

POPULATION MODELS

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Summary

This chapter presents an overview of the mathematical models associated with population ecology. Since the inception of the academic subject of ecology, mathematical models have been used to predict and understand changes in populations. Dealing with numbers of individuals of a species or interactions between species that change over time is a dynamical system. Such dynamical ecological systems include the interaction between competitors for limiting food, the effects of mutualists or the trophic effects of predator-prey interactions. This chapter begins with a broad introduction to population ecology and shows how mathematical models have been developed to explore a range of different ecological processes in continuous and discrete time. Towards the end of the chapter, brief consideration is given to stochastic formulations of these ecological processes. The chapter concludes with brief perspectives on the future role of mathematics in population ecology.

1. Introduction

Population ecology is the study of the changes in abundance and distribution of species over time and through space. It is a quantitative subject and relies heavily on the language of mathematics to formalize concepts. Four key parameters: births (B), deaths (D), immigration (I) and emigration (E) provide the fundamental basis for understanding the patterns of temporal abundance and spatial distribution of organisms. The changes in numbers (N) of a species through time and space can be expressed simply as:

$$N = B - D + I - E. \quad (1)$$

This expression (1) states that an organism will increase in numbers through births and/or immigration, and decrease through death and/or emigration. The overall objective of this chapter is to introduce how mathematical models and techniques can be applied to problems in population ecology. More specifically, in this chapter, the population processes associated with births and deaths are considered. Three major types of population models are presented: continuous-time models, discrete-time models and stochastic models. A comprehensive discussion of their role in understanding the patterns and processes associated with single species, competitive and predator-prey interactions is presented. The chapter concludes with a consideration of the prospects for models in population ecology and their general future role in biology.

The formulation of mathematical models provides a logical framework for developing, testing and criticizing ecological hypotheses. Mathematical models of ecological theory can be formulated in one of two ways. Firstly as deterministic models (i.e. using difference or differential equations) such as the continuous-time Lotka-Volterra model of interspecific competition or the discrete-time Nicholson-Bailey predator-prey model, or secondly, as stochastic models in which the occurrence of events is considered to be probabilistic even though the underlying rates remain constant. Although the use of mathematics in biology has often been controversial with biological realism often being ignored for the sake of mathematical generalities, mathematical models have provided biology (e.g. population ecology and population genetics) with a conceptual paradigm through which the occurrence of key patterns and processes can be expressed and explored.

2. Continuous-Time Population Models

2.1. Pure Birth Processes

The simplest ecological scenario to envisage is a pure birth process. This occurs if, over a short time period, a population increases without the constraints of crowding, competition or contests. If it is assumed that within this time frame death does not occur and the birth rate (λ) is the same for all individuals (genetic homogeneity) then the growth rate of the population may be considered in terms of an *ordinary differential equation*. If $N(t)$ denotes the population size at time t , in small time intervals of length τ , the increase in the population size from time t to $t + \tau$ is:

$$N(t + \tau) = N(t) + \lambda \cdot \tau \cdot N(t). \quad (2)$$

Subtracting $N(t)$ from each side of this expression (2) and dividing through by τ gives:

$$\frac{N(t + \tau) - N(t)}{\tau} = \lambda \cdot N(t). \quad (3)$$

Letting $\tau \rightarrow 0$ then yields the ordinary differential equation for a pure birth process:

$$\frac{dN(t)}{dt} = \lambda \cdot N(t) \quad (4)$$

such that the rate of change of N with respect to t is the product of the birth rate (λ) and the current population size ($N(t)$). Eq. (4) can be integrated to give (with appropriate initial conditions) the solution:

$$N(t) = N(0) \cdot \exp(\lambda \cdot t). \quad (5)$$

Given the initial assumptions of no death and constant birth rate, a pure birth process gives rise to an exponential increase in population size. A statistical test for a pure birth process would be to plot $\ln(N(t))$ versus t and check for an approximate positive linear relationship with slope λ and intercept $\ln(N(0))$.

