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

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with

David Alonso (Michigan)   Tim Newman (Arizona)

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1. Introduction

In the previous two talks the use of master equations and associated formalism in the study of stochastic models in population biology was described in the context of two very well known situations: competition between species and predator-prey interactions

Here the application of similar ideas to two other areas will be discussed:

(1) Metapopulation models (spatial and non-spatial)

Here the stochastic variable will not be the number of individuals of a particular type, but the number of patches which are occupied by a population

(2) Models of biodiversity

Here the stochastic variables will still be the number of individuals of a particular type, but there will be a large number of these different types

2. Metapopulations

A metapopulation is a population of populations — a group of local populations in patches which are either occupied or unoccupied

Population size of each patch unimportant — focus only on persistence

Patches can become occupied by colonisation from other patches, or may become unoccupied due to extinction of the local population

Suppose that there are N patches, of which n are occupied

Would like an equation for $P(n, t)$ — the probability that n patches are occupied at time t

If we also allow for the possibility of a mainland "raining down" migrants on to the islands, then there are 3 types of process:

- Extinction events: let e be the rate of extinction of a single population

- Colonisation events: let c be the rate of colonisation of an unoccupied patch from an occupied patch

- Migration events: let m be the rate of immigration into an unoccupied patch from the mainland

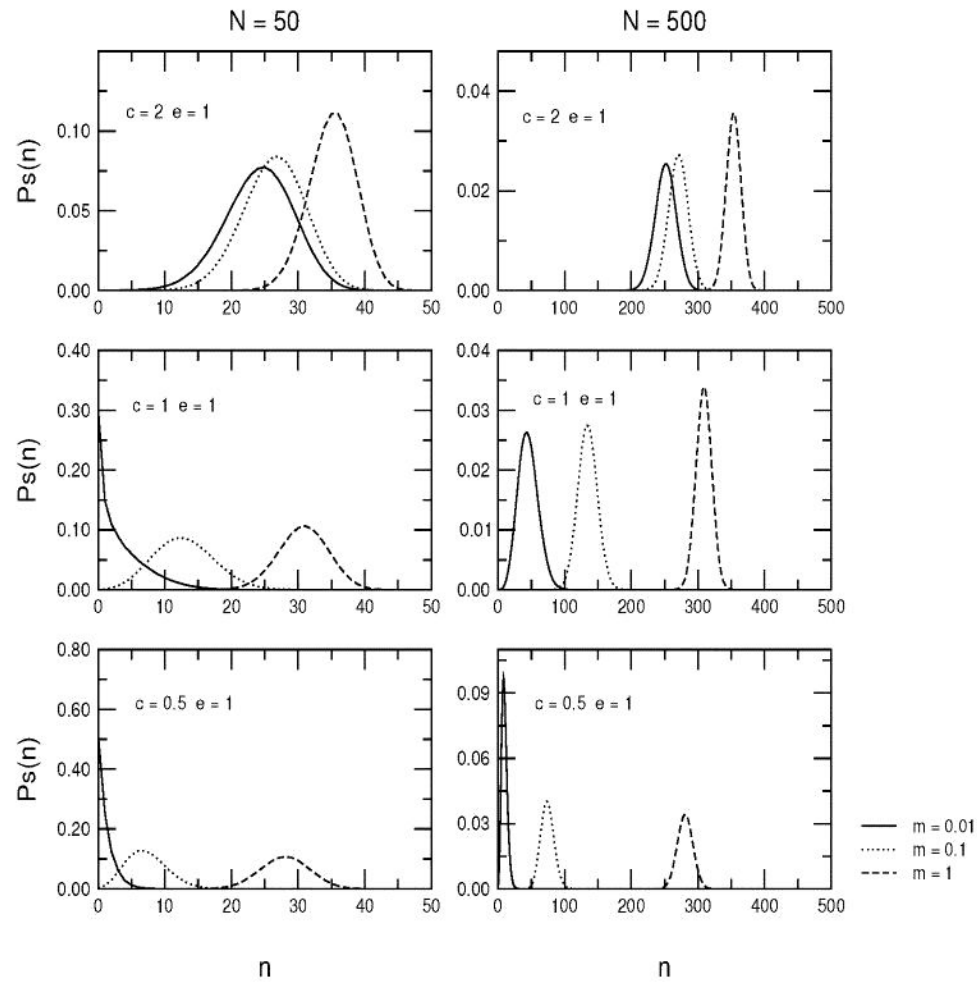This gives the following transition probabilities:

