

Explicitly Spatial Stochastic Reaction-Diffusion Models

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1 Introduction

There is a class of population models where dispersal is via diffusion. These are called reaction-diffusion models. Here we attempt to solve stochastic versions of such models numerically.

It was concluded that a stochastic technique which is both spatially and temporally discrete (though not with discrete individuals) gives a good match to the analogous deterministic reaction-diffusion models. This means that they displayed qualitatively equivalent dynamics. The proposed approach is more computationally demanding and allows less precise knowledge of the dynamics, but should be able to handle complex formulae more easily.

2 Background

Classic population models are deterministic and attempt to model the large-scale aggregated changes in population size. While they do provide insight into broad-scale population dynamics, they are of theoretical interest more than having direct application. For example, the model population may approach a limit continuously, coming within a fraction of an individual, but never reach it.

Models including environmental stochasticity address some of these problems. They incorporate random variables to represent, eg., unpredictable environmental variation. They are generally more realistic, especially for small populations. However, analysis of these models becomes very difficult as the formulation becomes more complex, which is often necessary for real populations.

Reaction-diffusion models also attempt to address a simplification in the classic models, that is, representing spatial heterogeneity. Clearly only a very small set of populations are well-mixed and spatially uniform. The diffusive dispersal represented in these models has wide applications including the dynamics of insects, plankton and mold. Solutions typically involve a continuous wavefront in

the transition between steady states (Murray 1993, p. 311). Specifically, if a small region is perturbed within a domain at unstable equilibrium, a wave may propagate at constant speed until it eventually completes the transition.

While diffusion is generally a stabilising influence, other terms in the model may be unstable and we potentially get some kind of balance. (The classic example is chemotaxis, movement *up* a chemical gradient.) Indeed May (1974, p. 137) has noted that spatial heterogeneity *per se* acts as a stabilising influence, for instance by allowing recolonisation of local extinction (refuge effects).

However, reaction-diffusion models have some of the same problems listed above – in particular, overly-precise solutions and difficulty of analysis. We will try to address these with a stochastic approach, but one that is spatially explicit. That is, the model processes, including diffusion, are performed directly on a spatial lattice – it is of course necessary to do this with a computer. If the method can be validated, this should allow more complex formulations which would be otherwise analytically intractable. One could include, for example, life expectancy or other history parameters. Another example might be the effect of habitat heterogeneity (such as variation of birth rate over space).

3 Theory

Deterministic reaction-diffusion models are of the form

$$\frac{\delta \mathbf{u}}{\delta t} = f(\mathbf{u}) + D \nabla^2 \mathbf{u} \quad (1)$$

where \mathbf{u} is the vector of species (or generally, reactant concentrations), $f(\mathbf{u})$ is the species interactions (non-linear reaction kinetics), and D is the matrix of diffusivities (usually just diagonal constant). The diffusion term can be derived analytically from a simple random walk (see Murray 1993, pp. 232-236).

In casting these models as lattice-based simulations we would like to go in the other direction, replacing the second derivative (diffusion) term with a simple random walk. This can be done with a uniform random variable in both spatial dimensions: repeated symmetric uniform displacement results in a gaussian distribution about the origin, just like diffusion.

We will apply the proposed method to the following models.

The simplest diffusion model is just the heat equation. In one spatial dimension this is:

$$\frac{du}{dt} = c \frac{d^2 u}{dx^2} \quad (2)$$

which is pure diffusion, conserving the population u . The diffusion coefficient c corresponds to the speed at which the initial conditions approach the steady state of spatial uniformity.

A slightly less trivial model is that of logistic growth with dispersal via diffusion. As a deterministic reaction-diffusion model this is the Fisher equation, derived in 1937 for describing the evolutionary success of a gene (Murray 1993, p. 277):

$$\frac{du}{dt} = ru\left(1 - \frac{u}{k}\right) + D\frac{d^2u}{dx^2} \quad (3)$$

where r is the intrinsic rate of increase and k is the carrying capacity.

