Evolution and Society

Manfred D. Laubichler and
Jane Maienschein

Evolution and society are connected in many different ways. First and foremost, humans, as a product of evolution, live in diverse societies. These are an outcome of evolution, albeit in more complex and often more indirect ways than the evolution of direct morphological and physiological adaptations. Second, the initial development of evolutionary theory occurred in a specific social milieu conducive to this particular intellectual endeavor, and subsequent development of evolutionary theory has also reflected its evolving historical settings. Evolutionary theory, like any other science, has thus been the product of a particular human society. Finally, and as probably the most visible connection of evolution and society, especially in the United States, we find surprisingly persistent debates about whether evolution or some form of creationism accounts for the origin of species (as Eugenie C. Scott discusses in the main essay "American Antievolutionism: Retrospect and Prospect" in this volume).

At some times, in some places, and in some ways, society has enthusiastically embraced evolution; at other times and places and in other ways, society has not. In the process *evolution* has meant different things, as has *society*. We therefore start with definitions and then look at society's impact on evolution in two ways: the way in which society in the sense of social, cultural, and intellectual context has shaped evolutionary theory, and also the social reception of evolution. Then we turn the direction of influence around and address how evolutionary theory today and in the past has contributed to explanations of society. In conclusion we discuss current relations between evolution and society in a forward-looking way.

We do not focus on much-discussed relationships such as standard interpretations of social Darwinism or retrace the history of ways in which social commentators have used (and misused) evolution. There is such a rich literature in these general areas that any general Google or Amazon search will yield dozens of offerings, of which Carl Degler's *In Search of Human Nature: The Decline and Revival of Darwinism in American Social Thought* (1992) or Richard Hofstadter's *Social Darwinism in American Thought* (1959) are just

two well-known and different types of examples. Readers can look to Herbert Spencer, Peter Kropotkin, Andrew Carnegie, and other popular examples of social thinkers who invoked evolution, or they can take up the evolution chapters in such recent books as Bernard Lightman's *Victorian Popularizers of Science: Designing Nature for New Audiences* (2007) for an introduction to less familiar popularizers. Again, it is not on this well-trod ground that we roam. Rather, we explore less familiar aspects of the intersections of evolution and society by asking about the relationships in a variety of ways.

Definitions

By *evolution* we mean the evolutionary theory of biologists rather than general evolutionary ideas, that is, naturalistic, materialistic explanations of the change of populations over time such that inherited variations are preserved and lead to divergence of forms and the origin of new species that are adapted to their environments. This process can happen more or less gradually, with variations of various sorts, inheritance working in complex ways, and species and populations defined differently. Nonetheless, there are constant themes: all accounts of evolution begin with naturalism rather than supernaturalism as a core assumption. All assume that organisms exist in an environment that in effect favors some variations over others since the favored are better *adapted*. And all versions assume that it is inherited variations that matter for evolution, though inheritance may come culturally with learning between generations, as well as biologically through genetic transmission.

We also share the view of Ernst Mayr and others that the Darwinian theory of evolution is composed of a variety of separate theories, and that at some times in the course of the history of evolutionary biology one or the other of these theories dominated the debates (Mayr 1982). Variation, heredity, struggle and competition, and emergence and preservation of the new are all part of evolutionary theory. Indeed, evolutionary theory is complex and consists of interconnected components that we explore in different ways in this essay.

By *society* we designate a variety of kinds of social groups. In some cases the relevant element of society centers on leaders who make decisions that affect many others. In other cases the relevant social group is more local, contingent, and populist, as when civic leaders may agree that evolution should be taught in the schools in any civilized society, but a vocal popular group demands a creationist antievolution account of the origin of man. Different social cohorts play different roles, obviously, and we will look at different groups as we go along. Similarly, when we discuss evolutionary explanations of (human) societies, we follow an equally catholic approach; *society* here means any group of animals or humans that interact with each other in a structured way and whose survival depends on these interactions (Wilson 1975; Boyd and Richerson 1985; Kuper 1994).

Evolutionary Theory Shaped by Society

Evolutionary theory exists in certain societies and is developed by members of these societies. That much is obvious. Darwin is the most visible central player, and historians have shown the significance of the facts that socially Darwin was upper middle class and a Victorian Englishman. For example, the British gentleman would presumably have found it easier than the poor son of a long-poor working-class family to come to Darwin's view of inheritance as a progressive and positive force in preserving variation or to see heredity as enabling rather than constraining. The way Darwin saw the world from HMS *Beagle* was surely shaped by his context and values, as historians have shown (Desmond and Moore 1991; Browne 1995, 2003; Hodge and Radick 2003). His world was the richly but gently entangled bank of an English garden rather than an arid desert, a diverse and pungent rain forest, or an Alpine tundra, each of which might have led him to different questions and emphases.

