

Evolutionary History

*Uniting History and Biology
to Understand Life on Earth*

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Matters of Life and Death

When I was thirteen, my grandfather died of a heart attack. He had entered the hospital for treatment of a prostate problem. Once there, he picked up an infection that led to heart failure. His death saddened me, of course, but it also puzzled me. I had seen wonder drugs such as penicillin cure ailments plaguing members of my family, so I could not understand why similar drugs would not have controlled my grandfather's infection. It seemed especially odd that he died in a hospital, where he should have benefited from the best treatment available. But the shelf of memory devoted to unsolved mysteries is long and dark, and I stored my grandfather's death there for decades.

Recently, I realized that a potential solution to the puzzle glowed on the computer screen in front of me. My grandfather's death might have been an example of this book's argument: people have encouraged evolution in populations of other species, which in turn has shaped human experience. I had known for decades that pathogens evolved resistance to antibiotics, but I had never applied that idea to the death of a loved one. The realization sent my heart racing and my fingers trembling so much I could not type for an hour.

Here is what might have happened. Before my grandfather arrived, doctors at a hospital in Omaha used a certain antibiotic (such as penicillin or a newer drug) after surgery to prevent and treat infections. It worked effectively. However, with time, a population of pathogenic bacteria living in the hospital evolved resistance to the drug. Alternatively, this strain may have evolved elsewhere and arrived at my grandfather's hospital in the body of a patient. (If evolution of resistance sounds mysterious, Chapter 2 is for you. For now, please take my word that

populations of pathogens can evolve resistance to antibiotics.) Because this population differed in a trait (drug resistance) from other populations of the same species, we call it a **strain**.

Initially, doctors did not realize that a new, resistant strain had infected their patients, so they continued prescribing the same antibiotic that had worked in the past. Bacteria belonging to that strain traveled from one patient to the next on equipment and the hands of hospital personnel. Some rode a catheter into my grandfather's urinary tract, thrived despite antibiotic treatment, challenged a weakened body, sparked a fever (which stressed his heart), and contributed to my grandfather's death.

We can predict the fate of the pathogenic strain with some confidence because the pattern has repeated itself in hospitals around the world. After enough failures, doctors realized that the drug had lost potency against the pathogen in their hospital. They substituted a second antibiotic drug, the hospital's population of bacteria evolved resistance to it, doctors substituted a third antibiotic, and so on up to the present.

As for my grandfather and pathogens, so for the world. This book makes four arguments that help us understand events ranging in scale from the personal to the global:

1. People have shaped evolution in populations of human and non-human species.
2. Human-induced evolution has shaped human history.
3. Human and nonhuman populations have coevolved, or continually changed in response to each other.
4. A young, synthetic field called *evolutionary history* can help us understand the past and present better than history or biology alone.

We shall see evidence for these arguments and their implications throughout the book. Here let me list some examples to illustrate their significance:

1. Human beings shape evolution today more powerfully than any other species. We have encouraged game animals and fish to shrink in size, pathogens and pests to evolve resistance to poisons, and domestic plants and animals to display traits we value. Organisms evolve in specific **environments**. We have modified terrestrial and marine environments over vast areas. Today our (probable) effect on climate is influencing the evolution of populations of species around the globe.

2. **Anthropogenic** (human-caused) evolution made possible the most important transition in human history, the agricultural revolution of about twelve thousand years ago, which was essential for nearly everything historians traditionally have studied. The agricultural revolution was an evolutionary revolution. It led to settled societies, which produced writing, class conflict, classical Greek philosophy, capitalism, nation-states, complex technologies, Kabuki theater, the Federal Reserve System, and management by objectives.
3. Anthropogenic evolution sparked the second most important transition in human history, the Industrial Revolution of the late eighteenth and early nineteenth centuries. One of the leading edges of the Industrial Revolution was mechanization of cotton textile manufacturing, which depended on the long, strong cotton fibers that Amerindians (peoples who inhabited the Americas before Europeans) had encouraged to evolve.
4. Coevolution between people and populations of agricultural species may have been responsible for the evolution of light skin, the trait that racists and segregationists used to divide social groups.
5. Linking history and biology in the new field of evolutionary history enables us to understand events more fully than either discipline can achieve in isolation. History may explain why my grandfather entered a hospital, but traditional historical approaches would have little to say about why an antibiotic would fail. Biology can explain the antibiotic failure, but it would have little to say about the rise of the organizations and technologies that brought antibiotics and pathogens together in the first place.
6. Social forces have been evolutionary forces. Historians usually study the impact of human beings on each other, but nearly all fields of history could widen their understanding of impact to include the evolution of populations of other species. Few political historians, to pick one example, have written about state building as an evolutionary force, but we shall see that the strengths and weaknesses of states have influenced the evolution of populations of elephants and mountain goats. Similarly, biologists could include state capacity as one of the variables in evolutionary models.
7. Anthropogenic evolution has been a social force. The previous point emphasized that historians can extend their understanding of impact beyond the human realm to include evolution in nonhuman species. Similarly, we can extend our understanding of causation

