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# **An Introduction to Mathematical Population Dynamics**

Along the trail of Volterra and Lotka



Springer

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# Preface

*The preface is that part of a book which is written last, placed first, and read least. As I approach my concluding task I am moved to reflect why a preface should be written at all. This question, if followed into all the intricacies of which it holds potentiality, should apparently result in a composition new in literature, a Preface to the Preface. Such precedent should not be lightly established, for it suggests a vista of future degenerations after the pattern of Josiah Royce's infinite succession of maps, each containing within itself its own replica on a reduced scale. But without going to such lengths as this, the philosophy of the preface may perhaps briefly be summarized to this effect, that it is the author subjective introduction to the more objective matter that should follow. Here he may, if this is deemed of any interest, say something regarding the circumstances that gave origin to the work, and the conditions under which it came into being. He may express his feelings as to its alleged purpose, and may follow custom by giving voice to pious wishes as to the function which the product of his presumptive mind may fulfill in an Universe in which no event, however trivial -be it no more than the addition of one more book to the groaning library shelves- is without distant reverberations.*

A.J. Lotka "Elements of Mathematical Biology", 1924

Almost a century has passed since Alfred Lotka wrote the preface to his book, whose title alone reveals the intention to be founding of Mathematical Biology as a new branch of Applied Mathematics. And indeed, in his view Mathematical Population Dynamics had a major role within the discipline to come.

After such a long lapse of time and such various and widespread developments concerning the interplay of Mathematics and Biology, we actually need to start our introduction considering what Mathematical Biology is today. In fact, the recent decades have seen an explosion in the use of mathematical methods in all areas of biology, from the use of advanced statistical methods in the analysis of medical trials, or in the alignment of DNA segments, to sophisticated pattern recognition methods in the analysis the signals from electroencephalogram data or the inference of vegetation structure from remote-sensing data.

This explosion may correspond to the joint high developments of specific mathematical methodologies and powerful implementation on computers, that contribute to make the Universe evoked by Lotka, full of reverberations difficult to follow and to understand in a unified view. Thus our work necessarily covers only part of this Universe, both concerning the object of our interest among the many fields of Biology, and our approach and methods of analysis within Mathematics, in short our idea of Mathematical Biology.

Actually, our view of Mathematical Biology, more or less corresponds to the scope of the journals or societies that have “Mathematical Biology” in their names as a distinctive character.

By “Mathematical Biology” we intend the use of mathematical models aiming at describing quantitatively and understanding the processes behind the data that have been observed and collected. In our view, mathematical biologists should not be satisfied in finding that, for instance, a parabola fits some data and can be used to make predictions; they should strive to understand the mechanisms yielding the parabola as a consequence of the laws they obey to. Indeed, mathematical modeling, in this sense, is becoming topical in all areas of biology, as can be seen from the very large number of publications involving mathematical modeling that can be found in generalist or specialized scientific journals. And still it would be impossible, not the least because of our limited knowledge, writing even an introduction to such a diverse field, and we were forced to make choices.

Biological systems are extremely complex and idiosyncratic. The case of Population Dynamics is emblematic, since a mathematical model that fits very well some data relative to a given species, may miss some factors that are quantitatively important in another one. Generally a model aiming at an accurate and quantitative fit to data must involve hundreds of relevant variables, and its properties may be understood only from numerical simulations at a computer. We see nothing wrong with that kind of models, but our basic choice here is to emphasize simple models that generically (i.e. over a reasonable range of parameter values) yield patterns in qualitative agreement with characteristic features of the biological phenomenon under study. In fact, in our view, understanding what are the consequences of model structure and assumptions in simple cases is essential also when one attempts to build a complex model, and to understand the result of its simulations.