Furthermore, as Darwin scholars have demonstrated clearly, the British context of natural theology shaped evolutionary theory. William Paley saw each organism and each type as adapted to its place in the world. Of course, it was Paley's Anglican God the Creator who had done the adapting in that case, but the fit of life form to environment carried over neatly to Darwin's view of life. True, a Thomas Robert Malthus might point to the human economic dilemmas intrinsic in the tendency of every individual to increase into a population that rapidly outgrows available resources. But Malthus did not call into question that humans were adapted to their environment. Indeed, the tendency to produce too many individuals just gives nature the opportunity to choose some over others. Or, as Malthus suggested, perhaps man could do the choosing with wise population control. At any rate, social views shaped the evolutionary theory that emerged, and the results were optimistic. For Malthus, population control would make life better for each person and for society as a whole. For Darwin, only the "healthy, vigorous, and happy" would survive and reproduce. A happy picture indeed (Ruse 1979, 2003; Hodge and Radick 2003).

Another part of Darwin's Victorian milieu that was extremely important for his eventual formulation of the theory of natural selection as an explanation of evolutionary change was his close contact over many years with many animal and plant breeders (Browne 2003). Indeed, the close comparison between artificial selection (with morphological and behavioral changes in populations that could be induced by continued breeding) and natural selection (changes that would be a result of the "struggle for existence" in nature) is a major part of Darwin's "long argument"

The German intellectual movement *Naturphilosophie,* with its romantic conception of nature, brought other perspectives that shaped evolutionary theory as it played out in Germany. Johann Wolfgang von Goethe's organicism that saw an unfolding of form, Friedrich Schelling and Georg Hegel's

assumptions of unity of nature, and Karl Marx's search for an unfolding of society shared the assumptions of emergence or of form from nonform and of change over time that leads to improvement and progress (Ruse 1996; Mocek 2002; Richards 2002). These social and philosophical threads helped shape the intellectual environment into which evolution arrived. Ernst Haeckel's particular version of evolutionary theory in Germany shared the positive and progressive implications of evolutionary change and developed the ideas in an explicitly and eccentrically materialistic way that had tremendous social impact, just as society had shaped the scientific ideas.

What was seen as an "eclipse of Darwinism" at the end of the nineteenth century also reflects impacts from outside science itself on evolutionary theory (Bowler 1983), shifting away from reliance on what Darwin had seen as randomly arising variations. Mendelism introduced genes, heritable units, and a focus on the internal workings of the organism more than on the organism in its environment. This brought a shift from the more organic interpretations that appealed to Marx and other late nineteenth-century social reformers who were calling for natural change. Instead, we see a rise of genetic determinist or hereditarian thinking, which in turn influenced evolutionary theory, and the determinism of which appealed to different social groups. If the heritable variations were genetically determined, then evolution could presumably be influenced by modifying these genes.

We cannot overemphasize that this is not simply a matter of science affecting society, though that has been the primary focus of historical discussion. Here the point is that forces within society were affecting science, shaping evolutionary theory, and influencing the choices made about which questions to ask and which assumptions to make in a complex theoretical arena of uncertainty where some assumptions must nonetheless be made. Social factors, as well as internal scientific developments, shape which methods to use to study evolution: naturalistic field work and description or experimental control and manipulation of variables, and study of populations or individuals, whole organisms, parts of organisms, invisible parts like genes, or emergent parts like behaviors and other traits.

August Weismann provided an inheritance-based evolutionary theory. His 1892 *Keimplasma* contained sequestered germplasm that was protected from environmental influence. This was the material of inheritance and the raw material of evolution, providing substance for evolutionary change through competition among his hypothetical ids, determinants, and idants, all arranged along visible chromosomes. The relevant population, that of these inherited material units, was now inside the individual organism, and this raised new questions about how far the action of natural selection can take us and about the fine details of the mechanisms of evolutionary change. For Weismann, who was part of a scientific tradition that focused on cell biology, development, and microscopic observation, the important natural selection took place inside each organism, and the environment was the internal environment.

