Simulating long distance dispersal processes in spatially heterogeneous landscapes

D. O'Sullivan[1] and G.L.W. Perry[1]

[1]School of Geography, Geology and Environmental Science,
University of Auckland, Private Bag 92091, Auckland 1142, New Zealand
Telephone: +64 9 373 7599 extn 84963
Fax: +64 9 373 7434
Email: {d.osullivan, George.perry}@auckland.ac.nz

1. Introduction

The interaction between dispersal processes and the spatial structure of landscapes is key to understanding the risks associated with the spread of invasive organisms. The critical question in dispersal ecology is how to explain the fact that organisms spread much more rapidly than classical models predict (Skellam 1951, Clark et al. 1998). The question is often addressed using mathematical and simulation approaches (see, e.g., Kot et al. 2004). In these contexts, the spatial extent of models is usually limited to individual organisms modelled at fine grains (e.g. less than 10 m).

Management-oriented models force us to consider a wider range of scales, from individual organisms (10^{-1} metre) to landscapes and regions (up to 10^6 metres) and require development of novel computational approaches to dispersal. Dispersal of propagules may depend on micro-turbulence or on decisions made by foraging animals, and are fine-grained in space and time (Nathan 2006). However, such mechanisms may resolve themselves on landscapes of hundreds, or even thousands of kilometres extent (Perry and Enright 2006). An obvious approach is individual-based models that represent individual organisms, along with the detail of their fine-grained behaviours. Recent simulations of forest succession may have as many as 10^8 individual trees (Chave 1999, Govindarajan et al. 2007). That such models are restricted to spatial extents of only around 100km^2 points to the challenges facing this approach, even with rapid developments in high-performance computing. In any case, analysis of such models is likely to be conducted only after data reduction, so that many painstakingly included details—especially the spatial details!—are lost when they are applied to ecosystem management.

2. Modelling dispersal more efficiently

The central difficulty of modelling dispersal processes from a management perspective is that most dispersal events occur over very short distances (up to perhaps 10 metres or so), but rates of spread are governed by rare long distance dispersal (LDD) events at distances two or more orders of magnitude greater (Nathan 2006).

In figure 1, a random walk of 1000 steps, with each step length drawn from an exponential probability distribution with mean length of $\lambda=0.1$ is shown. Over 1000 time-steps, the walk advances less than one whole grid square (from the red to the blue dot). Relative to the imposed grid, the walk may spend long periods oscillating back and forward between two cells along an edge. Thus, when the scope of the study requires a grid cell resolution on the order of 100's of metres (both because of the data available

and/or the extent being considered), but local dispersal occurs on the order of a few metres, substantial difficulties arise.

Two approaches are typically taken. One is to represent every individual in the population explicitly, but this becomes unwieldy when applied to real world problems, as we have seen. The alternative is to represent only total population or biomass in each grid cell. However, standard implementations of this approach may only crudely approximate the details of the dispersal process, typically applying simple rules of probabilistic contagious spread to adjacent cells (Birch 2006).
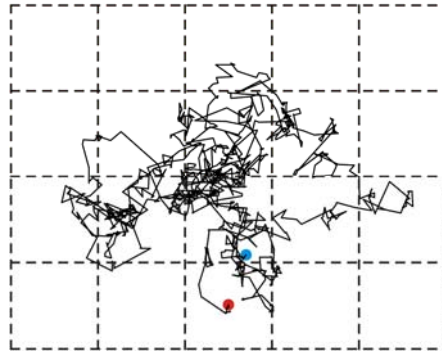

Figure 1. The scaling problem associated with dispersal.

Our approach conceptualises the presence of an organism in a grid cell as being in one of two 'phases' either the *core* or *buffer* phase. In the core phase, the probability of cell exit is determined by drawing a dispersal distance *d* from a probability distribution (or dispersal kernel) describing the process of interest (see for example Clark et al. 1998). A typical dispersal kernel might be an exponential distribution with mean $\lambda = 0.05$ where distances are expressed relative to grid cell resolution. Large values of *d* result in movement to a remote grid cell by applying simple geometry. For *d* <1, Buffon's needle result (Birch 2006, Shortridge and Goodchild 2002) is applied to determine the probability of exit to an orthogonal grid cell. The standard Buffon's needle probability results are scaled to account for additional cell-to-cell movements caused by the buffer phase mechanism described below, as detailed in O'Sullivan and Perry (2009). A uniform random number draw in the range 0 to 1 then determines whether cell exit actually occurs.

