Evolutionary Theory

Mathematical and Conceptual Foundations

Sean H. Rice

Sinauer Associates, Inc. Publishers
Sunderland, Massachusetts U.S.A.

The cover is adapted from Figure 8.14.

Fax: 413-549-1118
Email: publish@sinauer.com
www.sinauer.com

Library of Congress Cataloging-in-Publication Data

Rice, Sean H., 1961-
Evolutionary theory : mathematical and conceptual foundations / Sean H. Rice.
p. cm.
Includes bibliographical references (p.) and index.
ISBN 0-87893-702-1 (pbk. : alk. paper)
1. Evolution (Biology) 2. Evolutionary genetics. I. Title.
QH366.2.R523 2004
576.8—dc22
2004008054

Printed in U.S.A.

This book is dedicated to the memory of my parents,
Salem J. Rice and Ann R. Rice

Contents

Preface

This is first and foremost a book about evolutionary biology. Though it is filled with equations, it is not an applied mathematics book, nor is it a population genetics text, though that subject dominates half of the chapters. Rather, it is a book about the mechanics of evolution, as illuminated by mathematics, and about the conceptual structure of evolutionary theory. I hope to convey the fact that evolutionary theory is not just a collection of separately constructed models, but is a unified subject in which all of the major results are related to a few basic biological and mathematical principles.

The audience I had in mind while writing the book is made up primarily of graduate students in biology. These students know there is a body of formal evolutionary theory and are familiar with some of its conclusions, but often have never been shown where these conclusions originate from. I also hope that the book will be of interest to researchers in related fields, as well as to biology undergraduates who are frustrated with the fact that they learn calculus and then rarely use it in their courses. In short, my intended audience is composed of readers who know a bit of evolutionary biology and a bit of mathematics. My goal is to take these readers deep into the subject of evolutionary biology, and hopefully expand both their biological and mathematical knowledge in the process.

The single most difficult thing about writing a book that covers this range of material is deciding what to leave out. Most of the topics that I cover have entire books devoted exclusively to them. Giving a comprehensive treatment of each subject would make the book prohibitively long (for both author and readers) and would detract from the goal of uniting different fields and emphasizing the biological insights that they yield.

In deciding what to include and what to leave out, I chose to focus on those results that I feel have the greatest power to influence our thinking about how evolution works. By showing in detail how these central results are derived, I hope to convey some feel for how the different branches of evolutionary theory are constructed and connected.

Because I chose subjects based on their significance to understanding evolution rather than on the kind of mathematics that they require, the level of mathematical sophistication varies throughout the book. Some sections use only basic algebra and a bit of calculus while others, sometimes in the same chapter, use more sophisticated methods. I assume only that the reader is familiar with basic calculus. Beyond this, I strive to explain more advanced mathematical techniques when they arise or in the Appendices.

Acknowledgments

This book is based on a course that I have taught for a number of years. I am grateful to all of the students who, through challenging and insightful questions, lively discussions, and comments on my lecture notes, have not only improved my presentation of the material but have helped me to learn the subject more deeply.

My thinking about this subject has been influenced by many colleagues over the years. Those whose influence I clearly see when I look at what I have written include Jack Cohen, Paul Magwene, Monty Slatkin, Mike Rosenzweig, and Günter Wagner. David Houle and Mark Kirkpatrick read parts of the manuscript and provided helpful input regarding the material and presentation.

I am also grateful to Andy Sinauer and the folks at Sinauer Associates for working hard to keep the book on schedule while dealing with my constant underestimates of how long it would take me to complete each part. In particular I would like to thank Sydney Carroll, who worked overtime to pull the book together.

Most importantly, I would never have completed this book without the continuing encouragement and support of my wife, Melissa. When the project seemed daunting, she reminded me why it was worthwhile and inspired me to continue.

Introduction

All fields of science use mathematical models that allow us to draw accurate conclusions from empirical work as well as to address hypothetical "what if" questions. A few scientific fields go a step further. These sciences possess mathematical theory that is more than just a collection of special case models, it is fundamental to a basic understanding of the subject. In fields built upon this sort of theoretical foundation, discovery is often driven by mathematical arguments, followed by empirical tests. When a particular model fails an empirical test, researchers turn to the mathematical theory to understand why.

Only a few branches of science have this sort of formal mathematical foundation, but it is not surprising that evolutionary biology is one of them. When we look at the roots of evolutionary biology, we can see why this is so. The mechanism of evolution proposed by Darwin and Wallace, though not phrased mathematically, has a feeling of universality to it. The logic of natural selection is so clear and the premises so well founded, that critics—who are unable to find any logical flaws—are reduced to arguing that it has no empirical content. This is of course not true. The fact that offspring resemble their parents is an empirical observation, but the empirical basis of the theory is so well supported that it seems to blend into the logic of the arguments.

In this respect, evolutionary biology is unlike most biological sciences, where fundamental discoveries are usually the result of experiments. Mathematical models, when used at all, are seen more as ways to make numerical predictions than as ways to understand the basic science. In contrast, many of the central ideas in evolutionary biology originate in, or are justified by purely mathematical analysis. A short list of these central ideas includes: the fact that even seemingly weak selection can drive evolution; the existence of drift and its interplay with selection; the significance of frequency dependent selection for our understanding of adaptation; the importance of population structure in evolution; the role of kinship in the evolution of cooperation; the significance of mate choice as opposed to competition in sexual selection; and the conditions under which it is, or is not, reasonable to think of selection as acting at more than one level of organization. All of these subjects have also been studied experimentally, but none would have gotten far without rigorous mathematical analysis.

