Understanding Evolution

Current books on evolutionary theory all seem to take for granted the fact that students find evolution easy to understand when, actually, from a psychological perspective, it is a rather counter-intuitive idea. Evolutionary theory, like all scientific theories, is a means to understanding the natural world.

Understanding Evolution is intended for undergraduate students in the life sciences, biology teachers, or anyone wanting a basic introduction to evolutionary theory. Covering core concepts and the structure of evolutionary explanations, it clarifies both what evolution is about and why so many people find it difficult to grasp. The book provides an introduction to the major concepts and conceptual obstacles to understanding evolution, including the development of Darwin's theory, and a detailed presentation of the most important evolutionary concepts.

Bridging the gap between the concepts and conceptual obstacles, *Understanding Evolution* presents evolutionary theory with a clarity and vision students will quickly appreciate.

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To my wife, Katerina, and our children, Mirka and Giorgos, for turning an inherently purposeless life into a deeply meaningful one.

Contents

Prolegomena

Evolutionary theory is the central theory of biology. It explains the unity of life by documenting how extant and extinct species share a common ancestry. It also explains the diversity of life by describing how species have evolved from ancestral ones through natural processes. Charles Darwin laid the foundations for current evolutionary theory in his book *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (1859), where he argued for the common ancestry of all life and proposed natural selection as the mechanism by which evolution proceeds. Darwin briefly described the process as "descent with modification." This phrase still accurately describes the core of evolutionary theory. However, evolutionary biology has itself evolved since then, incorporating other disciplines such as genetics, **systematics**, or paleontology during the Modern Synthesis of the 1940s (Huxley, 1942), as well as others like developmental biology and genomics later in the twentieth century (which is described as the **Extended Synthesis**; see Pigliucci and Müller, 2010). Today scientists consider evolution to be a fact of life. An evolutionary perspective is dominant in many of the most active fields of biological research, such as genomics and evolutionary developmental biology, and also provides important insights in medical, agricultural, and conservation studies and applications. All in all, evolutionary theory is a powerful theory that organizes and provides coherence to our understanding of life.

Yet evolutionary theory and the idea of biological evolution more generally have been, and continue to be, enormously debated in the public sphere. Various polls taken around the world have shown that there is a rather low public acceptance of evolution (see, for example, Miller *et al.*, 2006). This low acceptance of evolution is often related to a high acceptance of Creationism in various forms (e.g., Intelligent Design [ID] is often considered as the most recent version of Creationism grabbing public attention – see Numbers, 2006, but also Numbers, 2011), and to the attempt to introduce an alternative, religiously founded "explanation" for the origin of species in biology courses (Branch and Scott, 2009). However, Creationism, in any form, does not exhibit the necessary prerequisites for inclusion in the biology curriculum (Sober, 2007; Audi, 2009; Brigandt, 2013). While Creationism is certainly an issue in the United States (see Berkman and Plutzer, 2010; Coyne, 2012), it is by no means restricted to there alone. It exists in the Muslim world, and it seems to be emerging in Europe as well (Graebsch and Schiermeier, 2006; Hameed, 2008; Curry, 2009; Numbers, 2009a; Blancke *et al.*, 2013). Interestingly enough, even literate citizens in countries like China and Japan seem to doubt that evolutionary theory can explain Earth's biodiversity (Cyranoski *et al*., 2010).

Research on undergraduate students' (both those pursuing degrees in biology and those pursuing degrees in other fields) understanding and acceptance of evolution suggests that they also face similar problems. Students from various countries and religious backgrounds often perceive a conflict between their worldviews and what evolutionary theory suggests (e.g., Brem *et al*., 2003; Sinatra *et al*., 2003; Ingram and Nelson, 2006; Deniz *et al*., 2008; Hokayem and Boujaoude, 2008; Athanasiou and Papadopoulou, 2011; Winslow *et al*., 2011). This raises serious concerns, as it is important that future scientists and other scholars acquire a clear understanding of what evolution is. This is especially crucial for students who intend to undertake studies in the life sciences, because evolution is its central unifying theory and, as Theodosius Dobzhansky (1973) famously stated, without evolution biology is a pile of sundry facts that make no meaningful picture as a whole. But it is also important that students in other sciences such as physics and chemistry, or even the social sciences and the humanities, also acquire a clear understanding of evolution. Scientific literacy is a demand of our times, particularly since some research fields of biology, such as genetics, genomics, stem cell biology, biotechnology, or conservation ecology, have enormous implications for our lives. Therefore, it is important that all literate people understand the central unifying theory of biology.

Rationale and aims

Many books on evolution have been published, written by evolutionary biologists, philosophers, or historians of science. Some books present the history of evolutionary thought (Larson, 2004; Bowler, 2009a; Ruse, 2009), analyze Darwin's theory in detail (Kohn, 1985a; Hodge and Radick, 2009a; Ruse and Richards, 2009, Ruse, 2013), explain what evolution is (Gould, 2002; Mayr, 2002; Pigliucci and Kaplan, 2006; Ruse and Travis, 2009), provide evidence for evolution (Prothero, 2007; Coyne, 2009; Dawkins, 2009; Rogers, 2011), or explain why it is important for our life (Dupré, 2003; Mindell, 2007; Stamos, 2008; Ayala, 2010a; Vermeij, 2010). Other books explain how evolution is related to religion (Ruse, 2001, 2010; Wilson, 2002; Ayala, 2007; Kitcher, 2007; Miller, 2007), describe the history of the evolution–creation struggle (Ruse, 2005; Numbers, 2006; Bowler, 2007), or explain why Creationism and ID cannot be considered as alternatives to evolution (Eldredge, 2000; Pennock, 2000; Pigliucci, 2002; Ayala, 2006; Sarkar, 2007; Avise, 2010). These are all valuable books, and they present sound arguments and suggestive evidence that shows not only that evolution is a fact of life, but also that evolutionary theory provides the best scientific explanation (so far) for all biological phenomena. However, in most of these books it seems to be taken for granted that it is simple for their readers to understand what evolution is. Therefore, it seems to be assumed that all people need is books which present arguments and evidence for evolution and/or against Creationism and ID. This is what readers will find in many of the excellent books sampled above. But if these books provide ample arguments for both purposes, why then do the public debates about evolution persist? Why is it the case that many people reject evolution or question its validity, despite the evidence for it and its enormous explanatory power in contemporary biological research?

