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WORKSHOP ON QUANTITATIVE ECOLOGY
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Stochastic Models in Population Biology - Part II

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OUTLINE

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- Predator prey model

- Summary

with

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1. Introduction

Stochastic models in population biology may be formulated as master equations and a $1/N$ expansion set up to analyse these equations

An analysis of the leading $(N \rightarrow \infty)$ behaviour for competition models recovered the standard phenomenological competition equations

But is novel behaviour found using this methodology?

Will look at two instances:

1. A spatially explicit model of competition between two species

2. $1/N$ correction to the population level predator-prey equations
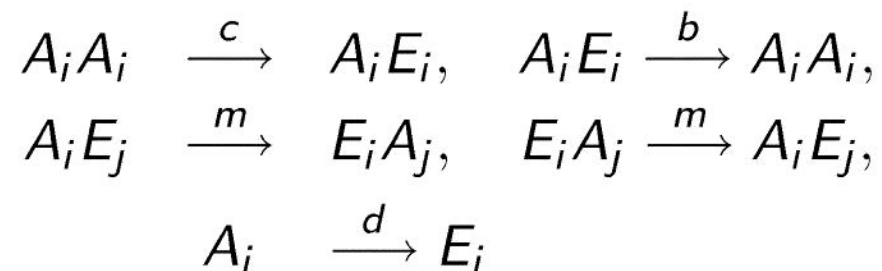
2. Spatially explicit model

Again formulate for competition models

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

For a single species the following interactions can occur:

$$A_i A_i \xrightarrow{c} A_i E_i, \quad A_i E_i \xrightarrow{b} A_i A_i,$$
$$A_i E_j \xrightarrow{m} E_i A_j, \quad E_i A_j \xrightarrow{m} A_i E_j,$$
$$A_i \xrightarrow{d} E_i$$

We can now find the transition rates and set-up the master equation as before

The population-level model (PLM) corresponding to this model can also be derived:

$$\frac{\partial N_A}{\partial t} = D_A \nabla^2 N_A + r_A N_A \left(1 - N_A/K_A\right)$$

The constants D_A, r_A and K_A can be given in terms of the parameters of the IBM.

This PLM is not a great surprise: it's the logistic equation with a diffusion term $\nabla^2 N_A$ added

However if a similar analysis is carried out for the two species model we find that the PLM is different from the one which is usually written down on phenomenological grounds:

$$\frac{\partial N_A}{\partial t} = D_A \nabla^2 N_A$$

$$+ \quad D_1 \left(N_A \nabla^2 N_B - N_B \nabla^2 N_A \right)$$

$$+ \quad r_A N_A \left(1 - N_A / K_A \right) - b_A N_A N_B$$

$$\frac{\partial N_B}{\partial t} = D_B \nabla^2 N_B$$

$$+ \quad D_2 \left(N_B \nabla^2 N_A - N_A \nabla^2 N_B \right)$$

$$+ \quad r_B N_B \left(1 - N_B / K_B \right) - b_B N_A N_B$$

These equations have the extra term $\left(N_A \nabla^2 N_B - N_B \nabla^2 N_A \right)$ which does not appear in phenomenological models
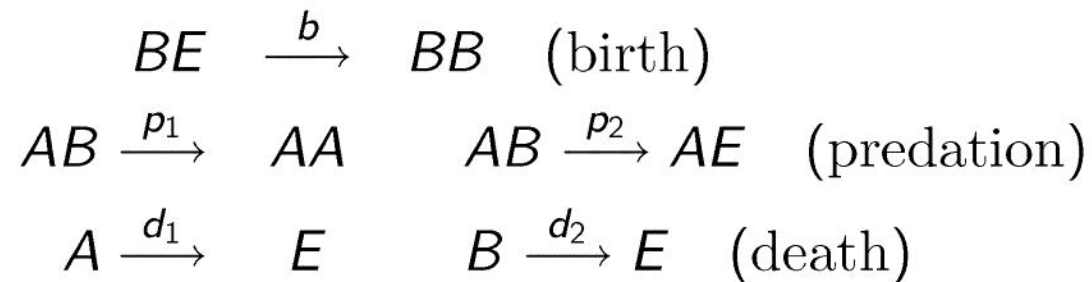
The phenomenological models simply add diffusion terms to the non-spatial model

3. Predator-prey model

Stochastic models are formulated and analysed in the same way as for competition models, but here we will be interested in $1/N$ corrections to the PLM

The IBM consists of n individuals of species A (the predators) and m individuals of species B (the prey)

The processes are taken to be

$$BE \xrightarrow{b} BB \quad (\text{birth})$$

$$AB \xrightarrow{p_1} AA \qquad AB \xrightarrow{p_2} AE \quad (\text{predation})$$

$$A \xrightarrow{d_1} E \qquad B \xrightarrow{d_2} E \quad (\text{death})$$

This gives rise to the following transition rates:

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

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

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

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

Now write

$$n/N = f_1 + N^{-1/2}x \text{ and } m/N = f_2 + N^{-1/2}y$$

in the master equation and expand systematically in powers of $1/N$

At leading order $(N \to \infty)$ this gives the corresponding PLM for $f_1 = \langle n \rangle / N$ and $f_2 = \langle m \rangle / N$

