Structure Analysis of the Spatial Lotka-Volterra Equations

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Introduction

The Lotka-Volterra coupled system of equations[1, 2] describing relationships between predators and prey has been applied to a number of spatial biological and ecological models by several authors. The equations need to be time-integrated for long times on a large system to fully appreciate the complex bulk behaviour that ensues spatially. We apply spectral analysis methods to spatial Lotka-Volterra models to study length scales and phased-locked spatial wave patterns at early and long time scales. We use spectral analysis techniques that allow construction of the Fourier images of the equation variables and their combination to construct numerical scattering experiments. Small-angle scattering[3] is a technique used in materials science[4], and it allows study of effects in a bulk field that would otherwise be difficult to spot or measure.

The Lotka-Volterra system is a framework for studying growth and fluctuations[5] in complex systems. Other authors have observed that the spatial system is a rich source of spatio-temporal fluctuations[6] and spatial variability[7]. Discrete models of predator-prey systems[8] also produce complex spatial emergent patterns such as spirals[9] and wavefronts. We show an example of the spatial wave fronts that oscillate between boom and bust in our simulated spatial Lotka Volterra system in Figure 2.

The Lotka-Volterra Equations

The Lotka-Volterra system of equations is usually written in terms of a n-vector $\mathbf{u}$ of relative populations of the 2 species in the system as:

$$\begin{aligned}\frac{du_0}{dt} &= Au_0 - Bu_0u_1 \\ \frac{du_1}{dt} &= Du_0u_1 - Cu_0\end{aligned} \qquad (1)$$

where the generalised interaction operator $\mathcal{F}$ is limited to the four terms shown with simple positive coefficients A, B, C, D. It is useful to fix ideas and think of a simple predator prey system such as "rabbits and foxes" where u_0 is the population of prey or "rabbits" and u_1 is the population fraction of predators or "foxes." This system has been well studied and is known to have a fixed point at $(x, y) = (\frac{D}{C}, \frac{A}{B})$. The implications of this are that a model system, initialised at some arbitrary point (x_0, y_0) will orbit around the fixed point for suitable non-zero values of A, B, C, D.

These four parameters can be interpreted in terms of the rabbit-fox predator-prey model as follows:

- **A** is the (exponential) prey growth rate
- **B** is the rate predators kill prey
- **C** is the growth rate of predators from killing prey
- **D** is the (exponential) death rate of predators

and are expressed this way as positive values.

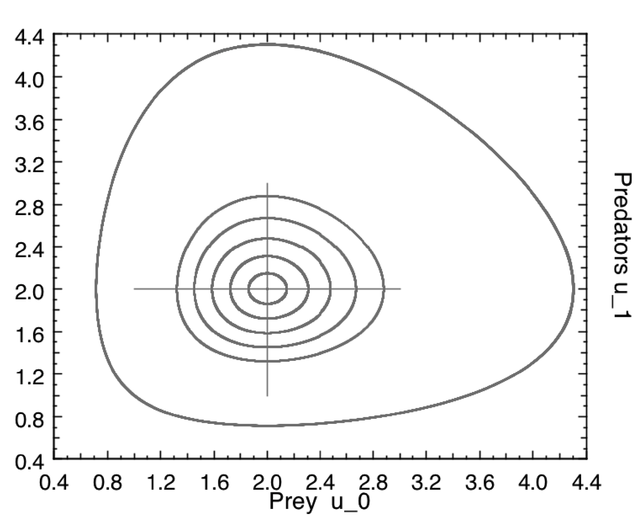

Figure 1: **Lotka-Volterra orbits in 2-species phase space, where the predator population phase-lags the prey by 90 degrees, manifested in boom-bust cycles.**

Figure 1 shows the typical fixed point attractor for the Lotka Volterra equations for the values: $A = 1, B = 0.5, C = 0.5, D = 1$. Any spatially isolated Lotka-Volterra cell with two species prey and predators shown on the x- and y-axes respectively, will orbit the fixed point anti-clockwise if initialised in the region of the fixed point. The figure shows points that have been initialised at $(1, 1), (1.5, 1.5), (1.6, 1.6), ..., (2.0, 2.0)$ which give rise to orbital trajectories that are seen to orbit the fixed point at $(2.0, 2.0)$, or stay at it.