beyond the human realm to include evolution. Manipulating the traits of populations of agricultural species has enabled states to conquer other states.

Subsequent chapters develop these arguments in stages. Chapters 2–8 explore the first argument, that *people have shaped the evolution of other species*. Chapter 2 defines evolution, explains how it works, clarifies the ability of human beings to influence it, and defines key terms (which also appear in the glossary). Chapters 3–8 provide examples of anthropogenic evolution, organized by types of human activity. We will look at hunting and fishing, eradication of organisms, environmental modification, domestication, intentional evolution, and coevolution.

Chapters 3–8 also develop the second argument, that *anthropogenic evolution has shaped human history*. We will see how changes we have wrought in populations of other species have circled back to shape human experience. Anthropogenic evolution has boosted and reduced our food supply, helped and harmed our health, added to and cut the cost of agriculture and medicine, perhaps helped rebels and cocaine producers circumvent government control, and expanded the gross national product of nations.

Chapter 8 explores the third argument: *people and populations of other species have coevolved*. This argument looks beyond one-way impacts to trace ways in which populations of people and other species have repeatedly evolved in response to each other.

Chapter 9 applies the ideas from previous chapters to show how evolutionary history can change our understanding of well-studied historical episodes. I will use one of the most important transitions in history, the Industrial Revolution, to make this argument. Scholars usually credit the English, their inventions, and their organizations with creating the Industrial Revolution. Using the history of the cotton industry as a case study, Chapter 9 suggests that anthropogenic evolution made the Industrial Revolution possible. The introduction of extra long cotton fiber from the New World, I suggest, enabled inventors to develop machines to spin and weave cotton. Extralong fiber evolved in the New World as a result of selection by Amerindians, so the Industrial Revolution in cotton was a response to anthropogenic evolution in the New World.

I hope these chapters will convince you that a synthetic field called **evolutionary history** can help us understand the past better than history or biology alone. Biologists already use *evolutionary history* to refer to the ancestry of species (as in the evolutionary history of elephants).

I propose broadening the term to mean the field (or research program) that studies the ways populations of human beings and other species have shaped each other's traits over time and the significance of those changes for all those populations.

Evolutionary history has the potential to expand the scope of many fields. As examples, I spell out implications for two fields – environmental history and history of technology – in Chapters 10 and 11. These chapters aim not to provide exhaustive reviews of the literature but rather to show how these fields lay the foundation for evolutionary history and could benefit from it. I envision evolutionary history as a crosscutting approach to scholarship rather than as a stand-alone field. In the concluding chapter, I suggest ways that evolutionary history might shape other fields of history as well.

One of the central goals of this book is to contradict the sense many of us have that evolution is something that happens “out there” – well away from us in time, well away from us in space, well away from us as a species, and certainly well away from us as individuals.¹ My grandfather's experience with evolution took place in an ordinary hospital in an ordinary city as a result of ordinary actions by ordinary people performing ordinary jobs with ordinary patients from ordinary families living ordinary lives.

Evolution is ordinary, not exceptional. It happens all around (and inside) every one of us – you, me, and the dog next door – every day. We rarely notice it, but it shapes our lives continually.