Perhaps the best-known of population models are predator-prey systems. A moderately complex Lotka-Volterra-type model with dispersal via diffusion is (from Murray, 1993, p. 315):

$$\begin{aligned} U_t &= AU\left(1 - \frac{U}{K}\right) - UV + Du_{xx} \\ V_t &= CV - DV + Dv_{xx} \end{aligned} \quad (4)$$

which, for simplicity, can be non-dimensionalised to

$$\begin{aligned} u_t &= u(1 - u - v) + Du_{xx} \\ v_t &= av(u - b) + Dv_{xx} \end{aligned} \quad (5)$$

where u is the prey and v the predator density at each location. D is a constant diffusion rate (in this case equal for the two species). The parameters are not as easily interpreted in this form, but we will refer to a as the predator amplification, and to b as the prey equilibrium (see below).

In analysing the deterministic reaction-diffusion systems, we can solve for wavefront solutions by transforming the spatial variable to a *wave variable* $z = x - ct$. It is then possible to construct phase plane equations and find singular points. A standard linear stability analysis for each shows that

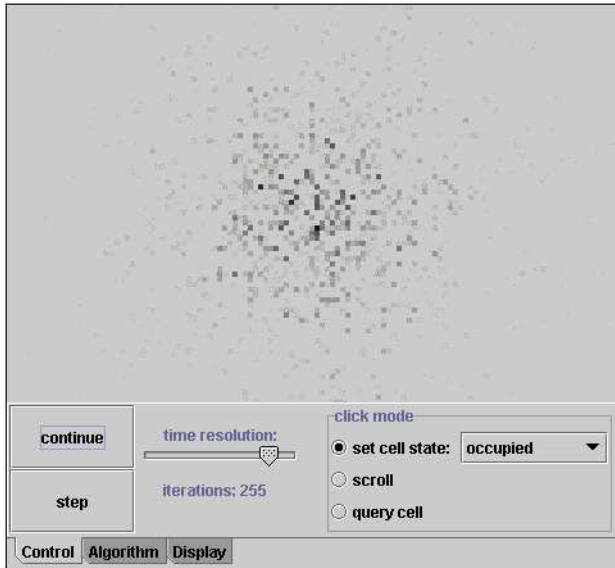
- $(u, v) = (0, 0)$ is unstable;
- $(u, v) = (1, 0)$ is unstable;
- $(u, v) = (b, 1 - b)$ is stable.

Further, looking at the characteristic polynomial from the analysis of the stable node, there is a critical value of the predator amplification a^* such that for $a < a^*$ there is a monotonic approach to the steady state, and for $a > a^*$ it is oscillatory. This procedure is due to Murray (1993, p. 315-318).

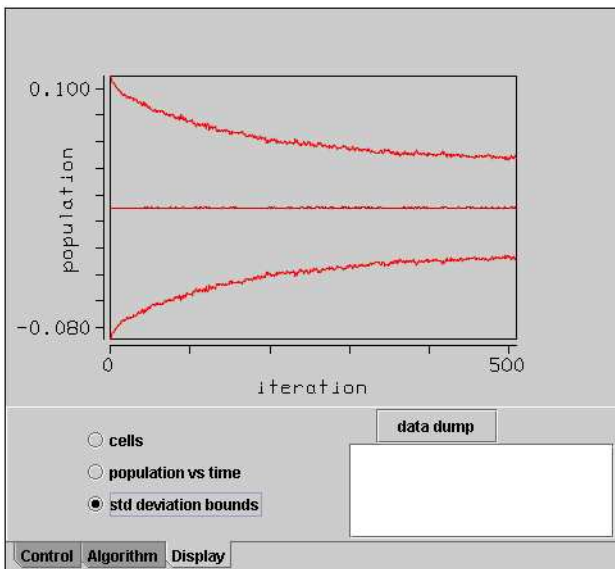
4 Results

The software was written as a reusable framework in Java. The interface uses interactive applets – these are available with the full source code at <http://www.nfrac.org/ca/>.

