Quasi-cycles in a spatial predator-prey model

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1. Introduction

The underlying approach will be to construct stochastic models at the level of individuals and to deduce the corresponding population level equations, and approximate stochastic equations, from these

So the plan is to:

- Construct an individual based model (IBM) which is stochastic
- Find the deterministic equation that it approaches for large population sizes (expect that population-level descriptions, such as the Lotka-Volterra equation, should emerge by taking the $N \to \infty$ limit of the IBM)
- Carry out the same procedure for spatially explicit models
- Investigate the nature of the stochasticity for large, but finite, N

In this talk we will illustrate the method on the simplest predator-prey interaction, but it can be applied to many other (and more complicated) systems in epidemiology and cell biology, for instance

2. Stochastic Formulation

We first construct the non-spatial model; it can then easily be generalised to include space

The IBM consists of n individuals of species A (the predators) and m individuals of species B (the prey). So the state of the system at a given time is specified by the vector of non-negative integers $\mathbf{n} = (n, m)$

The processes are taken to be

$$\begin{array}{ccccccc} & BE & \xrightarrow{b} & BB & \text{(birth)} & & \\ AB \xrightarrow{p_1} & AA & & AB \xrightarrow{p_2} AE & & \text{(predation)} & \\ A \xrightarrow{d_1} & E & & B \xrightarrow{d_2} E & \text{(death)} & & \end{array}$$

Here E is a null or space (in the spatial context) — it allows for the population of species A, n, to grow or decline, since the population of the nulls is $(N - n - m)$

This gives rise to the following transition rates:

$T(n-1, m|m, n) = d_1 n$

$T(n, m+1|n, m) = 2b\,\frac{m}{N}\,(N-n-m)$

$T(n, m-1|m, n) = 2p_1\frac{nm}{N} + d_2 m$

$T(n+1, m-1|m, n) = 2p_2\frac{nm}{N}$

What is the time evolution of the system?

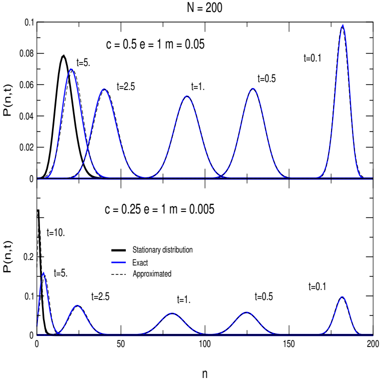
For a continuous time Markov process, the probability of finding the system in state $\mathbf{n}$ at time t changes according to the master equation:

$$\frac{dP(\mathbf{n},t)}{dt} = \sum_{\mathbf{n}'\neq\mathbf{n}} T(\mathbf{n}|\mathbf{n}')\,P(\mathbf{n}',t) - \sum_{\mathbf{n}'\neq\mathbf{n}} T(\mathbf{n}'|\mathbf{n})\,P(\mathbf{n},t)$$

Here $P(\mathbf{n},t)$ is the probability of finding the system in state $\mathbf{n}$ at time t and $T(\mathbf{n}'|\mathbf{n})$ is the rate of transitions from state $\mathbf{n}$ to state $\mathbf{n}'$ due to births, deaths, predation, and later migration

What methods are available to analyse master equations?

For large N can use van Kampen's approximation scheme — writing $n = N\phi(t) + N^{1/2}x$ and expanding master equation in powers of $1/\sqrt{N}$.



To leading order ($N \to \infty$) get equation for $\phi(t)$ (macroscopic equation). Next order get the Gaussian broadening of $P(n,t)$. Next order after this gives non-Gaussian corrections

3. Systematic Expansion in the System Size

For the non-spatial version of the model, the state of the system is specified by the two non-negative integers n and m. So in this case we write

$n/N = \phi + N^{-1/2}x$ and $m/N = \psi + N^{-1/2}y$

in the master equation and expand systematically in powers of $1/\sqrt{N}$

At leading order ($N \to \infty$) this gives the corresponding population-level model (PLM) for $\phi = \langle n \rangle / N$ and $\psi = \langle m \rangle / N$

