

# Dynamical systems and stochastic processes in ecology II

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## 2.1. Introduction

In the last lecture we introduced the master equation

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

where the transition rates  $T(n|n')$  are assumed given (this specifies the model)

This generalises to an arbitrary number of different types of individuals or individuals in different locations,  $\mathbf{n} = (n_1, n_2, \dots)$ :

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

In this lecture we will use the master equation to formulate individual-based models (IBMs) mathematically. IBMs are “microscopic models” which are frequently only studied by computer simulation, with the transition rates simply viewed as update rules in an algorithm

We will also *derive* the population level models (PLMs) from the IBMs by taking their average. PLMs are “macroscopic models” which are usually postulated phenomenologically, and not derived from microscopic models

An example is the Volterra equations for predator-prey reactions

$$\begin{aligned}\frac{dx}{dt} &= \lambda\rho xy - \alpha x, \\ \frac{dy}{dt} &= r y \left(1 - \frac{y}{k}\right) - \rho xy\end{aligned}$$

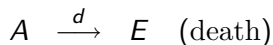
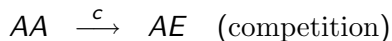
Deterministic, nonlinear differential equations such as these fall into the field of *dynamical systems*, and we will particularly be interested in the long-time behaviour of the solutions; whether they approach a fixed point of a limit cycle, for instance

We will always study well-mixed populations to begin with: additional features such as spatial distributions, age-structure will be added on later, once the initial, simple, model has been understood

## 2.2. Competition within one species

Let's begin with the simplest case, within species competition. An example would be the competition for space or resources

Suppose we denote an individual member of the species by  $A$ . Then the simplest population dynamics of the system can be essentially described by three processes:



We will denote the number of individuals in the system by the integer  $n$  and the maximum number of individuals allowed in the system to be  $N$

Here  $b$ ,  $c$  and  $d$  are the rates of birth, competition and death respectively. Also  $E$  is a null — it allows for the population of species  $A$ ,  $n$ , to grow or decline, since the population of the nulls is  $N - n$

This is a *well-mixed* system, and so spatial effects are disregarded. But if it were spatial, then the  $E$  would represent a vacant space

What is the time evolution of the system?

- Sample the patch — for  $\mu$  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:

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

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

Let us make the replacement  $2\mu b \rightarrow b$ ,  $\mu c \rightarrow c$  and  $(1-\mu)d \rightarrow d$  — in future we will not include the factors involving  $\mu$

We can analyse this model, but perhaps the first thing to do is to ask what the PLM is. That is, what is the equation satisfied by

$$x(t) = \lim_{N \rightarrow \infty} \frac{\langle n(t) \rangle}{N} ?$$

Well,

$$\frac{dx}{dt} = \frac{d}{dt} \frac{\langle n(t) \rangle}{N} = \frac{d}{dt} \left\{ \frac{1}{N} \sum_n n P(n, t) \right\} = \frac{1}{N} \sum_n n \frac{dP(n, t)}{dt}, \text{ as } N \rightarrow \infty$$

I leave it as an exercise for you to prove that

$$\sum_n n \frac{dP(n, t)}{dt} = \langle T(n+1|n) \rangle - \langle T(n-1|n) \rangle$$

Using the fact that  $\langle n^2 \rangle = \langle n \rangle^2$  in the limit  $N \rightarrow \infty$ , and defining a rescaled time by  $\tau = t/N$ , gives

$$\frac{dx}{d\tau} = r x \left( 1 - \frac{x}{k} \right)$$

where

$$r = (b - d) \quad \text{and} \quad k = \frac{(b - d)}{(b + c)}$$

This is the logistic equation

The long-time behaviour will be governed by the fixed points of the equation — those for which  $dx/d\tau = 0$ . For the logistic equation, there are only two:  $x^* = 0$  and  $x^* = k$



To look at the stability of these fixed points we apply a small perturbation and see whether this grows with time, or whether the system returns to the fixed point

So for *each fixed point* write  $x(t) = x^* + \hat{x}(t)$  and substitute into the differential equation keeping only terms linear in  $\hat{x}$ . One finds

$$\frac{d\hat{x}}{dt} = r x^* \left(1 - \frac{x^*}{k}\right) + r \left(1 - \frac{2x^*}{k}\right) \hat{x}(t) + \text{terms in } \hat{x}^2$$

The first term on the right-hand side is zero since  $x^*$  is a fixed point, so for small  $\hat{x}(t)$ :

$$\frac{d\hat{x}}{dt} = r\hat{x}(t) \quad \text{when } x^* = 0 \quad \Rightarrow \hat{x}(t) = e^{rt}\hat{x}(0)$$

$$\frac{d\hat{x}}{dt} = -r\hat{x}(t) \quad \text{when } x^* = k \quad \Rightarrow \hat{x}(t) = e^{-rt}\hat{x}(0)$$

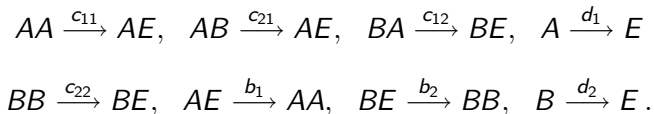
So in the case  $x^* = 0$ , the perturbation grows with time, but in the case  $x^* = k$ , it decays with time. So  $x^* = 0$  is an unstable fixed point and  $x^* = k$  is a stable fixed point

## 2.3. Models involving two species

### (a) Inter- and intra-species competition

Suppose now that there are two species,  $A$  and  $B$ , and there is not only competition between individuals of the same species (intra-species competition), but also between individuals of different species (inter-species competition)

