Chapter One

Introduction to Evolutionary Processes

In this chapter we introduce the basic elements and the empirical evidence of evolutionary processes. Since the groundbreaking work *The Origin of Species* by Charles Darwin (1859), a great deal of effort has been dedicated to the subject (see, e.g., Fisher, 1930; Haldane, 1932; Dobzanski, 1937; Mayr, 1942, 1963, 1982; Wright, 1969; Dawkins, 1976, 1982, 1986; Cavalli-Sforza and Feldman, 1981; Maynard Smith, 1989, 1993; Maynard Smith and Szathmary, 1995, just to mention a few masterpieces). Our discussion on the origin of evolutionary theory is mainly taken from the introduction by Ernst Mayr (2001) to the seventeenth printing of Darwin's famous book, and from Dieckmann (1994, Chapter 1), Schrage (1995), Rizzoli-Larousse (2003), and the web pages of the University of California Museum of Paleontology. Throughout the exposition we emphasize that, even though the major scientists who developed evolutionary theory were stimulated by the study of nature, their ideas not only apply to the biological realm, but also capture many phenomena of self-organization encountered in social sciences, economics, and engineering.

1.1 ORIGINS OF EVOLUTIONARY THEORY

The idea that living organisms have been diversifying themselves through time, starting from a common origin, goes back to the Greek naturalistic philosophy. Among the precursors of evolutionary theory, as we define it today, we can mention Anaximander of Miletus (610–546 BC), Empedocles of Acragas (495–435 BC), and later some clergymen, such as Saint Augustine (354–430). The evolutionary conceptions of Greek philosophy were known during the Renaissance. However, no further contribution arose until the eighteenth century, when European scholars still believed that the universe was created in essentially its present and final state. During the eighteenth century, the work of intellectuals known as "encyclopedists" spread the Illuminism doctrine and, in particular, the results of pioneering research in systematic biology, aimed at hierarchically classifying organisms into groups that successively share more and more visible structural characteristics. Their work brought a better understanding of the concept of species and highlighted fundamental similarities between widely disparate organisms. Such similarities were in contrast with the hypothesis of creation in final state and prepared the ground for evolutionary theory. A considerable contribution came from Georges-Louis Leclerc Buffon (1707–1788), author of a compendium of biological history, and from Erasmus Darwin (1731–1802), Charles' grandfather, who first discussed the conjecture that life could have evolved from a common ancestor and posed the question of how a species could evolve into another. The first explicit evolutionary theory was formulated by Jean Baptiste Lamarck (1744–1829), disciple of Buffon, who introduced the notion of inheritance. The "Lamarckian" hypothesis, that simple life forms continually come into existence from dead matter and continually become more complex, was strongly criticized by most naturalists of the time. In particular, one of the most active antievolutionists, Georges Cuvier (1769–1832), paradoxically provided evidence to the evolutionary hypothesis with his research in systematic biology, comparative anatomy, and paleontology.

At this point Charles Darwin (1809–1882) and Alfred Russel Wallace (1823–1913) formulated the evolutionary theory that we still accept today. In their papers published in the same issue of the *Journal of the Proceedings of the Linnean Society* (Darwin, 1858; Wallace, 1858, often cited as a single paper with the title "On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection") they presented their theory of evolution by *natural selection*, arguing that

– there is individual variation in innumerable characteristics of populations, some of which may affect the individual ability to survive and reproduce;

– there is likely to be a hereditary component to much of this variation, but evolutionary change ultimately relies on the appearance of new variant forms of organisms, called *mutants*;

– generation by generation there is a natural selection of the characteristics associated with greater survival and reproductive success, whose frequencies in the populations increase over time;

– the cumulative effects of mutations and natural selection, over a long period of time, alter the characteristics of species from those of their ancestors;

– all living organisms have descended with modifications from a common ancestor, thus developing hierarchical patterns of similarities.

Darwin and Wallace combined empirical observations with theoretical insights gained from Malthus' (1798) work on competition and population growth. They had a precise idea of natural selection and realized the need of mutations. However, they were not aware of the laws of heredity, discovered seven years later by Gregor Mendel (1822–1884), who realized the discrete nature of heredity determinants, which we now call genes (Mendel, 1865). Darwin actually introduced the concept of natural selection and deserves, more than anyone else, the credit for having started, and firmly supported, the scientific and philosophical revolution from the dogma of creation and constancy of species to evolutionary theory.