The explicit form of the PLM is found to be

$$\begin{aligned} \frac{d\phi}{dt} &= n(\psi)\phi - d_1\phi \\ \frac{d\psi}{dt} &= r\,\psi\left(1 - \frac{\psi}{K}\right) - g(\psi)\phi \end{aligned}$$

Here $r = 2b - d_2, K = 1 - (d_2/2b)$ and

$$n(\psi) = 2p_1\psi \; ; \; g(\psi) = 2(p_1 + p_2 + b)\psi$$

Note that $n(\psi) = \lambda g(\psi)$ — a frequent assumption when constructing phenomenological equations of this kind

The $1/\sqrt{N}$ corrections to the PLM are described by a linear Fokker-Planck equation, or alternatively by a set of linear Langevin equations

$$\begin{aligned} \dot{x} &= a_{11}x + a_{12}y + \eta_1(t)\,, \\ \dot{y} &= a_{21}x + a_{22}y + \eta_2(t)\,, \end{aligned}$$

where $\eta_\alpha(t)$ is a Gaussian white noise with zero mean and

$$\langle \eta_\alpha(t)\eta_\beta(t')\rangle = b_{\alpha\beta}\delta(t - t')$$

The $a_{\alpha\beta}$ and $b_{\alpha\beta}$ are calculated from the $1/\sqrt{N}$ expansion in terms of the original parameters of the stochastic model

At the fixed point of the PLM (after the transients have died away) these are constants and so since the Langevin equations are linear they can be solved exactly

Spatially explicit model

The area under consideration is divided into a large number of patches, each containing a number of individuals, which are then identified with the sites of a regular two-dimensional lattice (usually a square lattice)

Individuals are allowed to migrate to nearest neighbour patches — if space exists

But predation is between individuals of a particular patch and birth rate is also dependent on the population density of parental patch

The *local* processes are

$$\begin{array}{ccc} & B_i E_i \xrightarrow{b} B_i B_i & \text{(birth)} \\ A_i B_i \xrightarrow{p_1} A_i A_i & A_i B_i \xrightarrow{p_2} A_i E_i & \text{(predation)} \\ A_i \xrightarrow{d_1} E_i & B_i \xrightarrow{d_2} E_i & \text{(death)} \end{array}$$

with the new (nonlocal) processes being given by:

$$\begin{aligned} A_iE_j &\xrightarrow{\mu_1} E_iA_j, \quad E_iA_j \xrightarrow{\mu_1} A_iE_j, \\ B_iE_j &\xrightarrow{\mu_2} E_iB_j, \quad E_iB_j \xrightarrow{\mu_2} B_iE_j \end{aligned}$$

Here i and j are nearest-neighbour sites and μ_1 and μ_2 are the migration rates for individuals of species A and B respectively

We can now find the transition rates and the master equation as before. If we define the state of the system at a given time as $\mathbf{n} = (n_1, m_1, n_2, m_2, \ldots)$, then the master equation has exactly the same form as given earlier. Similarly the system-size expansion can be carried out as before

An alternative specification of the nonlocal processes is

$$A_i \xrightarrow{\mu_1} A_j, \quad B_i \xrightarrow{\mu_2} B_j$$

Clearly there are a wide range of choices for the IBMs, some give identical PLMs, others give PLMs which differ slightly from each other. The above choice is of this latter type

The deterministic limit of the spatial model is defined in terms of the populations $\phi_i = \lim_{N\to\infty}(n_i/N)$ and $\psi_i = \lim_{N\to\infty}(m_i/N)$:

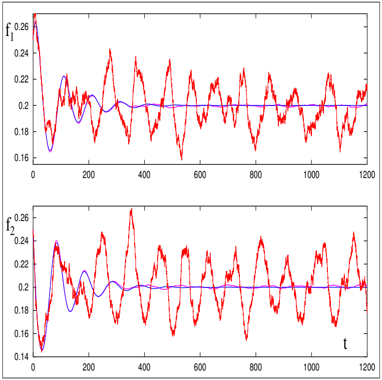
$$\begin{aligned}
\frac{d\phi_i}{d\tau} &= 2p_1\phi_i\psi_i - d_1\phi_i \\
&\quad +\mu_1\left(\Delta\phi_i + \phi_i\Delta\psi_i - \psi_i\Delta\phi_i\right)\,, \\
\frac{d\psi_i}{d\tau} &= -2\left(p_1+p_2+b\right)\phi_i\psi_i \\
&\quad +\left(2b-d_2\right)\psi_i - 2b\psi_i^2 \\
&\quad +\mu_2\left(\Delta\psi_i + \psi_i\Delta\phi_i - \phi_i\Delta\psi_i\right)\,,
\end{aligned}$$

where the symbol Δ represents the discrete Laplacian operator $\Delta f_i = \frac{2}{z}\sum_{j\in i}\left(f_j - f_i\right)$. A rescaled time, τ, has also been introduced.

Fluctuations about the spatially homogeneous stationary state solution of these equations are most conveniently studied by introducing spatial Fourier transforms

4. Results

As expected, for the non-spatial case, the ensemble averaged population density of the IBM, determined from numerical simulation (purple line), agrees perfectly with the solution of the PLM (blue line) showing a decaying oscillatory transient followed by a constant steady-state density



In marked contrast, individual realisations of the IBM show large persistent cycles (red lines). The amplitude of these cycles is much larger than would be naively expected

To search for oscillations in noisy data, one of the most useful diagnostic tools is the power spectrum $P(\omega) = \langle|\tilde{x}(\omega)|^2\rangle$, where $\tilde{x}(\omega)$ is the Fourier transform of $x(t)$. Taking the Fourier transform of the Langevin equations we find

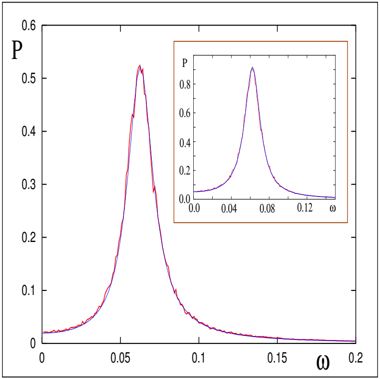
$$P(\omega) = \frac{\alpha + \beta\omega^2}{[(\omega^2 - \Omega_0^2)^2 + \Gamma^2\omega^2]}$$

where α and β are functions of the IBM rates:
$\alpha = b_{11}a_{22}^2 + 2b_{12}a_{12}|a_{22}| + b_{22}a_{12}^2$ and $\beta = b_{11}$. The constants in the denominator have the especially simple forms: $\Omega_0^2 = a_{12}|a_{21}|$ and $\Gamma = |a_{22}|$.

The spectrum given above is reminiscent of that for a simple mechanical system — namely a linear damped harmonic oscillator, with natural frequency Ω_0 and driven at frequency ω. Unlike the case of a mechanical oscillator the driving frequency is not tuned to achieve resonance

The noise which drives the system is not external, but arises from the demographic stochasticity contained in the individual processes which define the model; there is no environmental stochasticity in this model

The spectrum predicted by the above equation gives the solid line shown below. The agreement with the spectrum obtained from simulation of the IBM (noisy line) is very good



The naive $O(1/\sqrt{N})$ estimate of the size of stochastic fluctuations is comparable to the zero frequency value of $P(\omega)$. This clearly illustrates the very large amplification of these fluctuations due to the resonance effect

The amplitude of the cycles will be roughly given by

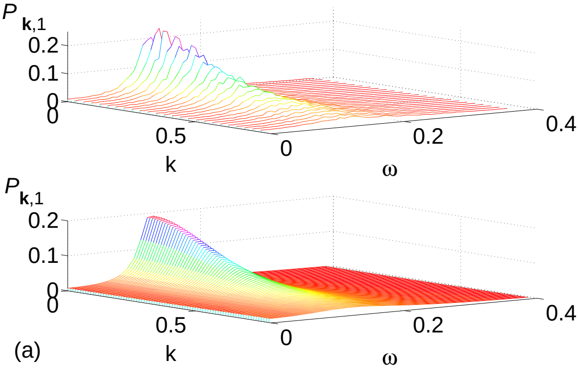
$$\text{Amplitude} \sim \frac{R}{\sqrt{N}}$$

