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Chapter 0

Introduction

'In time, those unconscionable maps no longer satisfied, and the cartographers guild drew a map of the empire whose size was that of the empire, coinciding point for point with it. The following generations, who were not so fond of the study of cartography saw the vast map to be useless and permitted it to decay and fray under the Sun and winters.'

Jorge Luis Borges *On Exactitude in Science* (1946).

'But everything takes a different shape when we pass from abstractions to reality. In the former, everything must be subject to optimism, and we must imagine the one side as well as the other striving after perfection and even attaining it. Will this ever take place in reality?'

Carl von Clausewitz *On War* (1832).

0.1 The goal of ecology: understanding the distribution and abundance of organisms from their interactions

Let us start from the beginning. Ecology can be defined as the scientific study of the distribution and abundance of organisms (Andrewartha 1961) or, more precisely, as the scientific study of the interactions that determine the distribution and abundance of organisms (Krebs 1978). Krebs' definition is both clear and comprehensive. And, in contrast to other definitions, avoids ambiguities or vagueness. Species distribution is the manner in which species are spatially arranged. Species distribution patterns depend on biotic (living) and abiotic (non-living) factors and change depending on the scale at which they are viewed. Abundance is an ecological quantity of paramount importance when making management and conservation decisions (Andrewartha and Birch 1954, Krebs 1978, Gaston 1994). Estimates of future

abundance are essential either for species of value to humans for regulating current and future harvests, or for species of conservation concern since their future numbers will be an important determinant of their extinction risk, or for harmful/toxic species to anticipate their blooms.

To analyze the relationships between living organisms and their environments, the interaction of organisms with one another, and the resulting patterns of abundance and distribution of organisms, ecology has progressed through the incorporation of sophisticated computational methods. The first major use of mathematics in ecology can be traced to the seminal models of Alfred Lotka (1925) and Vito Volterra (1926). They produced basic ecological models for competition and predation—now referred to as the Lotka–Volterra models—that have become the cornerstone for much of ecology today and particularly for two of its sub-disciplines: *community ecology* and *population ecology*. Community ecology is the study of the organization and functioning of communities, which are assemblages of interacting populations of different species coexisting at a particular location. Population ecology focuses on the dynamics of populations of single-species groups (or even a particular population within the same species). Since then, the above stylized mathematical models and their descendants have been used mostly to provide *qualitative* explanations for patterns in nature. An example is the use of competition models to explain species diversity (May 1974, Diamond and Case 1986). Simple competition models served to show that species that utilize the same resource can coexist and avoid competitive exclusion.

On the other hand, modelling efforts to provide *quantitative* results in applied fields have generally rejected simple mathematical models in favor of giant hyper-realistic simulation models (Onstad 1988). Individual-based models (DeAngelis and Grimm 2014) constitute an example of this modelling approach whose use in ecology has been growing rapidly in the last two decades. They simulate populations and communities by following individuals and their properties. These *individuals* might represent plants and animals in ecosystems. Individual-based models have been playing an increasingly important role in questions posed by complex ecological systems. For example, to understand the causes of vegetation change, an important long-term goal of ecology, we can link individual-based simulations of populations to models of detritus composition and nutrient release. These models provide important information on plant community processes, constraints over selection and biogeochemistry (Levin 1992). Individual-based models have also been used for addressing theoretical questions like understanding how traits of individual organisms are connected with the assembly of communities and food webs (DeAngelis and Grimm 2014). The problem with these more realistic simulation models is that they sacrifice understandability for ecological realism and can have hundreds of parameters and state variables.

However, in recent decades, an increased interest in applied questions among ecologists, and the resulting research has begun to suggest a different use for simple mathematical models, both for Lotka–Volterra models (Fort 2018a, 2018b, Fort and Segura 2018) as well as a general approach (Ginzburg and Jensen 2004, Hilborn and Mangel 1996, Ishida 2007, Lonegran 2014). In the last section of this chapter we

will comment on this well-known trade-off in mathematical modelling between realism and usability, which is captured by the saying ‘All models are wrong, but some are useful’ (Box 1976). But before this, in the section, we will review some of the basics of mathematical modelling, including why models are of central importance in scientific research, its principles and the classification of mathematical models.

0.2 Mathematical models

0.2.1 What is modelling?

Models describe our beliefs about how the world functions. They are idealizations that simplify reality and never provide a completely accurate representation of the real-world phenomena. Among the uses of models are: to describe the behavior or results observed; to explain why that behavior and results occurred as they did; to predict future behaviors or results that are as yet unseen or unmeasured.

modelling constitutes a central piece of the *scientific method* that roughly can be viewed as having four stages: observation, modelling, prediction and verification. The observation stage consists in measuring what is happening in the real world. Here we gather empirical facts and real-world data related to the phenomenon or phenomena we are interested in understanding/explaining. The modelling stage includes, first analyzing and filtering the above observations to only retain a reduced set of relevant data associated with this phenomenon and then to construct a hypothesis—an educated guess about how things work—that explains the phenomenon. For example, in physics this often means proposing a mathematical relation or a causal mechanism. In the prediction stage we use models to tell us what will happen in a yet-to-be-conducted experiment or in an anticipated set of events in the real world. These predictions are then followed by observations in the verification stage that serve either to validate the model or to suggest reasons why the model fails and then it either has to be changed or completely rejected. Actually, the above process is iterated so that scientists build up a better and better representation of the phenomena they want to explain or use for prediction as time goes on.

There is a large element of compromise in modelling. The majority of systems in the real world are far too complicated to model in their entirety. So it is crucial to identify the most important parts of the system. These will be included in the model, the rest will be excluded. This compromise between realism/accuracy and usefulness/practicality is well illustrated by the *map–territory relation*: the most accurate map possible would be the territory itself, and thus would be perfectly accurate and perfectly useless. The quotation from Jorge Luis Borges at the beginning of this chapter describes the tragic uselessness of the perfectly accurate, one-to-one map.