In my view, there is a gap in the existing literature on this topic. Evolution is a rather counter-intuitive idea (from a psychological point of view), and it should not be taken for granted that it is easy for all, or even most, people to understand it. In general, resistance to scientific theories may be due to intuitions that generate preconceptions about the natural world and often make scientific findings seem unnatural and counter-intuitive. For example, children's intuitions make it as difficult for them to accept that organisms may become adapted through natural, evolutionary processes, as it is to accept that the Earth is a sphere. In many cases, these intuitions persist into adulthood (Bloom and Weisberg, 2007). Moreover, it seems that preconceptions related to biology (e.g., the basic living/non-living distinction) are never completely overwritten, despite even a deep understanding of biological processes or expert scientific knowledge (Goldberg and Thompson-Schill, 2009). Such preconceptions make evolutionary concepts difficult to understand. Furthermore, people may misinterpret the implications of evolutionary theory for their lives, and they may also extend these to questions beyond the realm of science. What is necessary is that people realize that evolutionary theory, like all scientific theories, is a means to understand the natural world, and nothing beyond that. It is also a theory which can be put to the test and not something to which we should dogmatically subscribe.

I have written this book in an attempt to fill this gap in the literature, while also trying to present evolutionary theory in a comprehensible manner. To achieve this, I rely not only on evolutionary biology, but also on conceptual development research and on scholarship from both the history and the philosophy of biology. My main intention is to clearly describe the core concepts of evolutionary theory and the features of evolutionary explanations. However, before attempting this, I am being explicit about the obstacles that affect understanding of evolution, suggesting that the low percentage of acceptance of evolution among students is in part due to a lack of the required understanding. This book explains both what evolution is and why it is difficult to understand. Understanding evolution is neither simple, nor easy to achieve; it is a rather counter-intuitive idea given human intuitions and how we tend to perceive the world around us. Thus, I argue that whether people understand evolution or not *is* a major issue and one that may have been overlooked in the debates surrounding evolution. To the best of my knowledge only two edited books discussing conceptual issues relevant to evolution in some detail have been published (Taylor and Ferrari, 2011; Rosengren *et al*., 2012), but they are more technical and quite different from this one.

There is another reason for writing this book. Too much ink has been devoted to writing books against ID/Creationism, which has attracted public attention through court cases in the United States. This seems to be a major (political, not strictly religious) issue which, in my view, has misleadingly attracted most attention and as a result other important issues have been overlooked. An insightful research project by Michael Berkman and Eric Plutzer shows why this is the case (see Berkman and Plutzer, 2010, which is a must-read book for anyone interested in the teaching and the public understanding of evolution; see also Berkman and Plutzer, 2011, 2012 for overviews). They estimate that about 28% of US teachers are advocates of evolution and teach it in an appropriate manner; they also estimate that 13% of US teachers somehow advocate Creationism and ID by spending at least one hour of class time on it. Berkman and Plutzer argue that attention should be paid to the 60% of teachers that they call "the cautious 60%," who do not belong to either group of advocates, who cautiously (and reasonably in my view) want to avoid any kind of controversy and of whom 85% accepts evolution. Berkman and Plutzer rightly argue that this "cautious 60%" may do more in hindering scientific literacy than the 13% of explicit advocates of Creationism or ID. An important finding in their survey is that teachers' content knowledge can have a "dramatic effect" on their views and consequently on their teaching practices, as teachers belonging to the "cautious 60%" do not feel confident to teach evolution, although they do accept it. This is a very important point and this is part of the rationale for this book. Instead of trying to show that ID/Creationism is wrong, I have tried to provide the majority of teachers anywhere in the world with a book that explains the conceptual obstacles and the core concepts of evolutionary theory. This book could be used in an undergraduate or a teacher preparation course on evolution, but it could also be read by any biology teacher on his or her own.

I should note at this point that I do not overlook the cultural, religious, worldview, and other issues implicated in the problem of the public acceptance of evolution. I am aware that there are powerful social factors at work, especially among fundamentalist religious believers, that may have nothing to do with conceptual issues. These people usually associate evolutionary theory with a set of liberal values which they perceive as a threat to their own conservative values. They also usually perceive evolutionary theory as a threat to important social and moral issues – and militant modern atheists like Richard Dawkins are in part responsible for this (see Chapter 2 and my Concluding remarks on this). This notwithstanding, context seems to be important for how science is conducted, what conclusions are made, and what its implications are perceived to be. Thus, whether and why people perceive science in general, and evolutionary theory in particular, as a threat to their religious beliefs depends largely on context; generalizations cannot be made. David Livingstone (2003) has argued about the significance of place for the conduct of science, referring to "geographies of scientific knowledge." How science and religion relate to one another also varies around the world (Brooke and Numbers, 2010). However, many excellent treatments of the interplay between science and cultural, social, religious, and worldview factors have already been published. Thus, I have decided not to write much about these issues but to rather focus on conceptual ones, which in my view have not been given the required attention in the literature.

Let me now make clear where I come from and what the specific aims of this book are. I have worked for 12 years as a secondary biology teacher. I have taught evolution to secondary students (in a social context without any serious objection to evolutionary theory, I must note) and I have also conducted research on pre-school, elementary, and secondary students' preconceptions that are relevant to evolutionary theory

(Kampourakis and Zogza, 2007, 2008, 2009; Kampourakis *et al*., 2012a, 2012b). As a result I am quite aware of students' difficulties in understanding evolution. My main aim with this book is to explain to undergraduate students in the life sciences, some of whom may become biology teachers, why evolution is difficult to understand, and the minimum level of knowledge they should acquire. To achieve this, in this book I first discuss religious resistance to accepting and conceptual obstacles to understanding evolution; I then present some central evolutionary concepts in the light of these obstacles. Throughout the book I have tried to write in a comprehensible manner and I have included several figures which will hopefully contribute to a better understanding of the topics discussed. Reference is always made to articles in books and professional journals from various fields: science, history of science, philosophy of science, and cognitive psychology. In doing so, I am trying to fulfill a secondary aim of this book, which is to serve as a guide to a further and more detailed reading. Bringing together conclusions and insights from research in evolutionary biology, history and philosophy of biology, biology education, and conceptual development, this book might also serve as a guiding light to those wishing to learn more in some or all of these domains. The interested reader will find his or her way to additional literature of interest while reading the chapters of this book.

Consequently, this book is intended primarily for students in the life sciences, either at the undergraduate or graduate level. It provides an introduction to evolutionary theory by presenting not only the core concepts, but also the major conceptual obstacles to understanding evolution. The primary audience of this book also includes biology teachers and educators, as the presentation of concepts and conceptual obstacles is directly relevant to teaching about evolution. Students and teachers could read this book on their own, but it could also be used as a textbook in an introductory evolution course. The book will also be useful to curriculum developers, textbook authors, policy makers, journalists, and anyone interested in evolution or involved in the teaching of evolution and/or its public presentation. Finally, it will be of interest to historians and philosophers of science, as well as cognitive scientists who might be interested in reading how their disciplines can contribute to a proper understanding of science.