Weismann's evolutionary theory disallowed direct external environmental impact on the inherited chromosomes. His denial that Lamarckian use and

disuse of particular parts could have any effect on evolution is taken in retrospect as putting that idea to rest, though it did not actually do so. Instead, neo-Lamarckism continued to find a place in social and political contexts that emphasized the importance of change through effort and will, such as that of Richard Semon early in the twentieth century and with a line of less well-known supporters through subsequent generations (Semon 1908). By the second half of the twentieth century, political figures such as T. D. Lysenko gained considerable authority in the Stalinist Soviet Union, and not solely for distorted political reasons. Lysenko's neo-Lamarckism appealed to the hope that if only scientists could cultivate seeds in the right environment, they could produce enough grain to save the people from starvation. There was tremendous belief in the powers of science, and even though neo-Lamarckian ideas have later been identified with Soviet-style materialism, at least initially many of these proposals emphasized the role of culture and the social environment in shaping the fate of human societies.

Some would insist that this was clearly bad science, and for those fully familiar with contemporary scientific paradigms, it was. But for those for whom evolution was not a central part of their education and worldview, such an evolutionary theory that would place the causes of variations directly in use and disuse in response to the environment made sense. It was not a long stretch from Darwinian evolution to seeing temperature changes as a source of new variations through mutation and selection and therefore as the source and cause of the origin of species. Lysenko's version of neo-Lamarckism promised a speedier evolution, and since evolution was seen as progressive, it therefore offered a faster route to progress and improvement. Social needs shaped science, which then played out in society (Todes 1989).

We see another example in the so-called modern evolutionary synthesis of the late 1940s and after. Participants at key meetings, such as the 1947 Princeton meeting, saw this as a time of optimism for evolutionary biologists (Mayr and Provine 1980). The prewar tensions in Europe and the United States may well have encouraged the sort of synthesis that Julian Huxley, as a political activist with the United Nations, sought in his *Evolution: The Modern Synthesis* (1942). Huxley was not a major intellectual shaper of the perceived synthesis but a central voice in conceiving of it in that way (Smocovitis 1996). However, even while evolutionary biologists such as Ernst Mayr and George Gaylord Simpson eagerly embraced the idea of synthesis with evolution at the core, already other biologists were pushing in counter-directions. Cell biologists and geneticists cared more about the internal workings of cells and their contents than about the bigger pictures of evolution. Rapidly increased funding for medical research and medical demands of wars helped drive wedges between specialties within the biological communities. Evolutionary biologists often found themselves as comparative specialists in natural history museums, while more reductionist research programs gained priority in many universities and especially in medical schools.

Debates about the efficacy of adaptation reveal similar social shaping of evolutionary theory. Stephen Jay Gould, Niles Eldredge, and others began in

the 1970s to question how far natural selection can really effect change (Eldredge and Gould 1972). Is evolution really all gradualism and slow accumulation of morphological differences? Or could change be "punctuated" with more sudden "explosions"? Perhaps some changes could enable many others, as passing through a bottleneck to the opening beyond can do. Or external factors might lead to punctuation. Evolutionary theory could support competing interpretations of mechanisms, these researchers felt, though their views were interpreted by antievolutionary creationists as challenging the validity of evolution.

A central point here is that this critique and the revisions in evolutionary theory that resulted were, in part, shaped by the society in which they appeared. Old-school adaptationism and gradualism provided a slow process for change. Not coincidentally, those who were calling for punctuation were young and fancied themselves social reformers who favored rapid social change. This does not mean that they were wrong scientifically any more than those who favored gradualism. Nor does it mean that their challenges have not had tremendous positive impact on evolutionary theory generally. They have. Our point here is that the society and the social values the scientists absorbed have shaped the evolutionary theory significantly.

Today we see another transformation of the adaptationist paradigm in evolutionary biology in the form of a merger of developmental and evolutionary biology. Population genetic models have emphasized genetic changes within population. But genes do not interact with the environment, organisms do, and the way genetic variations relate to corresponding phenotypic variations has important implications for our understanding of evolutionary changes. Two notions, in particular, that are part of this new paradigm also have wider societal implications, namely, the ideas of constraints and of interactions (Maynard Smith et al. 1985). The idea of constraint emphasizes that not all variations are equally likely or even possible. It states that the developmental and physical boundaries of an organism limit the ways genetic variations can be translated into phenotypic variations because of the properties of the developing system. These are, of course, a consequence of multiple interactions among genetic, cellular, and environmental factors that together contribute to organismic development. The new synthesis of evo-devo (short for evolutionary and developmental biology) thus also emphasizes an epigenetic and interactive view of biology.

