Mathematical Ecology of Populations and Ecosystems

To
my grandparents, István and Erzsébet Szajkó,
my parents, Joseph and Mary Pastor,
my wife, Mary Dragich,
and my son, Andrew

Mathematical Ecology of Populations and Ecosystems

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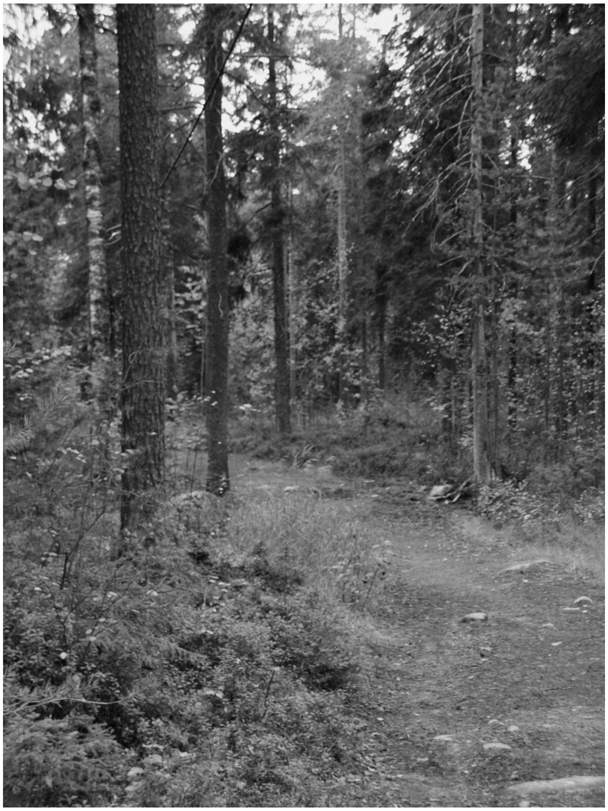
Prologue



Here is a photograph of a forest in northern Sweden. It is a pine forest near my office in the Department of Animal Ecology at the Swedish University of Agricultural Sciences in Umeå, Sweden, where I wrote much of this book while on sabbatical during 2005–2006. I would often take a break from writing about mathematical ecology and walk through this forest to refresh my contact with the natural world, as a stimulating contrast with the abstract world of this book.

The forest is used to teach forestry students about the measurement and management of such lands. Occasionally, parts are thinned, and the evidence of repeated thinnings and other management activities are readily apparent. Clearly, the large older trees were spared thinning to provide a seed source for the next cohort of pines.

None of the trees are "original old growth" but, according to my colleagues, there has always been a forest here, perhaps since the Vikings. There is a Viking burial ground on one of the knolls, looking out over what must have once been a bay of the Baltic Sea when the land was lower – it has risen by almost three meters since Linneaus's time because of rebound from the glaciers. Obviously, the forest had seen what mathematical ecologists dryly refer to as "perturbations" but equally obviously it had recovered and persisted in some recognizable form.

Questions about the persistence of the forest and recovery from repeated perturbations over the centuries suggested themselves. How is the current number of live trees of different ages related to the numbers of seedlings established decades and centuries ago? How do the decay of the annual cohorts of dead needles and other debris of the forest floor replenish and recycle nutrients taken up by the plants from the soil? What about the animals which wander through here, such as the moose who left pellets (more debris!) behind and browsed the pines? How do they affect the dynamics of the plant populations and the cycling of nutrients?

For that matter, what do we mean by all these abstract terms: *perturbation, persistence, dynamics, decay, growth, populations, cycles*? I could not point to any of these concepts like I could point to a pine tree or a moose or the soil, but I could not think about the forest without using them. How can we think clearly about how these abstract terms relate to the plants, animals, and soil?

That is what this book is all about.

Preface

This is an introductory textbook on mathematical ecology bridging the subdisciplines of population ecology and ecosystem ecology. The expected reader is you: a beginning graduate student, advanced undergraduate student, or someone who thinks of themselves as a student all their lives, with a working knowledge of basic calculus and basic ecology. While this is intended as a stand-alone text, the level is such that once you have read through it, you will be able to read more advanced texts and monographs such as Ågren and Bosatta (1998) and Kot (2001) with greater depth. While there are other very good introductory texts in mathematical ecology (e.g., Edelstein-Keshet 1988 [reissued but not revised 2005], Yodzis 1989 [now out of print], Gotelli 1995, Roughgarden 1997, Case 2000, and Kot 2001 are among the most widely used), none bridge the gap between population ecology and ecosystem ecology.

Ecological problems are complicated in ways that our language has not evolved to handle. Mathematics provides a more precise way than the spoken word of thinking and talking about the rates of change, nonlinearities, and feedbacks characteristic of populations and ecosystems. Even Edward Abbey, one of the sharpest thinkers who never solved an equation, once said: "Language makes a mighty loose net with which to go fishing for simple facts, when facts are infinite."* It is my hope that mathematics can help us tighten that net a bit, allowing us to catch a few facts that may have otherwise slipped through. At the very least, mathematics has precise tools for handling the infinite.

For the past 12 years, I have given courses in mathematical ecology and ecosystems ecology during alternate fall semesters. Often, the major topics of our discussions in each of these courses concern the relationships between population dynamics, species, and ecosystem processes such as productivity, nutrient cycling rates, and input–output budgets. These are leading research questions in ecology and have been major interests of mine for the past 25 years.

These are intellectually challenging questions. It is often easy to make a "plausible" argument that some hypothesized relationship between populations, species, and ecosystems must be true, only to find on more rigorous examination that it is not necessarily true, true only under certain restrictions, or simply not true at all. Framing the plausibility argument in mathematical terms and using the rules of mathematics to examine its logical structure is often the best way to uncover the sense in which it might be true. In fact, the mathematical examination of these arguments often uncovers hidden assumptions; these in turn suggests new experiments to determine

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**Desert Solitaire*, Author's Introduction.

whether they hold in the “real” world or new theoretical investigations to determine what happens when such hidden assumptions are relaxed in different ways.

Questions about the relations between populations and ecosystems are also challenging because the cultures of population ecologists and ecosystem ecologists differ so much. In part, these differences between population and ecosystem ecologists arise in their graduate training. Population ecologists are often trained to analyze the dynamics of populations’ and species’ interactions using analytical mathematical methods which allow them to calculate algebraic expressions for equilibria and their stability.