0.2.2 Why mathematical modelling?

Models can be of different types; conceptual models (abstractions of things that exist in the real world) to better understand, graphical models for visualizing purposes, mathematical models, etc. Formulating models into the language of mathematics has many advantages. It allows:

- **Precision and non-ambiguity.** Mathematics is a very precise language with well-defined rules for manipulations.
- **Algorithmic compression.** Mathematical models can condense vast arrays of data into compact formulas. According to Motz (1987), modern science began with Galileo and Newton and the quest for algorithmic compressibility: Newton's fundamental discovery that all the information recorded about the motion of bodies in the heavens or on Earth could be encapsulated in three simple rules he called 'the laws of motion' plus his law of gravitation. Algorithmic compression is crucial to understand why things are the way they are as well as to predict how they are going to be in the future.
- **To discover non-apparent relationships and develop scientific understanding.** Besides providing brevity and formality of description, quantitative expressions of current knowledge of a system also allow manipulation of the model and provide the opportunity of discovering emergent properties not apparent without mathematical reasoning and that are required to understand complex systems.
- **To use computers to perform numerical calculations.** Although mathematics has the potential to *prove* general results, i.e. of analytical proof, most systems of interest in ecology are described by equations whose analytical solutions (in terms of closed mathematical formulas) are unknown. However, these equations can be solved numerically by using computers, i.e. manipulating numbers directly to produce a numerical result rather than a formula.
- **To simulate virtual experiments.** Related with using computers, simulation allows one to perform virtual experiments that would be difficult or impossible to perform in the real world, for either practical or ethical reasons. This is particularly the case for many ecological systems for which experimentation is impossible. In fact, the complexity, cost or risk of many experiments make the use of simulations unavoidable. Furthermore, simulation can be useful when the real system does not yet exist (e.g. artificial ecological communities, like mixture of crops) or when the real system works too fast (e.g. an electrical network) or too slow (e.g. geological processes or evolution or speciation) precluding direct analysis. The systematic use of computer simulations—from climate science to high energy physics (Massimi and Bhimji 2015)—is undeniable.
- **Aid decision making.** Quantitative information, e.g. in the form of standardized indices, is helpful for making both tactical decisions by managers as well as strategic decisions by planners.

The importance of the application of mathematical methods to ecology has been discussed in several studies (Hallam and Levin 1986, Levin *et al* 1989, May 1974, 2004, Vandermer 2010). Mathematical models have been fundamental in describing many practical issues. A non exhaustive list covers from the fate and transport of pollutants in the environment, the spread of agricultural pests, the dynamics and control of epidemics, to the management of renewable and nonrenewable resources,

the response of ecological systems to global climate change, and fisheries management.

Indeed, there are few areas of science which cannot benefit from mathematical modelling. Our aim is that the methods covered in this book allow the reader to start developing her/his own models and provide insight into useful methods with a wide range of applications, including developing early warnings of catastrophic shifts in ecosystems, sustainable harvesting and conservation management.

0.2.3 What kind of mathematical modelling?

Mathematical models can be classified in several ways, according to their use (description, explanation, prediction, optimization), accuracy (qualitative or quantitative), degree of randomness (deterministic and stochastic), degree of specificity (specific or general), etc. Another possible distinction is between deductive and inductive models. A deductive model is a logical structure based on a theory. An inductive model arises from empirical findings and generalization from them. Mathematical models in ecology can also take many forms, including but not limited to dynamical systems, statistical models, partial differential equations, etc.

This book deals with models based on *differential equations* or their discrete counterpart, *finite difference equations* (and, in part III, with *cellular automata* resulting from spatial partial differential equations commonly used to describe systems such as vegetation patterns). These equations determine how a system changes from one state to the next and/or how one variable depends on the value or state of other variables (*state equations*). For instance, they describe the rates at which populations change due to birth, death, migration, etc. The majority of the models we will consider will be deterministic models, which ignore random variation, and so always predict the same outcome from a given starting initial condition. However, when needed, we will include stochastic variables to model uncertainty or randomness of some environmental condition. Take, for instance, a population of lynxes and hares. The lynxes need to eat hares in order to produce offspring. So the number of young each lynx produces is a function of the number of hares. But as the lynxes eat the hares, the number of hares decreases, thus the hare death rate is related to the number of lynxes. A model known as the *Lotka–Volterra predator–prey model* describes this kind of interacting system with a pair of coupled nonlinear differential equations. As we will see in the next chapter, this is an example of a *dynamical system*. More specifically, a deterministic dynamical system. That means that if you start with the same inputs, you always get the same prediction for the number of lynxes and hares over time.

There are several excellent textbooks on mathematical modelling. A completely non exhaustive list includes as general introductions to mathematical modelling the text by Giordano *et al* (2009) which offers a solid introduction to the entire modelling process across several fields with balance between theory and practice, and Bender (2000) using a practical ‘learn by doing’ approach. Mathematical biology is extensively covered by these two classics: Edelman-Keshet (1988) and Murray (1989). Highly valuable introductions to mathematical models, methods,

and issues in population ecology can be found in Kot (2003), May (1974) and Pastor (2008).

0.2.4 Principles and some rules of mathematical modelling

Mathematical modelling has both principles behind it and rules that are either necessary to warrant logical consistency or helpful to get insight with your model. The principles can be phrased as questions about the intentions and purposes of mathematical modelling (Dym 2004). We outline such principles in box 0.1, and we illustrate them with a practical problem. Next, we briefly review some of the rules and discuss them in the context of this illustrative problem.

Suppose our **goal** is to estimate when the population of yeast *Saccharomyces cerevisiae* inoculated into a culture medium will reach 80% of its maximum equilibrium value under the same experimental conditions used by Gause (1932) in his famous experiments. So **we want to know** the volume occupied by yeast as a function of the time after inoculation.

What do we know? Gause's experimental setting and details are as follows. As a nutritive medium the so-called 'yeast fluid' is employed; it was prepared in the following manner: 20 g of dry pressed beer yeast were mixed with 1 liter of distilled water, boiled for half an hour in Koch's boiler, and then filtered through infusorial earth. To this mixture 5 per cent of sugar was added, and then the medium was sterilized in an autoclave. The sterile medium was aseptically poured into the test-tubes which had been stopped by cotton-wool and first sterilized by dry heat. The

Box 0.1. A list of useful questions for guiding the process of mathematical modelling.