Our work is focused on the mathematical theory of Population Dynamics, an area where mathematical biology has generated new concepts that can be understood in their own. Initially, we thought we could include in this book other topics in Mathematical Biology such as molecular networks (how biomolecules can interact, and what are the consequences at the system level) and excitable media (a theory explaining phenomena such as neural impulse or cardiac beat); we believe that models in these areas share methods and approach with the models in population dynamics considered here, and a reader could find insightful connections between different topics. However, the need to limit the time needed to complete the book, and its number of pages forced us to conclude our work without going beyond ecological models.

What is there in this book, then? We follow a tradition that goes back to Lotka and Volterra, and use it as the area where to understand different types of mathematical modeling, and the possible meaning of qualitative agreement of modeling with data. Thus, Ecology is the basic scenario including also a part devoted to the spread of infectious diseases, an area where mathematical modeling is extremely popular, and is at the center of our current research. Our ambition was to follow the trail opened by Volterra and Lotka, to show where and how a century of modeling effort has conducted both Mathematics and Biology.

The material in this book has been used, in draft or oral form, in the courses (formerly *Biomatematica*, recently *Mathematical Biology*) we have been teaching at the University of Trento for more than 20 years. The courses have been aimed at students at their fourth year of studies in Mathematics, and this can presumably be seen in the structure of the book. We consider this book mainly as an introduction to *Mathematical Biology* for students with no experience in *Biology*, but with some mathematical background; in particular, we expect that readers have a reasonable working knowledge of calculus, mathematical analysis, linear algebra, probability theory and differential equations, although in the appendices we present the specific results we use in this book. We should also mention that, though we have not explicitly introduced and discussed the use of numerical methods for producing simulations, we strongly encourage the students to use their computer abilities and the available software to explore the models, check the theoretical findings, guess the behaviors beyond the analytical results.

The chapters aim at giving an idea of the biological problems that are examined, at presenting clearly the biological assumptions and the mathematical elaborations on those, and at discussing the biological insights, if any, that have been reached through the mathematical modeling. At the end of each chapter we propose a set of problems that ask the student to make an effort to go beyond the matter presented in the text. Thus most of them are not quite routine exercises, but they ask to try to proceed further in the modeling task and in the use of mathematical tools. For this reason some of the problems may not have a unique answer, but serve as a stimulus for discussion.

In the text some mathematical steps are proved in detail, while for others we ask the readers a leap of faith or the consultation of more advanced material; in all cases, however, we attempt to keep a clear distinction between what is a biological assumption, what a mathematical theorem (though we rarely use that term), what an approximation and what a reasonable conjecture, sometimes based on extensive numerical simulations. In this sense, we consider this book mainly a book of mathematics, that aims to give an idea of how mathematics is used in biological applications, without necessarily showing the most advanced results obtained, or the most advanced models examined.

We hope that the book can be of interest for everybody (student, researcher or other) looking for a first introduction to how to use mathematical modeling in biology. These are our pious wishes as to the function of our product in the Universe of Lotka who, as you see, indeed wrote a “Preface” to the Preface.

Trento  
March 2014

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On the other hand, we may say that our work has been influenced by the many inputs from the scientific world and by the many actors of the scientific adventure that, gathering the heredity of Lotka and Volterra, built Mathematical Biology through the last forty years, so our thanks go to them for their being our inspiring examples. Beyond the many books and articles that have inspired one chapter or another (and they are duly cited), we are particularly indebted to the book by Renato Casagrandi, Giulio De Leo and Marino Gatto, '101 problemi in ecologia', McGraw-Hill, a remarkable collection of problems connecting models with ecological problems and data.

We also thank Springer-Italia for giving us the opportunity of transforming our draft notes into a real book and in particular the Editors Francesca Bonadei and Francesca Ferrari, for their help and patience during our delayed writing.

Moreover, we have to thank our students through the years, for having answered to the call and having given us credit, when we started to teach something unusual for a curriculum in Mathematics, sometimes very demanding for the wide range of mathematical theories and methods necessary to analyze the models.

And, also, this book is dedicated to the future students who will accept to be challenged providing a precious feedback to our teaching and will contribute to improve and develop the contents of the present version.

The Authors

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