We are interested in formulations of this coupled (pair) or equations that extend to a spatial field - such as a two-dimensional square grid, so that each cell has population variable for the fraction of predators and prey on it. We further want to find a realistic way to couple the cells spatially so that the predators and prey are effectively moving around the system but that the number of a particular species is conserved by the spatial operation, even although it will oscillate and change in time. One form is:

$$\begin{aligned}\frac{du_0(\mathbf{r})}{dt} &= \mathcal{O}(u_0(\mathbf{r})) + Au_0(\mathbf{r}) - Bu_0(\mathbf{r})u_1(\mathbf{r}) \\ \frac{du_1(\mathbf{r})}{dt} &= \mathcal{O}(u_1(\mathbf{r})) + Du_0(\mathbf{r})u_1(\mathbf{r}) - Cu_0(\mathbf{r})\end{aligned} \qquad (2)$$

where a spatial operator $\mathcal{O}$ can either be formulated as a spatial average as above, or can simply be taken as the Laplacian operator ∇^2 which then turns equation 3 into a reaction-diffusion equation system.

Numerical Scattering

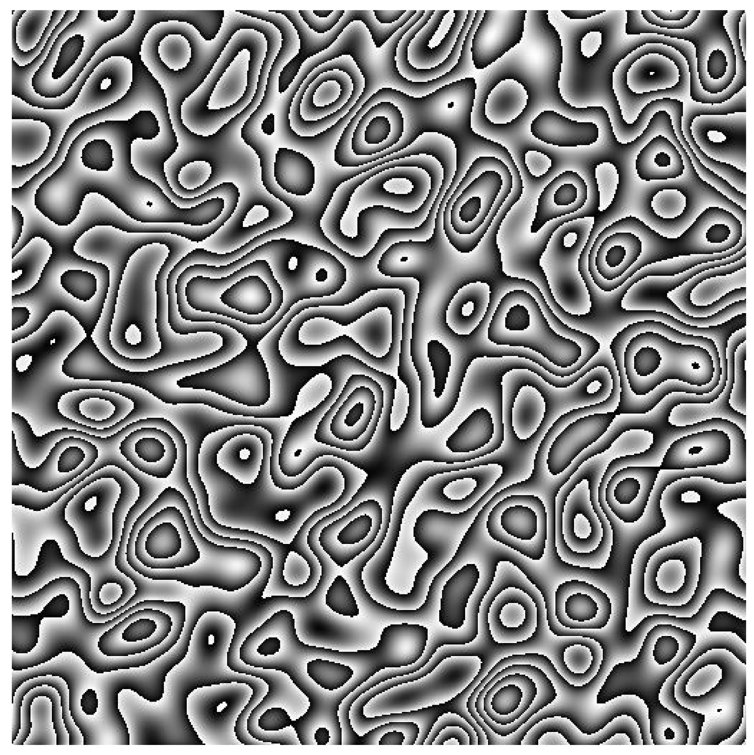

Figure 2: **Spatial Lotka-Volterra system at time 2048×0.05 after random start on 512×512 square periodic grid.**

Scattering experiments in materials science can use neutrons or x-trays or other particles. The essential physics is much the same and the end result is that a scattering experiment using an incident beam of particles van be used to probe the bulk average properties of a real sample. The scattering pattern formed by collecting the scattered particles in suitable detectors can give quantitative indications of the size and sometimes shape of spatial fluctuations and structures that are forming in the material. In the numerical simulation, a computation of the scattering pattern is possible and this can reveal properties of the simulated data field that would otherwise be hard to extract and observe. We give a brief derivation of the scattering formula.

A neutron scattering experiment conducted on a sample with volume V with scattering angle Ω and scattering cross-section (probability) of σ is given by:

$$\frac{d\sigma}{d\Omega} \approx (\rho_p - \rho_m)^2 \frac{1}{V} \left| \int_V e^{i\mathbf{Q}\cdot\mathbf{r}} d\mathbf{r} \right|^2 \qquad (3)$$

The term $(\rho_p - \rho_m)^2$ is the difference between the densities of the phase of interest and the background density and is known as the small angle scattering contrast, denoted as $\triangle\rho^2$. A large value of $\triangle\rho^2$ gives higher *relative* scattering intensity from the precipitate phase. Equation 3 can then be rewritten as:

$$\frac{d\sigma}{d\Omega} \approx (\rho_p - \rho_m)^2 \frac{1}{V} S(\mathbf{Q}) \qquad (4)$$

which defines the structure function as:

$$S(\mathbf{Q}) = \left| \int_V e^{i\mathbf{Q}\cdot\mathbf{r}} d\mathbf{r} \right|^2 \qquad (5)$$

which is strictly a dimensionless quantity.