where R is related to the height of the resonant peak

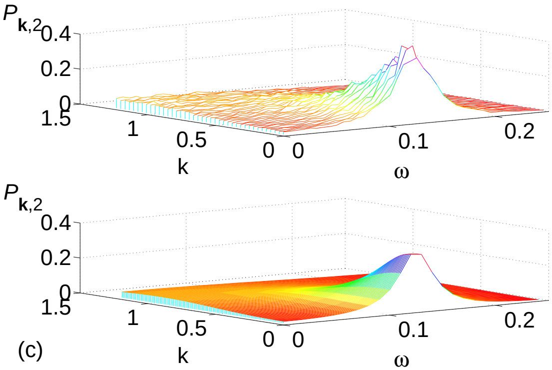
So for instance, if $R = 30$, then for $N \sim 1000$ the amplitude of the cycles are of order unity, whereas without the resonance they would be only 0.03.

Nevertheless, in the deterministic limit, $N \to \infty$, the cycles disappear

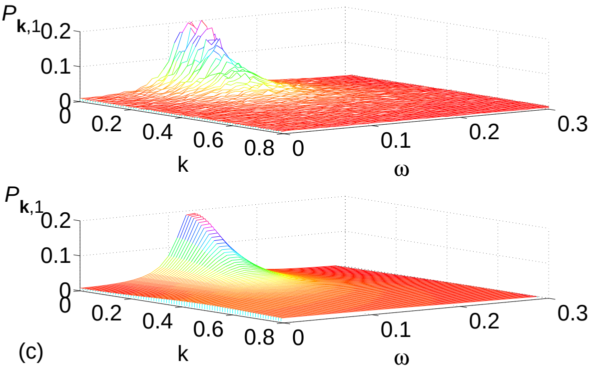
For the spatially explicit model, the power-spectrum has a similar form, but now the parameters are functions of the wave-vector **k**



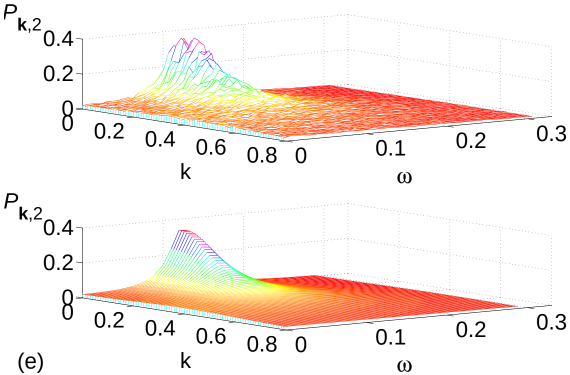
Power spectra for the predator species obtained from simulations (top) and from analytic predictions (bottom). Simulations were carried out in one dimension; the analytic form is known in any dimension



Power spectra for the prey species obtained from simulations (top) and from analytic predictions (bottom). Simulations were carried out in one dimension; the analytic form is known in any dimension



Power spectra for the predator species obtained from simulations (top) and from analytic predictions (bottom). Simulations were carried out in one dimension; the analytic form is known in any dimension



Power spectra for the prey species obtained from simulations (top) and from analytic predictions (bottom). Simulations were carried out in one dimension; the analytic form is known in any dimension

5. Summary and Conclusions

- Stochastic effects occur in many different areas of biological modelling. Master equations — and the associated formalism — are a useful way of analysing these systems
- The stochastic model may be investigated systematically within a $1/\sqrt{N}$ expansion
- The PLM may be derived and the parameters of the model related to those of the IBM
- The master equation formalism naturally generalises to spatial models
- In this simple model there is no peak at non-zero $|\mathbf{k}|$, but in models with more structure this is a possibility

Some references:

Phys. Rev. E **70**, 041902 (2004) ; Phys. Rev. Lett. **94**, 218102 (2005)

Phys. Rev. E **78**, 051911 (2008)