This first screenshot shows the basic diffusion process developing from an initial spike of 10x10 cells. The algorithm is supposed to correspond to equation 2. We can see that a distribution similar to the gaussian is indeed occurring.

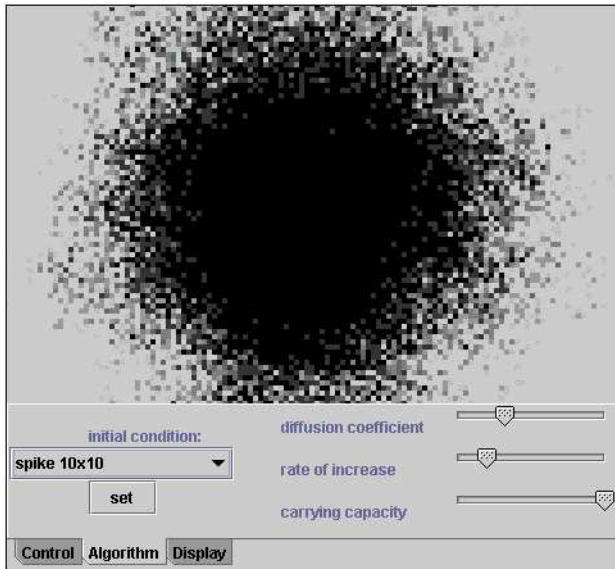


This is a plot of mean density (centre line) and one-standard-deviation bounds (outer lines) of the diffusion process. The system moves to a state which is more uniform, as expected from diffusion. Mean density is conserved.

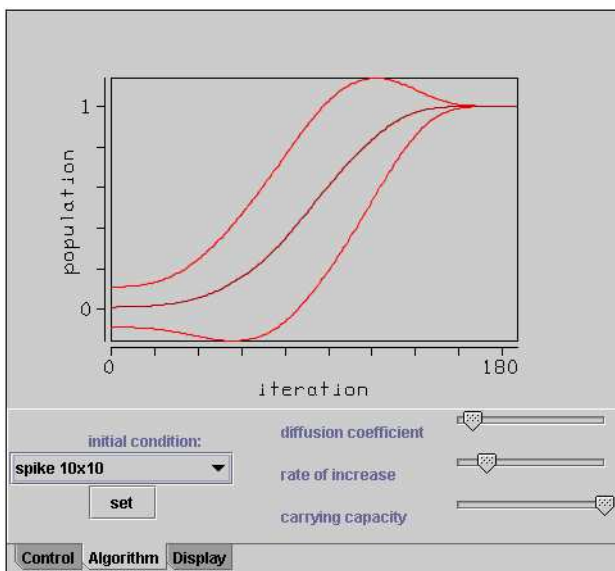


The following image shows the logistic growth process (equation 3) where $k=1$, developing again from a small spike. Of course, if $k < 1$, random variation

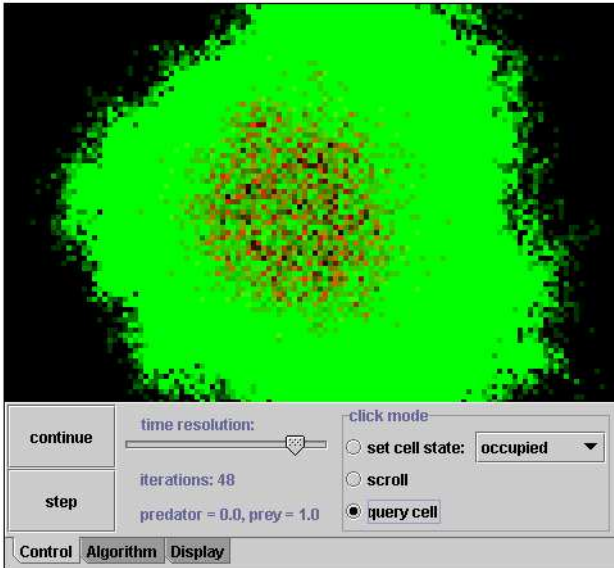
continues at the steady state. In this model it was observed that increasing the diffusion coefficient causes the mean density to drop. The general observation (and theoretical derivation) that models with more stochasticity support lower populations has been made, eg. in May (1974, p. 122).