This perspective has many scientific, cultural, and societal resonances; the idea of limits on what is possible within the boundaries of a natural system was first made popular in the context of the worry about a "population bomb" and the environmental movement. Similarly, the growing emphasis on interactions, even between distant parts of a large ecosystem, has found its first manifestations in this context. But today these concepts are also seen as relevant within developmental and evolutionary biology, where, quite ironically, the completion of the many genome projects—in many ways the culmination of the genetic paradigm—has led to insights into the highly interactive and epigenetic nature of both development and evolution (Hall 1998).

That evolutionary theory has not been insulated from social influences is no surprise to historians of science, but it is often surprising to scientists who see science as relatively insulated and progressing according to its own internal logic and responses to opportunities. It is also surprising to some social historians, who rarely study the history of science and who tend to take science as given and to see it as shaping society on occasion rather than to see the interactions in both directions. Darwinism, as Desmond and Moore (1991) and Browne (1995, 2003) have shown clearly, is just as much a story of Darwin in society as of Darwinism in society.

Society's Reception of Evolution

Historians have long described the reception of Darwinism, in particular, to show the variations in reaction. Why is evolution taken as a challenge to established values in some countries or local societies and not in others or to some religions and not others? Why have some groups readily endorsed the naturalism at the core of evolutionary theory, as Germany did in the late nineteenth century, while there is hostility at some times and in some groups to the apparent randomness and lack of purpose that they see in evolution? To what extent is the response shaped by local contingencies of dominant influential individuals, perhaps, and to what extent does the reaction flow from the logic of the values and assumptions within the culture? The answers to these questions are complex and involve detailed accounts of the social, cultural, economic, and political history of these societies and countries. For a more detailed account, the reader should consult the substantial body of literature in this area (for example, Hull 1973; Kohn and Kottler 1985; Wassersug and Rose 1984).

Here we want to point to just one aspect, namely, how different societies' reception of evolutionary ideas contributed to the further development of evolutionary theory. Within Darwin's inner circle Thomas Henry Huxley most visibly emphasized the importance of evolutionary theory to promote a liberal and materialistic agenda. To him, evolution implied that there is no intrinsic value in heritage and pedigree, and that all that should count are the abilities of people. As a consequence, he promoted science as a profession rather than a vocation and fought a constant battle against religion as the stalwart of received values (Desmond 1997). Similarly, Ernst Haeckel focused on the materialistic implications of evolutionary theory, which he expanded into a whole system of monistic philosophy. Neither Huxley nor Haeckel thought highly of natural selection as a mechanism of evolutionary change. Rather, each incorporated the principle of evolution into his scientific discipline (mostly morphology) and his highly successful teaching. In teaching they both interacted with and shaped current trends within their respective societies, while their scientific contributions influenced several generations of biologists.

A similar pattern can be seen in Russia, where ideas and observations about symbiosis and cooperation also challenged the dominance of natural

selection as an explanation of evolutionary change (Todes 1989; Ackert 2007). Another influence in Russia was the presence of a strong tradition of natural history and ecology, which laid the groundwork for subsequent studies of evolutionary changes within local populations (Adams 1994). Meanwhile, in Vienna emphasis on experimental work within physiology and developmental mechanics paired with focus on an organism's life history in the work of the biologists who worked in the Vivarium. This provided an experimental basis for proposals that questioned the then-emerging genetic context in favor of a developmental (including neo-Lamarckian) perspective on evolution (Przibram 1904).

All these examples show that the reception of evolutionary theory in a society never was just a one-way street. In all cases this was a highly interactive relationship that in turn contributed to the further development of evolutionary theory in interesting ways.

Evolutionary Theory Explaining Society

There are no a priori limits on what can be the subject of an evolutionary explanation as long as certain basic conditions apply. From monad to man, a multitude of different life forms and their behaviors, as well as their social and ecological interactions, have all been shaped by evolutionary forces (Ruse 1996). Obviously there are differences between the coordinated movements of slime molds that are forming a fruiting body and the members of an orchestra who are playing a Beethoven symphony, but both are ultimately the result of the interplay of complex behaviors that exist in accordance with the framework of evolutionary theory. In order to understand this last statement, keep in mind the ways in which any feature, morphological or behavioral, can be considered the product of evolution.