2.2. Pure Death Processes

In contrast to the pure birth process, a similar ordinary differential equation can be derived for a pure death process. This type of ecological process centers on how the longevity and survival of an organism affects changes in population numbers through time. Under a pure death process it is assumed that individuals do not give birth, they do not suffer the constraints of crowding, competition or contests and the death rate (μ) is the same for all individuals. If $N(t)$ denotes the population size a time t , then in small time intervals of length τ , the decrease in population size from time t to $t + \tau$:

$$N(t + \tau) = N(t) - \tau \cdot \mu \cdot N(t). \quad (6)$$

The ordinary differential Eq. (following the scheme for the pure birth process (3)) for a pure death process is:

$$\frac{dN(t)}{dt} = -\mu \cdot N(t) \quad (7)$$

and has solution:

$$N(t) = N(0) \cdot \exp(-\mu \cdot t) \quad (8)$$

Again given the assumptions, under a pure death process a population would decline exponentially. A simple test of this type of process would be to regress $\ln(N(t))$ on t and check for a negative linear relationship with slope μ and intercept $\ln(N(0))$.

2.3. Birth-death Processes

Given that populations change as a result of birth and death processes, the pure, individual, processes of birth and death can be combined to formulate a birth-death process that can be expressed as a continuous-time model for the changes in population numbers. Deriving the ordinary differential equation for the birth-death process proceeds in the same way as for a pure birth and pure death process. If it is assumed that individuals give birth at a rate λ and die at a rate μ , and do not suffer the constraints of crowding or competition, the deterministic ordinary differential equation is:

$$\frac{dN(t)}{dt} = (\lambda - \mu) \cdot N(t) \quad (9)$$

with solution:

$$N(t) = N(0) \cdot \exp((\lambda - \mu) \cdot t). \quad (10)$$

The net rate of change $(\lambda - \mu)$ may be positive or negative depending on whether $\lambda > \mu$ or vice versa. This can give rise to either exponential increase or decrease. This is a simple representation of how changes in population numbers may occur where the rate of birth and death are independent of population size.

In reality, population growth must be restricted by the availability of limiting resources. When these resources are fully utilized the population can grow no further: this upper bound or *carrying capacity* on population growth is determined by the environment. As the total abundance of an organism will only increase through births and immigration, or decrease through deaths and emigration, we seek general expressions that link these processes to population size and density.

For instance, if rates are functions of population numbers, the birth and death processes can be expressed as $B(N)$ and $D(N)$, respectively. These simple expressions allow virtually any functional form of birth or death to be modeled and in the limiting case when $B(N) = \lambda$ and $D(N) = \mu$, then the birth-death process described above (Eqs. (9) and (10)) is recovered.

If $N(t)$ denotes the population size at time t , then in small intervals of time of length τ , the increase in population size from time t to $t + \tau$ is:

$$N(t + \tau) = N(t) + (B(N) - D(N)) \cdot \tau \quad (11)$$

Subtracting $N(t)$ and dividing through by τ and allowing $\tau \rightarrow 0$ gives:

$$\frac{dN(t)}{dt} = B(N) - D(N) \quad (12)$$

Solutions to this ordinary differential equation are critically dependent on the functional forms of $B(N)$ and $D(N)$. Although analytical solutions may be difficult to obtain, numerical solutions are always feasible with an appropriate *numerical integration*

algorithm. Simple functional forms for the dependence of births and deaths on population numbers illustrate how the processes affect changes in population growth and abundance. For example, if in a birth-death process $B(N) = \lambda \cdot N$ and $D(N) = \mu \cdot N \cdot (N - 1)$, then Eq. (12) is:

$$\frac{dN(t)}{dt} = N \cdot [\lambda - \mu(N - 1)]. \quad (13)$$

One common question asked of population models is whether the ecological processes being modeled have any stable steady states. That is, over time will the population remain at a constant size or will it increase or decrease. A population will remain in a steady state for some value of N if both births and death rates are equal. A deterministic steady state (N^*) for the birth-death model (Eq. (13)), determined by setting $\frac{dN(t)}{dt} = 0$ and solving for N , is given by:

$$N^* = \frac{\lambda - \mu}{\mu} \quad (14)$$

This steady state is considered to be stable if after experiencing a small perturbation, the population returns to this steady state value (N^*). We can derive a formal test for this through local (as opposed to global) stability analysis: it is assumed that the population is displaced, through a small perturbation, from its steady state value and the subsequent population behavior is then monitored.