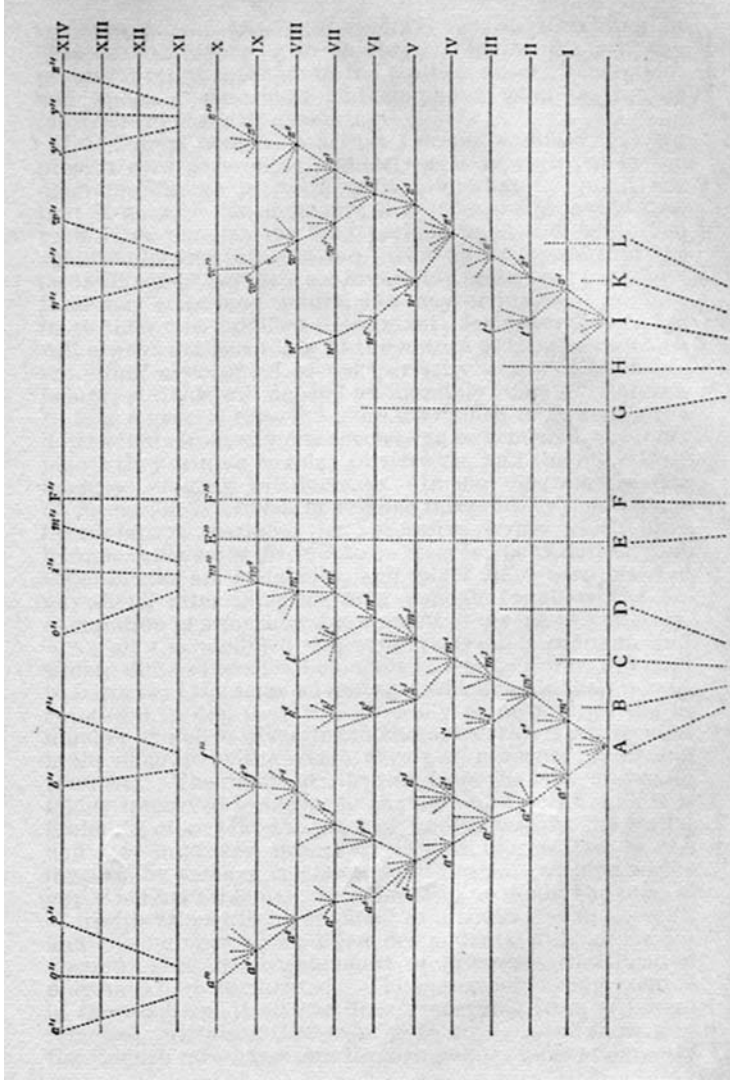
Evolution's Visible Hands

When discussing the ideas in this book with others, I have come to recognize a certain puzzled look. It usually involves a knitted brow and occasionally a sideways tilt of the head. Then a hand rises and objections follow. One of the most common objections has to do with the definition of evolution: “I think of evolution as **speciation**,” people have said. “Are you saying people create new species? Didn’t speciation take millions of years to accomplish, and didn’t it finish a long time ago?” Another common protest has to do with the mechanism of evolution: “Darwin showed that evolution happens because of natural selection. What you are describing is artificial selection, so it does not qualify as the same thing Darwin described at all. That is not real evolution.” If you have similar questions or objections, this chapter is for you.

The goals of this chapter are (1) to explain why processes described in this book qualify as evolution, (2) to provide a primer (or refresher) on ideas about evolution that will be essential for understanding the rest of this book, and (3) to clarify terminology. We will look at current concepts of evolution, list essential elements, and watch those elements at work in the wild and in everyday life. We will clarify the meanings of terms such as *natural selection*, *artificial selection*, *anthropogenic evolution*, *drift*, *sampling effect*, and *extinction*. If all these ideas are familiar to you, please feel free to skip to the next chapter.

It is not hard to see why many of us would equate evolution with speciation. The latter is the evolutionary outcome that has grabbed most of the headlines and sparked most of the controversy. Charles Darwin focused attention on speciation in the title of his landmark book *On the Origin of Species* (Figure 2.1), and for 150 years, religious fundamentalists

FIGURE 2.1. Darwin's branching bush of evolution. Darwin used this diagram to illustrate the idea that new species evolved from older species. Each branch (A-L) represents an ancestral species and its descendants. The diagram shows change through time, with the top horizontal line representing the present day and the bottom line representing an earlier era. Branches that end before reaching the top line represent extinct species. One can use the same diagram to represent the evolution of varieties and populations, although it would be more accurate to include horizontal lines to indicate that populations and varieties interbreed with each other. Darwin pointed out that there was no clear division between varieties and species. (From Charles Darwin, *On the Origin of Species by Means of Natural Selection; or The Preservation of Favoured Races in the Struggle for Life* [London: Odhams Press, [1859] 1872], 127.)



have challenged the idea that human beings evolved from other species rather than arriving on earth wholly formed on the sixth day of God's creation. They have sought to ban the teaching of evolution in public schools because of this aspect of evolutionary theory.

