

Elements of Evolutionary Genetics

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Since Maczulak's focus throughout the book is the detailed recounting of the history of microbiology, I wish she had also tackled the history of Carl Woese's reinvention of the field. This approach might have introduced and showcased archaea more effectively.

In other places, while trying to provide some basic biological information, Maczulak makes generalizations that are too casual, as when she declares that bacteria are less bound by the sort of spatial constraints that limit protozoa to aquatic places and fungi to soil. In a book this succinct, the background material must be chosen carefully and used with more precision. All bacteria and archaea are aquatic in that their reproduction and metabolisms require water in the environment, even if only a thin film around a particle. Maczulak also declares that the overwhelming majority of bacteria live in soil. If she is including all sediments in oceans and other bodies of water as "soil," as well as all of the tropical substrates that are not quite soil, then this statement might be true, but it is too loose a comment to be stated on its own as fact.

The history of microbiology can be presented as inspiring reading—Paul de Kruif being the leader of that genre. The strengths of *Allies and Enemies* all lie in the sections in which Maczulak delves into detail about the personalities and lives of her protagonists: The events in Koch's and Hesse's lab are nicely depicted, the interactions of Pasteur and Winogradsky are well developed, and the history of *Escherichia coli* is thoroughly researched and interestingly written. Maczulak's ability to tell a good story is highlighted again in her descriptions of the myriad bacteria in and on the human body. As an aside, I disagree with Maczulak that Hooke is a forgotten hero of bacteriology; he merits numerous pages from historians and philosophers of science for his many accomplishments. Hooke's particular microscope design, however, was never as effective as van Leeuwenhoek's. Hooke's subjects were much larger

objects, such as fleas and fly eyes, and never cells of bacterial size.

The tone of the book changes when Maczulak tries to clarify what we know and do not know about the origins of antibiotic-resistant bacteria. Although the origins of some antibiotic-resistant bacteria can be isolated to stockyard animals dosed with prophylactic antibiotics, she claims that "it can be difficult to prove" any real connection. I was at first puzzled by the prevarications in this section and then wondered whether Maczulak was speaking from some firsthand experience with the beef industry. (She has a consulting firm that deals with compliance audits for industries concerning microbes.) If so, I wish that she had told the story more directly in the book instead of presenting it as an intractable problem. A similar equivocal tone appears in the section on genetically modified food, another topic that might have benefited from a more forthright approach that included the author's experiences with such industries.

Segments of the book that are not about pathogens tend to be about bacteria as essential providers for specialized activities in industry and technology. This dichotomy of bacteria acting as either pathogens or industrial aids is already pervasive in the popular press and does not need such reinforcement. Another disconcerting theme I found in *Allies and Enemies* is the idea of "our" world being primarily inhabited by bacteria. Put more accurately, it is their world that we inhabit. Bacteria simply dominate the ecosystems; have been and continue to be intrinsically influential in our evolutionary history; and, quite simply, make nutrient cycles of life possible.

The final chapter concludes that bacteria are our best friends and that we should stop worrying about germs. Yet more than half of the book is focused on the pathogenicities of bacteria and their relentless resistance to the best antibiotics. The chapter "Bacteria in Popular Culture" emphasizes depictions of plague and tuberculosis in art and literature and then

segues into a discussion of bacteria as destroyers of the artwork itself. Alas, I had been hoping that Maczulak would review the growing body of art that celebrates bacterial ubiquity and diversity. Often, such art is colorful and transient, involving flows of living bacteria interacting on a substrate.

A surprising epilogue appears at the end of the book, containing information typically found in introductions to microbiology lab manuals. Maczulak includes instruction on how to do serial dilutions, how to count colonies, and even how to use logarithms to calculate large numbers. As one who has written a book on bacteria, I know it is a challenge to frame the audience. I think both Maczulak and I would like to envision our readers as so enthusiastic about microbes that dabbling in the laboratory would be their next irresistible step. But in the case of *Allies and Enemies*, those extra pages of instruction may have been better used to reinforce the grand scale of everything bacterial.

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SERIOUS EVOLUTIONARY GENETICS

Elements of Evolutionary Genetics. Brian Charlesworth and Deborah Charlesworth. Roberts and Company, 2010. 768 pp., illus. \$68.00 (ISBN 9780981519425 cloth).

Wherever the study of evolution intersects with the study of inheritance we have evolutionary genetics. Evolutionary genetics thus covers a huge chunk of evolutionary biology, as without inheritance there can be no cumulative change. The

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familiar core of evolutionary genetics is population genetics, the study of the ways in which evolutionary forces affect allelic variation within populations. Evolutionary genetics extends beyond population genetics to encompass why those evolutionary forces exist. By taking evolutionary genetics as their title topic, Brian and Deborah Charlesworth signal that this book, *Elements of Evolutionary Genetics*, aims to introduce their readers not just to population genetics but to the wider range of evolutionary problems that the consideration of inheritance informs.