Considering a small perturbation from a steady state (N^*)

$$n = N^* + N \quad (15)$$

where n is the resulting perturbed value of N , we can expand about the steady state for the birth and death processes through the use of a *Taylor series expansion*. This yields:

$$B(N) = B(N^*) + n \cdot \left(\frac{dB}{dN} \right)_{N=N^*} + o(n^2) \quad (16)$$

and

$$D(N) = D(N^*) + n \cdot \left(\frac{dD}{dN} \right)_{N=N^*} + o(n^2). \quad (17)$$

Substituting these Eqs. ((16) and (17)) into the original birth-death process (Eq. (12)) gives the rate of change of the population following a perturbation as:

$$\frac{dn(t)}{dt} = B(N^*) - D(N^*) + n \cdot \left(\frac{dB}{dN} - \frac{dD}{dN} \right)_{N=N^*} + o(n^2). \quad (18)$$

At the steady state, births and deaths are equal and following a small perturbation, terms of n^2 and higher terms of the Taylor expansion are assumed to be negligible. After a small displacement, the population is then expected, at least to a first approximation, to follow:

$$\frac{dn(t)}{dt} = n \cdot \left(\frac{dB}{dN} - \frac{dD}{dN} \right)_{N=N^*} \quad (19)$$

with solution

$$n(t) = n(0) \cdot \exp \left(t \cdot \left(\frac{dB}{dN} - \frac{dD}{dN} \right)_{N=N^*} \right). \quad (20)$$

This solution (Eq. (20)) implies that the population has steady state dynamics and that small perturbations decay away exponentially if

$$\left(\frac{dB}{dN} - \frac{dD}{dN} \right)_{N=N^*} < 0 \quad (21)$$

This occurs if $B(N) > D(N)$ whenever $N < N^*$ and $B(N) < D(N)$ whenever $N > N^*$.

2.4. Logistic Model

In many populations, the utilization of an available resource will eventually limit the long-term increase of a population. A development of the birth-death process (Eq. (12)) in which the net growth rate per individual is a function (f) of total population size (N) could take the form:

$$\frac{dN(t)}{dt} = f(N) \cdot N. \quad (22)$$

If N is large then $\frac{df(N)}{dN} < 0$ since the larger the population grows, the greater the inhibitory effect on further growth. The simplest assumption is to allow $f(N)$ to be linear: $f(N) = r - s \cdot N$ where r and s are positive constants representing the birth and death rates, respectively. This is the Verhulst-Pearl logistic equation. It predicts that, in the absence of interactions with other species, a population will grow to a carrying capacity (N^*), where $N^* = r/s$, the ratio of growth rate to death rate. The logistic model is a useful description of how populations grow in the presence of a limiting resource. Species, however, do not act in isolation but are embedded in webs of competitive and trophic interactions. Next, we explore the role of population models in understanding the effects of interspecific (between-species) competition before developing the theme further to examine predator-prey theory.

2.5. Competitive Interactions

2.5.1. Interspecific Competition

Species are likely to compete for limiting resources such as food or territory. The mathematical theory of these interspecific competitive interactions is well established. Although correlation does not necessarily imply causation, (for example, a negative correlation between populations of two organisms does not necessarily imply interspecific competition), simple mathematical models of competition do assume that a species growth rate is inhibited through both intraspecific (within-species) and interspecific (between species) processes. If N_1 and N_2 denote the numbers of individuals of species 1 and 2, respectively, then the single species logistic model (Eq. (22)) can be extended to a two species form:

$$\frac{dN_1}{dt} = N_1 \cdot (r_1 - s_{11} \cdot N_1 - s_{12} \cdot N_2) \quad (23)$$

$$\frac{dN_2}{dt} = N_2 \cdot (r_2 - s_{22} \cdot N_2 - s_{21} \cdot N_1) \quad (24)$$

where r_i is the growth rate of species i , s_{ii} is the inhibitory effect of species i on itself (i.e. the intraspecific effects) and s_{ij} is the effect of species j on species i (i.e. interspecific effects). To determine whether one species wins in competition or whether there is coexistence, requires an equilibrium solutions to Eq. (23) and Eq. (24): $\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$ at $N_1 = N_1^*$ and $N_2 = N_2^*$. Using this assumption, allows Eqs. (23) and (24) to be expressed in the form:

$$0 = N_1^* \cdot (r_1 - s_{11} \cdot N_1^* - s_{12} \cdot N_2^*) \quad (25)$$

$$0 = N_2^* \cdot (r_2 - s_{22} \cdot N_2^* - s_{21} \cdot N_1^*) \quad (26)$$

At equilibrium,

$$N_1 = \frac{r_1 \cdot s_{22} - r_2 \cdot s_{12}}{s_{11} \cdot s_{22} - s_{21} \cdot s_{12}} \quad (27)$$

$$N_2 = \frac{r_2 \cdot s_{11} - r_1 \cdot s_{21}}{s_{11} \cdot s_{22} - s_{21} \cdot s_{12}} \quad (28)$$

From Eq. (23), $N_1^* = 0$ when $N_2 = \frac{r_1}{s_{12}}$ and $N_2^* = 0$ when $N_1 = \frac{r_1}{s_{11}}$. From Eq. (24),

$N_1^* = 0$ when $N_2 = \frac{r_2}{s_{22}}$ and $N_2^* = 0$ when $N_1 = \frac{r_2}{s_{21}}$.

