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Principles and Origins of Darwinism

> There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.
>
> —CHARLES DARWIN, *ON THE ORIGIN OF SPECIES* (1859)

> Nothing in biology makes sense except in the light of evolution.
>
> —TH. DOBZHANSKY (1973)

The basic principles of Darwinian theory as outlined by Darwin in his abstract of a book that became the book of reference, the *Origin of Species* (Darwin 1859), are deceptively simple. Indeed, those principles can (in their most elementary form) be summarized in a single sentence: *"Inheritance with modification, coupled with natural selection, leads to the evolution of species."* We should not, however, be deceived by the simplicity of evolution's basic mechanism. After all, we take it for granted that scientific theories that can be summarized by a single formula can give rise to centuries of research, to work out its consequences in real (rather than idealized) settings. A framework of ideas such as Darwinism can never constitute the endpoint of inquiry into the origin and complexity of organic forms, but is rather the very point of departure. Within an extraordinarily complicated environment (made so complicated in part because of the organic forms in it), the Darwinian mechanism leads to such a vast diversity of seemingly unrelated consequences that a single scientist can spend their entire scientific career studying the mechanism's ramifications for a *single* species out of many millions.

Darwinism, as implied in the header quote, is what explains biology. Its claim is that it not only explains the complexity and variation in all the existing forms of life, but that the same mechanism allows an extrapolation backward in time to our, and all other terrestrial forms of life's, beginning. This is a magnificent and confident claim, and such a theory must therefore expect to be challenged strongly and repeatedly (as it has been and continues to be). This is the natural state of affairs for all scientific theories and so it is with evolution, except that challenges to established theories (for example, testing their applicability in extreme circumstances) usually does not imply a challenge to the very foundations and structure of the theory itself. In other words, theories that have withstood many decades of attempts at falsification are unlikely to be ultimately shown wrong *in their entirety,* but only in details. Thus, anti-Darwinian enthusiasts should keep in mind that they are as likely to disprove the Darwinian principles as Newton and Einstein will be shown to have been *completely wrong* about gravity.

While today's reader is sure to be already acquainted with the main principles of Darwinism, it is important to start by spelling them out as succinctly and clearly as possible. Each element will be treated in much more detail throughout the book. We shall be guided by the single italicized sentence at the beginning of this chapter and begin by fleshing out the terms that appear in it. After this exposition, we will explore the impact of each of the elements of the triad in a simple simulation of evolution, to show that each must be present for the process to work.

1.1 Principles of Darwinian Theory

1.1.1 Inheritance

That certain traits are inherited from parent to offspring is obvious to anyone who observes plants and animals, but this observation alone (like most of the components of Darwinism on their own) is unable to shed light on the origin of species and the evolution of complexity. A trait is an "observable feature" of an organism and does not necessarily have to be inherited (it can also be acquired as a response of the organism to the environment). Furthermore, a number of traits can be due to a single gene, or several genes can affect the character of a single trait. This explains (together with the complications engendered by sexual reproduction) why understanding the inheritance of traits has not led immediately to the discovery of the first central element of Darwinism: the *reproduction* of the organism, and the concomitant *replication* of information, in the form of the organism's genetic material. Indeed, inheritance is a *consequence* of reproduction, while the replication of genes is both a consequence and a necessity for reproduction. This (backward) inference from inheritance to reproduction to replication appears trivial from the vantage point gained by the discovery of the genetic code, but is far from obvious prior to that discovery.

From a purely mechanistic point of view, we can thus distill inheritance to the *replication of genes*, or, even more abstractly, to the *copying of information*. As we shall discuss at length in later chapters, the replication of genes, which encode the necessary information to grow the organism and increase the chances for its survival in the environment in which it lives, is the ordering force that preserves the continuity of lineages. We should keep in mind that only the faithful replication of an organism's genes is required for Darwinian evolution, *not* the faithful reproduction of the organism itself. As we shall see later in this chapter, however, a close correlation of the organism's phenotype (the sum of traits and characters) with its genotype (the sum of its genetic information) is required for selection to work properly.

1.1.2 Variation

If replication was perfect, all offspring would be identical to their parents, and therefore all members of such a population would be indistinguishable. Because selection (discussed below) implies a concept of ranking, selection would be impossible in the absence of variation. This variation, however, must occur at a genetic (that is, inheritable) level, because while selection can act on acquired characters, such selection does not give rise to evolution. Thus, variation must occur on the genotypic level: on the information stored in an organism's genome.

Perfect (error-free) replication of information also has another drawback. While it is ideal for protecting the information coded in the genes, it is counterproductive if new information needs to be discovered and incorporated into the genes. The importance of genetic variations is best understood by again taking a purely mechanistic, information-based view of evolution. If the genome alone contains the information about how to make an organism that best survives in the given environment, how does this information *get there*? Since acquired characteristics—changes to an organism's phenotype due to interactions with its environment, such as damage, injury, or wear and tear—do not change the genes, they cannot be inherited. For information to enter the genome, changes must occur in the genomic sequence itself. We thus need a force that works in the opposite direction to the replication process that keeps genes intact: this is the process of *mutation*. A mutation is an alteration of the genetic material (the genetic sequence) that is potentially transmitted to the next generation. In a sense, mutations are the natural consequence of a physical world: they reflect the difficulty of keeping an ordered state (the sequence) intact while it is being manipulated, and exposed to numerous potentially corrupting agents. For example, mutations are a natural by-product of replication simply because it is impossible to perform perfect replication using imperfect machinery. The replication of information (the replication of DNA for organisms based on terrestrial biochemistry) is a physical process that involves the duplication of the carriers of information in sequence. Because this process takes place in a physical environment, there will always be errors associated with this process (the process is "noisy"), and these errors give rise to an alteration of the original sequence: a mutation.

Even though point mutations (that is, replacements of one letter in the sequence by another) are the simplest way to account for genetic variation, they are by no means the only ones that occur. In retrospect, nature has taken advantage of essentially all possible ways in which information can be changed, including deletion and insertion of a letter, deletions and insertions of whole sequences of code, inversions, shuffling, and so on. One of the most well-known sources of variation in evolution is the genetic recombination of code during sexual reproduction. No matter the origin of the mutation, however, because the code defines the organism, variations in the genotype can give rise to variations in the phenotype. It is this variation that the next element of Darwinism acts upon: selection.

1.1.3 Selection and adaptation

Among the primary concepts of Darwinian evolution, selection and adaptation are perhaps those most often misunderstood. Natural selection as a mechanism is now part of our vernacular and occupies, for good reason, a central place in Darwinian theory. Natural selection is what happens if some organisms are better at surviving and/or reproducing than others. From what we saw earlier, this clearly implies that there must be some agent of variation, as otherwise all organisms would be the same, and some could not be better than others. If one type of organism is better at survival/reproduction than another, then the relative numbers of these two types must necessarily change. If, at the same time, the total number of organisms in this competition is fixed (either due to a finite amount of resources in the niche, or due to finite space), then it is clear that a constantly changing ratio of numbers between two competing species will result in the inferior species being driven into extinction. This is, in a nutshell, the mechanism of natural selection, but its consequences, as well as its subtle variations, are far from trivial.