Because population models focus on the dynamics of collections of live individuals, death is often treated as an export from the system. By contrast, the ecosystem ecologist considers dead material to still be in the system, simply be detached from the live populations and subject to different rules. Eventually, through microbial decay, the dead material is transferred to the resource pool which is then taken up by plants.

Because of the large number of compartments they generally consider and measure, ecosystem ecologists have not usually used analytical mathematical methods. Instead, large and complicated computer simulation models have traditionally been their method of choice in analyzing and synthesizing ecosystem data. Although these simulation models may make quite accurate predictions for specific situations, they are often almost as complex as the system being studied. Therefore, it is sometimes difficult to understand why their predictions are as they are, leading to an interesting paradox in which accurate prediction may not be the same as general understanding. Furthermore, through their investigations into the origin of chaos in single-species models, population ecologists have taught us that we can have understanding without predictability, a conclusion accepted with reluctance by some (but not all) ecosystem ecologists.

Therefore, ecosystem ecologists and population ecologists have been trained to speak different languages. Population ecologists have traditionally ignored nutrient feedbacks to populations through litter and its decay, whereas ecosystem ecologists traditionally dismiss analytical approaches in favor of simulation models. This lack of a common language or approach amongst population and ecosystem ecologists may impede our ability to address important practical problems. It is no wonder that many ecologists find the relationship between populations, species, and ecosystem properties extremely difficult to understand: each group has part of the answer but they find it difficult to speak to each other and frame questions in a common language.

In spite of the traditional dichotomy of using either simple analytical models of a few species or complicated simulation models of whole ecosystems, it is possible to couple interactions between species and the flux of an inorganic resource by simplifying the ecosystem to only a few compartments so that we can use analytical mathematical techniques to gain understanding about system behavior, especially how ecosystem properties emerge from an interaction between populations and the flux of inorganic resources. In this book, the same mathematical techniques will be used as a common thread to help unify population and ecosystem ecology.

These mathematical techniques are also essential for exploring how changes in controlling factors across thresholds often cause rapid changes between different states of an ecological system, which are sometimes called “regime shifts” (Scheffer et al. 2001). These rapid changes between different states are often accompanied by the appearance of new behaviors, such as limit cycles, extinction of species, or changes in top-down and bottom-up controls. Some examples of current interest are the possibility of rapid change in communities and ecosystems with slowly rising temperatures once some critical value of temperature is exceeded, the rapid changes in communities once critical thresholds of nutrient inputs are exceeded, and the rapid changes and extinctions in populations once critical values of harvesting rates are exceeded.

Different states of populations, communities, or ecosystems often correspond to different equilibrium solutions of a model. In turn, these solutions are often separated by a critical value of a parameter or a function of several parameters. Rapid changes in the nature and stability of solutions of equations as critical parameter values are crossed are known mathematically as bifurcations. Bifurcations between different equilibrial solutions appear suspiciously like the rapid changes in nature as controlling factors cross critical thresholds. Examples of bifurcations which we will meet in this book include: (i) saddle-node bifurcations, separating persistence from extinction of a species once a critical harvesting rate is exceeded; (ii) transcritical bifurcations, leading to shifts between two different communities once critical inputs of a limiting nutrient are exceeded; (iii) Hopf bifurcations, leading to stable limit cycles once critical values of carrying capacity are exceeded, otherwise known as the "paradox of enrichment" (Rosenzweig 1971); and (iv) Turing bifurcations, leading to the appearance of spatial patterns once critical values of diffusion rates of populations are exceeded. We shall explore examples of these and other bifurcations and their ecological implications throughout this book.

Bifurcation theory is therefore a powerful mathematical technique to help us understand sudden and interesting changes in the behaviors of ecological systems as some parameter or combination of parameters pass some critical value. Bifurcation theory draws heavily on the theory of eigenvalues and Jacobians and, insofar as bifurcation theory seems a promising mathematical approach to understand rapid changes in nature, one must have some grounding in eigenvalue analyses – indeed one must be able to frame questions and construct systems of equations with the use of these techniques in mind.

The purpose of this textbook is therefore to help you develop your thinking to bridge population and ecosystem problems using the mathematical tools of eigenvalue analysis and bifurcation theory as common threads. To successfully do this, you need a working understanding of calculus, especially the concept of limits; linear algebra, especially matrix operations required to analyze populations with age or stage structure or multiple species models; and differential and difference equations, especially the analysis of model stability by means of eigenvalues and eigenvectors. While all ecology graduate students have had training in calculus, it may have been a while since they used it; a few have had experience of linear and matrix algebra; very few have been exposed to eigenvalues and eigenvectors. Accordingly, Chapter 2 is a "mathematical toolbox" laying out the tools to be used in this book and providing some exercises for you to practice using these tools without much reference to any biology at first. This lays the foundations for a mathematical vocabulary for the book. Many of these exercises will appear later in more ecological form.

I try whenever possible to derive the standard equations of mathematical ecology from some more fundamental "first principles" of birth and death, probability of two individuals meeting, and conservation of matter. Typically, these derivations are motivated by uncovering or relaxing some “hidden assumption” to address an unrealistic behavior in some prior, simpler model. In addition, intermediate steps in these derivations often shed some light on what the final equation means: a lack of understanding of where the final equation came from can lead to misleading analogies and conclusions. In addition, many derivations and proofs often depend on some trick or turn of an argument in an intermediate step, and learning these tricks or turns of an argument both enriches the ecological and mathematical underpinnings of a model and often proves useful in derivations of other models.

Every chapter begins with an introduction to a new problem, usually motivated by some problems unearthed in the previous chapter or chapters. These problems are usually an unrealistic biological behavior of the previous, simpler models. We then try to uncover the assumptions that may be responsible for the problem behaviors. The chapters usually proceed by mathematically relaxing these assumptions in different ways and analyzing how this improves the model’s behavior (or not).

