An Introduction to Mathematical Ecology

3MC School on Quantitative Biology

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Part I: Modelling and Forecasting Ecological Dynamics

Ecological Dynamics

- Competition and cooperation within species
  - logistic growth
  - Allee effects
- Competition and predation between species
  - predator-prey dynamics
  - intra-guild predation
- Host-Pathogen dynamics
- Biological Invasions
  - forest insect pests
  - agricultural pests and pathogens
  - animal diseases
  - biological control

Heterogeneity

- variation between individuals
  - age
  - size
  - behaviour
- variation in landscape
- variation over time

Individual-based and Compartmental-based Models

- Compartmental models
  - The population is subdivided into *compartments* reflecting relevant heterogeneities.
  - The *state-space* of the system is the number of individuals in each compartment.
  - Individuals in the same compartment are interchangeable.
- Individual-based models:
  - The *state-space* of the model includes the state of each individual in the population.
  - Often more *natural* to develop, since the focus in describing the process at the level of the individual
  - Often more *complex* than necessary

Discrete-time vs Continuous-time Models

Many organisms have non-overlapping generations. Take, for example, an annual plant that does not survive through the winter, but produces seeds that germinate and sprout in the spring.

$$N_{t+1} = N_t \times \text{Fecundity} \times \text{Survival}$$

- Fecundity, or recruitment, is a number larger than one, for example, a ratio of offspring to adults, or juveniles to parents.
- Survival is a fraction, or a probability a given juvenile survives to the reproductive stage/age.

Age Structure

Or organisms may have life cycles that are synchronized, so taking a census of populations by age at fixed times makes sense.

$$
\begin{aligned}
N_{0,t+1} &= f_1 N_{1t} + f_2 N_{2t} + f_3 N_{3t} \\
N_{1,t+1} &= s_0 N_{0t} \\
N_{2,t+1} &= s_1 N_{1t} \\
N_{3,t+1} &= s_2 N_{2t}
\end{aligned}
$$

Size Structure

Many organisms are better described by size, not age.

$$
\begin{aligned}
N_{0,t+1} &= f_1 N_{1t} + f_2 N_{2t} + f_3 N_{3t} + (1 - p_0) N_{0t} \\
N_{1,t+1} &= (1 - p_1) N_{1t} + p_0 s_0 N_{0t} \\
N_{2,t+1} &= (1 - p_2) N_{2t} + p_1 s_1 N_{1t} \\
N_{3,t+1} &= (1 - p_3) N_{3t} + p_2 s_2 N_{2t}
\end{aligned}
$$

Stochastic vs Deterministic Modelling

Andersson and Britton (2012) raise several good arguments for using Stochastic models over deterministic models in Biology. Their interest is specific Epidemic Models, but the points pertain to Biology more generally.

1. The stochastic framework is the **most natural way to describe** most biological processes
2. Many phenomena of interest are inherently stochastic.
3. Quantifying our uncertainty in model elements, processes, and outcomes is necessary and inherently probabilistic.
4. Any forecast or assessment of the model is of little value without a corresponding assessment of its uncertainty.

Quantifying Uncertainty

An essential step in designing models is a *quantification of uncertainty*.

To be useful, a prediction must be accompanied by some measure of its accuracy and reliability.

Sources of uncertainty:

- uncertainty in model design, including
  - our understanding of the process being modelled,
  - our choice of model,
    - parameter selection, and
    - inherent variability in the process being modelled;
- uncertainty in observations,
  - measurement error.