To begin with, the previous sentence implies that natural selection acts on organisms that are "better at survival and/or reproduction." What exactly does that mean? This question addresses the concept of "fitness" within evolutionary biology, which is a central concept and deserves a brief discussion here (and a more detailed one later on). Much has been made from the apparent tautology that declares those organisms as the fittest who end up surviving. More precisely, this type of criticism has been leveled at the statement that "survival of the fittest" is a tautology if the fittest is defined as that which survives. There is no tautology, of course, because we do not, in biology, define "fit" as "one who survives." Fitness, instead, is a concept meant to characterize a *lineage,* not a single organism (even though the word is often used to describe individuals of that lineage). A lineage is a set of organisms that are tied together by their genes, that is, they all share the same genetic characteristics because of shared heritage. Any particular organism representing a lineage may be subject to random occurrences that may cause it to lose out in a competition with a representative of a less fit lineage purely through chance. This does not persuade us to change our fitness assessment of this lineage. Instead, on average, the representatives of the lineage that is fitter will outcompete the representatives of the less fit lineage, but any single competition may go either way.

This being said, the fitness of an organism is not always easy to estimate. Technically, the word "fitness" implies "adaptation," namely a lineage that "fits" its environment well. In evolutionary biology, fitness is defined as "expected reproductive success," where "reproductive success" implies success both in reproduction and survival. The reason we must emphasize our expectation is that, as we already saw, in a natural world expected success does not always equate with realized success. The phrase "survival of the fittest" is, therefore, really a poor rendition of the natural selection concept within Darwinian evolution. Selection is simply a mechanism by which the frequency of particular types of organisms are changed *depending on what genes they have,* and the mechanism is such that those genes that *increase* the carrier's relative numbers are precisely those that will carry the day. The logic of selection is so unassailable that it sometimes seems like an utter triviality. That this is not so is exemplified by the stupendous variety of mechanisms and technical complications that accompany natural selection, from sexual selection to a dependence on mutation rates, to neutral evolution and the selection for robustness.

Adaptation is perhaps even more misunderstood than selection. There is no doubt that adaptation is perhaps the most stunning result of Darwinian evolution, and can be observed in minute details of function in every organism inhabiting Earth. In the following chapters, we will largely do away with the concept of adaptation because it is too vague for a quantitative analysis. Some features of living organisms are easily identified as adaptations, namely traits that clearly further the reproductive and survival chances of a species. Other traits are not so easily interpreted, and the fitness value of any particular gene or trait cannot be linked directly to its adaptedness. Still, there is no doubt that adaptation occurs, when through natural selection those organisms are favored whose particular (well-adapted) trait allows them to exploit their environment in a more efficient manner. Adaptation, thus, is "adaptation to one's environment." Because the ability of an organism to exploit and thrive in its environment is directly related to the genes that code for such prowess, we can say that a well-adapted organism is in possession of a good amount of *information* about its environment, stored in its genes. Because the concept of information is a quantitative one, we shall use it in place of adaptation in most of what follows. We should keep in mind, however, that it is not guaranteed a priori that information is a good proxy for "adaptedness" or function, or even fitness for that matter. We shall have to examine this assumption in detail.

1.1.4 Putting it together

To get a better picture of how these three elements work together to generate evolution, it is instructive to put them all together in a computer simulation. We will keep this simulation as simple as possible so as to involve only the processes discussed above in their purest form, while making sure that we can turn off any of the elements independently to observe the dynamics that ensue. The simplicity of the simulation of course implies that it is not intended to simulate any actual evolving organism. Rather, its purpose is to illuminate the *interaction* between the elements, and to test their respective necessity.

The goal of our little simulation is to optimize the fitness of a population of alphabetic strings. The alphabet could be anything as long as it is finite. It could be binary (bits), quaternary (like DNA and RNA), base 20 (such as with amino acids), or base 26 (English lowercase alphabet). Here, we arbitrarily choose an alphabet consisting of the first twenty letters, (from a to t). Also, we will fix the length of any sequence to one hundred letters. To enact selection, we can construct a simple fitness landscape by arbitrarily declaring one particular (randomly chosen) sequence of letters the most fit, and stipulating that you lose fitness the more mutations away you are from that sequence. The number of point mutations it takes to get from one sequence to another is called *Hamming distance* in the mathematical literature, so in this case the fitness is based on a sequence's Hamming distance to the optimum.

Clearly, this fitness landscape does not resemble anything like what we would encounter in natural systems. In particular, no natural fitness peak is this cleanly designed from the outside, and even more importantly, the Hamming distance fitness implies that each site in the string of length 100 contributes *independently* to the fitness of the string. As a consequence, there are only one hundred different fitness values in this landscape, and the order in which the beneficial mutations are acquired is inessential. As we will see as the chapters unfold, this is so far removed from realistic fitness landscapes for nucleotides or proteins or even genes that such a simulation is little more than a caricature of the evolutionary process. Indeed, if all mutations were to depend on each other instead, that is, if the fitness effect of one mutation at one site depends on the state of all other sites, then a string of length 100 can encode up to D^{100} different fitness values, where D is the size of the alphabet. For proteins ($D = 20$), the difference in the "richness" of the fitness landscape amounts to about a factor 10^{128}! Mutations that depend on each other are called *epistatic*, and we will see that the interaction between mutations is the single most important factor in the emergence of complexity via Darwinian evolution. To some extent, the simulation we study below can be viewed as representing evolution with all its interesting bits (namely epistasis) stripped off. Its only purpose is to illustrate the combined effects of replication (inheritance), mutation (variation), and selection. Any fitness landscape suffices for this purpose, as long as it is not completely flat, that is, if there are any fitness differences at all.

Evolution occurs on sequences within a population, so in this simulation we shall observe the fate of a population of fixed size (here, 200), in competition with each other. Later, we will relax even this condition, to see what happens to evolution in the absence of competition (by allowing the population to grow indefinitely). Mutations are implemented so that each generation, an arbitrary string will suffer on average one mutation per replication cycle. This means that oftentimes they will suffer no mutations, more likely only one, and in rarer cases two or more mutations. This mechanism can be applied even if sequences do not replicate. The replication of these sequences is implemented in a probabilistic manner, so that those sequences that are ranked the highest according to the fitness criterion discussed above are accorded multiple offspring, while the sequence with the smallest score is assured not to leave any descendants.

If all this is put together, the algorithm effectively implements a parallel search (parallel because the search occurs in a population) for the optimum sequence. Algorithms just like that are indeed often used in engineering and other applications, and are termed *Genetic Algorithms* (see, e.g., Mitchell 1996 for an introduction or Michalewicz 1999 for a more advanced exposition).

Figure 1.1 shows a typical result of such a simulation when all elements of Darwin's triad are present. The mean fitness (solid line) of a population of 200 random sequences is steadily increasing, and the optimum fitness is found after 71 generations (the dashed line is the fitness of the best-in-population). Also note the population diversity (dotted line), which here is the logarithm of the number of different types of sequences n_s in the population (where we use