<i>Question</i>	<i>Task</i>
• Why? What is the goal?	Identify the need for the model.
• Find? (output) What do we want to know?	List the data we are seeking.
• Given? (Input) What do we know?	Identify the available relevant data.
• Assumptions? What can we assume?	Identify the circumstances that apply.
• How? How should we look at this model?	Identify the governing rules or principles and the equations that will be used.
• Predictions? (Output) What will our model predict?	Identify the calculations that will be made, and the answers that will result.
• Valid? Are the predictions valid?	Check the accuracy of the model's representation of the real system.
• Improve? How can we improve the model?	Identify parameter values that are not adequately known, variables that should have been included, and/or assumptions/restrictions that could be lifted.

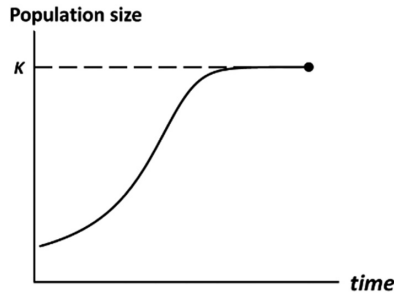


Figure 0.1. Logistic curve for the population size as a function of time, $N(t)$.

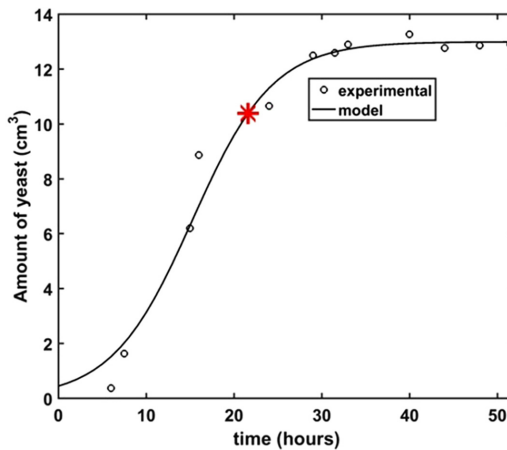


Figure 0.2. The growth of the volume of *Saccharomyces* (o) and the logistic curve (filled). The * symbol denotes when the yeast reaches 80% of its carrying capacity.

experiments were made in a thermostat at a temperature of 28 °C. The volume of yeast was measured and the number of cells were counted in a counting chamber under the microscope for 6, 7.5, 15, 16, 24, 29, 31.5, 33, 40, 44, 48 and 51.5 h after inoculation (circles in figure 0.2).

We should list any relevant **assumptions**, so any assumptions made about population growth should be spelled out. The reader can find a list of relevant assumptions in table 1 of the next chapter. For example, that there is a continuous overlap of generations so that a continuous time variable can be used, the population is isolated (i.e. there are no in or out fluxes), the environment is considered homogeneous (i.e. there are no sharp gradients of resource distribution), etc. It turns out that all these assumptions are consistent with the experimental conditions.

Which rules or principles apply to this model? As we will see in the next chapter, the growth of a homogeneous population within a limited environment exhibits a sigmoid behavior, i.e. at first the population N grows exponentially with time until it reaches an inflection point where it changes concavity and finally it saturates to a

maximal equilibrium population or carrying capacity \mathfrak{K} (figure 0.1). Mathematically the population growth is described by the logistic equation (see next chapter)¹

$$dN/dt = rN(1 - N/\mathfrak{K}), \quad (0.1)$$

where r denotes the population growth rate. Solving this equation we get the logistic curve

$$N(t) = \frac{\mathfrak{K}}{1 + (\mathfrak{K}/N_0 - 1)e^{-rt}}, \quad (0.2)$$

where N_0 is the initial population. In our problem, the variable will be the volume $V(t)$ rather than the number of cells $N(t)$.

Predictions. Our model will predict the time t_{80} when the fraction $x = N/\mathfrak{K}$ reaches 80%. From equation (0.2), this function as a function of the elapsed time t can be expressed as

$$x(t) = \frac{1}{1 + (1/x_0 - 1)e^{-rt}}. \quad (0.3)$$

The parameters \mathfrak{K} and r as well as N_0 can be obtained from the experimental values by a simple least square regression (see exercise 1.2) producing $\mathfrak{K} = 13.0$, $r = 0.218$ and $N_0 = 0.45$ ($x_0 = 0.45/13 = 0.035$).

Therefore t_{80} can be obtained by solving equation (0.3) for $x = 0.8$, which gives:

$$\begin{aligned} t &= \frac{1}{r} \ln \left(\frac{1/x_0 - 1}{1/0.8 - 1} \right) = \frac{1}{0.218} \ln \left(\frac{1/0.035 - 1}{1/0.8 - 1} \right) \\ &= 21.6 \text{ h (indicated as an asterisk in figure 0.2)}. \end{aligned}$$

Validation. From figure 0.2 we can see that the theoretical logistic curve, with estimated parameters $K = 13.0$, $r = 3.328$, agrees pretty well with the experimentally measured amounts of yeast (circles).

If we find that our model is inadequate or that it fails in some way, we then enter an iterative loop in which we cycle back to an earlier stage of the model building and re-examine our assumptions, our known parameter values, the principles chosen, the equations used, the means of calculation, and so on. This iterative process is essential because it is the only way that models can be improved, corrected, and validated.

Now we will review some rules that need to be followed as well as some recipes that are generally useful.