When exit to an adjacent cell occurs, the organism enters the adjacent cell in the *buffer* phase and movement is handled differently. Each time-step the organism stays in the buffer phase with probability *s*. An organism determined as not staying moves back to the grid cell from which it originally arrived in the cell, *remaining in the buffer phase*, with probability *b*. Finally, an organism which is neither staying in, nor returning to its original cell, moves forward into the core phase in its new grid cell. This mechanism is a Markov chain governing movement from grid cell to grid cell (figure 2).
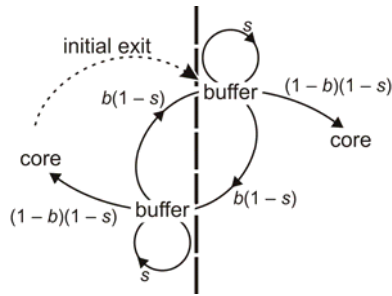
Figure 2. Schematic illustration of movement across a cell boundary (the dashed line) showing core and buffer phases, and associated probabilities.

O'Sullivan and Perry (2009) show that this mechanism can be tuned by appropriate choice of s and b to match dispersal rates associated with continuous-space random walks on the same gridded landscape. This is true even for dispersal kernels with mean distances that are short (down to ~0.01) relative to the grid resolution.

3. Population-level dispersal and the complete model

The model described above represents an individual random walk across a gridded landscape. Up-scaling the approach to a population level is illustrated in figure 3.
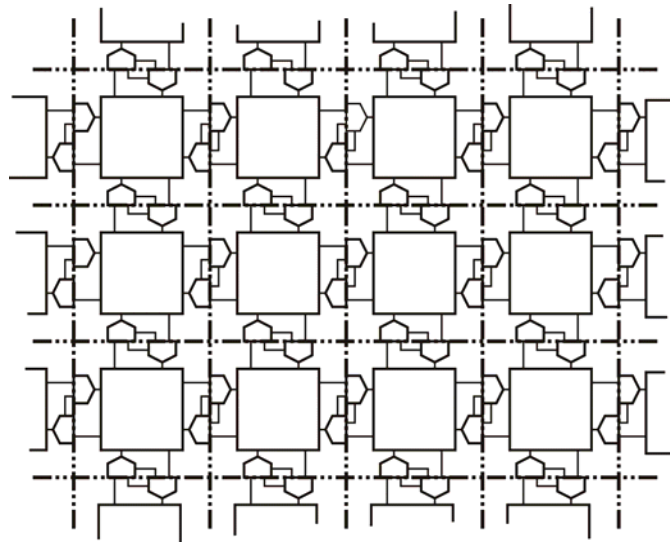

Figure 3. The structure for up-scaling the dispersal mechanism to the grid-level.

Each grid cell holds five 'containers' for each population, one core phase, and four 'in-bound' buffer phase containers. At each time-step a grid-cell's population is the sum of its five containers. Movement from core containers to buffers in adjacent cells is governed by drawing dispersal distances from an appropriate dispersal kernel. Movement in the buffer phases is stochastic. For example, if there are N occupants of a particular buffer phase container, a binomial distribution with probability s determines how many stay. Of those leaving, a binomial process determines how many move back

to the neighbouring cell buffer phase, and how many move forward to the current grid cell core.