The decisive event in Darwin's life was the five-year period spent as a naturalist on the vessel Her Majesty's Ship *Beagle* (from December 1831 to October 1836), in which he surveyed the coast of South America and the off-lying islands, collecting invaluable observations on the tropical forests of Brazil, on fossils in the Pampas of Argentina, on the geology of the Andes, and on the animal life of the

Galapagos Islands (Darwin, 1839). After the return of the *Beagle*, Darwin spent most of his time in the analysis and interpretation of his findings and became later more acknowledged than Wallace, thanks to his famous book *The Origin of Species* (1859).

A third important scientist in the development of evolutionary theory, though by far less acknowledged than Darwin and Wallace, is Patrick Matthew (1790–1874). In a letter to Charles Lyell (April 10, 1860) Darwin says: "In last Saturday Gardeners' Chronicle, a Mr. Patrick Matthew publishes long extract from his work on Naval Timber & Arboriculture published in 1831, in which he briefly but completely anticipates the theory of Natural Selection. — I have ordered the book, as some few passages are rather obscure but it is, certainly, I think, a complete but not developed anticipation." Matthew's evolutionary insights lie buried in an appendix of a book he wrote on raising trees of optimal quality for the Royal Navy (Matthew, 1831). In that appendix Matthew expressed his theory based on how tree species might vary in form and how artificial selection might improve cultivated trees.

Let us now listen directly to Darwin, Wallace, and Matthew. "The affinities of all the beings of the same class have sometimes been represented by a great tree. I believe this simile largely speaks the truth. The green and budding twigs may represent existing species; and those produced during each former year may represent the long succession of extinct species... The limbs divided into great branches, and these into lesser and lesser branches, were themselves once, when the tree was small, budding twigs; and this connexion of the former and present buds by ramifying branches may well represent the classification of all extinct and living species in groups subordinate to groups... From the first growth of the tree, many a limb and branch has decayed and dropped off, and these lost branches of various sizes may represent those whole orders, families, and genera which have now no living representatives, and which are known to us only from having been found in a fossil state... As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all a feebler branch, so by generation I believe it has been with the Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications" (Darwin, 1859).

"We have also here an acting cause to account for that balance so often observed in Nature — a deficiency in one set of organs always being compensated by an increased development of some others — powerful wings accompanying weak feet, or great velocity making up for the absence of defensive weapons; for it has been shown that all varieties in which an unbalanced deficiency occurred could not long continue their existence. The action of this principle is exactly like that of the centrifugal governor of the steam engine, which checks and corrects any irregularities almost before they become evident; and in like manner no unbalanced deficiency in the animal kingdom can ever reach any conspicuous magnitude, because it would make itself felt at the very first step, by rendering existence difficult and extinction almost sure soon to follow" (Wallace, 1858).

"As Nature, in all her modifications of life, has a power of increase far beyond what is needed to supply the place of what falls by Time's decay, those individuals who possess not the requisite strength, swiftness, hardihood, or cunning, fall prematurely without reproducing — either a prey to their natural devourers, or sinking under disease, generally induced by want of nourishment, their place being occupied by the more perfect of their own kind, who are pressing on the means of subsistence…a law universal in Nature, tending to render every reproductive being as the best possibly suited to its condition…There is more beauty and unity of design in this continual balancing of life to circumstance, and greater conformity to those dispositions of Nature which are manifest to us, than in total destruction and new creation. It is improbable that much of this diversification is owing to commixture of species nearly allied, all change by this appears very limited, and confined within the bounds of what is called species; the progeny of the same parents, under great differences of circumstance, might, in several generations, even become distinct species, incapable of co-reproduction" (Matthew, 1831).