Every chapter ends with two sections, the first entitled: “Summary: what have we learned?” which, besides the obvious summarizing of the main points, also brings the discussion back to a wider plane. The final concluding section of each chapter (except the Introduction and Mathematical Toolbox) is a section called “Open questions and loose ends.” Here, I point you in some directions and towards some papers or texts about problems that lack of space does not allow me to go into. I also suggest some open questions for you to consider. Some of these are small questions for you to explore, perhaps as additional homework problems, but they may lead to larger questions. Some of these are large open questions (such as control of chaos in population models) which are at the current edge of research. I hope that these may help you choose a thesis problem (if you are a graduate student) or research problem (if you are already establishing your own program). I would welcome learning from you any findings along these lines or about any papers that have addressed them that I may not know about (and for which I apologize to the authors).

By introducing you to the mathematical tools required to analyze models of populations, communities, and ecosystems, I hope to help you develop more rigorous ways of thinking about the interaction of population and ecosystem dynamics. It is my further hope that these ways of thinking will spawn more creative approaches to these problems.

I have learned much by writing this book: oftentimes, connections have emerged that neither I nor (I believe) anyone else has seen before. If you are already a professional mathematical ecologist or mathematician, I hope that these connections will surprise you as much as they did me. If you are a student, I hope you will learn as much or more than I did and, in turn, teach me through the papers you will write.

Acknowledgments

This book grows out of a graduate course in Mathematical Ecology which I have taught for the past twelve years, in both the Biology Department at the University of Minnesota Duluth and in the Department of Animal Ecology at the Swedish University of Agricultural Sciences in Umeå, Sweden. Teaching this course is always one of the high points of my year. I must therefore first thank all the students who have taken this course over these years. They have helped me clarify and simplify various explanations of mathematical ecology in my lectures and I hope some of their help has worked its way into this book. During 2006, students in both Sweden and Minnesota read through drafts of these chapters during class and I thank them in particular for catching typographical and other errors, for pointing out where more explanation is required, and for suggesting simplifications of some explanations and derivations.

Most of these chapters were written during 2005–2006, while I was on sabbatical leave in Umeå. Financial support for this leave came from the College of Science and Engineering at the University of Minnesota Duluth, the Department of Animal Ecology at the Swedish University of Agricultural Sciences, and the Kempe Foundation, and I thank them all for their generosity.

I am especially grateful to my colleague Kjell Danell of the Department of Animal Ecology at the Swedish University of Agricultural Sciences for helping to arrange my sabbatical visit and the grant from the Kempe Foundation. Through Kjell's help, I was provided with a quiet office with a view of a forest where I could write and think about mathematics and ecology, and my wife Mary and I were provided with an excellent apartment from which we could ski off into the forest right from our door. Kjell, his family Kerstin Huss-Danell and Markus Danell, and my colleagues at the Department of Animal Ecology provided superb hospitality in the best Swedish tradition, and to all of them I say: *Tack så mycket*!

Special mention must be made of my colleagues Bruce Peckham and Harlan Stech of the Department of Mathematics and Statistics at the University of Minnesota Duluth and Yossi Cohen of the Department of Fisheries and Wildlife at the University of Minnesota St. Paul. I have collaborated with them over the years on topics both mathematical and ecological. I have learned much from each of them, and I hope the things I have learned from them show in this book. Bruce Peckham helped clarify my thinking on several of the topics and Harlan Stech read through the entire book and made many helpful comments and suggestions and corrected some errors. Tom Andersen of the University of Oslo also read many of these chapters and offered helpful comments and encouraging words. I thank Harlan, Bruce, and Tom for their help. Any remaining errors remain my own and I ask that if you spot one, please notify me of it.

Parts of several of these chapters were presented at the weekly seminar of the Department of Mathematics and Statistics at the University of Minnesota Duluth. I thank the faculty and students at these seminars for their insights and helpful comments.

Alan Crowden guided the proposal for this book through the review process and presented it to Blackwell Publishing. Without his encouragement to begin writing and his help and assistance with the publishing world, this book may not have been begun at all. Ward Cooper of Blackwell also provided publishing assistance, and I appreciate his efforts and those of his staff, especially Rosie Hayden, Pat Croucher, and Delia Sandford, as well.

Rachel MaKarrall scanned and lettered the figures; their clarity owes much to her artistic eye.

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But above all, I must thank Mary Dragich, my wife, who has always given me support and encouragement, especially during the writing of this book, and who has listened patiently and helpfully to my long explanations of ecological and mathematical problems over the dinner table.

John Pastor

Part 1

Preliminaries

1 What is mathematical ecology and why should we do it?

Let's begin by looking again at the photograph in the Prologue and imagine yourself walking through this forest. What do you see? Jot down a few things (this is your first exercise). They need not be profound – in fact, it is best not to try to make them profound. After all, Darwin constructed the most profound theory in biology by asking ordinary questions about barnacles, birds, and tortoises, amongst many other things.

Perhaps you see big trees and little trees and think that big trees are older than little trees. You also might notice that there are more little trees than big trees, and so not every little tree grows up to be a big tree – most die young. But the little trees must come from somewhere, namely seeds produced and shed by the bigger trees. These are the core ideas of population ecology.

Or perhaps you might notice that there are some dead needles and leaves on the ground and some standing dead trees which will eventually fall to the soil, the result of the deaths of those young trees and plant parts. You also note that the live trees have roots in the soil formed partly from those dead leaves and logs and surmise that the trees obtain some nutrients from them. These are the core ideas of ecosystem ecology.

These two views of the forest look very different, but they both contain biological objects that interact with each other through hypothesized processes. When we model a biological object such as a population, we begin by offering an analogy between it and a mathematical object. Mathematically we will term these analogs *state variables*. The processes usually represent a transfer of something (live individuals, seeds, nutrients) from one biological object to another. Processes will be modeled by mathematical *operations*, such as addition, multiplication, subtraction, or powers. One or more operations and the objects they operate on will be encapsulated into an *equation*, specifically an equation which relates how one state variable partly determines the state of itself and perhaps another at some point in the future. These equations will contain, besides mathematical operations and state variables, some *parameters*, whose values remain fixed while the state variables change. Each state variable will be described by one equation. The time-dependent behavior of the state variables and the magnitudes of the state variables at equilibrium are called the *time-varying* and *equilibrium solutions* of the model, respectively. We then use the rigor of mathematics to work through the logic of our thinking to gain some insight into the biological objects and processes.