Modelling Theory vs Modelling Data

- Modelling Theory
  - model hypothesized processes
  - compare predictions and observations
  - how well does theory explain observation?
  - robust, *extrapolate* to other scales, regions, ...
- Modelling Data
  - descriptive
  - interpolation
  - near-term forecasting
  - no inference can be made on underlying processes

Incorporating Uncertainty and Variability

$$
\begin{aligned}
N_{0,t+1} &= f_1 N_{1t} + f_2 N_{2t} + f_3 N_{3t} + (1 - p_0) N_{0t} \\
N_{1,t+1} &= (1 - p_1) N_{1t} + p_0 s_0 N_{0t} \\
N_{2,t+1} &= (1 - p_2) N_{2t} + p_1 s_1 N_{1t} \\
N_{3,t+1} &= (1 - p_3) N_{3t} + p_2 s_2 N_{2t}
\end{aligned}
$$

Process Variability: f_i, p_i, s_i are nonlinear operators returning random variables.

Environmental or Temporal Variability: f_i, p_i, s_i are deterministic, but parameters are random variables.

Observation Uncertainty: not propagated through time

$$Y_{it} = N_{it} + \epsilon_{it}$$

What is a Forecast?

The process of **predicting** the state of ecosystems, ecosystem services, and natural capital, **with fully specified uncertainties**, and is **contingent on explicit scenarios** for climate, land use, human population, technologies, and economic activity. Forecast state at future time from state at current time given assumptions about parameters. – (Clarke et al, 2001)

Forecasts for Policies, Strategies, and Decisions

- Serviceable Truths
- Working Hypotheses
- Actionable Intel

All models are wrong, but some models suggest *serviceable truths*.

Forecasting is part of the Scientific Method

- Observe
- Formulate Research Question
- Formulate Model and Hypothesis
- Predict/Forecast
- Gather data and test model/hypothesis
- Report and Repeat

The general *process-based* framework

$$\frac{dN}{dt} = B(t, N) - D(t, N)$$

- $N(t)$ is the population at time t
- continuous state: $N \in \mathbb{R}$
  - interpret N as a density or expected population
- continuous time: $t \in \mathbb{R}$
- $B(t, N)$ is the birth rate at time t and population N
- $D(t, N)$ is the death rate at time t and population N

Objective: study solutions of the ODE and their dependence on initial conditions and parameters.

Exponential Growth

Suppose the birth and death rates are both independent of time and proportional to the population size.

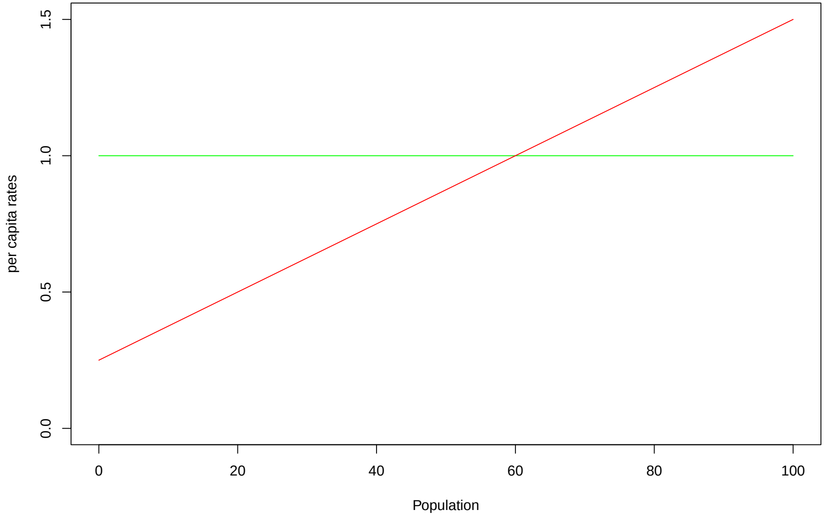
$$\frac{dN}{dt} = bN - dN$$

with $N(0) = N_0$.

- The constants b and d are referred to as the *per-capita* birth and death rates.
- The solution grows exponentially at rate $b - d$ if $b > d$, or decays if $b < d$.

Logistic Growth

$$\frac{dN}{dt} = bN - (d + aN)N$$



Allee Effects

$$\frac{dN}{dt} = \frac{bN^2}{c+N} - (d + aN)N$$