Natural selection favors variants with higher fitness, namely, those that manage to increase their representation in the next generation. This process is described by the universal replicator equation that mathematically describes the consequences of natural selection and that applies to all objects that can reproduce themselves (Dawkins 1976; Hofbauer and Sigmund 1998). The replicator equation does not specify what properties of these objects actually contribute to fitness differences; it only predicts that whatever variable features are responsible for these effects, these will eventually reach a (local) optimum as long as environmental conditions do not change. Furthermore, the replicator equation does not specify how those variants manage to reproduce themselves. All that is required for natural selection is that reproduction happens with a sufficient degree of accuracy that the favorable properties do not disintegrate too fast. Many different structures can thus be potential and actual replicators, or units of selection. These include molecules, genes, cells, clones (in the botanical sense), groups, including social groups, and ideas, so-called memes (Dawkins 1982; Brandon and Burian 1984; Sober and Wilson 1998).

The replicator equation specifies the broad limits of what kind of properties can evolve—those that either increase the fitness of their carriers or those that are neutral with regard to fitness (those, however, are the subject of a different dynamics; see Kimura 1983). If we now ask in what way a specific new phenotype such as a morphological feature or a form of behavior can be the product of evolution, we have to address an additional question. Before such novel phenotypes can contribute to fitness, they must first emerge within their carriers; that is, they must themselves be products of evolution. In other words, the molecular, cellular, and developmental context of organisms is the first part of the explanation of any new feature. Only those phenotypic variants that are possible at all can become the raw material for natural selection, because phenotypes determine the fitness of their carriers. The fact that development plays a crucial role in this generation of variation has recently been the subject of increased attention (Raff 1996; Hall 1998).

For our discussion of evolutionary explanations of societies, a different aspect of the evolutionary process is also of interest. As we have seen, all that is required for natural selection to act is the availability of accurately transmitted variation in fitness. This relationship is commonly measured by heritability of a character. Heritability is actually defined as the correlation between parents and offspring, and even though in many cases the reason for this correlation will be genetic, it is not limited to the effects of genes (Falconer 1989). This aspect of heritability is especially important in the context of discussions about cultural evolution. Not only can ideas or memes be interpreted as replicators, but in the context of human, as well as animal, societies learned behaviors can be transmitted to the next generation. From this abstract perspective there is thus no contradiction between the intricate patterns of human history reflected in the changes and transformations of human societies and the basic principles of evolutionary biology. There are, of course, many additional factors besides genes that contribute to human history. Nothing less would be expected from the viewpoint of evolutionary theory because more complex systems add many different levels and degrees of freedom, but all this happens within the confines of evolutionary principles.

It is important to note that this perspective does not imply any form of biological reductionism; rather, the evolutionary analysis of complex systems, such as human societies, requires that we simultaneously consider effects at all different levels of complexity. Indeed, in evolutionary biology the most interesting questions always arise in situations where any simple explanation reaches its limit and where we find a conflict between different entities. These are the "major transitions in evolution" described by the late John Maynard Smith and Eörs Szathmáry that bring about something fundamentally new, such as the first multicellular organisms or the first human societies (Maynard Smith and Szathmáry 1995). In order to survive, these new entities need to "control" the behavior and selfish interest of the parts; in higher organisms, cells have to give up their own reproductive interests, and in a complex society with a high degree of division of labor, these activities also need to be

coordinated. How these regulations come about and evolve is one of the most fascinating problems of evolutionary biology (Margulis 1981).

These brief technical comments about the basic assumptions of evolutionary theory also help us see the long-standing controversy over nature versus nurture in a different light. In the context of evolutionary biology this distinction is one only of degree and not of kind. There is no clear-cut separation between nature (or biology) and nurture (or culture and society). A multitude of factors, both biological and cultural, contribute to the development and formation of any human being; indeed, our developmental program requires all these different stimuli as crucial inputs.

As we have learned from evolutionary biology, compared with our closest relatives, we are born prematurely (Portmann 1951). One consequence of this fact is that in human infants the developing brain is stimulated by a multitude of environmental and social factors. In addition, we have learned that in our evolutionary history the emergence of social skills, including the evolution of language, was much more important than accumulated genetic differences (Diamond 1992; Kuper 1994). Of course, precisely those characteristics also enable learning and the transmission of acquired knowledge. In conclusion, all evidence thus far points to highly interactive relationships among different factors (biological and cultural) in human evolution. Consequently, in explanations of human evolution and society we cannot give priority to any one of these factors over all the others. This realization should also help us avoid the naturalistic fallacy; knowing the evolutionary history of some aspects of our behavior and social organization does not imply any value judgment about these properties. But realizing the evolutionary reasons for these behaviors does help us if we want to enforce societal roles, a fact that is increasingly realized by a growing community of legal scholars, economists, and management consultants.