- A. **Abstraction and the value of idealized systems.** An important decision in modelling is choosing an appropriate level of detail for the problem at hand. This abstraction process requires a thoughtful approach to identifying those phenomena on which we want to focus. Finding the right level of detail is therefore intimately connected with finding the right level of abstraction. With this aim, using ideal systems, i.e. simplified or stylized representations

¹ A note on notation, as we will see at the end of this chapter, variables (like ' N ' and ' t ') are denoted in regular italic while parameters (such as ' r ' and ' \mathfrak{K} ') are denoted by manuscript font.

of real systems, as a starting point to model a phenomenon and then complicating things if this simplest model fails in capturing important aspects of this phenomenon is a common practice in many fields of science that has demonstrated its usefulness. An example of such idealized systems in physics is the *ideal gas*, a theoretical gas composed of many randomly moving point particles whose only interactions are perfectly elastic collisions, like the ones between billiard balls. For a mol of an ideal gas the well-known equation of state $PV = \mathcal{R}T$ (where P , V and T denote, respectively, pressure, volume and temperature, and \mathcal{R} is the gas constant $8.314 \text{ J K}^{-1} \text{ mol}^{-1}$), the *ideal gas law*, can be derived using Maxwell's kinetic theory of gases. There are no 'ideal gases' in reality, however, the ideal gas law, is a good approximation. Under usual conditions, most real gases behave qualitatively like an ideal gas. Furthermore, many gases such as, noble gases, nitrogen, oxygen, and hydrogen can be treated like ideal gases within reasonable tolerances. For example one mol of nitrogen, the most common pure element in the Earth and making up 78.1% of the entire volume of the atmosphere, occupies at standard temperature and pressure (a temperature of $20 \text{ }^\circ\text{C} = 293.15 \text{ K}$ and an absolute pressure of $1 \text{ atm} = 101\,325 \text{ Pa}$) a volume of 24.00 l . And, under the same standard conditions, the ideal gas law predicts a volume of $8.314 \times 293.15/101\,325 = 0.024\,05 \text{ m}^3 = 24.05 \text{ l}$, i.e. a relative difference of 0.21%. However, it turns out the ideal gas model tends to fail at lower temperatures or higher pressures, when intermolecular forces and molecular size becomes important. It also fails for most heavy gases, such as many refrigerants, and for gases with strong intermolecular forces, notably water vapor. At high pressures, the ideal gas law generally underestimates the volume of real gases and at low temperatures overestimates the pressure of real gases. Most importantly, at some point of low temperature and high pressure, real gases undergo a phase transition, such as to a liquid or a solid. The model of an ideal gas, however, does not describe or allow phase transitions. These must be modelled by more complex equations of state.

History has shown, not only in physics, but also in ecology, that one can make considerable progress with simple models. For example, in population ecology a well-known ideal system is a population growing at a constant rate, i.e. governed by the Malthus equation $dN/dt = rN$ (see next chapter), which can be obtained as a limiting case of the more realistic logistic equation (0.1) when N is much smaller than \mathcal{K} . And, although it is very unrealistic as a general description of population growth, bacteriologists have used it for differentiating species by restricting the model to the initial stage of exponential growth. Indeed, as we will discuss in chapter 4, there is an interesting formal analogy between the equation of state of a real gas and its ideal gas limit for one side and the logistic equation and its Malthus limit for the other. In the next section we will get back to the value of using idealized systems and situations to get insight into the phenomena we want to understand.

B. **Aggregation and compartmental modelling.** Compartmental modelling can help the above abstraction process. Compartmental models are composed of sets of interconnected ‘compartments’ or ‘chambers’. Each compartment of the system is considered to be homogeneous (perfectly mixed, with uniform concentration or density). Compartments can be used as ‘black’ boxes without explicit internal structure, connected by ‘flows’ that simulate how individuals in different ‘compartments’ interact. In population ecology, the plants or animals in each compartment are assumed to be the same as all the other plants or animals in that compartment. Flows between compartments of the model can represent interactions. For instance, predators eating prey is described as a ‘biomass flow’ from the prey compartment into the predator compartment. This flow represents the fact that the number of predators that can survive is related to the number of prey available for them to eat and, vice versa, the survival of prey depends on the number of predators around to eat them. Another example is live individuals that flow to a ‘dead’ compartment with a certain rate. The rates of flow between compartments, and interaction rates between compartments, are parameters of the model. For instance, a compartmental model could be used to simulate the number of animals over time in a predatory/prey system like lynxes and hares. One compartment would be the predators (the lynxes), and they would be assumed to all be the same, with the same death and birth rates, ability to catch prey, no distinction between ages, etc. The other compartment would be the hares, and they would also be assumed to all be the same and have the same probability of being caught by lynxes. Actually, this model of two boxes, one for prey and the other for predator, is the basis behind the Lotka–Volterra predator–prey model we already mentioned.

Aggregation of species which are similar regarding traits or function into sets or groups can also be helpful. For example, functional groups are non-phylogenetic, aggregated units of species sharing an important ecological characteristic and playing an equivalent role in the community (Cummins 1974). In the second part of this book we will consider a compartmental model obtained by aggregation of species of plants and pollinators in plant–pollinator networks.

C. **Dimensional homogeneity and consistency.** Biology, physics and chemistry, rest on a number of measurable entities or *quantities* such as length, mass or time. To each such quantity a unit of measurement is assigned. For example, length measured in meters, mass in kilograms and time in seconds define the MKS (meter–kilogram–second) *system of units*. We associate to each of these three quantities the *physical dimensions* of length, mass and time, respectively. The concept of physical dimension was introduced by the physicist/mathematician Joseph Fourier in 1822. Physical quantities that are of the same kind (called *commensurable*) have the same dimension (length, time, mass) and can be directly compared to each other, even if they are originally expressed in differing units of measure (such as yards and meters). If physical quantities have different dimensions (such as length versus mass),

Table 0.1. Dimensions for standard units in the SI system.

Quantity	Unit	Abbreviation	Dimension
Length	Meter	m	$[L]$
Mass	Kilogram	kg	$[M]$
Time	Second	s	$[T]$
Temperature	Kelvin	K	$[\theta]$
Amount of substance	Mole	mol	$[N]$
Charge	Coulomb	C	$[Q]$
Luminous intensity	Candela	cd	$[I]$

they cannot be expressed in terms of similar units and cannot be compared in quantity (also called *incommensurable*). The dimensions of length, time and mass—denoted, respectively, by L , M , and T —are *fundamental* in the sense that the dimension of any mechanical quantity can be written as a product of powers of them. Thus, the dimension of an area is $[L^2]$, of a speed $[LT^{-1}]$, of an acceleration $[LT^{-2}]$, and of a force $[MLT^{-2}]$. For phenomena outside mechanics, more dimensions are required. For instance, in thermodynamics and bioenergetics the additional dimension is temperature, denoted by $[\theta]$. The standard unit is 1 degree on the Kelvin scale, denoted as K. In the same way, if we want to address electromagnetic phenomena we need to add the charge dimension $[Q]$ for electromagnetic quantities, etc. Table 0.1 shows the dimensions for each of the seven standard units of the International System of Units (SI, abbreviated from the French *Système International*).