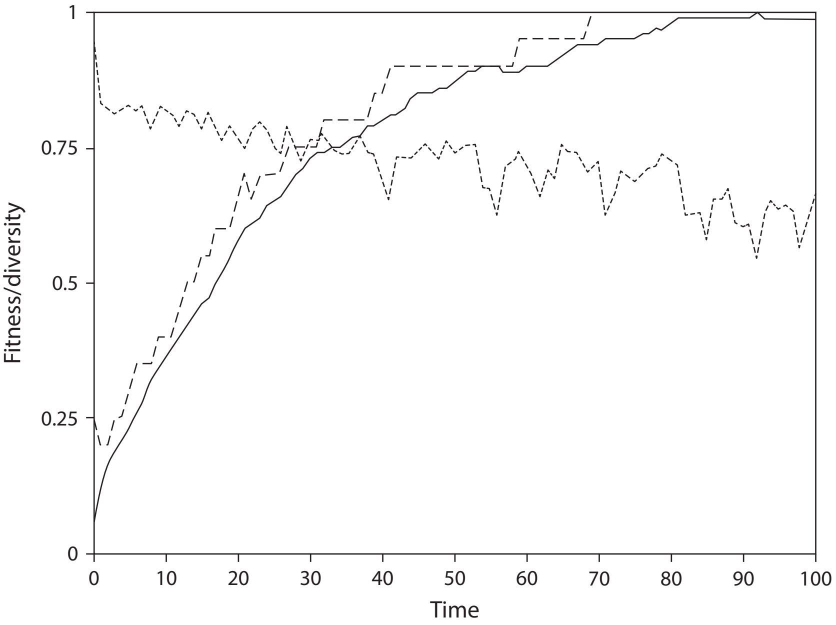

FIGURE 1.1. Mean fitness (solid line), fitness-of-best (dashed line), and population diversity (dotted line) in a simulation of evolution with mutation, reproduction, and selection. Fitness is measured in arbitrary units between one (optimum) and zero (worst), while time is measured in generations. Diversity is measured as the logarithm of the number of different sequences n_s, to the base of the population size $\log_{200}(n_s)$, which also lies between zero (no diversity) and 1 (all sequences different).

the population size as the base). It starts at approximately its maximal value 1 and declines to a steady state that remains below the maximum.

Let's first consider the same exact process, but in the absence of mutations. We start with a random population, so there is plenty of variation to begin with, but none is added as time goes on. Because the population size is so much smaller than the possible number of sequences, the chance that the fitness peak is accidentally already in the population is astronomically small. The best-of-population fitness is constant throughout since it is given by the highest fitness individual present (by chance) at the beginning, while the mean fitness of the population quickly increases (see Fig. 1.2[a]) because selection is working. The best sequence in the population quickly gains in numbers at the detriment of the less fit ones. At the same time, you can see the population diversity plummet drastically, because less fit variants are replaced by copies of the fitter variant, all of them identical but far from the maximum

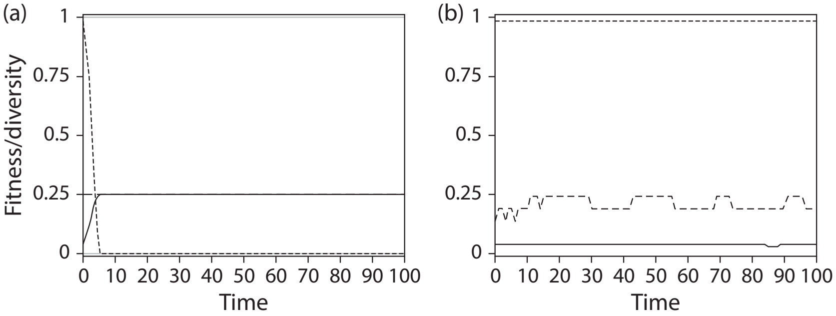

FIGURE 1.2. (a) Simulation of evolution with reproduction and selection, but without mutation. (b) Simulation of evolution with selection and mutation, but without reproduction. Legend as in Figure 1.1.

fitness possible). After nine generations, all two hundred individuals in the population are identical, and nothing else will ever happen here.

Next, we study the importance of reproduction. We can perform the same simulation, including a ranking of organisms according to their Hamming distance to the optimum, but now this ranking does not affect a sequence's reproduction rate (they do not reproduce at all). Mutations continue to occur, so in principle the optimum sequence could still be found because the sequences are immortal in this setting; however, the probability of this happening here is exponentially small. In Figure 1.2(b), we can see that the fitness of the best organism in the population is fluctuating (the fitness is taking what is known as a *random walk*), and the mean fitness mirrors that. Population diversity is maximal and unchanged from the initial diversity, since replication is the only process that can appreciably reduce the diversity. It is possible, of course, that random mutations create several copies of the same exact sequence by accident, thus lowering the population diversity. However, the probability of this occurring is again exponentially small, and such a state would be replaced by a more probable one in the next instant.

Finally, we consider the case where we have both mutation and reproduction, but no selection. To turn selection off, we can simply rank all sequences equally, independently of their Hamming distance to the optimal sequence. As a consequence, each individual is guaranteed exactly one offspring, regardless of the sequence of instructions. This case is interesting because even though there is no selection, random fluctuations can give rise to differences in reproductive ability, and sometimes certain mutations can become quite common in the population even though they have the same fitness as all others. (This case is known as "neutral evolution," and will be treated in detail in chapter 6.)

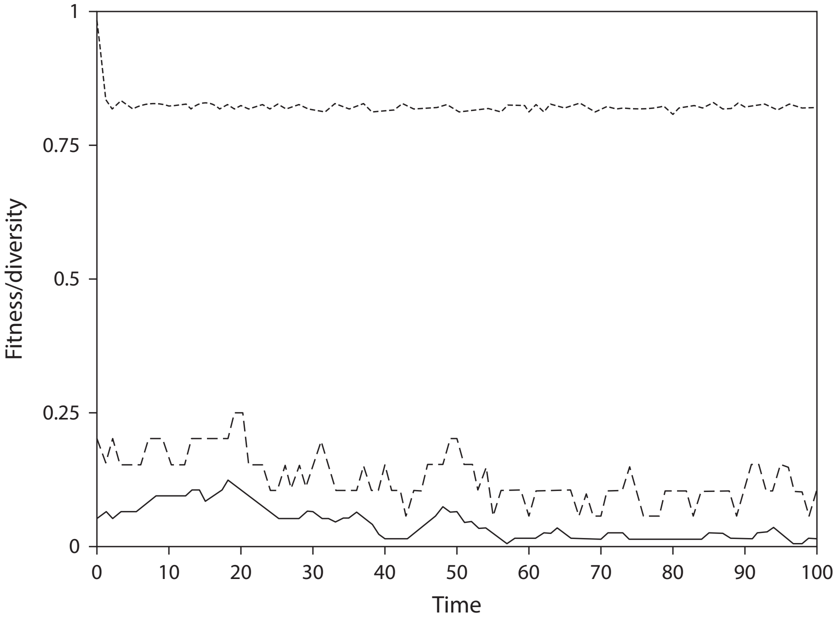

FIGURE 1.3. Simulation of evolution with reproduction and mutation, but without selection (neutral evolution). Legend as in Figure 1.1.

As a consequence, the dynamics are quite a bit different from the case we treated just before (no replication). The population diversity is not maximal, and the average and best fitness fluctuate more strongly (see Fig. 1.3). In each of the three cases where one of the necessary elements is absent, it is patently obvious that evolution does not occur even though two of the required three elements are present. Such is the interaction of the three elements of the Darwinian triad: all for one, and each for all!

1.1.5 Speciation

The species and its origin, while clearly a central concept in Darwinian theory, is not actually a central element of the Darwinian mechanism (the first three in this chapter are all that is needed), but rather one of its consequences. Still, it deserves to be treated in this quick tour of the principles because of its pivotal role in evolutionary biology.