I hope the presentation of concepts that takes into account the respective conceptual obstacles will be effective in promoting an appropriate understanding of evolution. Since research suggests that adult resistance to science in general, and to evolutionary biology in particular, may originate in childhood, the various conceptual obstacles are addressed in this book by taking into account students' intuitions, especially those related to teleology and essentialism, which generate preconceptions that in turn make evolutionary theory seem counter-intuitive. Readers of the book will realize which obstacles make evolution difficult to understand, as well as why they persist. Hopefully, they will even be guided to overcome these obstacles themselves. Having understood evolution, readers may then realize that science studies the natural world only. If a supernatural realm exists, it cannot be studied by the rational tools of science. Science does not deny the supernatural, but only acknowledges that it has nothing to say about it. Most importantly, science in general and evolutionary theory in particular is a useful tool in our quest to explore nature and understand life; we should not expect more than that. Consequently, this book is explicit not only about the content of evolutionary science, but also about the nature of science in the wider sense: what science is about, and what its aims are.

Overview of contents

The book consists of six chapters and is divided into two parts. The first part includes the first four chapters which address wider issues relevant to understanding and accepting evolution, such as the nature of evolutionary biology (Chapter 1), religious worldviews and how they relate to evolutionary theory (Chapter 2), conceptual issues and obstacles to understanding evolutionary theory (Chapter 3), and the development of Darwin's theory as a historical case study of conceptual change (Chapter 4). The second part consists of two chapters that are more technical than the earlier ones and which present the core concepts of evolutionary theory along with contemporary knowledge about the evolution of life on Earth, focusing on common ancestry (Chapter 5) and evolutionary change (Chapter 6). Each chapter can be read independently; however, it will be useful for the reader to be aware of the discussion of the conceptual obstacles and conceptual change before reading about concepts.

As students are the main target audience of this book, it includes suggestions for further reading at the end of each chapter. Most major books on evolution published so far are included and their contents are briefly described. Students will thus have a guide for exploring further the issues raised in this book. The book also includes a glossary. Although all concepts will be defined and/or explained in the main text, detailed definitions are also included in the glossary. This can be a useful reference tool that, although is intended to complement the text of the book, also stands on its own. Readers will thus be able to read definitions of the most important evolutionary concepts, and in the main text of the book they will also find references to articles and books that provide further analyses of these. In what follows, I outline the contents of each chapter.

In Chapter 1 I explain how evolutionary biologists work in order to obtain data and what conclusions they can make from it. I then go on to elucidate which questions are answered by evolutionary biology, and how it provides understanding of the world around us, focusing on domestication and infectious disease as examples. Particular cases are described in detail, such as the diversity of dog breeds and the AIDS epidemic, and I argue that evolutionary theory provides a sound explanation for what we observe. This introductory chapter outlines the main features of evolutionary processes and shows that the same basic propositions and models can be used to explain a variety of phenomena. The cases described in this chapter are just some representative ones, discussed for illustrative purposes. The logic of evolutionary theory applies to a lot more.

In Chapter 2 I focus on the relationship between evolutionary theory and religion, in an attempt to explain why many people reject evolution. First, I show that human intuitions about design may not stem from religious beliefs, but rather from our understanding of artifacts. People may think of God as the Creator of our world not (only) because they are religious, but due to their intuitions that make them think of the world as an artifact that consequently demands an artificer. I suggest that people may consider evolution incompatible with their beliefs and worldviews not only because they mistakenly perceive the world as an artifact, but also because they inappropriately extend the applications of evolutionary theory to domains beyond the realm of science. To illustrate how even scientists may do this, the views of three evolutionary biologists – Richard Dawkins, Stephen Jay Gould, and Simon Conway Morris – are compared. An atheist, an agnostic, and a religious person, respectively, make conclusions about the implications of evolutionary theory which are influenced by their worldviews and beliefs. I conclude that in order to seek answers to "big questions" it is necessary to distinguish between what one *knows* and what one *believes*. I suggest that making this distinction clear and achieving conceptual understanding of evolutionary theory are prerequisites for accepting it.

In Chapter 3 I focus on obstacles related to understanding evolution. Having already argued in the previous chapter that the conflict with religious views is only part of the problem and that the real problem may be that people intuitively think of the world as an artifact, I focus on conceptual change in evolution. After explaining what conceptual change in science consists of, I discuss in detail two major conceptual obstacles relevant to evolution – namely, design teleology and psychological essentialism. I analyze these from philosophical and psychological perspectives in order to explain why people tend to think intuitively about the world in teleological and essentialist terms and why thinking this way can make the idea of evolution seem counter-intuitive. I argue that conceptual change in evolution can only take place if these obstacles are properly addressed. To make my case, organisms are compared to non-living natural objects and artifacts, and I explain how organisms differ from artifacts and why organisms therefore require different kinds of explanations than artifacts. Artifacts are objects intelligently designed for some purpose; consequently they have fixed essential properties (as a result of their being designed) and they may be said to exist for some purpose (because this is what they were intentionally created for). This is not the case for organisms. If organisms have essences, these are not fixed; if organisms seem to have purposes, these are evolved, natural ones. I conclude that thinking in essentialist and teleological terms for organisms as if they were artifacts is a major issue that may impact understanding of evolutionary theory. Understanding the differences is crucial for overcoming the obstacles and consequently for understanding evolution.

In Chapter 4 I describe the development of Darwin's theory and I also provide an overview of what he actually wrote in the *Origin*. The chapter starts with the context in which Darwin's theory was developed, taking into account the theories and debates before the *Origin*. By the time the *Origin* was published in 1859, Darwin himself had undergone a conceptual change from his initial views in the 1830s and had developed his theory as an alternative to the views of his times, providing a new explanation for both the common features and the distinctive adaptations of organisms. The important point here is that it took Darwin himself a significant amount of time to develop his theory and to overcome his own initial views. Then the conceptual foundations of the *Origin* are presented, focusing on the influences on Darwin's central arguments (transmutation, common descent, and natural selection). What I also emphasize is that, religious reaction notwithstanding, there were important scientific criticisms of Darwin's theory which were well grounded, and that Darwin was well aware of them and had even sincerely admitted some of them in the *Origin*. These criticisms came both from Darwin's supporters such as Huxley, as well from less sympathetic critics such as Owen and Wilberforce. Consequently, there was more in the reaction to the *Origin* than just religious sentiment, and this chapter also aims to show that disagreement on scientific grounds is possible despite personal views.

In Chapters 5 and 6 I provide a philosophical analysis of some core concepts of contemporary evolutionary theory. Chapter 5 focuses on common ancestry. First, I provide an overview of the evidence that supports the common ancestry of life on Earth, describing what the evolutionary network of life is. I also describe the important insights that the study of microbial life brings to our understanding of evolution in particular, and of life more generally. However, since the main problem with understanding evolution is how complex, multicellular organisms have evolved, I turn my attention to vertebrates (the group which includes humans) to show how evolutionary theory can account for the similar characters we find in organisms. These similarities are either homologies due to common descent or homoplasies due to convergence. There seems to be a continuum of phenomena from homology to homoplasy, and it seems that the study of how characters develop is crucial. This is why I then turn to evolutionary developmental biology, which provides novel insights to the evolution of life on Earth by showing how apparently large morphological transitions may not be so difficult to achieve due to shared underlying molecular networks and mechanisms. Thus, similarities between different organisms may be deeper than was previously thought.