Four types of population behavior are possible depending on whether (i) $\frac{r_1}{s_{12}} > \frac{r_2}{s_{22}}$, (ii) $\frac{r_1}{s_{12}} < \frac{r_2}{s_{22}}$ (iii) $\frac{r_1}{s_{11}} > \frac{r_2}{s_{21}}$ and (iv) $\frac{r_1}{s_{11}} < \frac{r_2}{s_{21}}$. These invasion conditions can be represented graphically.

If $\frac{r_1}{r_2} > \frac{s_{12}}{s_{22}}$ and $\frac{r_1}{r_2} > \frac{s_{11}}{s_{21}}$ species 1 wins out. If $\frac{r_1}{r_2} < \frac{s_{12}}{s_{22}}$ and $\frac{r_1}{r_2} < \frac{s_{11}}{s_{21}}$ species 2 wins out. If $\frac{s_{12}}{s_{22}} < \frac{r_1}{r_2} > \frac{s_{11}}{s_{21}}$ a stable equilibrium exists and the species coexist. If $\frac{s_{11}}{s_{21}} < \frac{r_1}{r_2} > \frac{s_{12}}{s_{22}}$ there is an unstable equilibrium such that if species are perturbed from the equilibrium, one of the species will ultimately become extinct.

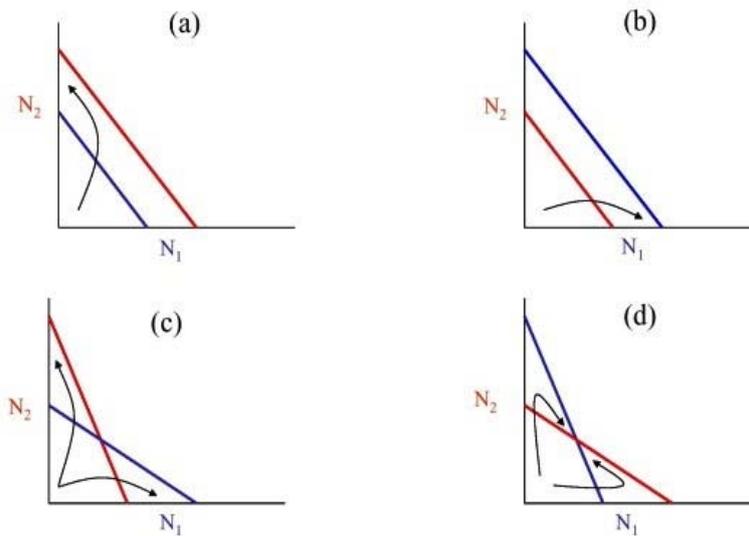


Figure 1. Conditions for coexistence and competitive exclusion. (a) Exclusion of N_1 by N_2 as N_2 is the stronger competitor. (b) Exclusion of N_2 by N_1 as N_1 is the stronger competitor. (c) Unstable equilibrium: outcome of competition dependent on initial conditions. (d) Coexistence of N_1 and N_2 . Blue line is the growth isocline for N_1 and red line is the growth isocline for N_2 .

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Biographical Sketch

Michael Bonsall , is a Royal Society University Research Fellow and Head of Ecology in the Department of Zoology at the University of Oxford. Michael graduated from Imperial College London. He completed his PhD on theoretical and empirical insect population dynamics and completed postdoctoral positions at Silwood Park, Imperial College, London. He joined the Zoology Department in Oxford in April 2005 and is the Biology Fellow and Tutor at St. Peter's College. Michael's overall research focuses on mathematical biology and aims, broadly, to understand how species coexist in time and space. This is approached using mathematical models, observations and experiments. He has grant-funded projects exploring the role of insect on predator-prey communities and the evolution of insect resistance to microbial insecticides, and works with a range of international collaborators.