We can treat the S(Q) as a scattering intensity and which corresponds to the Fourier transform of the "contrast" or the physical configuration in the model system. We can take the contrast as simply the value of the field. So $S(Q)$ or $I(q_x, q_y)$ can be computed by a two-dimensional Fast Fourier Transform (FFT) of the data field u_0 or u_1. In practice since the two variables are related though the phase coupling for the Lotka Volterra system, we find little difference in whether the FFT is computed by u_0, or u_1 for the data in Figure 3.

It is useful to consider the circular average - replacing the wave-vector $Q = (q_x, q_y)$ with a single wave number q which is inversely related to a spatial length l scale by $q \approx 2\pi/l$. A circular binning scheme can be used to obtain the numerical scattering as a function of the one-dimensional wave number q. This analysis is discussed in greater detail in[10].

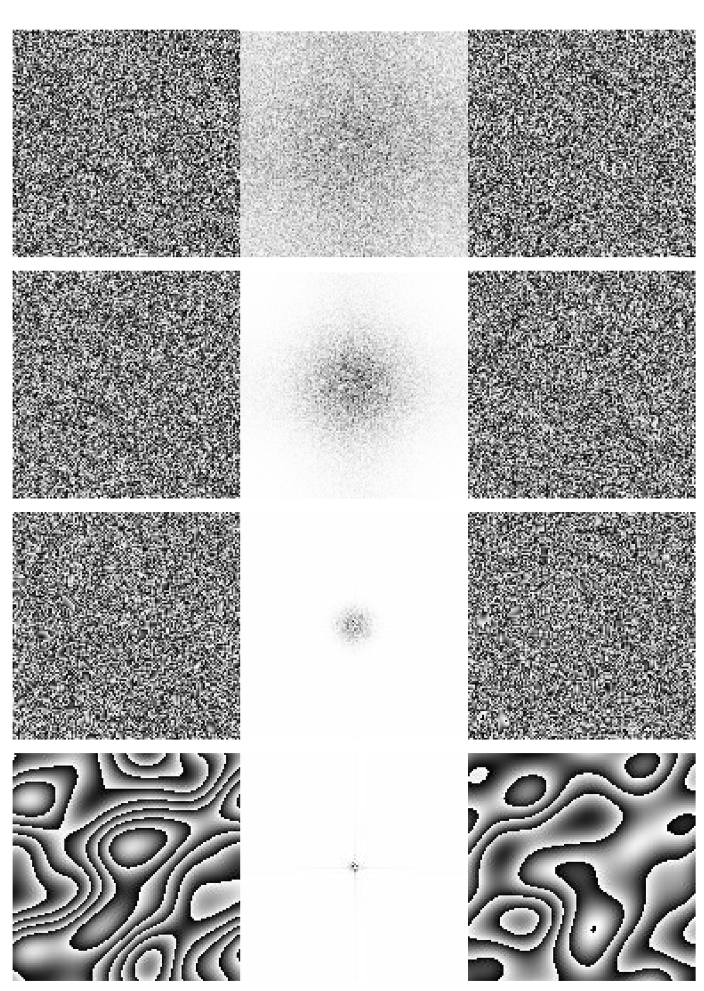

Figure 3: **Spatial System configuration (u_0 on left, u_1 on right, with $I(q_x, q_y)$ in middle. Times shown top to bottom are: $t = 0.1, 0.3, 5.0, 100.0$. The scattering pattern reveals structure not directly visible in u.**