Likewise, an extra dimension, the population $[N]$ is needed for biological entities. The corresponding base unit is a biological entity # rather than a mole. Examples of biological entities are individuals, species, or cells. Therefore, growth rates have dimension of population divided by time $[NT^{-1}]$, densities of individuals have dimension of population divided by area $[NL^{-2}]$, etc.

A requirement that is central to mathematical modelling, is that every equation we use must be dimensionally homogeneous or dimensionally consistent. It is quite logical that every term in the second law of Newton, force = mass \times acceleration, has total dimensions of force. In the same way, a population dynamic equation with the temporal variation of a population density on the left-hand side, must have total dimensions $[NT^{-1}]$. Therefore, equations will involve four quantities:

- i. Dimensional variables, e.g. yield (biomass density), of dimensions $[ML^{-2}]$ and measured in g m^{-2} .
- ii. Dimensional parameters, e.g. yield growth rates, of dimensions $[ML^{-2}T^{-1}]$ and measured $\text{g m}^{-2} \text{t}^{-1}$.

iii. Dimensionless variables, e.g. relative yields, defined as yields in polyculture divided by yields in monoculture.

iv. Dimensionless parameters.

D. **Constructing linear approximations.** Linearity is a concept of central importance in mathematical modelling. A model or system is said to be linear when its basic equations are such that the magnitude of its behavior or response produced is directly proportional to the excitation or input that drives it. Even though most systems in nature are more fully described by nonlinear models, their behavior can often be approximated by linearized models whose equations are, in general, easier to solve analytically than nonlinear equations. Additionally, a linear system obeys the *principle of superposition*: the response of that system to the sum of many individual inputs is obtained by adding or superposing the separate responses of the system to each individual input. Therefore, as engineers do all the time, we can use this principle to predict the response of a system to a complicated input by decomposing or breaking down that input into a set of simpler inputs that produce known system responses or behaviors. For example, we know that the relation between force F and relative extension x of a simple coiled spring, e.g. an automobile spring, is nonlinear, i.e. $F(x) = -k_1x + k_2x^2 + \dots$. However, civil engineers frequently use, as a first approximation, a simple linear elastic spring ($F(x) = -k_1x$) to model the static and dynamic behavior of a tall building, from wind loading to how the building would respond to an earthquake (Dym 2004). Indeed, this linear spring is an example of a *harmonic oscillator*, which, like the ideal gas, is another fruitful idealized system. Notice that if we write the logistic equation as $dN/dt = rN - (r/K)N^2$, its right-hand side term looks similar to the one of the nonlinear spring. So a Malthusian population would be like the ‘linear spring’ of population ecology (while the logistic equation would correspond to a more realistic nonlinear spring). As we will see in the next chapter, linearization is also crucial to study the stability of equilibria of dynamical population equations.

E. **Heuristics for problem-solving.** *Heuristic* as an adjective means ‘serving to discover’. A heuristic method, often called simply a heuristic, is any approach to problem-solving or self-discovery that employs a practical method, not guaranteed to be optimal, perfect, logical, or rational, but instead sufficient for reaching a quick estimation. Heuristics are ‘rules of thumb’, educated guesses, intuitive judgments or simply common sense. Here are a few other commonly used heuristics, from George Pólya’s book, *How to Solve It* (Pólya 2014):

- If you are having difficulty understanding a problem, try drawing a picture.
- If you can’t find a solution, try assuming that you have a solution and see what you can derive from that (‘working backward’).

- If you cannot solve the proposed problem try to solve first some related and more accessible problem or look for a similar problem you already solved or know the solution for.
- If the problem is abstract, try examining a concrete example.

Another example of useful heuristic methods in science and engineering are *back-of-the-envelope calculations*, i.e. rough calculations, typically scribbled on any available piece of paper (such as an envelope). It is more than a guess but less than an accurate calculation or mathematical proof. This estimation technique is also called *Fermi order estimate*, after physicist Enrico Fermi as he was known for his ability to make good approximate calculations with little or no actual data. Fermi estimations typically involve making justified guesses about quantities and their variance or lower and upper bounds. Depending on the difficulty of the problem, and the number of estimation sub-problems required, one can usually hope to be correct to within a factor of 2 or 3, and other times to within the correct order of magnitude (i.e. the closest power of 10).

Why bother with Fermi estimates, if they are likely to be off by a factor of 2 or even 10? Well, often, getting an estimate within a factor of 10 or 20 is enough to make a decision. So Fermi estimates can save you a lot of time. Actually, scientists often look for Fermi estimates of the answer to a problem before turning to more sophisticated methods to calculate a more accurate answer. While the estimate is almost certainly incorrect, it provides a useful and simple first check on the results. By contrast, precise calculations can be extremely complex and time consuming. The far larger number of factors and operations involved can obscure very significant errors, either in mathematical process or in the assumptions the modelling equations are based on. Without a reasonable benchmark to work from it is unclear if a result is acceptably precise. The Fermi estimation gives a quick, simple way to obtain this benchmark for what might reasonably be expected to be the answer, giving context to the results.

In addition, practicing Fermi estimations enables you to:

- i. Develop important modelling skills, like choosing relevant information, making reasonable estimates of size and quantity and combine bits of information, your estimates and rates appropriately.
- ii. Get you comfortable estimating, visualizing and working with unknown quantities or incomplete information.
- iii. Rapidly and approximately calculate an unfamiliar quantity.
- iv. Learn dimensional analysis and master approximation techniques.

One famous instance came during the first atomic bomb test in New Mexico on 16 July 1945. As the blast wave reached him, Fermi dropped bits of paper from a known height (his outstretched arm). Measuring the distance they were blown, gave him an approximation of wind speed which, together with knowing the distance from the point of detonation, provided an estimation of the energy of the blast. Fermi concluded that the blast must be greater than 10 kilotons of TNT. His guess was remarkably accurate for

having so little data: the true answer turned out to be 18.6 kilotons (Kelly 2004). Another illustrative example of a Fermi estimation is in box 0.2.

