Preface

Darwin's *Origin of Species* has been described as one of the books that is most widely referred to, but least likely to be read. My goal is to make the *Origin* accessible to a larger audience and to do so by placing it in a continuum of science. The *Origin* was the inception of a new, unifying theory of the life sciences, but it was also strongly influenced by the science that preceded it; so understanding the *Origin* requires looking back in time to define the context in which it was written. Sometimes this also means understanding that some details that were critical to Darwin's theory were not yet known. The *Origin* was an inspiration to science because it highlighted these gaps in our knowledge and why it was important to fill them. It was much more of an inspiration because it defined so many new areas of inquiry. To appreciate the *Origin*, then, it is also important to look forward in time to see how it changed science.

I am an evolutionary biologist and have been studying evolution for over thirty years. I have specialized in the experimental evaluation of facets of the theory of evolution in nature. No one should be surprised to hear that someone like me is a fan of Charles Darwin. But being a fan of Darwin and his ideas is different from being an admirer of the *Origin of Species*. I first read the *Origin* during the summer break between completing my bachelor's degree at Washington University and beginning PhD studies at the University of Pennsylvania. I cannot recall much about what I learned from that first reading. I do recall finding it very hard going. I finished it out of a sense of obligation. I did not read the *Origin* again until I was an assistant professor at the University of California, when I decided to use it as part of a graduate class. It was not until I had read the first and sixth editions a few times, plus learned more about the development of evolution as a discipline, that I appreciated the scope and lasting importance of the book. More

than a decade later I found myself, as a guest professor at the University of Konstanz in Germany, leading a seminar on the *Origin of Species* for a polyglot group of graduate students and postdocs. That is when I got a full sense of what the difficulties of the book were, but also of the potential for turning it into a document that would be accessible to a much wider audience. That is my goal with this book. I intend it to be a reader's guide to the *Origin* that addresses the issues that make Darwin's masterpiece a challenge to read and yet emphasizes the importance of reading it today, not as a historical benchmark, but as a living, relevant document.

Why is this worth doing? I think that a working knowledge of evolution can enhance anyone's understanding of any aspect of biology. For the majority of professional scientists, this knowledge represents a void that will rarely be filled; the growth of biological sciences and the extent to which we have become specialized means that most biologists get little or no exposure to evolution and often do not see its relevance. The general public hears about evolution in the news, mostly as sound bites from the opposing sides of the evolution-creation controversy. People in this wider audience can benefit as much as any student or scientist from understanding the theory of evolution because it has become a central issue in the design and delivery of science education. Understanding will lead to more informed decisions about how education is delivered.

Evolution is also an underappreciated feature of our day-to-day lives. Understanding evolution can help us understand the ever-changing risk of disease (e.g., why antibiotics and insecticides can do more harm than good if overused) or appreciate some of the risks associated with using genetic engineering to modify crops. The properties of plants and animals that make evolution inevitable are central to the development of domesticated breeds, without which life as we know it could not exist. Evolution plays a central role in understanding the impact of humans on the natural environment too, since organisms can evolve on short timescales. It plays a role in determining which species will survive and which will go extinct as climates change. It can play a key role when species are accidentally transported to new environments and become pests that invade and change local communities. Humans cause evolution by being predators—when hunting or catching fish, for example. The cod of today are genetically different from the cod that were fished fifty years ago and are less valuable as a source of food because of genetic changes promoted by human predation. All the

above represents evolution that happens quickly, within a single person's lifetime, and that profoundly affects our welfare.

All these observations support an argument for understanding the basics of evolution, but these basics can be gained from any general biology textbook. They are not an argument for reading the *Origin*. One argument for reading the *Origin* is that it is the first comprehensive statement of the mechanism of natural selection and of the extent to which evolution by means of natural selection can serve as a unifying concept in biology. The *Origin* brings into its fold the entire scope of the natural sciences that become explainable by evolution. But this is still an incomplete argument; there are other sources for the same information. Reading the *Origin*, as opposed to turning to some other source, also provides a basis for understanding how science evolves and how we define the important unanswered questions to be addressed with future research. This is why we continue to include the *Origin* in our graduate classes.

