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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

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[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."

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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;

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[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)

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[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.

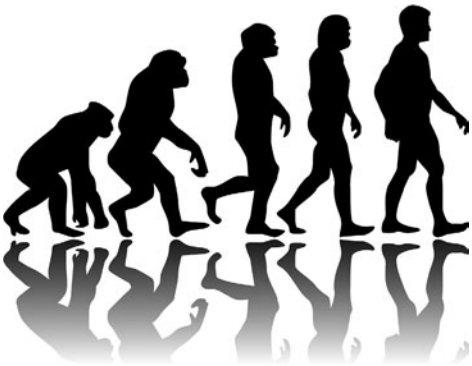

Figure 1.2 One of the usual misrepresentations and wrong portrayals of evolution in general and human evolution in particular. Image © Williammpark.

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

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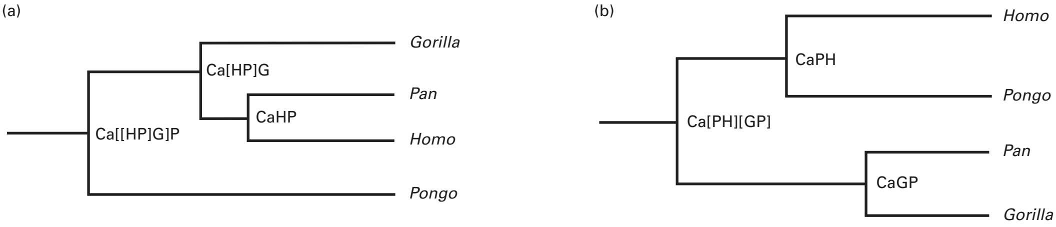

Figure 1.3 (a) Humans and chimpanzees are depicted as the most closely related genera because their common ancestor (CaHP) is closer to the present. These also share a common ancestor with the gorillas (Ca[HP]G), while the orangutans are less related to humans since they share the oldest among the common 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

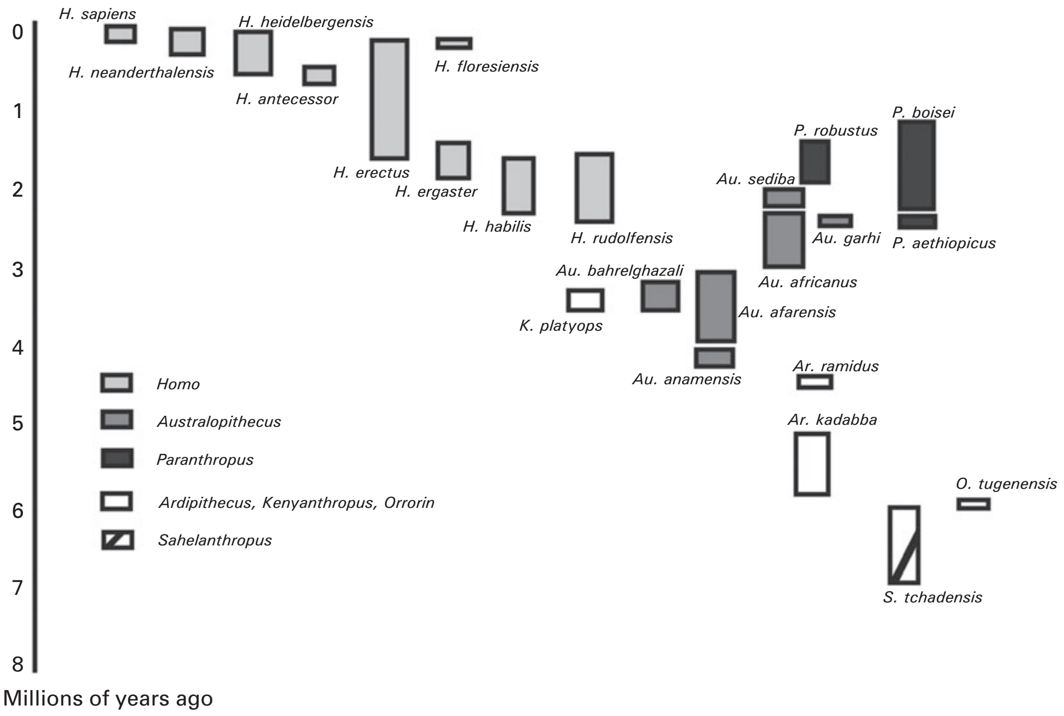

Figure 1.4 This is not an evolutionary tree such as the ones depicted in Figure 1.3, because species are not connected with lines. We only have fragmented data about human evolution; much is still missing. The various boxes have different lengths which correspond to the time length (millions of years) 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