Having described what we know about the common ancestry of all life on Earth, in Chapter 6 I describe the processes of evolutionary change. Adaptations, features or properties that facilitate the survival and reproduction of their possessors in a given environment, are outcomes of natural selection. I describe the various definitions of adaptation and the various perceptions of the process of natural selection. I also argue that stochastic processes have an important role in evolution. There is an important component of unpredictability in evolution, which makes it inherently purposeless. History matters, and one problem we have is how to understand macroevolutionary phenomena, such as speciation and extinction. Epistemic access to the past is difficult to achieve, and so in large part evolutionary explanations have a historical dimension. I conclude that the crucial element for historical explanations is antecedent conditions; particular conditions may have a causal influence on natural processes and turn evolution to one or the other direction.

In my Concluding remarks I describe the virtues of evolutionary theory, and I argue that it cannot, and should not, be used to answer all kinds of questions. My final suggestion is that one should try to understand evolutionary theory without worrying about its religious, metaphysical, or other implications. Having achieved this, one could then decide what these implications are. I believe that evolutionary theory has such implications, but these depend on one's worldview; and this is why there is a variety of reactions to the theory, from dogmatic acceptance of it as a form of secular religion to outright rejection as a form of atheistic dogma. I believe that evolutionary theory shows that life has no inherent purpose, but at the same time it has nothing to say about whether one can find purpose or meaning in life. In contrast, I take evolutionary theory to suggest that each of us can find his or her own meaning and purpose in life. Actually, that humans are able to do this seems to me to be a triumph of evolution; believing that I have achieved this myself makes it a joy. This is, in my view, what an understanding of evolutionary theory can offer: liberate one from fatalistic notions and let one understand the world around us and then find meaning in life through religion, philosophy, art, or any other means one wants.

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I have been working on conceptual issues relevant to understanding evolution for more than ten years. I am indebted to Vasso Zogza, my PhD dissertation advisor, who guided me as a graduate student to understand that conceptual development research has a lot to contribute to understanding science concepts. I am also indebted to my old friend Giorgos Malamis, who guided me through my first forays into the vast literature of philosophy and history of science when I was an undergraduate student. All my research in evolution education was conducted in Geitonas School in Athens, Greece, where I worked as a biology teacher for 12 years. I am grateful to Eleftherios Geitonas, founder and director of this school, and to all my former colleagues there who supported this research in many ways.

While I was writing this book, I was also editing a volume entitled *The Philosophy of Biology: A Companion for Educators* (Kampourakis, 2013a). That book includes important contributions from professional philosophers of biology, and editing it has been an intellectually rewarding experience. I benefited enormously for writing this book by editing that one. Throughout the present book are references to chapters of that book which contain extremely useful analyses of important philosophical topics, all written in a very accessible manner.

Last, but not least, I am indebted to the Cambridge University Press staff. I am very grateful to Martin Griffiths, who supported this book right from the start and guided it in the right direction. I am also grateful to Ilaria Tassistro, Beata Mako, Gary Smith, and

Lynette Talbot for their support during the preparation of this book. Finally, I thank Simon Tegg for drawing those figures I could not draw myself.

The first three sections of Chapter 4 draw in part on sections 3 and 4 of Kampourakis and McComas (2010). The first section of Chapter 6 draws in part on section 2 of Kampourakis (2013b). I was able to draw on and use part of that research with the kind permission from Springer Science + Business Media B.V.

Many authors say that writing a book is a very lonely experience. I managed to write most of this book in my home, surrounded by my family. Much of the writing took place late at night, when they were all asleep. However, in many instances I was also writing with my wife and our children around me, during weekends and holidays. Although having them around may sound as if they were a potential source of distraction, seeing them was a kind of inspiration for me. Over the years I have extensively discussed many of the issues raised in the book with my wife, Katerina, my best friend and companion in life who has a background in the life sciences. Her thoughts, comments, and fierce criticism have always been valuable. Moreover, as I was writing I was thinking that this book should be appropriate for our children, Mirka and Giorgos, to read when they grow up. Existential questions will come up at some point and I wanted to be able to give them this book in order to read about how scientists study the natural world and what they can, and cannot, conclude about it. Thus, I have written this book with my own children and their intellectual/conceptual development in mind.

For being a source of inspiration and for making me feel sentimentally rich, I dedicate this book to my family: my wife and our children for turning an inherently purposeless life into a deeply meaningful one.

1 An evolving world

What is **evolution**? One might define it in many different ways. The term "evolution" might refer either to the fact that organisms have changed over the course of eons, or to the process by which this has taken place or to the outcome of this process, which includes both the exquisite adaptations of organisms and their outstandingly common features. As I do many times in this book, I rely on Charles Darwin's *The Origin of Species* (1859),[1] the foundational text of current **evolutionary theory**,[2] to define evolution. Darwin proposed a "theory of descent with modification through **natural selection**"[3] (Darwin, 1859, p. 343), as an explanation for "the origin of species – that mystery of mysteries" (p. 1). In particular, he aimed to explain the origin of the adaptations of organisms: "how the innumerable **species** inhabiting this world have been modified, so as to acquire that perfection of structure and coadaptation which most justly excites our admiration" (p. 3). The phrase "descent with modification" includes the two central ideas of evolution: All organisms are related to each other because they have descended from a common ancestor through a process of modification that has produced new life forms from pre-existing ones. Thus, evolution might briefly be defined as the natural process by which new species[4] emerge as the modified descendants of pre-existing ones. Evolutionary theory is the scientific theory that explains how this process has

[1] The full title of the book was: *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. In the rest of this book I refer to Darwin's book simply as the *Origin*.

[2] It should be noted right from the start that the word theory has an entirely different meaning in science compared to the colloquial use. Thus, in science a theory is not simply a hypothesis, a thought, or a speculation (this is what is usually implied with the everyday use of the word), but rather an area of inquiry with widely accepted principles, methods, and foundations or a body of explanatory hypotheses which are strongly supported empirically (Rosenberg, 2005, p. 69).

[3] One major problem that non-experts face with natural selection is to clearly understand what is selected: genes, individuals, or groups? Different views exist on this and experts describe this as the debate about the **levels of selection** (Okasha, 2006). However, it should be made clear that when experts are talking about natural selection, they are referring to an unconscious process of selection taking place in nature, and not to nature consciously selecting anything. Why non-experts tend to favor the latter sense over the former will be discussed in Chapters 2 and 3. An alternative metaphor to describe this process is environmental filtration (Rosenberg and McShea, 2008, p. 18). However, in this book I will stick with Darwin's metaphor, having clarified that natural selection refers to an unconscious process of selection taking place in nature (which is discussed in detail in Chapter 6).

