



The Abdus Salam
International Centre for Theoretical Physics



SMR 1655 - 3

WORKSHOP ON QUANTITATIVE ECOLOGY
9 to 20 May 2005

Stochastic Models in Population Biology - Part I

Alan J. McKANE
Theory Group, School of Physics & Astronomy
University of Manchester
M13 9PL Manchester, U.K.

Stochastic models in population biology I

Alan McKane

Theory Group, School of Physics and Astronomy, University of Manchester

Trieste May 2005

OUTLINE

- Introduction
- The master equation
- Individual and population level models
- Summary

with

David Alonso (Michigan)

Tim Newman (Arizona)

Ricard Solé (Barcelona)

1. Introduction

One of the most well known aspects of quantitative ecology is the study of deterministic differential equations for the change in time of populations of individuals — different species, for example

An example is the Lotka-Volterra equations describing competition between species A, having N_A individuals in the population, and species B, having N_B individuals in the population:

$$\frac{dN_A}{dt} = r_A N_A (1 - N_A/K_A) - b_A N_A N_B$$
$$\frac{dN_B}{dt} = r_B N_B (1 - N_B/K_B) - b_B N_A N_B$$

In reality, population dynamics is stochastic — populations fluctuate due to random births and deaths, for instance

For large populations expect that deterministic description is valid, but for small population sizes stochastic effects will be important

For the example of two species in competition — and more generally — would like to:

- Formulate 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 $N \rightarrow \infty$ limit of the IBM)
- Carry out the same procedure for spatially explicit models
- Investigate the nature of the stochasticity for large, but finite, N

2. The master equation

We begin with a stochastic system which consists of a set of N states labelled $n = 1, 2, \dots, N$

For example, n could be the number of individuals in a population or the number of occupied patches in a metapopulation (to describe the number of individuals in two populations we would need m and n)

There will be a transition rate from state n to state n' caused by births, deaths, competition, predation, colonisation, extinction,... This rate will be denoted by $T(n'|n)$.

Then the probability of finding the system in state n at time t changes according to the master equation:

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

For a one-step process, transition rates are only non-zero when $n' = n + 1$ and $n' = n - 1$:

Then the master equation takes the simpler form

$$\begin{aligned} \frac{dP(n, t)}{dt} &= T(n|n+1)P(n+1, t) + T(n|n-1)P(n-1, t) \\ &\quad - \{T(n-1|n) + T(n+1|n)\} P(n, t) \end{aligned}$$

Given the $T(n|n')$, the master equation is a differential-difference equation for the probabilities $P(n, t)$

A simple example is the asymmetric random walk:

$$T(n+1|n) = \lambda; \text{ move in the positive direction}$$

$$T(n-1|n) = \mu; \text{ move in the negative direction}$$

What methods are available to analyse master equations?

- Linear one-step processes may be solved exactly by first finding the generating function $f(z, t) = \sum_n P(n, t)z^n$

Example The birth and death process: $T(n+1|n) = \lambda n$ and $T(n-1|n) = \mu n$ where λ and μ are constants.

Then $f(z, t)$ satisfies the equation

$$\frac{\partial f}{\partial t} = (z-1)(\lambda z - \mu) \frac{\partial f}{\partial z}$$

The general solution to this equation is

$$f(z, t) = \Phi \left(\frac{(z-1)}{(\lambda z - \mu)} e^{(\lambda - \mu)t} \right),$$

where Φ is an arbitrary function.

If the initial condition that there are m individuals at $t = 0$ is imposed then

$$f(z, t) = \left[\frac{\mu(z-1)e^{(\lambda-\mu)t} - (\lambda z - \mu)}{\lambda(z-1)e^{(\lambda-\mu)t} - (\lambda z - \mu)} \right]^m$$

- The stationary state can be expressed as a simple product:

$$P_s(n) = \frac{g_{n-1}g_{n-2}\cdots g_0}{r_n r_{n-1}\cdots r_1} P_s(0); \quad n = 1, \dots, N,$$

where $g_n = T(n+1|n)$ and $r_n = T(n-1|n)$

The constant $P_s(0)$ is determined by normalisation:

$$\begin{aligned} \sum_{n=0}^N P_s(n) &= P_s(0) + \sum_{n>0} P_s(n) = 1 \\ \Rightarrow (P_s(0))^{-1} &= 1 + \sum_{n=1}^N \frac{g_{n-1}g_{n-2}\cdots g_0}{r_n r_{n-1}\cdots r_1} \end{aligned}$$

Example The Hubbell model. If n_i is the number of individuals of species i in the local community, J is the total number of individuals of all species and m is the immigration parameter, then

$$T(n_i + 1|n_i) = (1 - m) \frac{(J - n_i)}{J} \frac{n_i}{J - 1} + m \frac{(J - n_i)}{J} p_i$$

$$T(n_i - 1|n_i) = (1 - m) \frac{n_i}{J} \frac{(J - n_i)}{J - 1} + m \frac{n_i}{J} (1 - p_i)$$

The stationary probability distribution, $P_S(n_i)$, can be determined in closed form to be:

$$P_S(n_i) = \binom{J}{n_i} \frac{B(n_i + p_i^*, n_i^* - n_i)}{B(p_i^*, n_i^* - J)},$$