$$
\begin{aligned}
T(n+1|n) &= \left(c\frac{n}{N} + m\right)\left(1 - \frac{n}{N}\right) \\
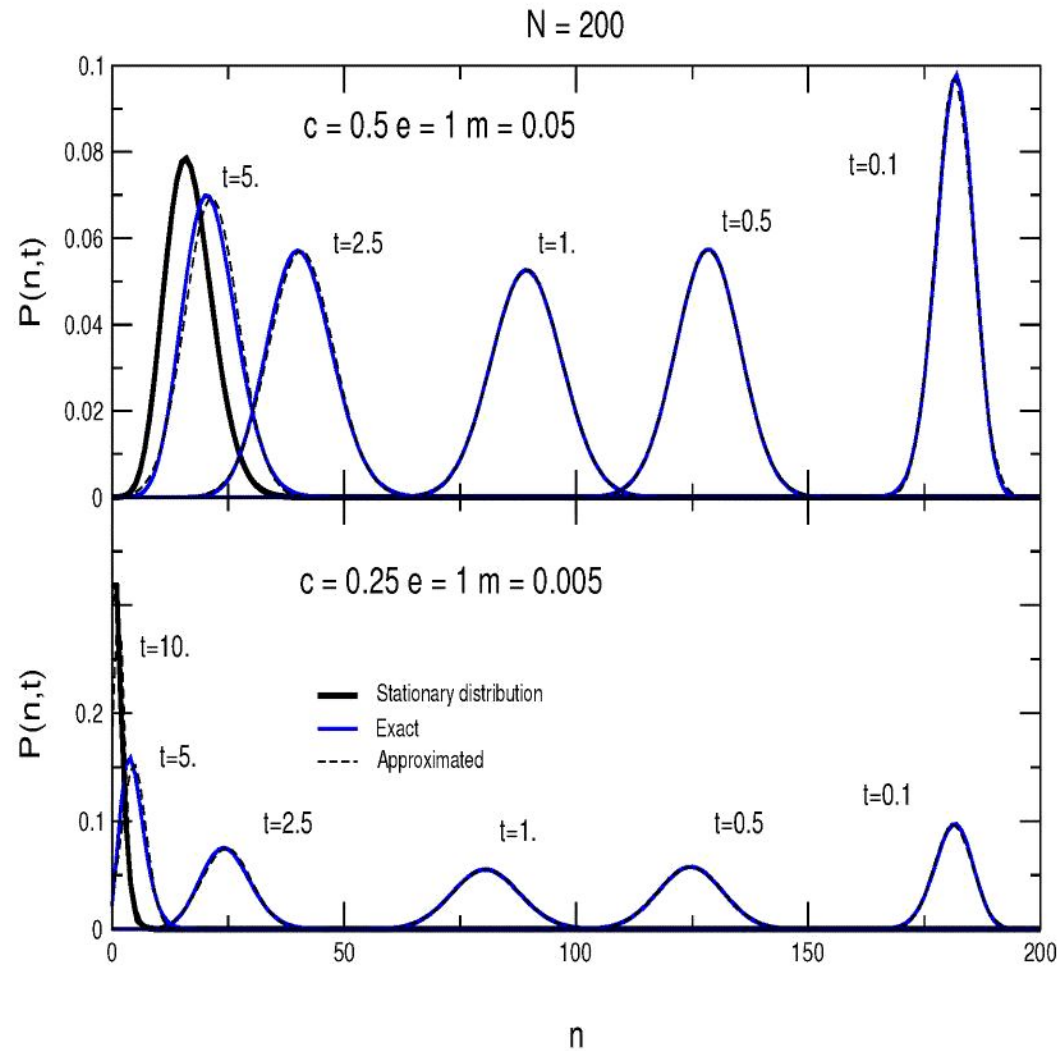T(n-1|n) &= e\frac{n}{N}
\end{aligned}
$$

The $N \to \infty$ limit of the model is the Levins model:

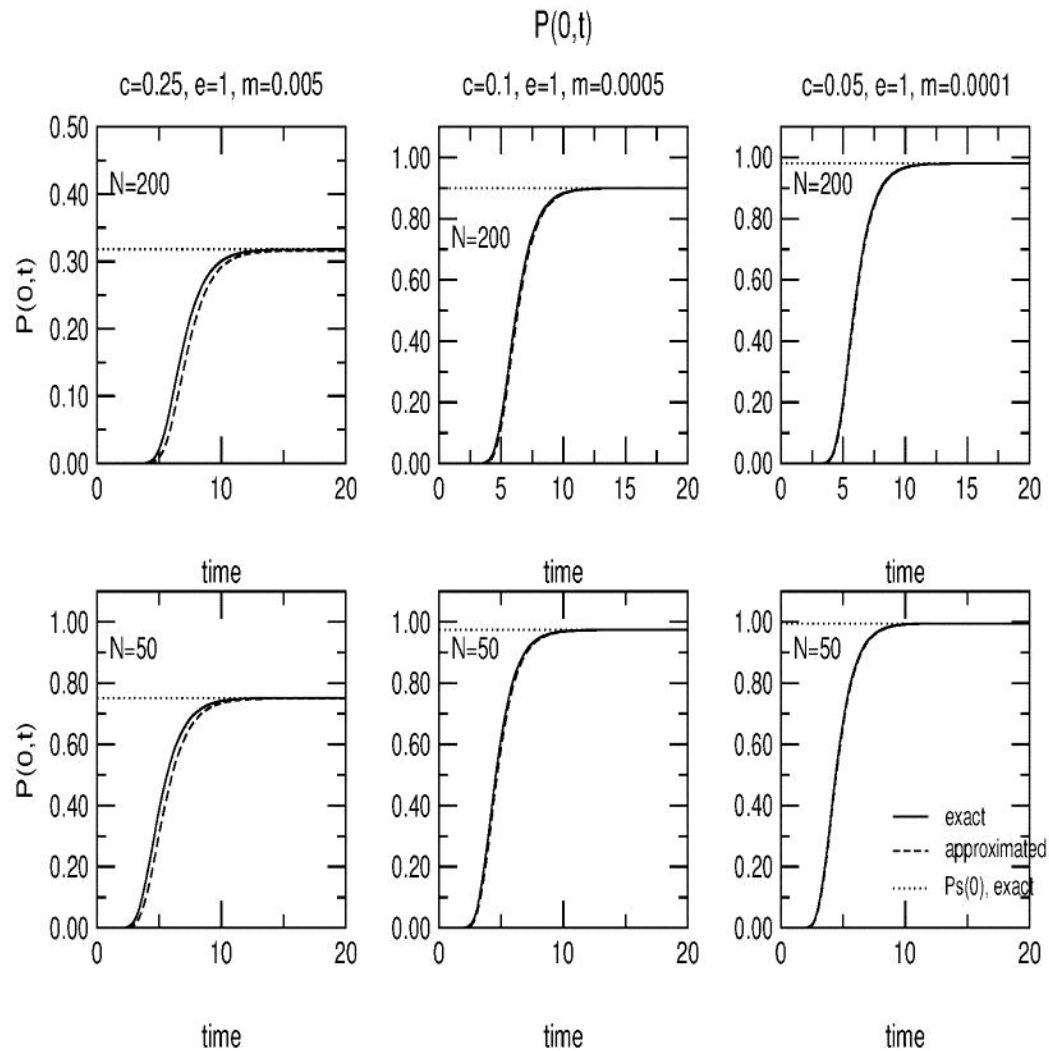$$
\frac{df}{dt} = (cf + m)(1 - f) - ef \, ,
$$

where $f(t)$ is the fraction of occupied sites at time t

Stationary probability distribution $P_s(n)$

N = 200

"Exact" = Numerical integration of equation; "Approximated" = Large N approximation

$P(0,t)$

Probability of metapopulation extinction at time t; "approximated" refers to a linear approximation used to solve the equations

3. Spatial metapopulation models

In spatially explicit metapopulation models can incorporate more realistic features e.g. internal colonisation should depend on local density of occupied sites

<u>Model 1:</u> The lattice metapopulation model. Patches are sites on a regular square lattice.
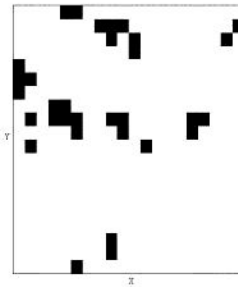
Colonisation takes place only from the z nearest neighbours of an available site