Therefore, mathematical ecology does not deal directly with natural objects. Instead, it deals with the mathematical objects and operations we offer as analogs of nature and natural processes. These mathematical models do not contain all information about nature that we may know, but only what we think are the most pertinent for the problem at hand. In mathematical modeling, we have abstracted nature into simpler form so that we have some chance of understanding it. Mathematical ecology helps us understand the logic of our thinking about nature to help us avoid making plausible arguments that may not be true or only true under certain restrictions. It helps us avoid wishful thinking about how we would like nature to be in favor of rigorous thinking about how nature might actually work.

What equations should we choose to use to model the dynamical relations amongst the state variables? Of course, there are an infinite number of equations we can choose, but we prefer equations that are simple to understand, are derived from simple "first principles," have parameters and operations that correspond to some real biological process and are therefore potentially measurable, and produce surprising results that lead to new observations. These four properties of these equations are components of mathematical beauty. They are important criteria by which we judge the utility of an equation or model because they help clarify our thinking. They often force our thinking into new directions.

This is all well and good, but why should we play this game? Why not just state hypotheses as clearly as we can and do the experiments to test them? One reason is that we are often not sure of either the internal logic of our ideas and hypotheses or their consequences. For example, state variables often affect and are affected by another state variable. This mutual interaction between state variables is termed *feedback*. Feedbacks are common in ecological systems – in fact, they are characteristic of all interesting ecological systems. Systems with internal feedbacks are almost impossible to completely understand in an intuitive way. Without a clear understanding of how the feedback works, it is also very difficult to do an experiment which manipulates the feedback. It is easy to understand a chain of events where X influences Y and Y influences Z, but what if Z also affects X? What then happens to Y? By writing a system of equations, one for each of the state variables and using the rules of mathematics, we can examine the logical structure of feedbacks and their consequences.

Examining the properties of a system of equations allows us to pose further questions and determine how their answers might follow logically from their structure and properties. For example, the population ecologist might wonder how the proportion of individuals of a given age class changes over time, whether the proportional distribution over all age classes ever settles down to a stable distribution, and what that distribution is. The ecosystem ecologist might note that the world surrounding the forest contributes material to it (in rainwater, for example) and the forest contributes material back to the surrounding world (in the water leaching out of the soil). He or she might wonder what difference it makes how and where the material enters and leaves the ecosystem. Both ecologists might also wonder what happens if we harvest some of a population or ecosystem: does the population or ecosystem recover to its earlier state? How will it recover? Can we harvest so much that the population or ecosystem will never recover? And what exactly is meant by "recover"?

Examining these equations also allows us to uncover hidden assumptions about our ideas and ask what happens when we relax those assumptions. For example, we have assumed that each equation in our model applies equally well to every species that is reasonably similar to the one we are studying. Well, do they? What difference does it make if they aren't similar to each other? How different do things have to be to make a difference in the system's behavior? How do different species affect each other? How does including additional tropic levels or other components affect the behavior of the models?

Finally, mathematical modeling allows us to rigorously connect the two different views of population and ecosystem ecologists. For example, the ecosystem ecologist notices that the forest floor contains layers corresponding to different ages of leaf litter from many years in the past. One year's leaf litter is transferred into older decay classes with each passing year. If the leaves are decomposing, something is being lost from each age class of litter. The ecosystem ecologist pauses and notices that these ideas bear a great deal of resemblance to the age class model of the population ecologist. Can we take the equations for the dynamics of the live populations and extend them belowground into the leaf litter? This shows the real power of mathematical abstraction. Once you recognize a structural correspondence between two different systems, then the same equations and same mathematical techniques could apply to both. If it turns out that this is the case, then the ecologist has discovered some underlying principle of organization in nature, a principle which he or she did not expect when first observing a particular forest (or prairie or lake) and jotting down what first caught his or her eye.

And that is what mathematical ecology is about.

The nature of theoretical problems and their relation to experiment

In the process of abstracting nature into a mathematical model, we run into a number of theoretical problems. These are distinct from the sorts of problems experimenters have to deal with. Most ecologists are familiar with experimental questions such as measuring the response of an individual, population, or ecosystem to manipulations, or determining the proper number of samples required to detect a difference between mean values of measurements. In contrast to these experimental problems, mathematical models of ecological systems address a variety of theoretical questions regarding the logical consistency and consequences of ideas (Caswell 1988). While measuring devices are the tools of the experimental ecologist, equations are the tools of the mathematical ecologist. Equations are used to examine the following theoretical problems (Caswell 1988):

Exploring the possible ranges of behavior of a natural system. In order to understand why a particular natural system behaves as it does, it is useful to discover the range of behaviors that is possible for the system to exhibit. The behavior of a particular natural system is simply one realization of a family of possible behaviors. Models delimit the theoretical range of behaviors that follow from simple assumptions (mass balance, birth and death, etc). Experiments delimit the actual range of behaviors realized in nature, or the realized subset of the set of possible behaviors. Sometimes, by delimiting the full range of possible behaviors, models indicate new areas where experiments need to be performed that no one had previously realized, such as in extreme environments.

Exploring the logical consistency of ideas with a set of common axioms. Upon detailed examination, we often find that many plausible ideas are not consistent with some simple assumptions we must make about nature. Mathematical models allow one to logically connect an idea or a hypothesis with some axiom about nature. Reiners (1986), for example, offers several axioms upon which ecosystem ecology might be based. Often, such theoretical exercises show that our hypotheses may be simply wishful thinking. It is often said that beautiful theories are killed by ugly facts, but it is equally true that a beautiful hypothesis can be killed by being inconsistent with some more fundamental axiom of how nature works.

Exploring the connections between different ideas or experimental results by deriving them from a common set of assumptions. Oftentimes in ecology, different camps take up one side of an argument or another, resulting in "either–or" false dichotomies. Ecology is rife with these "either–or" arguments: either competition is important, or it is not; food webs are controlled either by top-down forces or by bottom-up forces; etc. The key word in all these arguments that creates the problem is the conjunction "or." Usually, there is ample experimental evidence for both sides of the argument and so it is impossible for experimental ecology to clearly decide on one side or the other. At such times, it is useful to ask: when does one thing happen and when does the other thing happen? It may well be that there is some common underlying model that produces both sides of the argument at different time scales, for different parameter values, or for different initial conditions. Finding such a model and showing the conditions that lead to one system behavior or the other is a very important theoretical problem.