Biologists think of evolution as a broader process than speciation alone. To understand why, let us look at an example from the islands that Charles Darwin helped make famous: the Galapagos. Peter and Rosemary Grant of Princeton University began studying birds there in 1973. They and their collaborators have shown that the traits of finch populations change rapidly. During a drought in 1977, for example, the supply of small seeds on one of the islands plummeted, forcing finches to rely on big, tough seeds for food. Finches with bigger beaks opened these seeds more easily than finches with smaller beaks, and bigger-beaked individuals survived more often than their smaller-beaked relatives. Offspring resemble their parents when it comes to beak size, and the average size of beaks increased in the next generation.¹

The increase in beak size fits the definition of **evolution** that is common among biologists: *change in inherited traits of populations over generations.*² This definition requires several things, some explicit and others implicit, that we can illustrate with the finches:

1. **A population**, which we can describe roughly as *a group of individuals of a given species living in a certain place*. The population we mentioned consists of members of a species of ground finch (*Geospiza fortis*) living on one island (Daphne Major) in the Galapagos.
2. **Variation** among individuals in **heritable** traits. Within the ground finch population on Daphne Major, individuals grow beaks of various sizes. Big-beaked finches have big-beaked offspring, and small-beaked finches have small-beaked offspring.
3. **Reproduction**, which is essential to pass traits to future generations.
4. **Change in inherited traits of a population over generations**. The average size of beaks in this population increased from one generation to the next.

Note that this definition does not require several things that many of us associate with evolution. It does not limit evolution to speciation because any change in traits in a population qualifies. It does not require millions of years because a population can evolve in just one generation. It does not require natural selection because the mechanism for change in traits goes unspecified. (The finch population did change as a result of natural selection, but the definition allows other mechanisms as well. We will see

TABLE 2.1. *Understanding of Evolution*

Criterion	Popular Ideas	Evolutionary Biology
Definition of evolution	Speciation	Change in traits of populations over generations
Most common form of evolution	Speciation	Changes in populations short of speciation
Reason for speciation	Goal of evolution	One outcome of evolution, which has no goal
Direction of evolution	Toward speciation	Multiple, changing directions
Time required for evolution	Long (thousands or millions of years)	Long or short (hours for bacteria)
Cause of evolution	Natural selection only	Anything that influences traits of populations over generations, including natural selection, sexual selection, methodical selection, unconscious selection, sampling effects, genetic engineering
Role of people in evolution	None – we cause artificial selection, not natural selection	Important because we affect traits of many populations over generations
Composition of species	Unitary	Made up of populations with overlapping genes and traits
Options people create for species	Survive in same form or go extinct	Survive in same form, evolve, or go extinct
Extinction	Only species can go extinct	Any population can go extinct
Status of evolution today	Largely complete	Continuing (no more complete or incomplete than other periods)

Note: Not everyone thinks of evolution the same way as evolutionary biologists. This table highlights some of the most common differences. This book builds its arguments on the ideas in the evolutionary biology column.

examples later.) The definition does not require that we exclude human beings as evolutionary forces because it does not limit evolutionary forces to so-called nature. Finally, it does not require that evolution be random because the definition is silent on intentionality (Table 2.1).

Those who believe evolution happens only as a result of natural selection might be shocked to learn that Charles Darwin identified not one but four types of **selection**. Two of them occur in the wild. The first and most famous is *natural selection*, which Darwin defined as “the preservation of favourable individual differences and variations, and the destruction of those which are injurious.”³ Darwin considered natural selection to be the most important force driving evolution. The second is *sexual selection*, which Darwin described as “a struggle between the individuals of one sex, generally the males, for the possession of the other sex. The result is not death to the unsuccessful competitor, but few or no offspring.”⁴

The other two occur under domestication. One is *methodical selection*. Darwin wrote, “Nature gives successive variations; man adds them up in certain directions useful to him.” Darwin thought this process helps create breeds of animals and plants that are well adapted to human desires.⁵ The other is *unconscious selection*. Darwin believed that this process “results from every one trying to possess and breed from the best individual animals. . . . [The owner] has no wish or expectation of permanently altering the breed. . . . This process, continued during centuries, would improve and modify any breed.”⁶

The striking fact about this list is that Charles Darwin included things that many of us believe Darwinian evolution excludes. Changes short of speciation? Check. Mechanisms other than natural selection? Check. Human beings as evolutionary actors? Check. Domestic plants and animals? Check. Human intentionality? Check. It is not Darwin’s fault if, in popular retelling, people have confined his ideas to natural selection.