[4] It is difficult to provide a single definition for this concept (see Wilkins, 2009; Ereshefsky, 2010b; Richards, 2010). I describe these difficulties in some detail in Chapter 6. This concept is used throughout this book, rather loosely, to refer to a group of individuals which are reproductively isolated from other groups and/or

taken, and still takes, place on Earth, with reference to particular, old and current, aspects of life on Earth and to particular episodes of its history. What is most important is that evolutionary theory can account for both the unity and the diversity of life. Life has evolved from one or a few universal common ancestor(s) to many different forms of various shapes, sizes, colors, behaviors, and habits. This notwithstanding, they all share some major **characters**,[5] inherited from the common ancestor(s). Evolutionary theory provides the best explanations (so far) for all these phenomena.

In this chapter I provide a broad overview of how evolutionary biologists work to understand both the common origin and the divergence of various life forms. I focus on how evolutionary biologists study nature and obtain data to construct such explanations and reconstruct past events of the history of life on Earth, based on what is often called the "evidence for evolution," e.g., fossils, biogeography, and DNA evidence. Several books presenting the **evidence** for evolution have been published recently (e.g., Coyne, 2009; Dawkins, 2009; Rogers, 2011). Consequently, in this chapter I only provide some illustrative examples. Then, I turn to particular questions about issues relevant to **domestication** and epidemic infectious disease, which serve as case studies. I argue that evolutionary theory provides rational and legitimate answers to these questions, providing sufficient explanations for what is observed.

Before turning to how scientists study evolution, let me make clear an approach which is central in this book. The study of genes and of gene-related phenomena (changes of gene frequencies; changes of gene sequences, etc.) is central in the study of evolution. However, it is difficult to give a single definition for the *gene* concept (see Burian and Kampourakis, 2013 for an overview). Most problematic is the notion of "*genes for*," i.e., genes that *control*/*encode* **phenotypes**. Genes do not control anything on their own, but operate within cellular environments which affect their expression. If you and I own the same cookbook (DNA) and cook some food, the outcome (phenotype) could be very different even though we have both followed the same recipe (genes). The expression of the **information** in the cookbook (DNA or genes) depends on the cook (developmental system) that will implement it. Consequently, it is useful to mention **development** alongside **heredity**, particularly for multicellular organisms, as developmental processes may produce outcomes different to those expected by reading the DNA sequences alone. To achieve this, throughout the book I refer to DNA sequences which are implicated in phenomena instead of using the overly genetically deterministic language of *genes for* (see Moore, 2002, 2013; Keller, 2010; Burian and Kampourakis, 2013). In a way, this book serves as an experiment to see whether a scientific text can be accurate without any reference to gene **concepts** or "genes for."

genetically distinct. For sexually reproducing organisms, a species is defined as a number of, usually similar, organisms that can interbreed and produce fertile offspring.

[5] To avoid inconsistencies by referring to features, traits, characteristics, etc. interchangeably, I will be using the term "character" throughout this book, defined as any recognizable feature of an organism that can exist in a variety of character states, at several levels from the molecular to the organismal (Arthur, 2004, p. 212).

How we know what we know about evolution

Evolution has been taking place on Earth for billions of years. Consequently, although it is still taking place now, much of the information about it comes from the past. In Chapter 6 I describe the importance of history for evolutionary explanations. For now, let me provide an illustration of how evolutionary biologists work. Imagine that you turn on your TV and start watching an episode of a series you have never watched in the past, although its premiere was 20 years ago. You realize that you know nothing about the characters or their relationships, and the plot is too complicated and you can hardly understand what is going on. However, you find it interesting and decide that it is worth the effort to try finding out more about previous episodes. What you might do is try to find them on DVD, or find some information about them on the producer's official website. You might also look for someone who watched the series for a long time and who might thus give you a narrative of past episodes. Eventually, you might end up with much information that would help you follow the plot and keep watching what has become your favorite TV series.

Unfortunately, studying evolution and obtaining evidence from the past is much more difficult than this. Scientists only have access to what they currently observe; there is no complete record of what happened in the past and, of course, no one was there to witness it. Imagine that in your quest to uncover the plot of previous episodes of your favorite TV series you were unable to find a complete DVD boxset, a website on which the script was available for download, or a friend who had watched it from the very beginning or at least for some time in the past. Imagine that you were only able to find some old episodes from different seasons, a couple of torn pages with a critique of some of the first episodes, some video clips of different episodes uploaded on YouTube without indicating the respective season, and an old interview with one of the members of the cast. What you would have to do would be to watch or read what you managed to obtain and look for clues to events that had taken place in past episodes. But you could also keep watching the current episodes and note down any references to past events that would help you reconstruct the story up to the point that you started watching the series. This is, in part, what evolutionary biologists do. They do not have a direct view of the past, but they can infer past events from what they currently observe. There are three distinct, complementary lines of evidence. The first is quite similar to the one you might try to obtain in your quest to learn more about your favorite series. The other two are more characteristic of doing science.[6]

What evolutionary biologists do is look for evidence of the past, analogous to the torn pages or the YouTube clips. They look for remnants of the history of life on Earth;

[6] Another, perhaps more commonly used, analogy is between an evolutionary biologist and a criminal investigator (e.g., see Cleland, 2002). However, criminal investigators usually investigate individual events (crimes) and do not aim to reveal general patterns (unless a serial killer is involved). Most importantly, they may not be interested in finding out more about sequences of events which may or may not be related. In contrast, to understand what is happening in a TV series, one should try to learn as much as possible about the whole story and not about single events or ones involving individual characters.

these usually exist in rocks and in DNA molecules. For example, human evolution is currently very well understood thanks to both fossil and DNA evidence. This, of course, does not mean that biologists have resolved everything or that no unanswered questions remain. For example, scientists do not agree yet on how exactly humans should be classified. Some scientists use the term Hominini for both chimpanzees/bonobos and humans, whereas others use the term Hominini to refer to the human **clade** only. But this does not mean that any of them questions the fact that the genera *Gorilla*, *Pan*, and *Homo* are closely related.[7] Quite the contrary! Until recently the human clade was distinguished from that of non-human great apes (chimpanzees, bonobos, gorillas, and orangutans) as the Hominidae and the Pongidae family, respectively. However, some scientists now include both humans and great apes under the family Hominidae (Harrison, 2010; Wood, 2010).