$z = 4$ or 8 (depending on the neighbourhood scheme chosen)
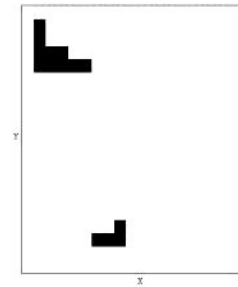
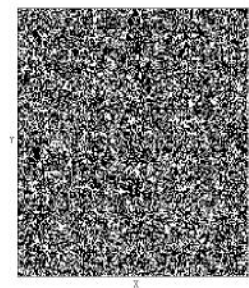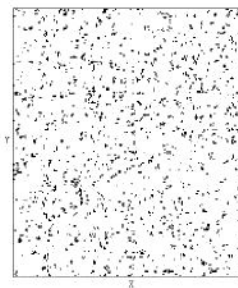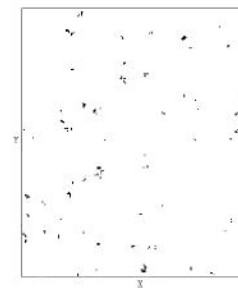LOCAL LATTICE MODEL

t=0.64   t=7.44   t=15.02

t=0.71   t=7.16   t=17.97

Upper plots: 20×20 lattices

Lower plots: 200×200 lattices

$(c = 1, e = 1, m = 0.0001)$

<u>Model 2:</u> Spatially realistic model (Hanski). Incorporates landscape structure: position and area of every patch in the metapopulation

- Patch extinction rate inversely proportional to patch area: $E_i = e/A_i$

- Probability of an extinction event in whole patch network in time δt

$$= \sum_{i=1}^{N} E_i p_i \delta t = \sum_{i=1}^{N} \frac{e}{A_i} p_i \delta t \,,$$

where

$$p_i = \begin{cases} 0, & \text{if patch } i \text{ is empty} \\ \\ 1, & \text{if patch } i \text{ is occupied} \end{cases}$$

- Probability of a colonisation event in the whole patch network in time δt

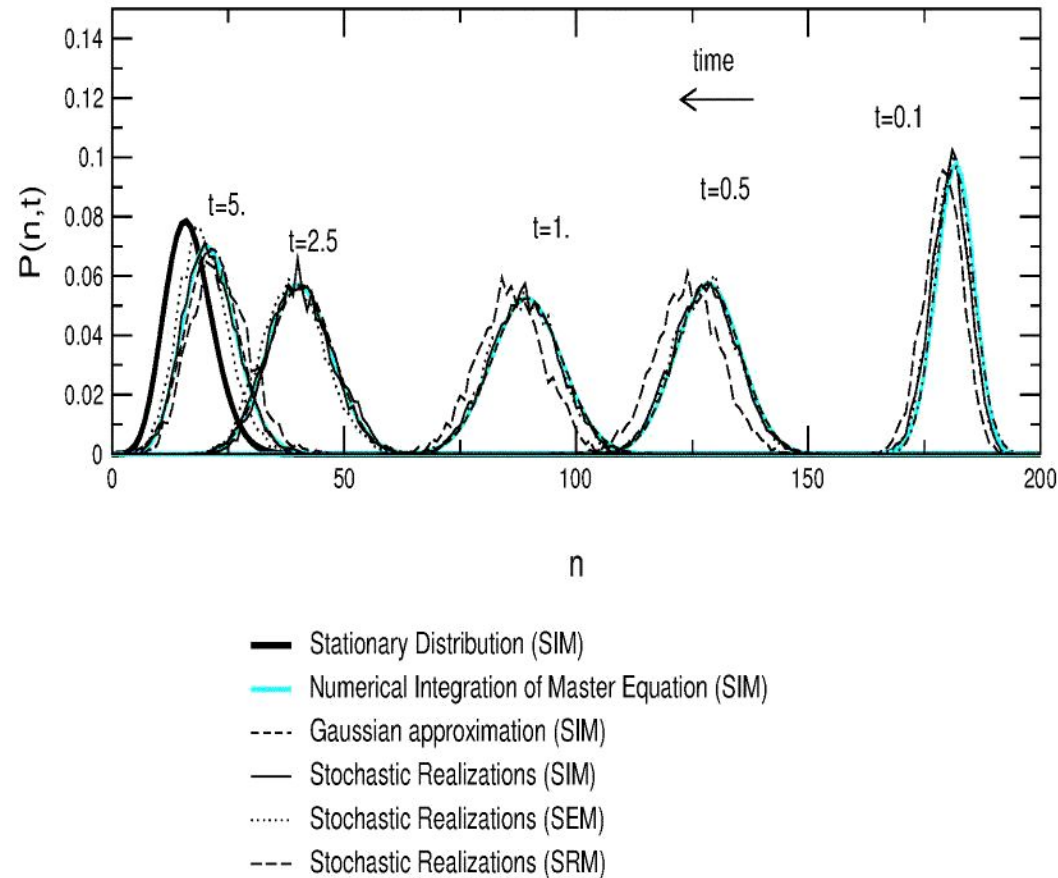$$= \sum_{i=1}^{N} C_i (1 - p_i) \delta t \,,$$