I teach a graduate course in evolutionary genetics, and my goal is for the students to be able to read and understand the important papers in their area of interest. Such papers are usually empirical but depend on a critical backbone of theory for their ultimate impact. Students readily learn to read and interpret empirical work in evolutionary genetics; the challenge is to bring them up to speed on theory. What students need to understand about theory is fairly basic: Assumptions dictate results, most theory is based on rather simple mathematical techniques that can be understood when you really need to understand them, and one cannot understand empirical results without understanding the theory.

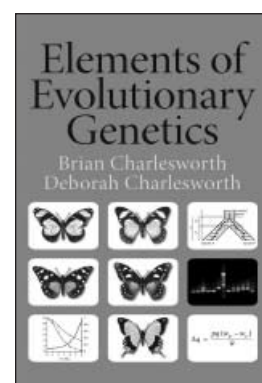
I have long struggled to find a suitable text for this course, having tried various combinations of population genetics and theoretical textbooks and primary readings. Using this patchwork of material, it has rested primarily on me to make the crucial connections between theory and data, to bring students up to speed on the basic mathematical concepts used in the theory, and to cover quantitative genetic and optimality approaches that are usually omitted from nonspecialized texts. *Elements of Evolutionary Genetics* has changed all that. The target audience for this book includes my students—people interested in the study of evolution who want to achieve a sophisticated understanding of how evolutionary theory illuminates the evolutionary process.

As two of the most influential evolutionary geneticists working today, the Charlesworths are uniquely positioned to write this book. Their work has spanned the range of problems in evolutionary biology, from phenotypic phenomena such as butterfly mimicry and life history to allelic variation such as protein allozymes to their current work on genome-level phenomena such as the evolution of recombination. As a postdoctoral researcher with the Charlesworths 20 years ago, I realized how little evolutionary biology I knew when I listened to them discuss the papers of the day (*every* paper, it seemed to me) and their own ongoing work.

Most of us are inclined to skip mathematical detail whenever possible, and how a textbook deals with this problem is a key to its success. Here the Charlesworth book is nearly ideal.

This book is an introductory but comprehensive graduate-level text and reference guide to much of evolutionary genetics. At its core is population genetics, enhanced by substantial forays into topics such as quantitative genetics, models of adaptation, the evolution of phenotypic phenomena such as life histories, breeding systems, and genome evolution. The breadth and depth of scholarship on these topics are superb. I find the combined presentation of older and newer work to be particularly stimulating. Those studying primarily genomic data are sometimes unaware of the value of evolutionary genetic research before the invention of DNA sequencing, whereas those of us who are older sometimes fail to follow the scaling up of analyses to the genome scale. The Charlesworths remember the old and read the new.

Each section of the book is a mixture of data and theory, culminating in several detailed examples that relate the two. Typically, one will find an introduction to the data, the potential explanations of that data, the theoretical models that instantiate those hypotheses, the methods of analysis used to work those models, and finally, the analyses that test particular hypotheses. The examples are interesting and accessible, given the detailed material. The result is a brisk, readable book that is refreshing to the initiated and, according to my students, reasonably accessible to the novice.



Most of us are inclined to skip mathematical detail whenever possible, and how a textbook deals with this problem is a key to its success. In this, the Charlesworth book is nearly ideal. By interweaving theory and empirical work they make it relatively attractive to pay attention even to equations. When the mathematical details are not as important to following an argument, they are set off in boxes. Basic mathematical techniques in calculus and linear algebra are neatly introduced in one appendix, and basic statistics and probability are covered in another. Each chapter includes numerous mathematical exercises that range from simple applications of summary measures to more challenging derivations of theoretical results. All of these are answered and fully resolved at the end of the book. Unfortunately, many of my students still need a boost

up to the level at which this book begins. In particular, more graphical representations of model logic and results would be particularly valuable to these students. The Charlesworths are not visual thinkers.

In addition to being readable, *Elements of Evolutionary Genetics* is also organized to make it a very effective reference. The chapters are structured into sections and subsections that are extensively cross-referenced. Getting to a particular topic is usually easy using the book's adequate (although less than comprehensive) index or by perusing the well-organized table of contents that repeats the section and subsection information. The book avoids redundancy through this cross-referencing, but a cost is that one is likely to be led back through several previous sections to get fully up to speed on the topic of interest.

My problems with the book are in what is omitted, rather than what is covered. To me, evolutionary genetics is significantly broader than the material covered in this text. In particular, to deal with genomic-level data, evolutionary genetics must be extended in two directions: First, genome evolution is entirely an evolutionary genetic topic, but the Charlesworths choose to cover only special topics, largely omitting consideration of important phenomena such as gene and genome duplication and the evolution of multigene systems such as regulatory networks. On the other end of the spectrum, the recent collapse of the genomewide association paradigm suggests that more attention must be given to traditional phenotype-based quantitative evolutionary genetics. I would also love to see more information on inferring the phenotypic causes of natural selection and estimating its strength. Many clever, older approaches to these problems seem to have been forgotten.

Overall, *Elements of Evolutionary Genetics* is a superb introduction to evolutionary genetics for the serious and motivated student of evolution. The writing is clear, the scholarship authoritative, and the blending of theoretical and empirical approaches is

simply without parallel among books aimed at this audience. I expect to be using this book as a text and as my first-line reference for many years to come.

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