After more than a century since the publication of Darwin's famous book, we can say that the impact it had on man's concept of himself and his activities has been dramatic and has gone far beyond biology. Reduced to the essential, evolutionary change can be described as a two-step process: the first step consists of *innovation*, namely the production of variations, while the second is ruled by *competition* and leads to the selection of the best-performing variants. This abstract paradigm can be applied to many processes of self-organization that drive the evolution of complex natural and artificial systems, composed of several interacting agents, or units, each characterized by individual traits that are transmitted, with possible modifications, to agents or units of next generation, and naturally or artificially selected by their effectiveness or by optimization criteria. In other words, after the Darwinian "revolution," networks of socio-cultural relationships, the global economy, and the design of several industrial processes can be interpreted and studied as evolutionary processes.

In particular, Richard Dawkins reformulated the paradigm of evolution independently of genetic inheritance to explain the evolution of culture. In his books *The Selfish Gene* (1976) and *The Extended Phenotype* (1982) he argued that cultures, namely the clouds of ideas, behavioral traits, and artifacts developed and produced by animal and human populations, compete, cooperate, mutate, and are transmitted as well as genetic traits. Thus, the constitutive elements of cultures do evolve, and actually coevolve with genetic traits in a whole biological-socio-cultural evolutionary process. Dawkins introduced the concept of a *replicator* as the minimum natural or artificial unit evolvable through a *mutation-selection* (or better *innovation-competition*) *process*. Replicators are characterized by four fundamental properties:

– *replication*: units generate or are replaced by new units;

– *transmission*: units are characterized by distinctive features that are passed to the units of next generation;

– *innovation*: transmission is not a perfect copy but allows for variations;

– *competition*: survival and effectiveness of units are regulated by the characteristic features of interacting units.

Dawkins' idea of a replicator was elaborated on just a few years after Francis Crick and James Watson's (1953) discovery of the double helix molecular structure of the *deoxyribonucleic acid* (DNA). Although this idea might simply seem an abstract summary of Darwin and Wallace's evolutionary theory, its conceptual impact is enormous because it offers a paradigm of evolution that can be scaled from DNA to macroscopic natural and artificial systems. In fact, even if Dawkins' work is focused on animal and, in particular, human biological and cultural coevolution, the concept of replicator is fully independent of biology and can in principle be applied to describe any innovation-competition process. However, for tradition, simplicity, and uniformity, we will mainly refer throughout this chapter to biological evolution, pointing out here and there, and, in particular, in Section 1.9, the analogy with the evolution of social and economic systems. Later, in Chapter 4, we will interpret and analyze the process of technological change as an evolutionary process, where replicators are commercial products competing in a market, which replicate in production and transmit, with possible innovations, technological characteristics to new generations of products. Through a stylized model we will show that the evolutionary interpretation of technological change supports the emergence of technological variety from a single ancestral technology.

In the next three sections we introduce the basic biological elements of evolutionary processes, namely the structure of the genetic material and the laws of heredity, underpinning the way of being and reproducing of all living organisms, the appearance of mutations, ultimate source of organisms variability, and the mechanisms of selection of successful mutants. Among the innumerable options, we closely follow Charlesworth and Charlesworth (2003), a lucid and concise introduction to evolutionary theory, presenting some of their contributions in a form appropriate for this book. Sections 1.5–1.8 describe the evolutionary patterns we might expect to emerge as long-term consequences of evolutionary processes, while the last section shows many examples of such patterns in biological as well as nonbiological contexts.

1.2 GENOTYPES AND PHENOTYPES

Starting with Mendel's (1865) work and passing through the achievements of modern molecular biology, we now know that the similarities between living organisms are not confined to visible structural characteristics, but are profound and extend to the smallest microscopic scale. All living organisms other than viruses (which are on the borderline of life) are composed of a single unit or an assembly of essentially similar units, the *cells*. In so-called *eukaryote* organisms, which include all multicellular species (animals, plants, and fungi) as well as some unicellular species, cells are delimited by a membrane and contain the *cytoplasm*, a gel with floating subcellular structures, and the *nucleus*, which carries the genetic material. The remaining unicellular organisms, called *prokaryotes* and including bacteria and similar organisms called *archaea*, are simpler cells in which the genetic material is floating in the gel with no subcellular structures and nucleus. Viruses are parasites that reproduce inside the cells of other organisms and consist of a chemical coat