A minimal set of interactions which reflect this is



It is left as an exercise to write down the transition rates corresponding to these interactions. From this, the master equation may be written down, and the deterministic equations which hold in the limit  $N \rightarrow \infty$  may be derived

They are found to be

$$\frac{dx_A}{dt} = r_A x_A (1 - x_A/k_A) - a_A x_A x_B$$

$$\frac{dx_B}{dt} = r_B x_B (1 - x_B/k_B) - a_B x_A x_B$$

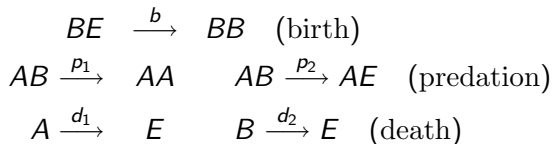
As an exercise you might like to find the fixed points, and for those who want to go further, to find the stability of these fixed points

### (b) Predator-prey interactions

These are fundamentally different from competitive interactions — there is an asymmetry between the species, and also there are feedback effects

To see this, suppose  $A$  is the predator species and  $B$  is the prey species. If there are a large number of predators, then the number of prey will decrease due to predation. But then the number of  $A$  will decrease due to a scarcity of food, so the number of  $B$  will increase. Therefore we should see cycling of predator and prey numbers out of phase with each other

The simplest predator-prey model has the structure



If the population of species  $A$  and  $B$  are  $n$  and  $m$  respectively, the transition rates are

$$\begin{aligned}
 T(n-1, m | n, m) &= d_1 n \\
 T(n, m+1 | n, m) &= 2b \frac{m}{N} (N - n - m) \\
 T(n, m-1 | n, m) &= 2p_1 \frac{n}{N} m + d_2 m \\
 T(n+1, m-1 | n, m) &= 2p_2 \frac{n}{N} m
 \end{aligned}$$

Here a factor of  $N$  has been taken out, by rescaling the time in the master equation (introducing a new time  $\tau = t/N$ )

The explicit form of the deterministic equations is found to be

$$\begin{aligned}\frac{dx}{dt} &= \lambda \rho xy - \alpha x, & x &= \lim_{N \rightarrow \infty} \frac{\langle n \rangle}{N} \\ \frac{dy}{dt} &= r y \left(1 - \frac{y}{k}\right) - \rho xy, & y &= \lim_{N \rightarrow \infty} \frac{\langle m \rangle}{N}\end{aligned}$$

There are two fixed points to these equations. The first is not very interesting. It has  $x^* = 0$ , corresponding to no predators. The prey then just obey a logistic equation

The second one is non-trivial:  $x^* \neq 0$  and  $y^* \neq 0$ . It turns out to be stable for a range of parameter values, but this is rather puzzling, since we would have expected to see oscillatory behaviour, following the argument about the population cycles given earlier

The resolution of this paradox will be discussed in the next lecture

## (c) Models of epidemics

One of the simplest models of childhood diseases, such as measles, whooping cough,... is the SIR (Susceptible-Infected-Recovered) model

The IBM (individual-based model) consists of  $m$  individuals of type  $S$  (the susceptibles),  $n$  individuals of type  $I$  (the infectives) and  $\ell$  individuals of type  $R$  (the recovered)

The processes may be divided into four groups:

1. Infection. An infected individual may come into contact with a susceptible individual or be infected by an external agent (that is, from the environment). These two mechanisms may be expressed as  $SI \xrightarrow{\beta} II$  and  $S \xrightarrow{\eta} I$ .
2. Death. This is a demographic effect rather than an epidemiological one:  $S \xrightarrow{\mu} E$ ,  $I \xrightarrow{\mu} E$  and  $R \xrightarrow{\mu} E$ .
3. Birth. This is again a demographic effect, but with all newly-born individuals being susceptible:  $E \xrightarrow{\mu} S$ .
4. Recovery:  $\gamma: I \xrightarrow{\gamma} R$ .

① Infection:  $S + I \xrightarrow{\beta} I + I$  and  $S \xrightarrow{\eta} I$

$$T(m-1, n+1|m, n) = \left( \beta \frac{m}{N} n + \eta m \right)$$

② Recovery:  $I \xrightarrow{\gamma} R$        $T(m, n-1|m, n) = \gamma n$

③ Death of an infected individual:  $I \xrightarrow{\mu} S$

$$T(m+1, n-1|m, n) = \mu n$$

④ Death of a recovered individual:  $R \xrightarrow{\mu} S$

$$T(m+1, n|m, n) = \mu(N - m - n)$$

We have assumed that births and deaths are coupled, so that  $n + m + \ell = N$ , which means that there are only two degrees of freedom:  $\ell = N - n - m$

The deterministic equations for the SIR model are

$$\begin{aligned} \dot{x} &= \beta xy + \eta y - (\mu + \gamma)x, & x &= \lim_{N \rightarrow \infty} \frac{\langle n \rangle}{N} \\ \dot{y} &= -\beta xy - \eta y + \mu(1 - y), & y &= \lim_{N \rightarrow \infty} \frac{\langle m \rangle}{N} \end{aligned}$$

## 2.4. Other ecological models

An example of another type of ecological model which can be formulated in a similar way, is that of a metapopulation model. We will discuss this here, other examples will be given in the next lecture

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 is 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 three 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:

$$T(n+1|n) = \left(c\frac{n}{N} + m\right) \left(1 - \frac{n}{N}\right)$$

$$T(n-1|n) = e\frac{n}{N}$$

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

$$\frac{dx}{dt} = (cx + m)(1 - x) - ex,$$

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