Evaluating the robustness of different approaches. An experimental result may be consistent with a particular way of simplifying nature, but how robust are our conclusions to uncertainties in the details of the structure of the natural system? Do we need to represent every age class in a population model, or can we aggregate age classes? Do we need to measure the population dynamics of every microbe to predict the fate of a nutrient during decomposition, or can we aggregate microbes into "microbial biomass"? How precisely do we need to measure minute-by-minute changes in photosynthesis to predict tree growth several years into the future? Can we even make predictions far into the future or is the natural system inherently sensitive to very small differences in initial conditions? How fast does the accuracy of our predictions decay with time?

Finding the simplest model capable of generating an observed pattern in nature. Such a model would suggest the simplest set of experimental protocols required to experimentally characterize a natural system. It could also pinpoint exactly which processes, interactions, or parameter values are responsible for observed behavior. Whether such a model is true to reality remains to be tested by experiment.

Predicting critical (falsifiable) consequences of verbal or conceptual theories. Prediction is considered to be a precise numerical value for something that can be measured, and so it often is. But prediction can also be qualitative, such as the shape of a response curve. The shape of a response can distinguish one mechanism from another. For example, different theories of nutrient uptake may yield response curves with different shapes, suggesting that experimenters test hypotheses about mechanisms of nutrient uptake by distinguishing between uptake curves of different shapes (O'Neill et al. 1989). Prediction can also be as simple (and as powerful) as postulating the existence of a particular behavior, such as the existence of limit cycles or other forms of complex population dynamics (Turchin 2003) or a decline in nutrient use efficiency at low levels of nutrient availability (Pastor and Bridgham 1999). At an early stage of experimental investigation, precise prediction of the magnitude of response may be unnecessary and being overly concerned with precise prediction or "validation" may even obscure broader issues of which mechanism is actually operating. We will have more to say about prediction and its role in model evaluation shortly.

Errors of perception of mathematical models

There are several common errors of perception of mathematical models (Caswell 1988):

The only thing to do with a theory is to test its predictions with experiments. This has to be done, but this ignores the role that rigorous mathematics can play in helping us work out the logic of our ideas before we even begin to design or execute an experiment. Much effort has been spent by myself and others on collecting data that in the end bears no relationship to the hypothesis being tested. Sometimes, this is fine because it helps us put the experiment in a larger context. It also allows us to serendipitously make connections between processes that might otherwise not have been made. But, since it also takes time and effort to collect data which may turn out to be unnecessary, we may also miss collecting data that is essential. Every modeler has had the experience of an experimentalist friend showing up with a boatload of hard-won data and asking for help to construct a model, only to have to say upon examining the data that much of it is not relevant to the experimenter's own statement of their hypothesis or that some key data required to construct a model of the hypothesis was not collected. In the latter case, the modeler then says that we will have to assume certain values. The conversation then usually deteriorates. The point here is that we should know which data are essential to the test of a hypothesis and which are ancillary, albeit desirable for other reasons. When we translate a hypothesis into a mathematical model, the attempt to precisely define each parameter and variable in terms of an analogous biological process or object helps clarify the essential data we need to collect.

Theories that are refuted by experiment should be abandoned. They can also be modified. Perhaps the experiment is in error or itself has ignored an important process. Data themselves may be in error, perhaps because of an unrecognized sampling bias. We should be as skeptical of data as we are of theories. As Sir Arthur Eddington once said, "Do not believe an experiment unless it is confirmed by theory."

Modelers make assumptions, which are evil, and the worst assumption is that the system is simple. Like many models, every experiment is based on a set of hidden assumptions. For example, the statistical analysis of experimental data makes the assumption that the natural system can be explained by linear models even though the system being manipulated is clearly non-linear. Models at least make assumptions explicit and also explicitly show the logical consequences of those assumptions, while the assumptions of an experiment often go unrecognized. In addition, uncovering and relaxing hidden assumptions of a model is a powerful theoretical tool to advance our understanding, one that we shall use throughout this book.

The simplicity of many models often brings out strong reactions from many experimenters, who are often upset when a process that they have spent their career studying and which is clearly operating in nature is not included in a model. The model is then often said to "oversimplify" nature and should therefore not be trusted. This is a healthy skepticism but it could also be directed against the experiments themselves. For example, most experiments (including my own) manipulate only two or three factors and measure the response of a single state variable, while many models consider two or more state variables and more than two or three parameters. Therefore, many experiments often simplify the natural system of interest even more than models.

What do we expect of mathematical models?

Some ecologists (e.g., Peters 1991) have argued that ecologists should concentrate solely on making quantitative predictions from models. Such a recommendation has much to recommend it, not least of which is that it will facilitate the interface between models and experiments by demonstrating very specific and falsifiable consequences of hypotheses.

Prediction is a good thing when you can get it, but we cannot always get it. Prediction is often regarded as the highest test of a scientific theory – indeed, the ability to quantitatively predict something is often taken as the hallmark of a "hard" science. The epitomes of the hard, predictive sciences are, of course, physics and astronomy. However, predictive capability or the lack thereof may be ". . . an essential difference between the biological as against the physical sciences, rather than a *sine qua non* of scientific synthesis as such" (Holton 1978). There are several reasons why quantitative predictions are easier in physics than in ecology.

First, the entities that much of physics deals with, such as electrons and other particles, are identical in all pertinent respects, whereas the basic entities of ecology, namely individual organisms, vary quite a bit in their pertinent properties (and necessarily so, as Darwin taught us). Second, physical relationships are often linear. A linear model is one in which the size of something changes in proportion to itself or the size of something else (we will explore linearity in more rigor in Chapter 2). Linear models, as we shall see, exhibit simple behaviors. After all, much of the physics of the everyday world is derived from $F = ma$, which is a linear model. Ecological processes are inherently nonlinear (the size of something changes out of proportion to itself or the size of something else), and we shall see that nonlinear models exhibit very complex and surprising behaviors, stabilities, and instabilities (or bifurcations) with small changes in parameters near critical values. Predicting the behaviors of nonlinear systems using nonlinear models is a daunting task.

The statistical design and analysis of experiments is based on linear models of expected values of variables. We do not know how to design and analyze a nonlinear experiment. Instead, we experimentally break the system into linear chunks within which predictions are robust and easily falsifiable or verifiable. Models are useful in reassembling those chunks and synthesizing results of many experiments. Finally, it is well to note that in the branches of physics that deal with nonlinear processes, such as turbulence in fluid dynamics, prediction is every bit as difficult as in ecology.