Our brief analysis of the relationship between evolutionary theory and society notwithstanding, it is also true that throughout the history of evolutionary biology the majority of attempts to apply evolutionary principles to explanations of human societies have been grandiose failures (Hofstadter 1959). Seen through historians' eyes, these cases are prime examples of the mutual relationship between science and society discussed in the first section; at certain times specific societal beliefs and assumptions resonate with elements of the then-current state of evolutionary theory and become the foundation of wide-ranging "explanations" of nature and society. Seen through the eyes of an evolutionary biologist, these cases take on a different meaning. On the one hand, one might argue that these cases are a reflection of the then-incomplete status of evolutionary theory, at least when compared with our present understanding. Taken at face value, this view is problematic because it implies a rather naive conception of scientific progress. Another observation an evolutionary biologist would make, looking back at previous cases of evolutionary explanations of society, is that all these proposals tend to emphasize only one or a few elements of what Ernst Mayr and others have identified as the multiple elements of evolutionary theory (Mayr 1982).

This observation allows us to combine historical contextualization of evolutionary explanations of society (what was the scientific, social, political, and economic context of these proposals?) with evaluation in terms of their scientific merit (what were the problems with and wrong assumptions of these proposals? what was left out, and what was exaggerated?). This approach allows us to analyze these various proposals both in relation to their historical context and with regard to their scientific content. Unfortunately, we do not have the space to discuss these ideas in detail, but we want briefly to present a few examples of how evolutionary ideas were applied to human societies in the past before concluding with a sketch of how present-day evolutionary biology approaches the issue of human societies.

It will come as no surprise that as soon as there was evolutionary theory, it was applied to explain aspects of human society. Herbert Spencer, a popular philosopher and advocate of ideas similar to those of Darwin, coined the term *survival of the fittest* to describe the consequences of natural selection. Detached from its strictly biological meaning, this term could be (and was) applied to a variety of social contexts. It could be taken to support a conservative status quo when it was combined with ideas and observations that evolution favors conservation of existing traits and behaviors. In this way evolutionary theory provided a naturalistic and materialistic explanation of social differences by demonstrating how some people are more successful because they are fitter in Herbert Spencer's sense. Their variations are better adapted to the competitive social environment in which they live, and they therefore naturally enough rise to the top.

Not surprisingly, it was the great industrialist Andrew Carnegie who most enthusiastically embraced this interpretation of evolutionary theory as explaining society. But the idea of natural selection was also used in support of radical transformation of society, as the initial positive reception of Darwin by Marx, Engels, and other leading social democrats attests. They, of course, emphasized the transformative powers of natural selection rather than the conservative ones.

What all these initial applications of evolutionary theory to society have in common is that they focus mostly on competition, struggle, and a progressive interpretation of (evolutionary) history, as well as a hierarchical notion of different social classes and races. Furthermore, their notion of competition is more or less direct or hands-on. Struggle was often seen as a consequence of different strengths of individuals, groups, states, or races. Indeed, the early years of the twentieth century brought several attempts to adapt Darwinian logic to work as a guide to international affairs and politics (Ziegler 1918). What all these applications of evolutionary theory to society missed was an understanding of the internal conditions of organisms and the modes of transmission of hereditary material, which were, after all, crucial elements of Darwin's theory.

The centrality of heredity to the theory of evolution was not missed by Darwin's cousin Francis Galton. In his *Hereditary Genius* (1869) he realized that the cumulative effect of natural selection, necessary for gradual evolu-

tion, crucially depended on both the availability and the stability of adequate hereditary material. Focusing on inheritance and stability across generations, Galton saw possibilities for controlling populations and thereby controlling evolution and the future of human populations. This was an enticing idea to the Victorian progressivist. Not only could we have progress, but we could cause and control it through biology, Galton suggested with his call for good breeding with the negative and positive selections of eugenics.

In *Man and Superman* (1903), George Bernard Shaw also reflected a more progressive interpretation, though still very much grounded in assumptions that some are naturally better than others. Why not acknowledge that our society is currently weaker than it could and should be because we have no informed breeding program, Shaw suggested. We can explain our imperfections now and also seek to improve, generating a society of men and supermen.

Indeed, eugenics brought hope for progress especially to European and American visionaries in the early twentieth century. Leading geneticists joined the call for good breeding and for better society through biology. Only gradually did scientists accept how little solid scientific knowledge really undergirded the eugenic assumptions, so that in the 1910s and into the 1920s eugenics was not as ridiculously unscientific as it has seemed to commentators in retrospect. Social selective pressures reinforced those who adopted eugenic programs based on biological claims (Kevles 1985; Paul 1995).