Discussion

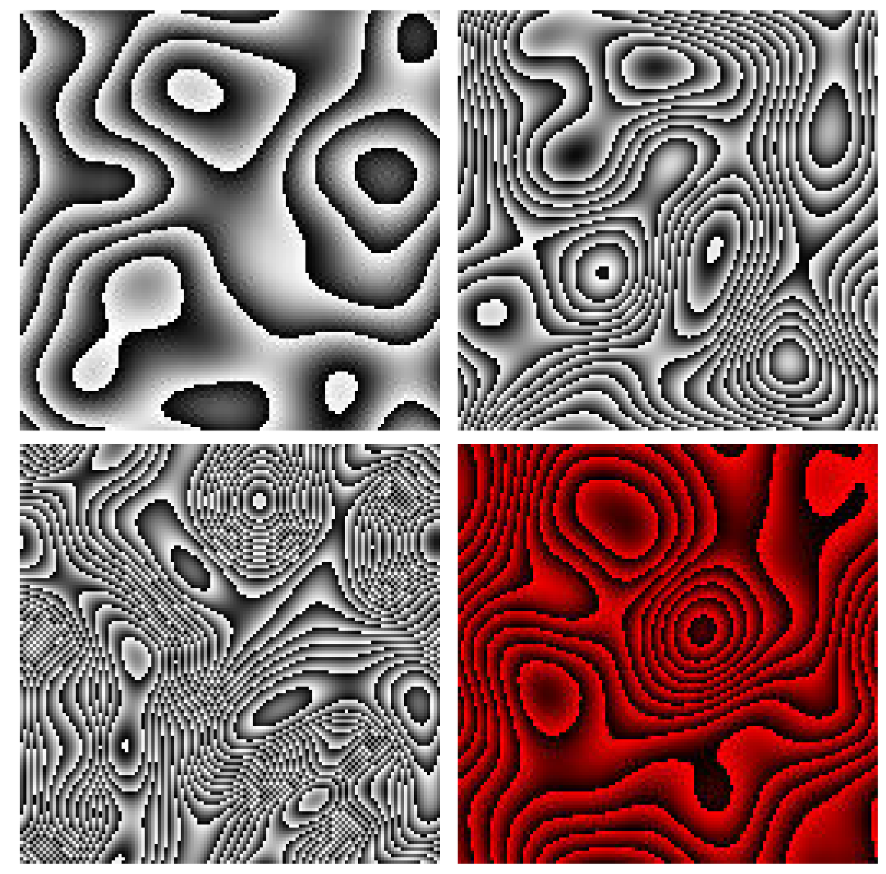

Figure 4: **Predator configurations at different Prey growth rates: $A = 1.0, 0.5, 0.25, 1.25$ for top left, top-right, etc respectively.**

We can use these techniques to study the effect of different growth rate parameters. Figure 4 shows configuration snapshots of the predator population (u_1) system with different values of the prey growth rate $A = 1.0, 0.5, 0.25, 1.25$. Generally it is seen that the spatial features are smaller and the oscillations more rapid if the prey population growth is reduced. Lowering A shifts the fixed point to the left on the phase plots and raising it shifts it to the right.

Physically one might intuit that lower growth rates of prey makes the system more vulnerable to spatial fluctuations such as food shortages and local extinctions. Higher prey growth might be expected to dampen the effect of local populations a nd support growth of larger spatial regions. However As the lower right image in Figure 4 indicates that raising A also leads to more rapidly changing spatial waves in the system. It appears that too much prey will also drive the system to frantic oscillation spatially.

Summary & Conclusions

We have described how the spatial Lotka-Volterra equations can be studied on a relatively large period mesh for long integration times using custom simulation codes. We have explored coupling mechanisms such as simple inclusive and exclusive neighbour averaging and found they give rise to individually stable behaviour but do not lead to phase-locking that can support large spatial structures such as waves. Using a proper Laplacian in the spatial equations couples cells together so that long-range spatial structures can develop, propagate and oscillate. The oscillations lead to the merging and dissipation of spatial waved structures which continue to oscillate together, phase-locked by the diffusive coupling between spatial cells.

We have used spectral methods from material science that are based on small-angle scattering and have presented calculated scattering images of the evolving spatial model. The scattering patterns illustrate effects that are not discernible in the early to medium time-scales of the model and can also give a quantitative estimate of the fractal or effective dimension of small scale phenomena and features at all time scales.

More information on this work on the Spatial Lotka-Volterra system of equations is described in technical note CSTN-092, available online at

`http://www.massey.ac.nz/~kahawick/cstn/092`

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