Despite the differences between the skeletons of humans, chimpanzees, and gorillas, there also exist some marked similarities noticed since Darwin's time. Darwin refrained from discussing human evolution in the *Origin*, but was aware that his theory would have relevant implications:

> The whole history of the world, as at present known, although of a length quite incomprehensible by us, will hereafter be recognised as a mere fragment of time, compared with the ages which have elapsed since the first creature, the progenitor of innumerable extinct and living descendants, was created. In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history. (Darwin, 1859, p. 488)

Darwin's biographers, Adrian Desmond and James Moore (2009), have made the interesting suggestion that Darwin's hatred for slavery made him want to show that all humans had the same ancestry. However, it was not until 1871 that Darwin made public his views on human evolution by suggesting that "It would be beyond my limits, and quite beyond my knowledge, even to name the innumerable points of structure in which man agrees with the other Primates" (Darwin, 1871, p. 191). He then quoted Huxley who, after studying the available evidence, concluded that:

> The structural differences between Man and the Man-like apes certainly justify our regarding him as constituting a family apart from them; though, inasmuch as he differs less from them than they do from other families of the same order, there can be no justification for placing him in a distinct order. And thus the sagacious foresight of the great lawgiver of systematic zoology, Linnaeus, becomes justified, and a century of anatomical research brings us back to his conclusions, that man is a member of the same order (for which the Linnaean term PRIMATES ought to be retained) as the Apes and the Lemurs. (Huxley, 1863, p. 124)

[7] In many cases those who oppose evolution, for whatever reason, present such disagreements as evidence that science cannot provide conclusive answers. In this case they might consider the fact that some scientists distinguish the human clade from that of the apes, whereas others do not as a controversy pointing to the insufficiency of science, overlooking the fact that all of these scientists consider humans and apes as closely related in an evolutionary sense.

Figure 1.1 The skeletons of gibbons, gorillas, chimpanzees, orangutans, and humans. A picture like this was included in Huxley's book, serving as evidence for the similarities in skeletal structure among these groups. Image © Morphant Creation.

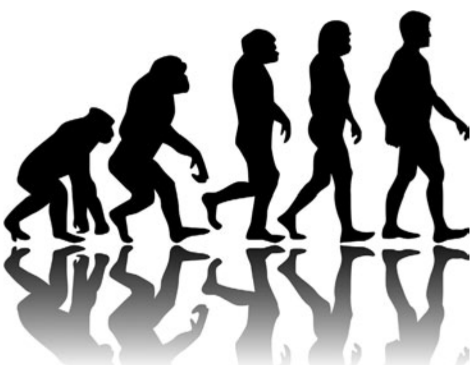

Figure 1.2 One of the usual misrepresentations and wrong portrayals of evolution in general and human evolution in particular. Image © Williammpark.

Figure 1.1 shows the similarities in skeletal structure between humans and the other primates. Since that time, several human fossils have been found (for an overview, see Tattersall, 1998; Wood, 2005). As Darwin had hypothesized, it now seems clear that humans originated in Africa (Tattersall, 2009) and new evidence continuously contributes to a better understanding of human evolution (e.g., White *et al.*, 2009; Berger *et al.*, 2010). However, the idea of evolution in general and of human evolution in particular is usually misrepresented in the public sphere, with illustrations such as the one in Figure 1.2. There are two main problems with this representation of human evolution. First, it portrays evolution as a linear process where each of the species changes into another one. As will be explained in Chapters 4 and 5, evolution is more accurately represented as a branching and not a linear process. Second, this representation shows humans evolving from apes. This is misleading too, because a species cannot evolve from another contemporary species. What is actually happening is that humans and apes share common ancestors, from which they have evolved independently, like branches

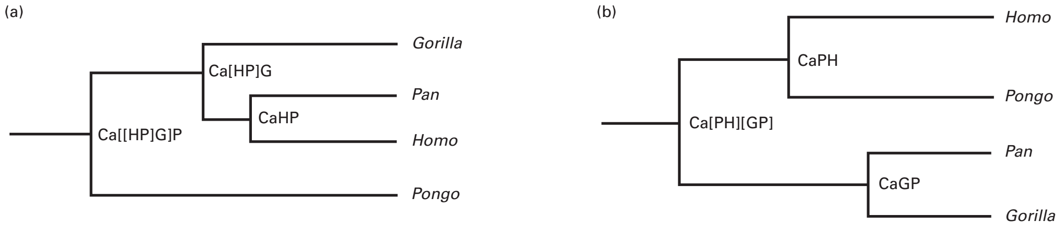

Figure 1.3 (a) Humans and chimpanzees are depicted as the most closely related genera because their common ancestor (CaHP) is closer to the present. These also share a common ancestor with the gorillas (Ca[HP]G), while the orangutans are less related to humans since they share the oldest among the common ancestors (Ca[[HP]G]P) (adapted from Fabre *et al.*, 2009) (*Homo*: humans; *Pan*: chimpanzees; *Pongo*: orangutans). (b) Chimpanzees and gorillas are depicted as the most related genera, sharing a relatively recent common ancestor (CaGP). Humans are depicted closer to orangutans, having diverged from their common ancestor (CaPH) at earlier times, compared to chimpanzees and gorillas. Finally, the two pairs share a common ancestor (Ca[PH][GP]) from which each genus evolved (adapted from Grehan and Schwartz, 2009) (*Homo*: humans; *Pan*: chimpanzees and bonobos; *Pongo*: orangutans). How evolutionary trees are constructed and what kinds of information they provide is discussed in detail in Chapter 5.

starting from a common shoot. Common ancestry and evolutionary change, or descent with modification as Darwin put it, are explained in Chapters 5 and 6, respectively.

Recent advances, such as comparative **genomics** and DNA sequence expression analyses, have contributed to a better understanding of human evolution (Carroll, 2003). Molecular evidence supports the conclusion based on fossils that humans and apes are closely related. A molecular analysis that focused on 27 (from a total of 43 nuclear and 15 mitochondrial) DNA coding sequences, and allowed sampling of 73% to 85% of primate species (Fabre *et al.*, 2009), has concluded that humans are more closely related to chimpanzees (genus *Pan*) than the latter are to gorillas (genus *Gorilla*) (Figure 1.3a). Another line of evidence based on structural, behavioral, and physiological characters, probably not of equivalent status with molecular phylogeny, suggests that humans and orangutans (genus *Pongo*) share a common ancestor not shared by the extant African apes (Grehan and Schwartz, 2009) (Figure 1.3b). Many details on how human evolution actually took place are certainly still missing. Currently we have several scattered pieces of the whole puzzle (Figure 1.4). Nevertheless, the close relatedness between humans and the primates is consistently supported by several different kinds of evidence currently available.