The explicit form of the PLM is found to be

$$\frac{df_1}{dt} = n(f_2)f_1 - \mu f_1$$

$$\frac{df_2}{dt} = r f_2 \left(1 - \frac{f_2}{K}\right) - g(f_2)f_1$$

where $\mu = d_1$, $r = 2b - d_2$, $K = 1 - (d_2/2b)$ and

$$n(f_2) = 2p_1 f_2 \; ; \; g(f_2) = 2(p_1 + p_2 + b)f_2$$

Note that $n(f_2) = \lambda g(f_2)$ — a frequent assumption when constructing phenomenological equations of this kind

These equations are the Volterra equations — distinguished from the Lotka-Volterra equations by the logistic growth for f_2

The $1/N$ corrections to the PLM are described by a <u>linear</u> 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 $\eta_i(t)$ is a Gaussian white noise with zero mean and

$$
\langle \eta_i(t)\eta_j(t') \rangle = b_{ij}\delta(t - t')
$$

The a_{ij} and b_{ij} are calculated from the $1/N$ 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

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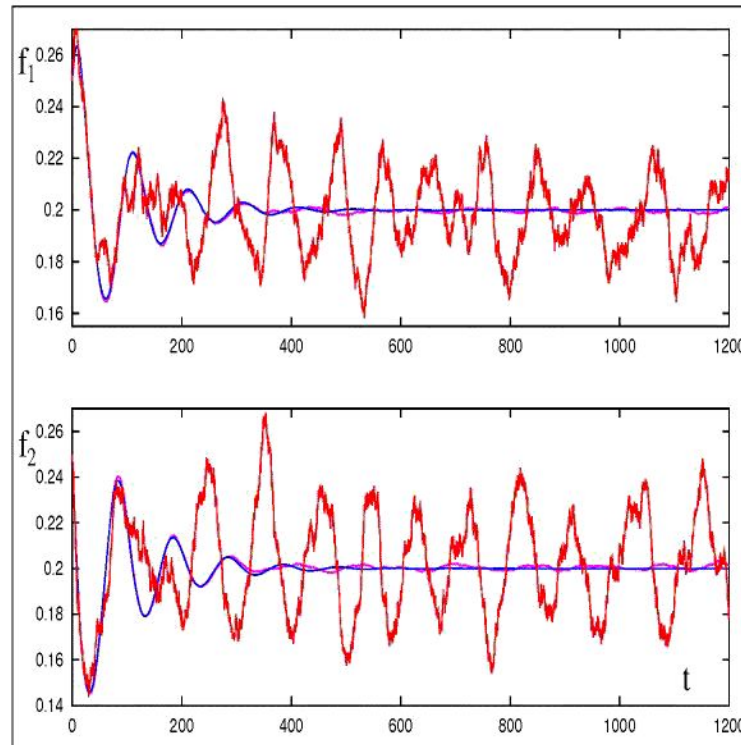
In marked contrast, individual realisations of the IBM show large persistent cycles (red lines). The amplitude of these cycles is much larger than would be naively expected

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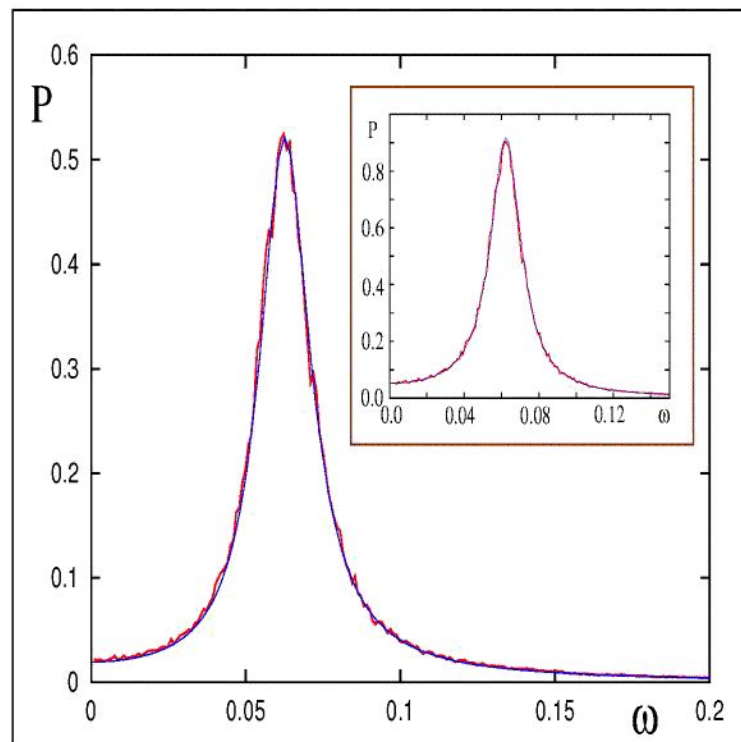
Note, the naive $O(1/\sqrt{N})$ estimate of the size of stochastic fluctuations corresponds to the zero frequency value of $P(\omega)$. This clearly illustrates the very large amplification of these fluctuations due to the resonance effect

4. Summary

- The master equation formalism naturally generalises to spatial models

- The $N \to \infty$ limit of stochastic models may give a PLM which is not the one which is typically written down on phenomenological grounds

- Cycles in the simplest predator-prey model are not present in the PLM, but do exist in the stochastic version of the model.

- The cycles present in the stochastic model are much larger than would naively be expected because of a resonant amplification due to the demographic stochasticity

Some references:

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