Theoretical science begins with what we know and leads us to conclusions that could not have been made without rigorous analysis. How far a theory can take us is determined in large part by how solid the foundation is on which it is built (what we know). This foundation is what allows us to decide when we can or can not apply the results of our theory, how and when these results can be combined, and how to interpret cases in which the theory fails. There are two main types of foundations that underlie successful theories. The first is a set of well-understood empirical rules that apply to a wide range of systems. The second is a set of mathematical theorems derived from unambiguous principles, that apply exactly to a well-defined set of systems. Evolutionary theory provides good examples of both of these foundations.

It is no accident that classical population genetics emerged soon after the rediscovery of Mendel's work in 1900. Mendel's laws have the appropriate combination of precision and generality to form the basis of a body of mathematical theory. The introduction of linkage and recombination fit right into the basic Mendelian framework, and the discovery made in the middle of the 20th century of the chemical basis of genetic transmission only substantiated and explained the basic patterns.

It is interesting to note that other models of inheritance were proposed in the 35 years between Mendel's work (Mendel 1865) and its rediscovery in 1900. One of these models, proposed by Galton (1898), posited that an individual's inherited makeup is a combination of separate contributions from parents, grandparents, and all of the individual's ancestors, each skipping over intervening generations. If this had turned out to be correct, subsequent evolutionary theory would probably not have gone very far, since understanding how a population changes could only be based on a detailed study of its entire history, rather than on its current state and a set of well-established rules.

The first half of this book is concerned with the mathematical analysis of what happens when we combine population level processes, such as selection, with the basic rules of transmission genetics. This kind of theory, focusing on genes and drawing on the mathematics of sampling, was the only well-developed mathematical evolutionary theory for most of the 20th century.

Of course, not all genes behave in a Mendelian fashion. Meiotic drive, in particular, subverts the evenness of transmission that Mendel observed. We will see in Chapter 2, though, that we can still use the formalism of population genetics to model meiotic drive because we understand the basic process that meiotic drive distorts. In analogous ways, classical population genetics has expanded to address a number of subjects, including the evolution of recombination and maternal inheritance, that would have confounded Mendel's experiments.

Some problems, though, never fit well into the framework of population genetics. Though modified Mendelian genetics provides a good foundation for one- and two-locus population genetics theory, it does not give us so solid a footing when we are concerned with phenotypic evolution. Phenotypes, both morphological and behavioral, do not generally exhibit the kinds of simple, regular patterns that we see in the transmission of alleles. The assumptions required to connect morphology to a well-behaved Mendelian process are so extensive and arbitrary that models based on such assumptions cease to have the foundational quality discussed at the beginning of this introduction.

One possible approach would be to search for "laws" of development that could substitute for Mendel's laws as the foundation of a general theory of morphological evolution. This approach appealed to many researchers, and a number of putative developmental or morphological "laws" were proposed. However, though there are many tantalizing generalizations about development which make evolutionary developmental biology an exciting field, there are no empirical rules that are either universal enough or precise enough to form the foundation of a truly general theory of morphological evolution.

Fortunately, there is another route to developing such a theory. As mentioned earlier, a body of theory can be built on a set of purely analytical results as long as those results are derived from unambiguous premises and apply exactly to a well-defined set of systems relevant to our interest. The beginning of such an analytical foundation for evolutionary theory was provided by Price (1970). In one sense, Price's theorem is just a formalization of the basic ideas of Darwin and Wallace. The premise is the same: A population of phenotypically variable organisms (or things of any sort) leave descendants bearing some resemblance to their parents. Add to this the fact that organisms with certain phenotypes leave more descendants than those with other phenotypes and you get evolution. Like Darwin and Wallace, Price assumed a causal connection between phenotype and survival or reproduction and he thus phrased his theory in terms of selection. However, we will see in Chapter 6 that the same mathematics describes drift if we allow the relation between phenotype and reproduction to be random.

Like the ideas of Darwin and Wallace, Price's theorem shifts back and forth between seeming so obvious that it must be universal, and so simple that it must be missing something. Simply looking at the theorem does not provide much insight beyond our intuitive understanding of selection. The value of Price's theorem lies not in the fact that it says anything shocking, but in the fact that it is an exact statement of the relationship between differential reproduction, inheritance, and evolution that was intuitive to Wallace and Darwin and to most biologists since. As such, this theorem provides the beginning of an evolutionary algebra; a set of mathematical results that by virtue of their exactness do for general phenotypic evolution what Mendel's work did for population genetics. This is what gives us a foundation from which to derive more elaborate theories and a standard against which we can check our results.

The theory of phenotypic evolution forms most of the second half of this book. In Chapter 6, we will discuss the basic theory and see how it unites the gene based theories that came before with the phenotype based theories that follow in subsequent chapters. In Chapter 8, we will add some further results to the algebra of evolution that are appropriate to the study of development.

Just saying that evolutionary theory has a solid analytical foundation is not the same as saying that the field of evolutionary theory is anywhere near complete. There are many areas within evolutionary biology that still consist largely of loosely connected models with no unifying theoretical framework. Expanding the general theory to include these will likely change how we think about the entire subject, but looking at the history of other sciences that use mathematical theory as a foundation, it seems likely that future developments in evolutionary theory will not discard the theoretical foundations discussed here, but will retain them as special cases and build upon them.