The second line of evidence is a consequence of the ability of evolutionary biologists to make predictions based on existing evidence and test them against it. They might look for particular fossils of particular organisms at particular places, or for particular similarities between specific DNA sequences of certain organisms. Both types of predictions not only have been repeatedly confirmed so far, but have also yielded new evidence of the same kind. You could probably do something like this for your favorite series. You might predict that the producer of the series or a member of the cast would have copies of the old episodes or a copy of the script, and you might look for that person and request these copies. Or you

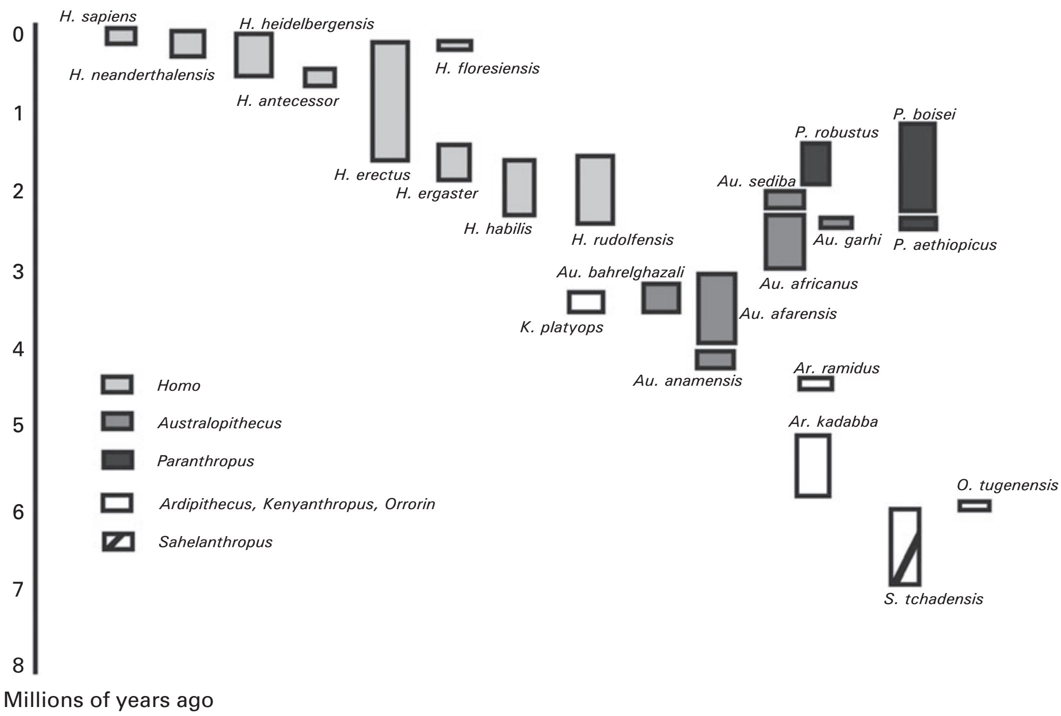

Figure 1.4 This is not an evolutionary tree such as the ones depicted in Figure 1.3, because species are not connected with lines. We only have fragmented data about human evolution; much is still missing. The various boxes have different lengths which correspond to the time length (millions of years) during which scientists have found fossils of these species. The various species are not connected with lines because scientists do not know the exact evolutionary relationships (adapted from Wood, 2010). Missing details notwithstanding, we still have a good sense of how our evolution took place. In this figure two words are used to indicate the name of each species; the first refers to the genus and the second to the species. Our species is described as *Homo sapiens*: the word *Homo* indicates the genus and *sapiens* the species.

might predict that some fans of the series would possess what you want and so you could look for their websites or blogs. You might also post a request on your own webpage. Of course, evolutionary biologists cannot find evidence by sending out calls like "fossils of this and that kind wanted." They have to go and look for these themselves. Nevertheless, they often know quite well where to look for evidence and they have been quite successful in finding it. In some cases their predictions would be more successful than your own on finding out what happened previously in the TV series you are watching, because they can have a more solid basis for making predictions.

Although the evolution of tetrapods (four-limbed vertebrates) from sarcopterygian (lobe-finned) fish was generally accepted, there existed few fossils that might suggest how this evolutionary transition might have taken place. The discovery of *Tiktaalik* in Canada has contributed enormously to current **knowledge** of the transition from fish to tetrapods (Figure 1.5). Its skeleton represents a shift from the structure of primitive sarcopterygian fish, toward the structure of tetrapods (Daeschler *et al*., 2006; Shubin

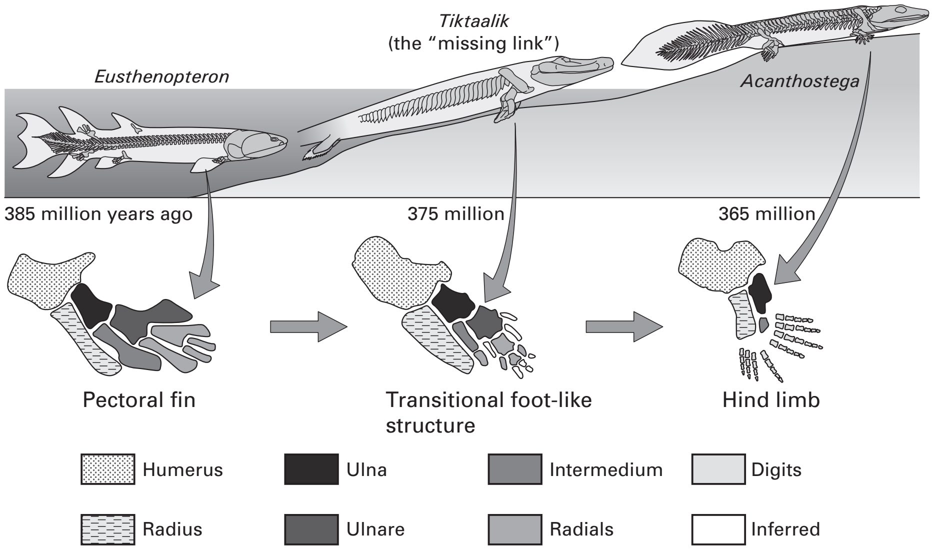

Figure 1.5 The fossils of *Tiktaalik* were found where they were predicted to be and provide evidence about how the transition from fish to tetrapods could have taken place (based on Daeschler *et al*., 2006; Shubin *et al*., 2006). Note that this figure does not present the actual transition, but only how it could have been possible. *Tiktaalik* is not the intermediate form or the "missing link," but one that resembles that. Image © Simon Tegg.

et al., 2006). But what is most interesting is why and how these scientists decided to look for the particular fossils at the particular site they did. In his personal account of the discovery, Neil Shubin (2008, pp. 4–5) wrote that: "Most people do not know that finding fossils is something we can often do with surprising precision and predictability. [. . .] Of course, we are not successful 100 percent of the time, but we strike it rich often enough to make things interesting." Shubin then describes how he and his colleagues took into account previous discoveries and decided where to look for fossils of organisms which would be intermediate forms between fish and tetrapods. They had to find rocks of the right age, of a type in which fossils would have been preserved and exposed at the surface. They were aware that amphibian fossils had been recovered from rocks about 365 million years old and that fish fossils had been recovered from rocks about 385 million years old. Consequently, they should look for transitional forms in rocks aged 365–385 million years old. In addition, knowing that sedimentary rocks usually preserve fossils, they had to look for rocks formed in oceans, lakes, or streams, ruling out volcanic and metamorphic rocks in which fish fossils would not likely be found. Finally, they wanted to find areas that were not inhabited and where fossils might be exposed on the surface of rocks. Shubin and his colleagues concluded that the Canadian Arctic was of the right age, type, and exposure, as well as unknown to vertebrate paleontologists. It therefore fulfilled all their criteria. And it was there, at the Fram Formation in Nunavut Territory, Canada, where *Tiktaalik* was eventually found, as they had predicted (Shubin, 2008, pp. 4–27). This discovery, of course, took much time, money, and effort. What is important is that it was based on valid scientific predictions.