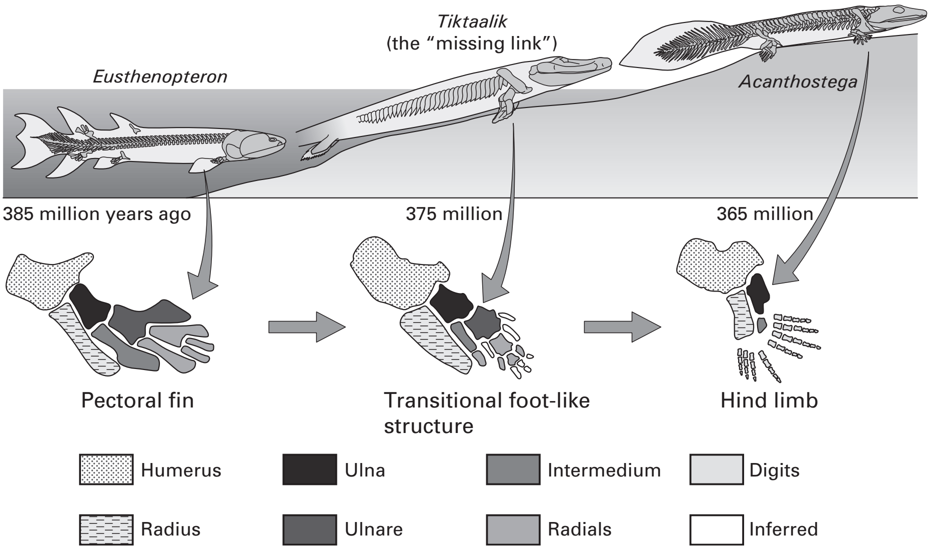

Figure 1.5 The fossils of *Tiktaalik* were found where they were predicted to be and provide evidence about how the transition from fish to tetrapods could have taken place (based on Daeschler *et al*., 2006; Shubin *et al*., 2006). Note that this figure does not present the actual transition, but only 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.

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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

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[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**.

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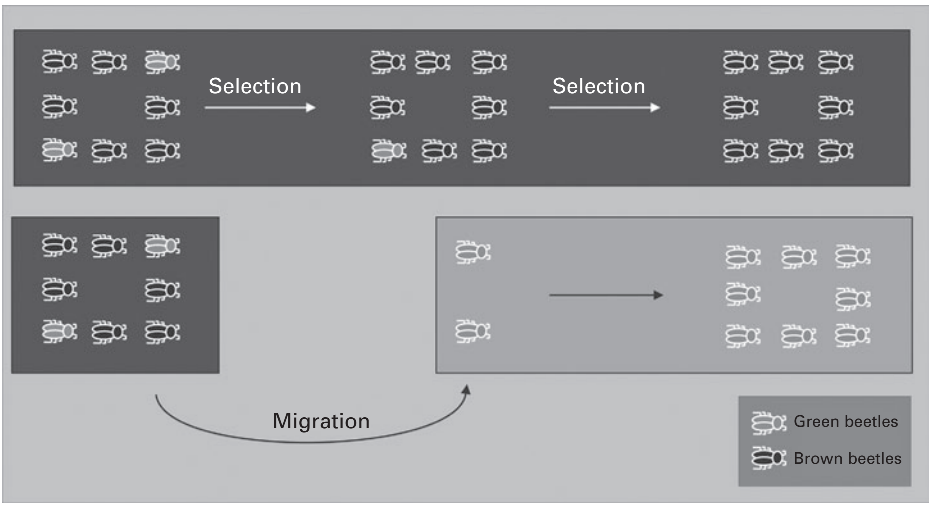

Figure 1.6 Selection and migration; in each case ratios rather than actual numbers of organisms of each type are depicted (see text for the details of the processes).

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

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[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).