Nonetheless, the physicist's ability to simplify a problem to its essentials so that first and foremost the tools of mathematical rigor and logic can be brought to bear on the problem is a useful lesson for ecologists. When certain reasonable and almost axiomatic constraints – such as the conservation laws – are imposed on our equations, the number of solutions is minimized. The constraints on the model also tend to sharpen the differences between the solutions. This style of research produces insights of remarkable clarity. The solutions could represent different communities, for example, and discovering how the parameters and variables of a model lead to different solutions can give great insight into what controls the diversity of life without needing the model to make quantitative predictions. Predictive ability is sought only after a general mathematical analysis of the situation and the possible controlling factors. It is this style of thinking – the homing in on the essentials of a problem and its translation into mathematics – that I think ecologists can borrow from physicists, not the ability to make extremely precise predictions of properties, which may be something peculiar to much of physics.

Not being able to make a prediction should not prevent us from grappling with ideas. I don't think Peters is saying that we should abandon an approach when it cannot give a quantitative prediction. Rather, I believe he is saying that we should always have prediction in mind as a goal to work towards and in this I agree with him. But too much of an emphasis on quantitative prediction can blind us to the often more important and interesting qualitative behaviors of a model, such as when limit cycles or spatial patterns suddenly appear.

Another problem with concentrating solely or even mainly on prediction is that it can be quite easy to get very good predictions without gaining any understanding of nature. For example, one can obtain a very long time series of data (weather data or long-term population data, for example) and fit a model to it that is essentially a sum of sine functions of different amplitudes, frequencies, and phases. In principle, one can eventually get a model that goes through every point and will probably make accurate predictions into the future, for a while at least. But why do the sine waves have different frequencies, amplitudes, and phases, or for that matter why should sine waves describe the data at all? What are the sine waves trying to tell us about how nature works? Again, building models solely by fitting sine waves to data is a bit of a caricature and nobody is really suggesting that this and only this is what we should be doing, but it does serve to point out the problems of an overemphasis on predictability as the goal of modeling.

Finally, there is the class of models (used frequently in ecosystem ecology) known as simulation models, which are very complicated computer codes that try to depict processes explicitly and often give very good predictions. These are valuable tools and have certainly helped advance ecology and should not be abandoned. But, in my own experience with simulation models whose development I have been a part of, these models are often nearly as complicated as the system they are attempting to depict. Therefore, while it is wonderful to see trajectories of ecosystem development emerging on your computer screen when these models are run, why those trajectories are developing the way they are can be rather mysterious. There is a temptation (which I myself have felt) for simulation modelers, when asked: “How do you think such-and-such system works?,” to hand the questioner a disk containing computer code and say “Just run this and you will see precisely what I think.” Needless to say, the questioner does not always feel enlightened by this answer. Precise prediction of a wide variety of natural phenomena using a model that incorporates many conceivable ecological processes operating over a wide range of spatial and temporal response scales is impressive output, but we want something other than this from a model or theory.

What we require first and foremost of a model or theory is not prediction or reproduction of experimental results, but that it deepens and extends our understanding of nature, or at least our understanding of how we think about nature. By understanding I mean that the model transparently shows how various complicated phenomena, such as population cycles or sharp boundaries between ecosystems, emerge naturally from the basic ecological processes of birth, death, immigration and emigration, uptake of nutrients and water through roots or uptake of carbon dioxide and energy through leaves, and consumption of one species by another. How much of the complicated phenomena we see around us can be explained through these few processes? Transparency of assumptions and model structure, how the model relates to basic biological processes, and emergence of surprising results that bear some resemblance to complicated behaviors of natural systems are the main things we expect from models.

How mathematics helps us better understand nature is actually not well understood. Eugene Wigner called this "the unreasonable effectiveness of mathematics in the natural sciences" (Wigner 1960). Wigner asked why should some of the most abstract mathematical ideas of which we have no direct sensory experience have such an uncanny ability to describe the natural world and deepen our understanding of it? Neither Wigner nor anyone else has been able to answer that, but anyone who has experienced this consilience between mathematics and the natural world knows that it is a beautiful gift (Wilson 1998).

The mathematical models we will explore in this book have had a long history of deepening our understanding of the ecological world. Their simplicity makes some of the consequences of basic biological processes transparent but at the same time they exhibit behaviors that surprise us. As we think more deeply about why we are surprised by a model's behavior and why it conforms to similar behaviors of real populations and ecosystems, we gain a deeper understanding of why certain things and not others might be happening in nature. Simplicity, transparency, emergence of surprising results, and understanding are what we seek. You must be the judge of whether you find them in any model.

2 Mathematical toolbox

In Chapter 1 we drew attention to the analogical, even metaphorical, relation between mathematical objects and operations and biological objects and processes. The use of metaphor and analogy in scientific reasoning is very deep and perhaps not as well appreciated as it should be (Holton 1986). Because analogies between two things are slippery, before we can properly use an analogy we must have a solid understanding of both sides of it. Otherwise, an analogy becomes ". . . a form of reasoning that is particularly liable to yield false conclusions from true premises" (Holton 1986). But if mathematical reasoning about the real world is an analogy, it has the peculiar strength of allowing us to determine exactly where our reasoning went false or whether we would arrive at the same conclusions from different but equally true premises. In order to do this, we must understand mathematical objects and operations *as mathematical objects and operations* first before we offer them as analogs of biological objects and processes.

In this chapter, we will develop and explore some basic mathematical objects and operations which will be used as analogs of biological objects and processes, respectively. We will use this material in the rest of the book to sharpen our thinking about ecological objects, the processes that they affect and which, in turn, act upon them. If you have a working familiarity with limits, matrices, and eigenvalues, you can skip this chapter. If not then it would be useful to spend time on this chapter so that later we can concentrate on the biological meaning of the derivations and analyses of these models without making too many side diversions into the mathematical techniques. I hope that this chapter will introduce you to some of the ways mathematicians think about things. I will occasionally "look ahead" and let you know the type of ecological problems for which this chapter's material will be used. But for now, I mostly want you to just think about mathematics without worrying too much yet about how it will be applied to ecology. Let's begin with numbers, which are perhaps the simplest of all mathematical objects, but as you shall see, they are deceptively simple.