The third line of evidence is even more characteristic of science. Contrary to your favorite series, the story of which was the product of human fiction, the history of life on Earth is the product of actual events that are based on natural causal processes such as mutation/recombination, migration, drift, and selection. Under particular circumstances, these processes can cause evolution of a population. For instance, mutation/recombination can produce new DNA sequences and perhaps new characters in a population. In the subsequent generations the population will be different from the initial one, so evolution will have occurred. In the case of migration, some individuals might migrate to new areas, giving rise to a new population which could be different from the old one if some types of individuals but not others from the initial population migrated. Drift results from the random sampling of individuals independently of the characters they possess and of whether these provide them with a particular advantage or not. Some individuals but not others might reproduce, and so the structure of the population might change; the smaller the population, the more significant the effect would be. Finally, during the process of selection some individuals manage to survive and reproduce because they possess characters which contribute to this, whereas others who do not have them fail to survive or reproduce. These processes are discussed in more detail in Chapter 6.

Scientists can make predictions for future outcomes based on their understanding of how these processes take place.[8] Let me give an example. Imagine: a population consisting of green beetles and brown beetles, of the same species, exists in a forest; their color is an inherited character, the **allele**[9] for brown color is dominant[10] and **heterozygotes**[11] exhibit brown color; birds can spot the green beetles on the ground and on the trunks of trees more easily than the brown ones; birds can also spot the brown beetles on the leaves and on the green parts of the plants more easily than the green ones; under these conditions both types of beetles exist in a particular ratio (25% green, 75% brown) in the particular region. It can be predicted that under particular environmental conditions such a population may evolve.

If a new predator is introduced, which lives on the ground and is unable to spot the brown beetles and thus feeds only on green ones, after a number of generations the total number of brown beetles will probably rise. Brown beetles have an advantage because they are concealed in the soil, whereas the green ones are more prone to becoming prey for the new predator on the ground. Consequently, one can make the prediction that

[8] Whether these processes are based on laws or law-like (nomological) principles is a discussion that goes beyond the scope of this book (see Sober, 1997; McShea and Brandon, 2010).

[9] An allele is one of several variants of a particular DNA sequence that "encodes" a particular protein or RNA molecule and thus affects a particular biological process. Alleles are identified with particular parts of chromosomes which are described as loci (sing. locus).

[10] Dominance is a concept you probably heard of in your high-school genetics courses: a dominant allele is the one that is "expressed" and the recessive is the one that is not "expressed" when carried together by the same (heterozygous) organism. This concept is problematic as it actually refers to a minority rather than a majority of cases (see Allchin, 2005; Jamieson and Radick, 2013). However, for the purpose of comprehensiveness I will occasionally use the typical terminology of Mendelian genetics taught in high-school biology as most readers of this book will probably be familiar with it.

[11] An individual that carries two different alleles is called a heterozygote. An individual that carries the same allele on both homologous chromosomes is called a **homozygote**.

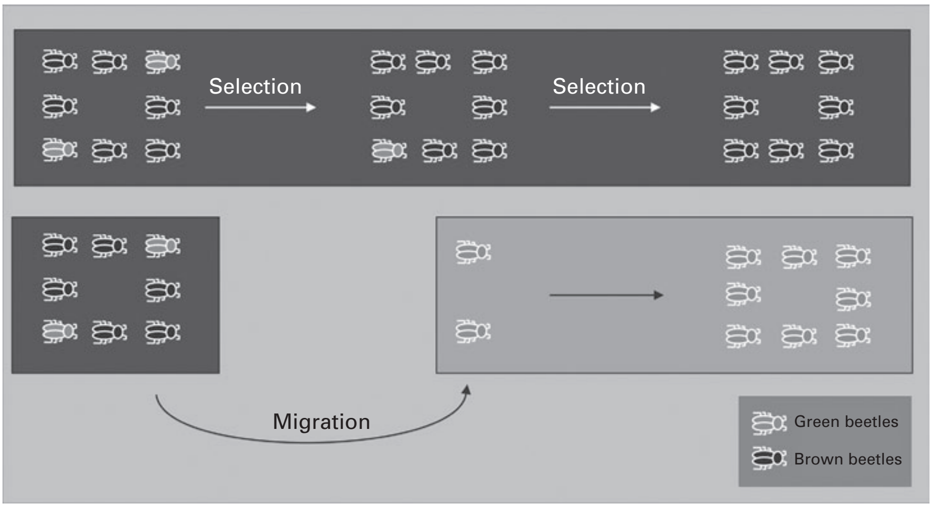

Figure 1.6 Selection and migration; in each case ratios rather than actual numbers of organisms of each type are depicted (see text for the details of the processes).

after a number of generations the population will probably change to one consisting mostly of brown beetles. This will be due to the fact that the brown beetles (and/or the DNA sequence involved in the production of brown color) will be selected. When there is genetic and consequently phenotypic[12] variation in a population (the green and brown colors are inherited characters, i.e., are produced through the expression of particular DNA sequences), natural selection may occur. Not all organisms are equally able to survive and reproduce in a particular environment; some will, others will not. The former are those which are said to be selected. Of course, there is no external agent doing any kind of selection, but one might think that the environment drives the (unconscious) selection of some organisms while others die out. Given this, we can predict that the green beetles in this area will at some point die and the initial population will evolve to one consisting exclusively of brown beetles (Figure 1.6).

Now, consider again the initial population that consisted of 75% brown beetles and 25% green beetles. Imagine that some green beetles only, but not a single brown one, happen to migrate to another area, where they can survive and reproduce without any significant selection pressure. Although brown beetles were greater in number in

[12] Which alleles an individual possesses is its genotype. The outcome of the expression of these alleles is described as its phenotype. Alleles may interact in various ways in producing the phenotype. A homozygous individual usually has a particular phenotype, which is determined by its alleles. According to Mendelian genetics usually taught in high-school biology, in a heterozygote one allele may be expressed (dominant) while the other is not (recessive) or in other cases both alleles may contribute to the phenotype observed (co-dominant). It should be noted, though, that how alleles influence phenotype is much more complicated than this simple description because the effect of an allele at one locus may hide the effect of an allele at another locus (**epistasis**) or affect multiple phenomena within the organism (pleiotropy) when, e.g., a protein performs multiple distinct functions or is expressed in multiple tissues (see Stern, 2011 for details).