Species are all around us, and are (usually) easily identified by eye as those members of a population that share certain phenotypic (meaning here, manifested) properties of an organism. That there is a "species problem" (this is what Darwin told his friends and colleagues he was working on before the publication of his *Origins*) takes a little thinking, because at first glance one might think that it is only too obvious that "populations of closely related organism that are mostly similar," namely species, will form as a consequence of the mechanisms described above. After all, a mutated organism is necessarily directly related to its progenitor if the mutation happened during the reproduction process. Furthermore, the probability that a mutation creates a dramatically different organism (one that would be classified as a different species) is expected to be exceedingly low. However, these obvious observations are precisely those that lead to the species question. If organisms naturally form populations of closely related specimens, why do new species arise at all? And how can it be that the process of species formation has led to types so dramatically different that it is well nigh inconceivable that they were once siblings, in particular while relatives of the original stock still exist today largely unchanged? What, then, drives the changes that species undergo, this fragmentation of populations into distinct groups, and why do they not coalesce into a muddled amalgam of types that blend one into another, with intermediate organisms everywhere between bacteria and the giraffe?

For sexual organisms, the standard species definition is that all organisms that can produce fertile offspring are considered as belonging to the same species and are different species if they cannot. This idea is called the "biological species concept" (Coyne and Orr 2004). It is a very sensible way of defining species because groups that cannot produce offspring with each other are effectively genetically isolated, as no gene mixing can occur between them. As a consequence, two groups that are isolated in this manner will evolve independently and become more and more different. On the other hand, it is not a perfect criterion because examples exist of distinct species that can produce fertile hybrids. In any case, defining species in this manner does not solve the species problem, as we now have to understand how it can happen that one species breaks into two or more "proto-species," who then gradually lose the ability to interbreed.

There are two main ways in which we can imagine that this breakup happens. First, it is possible that a species is accidentally separated into two groups due to a geographic partition, say, one group crosses a river while another does not. If subsequently the river grows so large that it renders any other crossing impossible, the groups are *reproductively isolated* and can evolve independently without mixing of genes *as if* they were different species. After some time, the different evolutionary paths taken by the respective groups is likely to have resulted in changes that make interbreeding biologically impossible (not only practically) so that the species will remain separate even if the river dries up and the groups are reunited. This process is called *allopatric speciation* in the literature ("allopatry" translates literally to "having different fatherlands").

Another (much more controversial) possibility is that groups can drift apart *without* geographic separation, a process termed *sympatric speciation*. As the name suggests, this is a mode of speciation where the future species occupy the *same* homeland. The difficulty with this mode is that it is hard to understand how the small genetic changes that occur within a population can give rise to separate species if the organisms are able to interbreed. The genetic mixing implied by interbreeding should wash out any genetic differences that may have arisen. Thus, interbreeding is a force that opposes speciation. To understand speciation in sympatry, we would have to assume that small genetic changes can cause some reproductive isolation that ultimately stops the gene flow between the incipient species (there is actually direct evidence for such an effect, see for example Uy et al. 2009). Most theories of sympatric speciation invoke local adaptation to different resources (so-called microhabitats). But because adaptation to different local resources (for example, changing your diet via a genetic mutation) does not prevent such differently adapted groups to interbreed, we usually have to assume that the change in diet must be directly associated with mate choice behavior also. In other words, the change in diet has to turn the prospective partners off sufficiently so that interbreeding is prevented.

It should be clear that one of the difficulties in testing theories of speciation is that it is rare that the process can be observed in real time. One of the most laudable exceptions is perhaps the decades-long work of the Grants (Grant and Grant 1989; Grant and Grant 2008), but other examples exist such as speciation in flowering plants (Soltis and Soltis 1989), sticklebacks (Colosimo et al. 2005), and cichlid fish (Schliewen et al. 1994; Seehausen et al. 2008).

The species concept can also be applied to asexual organisms, albeit in a different form, naturally. Bacteria and viruses, for example, do occur in distinct groups rather than in genetically fluid amalgams even though they do not reproduce sexually. For asexual organisms, allopatric and sympatric modes of speciation can occur, but the difference is not so profound because asexual species do not mix genetic material to begin with (I am ignoring lateral gene transfer here for the purpose of simplicity). Thus, within asexual organisms, a new species can be born simply by one (or several) propitious mutations. The difficulty for the bacterial species concept that arises in this case is somewhat different. If new species can arise within asexual organisms with every beneficial mutation, why do we not see have an almost infinite number of them, one corresponding to each such mutation? The answer to this question naturally lies in selection: when such a beneficial mutation sweeps a population, the inferior kind is driven to extinction. This seems to imply that evolution in asexual populations simply proceeds by one species supplanting another. Where, then, do all the different bacterial and viral species come from? This

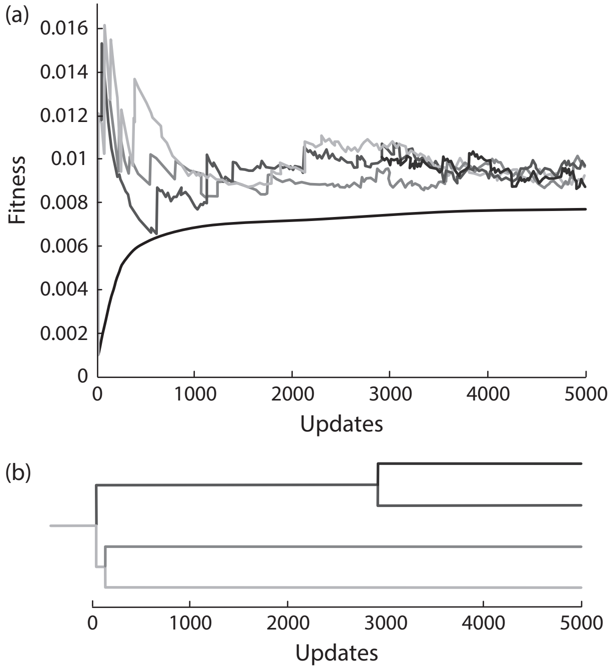

FIGURE 1.4. Evolution of an ecosystem of different species that specialize for survival on different limited resources. Each species discovers and then specializes on a different resource. (a) Lines in different shades of gray show relative fitness of the different species, splitting off ancestral species. Overall fitness of ecosystem in black at the bottom of the figure. (b) Ancestral reconstruction (phylogeny) of the simulated species (shades of gray the same as those in panel (a)). Adapted from Østman et al. (2014).

question seems to find its explanation in a resource-based sympatric process, where different species can coexist because they all “make their living” in a different manner, which means that they do not directly compete against each other anymore. A typical example that shows the emergence of new species (in a computational simulation, see Østman et al. 2014 for more details) in a resource-limited environment is shown in Figure 1.4. As new species emerge, the relative fitness of each depends on the frequency of that species in the population, as well as the frequency of others in some cases. When rare (that is, when it just emerges), a new species has a competitive advantage because the resource it relies upon is very abundant—nobody else relies on it yet. As a consequence, the emerging species has no trouble invading the existing type (see, for example, the new species in black that splits off the dark-gray species just before generation 3,000 in Fig. 1.4).

Ultimately, the relative fitness (here the overall reproductive rate) of each species must match those of any other species in the same ecosystem, as otherwise the equilibrium among the different types would be disrupted. In the case of speciation via adaptive radiation in a resource-limited environment, this equilibrium is stable because any time a species increases in number beyond what the ecosystem can carry, its relative fitness must drop, adjusting the number down. The mathematics of species equilibrium in a global ecosystem should give us pause, of course, because once the connection between resource limits and species fitness is broken, unimpeded replication can catastrophically exhaust a resource, leading ultimately to the demise of that species.

It is clear then that a theory of biocomplexity must also address the species problem. Not only is it important to understand how a diversity of species is created and maintained by Darwinian processes, we should also strive to understand how the *interaction* between these species and the ecological networks they form are created, maintained, and nurtured.