Eugenic ideas, together with a biological concept of racial superiority and racial hygiene, contributed to the Nazi genocides, the campaign to exterminate "unworthy life," and finally the Holocaust. As a consequence, a growing coalition formed to counteract what was perceived as an inappropriate biological definition of human races, culminating in the 1950 UNESCO statement on race. This statement then became the foundation for further antidiscrimination policies and laws. These declarations emphasized ethnic rather than biological differences between human populations, which seemed consistent with studies that showed that the vast majority of genetic differences among humans occur within populations. However, in recent years genetic differences in mitochondrial and Y-chromosomal DNA between human populations have also been used to illuminate migration patterns and genealogical relationships between human populations, including the origin of our species in East Africa about 130,000 years ago. Today, even though the subject of genetic differences between human populations is still touchy, we find a growing consensus that neither the biological nor the cultural history of mankind can be ignored. This is especially true as several technological developments in the postgenomic age increase our abilities to customize medical treatment on the basis of the genetic constitution of patients.

The two most important theoretical insights into the evolution of (animal and human) behavior were Hamilton's notion of kin selection as an explanation of seemingly altruistic behavior and the application of game-theoretic notions, and here especially the concept of strategies, by John Maynard Smith and others (Hamilton 1964; Maynard Smith 1982). These ideas represented a

major change in evolutionary explanations of behavior and set the stage for the development of rigorous mathematical models.

The theory of kin selection and of inclusive fitness focused the debate on the appropriate units of selection in explanations of behavior. Rather than just looking at one individual's fate as the sole determinant of fitness, the theory of kin selection changes the ways in which evolutionary accounting is done. Within the framework of population genetics changes, evolution is represented as changes in gene frequencies. What Hamilton realized was that there is more than one way in which a specific gene in a specific individual can make it into the next generation. It can be passed on to its offspring directly or through the reproductive success of close relatives, who will share the same gene with a certain probability (.5 for siblings, .125 for cousins). In calculating the fitness of a specific gene, one thus has to focus on the inclusive fitness, which is the sum of all the different means by which a specific gene can come to be represented in the next generation.

Previous vague notions, such as the idea that a behavior can evolve because it is good for the species or the group, were replaced by concepts that accorded with the predictions of population genetics and the theory of natural selection. However, it is also important to note that these notions were highly abstract, and when they were first proposed, scientists did not really know anything about how these proposed genetic replicators actually could cause the respective behaviors. At this time the arguments were largely theoretical: if a gene/replicator causes altruistic behavior, it can be favored by natural selection as long as the cost to the individual acting selflessly is smaller than the benefit to its recipients multiplied by the coefficient of relatedness between those individuals. A similar approach guided the many game-theoretic concepts, such as the prisoner's dilemma and ideas about repeated games and reciprocal altruism that were used to explain many aspects of animal behavior.

The appeal of these new ideas was enormous, and biology seemed capable of explaining much of social behavior. The ideas provided an important boost to many disciplines, such as behavioral ecology, but also invited far-reaching generalizations and in turn generated many, often polemical, controversies. The most visible of the scandals erupted with the publication of E. O. Wilson's *Sociobiology* in 1975. In this encyclopedic tome Wilson, an expert on ants and social insects, collected an enormous amount of empirical data on what was then known about animal behavior and organized it in the context of the new theoretical framework. In the final chapter he applied these ideas to human behavior and the evolution of human societies. Furthermore, he proposed that this new synthesis would lead the social sciences to be integrated within the framework of the biological sciences. The reaction was vivid. However, ensuing debate focused mostly on the feared political implications—Wilson's most vocal critics belong to the Left—and on the consequences of the reductionism implicit in Wilson's emphasis of genetic explanations and in his model of the relations among the sciences. Surprisingly little attention was paid to the bulk of the book, the enormous amount of

empirical data and the rigorous application of evolutionary principles to animal and human behavior.

The sociobiology debate resembled the many other attempts to apply evolutionary explanations to human societies in that it overemphasized just one of the many dimensions of evolutionary theory. Wilson's genetic reductionism, supported by his experience with social ants, as well as the state of population genetics at this time, left little room for other factors or for the more interactive perspective that has emerged more recently. Wilson, his supporters, and his critics were all products of their social and political, as well as scientific, environments (at that time dominated by the recent successes of molecular biology). This led to a rather polarized climate within the life sciences of that time, which in part explains the confrontational tone of these debates.