where

$$C_i = c \sum_{j \neq i}^{N} p_j A_j \exp\left(-\alpha d_{ij}\right) + m$$

$d_{ij} = $ distance between patches i and j

$1/\alpha$ is the average migration distance

Temporal evolution of the probability of having n patches occupied at time t for different models of metapopulation dynamics

4. Model of biodiversity

Imagine an island (the *local community*) consisting of N individuals of S possible species (typical values used in simulations might be $N = 50,000$ and $S = 300$). The number of individuals is fixed, and not all possible species may be represented on the island

Immigration occurs from a *metacommunity*, but in such a way that any immigrants simply displace individuals in the local community, so that N still remains fixed

We can think of the species as nodes of a graph labelled by $i = 1, \ldots, S$, and the links between the nodes as representing the (predator-prey) interactions between the species of the two nodes being joined

This interaction will be given by the single real number Ω_{ij} for the link from j to i

Links from a node to itself are not allowed, and so the matrix Ω has zero entries on the diagonal

The antisymmetric matrix $S_{ij} \equiv \Omega_{ij} - \Omega_{ji}$ has a more direct interpretation as the "score" of species i against species j:

(i) If $S_{ij} > 0$, then j acts as a resource for i

(ii) If $S_{ij} = 0$, there is no interaction between i and j

(iii) If $S_{ij} < 0$, then i acts as a resource for j

How do we specify Ω?

Since connectivity seems to be an important quantity will assume that Ω has a fixed connectivity C.

Other than this, and the fact that the diagonal entries are zero, we will not impose any other restrictions on Ω

If the connectivity of Ω is C, then the connectivity of $\mathbf{S}$ is
$$C^* \equiv 1 - (1 - C)^2$$

What are the dynamics of the process?

(1) With probability $(1 - \mu)$, pick two individuals at random. Suppose they belong to species i and j, and that $S_{ij} \neq 0$. Replace the individual belonging to the species which has a negative score against the other species by a new individual of the more highly scoring species

For example, if $S_{ij} > 0$, the total number of individuals belonging to species i goes up by 1, and the total belonging to species j goes down by 1.

If $S_{ij} = 0$, no action is taken

(2) With probability μ, pick an individual at random. Replace it by another individual of *any* of the S species

A numerical simulation can now be carried out — starting with, for instance, the off-diagonal entries of Ω assigned in a purely random way at $t = 0$

But can any progress be made analytically?

A mean-field approach can be used to write down a master equation which is tractable as follows:

Focus on one species — call it species A. Lump the other $(S - 1)$ other species together and call this species B. It can be regarded as some kind of average species — a kind of effective background population with which species A interacts

Rule (1) involves picking two individuals. If both individuals belong to species A or species B no action is taken.

The probability of selecting an A and a B is

$$2\frac{n}{N}\frac{(N - n)}{N - 1}$$

The probability that S_{AB} is non-zero is C^* and, on average, in half the events the individuals from species A will have a higher score than the individuals from species B, i.e., $S_{AB} > 0$, and the other half of the events $S_{AB} < 0$.

This gives the following transition rates:

$$T(n+1|n) = C^* \frac{1}{2} 2 \frac{n}{N} \frac{(N-n)}{(N-1)}$$

$$T(n-1|n) = C^* \frac{1}{2} 2 \frac{n}{N} \frac{(N-n)}{(N-1)}$$

Using only rule (1) leads to a process where eventually only one species survives. To create diversity, we need rule (2): with a probability μ, pick an individual at random. Replace it by another individual of any of the S species, with a probability p, the relative abundance of species A in the metacommunity.