1.2 Origin of Darwinian Thought

Successful theories, meaning those that are particularly good at explaining observations, often seem so obvious that it is impossible to imagine a time when the world was looked at without this piece of knowledge. The idea that the Earth is round and not flat is one good example, perhaps the heliocentric worldview somewhat less so (but only because it is somewhat less obvious). With respect to evolution, its general principles have so permeated our everyday thinking that to delve into pre-Darwinian thought processes might seem like an exercise without merit. Yet, if you think about the simplicity of the main elements of Darwinism, it could appear like a preposterous accident that they have been discovered comparatively late.

To fully appreciate Darwin's insight, and perhaps to get a better gut feeling for these seemingly innocuous "three principles," we are going to take a little detour back in time to search out the roots of Darwinist ideas, to get a feel for the mindset of the era into which they were flung, and to follow the fits and starts of other scientists, who got little pieces of the story, but did not solve the puzzle.

1.2.1 Eighteenth century

The origins of Darwinian thought can be found scattered among the writing of naturalists, theologians, and geologists of the eighteenth century. To do justice to the sometimes timid attempts at making sense of the natural world during this time, it is important to understand that the century was steeped in religious dogma, which did not allow any opinion to be held that contradicted the Bible's creation story or its affirmation of the fixity of the Earth and the animal life that inhabits it.

In those times, you would be hard-pressed, therefore, to find someone to openly consider the question of "the origin of species," because this question was considered solved by a singular act of creation. Within this era, however, a few people were willing to ask questions which, perhaps, could be construed as heretic, but which nevertheless were openly dedicated to the "Glory of God." Because at the time it was modern to consider Nature as "the other great book" through which one could discover God,[1] some of the foremost naturalists of the time were in fact reverends and priests.

Two church doctrines governed all discussions about biological diversity in the eighteenth century. The first is the idea that all species were created at once, independently from each other, and arranged into the famous "great chain of being" with God, angels, and then humans at its top (see Fig. 1.5). This concept is actually an old philosophical one dating back to Plato and Aristotle, and has inspired thinking about the world order up until the nineteenth century.[2]

The second doctrine prescribed the age of the Earth, namely about 6,000 years. Both doctrines essentially prevented any thinking about *time*, thereby locking the universe, the Earth, and its inhabitants into a static stranglehold from which only the adventurous thinker could free himself.

The questions that at that time were encouraged were mostly concerned with classification. The first name to mention here is of course that of Carl Linnaeus (1707–1778), the Swedish botanist (and son of a pastor) who instead of following in his father's footsteps became obsessed with collecting and studying plants. He became known as the first *taxonomist* (meaning one who studies the general principles of classification of biological organisms) largely through his main work, the *Systema Naturae* (first published in 1735) which went through many editions (Linnaeus 1766).

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[1] Thomas Browne (1643) famously wrote: "Thus there are two Books from whence I collect my Divinity, besides that written by God, another of His servant Nature, that universal and publick Manuscript that lies expans'd unto the Eyes of all: those that never saw Him in the one, have discovered Him in the other."

[2] Alexander Pope, in his *Essay on Man* (1733) pronounces:

> "Vast chain of Being! which from God Began,
> Natures aethereal, human, angel, man,
> Beast, bird, fish, insect, what no eye can see,
> No glass can reach; from Infinite to thee(. . .)"

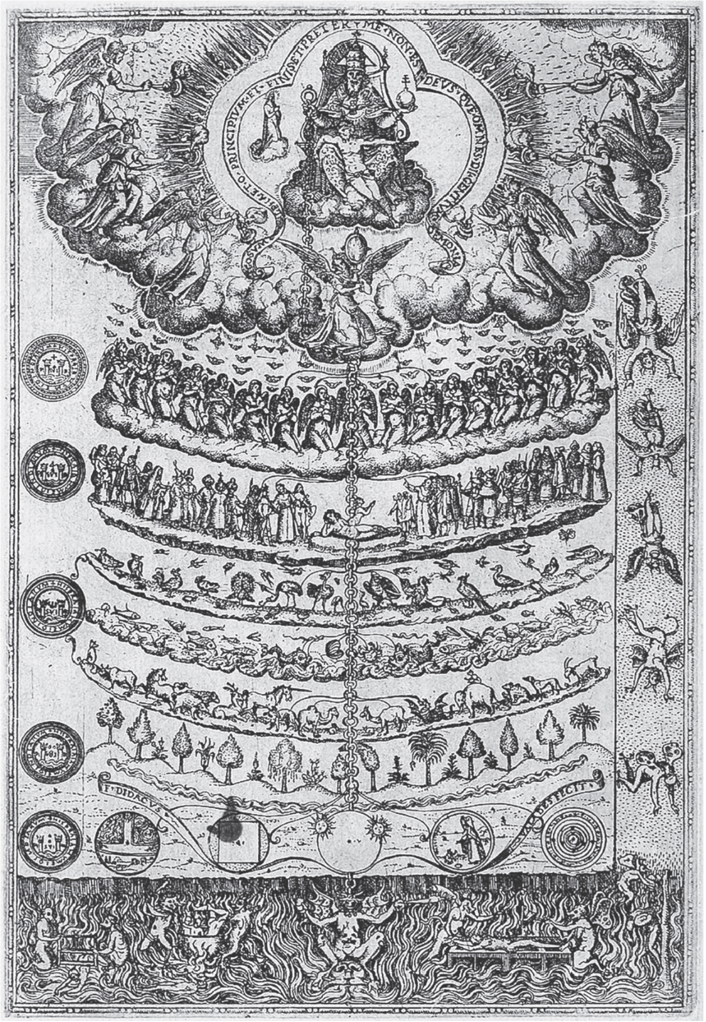

FIGURE 1.5. Depiction of the great chain of being, from *Rhetorica Christiana* (1579) by Diego de Valadés.

Linnaeus's work was important not just because of its attempt to put order into the seemingly unbounded variety of plants and animals, but also because it started a fashion trend of sorts: to find hitherto undiscovered species and have them named after the discoverer. It was only through this combined effort of classification and discovery that the people of the eighteenth century would slowly acquire a grasp of what kind of life was out there sharing the planet with them. This was, after all, a time when tales of monsters with

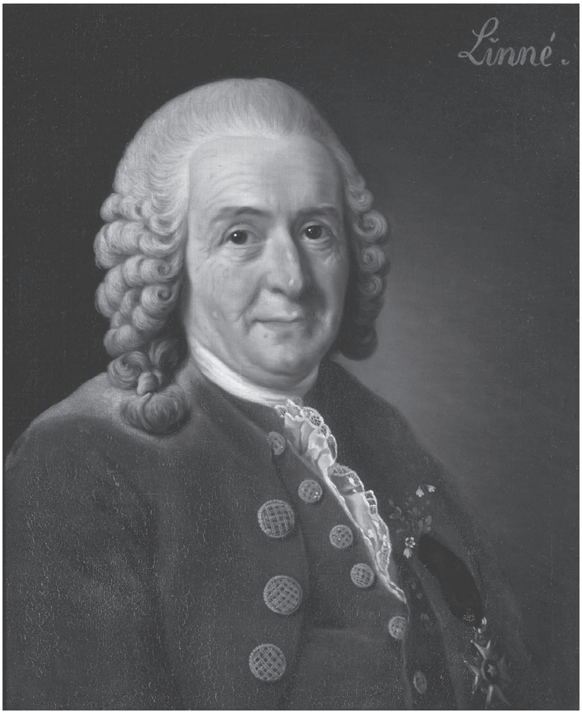

FIGURE 1.6. Portrait of Carl Linnaeus by Alexander Roslin (Nationalmuseum Stockholm).

several heads, giants, mermaids, men with tails, etc., were widely believed by the literate public.