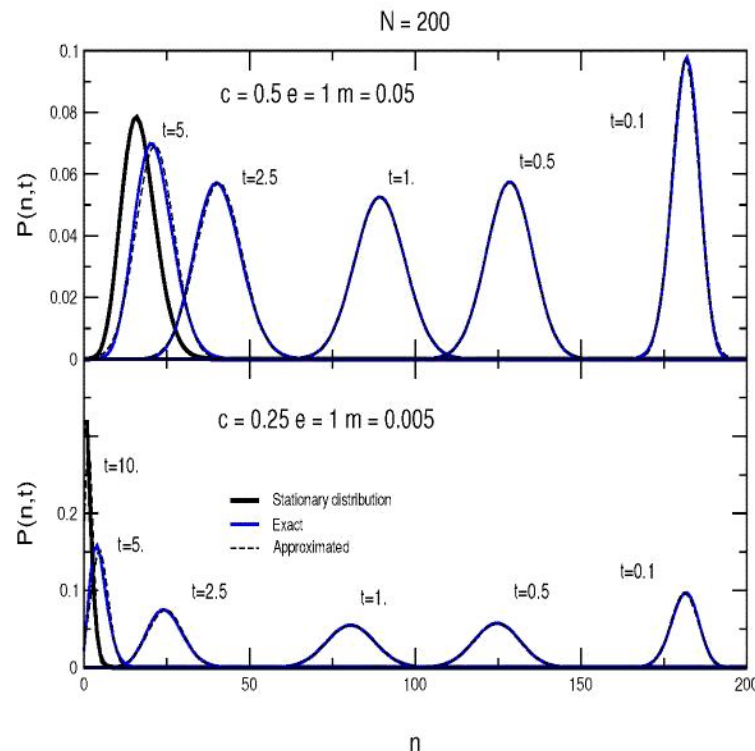
where

$$p_i^* = \frac{m(J - 1)}{1 - m} p_i$$

$$n_i^* = \left(\frac{J - m}{1 - m} \right) - p_i^*$$

and $B(a, b) = \Gamma(a)\Gamma(b)/\Gamma(a + b)$ is the beta-function

- 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 $1/N$.

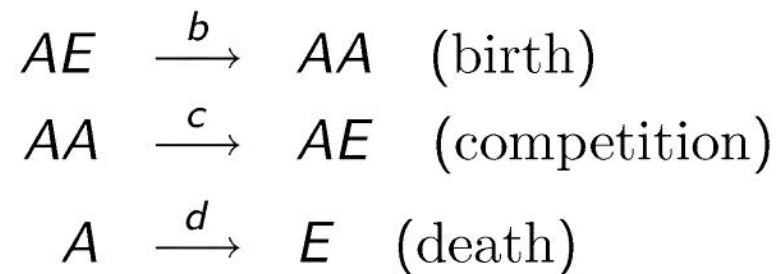


To leading order ($N \rightarrow \infty$) get equation for $\phi(t)$ (macroscopic equation).
 Next order get the Gaussian broadening of $P(n, t)$. Next order after this
 non-Gaussian corrections

3. Individual and population level models

Begin with the simplest case of competition within one species

We suppose that the population dynamics of the system can be essentially described by three processes:



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 $N - n$

What is the time evolution of the system?

- Sample the patch — for μ of the time randomly choose two individuals and allow them to interact. For $(1 - \mu)$ of the time choose only one individual randomly
- Simple combinatorics gives:

$$\text{Probability of picking } AA \text{ is } \mu \frac{n}{N} \frac{(n-1)}{(N-1)}$$

$$\text{Probability of picking } AE \text{ is } 2\mu \frac{n}{N} \frac{(N-n)}{(N-1)}$$

$$\text{Probability of picking } A \text{ is } (1 - \mu) \frac{n}{N}$$

This gives the following transition rates:

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

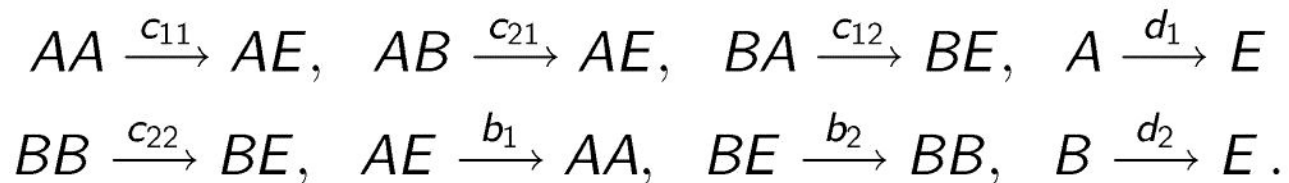
$$T(n-1|n) = \mu c \frac{n}{N} \frac{(n-1)}{N-1} + (1 - \mu) d \frac{n}{N},$$

Writing $n/N = \phi(t) + N^{-1/2}x$ in the master equation and equating terms of order $N^0, N^{-1}, N^{-2}, \dots$ gives at leading order the following deterministic equation

$$\frac{dN_A}{dt} = r_A N_A (1 - N_A/K_A),$$

where r_A and K_A are given in terms of b, c and d

For two species A and B the interactions are



Taking the limit $N \rightarrow \infty$ gives the deterministic equations given in the Introduction:

$$\frac{dN_A}{dt} = r_A N_A (1 - N_A/K_A) - b_A N_A N_B$$

$$\frac{dN_B}{dt} = r_B N_B (1 - N_B/K_B) - b_B N_A N_B$$

4. Summary

- 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 stochastic model may be investigated systematically within a $1/N$ expansion
- The PLM may be derived and the parameters of the model related to those of the ILM

Some references:

Phys. Rev. E **62**, 8466–8484 (2000)

Theor. Popul. Biol. **65**, 67–73 (2004)

Phys. Rev. E **70**, 041902 (2004)