These clarifications make it easier to see why events in my grandfather’s hospital (see Chapter 1) qualify as evolution. We saw four elements coincide to shape evolution among finches in the distant and exotic Galapagos. The same four elements shaped evolution among pathogens in the more familiar setting of a hospital room in the United States:

1. **A population of a pathogenic species lived in a hospital** (more specifically, in the hospital’s patients). We do not know the name of the species, but we know it existed because it caused infections.
2. **There was variation in a heritable trait.** In one or more patients, some individual members of the pathogen population survived treatment with an antibiotic, and some did not. We call the individual pathogens that survived treatment **resistant** and those that did not **susceptible**. Individual pathogens inherited resistance or susceptibility from the previous generation.

3. **Reproduction occurred.** Members of the pathogen population reproduced themselves in patients. Hospital equipment and personnel helped the population survive by carrying its members (germs) from one patient to the next.
4. **Change in inherited traits of a population over generations occurred.** Before doctors used an antibiotic on patients in the hospital, most individual pathogens in the population were susceptible (otherwise, doctors would have abandoned the drug immediately). One or more generations later, resistant individuals made up a higher percentage of the pathogen population than they did before the antibiotic arrived.

Our understanding of the second element, inheritance of traits, has changed over the past 150 years. Darwin's study of breeding convinced him that parents passed traits to their offspring, but the mechanism stumped him (a fact he freely admitted). It was hard to fathom, for example, how a trait might appear in one generation, disappear in the next, and reappear in the following.

Darwin made a game effort by hypothesizing a mechanism he called *pangenesis*, in which individual parts of the body throw off *gemmules* that concentrate in sperm and egg. As an offspring develops from the fertilized ovum, the parents' gemmules travel to the appropriate body parts in the offspring. If external conditions alter a part of the parent's body, that part throws off modified gemmules and the offspring inherits modified traits.⁷ Darwin's hypothesis might come as a surprise. Many of us learned to contrast Darwinian evolution with **Lamarckian evolution**, the key difference being that Darwinian evolution rejects the idea of inheritance of acquired traits, whereas the latter embraces it. In fact, Darwin and Lamarck both believed in inheritance of acquired traits.

The development of the field of genetics supplied a more durable mechanism than Darwin's gemmules. Gregor Mendel and others documented predictable patterns of inheritance that involved, among other things, dominant and recessive traits. Biologists dubbed the hypothesized units that controlled traits *genes*. Over the twentieth century, scientists figured out that genes were stretches of DNA that carried instructions for cell functioning. Some geneticists broadened their perspective from genes as traits of individuals or families to genes as traits of populations, giving rise to the field called population genetics.

In the mid-twentieth century, evolutionary biologists and population geneticists merged their insights in the modern (or neo-Darwinian)

synthesis. The synthesizers held that the laws of genetics and evolutionary biology were compatible. Though this idea may seem obvious today, it was not so clear early in the twentieth century. In the synthesis, genes explained inheritance of traits, genetic variation explained variation in traits, and mutations explained the generation of new traits. The synthesizers placed populations at the center of evolutionary processes, and they credited natural selection with the biggest role in driving evolution. The neo-Darwinian synthesis remains the dominant model in evolutionary biology today.⁸

The synthesis led to a new definition of **evolution** as *changes in the genetic makeup of populations of organisms over generations*.⁹ This definition is common among biologists but unfamiliar to many members of the public. The key idea is that genetic change is the measure of evolution. If even a single gene becomes more or less common in a population over generations, evolution has occurred. One of the most important benefits of this definition is that it helps us understand evolution across all scales, from individual populations to species and on up to kingdoms. There is no difference in mechanism between what some call microevolution and macroevolution. The degree of change differs across scales, but the process does not.