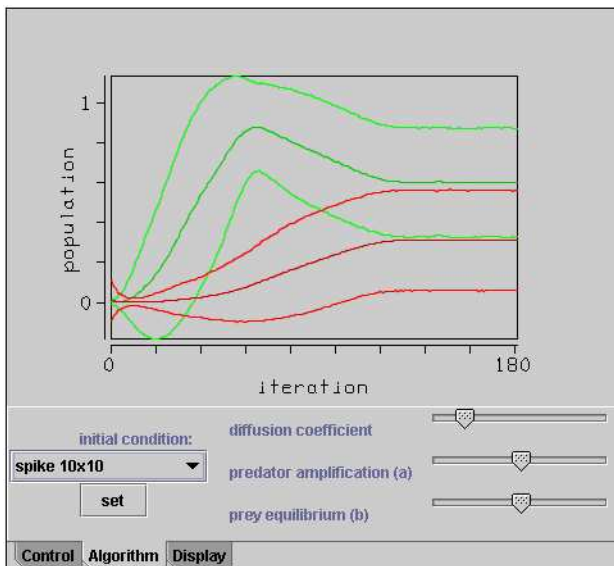
Below is a time series plot of the same process with standard deviation bounds. This waveform is as expected from the logistic growth equation (Murray, 1993, p. 279).



The screenshot below shows initial development of the predator-prey model with similar starting conditions as the previous ones. The algorithm is of course based directly on equation 5. Green corresponds to prey density and red to predator density. This is a good example of “waves of pursuit and evasion”, although it is not so much evasion as growth into empty space.

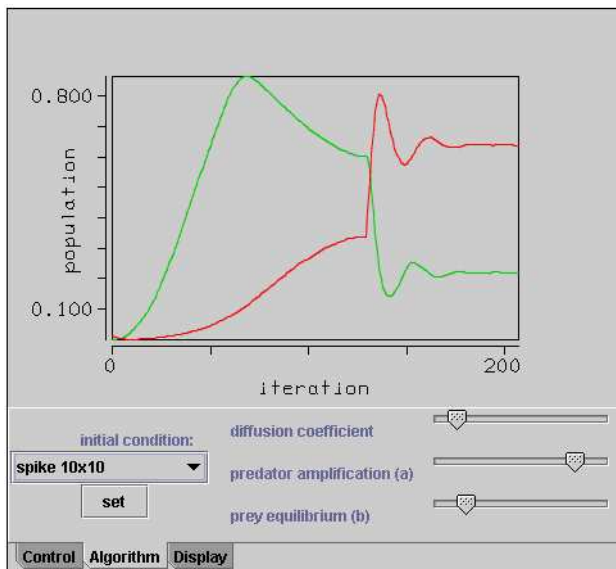


The same situation after equilibrium is reached is shown in this time series plot; again green is the prey and red the predator, with mean density and standard deviation of each. With $b=0.5$, the deterministic model predicts that predator and prey densities should be equal. What we observe is that the predator is lower than the prey. It seems that the predator is susceptible to environmental variation (as with the logistic model above) but the prey are able to recover to their previous stable level following an increase in diffusion coefficient. The parameter b does however have the expected relative effect – increasing it increases the prey density (and decreases the predator), and vice-versa.

