neighbor distribution process, but each cell in the kernel can only contain one constant density, while a continuous dispersal kernel can change value over the same space. For some applications, a fine temporal scale may be desired. As the time step decreases, dispersal kernels become smaller and more coarse-grained. As the grain size is increased and the number of cells in a dispersal kernel shrinks, the information contained within the kernel also shrinks, and the kernel tails become less well defined. Very coarse kernels can essentially be reduced to a nearest-neighbor situation. These coarse kernels can be expected to contain large spatial errors (Hall and Wand, 1996; Fig. 1).

Errors that are generated by the discretization of spatial processes have always been tacitly acknowledged by researchers performing traditional numerical solutions to continuous spatial processes, so they use very fine grain sizes or error-controlling numerical methods (such as Runge-Kutta) in their simulations. Recently, uncontrolled error that appears in discrete model systems where the grain size is pre-selected and large is receiving attention in the literature (Chesson and Lee, 2005; Holland et al., 2007; O'Sullivan and Perry, 2009). Significant dispersal errors were found in a model described by Slone et al. (2003), caused by small size dispersal kernels on a large-grained landscape. For that model, the authors corrected the specific kernels used on an ad-hoc basis, but questions remained about the general error rates of small kernels. Measuring and correcting these errors will be the central focus of this paper.

2. Methods

2.1. Defining and correcting errors

Accurate dispersal kernels are necessary for spatial models to be reliable tools for answering management questions. As grain size decreases towards zero, results from a discrete simulation will asymptotically approach that of a continuous-space simulation (i.e. – have zero error). Two questions that arise are (1) at what grain size does the error between the discrete and continuous system become negligible for answering research questions, and (2) at coarser resolutions, can the error be corrected so that more efficient coarse-grained simulated landscapes can be used?

The research has the following three objectives:

1) quantify error in discrete Gaussian and Laplace dispersal kernels, and the invasion speed of these kernels when applied to a spatial model;
2) explore methods to correct kernel error, thus allowing the output from coarse-grained discrete spatial systems to match theoretical or field-measured dispersal rates; and
3) determine a minimum grain size where no correction is required (<5% error in invasion speed).

Though population redistribution functions are often non-normal (Kot et al., 1996), the bivariate Gaussian distribution was explored first because it exhibits "closure" (Chesson and Lee, 2005): that is, as organisms disperse from a single cell through time with a Gaussian dispersal kernel, their overall distribution will remain Gaussian, with known parameters. This property enables a simple but powerful test: as a Gaussian dispersal kernel becomes very small, do the propagules still disperse in the expected pattern and retain the expected Gaussian distribution? Other kernel shapes do not lend themselves so readily to this type of analysis. The Gaussian kernel – assuming non-directional circular dispersal ($\mu_x = \mu_y = 0$; $\sigma_x = \sigma_y = \sigma$) – has an additional simplifying property that it has only one parameter (σ; see Table 1 for notation).