Recent discoveries in a field known as **epigenetics** have challenged the dogmas that limit evolution to genetic inheritance and exclude the inheritance of acquired traits. It appears that the addition or removal of a certain chemical structure (methyl) on DNA can turn genes on or off, which in turn can influence the traits of organisms. It also appears that offspring can inherit methylation from their parents. Methyl groups are not genes, so they do not qualify as genetic inheritance, but they do provide a nongenetic means of inheriting acquired traits. Epigenetics is a young, fast-changing field that might lead to revisions in the neo-Darwinian synthesis.¹⁰

Readers familiar with the term **artificial selection** may wonder why it rarely appears in this work. It is, after all, a popular term. A Google search for it turned up 311,000 hits. Biologists have applied it to processes described in this book such as the development of resistance and breeding. It is a legitimate term but one I avoid because it obscures more than it clarifies.

One source of confusion is disagreement over the meaning of *artificial selection*. Some authors, especially in textbooks, have more or less equated the term with breeding. Following are a couple of examples:

- Douglas Futuyma's evolutionary biology textbook defines *artificial selection* as "selection by humans of a consciously chosen trait or combination of traits in a (usually captive) population; differing from natural selection in that the criterion of survival and reproduction is the trait chosen, rather than fitness as determined by the entire genotype."¹¹
- Helena Curtis's introductory biology textbook defines *artificial selection* as "the breeding of selected organisms for the purpose of producing descendants with desired traits."¹²

Both definitions highlight a conscious desire to shape future generations, human control of reproduction, and the development of desirable traits.

Other biologists have used *artificial selection* to refer to processes with opposite features – accidental effects on future generations, no human control of reproduction, and the development of undesirable traits. Following are examples from the peer-reviewed literature:

- Stephanie Carlson et al. describe trait-selective harvesting (catching big fish, in this case), which accidentally leads wild fish populations to become smaller, as *artificial selection*.¹³
- Jean-Marc Rolain et al. describe the evolution of pathogens resistant to multiple antibiotics as *artificial selection*.¹⁴

Biologists use *artificial selection* in contradictory ways, but they agree on one thing: artificial selection is something people do. In practice, if not in theory, then, the major job of *artificial selection* is to separate human beings from all other actors (which we usually call *nature*). The first definition of *artificial* in the *Oxford English Dictionary* is "opposed to natural." Every time we use *artificial selection*, we confirm our self-image. If we are fundamentally different from nature, then our actions and their effects are also fundamentally different. Once *artificial* slips its nose into the evolutionary tent as a synonym for *human-influenced*, it wastes little time dragging in other meanings. Two of the most insidious are *false* and *feigned*. Familiar with artificial flowers and artificial fruit, we might easily conclude that artificial selection is an imitation of real selection. This conclusion would, quite logically, lead us to see the effect of artificial selection as imitation evolution. But this idea is mistaken. Changes in traits of populations are just as real whether they take place on a remote island or in a barnyard.

To head off the confusion created by *artificial*, this book relies on terms such as *human-induced*, *human-shaped*, and *anthropogenic*. These terms (which I use interchangeably) identify human beings as evolutionary actors without implying that the effects of our own species are any less real or important than those of other species. My preferred terms also enable us to sidestep the confusion over whether *artificial selection* includes accidental impacts. When intentionality or its absence matters, I rely on Darwin's adjectives *methodical* and *unconscious*.

Given that authors attribute the term *artificial selection* to Darwin, it is worth clarifying that the evolutionist did not push the term very hard. He did use it in contrast with *natural selection*, but he never defined it or listed it in his taxonomy of selection. *Artificial selection* appears twice in *On the Origin of Species* and once in *Variation of Animals and Plants under Domestication*. The latter is a detailed, two-volume study of plant and animal breeding, so the term's lone appearance is striking. *Artificial selection* does not appear in the indexes to *Origin* or *Variation*. As we saw earlier, Darwin did highlight two other terms for human actions: *methodical selection* appears seven times in *Origin*, twenty-three times in *Variation*, and in the indexes of both books; *unconscious selection* appears seven times in *Origin*, forty-three times in *Variation*, and in the indexes of both books.¹⁵

Darwin may have used *artificial* sparingly because he ranged types of selection along a continuum rather than assigning them to separate boxes. Methodical selection anchors one end. It shades into unconscious selection, which shades into natural selection at the other end.¹⁶ In a passage worth quoting at length, Darwin took to task authors who cleaved the continuum into the artificial and the natural:

Some authors have drawn a wide distinction between artificial and natural breeds; although in extreme cases the distinction is plain, in many other cases it is arbitrary; the difference depending chiefly on the kind of selection which has been applied. Artificial breeds are those which have been intentionally improved by man. . . . The so-called natural breeds, on the other hand, . . . have been rarely acted on by man's intentional selection; more frequently by unconscious selection, and partly by natural selection.¹⁷

We owe Darwin's most famous term, *natural selection*, to his desire to emphasize commonalities rather than contrasts between human and natural selection. In the nineteenth century, *selection* referred to what we call *breeding* today. Darwin's readers knew that *selection* involved human actions, so he had no need to add *artificial* to imply human action.

Quite the opposite: he had to add *natural* to give the term a new twist. It was a risky move. As he noted, “the term ‘natural selection’ is in some respects a bad one, as it seems to imply conscious choice.”¹⁸ But Darwin thought the risk was worthwhile because he wanted to blow down the walls separating the human from the natural. He wrote, “The term [*natural selection*] is so far a good one as it brings into connection the production of domestic races by man’s power of selection, and the natural preservation of **varieties** and species in a state of nature.”¹⁹

Another term that can spark confusion is *extinction*. Consistent with the idea that evolution equals the birth of a species, many of us have the idea that extinction equals the death of a species. This belief has led to objections when other taxonomic units, such as varieties of plants or breeds of animals, are described as going extinct. The broader view of evolution developed in this chapter points a way out of this confusion. Populations stand at the center of evolution. In some cases, we aggregate populations into entities we call *varieties* and *species*. The extinction of a variety or species happens when all its populations disappear, that is, go extinct. Extinction, like evolution, is a population process. All disappearances of species are extinctions, but not all extinctions are disappearances of species.

Darwin held much the same view. He emphasized that species assignments reflect a scientist’s judgment and that no clear line demarcates varieties from species. “I look at the term species as one arbitrarily given, for the sake of convenience,” he wrote, “to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with more individual differences, is also applied arbitrarily, for convenience sake.”²⁰ Out of this idea flowed Darwin’s conclusion that varieties (as well as species) “may become extinct, or they may endure as varieties for very long periods.”²¹

Darwin’s ideas have proved so powerful that many people equate evolution with evolution by natural selection. We have already seen one flaw in this equation, which is that Darwin thought evolution proceeded by sexual, unconscious, and methodical selection as well as by natural selection. Here we turn to another flaw, which is to limit evolution to the effects of selection of any stripe.

Evolution can occur without selection, especially in small populations, as a result of **sampling effects**. If **chance** limits reproduction to an unrepresentative subset of individuals in a population (e.g., only members of professional basketball teams rather than all Americans), the traits of the

population will change over generations (individuals in the next generation will be taller, on average, than individuals in the previous generation). Selection also limits reproduction to an unrepresentative subset of individuals, so the distinction between selection and sampling effects is subtle. The key lies in the role of variation in traits. In selection, a subset of individuals reproduces because of advantageous traits. In sampling effects, a subset of individuals reproduces by chance, independent of traits. (Selection and sampling effects can also operate at the same time in a population.) Chapter 3 provides examples of sampling effects, so here our purpose is to flag the process.

Knowing about sampling effects helps us nail down the difference between evolution and selection. Evolution involves changes in inherited traits or genes of populations over generations. It can result from any mechanism, including selection and sampling effects. The key idea in selection is that an individual's traits affect its reproduction. Selection includes natural, sexual, methodical, and unconscious selection. The key idea in sampling effects is that they affect all individuals in a population with equal likelihood. If variation in traits has no impact on reproduction, selection is not at work. All cases in which selection affects the genetic makeup of populations over generations is evolution, but not all cases of evolution happen because of selection.

I like to think of this book as following in the Darwinian tradition, which partly explains my fondness for appealing to Darwin's ideas. Although we associate him with natural selection, Darwin believed one of the best ways to understand this process was to study selection in domestic plants and animals. He was glad he did. When puzzled, he wrote, "I have invariably found that our knowledge, imperfect though it be, of variation under domestication, afforded the best and safest clue. I may venture to express my conviction for the high value of such studies, although they have been very commonly neglected by naturalists."²² I am not a Darwin, but I take inspiration from his belief that one of the best ways to understand evolution is to look at what we ourselves have wrought.