But I am aiming for a bigger audience than students of the life sciences. Reading the *Origin* can teach anyone at any level important lessons about the structure of science and the meaning of the word *theory*. Another goal of this book is to define the word *theory* as it is used in the sciences and to detail how and why Darwin developed evolution as a scientific theory. Reading the *Origin* can also highlight the role that evolutionary theory played in shaping the future development of science. For example, the growth of genetics in the early twentieth century was strongly influenced by an interest in evolution. The connection between genetics and the *Origin* is that inheritance—the passing of characteristics from one generation of organisms to the next—was a critical component of the mechanism of natural selection. Darwin did his best to come to grips with how inheritance worked. What he saw and reported is a time capsule of what any acute observer would think of inheritance without the benefit of knowledge of Mendel. A good observer would rarely see anything like Mendelian inheritance governing the similarities between parents and offspring, which is why it took so long for Mendelism to be universally accepted. Darwin highlighted the importance of understanding how inheritance works. It was those who were influenced by Darwin who rediscovered and appreciated Mendel's laws.

The *Origin* can also still inspire new research because of the broad implications of some of Darwin's ideas. One example is the development of molecular evolution. Darwin knew nothing about DNA, but he was very clear

about how the theory of evolution predicts that organisms will contain clues to their history. He applied this idea to the fossil record and the comparative anatomy and embryology of living organisms. It was for those who followed to realize that this same logic could be applied to the structure of DNA and proteins, and then to integrate evolutionary and molecular biology.

Reading the *Origin* also highlights basic issues that have yet to be fully resolved. Some of these include the causes of gaps in the fossil record, the relationship between micro- and macroevolution, the evolution of complex organs (what Darwin referred to as "organs of extreme complexity"), or the mechanisms of population regulation in living organisms. All these phenomena and more appear in the *Origin* as part of Darwin's development of the theory of evolution, and all represent active areas of research.

For all these reasons, the *Origin* represents far more than a book of historical interest. It is as relevant to science today as it was in 1859.

This is all an abbreviated argument for why we should read the *Origin*, yet very few people try to. Of those who try, few finish it, and even fewer understand it. I sympathize with anyone who has tried, given my own experience. I have tried to make the *Origin* more accessible by rewriting it, and by identifying and addressing the difficulties inherent in the original document. People often talk about the difficulty of Darwin's Victorian prose, but this is a minor issue. I have learned to like and admire his writing. One of the more substantive reasons that the *Origin* is difficult to read is that Darwin draws on a breadth of scientific expertise that exceeds that of virtually any layman but also most scientists. As the life sciences have expanded since 1859, we have tended to become far more specialized than were the scientists of Darwin's day. A second source of difficulty is that Darwin's presentation is rooted in the science of 1859, which is quite different from the science of today. A third source is that Darwin had multiple goals that are interwoven throughout the book, rather than being neatly separated. One main goal was to define natural selection. A second was to show how natural selection causes speciation. A third was to develop evolution as a theory, which means to show how the single mechanism of natural selection can help to explain a diversity of phenomena that were previously thought to be unrelated to one another. His fourth main goal was to anticipate the debate that his new ideas would generate, since he was attempting to overturn established dogma. These themes are often presented together as a complex fabric, rooted in the science and arguments of the past.

I have tried to simplify the presentation of the *Origin* by deconstructing the original, then presenting its themes separately as the three main sections of this book. Part 1 presents "natural selection," which Darwin proposed as the universal mechanism that causes organisms to evolve. Part 2 presents "speciation," which is one possible consequence of evolution by natural selection. Part 3 presents the "theory of evolution," which develops the explanatory power of evolution and defines its potential as the central, organizing theme of the life sciences. The fourth theme, Darwin's response to anticipated criticisms of his theory, is presented throughout this book in a fashion that is loyal to Darwin's description of the *Origin* as one long argument. In the last chapter I apply Darwin's principles to a topic he avoided in the *Origin*—the evolution of humans.

In each section, I present Darwin's arguments and use his examples, but also offer the background needed to understand his arguments. In so doing, I highlight some areas of growth in science inspired by the *Origin*. I also present observations about the expanded influence of the *Origin*; these extra topics appear as "evolution today" segments at the end of some chapters and as several independent chapters dispersed through the book. Unless I say otherwise, I present what I believe to be Darwin's understanding of evolution, which is not necessarily the same as our understanding of evolution today. I maintain the connection between this book and the *Origin* by often quoting Darwin from the facsimile of the first edition that is now available from Harvard University Press. All page references are to the first edition, unless otherwise noted. Many people may not want to read this book and the *Origin* together, so I have written this book to serve as either a stand-alone explanation of the *Origin* or a reader's guide to the *Origin*. I hope that some readers will be inspired to read the original.