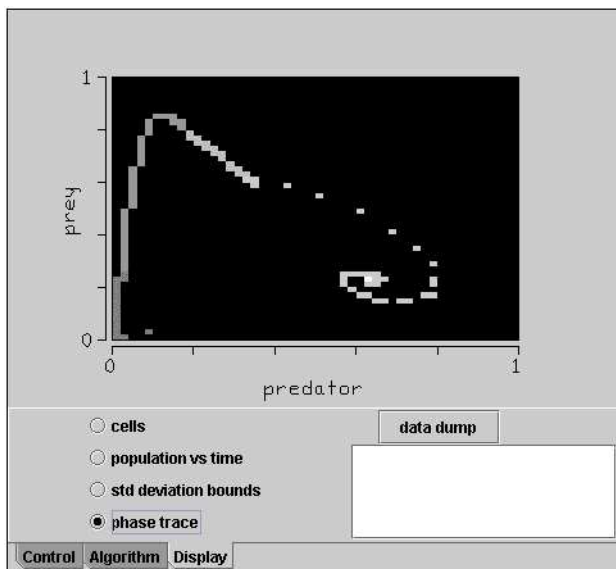


We will now test whether the theoretical result about a critical value of the 'predator amplification' (a) can be observed. The basic situation starts from

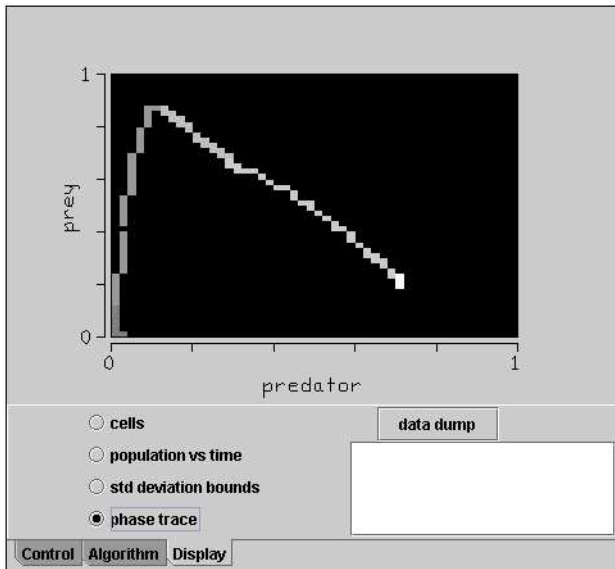
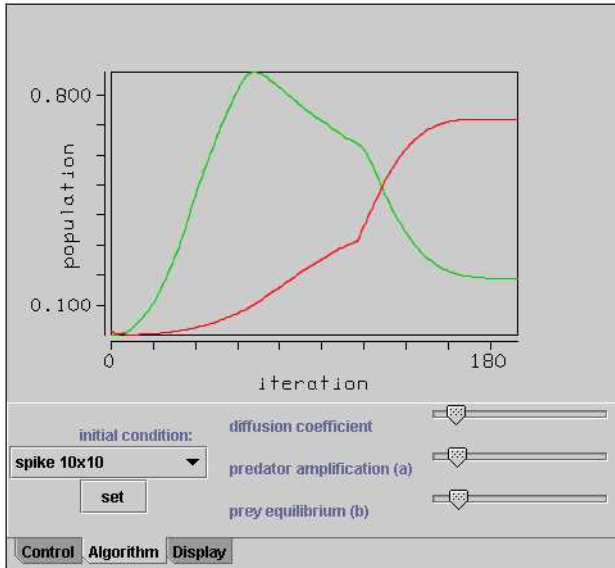
a 'spike' initial condition and lets the wavefronts move to a steady state with a high value of the prey equilibrium (b). Then the prey equilibrium is instantly changed to be low, causing a transition to the new steady state. In the first case we do this with a high value of a , so we should expect an oscillatory approach. This can indeed be seen on the following time series...



...and equivalent phase plane trace (brighter points occurred later in time).



A contrast can be made with the following plots, which show the same situation but with a low value of a . We expect monotonic rather than oscillatory behaviour, and that is clearly observed.



We can conclude that there is a critical a^* in this implementation of the predator-prey model.

All tests on these explicitly spatial stochastic reaction-diffusion models have shown a qualitative correspondence to the analytical forms.

5 Conclusion

The simulations were successful within the aims of this project.

6 Bibliography

May, R. M. (1974) *Stability and Complexity in Model Ecosystems* (2nd ed.).
Monographs in Population Biology. Princeton University Press.

Murray, J. D. (1993) *Mathematical Biology* (2nd ed.). Springer.