Because this effort of classification was ostensibly one of cataloguing God's creation, the idea of extinct species, or even *novel* ones, was still not one anybody would openly entertain. But, because it is clear that without a serious classification effort it would hardly have been possible even to make a claim about extinct or recent species, we can see that Linnaeus, while steeped in his time, was preparing the world for far greater discoveries.

Among those who conformed to the general belief system walked a few who dared to heretically question some of those most deeply held beliefs. Around the time of publication of Linnaeus's book, another famous tome was being read and discussed, this one by Benoit de Maillet (1656–1738), a French nobleman, later appointed Consul General of King Louis XIVth in Cairo.

De Maillet was an amateur as far as geology and natural history was concerned, but he showed a shrewd sense of discovery and deduction. Armed

FIGURE 1.7. A portrait of Benoit de Maillet (from de Maillet and Mascrier 1735).

with those, he attempted to make sense of the evidence available to him, link it, and construct a view of the universe. What is remarkable is that his theory of the universe does not involve a God, and envisions an Earth that is subject to external natural forces that change it, as opposed to catastrophes willed by a creator. He thus implicitly questioned one of the most important of church doctrines, namely that of the fixity of the Earth.

In his book *Telliamed* (de Maillet 1750), first published anonymously and widely read only after his death, de Maillet staunchly opposes the biblical deluge myth and suggests a much older age of the Earth. He deduces both opinions from observations, which he insists should hold preponderance over beliefs handed down from generations. In this sense, de Maillet was a radical revolutionary. His attack on religious dogma is particularly vitriolic in the following passage, where he speaks about the type of people who might reject his theory without giving due consideration to his facts:

> The Case is not the same with another Class of Persons, to whom this Idea of Novelty and Singularity will perhaps appear a just Reason for

> condemning the Work; I mean those persons remarkable for their excessive Scruples and Delicacies in point of Religion. I grant indeed, we cannot too much respect this Delicacy, when it is enlightened and guided by reason; but it is equally certain, that this excessive Zeal sometimes only proceeds from Ignorance and Meanness of Spirit, since it often degenerates into false Prejudices, and a barbarous and ridiculous Blindness; that without giving a Shock to Religion, we may boldly attack ill-grounded Scruples, which are only the Effects of an inexcusable Superstition; and that if we were obliged to support the pure and salutary Ideas of the former, we are equally bound to oppose the Propagation of the stupid opinions set on Foot by the latter (. . .)

Even though the theory of the universe in *Telliamed* is being advocated by an Eastern philosopher (by the name of Telliamed) who is being interviewed by the God-fearing author, this ruse is only thinly disguised given that *Telliamed* is the author's last name spelled backward!

This is not to say that de Maillet anticipated Darwinism in any real sense. While he advocated the possibility that species could transform, and some species would evolve from sea dwellers to land animals, he also believed the stories of giants, and mermaids and mermen. So while he mixed legends and observations in support of his theories of the universe, he was unequivocal about the interpretation of fossil shells and animals discovered in strata far higher than the current sea level: species can go extinct, new ones can emerge, and the Earth is subject to constant forces of erosion that shape its appearance. Because de Maillet was born in 1656, we should really see in him a precocious precursor of the enlightenment that was to follow in the eighteenth and nineteenth centuries.

Perhaps the most important figure in natural history in the middle of the eighteenth century was the Comte de Buffon (1707–1788), more precisely George-Louis Leclerc, Comte de Buffon. Buffon's influence on the history of science would likely have been far greater had he not become obsessed with the idea of cataloging all existing knowledge in the fields of natural history, geology, and anthropology, which he did in his forty-four-volume *Histoire Naturelle* (Buffon 1749–1804).

Within the volumes depicting animal life, however, can be heard the voice of the scientist who attempts to make sense of all this variety. And, scattered among the many volumes that he wrote can be found essentially all the elements that are necessary to put together the theory of evolution. In particular, he advocated a theory of "degeneration" (by which he essentially meant change and progress) to link one species to another. He also clearly saw the evidence of fossils and therefore maintained that not only are there extinct species, but that new types emerge continuously. Finally, using

FIGURE 1.8. George-Louis Leclerc, Comte de Buffon, detail of a painting by Francois-Hubert Drouais at Musée Buffon.

geological arguments he refuted the church's claim of a 6,000-year-old Earth and proposed a much longer one (while still far off from what we know today). According to the sign of the times, though, he made these claims not as forcefully as Darwin would later dare, but somewhat timidly, followed immediately by affirmations of the church's general doctrines of thinking, often thereby contradicting himself in subsequent sentences.

While Buffon's *Histoire Naturelle* was widely read and admired in his time, he was less well known as an original thinker in natural history, simply because he never portrayed his thoughts as theory. It is entirely likely that he thought it best to throw in such ruminations to break the monotony of the animal descriptions that make up the bulk of his work. Still, in retrospect we can see that every one of the elements that Darwin used to synthesize his theory were already available at the middle of the eighteenth century, for somebody who had the perspicacity to appreciate their importance and the courage to put them together.

Inspired by the ideas of Buffon, Erasmus Darwin (1731–1802) forms a link to the nineteenth century. A respected physician and poet, Erasmus—who is the grandfather of Charles Darwin—had a serious interest in natural history and strongly entertained the idea that *species can change without limits*. In particular, he was convinced that the similarities between the different forms of life were due to ancestral relationships, and were changing and adapting through time. Still, these ruminations of the grandfather of the famous grandson (Erasmus Darwin died seven years before Charles was born) were not formulated as a coherent theory, but rather were observations about nature contained in his books *The Botanic Garden* (E. Darwin 1791) and *The Temple of Nature* (E. Darwin 1802), both in verse. His vision of such a theory, however, cannot be denied, as we can read in his *Botanic Garden*:

> As all the families both of plants and animals appear in a state of perpetual improvement or degeneracy, it becomes a subject of importance to detect the causes of these mutations.

Before venturing into the nineteenth century, two more influences on Darwin should briefly be mentioned. Thomas Malthus's (1766–1834) *Essay on the Principle of Population* (Malthus 1798) is often cited as having given Darwin the inspirational spark for his theory by emphasizing the "struggle of existence" going on everywhere, among animals and plants as well as humans. The main point that Malthus tried to make in his essay concerned the danger of overpopulation in the face of limited resources, in particular among the poor. Indeed, Darwin himself remarks in his autobiography edited by his son Francis (F. Darwin 1887, p. 68):

> In October 1838, that is, fifteen months after I had begun my systematic inquiry, I happened to read for amusement Malthus on *Population*, and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The results of this would be the formation of a new species. Here, then I had at last got a theory by which to work.

It seems somewhat odd, though, that it would be in Malthus's essay that Darwin first heard about the idea of a struggle of existence (see Eiseley 1958, 180 for a discussion of this point), as several authors had already extensively discussed it by the time Darwin read Malthus, in particular his good friend Lyell (whom we meet later), and the Reverend William Paley (1743–1805), whose writings concerning the "Evidence for Christianity" were required reading at

FIGURE 1.9. Erasmus Darwin by Joseph Wright of Derby (1792), at the Derby Museum and National Gallery.