When getting started with Fermi practice, it is recommended estimating quantities that you can easily look up later, so that you can see how accurate your Fermi estimates tend to be. You might allow yourself to look up particular pieces of the problem—e.g. the world electric energy consumption, or the gross domestic product of a country—but not the final quantity you’re trying to estimate. In appendix I we develop some other examples of Fermi estimations.

Box 0.2. Fermi estimation: ‘How many piano tuners are there in Chicago?’

A problem Fermi posed to his students is ‘How many piano tuners are there in Chicago?’ A typical solution to this problem involves multiplying a series of estimates that yield the correct answer if the estimates are correct. For example, we might make the following assumptions:

1. The population of Chicago is approximately 3 000 000.
2. On average, there are two persons in each household in Chicago.
3. Roughly one household in twenty has a piano that is tuned regularly.
4. Pianos that are tuned regularly are tuned on average about once per year.
5. Each piano tuner works eight hours in a day, five days in a week, and 50 weeks in a year.
6. Each day a piano tuner tunes 3 pianos (it takes about two hours to tune a piano, plus travel time).

From these assumptions, we can compute that the number of piano tunings in a single year in Chicago is

$(3\,000\,000 \text{ persons in Chicago}) \div (2 \text{ persons/household}) \times (1 \text{ piano}/20 \text{ households}) \times (1 \text{ piano tuning per piano per year}) = 75\,000 \text{ piano tunings per year in Chicago.}$

We can similarly calculate that the average piano tuner performs

$(50 \text{ weeks/year}) \times (5 \text{ days/week}) \times (3 \text{ pianos per day}) = 750 \text{ piano tunings per year.}$

Dividing gives $(75\,000 \text{ piano tunings per year in Chicago}) \div (750 \text{ piano tunings per year per piano tuner}) = 100 \text{ piano tuners in Chicago.}$ Depending on the specific values you chose, you would probably get answers in the range 30–300. In 2009, the actual number of piano tuners in Chicago was about 290 (Wolfram alpha 2019).

A couple of lessons from the piano tuners example. First, suppose the precise answer tells you there are many thousands of piano tuners in Chicago. Then you know you need to find out why there is this such a divergence from the expected result. Maybe you missed something important. For example, Does Chicago have a number of music schools or other places with a disproportionately high ratio of pianos to people? Or perhaps, most piano tuners have other jobs and they only work part-time? etc. Second, although this Fermi calculation is not very accurate, it may be good enough for practical purposes. Imagine we want to start a store in Chicago that sells piano tuning equipment, and we calculate that we need 10 000 potential customers to stay in business. So we quickly conclude that we should consider a different business.

0.3 Community and population ecology modelling

0.3.1 Parallelism with physics and the debate of the 'biology-as-physics approach'

Much of the rationale of mathematical population theory is explicitly derived from physical science. In fact, its major proponents in the 1920s, Alfred Lotka and Vito Volterra, have been physicists and mathematicians. For instance, Lotka analyzed populations as chemical systems with exchanges of energy and matter governed by the second law of thermodynamics and treated organisms as engaged in competition for energy. According to Lotka, evolution would increase the flow of energy and matter through the system. Furthermore, it seems that the audience which Lotka hoped to reach consisted of physicists, and it was the ecologist C C Adams who pointed out to him the connection of his work with ecology (Kingsland 1981). Volterra, although he was interested in explaining the dynamics of fish populations in the Adriatic, used similar physical analogies to Lotka. The physicist V A Bailey in the 30s modelled organisms as gas molecules obeying the gas laws. Beginning in the 1940s, concepts like 'energy flow', 'trophic levels' and 'ecosystem' became popular in the leading ecology journals, and they indicated a view of nature shaped more by physics than by botany (Worster 1993).

This similarity with physics may be regarded as a virtue for those seeking to turn ecology into a 'hard' science but also as a vice for those who believe that ecology has specificities that make it intrinsically different from physics. From the very beginning mathematical population theory received criticism. Reviewing Lotka's book Charles Elton wrote a common complaint of many later ecologists: 'Like most mathematicians he takes the hopeful biologist to the edge of a pond, points out that a good swim will help his work, and then pushes him in and leaves him to drown.' A common criticism was that so many assumptions have been made in order to simplify the mathematical treatment that the entities considered can nowhere be found in the roster of living organisms (Stanley 1932), i.e. organisms do not behave like gas molecules, a common assumption of population theory (McIntosh 1985). Another concern, common to many ecologists working with natural populations was that the diversity and complexity of natural populations could not be expressed in simple mathematical formulations, i.e. the authors of mathematical population ecology generalized too much, simplified too much (Nice 1937).

This debate between those leaning towards the biology-as-physics approach and those leaning towards the natural history tradition has continued until the present. Those supporting the first viewpoint think that biology would be best served by emulating the physical sciences in selecting simple models that generate testable hypotheses with research questions structured as branching logical trees (Platt 1964). They consider that the fundamental reason of why there is little progress in ecology is that biologists do not follow the four rules of reasoning formulated by Newton (Murray 1992). The first rule is Occam's Razor or the principle of parsimony for the determination of the causes of natural phenomena. The second is the causality principle, i.e. the same cause always produces the same effect. The third corresponds to the generalization by induction in order to allow the extension of the range of applicability of a theory to all natural things. 'The process of

induction is the process of assuming the simplest law that can be made to harmonize with our experience' (Wittgenstein 1922). The fourth rule states that a hypothesis is only as good as the extent to which its predictions conform to fact. Murray (1992) goes on by developing a metaphor in terms of the motion of a cart pushed along the street. To understand this motion it is wise to begin with the simplest possible situation, and proceed gradually to the more complicated ones (Einstein and Infeld 1938). For example, if we give a cart a push along a level road it will move some distance before coming to rest. How can we increase this distance? There are various ways, like oiling the wheels or making the road smoother to reduce friction both in the wheels and between the wheels and the road. The more the friction is reduced, the longer the cart will travel before stopping. One significant step farther is to imagine this simplest idealized situation: the road is perfectly smooth, and wheels with no friction at all. Then there would be nothing to stop the cart, so that it would move at a constant speed in a straight line forever. But, we cannot actually perform this experiment since it is practically impossible to eliminate friction completely. It is a *gedankenexperiment* (from the German, a thought experiment), we can only think it. Therefore, 'the first law of motion or principle of inertia cannot be derived directly from experiment, but only by speculative thinking consistent with observation. The idealized experiment can never be actually performed, although leads to a profound understanding of real experiments' (Einstein and Infeld 1938). Moreover, it allowed Newton to predict from how far an apple would fall near the Earth's surface to the elliptical shape of planetary orbits. Murray (1992) regrets biologists do not approach problems in this way. Rather, 'biologists called in to study the physics of motion would be designing experiments to determine the role of those factors impeding the forward progress of the cart, such as the nature of the ball bearings, the viscosity of the lubricating oil, the shape of the cart, wind speed and direction, temperature and humidity, the road materials, and so on'. And he concludes: biologists shouldn't be 'distracted by the biological equivalents of friction, if we are interested in discovering the biological equivalents of inertia'.

