

# Preface

Structures and processes studied in biology range from molecules in cells to populations or ecosystems, or to brains consisting of billions of interacting neurons, and the formal models employed in biology range from graphs as abstract representations of pairwise interactions to complicated systems of partial differential equations that try to capture all details of some biological system. Therefore, also the mathematical methods and tools employed in biology and neurobiology are quite diverse and heterogeneous. A student wanting to learn and apply mathematical techniques in biology might be confronted with the problem that she or he does not possess an overview of the available mathematical tools and does not know which method could be appropriate for a specific biological problem. A biological structure, in fact, can be modeled at various levels of details, and it is not necessarily the case that a more detailed and precise model yields better quantitative predictions.

In that situation, this book presents a spectrum of mathematical methods that are relevant and important for biology and neurobiology. Thereby, the student should be equipped with an overview and a working knowledge of the most important mathematical tools. These methods fall into three categories: First of all, there are the discrete methods, from combinatorics and graph theory. Graphs can be used to model the structure of pairwise interactions between elements in some network, whatever their precise biological nature might be. They can also be utilized to analyze empirical network data. A particular class of graphs, the trees, plays a special role in biology because they model descent relations. The second class of models comprises the stochastic ones. Much of biology, in fact, is modeled in stochastic terms, be it the firing of neurons in the brain or the random forces of evolution. Therefore, I provide a systematic introduction to stochastic processes. Finally, there are the analytical methods from the theory of differential equations, like dynamical systems or partial differential equations, that are used to explain the formation of biological patterns, ranging from the molecular scale to that of interacting species. Often, such models are derived from optimization principles, the theoretical rationale being that evolutionary competition has produced structures that best perform certain functions. Therefore, we also devote a chapter to optimization schemes. A final chapter then deals with a particular area of mathematical biology, population genetics. That has been the field of biology where mathematical methods first have been applied in a very

systematic manner. It continues to be alive today, and I present a new geometric approach to population genetics that will, as I hope, clarify the underlying mathematical structure.<sup>1</sup> These last two chapters are thus both concerned with issues of evolutionary biology, but from two different perspectives, that of optimization versus that of random processes. For a mathematical understanding of evolution, the combination of these two perspectives is essential.

The exercises are concerned with both the mathematical techniques developed in this book and their application in biological modeling. While some exercises are more of the traditional drill type that is needed to master some technique, others are more open in order to stimulate and encourage your own thinking.

In this book, I try to explain the underlying mathematical concepts and to prove the easier statements so that the reader can develop some feeling for the abstract mathematical structures. Throughout the text, I also develop applications to biology, from intracellular structures or the dynamics of neurons to those of populations. Thus, the applications span many physical orders of magnitude, but perhaps somewhat surprisingly, often the same mathematical structures turn out to yield useful models at several rather different levels. In any case, the systematic arrangement of the material is according to mathematical and not to biological principles. This seemed the natural choice for the material to be presented here, but in order to compensate for that, I am writing a companion volume “Biology and Mathematics” [2] where I attempt a systematic presentation according to biological principles and structures. Actually, I have recently also written a book entitled “Mathematical Concepts” [3] where the mathematical structures are developed at a much more abstract level. I believe that this may be relevant for biology because theoretical biology needs to develop more abstract and encompassing concepts in order to organize and understand the multitude of biological structures and processes and the increasing wealth and heterogeneity of biological data more deeply. This aspect, however, is not addressed in the present book which rather concentrates on established mathematical methods and their biological applications. In contrast to such an abstract systematic treatment, this book emphasizes the richness and diversity of the applications of mathematics to biology.

The literature in mathematical biology is too extensive to be adequately covered in this book. Therefore, the references are very selective, and you should consult the monographs and survey articles listed in the bibliography for further or more precise references. I apologize to any authors whose work is not, or not correctly, referenced in this book.

In any case, while this book certainly aims at teaching a range of mathematical concepts and methods that are relevant for the modeling and analysis of biological structures and processes, it also wants to stimulate your curiosity about biological phenomena and your independent thinking about how to model and analyze them with mathematical tools.

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<sup>1</sup> A more detailed exposition of this theory will be given in [1].

This book is based on graduate courses at Leipzig (in a joint program between the Max Planck Institute for Mathematics in the Sciences and the Department of Mathematics and Computer Science of Leipzig University, the International Max Planck Research School “Mathematics in the Sciences,” directed by Stephan Luckhaus) and at the Ecole Normale Supérieure in Paris (organized by Benoît Perthame).

Thus, a student who would like to use this book should have some basic mathematical knowledge, including in particular calculus. Some background in biology might help to appreciate the significance of the mathematical methods, but is not indispensable for reading this book. In fact, the book can also be taken as a survey over a rather wide range of mathematical structures, for any student of mathematics or the sciences.

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