Cambridge University, where Darwin took his B.A. In fact, Darwin professed to be fascinated by the logical deductive approach taken by Paley, almost as if theology was a subbranch of mathematics. In his book *Natural Theology* (Paley 1802) (famous for its comparison of complex life to a finely tuned watch, and the argument that just as the watch needs a watchmaker, life would need a creator) the Anglican priest Paley attempted to prove the existence of God by observing and showcasing astonishing details of adaptation. While we now know Paley's solution to the puzzling complexity of organic life to be wrong, he was certainly right to be puzzled, and his zeal to document the extent of the intricate complications and adaptations of life make him a worthy naturalist on the cusp of the nineteenth century.

1.2.2 Nineteenth century

The eighteenth century was marked more by the recognition that natural laws govern the movements of planets, and a growing awareness of the universe around us through astronomical discoveries, than a leap in our understanding

FIGURE 1.10. Thomas Robert Malthus, Mezzotint by John Linnell. From Wellcome Collection (CC BY 4.0).

of the natural world. But the groundwork had been laid, and in short succession several important new elements and ideas emerged.

In the year Erasmus Darwin passed away, the German physician (later professor of medicine and mathematics at the University of Bremen) Gottfried Reinhold Treviranus published his ruminations about the origin of species in a book entitled *Biologie, oder Philosophie der lebenden Natur*[3] (Treviranus 1802). In this book he set forth a theory of the "transmutation of species," arguing that each species had the potential to change in response to changes in the environment, and that it is this capacity that lies at the origin of the observed diversity of species. He writes:

> In every living being there exists a capacity of endless diversity of form; each possesses the power of adapting its organization to the variations of the external world, and it is this power, called into activity by cosmic changes, which has enabled the simple zoophytes in the primitive world to

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[3] Biology, or Philosophy of the Animate Nature

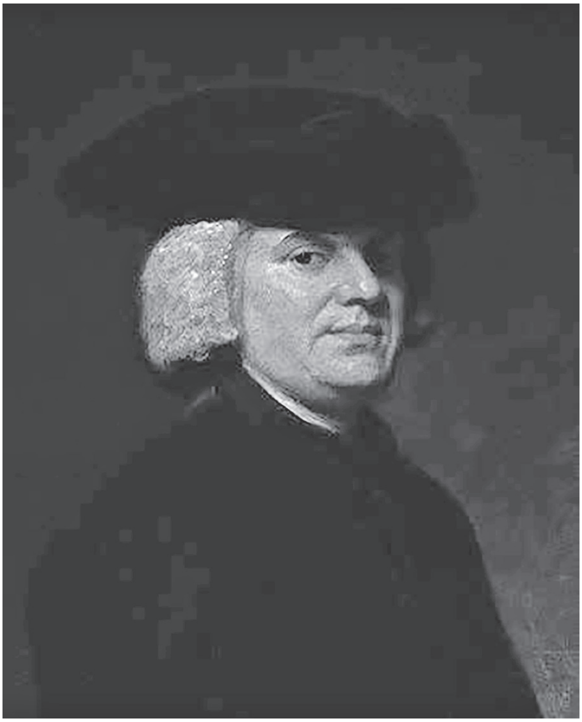

FIGURE 1.11. Reverend William Paley, painting by George Romney (National Portrait Gallery, London).

> climb to higher and higher stages of organization, and has brought endless variety into nature.

While it is clear that Treviranus does not pretend to know the origin of the power to change that he sees inherent in every organism, he does glimpse lines of descent (in the form of "lines of transmutations") that span from the simplest forms all the way to us.

The idea of "adaptation" as the core of species diversity was (presumably independently) taken up by Jean-Baptiste Lamarck (1744–1829), who thought that he had (unlike Treviranus) hit upon the origin of the power to change: the use and disuse of organs in response to environmental changes. Lamarck echoed the poetic ruminations of Erasmus Darwin in a more scientific manner and, while influenced by Buffon just like Erasmus Darwin, was a man more on the cusp of the new century. After a career in the army, Lamarck took a post at the National Museum of Natural History in Paris, where he attempted to classify "insects and worms" (for which he coined the

FIGURE 1.12. Gottfried Reinhold Treviranus (1776–1837).

word "invertebrates"). For him, it was clear that species could change, but he also speculated that this change was not random, but instead occurred as a response to the environment. In particular, he figured that the influence of the environment was *direct*: if the leaves on an acacia tree are so high to be almost out of reach (to quote a famous example), then those giraffes that stretch their necks highest will survive preferentially. However, contrary to the genetic and heritable origins of an elongated neck that constitutes Darwinian evolution, Lamarck reckoned that a giraffe that had acquired a longer neck due to a lifetime of straining to reach the leaves would bear offspring with just as long a neck. In other words, his theory of evolution—and the system he outlined in *Philosophie Zoologique* (Lamarck 1809) certainly qualified as such—was based on the inheritance of such *acquired* characteristics.

Apart from invoking this particular mechanism to create diversity (after all, the laws of inheritance were only discovered quite a bit later by Mendel) Lamarck's theory reads curiously like that laid down later by Charles Darwin, but with *adaptation* at its core. Unlike Darwin, who professed that while there seems to be a general trend from the simple to the complex in evolution (a concept we will examine in detail in later chapters) and who could see

FIGURE 1.13. Jean-Baptiste de Monet, Chevalier de Lamarck. Portrait by Jules Pizzetta in *Galerie des naturistes,* Paris: Ed. Hennuyer (1893).

adaptation giving rise to more *or less* complex organisms, Lamarck believed fervently that evolution would produce *only* advancements, that nature was constantly improving organisms. Note, however, that because *all* animals, according to Lamarck's view, would "improve" their organs through use (and lose functions of others through disuse) natural selection through competition for limited resources is not an important element in this system. While being very much inspired by Lamarck's book, Darwin would later dismiss it as an "error" for its failure to recognize the importance of natural selection.

Even though Lamarck's *Philosophie Zoologique* should have shocked and amazed his contemporaries as the first system to explain the diversity and evolution of species, it went largely unnoticed. Lamarck's success was constantly being undermined by his much more successful colleague Cuvier (whom we meet momentarily), and he died blind, destitute, and forgotten.

Georges Cuvier (1769–1832) plays a starring role in any exploration of the origins of Darwinian thought because he was the first one to pay attention to the details of anatomy in a scientific manner. Cuvier worked and taught at the National Museum of Natural History alongside Lamarck and developed a system of comparative anatomy that would allow him to reconstruct the skeleton of entire organisms from the examination of a few or even a single bone. This system was based on correlations and similarities between bones that he had studied, and a belief that each organism's manner of living and precise function

FIGURE 1.14. George Cuvier (1831). Engraving by George T. Doo after a painting by W. H. Pickergill.

would affect each and every bone in its body; that the functioning of one organ would affect all others in such a manner that the entire *plan* of the organism was defined by them. While such a holistic view of organism structure appears somewhat mystic by today's standards, there is no denying that Cuvier took his skills in comparative anatomy to heights resembling magic.

For example, an ongoing excavation of the rock formation of the Paris Basin provided him with heaps of bones of large and extinct animals, which he proceeded to resurrect (so to speak), classify, and name. The importance of this skill for the development of a theory of evolution can be felt from retelling just two of his exploits. In another example, he examined a slab of granite containing a fossil that was described in 1726 and that was thought to contain the remains of the skeleton of a man who lived before the floods. This "relique" was soon put into its place when Cuvier demonstrated that the fossil was really that of a giant (now extinct) salamander. Clearly, this was *not* the eighteenth century anymore! In 1798, he published a study of elephant bones that proved that not only were the African and Indian elephants different species, but that they were also quite different from the fossil mammoths discovered in Europe and Siberia. Thus, he established evolution as a *fact*, and proved without the possibility of doubt that certain animal species were indeed extinct (as has been suggested by others before, of course).