Many ecologists reply that biologists should not think like physicists since biology has developed in a way that is distinctly different from the physical sciences (Aarsen 1997). For example, biology is largely context dependent; often deals of necessity with small sample sizes; and for a broad range of organisms, the most interesting phenomena occur over longer timescales than the feasible long-term studies (Anderson 2017). Naturalists have been fascinated by biological diversity and do not view organisms merely as models, or vehicles for theory, but rather as the thing itself that excites their admiration and their desire for knowledge, and understanding (Schmidley 2005). A common claim of ecologists that deplore the biology-as-physics approach is that because of the nature of biological science, progress in ecology has been hampered by an excessive focus on simple models, which fail to adequately capture important processes driving ecosystem dynamics. Rather, complex, system-specific models are often needed to provide the ability to predict the current and future behavior of systems. These models need to incorporate all relevant processes and then be tested, perhaps by simulation, to assess which processes most influence the predictions of the model (Evans 2013). It was also argued that biology needs

historical explanations which do not systematically follow the methods of Newtonian physics (Quenette and Gerard 1993). On both sides of the debate, there is a widespread belief that ecology is different from physics because (A) it lacks general laws, and (B) it is not a predictive and, therefore, not a ‘hard’ science (Turchin 2003).

Freeman Dyson summarized the reason of this ‘clash of cultures’ (1988). According to him, there are two kind of scientists, the unifiers and the diversifiers. The driving passion of unifiers is to find general principles which will explain everything. They are happy if they can leave the Universe looking a little simpler than they found it. Diversifiers are people whose passion is to explore details and are in love with the heterogeneity of nature. They are happy if they leave the Universe a little more complicated than they found it. Whereas physicists are unifiers, many ecologists are diversifiers.

0.3.2 Trade-offs and modelling strategies

The main trade-offs we face when modelling population dynamics as well as the different choices we have were analyzed by Richard Levins in an essay of 1966 that became a classic (Levins 1966). He stated that an optimally general, precise, and realistic model would require using a very large number of simultaneous partial differential equations involving a huge number of parameters to estimate from measurements. These equations would be analytically insoluble, and even if soluble (in the form of quotients of sums of products of parameters) would be uninterpretable, i.e. they would have no meaning for us. It is true that, from 1966 to today, we have augmented our computational abilities and power by simulations, including individual-based models, for addressing both applied and theoretical questions. However, as we already mentioned, these more realistic simulation models (a) can have hundreds of parameters which are impossible to measure in practice by limitations of time and resources, and (b) by including so many variables they sacrifice understandability for ecological realism. Therefore, there is an unavoidable trade-off for us between the generality, precision, and realism of the mathematical models if they are to be of any use to ecologists. Levins thus concludes the above trade-offs suggest three alternative strategies for building models:

Type I models sacrifice generality to precision and realism.

Type II models sacrifice realism to generality and precision.

Type III models sacrifice precision to generality and realism.

Type I models are large models preferred in applied fields, like Fisheries, or by *systems ecology* practitioners who advocate for a holistic approach of ecology that takes all the various components into account (Odum 1994, Watt 1968). The stylized type II models would correspond to the biology-as-physics approach we already reviewed. Type III models are favored when ecologists are concerned with qualitative rather than quantitative results.

This book is structured around practical applications and ours will be an instrumentalist viewpoint, regarding models primarily as operational tools to

make quantitative predictions. However we will attempt to maintain balance between the simplicity of the unifiers and the complexity of the diversifiers. In that sense, a general recipe that has worked very well in science is the so-called *principle of parsimony* aka *Occam's razor*: 'plurality should not be posited without necessity', meaning that all things being equal, the simpler theory is more likely to be correct. Simpler models are less prone to overfitting occurring when, in the effort to refine the model to the maximum, we end up adjusting the model to the imperfections of the data we have, worsening our predictive capacity and confusing signal with noise. Therefore, we will adopt a parsimonious approach for model-building. This implies that, since most of the applications we will consider require quantitative output, we will mainly deal with type II models (much simpler than type I models and more adequate than type III models for quantitative analysis).

Besides being parsimonious, our approach will also be pragmatic since we want to overcome the existing trade-off between efficiency and robustness. Something is efficient if it performs optimally under ideal circumstances, while something is robust if it performs pretty well under non-ideal circumstances. It turns out that robust (simple) models are often more efficient than efficient (complex) models are robust. When facing practical problems the conditions are in general far from ideal. There are model parameters that are unknown, let alone errors in the parameters. Moreover, the data are usually incomplete and/or contaminated and/or the statistics is not clearly sufficient, etc. Under these conditions complex efficient models can fail spectacularly because the assumptions they're based on don't hold. We will show how simple models can contribute to solve practical problems in fields like agriculture and environmental sciences. However, since no single model can meet all the requirements of generality, realism, precision, and manageability, for those specific applications for which type II models are unfit we will consider models that could be considered of type I or of type III.

Framing ecology as physics is probably neither possible nor desirable. Nevertheless, there are practices that have paid off. Firstly, borrowing ideas from other sciences, especially physics, and incorporating them into ecology. This is a tradition that has existed at least since the days of Lotka (1925). Secondly, embracing the spirit of physics, do not be afraid of relying on partial aspects and partial relations of things which we only understand partially. Amazingly, in spite of all our ignorance, we can make rather precise statements and predictions about certain aspects of phenomena. Thirdly, whether you are a diversifier or a unifier, it is undeniable that using idealized systems has been crucial in providing us with insight and understanding of several natural phenomena. Therefore, we will adopt these three practices throughout this book.