Numbers, operations, and closure

The origin of mathematics may lie in the needs of primitive humans to characterize the magnitude of foods in relation to the size of a social unit: is there enough of something to feed all of us? Numbers might have been invented as convenient shorthand to keep track of essential resources and to determine if there is at least a 1:1 correspondence between the magnitude of resources and the size of the social unit among which the resources need to be shared (Barrow 1993). It is interesting to think that at least one plausible reason for the origin and early development of mathematics might be a problem that will concern us throughout this book, namely the relationship between a population and the resources that it must draw upon.

It is difficult to imagine how one could even begin to "think" about population density or the size of a pool of a particular nutrient without using numbers. Thinking about populations or nutrients seems to require using numbers at such a basic level that ecologists rarely give numbers and their mathematical properties a second thought. It may come as a surprise to many "pure" experimentalists that when they take data, they are implicitly doing mathematical modeling because they are associating a mathematical object (a number) with a property of a biological object. Indeed, we often proceed as if properties are defined in terms of numbers without realizing that numbers are mathematical objects used to model some perceived magnitude of a property. And so it may be good to begin our exploration of mathematical ecology by examining the properties of numbers and the basic operations which are performed upon them. Much of the discussion of numbers that follows is loosely based on chapter 22 from Feynman et al. (1963), which belongs in the repertoire of any literate scientist.

We need to develop a set of numbers upon which we can perform operations. We wish the set to be closed under the operation. By closure is meant that an operation on any element of a set of objects will produce another object that is also a member of that set. Closure avoids the problem of generating, by means of a mathematical operation analogous to a biological process, a mathematical object which does not belong to the set of mathematical objects that represents a set of biological objects. Without closure, the analogy between mathematical and biological objects and operations/processes would break down.

The natural numbers 1, 2, 3, . . . and 0 are the simplest sort of number. We will take these as given and not go into the set theoretic notions required to construct them from more basic concepts. What sort of operations are the natural numbers and zero closed under? Which biological processes are modeled by these operations and are these all the operations we need?

Beginning with 0, we generate the next natural number by adding 1:

$$a' = a + 1$$

Adding 1 to an object b times always generates a new natural number:

$$a' = a + b$$

And so natural numbers are closed under addition. Suppose we start with 0 and add a to it b times. We then get the operation of multiplication:

$$a' = 0 + a \times b$$

Since

$$a \times b = \underbrace{b + b + b + \cdots + b}_{a\ times}$$

natural numbers are also closed under multiplication. If we start with 1 and multiply it by a b times in a row, we get the operation of powers, under which natural numbers are also closed:

$$a' = a^b$$

Besides the condition of equality, there is also the inequality conditions of > (greater than) and < (less than), which we will also find useful. Addition and multiplication of natural numbers are also closed under these inequality conditions, sometimes known as monotonic laws (Klein 1932):

if $b > c$, then $a + b > a + c$

if $b > c$, then $a \times b > a \times c$

Natural numbers are closed not only under addition, multiplication, taking powers, and the monotonic laws individually but also under various combinations and sequences of these operations. Combining these three operations give us a rich set of possibilities with which to manipulate natural numbers. Natural numbers are closed under the following sets of combinations of these operations:

$$a + b = b + a \qquad a + (b + c) = (a + b) + c$$

$$ab = ba \qquad a(b + c) = ab + ac$$

$$(ab)c = a(bc) \qquad (ab)^c = a^c b^c$$

$$a^b a^c = a^{(b+c)} \qquad (a^b)^c = a^{(bc)}$$

There are also identity operations which take a number and return it. The natural numbers are obviously closed under the identity operations. The identity operation for addition is adding zero, that for multiplication is multiplying by 1, and that for powers is raising any number to the power 1.

Functions are particular combinations of objects and operations. A function takes some mathematical object or objects, $x \in A$, performs operations on them, and returns exactly one other object $y \in B$. The objects, x, which functions take and change are called the arguments of the function, or the independent variables. Independent variables are usually acted upon by parameters, which are constants. The returned value, y, is the dependent variable. The set of values which the function takes, A, are called the *domain* and the set of acceptable values for the returned value, B, is called the *range* of the function. Although a function must return only one value y for each value of x, it can return the same value for several values of x. Functions are usually expressed as equations, but a table consisting of a column of values of an independent variable with a corresponding paired column of values of the dependent variable is also a function. A contour map is also a function that takes a latitude, longitude pair of numbers and returns a single elevation for that point on the surface of an object (such as the Earth). Whether they are tables, maps, equations or algorithms, functions associate each argument with a single returned value through their operations.

The standard symbol for the value of an argument is x (or, for many population models, N) and the returned value from the function is $f(x)$ (or $f(N)$). Strictly speaking, the function itself is not $f(x)$ – the function is f, which stands for the "rules" or sequence of operations. Sometimes we see the statement $y = f(x)$, but that means y is the returned value after the function operates on x; y is not the function. For example, in the function $b = 5a$, a is the argument, 5 is a parameter, b is the returned value, and the function is the rule: "multiply a by 5 and return the value b."

One of the keys to creating helpful biological models is to be able to associate each variable with a measurement of a biological object that can change in time or over space (e.g., mass, population density, nutrient content), each parameter with some constant property of the object (e.g., specific heat, input, per capita birth rate or death rate), and the operations with some biological process (e.g., birth, death, decay, harvesting, etc.). The relationship between a hypothesis about how a process operates on biological objects and the analogous mathematical function is then clarified.

For each operation, we also want to have an inverse operation that undoes the result of the first operation. The inverse of addition is subtraction. If $a + b = c$, then $a = c - b$. Now, the set of natural numbers is not closed under subtraction because subtraction of one natural number from another does not always yield another natural number. For example the operation $3 - 5$ makes no sense in the set of natural numbers. What should we do? Clearly, subtraction is sometimes very useful as the above example shows. Let's assume that subtraction is "true" in some sense and define new mathematical objects that are closed under subtraction so that we can use them to solve equations without generating something undefined. This is of course the set of integers, which is all the natural numbers plus negative whole numbers. This object allows us to solve the above equation, yielding $3 - 5 = -2$. Enlarging the set of objects to maintain closure under new operations is the strategy that mathematicians have used when faced with similar situations. This strategy has the advantage that the new set of objects remains closed under all the previous operations that the more restricted set is closed under and it is also closed under the new operation.