More generally, Cuvier's precise analysis of anatomy led to the total destruction of the idea of a greater chain of being, that all organisms could be arranged in an unbroken chain reaching from the simplest all the way to God. Instead, he showed that a number of different body types had been evolving for ages completely in parallel, and that there was no conceivable way in which they could be put into a sequence. Thus, evolution did not proceed as the ladder or chain that was imagined during antiquity, but instead rose up more like a bush, with innumerable twigs, some prospering, some not. This type of insight, and the precision and diligence with which it was obtained, proved to be inspirational for Darwin, along with the momentous changes that occurred in the field of geology.

When discussing the thoughts that influenced Darwin and moved him on to the path to the *Origins*, most agree that the work of the geologist Charles Lyell (1797–1875) takes the crown. To gauge the importance of Lyell's work, we should remind ourselves again of the thinking with respect to geology that was current in this era. Up until the time that Lyell published his most important work, the three-volume *Principles of Geology* (Lyell 1830–1832), it was almost universally accepted that the present state of the Earth was a result of the biblical deluge, and that the forces that shape the Earth were due to divine interventions. This theory of *catastrophism* was popular despite the work of James Hutton (1726–1797), who in the eighteenth century had argued against catastrophism by invoking an eternal cycle of natural forces to which the Earth's features are exposed, building and reshaping surfaces, mountains, and seas. Hutton's *uniformitarianism* was the first blueprint of a physical theory of the Earth, in which processes of erosion and rebuilding are the main characters, and the surface of the Earth itself serves as the memory of bygone days. In particular, it was Hutton who boldly exclaimed that this process of erosion and regeneration showed that time was unlimited, "that we find no vestige of a beginning, no prospect of an end" (Hutton 1795). On the other hand, Hutton was a devout Christian who believed that the Earth was formed in this manner by God to allow human habitation, and the influence of his ideas gradually waned.

Enter Lyell, who after a brief career as a lawyer decided to devote himself full-time to his geological studies, while marshaling his talents of persuasion. The publication of the *Principles* irrevocably cemented the concept of unlimited time and the operation of natural forces into geology. Lyell's book was extraordinarily popular not only within scientific circles but also with

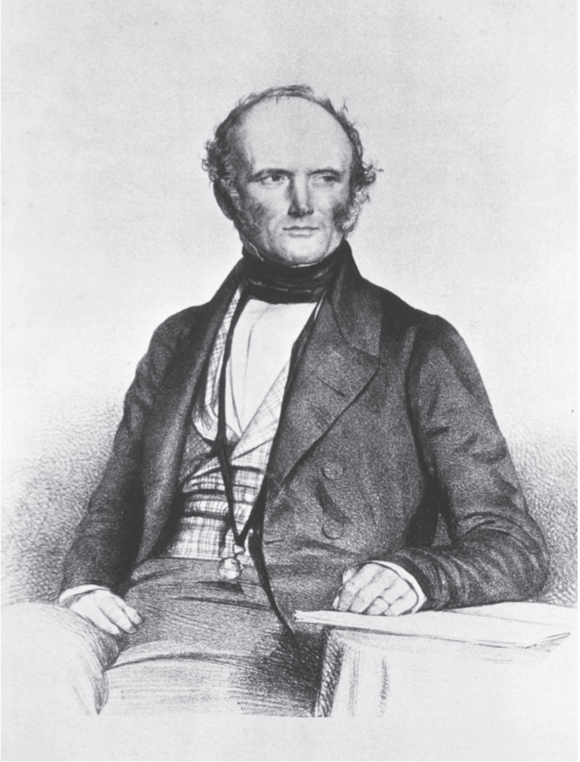

FIGURE 1.15. Charles Lyell, drawn by H. Maguire (National Library of Medicine).

the public at large, and contributed to a change in attitude among what would later constitute Darwin's audience. Darwin read the first edition of the *Principles* while on board the *Beagle* and was deeply impressed. Lyell's version of uniformitarianism, sans the mystic and obscure overtones of Hutton's theory, argued for a natural origin of the features of the Earth, while Darwin himself was searching for a natural origin of the species inhabiting it. The style of argumentation and the abundance of evidence presented to make his case deeply resonated within Darwin, and he appears to have copied some of Lyell's style in writing the *Origins,* which is dedicated to Lyell.

Armed with so much geological evidence and knowledge of the fossils, it may appear somewhat curious that Lyell did not discover evolution himself, or even strongly believe in its reality until very late in life. After all, Lyell wrote abundantly about the diversity of flora and fauna, as well as its distribution in relation to geology and geographic location; indeed, he was even the first to use the words "struggle for existence"! The reason for Lyell's failure to see the

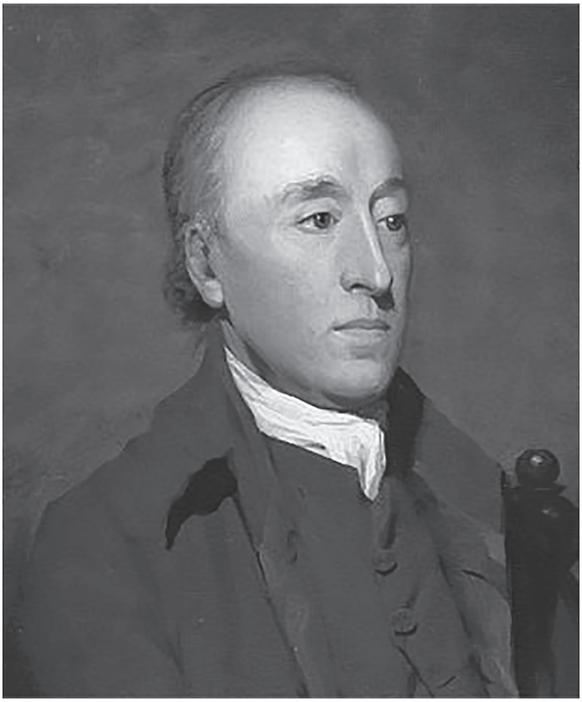

FIGURE 1.16. James Hutton. Detail of a painting by Sir Henry Raeburn (1776) (Scottish National Portrait Gallery).

natural forces operating on the level of species can be found in his deep belief in the principles of uniformitarianism. This view argues for constant natural forces shaping and reshaping the Earth, but it does not call for *progress*. Indeed, right around the time that Darwin prepared the *Origin* for publication, Lyell was advocating a theory of *nonprogressionism* for the species problem, which mirrored his uniformitarianism. On the one hand, it is astounding how close Lyell came to anticipating Darwin when he was describing the mechanisms by which old species are being replaced by new ones in their struggle for existence in an environment with limited food supply. On the other hand, these thoughts are permeated with the concept of a cyclic nature of uniformitarian forces and do not anticipate the evolution of radically new forms of life and their common descent. Instead, the species that come and go and succeed each other in Lyell's view are all somewhat similar variations on a theme, coming and going eternally.

It is of course impossible to close a chapter on the evolution of Darwinian thought without mentioning the influence of Alfred Russel Wallace (1823–1913), a naturalist and explorer from Wales, whose forays into

(continued...)

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