This mechanism has been implemented using *NetLogo* (Wilensky 1999). The full model includes a logistic population model (Gotelli 2008), and landscape structure is represented by multi-cell 'patches' of uniform carrying capacity, initialised by a voter model (Liggett 1999) where the number of rounds of voting controls the spatial scal. Alternative landscape structures can be easily accommodated with SIMMAP (Saura and Martinez-Millan 2000) an attractive option. Figure 4 shows the complete model.
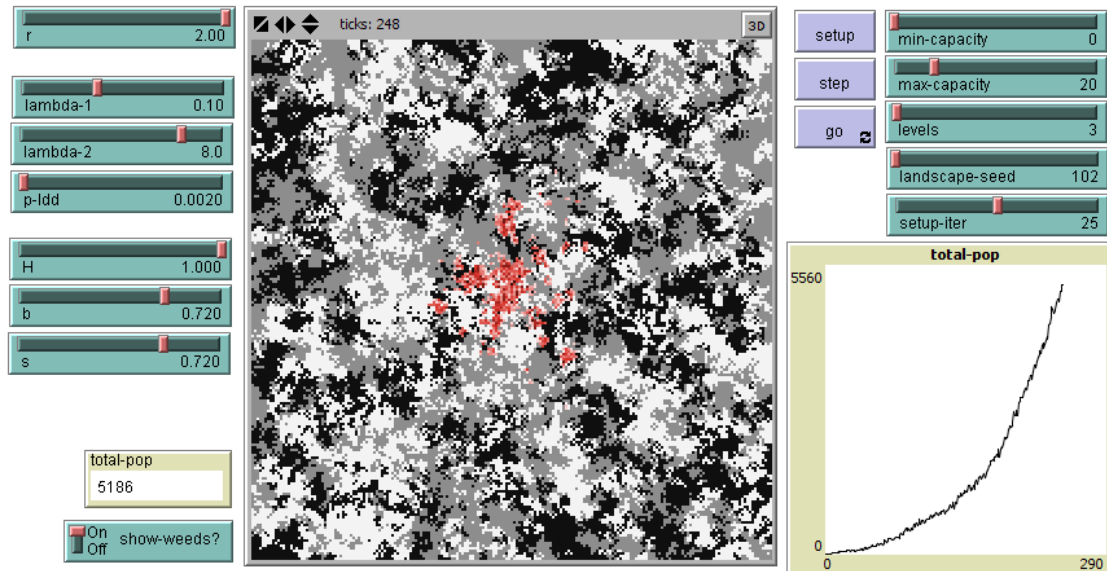

Figure 4. The complete model prototype. Carrying capacity in each cell is coloured from white to black as capacity increases, and a population of mobile organisms is shown in shades of red.

5. Conclusions

A mechanism for efficiently representing dispersal processes with a significant long-distance component on large landscapes has been developed and integrated into a general model. Preliminary results on the interaction between the scale of landscape structure and dispersal kernel properties will be presented.

6. References

Birch, C. 2006. Diagonal and orthogonal neighbours in grid-based simulations: Buffon's stick after 200 years. *Ecological Modelling*, 192: 637-644.

Chave, J. 1999. Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. *Ecological Modelling*, 124: 233-254.

Clark, J., Fastie, C., Hurtt, G., Jackson, S., Johnson, C., King, G., Lewis, M., Lynch, J., Pacala, S., Prentice, C., Schupp, E., Webb III, T., Wyckoff, P., 1998. Reid's paradox of rapid plant migration: dispersal theory and interpretation of paleoecological records. *BioScience* 48: 13–24.

Gotelli, N.J. 2008. *A Primer of Ecology*, 4th Edition (Sinnauer Associates, MA).

Govindarajan, S.; Dietze, M.C.; Agarwal, P. and Clark, J.S. 2007. A scalable algorithm for dispersing populations. *Journal of Intelligent Information Systems*, 29: 39-61.

Kot, M., Medlock, J., Reluga, T.C., and Walton, B.D. 2004. Stochasticity, invasions, and branching random walks. *Theoretical Population Biology*, 66: 175–184.

Liggett, T.J. 1999. *Stochastic Interacting Systems: Contact, Voter and Exclusion Processes* (Springer, New York).

Nathan, R. 2006. Long-distance dispersal of plants. *Science*, 313: 786-788.

O'Sullivan, D. and G.L.W. Perry. 2009. A discrete space model for continuous space dispersal processes. *Ecological Informatics,* 4(2): 57-68.

Perry, G.L.W. and Enright, N.J. 2006. Spatial modelling of vegetation change in dynamic landscapes: a review of methods and applications. *Progress in Physical Geography*, 30: 47-72.

Saura, S. and Martinez-Millan, J. 2000. Landscape pattern simulation with a modified random clusters method. *Landscape Ecology*, 15: 661-677.

Shortridge, A.M. and Goodchild, M.F. 2002. Geometric probability and GIS: some applications for the statistics of intersections. *International Journal of Geographical Information Science*, 16: 227-243.

Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38: 196-218.

Wilensky, U. 1999. *NetLogo* [Computer software]. Evanston, IL: Center for Connected Learning and Computer-Based Modeling, Northwestern University. http://ccl.northwestern.edu/netlogo