Definitions and tips for non mathematicians

Many people, including agronomists and ecologists, often dislike reading books full of equations. One reason is they are not used to mathematics and find it hard, but so was any language before we learned it. Comprehension and eventual proficiency in handling equations results from repeated encounter and practice. Another reason is that they don't know how to relate equations to anything real. This lack of clear meaning is a source of frustration to the reader. If that happens, you're doing it wrong. Math is nothing more than a concise language for describing relationships between objects. So if you are not a mathematician (and maybe even if you are) but someone who sees calculus as a tool, rather than an end in itself, the definitions and tips below hopefully will be useful to finding meaning in equations, to manipulating equations in order to facilitate understanding, and to making you feel comfortable reading/writing equations.

Basic definitions and notation

The first step is to specify the different entities coexisting in an equation. Most equations contain *variables*, denoted by letters in italic font signifying things that are known or unknown. That is, variables can be classified as dependent and independent. The values of **dependent** variables depend on the values of **independent** variables. The dependent variables represent the output or outcome whose variation is being studied. The independent variables represent inputs or causes. In other words, the dependent variable is a **function** of the independent variable. For example, the population density of a species N is a function of time t . And, using the notation first introduced by Leonhard Euler in 1734, this *functional dependence* is denoted explicitly as $N(t)$, i.e. by a symbol consisting generally of a single letter in italic font, followed by the independent variable between parentheses. The notation reads: ' N of t '.

Some widely used functions are represented by a symbol consisting of several letters (usually two or three, generally an abbreviation of their name). By convention, in this case, a roman type is used, such as 'sin' for the sine function, in contrast to italic font for single-letter symbols.

Besides variables there are quantities which are assumed to be constant or fixed and are called *parameters* (from the Greek word *para-*, meaning 'beside,' and *metron*, meaning 'measure'). To distinguish parameters from variables we will denote parameters using manuscript font. For example the per-capita growth rate and the carrying capacity of a population are denoted, respectively, by ' r ' and ' K '.

When parameters are present, they actually define a whole family of functions, one for every valid set of values of the parameters.

Historically, the concept of function was elaborated with the infinitesimal calculus at the end of the 17th century, i.e. the functions that were considered were differentiable (that is, they had a high degree of regularity). So besides algebraic equations, relations only involving variables (and parameters), we have differential equations. A **differential equation** is a mathematical equation that relates some function with its derivatives. The first equation that appears in this book, equation (0.1), is an example of a differential equation, that contains all the ingredients mentioned up to now:

- an independent variable (the time t),
- a dependent variable or a function of t (the population density $N(t)$),
- the derivative of this variable (dN/dt),
- and two parameters (r and K).

To emphasize that the population density N is a dependent function of t , equation (0.1) can be re-written as

$$dN/dt = rN(t)[1 - N(t)/K]$$

Finally, sets of variables or sets of parameters can be arranged into *arrays*, for example one-dimensional arrays or *vectors*, and two-dimensional arrays or *matrices*. We will denote vector and matrices as bold symbols. Unless we specify otherwise, we will use lowercase for vectors and uppercase for matrices. For example, if we have S species coexisting in a community with densities N_1, N_2, \dots, N_S , we can group them into a column vector denoted as the column of densities between square brackets:

$$\mathbf{n} = \begin{bmatrix} N_1 \\ N_2 \\ \vdots \\ N_S \end{bmatrix}.$$

Likewise, we will arrange the pairwise interaction coefficients a_{ij} between these species (which are parameters) into an $S \times S$ square matrix:

$$\mathbf{A} = \begin{pmatrix} a_{11} & \dots & a_{1S} \\ \vdots & \ddots & \vdots \\ a_{S1} & \dots & a_{SS} \end{pmatrix}.$$

Reading and writing equations

When reading an equation it becomes crucial to understand what the equation is telling you; you should try to ‘inhabit’ the situation this equation describes. Translating equations into words is a crucial step for understanding them. Then you should answer the following questions (Pólya 2014):

- What is the unknown?
- What are the data?
- How are the various items connected?
- How is the unknown linked to the data?

Let us suppose we have a differential equation for the growth of a certain population N living in a given area. Something of the form:

$$\frac{dN}{dt} = i(N(t); \{c_\alpha\}) - o(N(t); \{c_\beta\}),$$

where $i(N(t); \{c_\alpha\})$ and $o(N(t); \{c_\beta\})$ correspond, respectively, to ‘input’ and ‘output’ terms (corresponding for instance to birth and immigration rates and death and emigration rates) which are functions of the variable population $N(t)$ and of sets of parameters denoted by curly brackets as $\{c_\alpha\}$ and $\{c_\beta\}$, $\alpha = 1, 2, \dots, \beta = 1, 2, \dots$, (we use Greek indices for parameters).

A helpful recipe to qualitatively analyze this kind of differential equation is to break it down into chunks and visualize what the relationship between variables looks like. You can follow these steps:

1. Check that all terms in both sides of the equation have the same dimension. (In our case $[NT^{-1}]$).

2. Identify which of the quantities are constants and which are variables. (Variables: t , N ; constants: $\{c_\alpha\}$ and $\{c_\beta\}$).
3. As a first approximation, ignore the constants; you can just set them all to 1.
4. Break each term down and visualize what it would look like when plotted on an x - y graph. (Plot $i(N(t); \{1\})$ and $o(N(t); \{1\})$ versus $N(t)$).
5. Add or subtract the terms as the equation says, and visualize the resulting curve. ($i(N(t); \{1\}) - o(N(t); \{1\})$).
6. Go back and look at the constants to see how this curve scales.
7. If you are interested in the behavior of $N(t)$, remember that to solve the above differential equation it is necessary to integrate it. And, that the geometrical interpretation of the integral is the 'area under the curve' between the initial and final times t_i and t_f . (The area under $i(N(t); \{c_\alpha\}) - o(N(t); \{c_\beta\})$ varying t_i and t_f .)

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