In our model we took $p = 1/S$

So the total transition rates are:

$$T(n+1|n) = (1-\mu)C^* \frac{n}{N} \frac{(N-n)}{(N-1)} + \mu \left(1 - \frac{n}{N}\right) \frac{1}{S}$$

$$T(n-1|n) = (1-\mu)C^* \frac{n}{N} \frac{(N-n)}{(N-1)} + \mu \frac{n}{N} \left(1 - \frac{1}{S}\right)$$

The above model differs from the Hubbell model in two ways:

(i) The Hubbell model has an evolved metacommunity, while the above model has a uniform metacommunity

(ii) There is no equivalent of the matrix S_{ij} which gives a "score" to each species i against other species j in the Hubbell model. In other words, it has no rule which ranks one species of the local community above another

Once the mean field approximation has been made, the model described above reduces to the Hubbell model. Then exactly the same calculations may be carried out, for example, the stationary probability distribution, $P_S(n_j)$, can be determined in closed form and it has exactly the same form as in the Hubbell model

The species abundance distribution, $S(n)$, is the number of species in the system having n individuals. It is proportional to the stationary probability distribution, $P_S(n)$, in the model

N = 5000, S = 300, C = 0.5
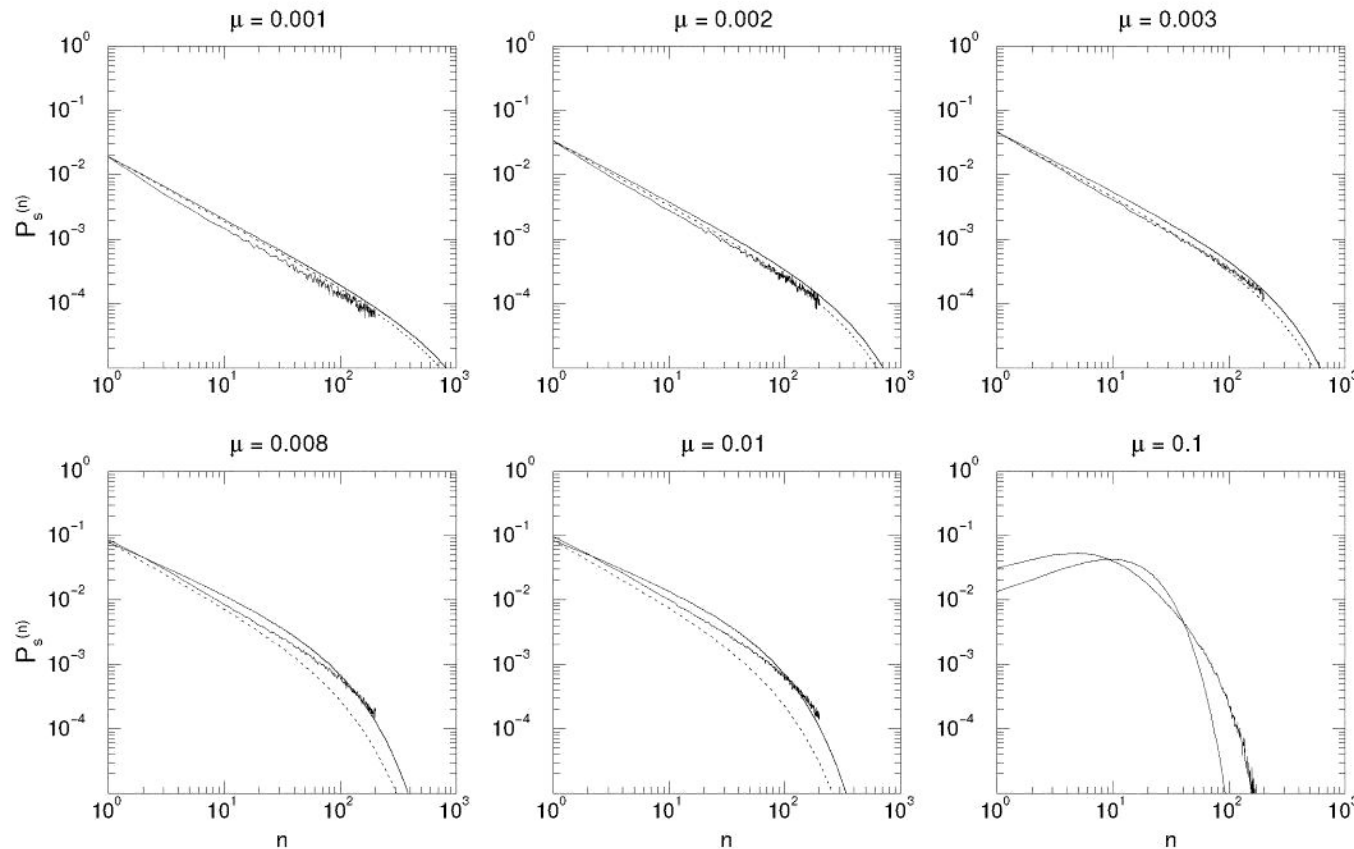
Stationary probability distribution $P_S(n)$ (solid line); log-series approximation (dotted line); simulation of IBM (noisy solid line)
$N = 5000, S = 300$
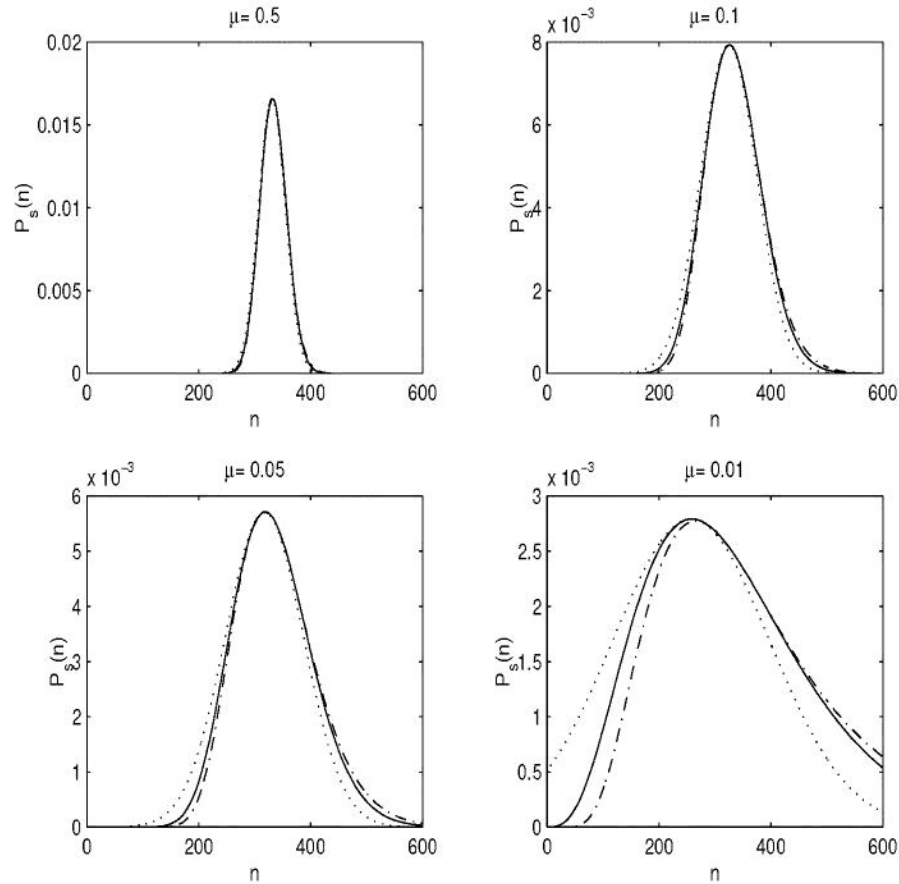
Stationary probability distribution $P_S(n)$ (solid line); log-normal approximation (long-dashed line); normal approximation (dotted line) $N = 100000, S = 300$

4. Conclusions

Stochastic effects occur in many different areas of ecological modelling. Master equations — and the associated formalism — are a useful way of analysing these systems

The formalism naturally generalises to spatial models

The $1/N$ expansion provides a systematic method for investigating stochastic models of these types. It can uncover novel effects such as a PLM which differs from the one usually written down on phenomenological grounds and cycles in predator-prey systems which are significant for moderate values of N, but which vanish when $N \to \infty$

<u>Some references:</u>

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