Using the set of integers, addition, and its inverse subtraction, we are now ready to make our first mathematical model of a biological process. This is a model for the population growth of a bee colony: There is one queen that produces b offspring over some as yet unspecified but still definite period of time and a workers who don't reproduce. The set of positive integers is the mathematical object of which one member is analogous to the size of the hive, b is another object from the set of positive integers analogous to the number of new offspring, and adding is the mathematical operation analogous to reproduction by one queen. N_0 is the size of the original colony of one queen and a workers before the queen reproduces and N_1 is the size of the colony after the queen produces b offspring. Thus, the new population is formed by the bees in a manner analogous to addition on natural numbers:

$$N_0 = a + 1$$

$$N_1 = N_0 + b = (a + 1) + b$$

If we subtract the first equation from the second we get:

$$N_1 - N_0 = (a + 1) + b - (a + 1) = b$$

and so b is the rate of change of the bee colony (number of new individuals) over some span of time.

Let's make a model of a different kind of population in which each of a organisms can produce b offspring apiece during some unspecified but still definite time period, such as a population of protozoan that can reproduce by mitosis or that of a plant species in which each individual can produce viable seeds. We now have a new population which requires the operation of multiplication to stand for reproduction instead of addition:

$$N_0 = a$$

$$N_1 = N_0 + bN_0 = a + ba$$

Subtracting the first equation from the second gives the net change in the population during the time period, or

$$N_1 - N_0 = a + ba - a = ba$$

Thus, multiplication on the set of integers is a mathematical operation that yields a new model of population growth, one that is faster than addition because $a > 1$ and therefore $ba > b$. We will later show that this is the basic idea underlying exponential growth. Therefore, not only is the growth of a bee colony slower than that of populations of many other organisms, also it is fundamentally different because it is modeled by different mathematical operations.

These two examples are known as recursive models because they take the previous returned value of the dependent variable and use it in the next step as the argument to get or "map" the next value for the dependent variable. Recursive models operate in steps and the rate of change obtained by subtracting one step from the next is called a difference equation. There is an implicit delay in the process going from one step to the next. This delay in recursive models causes some peculiar behaviors, as we shall see in Chapter 6.

Integers thus allow us to count discrete objects such as individuals and manipulate them by means of multiplication, addition, and its inverse subtraction. But there are many quantities that interest us which can't be counted because they vary continuously, such as mass, population density per unit area, light levels, nutrient content, and nutrient concentration. These we must measure, not count. The measured values usually fall between the discrete values used for counting. Thus, to model measurements we must be able to express a fraction of an integer unit. This, of course, requires division. Division is also the inverse of multiplication but the integers are not closed under the operation of division: 3/5 does not yield a number that can be expressed as an integer. Therefore, for the empirical reason of being able to express continuous measurements and also the mathematical reason of being able to use the operation of division, we have to proceed further by assuming division to be closed for all members of another class of numbers and define that class, which is the set of rational numbers (e.g., 3/5 = 0.600 000). A feature of all rational numbers is that the sequence of numbers to the right of a decimal point eventually either falls into a repeatable pattern, or ends with 000 . . .

It is easy to prove there are an infinite number of rational numbers. Take any rational number p/q in which p and q do not have any common divisors (otherwise we can simply factor them out). Add 1 to either p or q or both. The result is another rational number, p'/q' because p and q are both integers and integers are closed under the operation of adding 1. Generate yet another rational number by applying the same processes to p' and q', *ad infinitum*.

But unlike the integers, rational numbers are "dense" in the sense that the gaps between successive integers are filled by the rational numbers such that between any two rational numbers, no matter how close, we can always construct another. Here's how: take any two rational numbers p and q where $p > q$. Then there is some distance $p - q$ between p and q. Divide this distance by any number (2 will give the midpoint of the distance, so let's use 2 for convenience). Add this new number, $(p - q)/2$, to q. We now have a new number $q' = q + (p - q)/2$, which is also rational because it can be put into the form $(p + q)/2$. Therefore, the average of p and q is another rational number, q', that lies between p and q (i.e., $q < q' < p$). Now construct another rational number between q and q' in the same way and iterate *ad infinitum*. We have just demonstrated how to construct a sequence of rational numbers that gets as close to q as we please and without ever reaching a stopping point by remaining in an interval from q to q' which is arbitrarily small. Note that we have not defined density as every rational number being "next to" or "immediately adjacent to" another rational number. Instead we have defined density as a sequence of operations which yields a rational number which can be made arbitrarily close to q by constructing intervals that are arbitrarily small but that still contain at least one rational number. This is a preview of problems that will be addressed by the concept of limits.

What happens when we take negative numbers as a power? In other words, what is the value of: $a^{(3-5)}$, where a is a natural number? Division provides the answer. We know from one of the above operations under which natural numbers are closed that

$$a^{(3-5)}a^5 = a^3$$

and by using the definition of division as the inverse of multiplication on a number,

$$a^{(3-5)} = a^3/a^5 = (a \times a \times a)/(a \times a \times a \times a \times a) = 1/(a \times a) = 1/a^2$$

but $a^{(3-5)}$ also equals a^{-2}, so $a^{-2} = 1/a^2$. Therefore, taking a negative power of a natural number is equal to the multiplicative inverse of a number raised to the positive magnitude of that power.

Division gives us the ability to more precisely and operationally define what we mean by "rate of change." In the above simple models of population growth, the rate of growth is somehow captured by b new individuals per reproductive individual over some unspecified but still definite period of time. How do we measure b? Well, we go out and watch a single reproductive individual over some period of time and count the number of new individuals produced. But clearly the data we obtain will depend on how long we count – someone else could get a different estimate of b simply by counting for a different length of time. We don't want our measurements to depend on such trivialities as how long to count, so we need to express rate in terms of some basic unit of time. To do this, we must count not only the numbers of new individuals but the numbers of time units elapsed during the measurement. We then divide $N_1 - N_0$ by $t_1 - t_0$, where t_1 and t_0 are the end and beginning clock readings during the time of our counting:

$$\frac{N_1 - N_0}{t_1 - t_0} = \frac{(a + 1) + b - (a + 1)}{t_1 - t_0} = \frac{b}{t_1 - t_0} = b'$$