Today, more than 30 years after the publication of *Sociobiology,* evolutionary explanations of society and discussions of cultural evolution are still popular within biology. However, the conceptual, as well as the empirical, basis for this research has become much more pluralistic. There is still considerable debate and controversy, especially surrounding evolutionary psychology. Yet some of today's approaches to understanding human (and animal) societies better reflect the insights of evolutionary theory sketched earlier. Many different fields of evolutionary biology contribute, and indeed the study of the evolution of complex social systems has become a paradigmatic case for interdisciplinary research. As such, it faces all the challenges of this kind of research; as each specialty takes on one aspect of society and human behavior, it is in danger of overemphasizing that part. And the ensuing debate, even if scientifically productive, is received by a society that is uneasy about evolution in general.

Conclusions

Evolutionary theory is unquestionably the foundation of biology. And of all the sciences, biology has the largest impact on today's societies. Biotechnology and biomedicine carry the hopes of billions that their, or at least their children's, lot will improve, while environmental sciences warn almost daily about the negative consequences of our own actions. Nothing less than the future of human societies—some might call it their evolutionary fate—seems to be at stake. Biology offers both gloom and glory, utopian dreams and conservative longings for an idealized past, and evolutionary biology with its focus on the history of life, as well as the mechanisms of change, is at center stage.

It seems almost inevitable that today's rapid scientific developments and associated transformations of society and human (self-)understanding might trigger reaction by fundamentalists, with their desires for sure answers. In the context of evolution and society, the popularity of fundamentalist movements highlights important failures in communicating what is promising in

the fundamental principles of evolutionary theory and in exploring implications and limitations of these scientific insights for our current societies and for human self-understanding (see the main essays "Evolution and Religion" by David N. Livingstone and "American Antievolutionism: Retrospect and Prospect" by Eugenie C. Scott in this volume). We thus offer a few remarks on future directions.

Evolutionary analysis of human behavior and social organizations will remain an important research area within evolutionary biology and will have a high potential for insights, as well as for conflict. Evolutionary medicine is already transforming the ways we understand and treat certain diseases (see the main essay "Evolutionary Biology of Disease and Darwinian Medicine" by Michael F. Antolin in this volume). Evolutionary psychology offers insights into the history of human behavior and our potential to modify and control behavior, including possible transformations in our legal systems and practices (see the main essay "Social Behavior and Sociobiology" by Daniel I. Rubenstein in this volume). The merging of economic theory with evolutionary theory benefits both fields and has given evolutionary theory new conceptual and mathematical tools, such as game theory and the notion of strategies. It has also introduced new questions by replacing traditional ideas of an "invisible hand" with the behavior of individual actors shaped by their evolutionary history and constraints. Applications of evolutionary theory even transform certain fields of engineering and computer science as the principles of evolutionary design and of genetic algorithms have opened new venues for solving complex optimization problems, such as the design of airplane wings (Rechenberg 1973; Holland 1995).

The relationship between evolution and society also provides an important case study for interactions between science and society more generally. The history of evolutionary theory is among the best-studied areas in the history of biology and has revealed interesting ways in which scientific results emerge in a complex interplay between scientific investigations and what can be called their social and cultural contexts. Although these studies have led to insights about how science happens and thus have contributed to popular understandings of science, they also challenge philosophers of science to rethink some fundamental assumptions about the nature of scientific evidence and how historically contingent experimental and theoretical practices can lead to increasingly "accurate" representations of natural phenomena. Some even go so far as to describe this "social" process of finding the "truth" in science in evolutionary terms, thus coming full circle.

But the most important aspect of the ongoing interactions between evolution and society lies in the ways in which evolutionary theory transforms our self-understanding as both biological and social/cultural beings. As proponents of cultural evolution suggest, there is no inherent difference between the ways our bodies and behaviors and our societies and cultures evolved. Indeed, the rigorous application of evolutionary theory to such areas as the evolution of language and of cultural transmission has allowed these proponents to formulate a theory of human society and culture that is materialistic

without being unduly gene centered and reductionistic. The insight that social organization and cultural transmission are governed by the same general principles of the replicator equation implies (1) that not everything that is the product of evolution has to be genetically determined and (2) that many phenomena (such as the evolution of cooperation) that remain puzzling when studied within just one level of analysis (genetic or social/cultural) can be resolved when they are approached from both directions. Without doubt this current extension of evolutionary theory to society will be an important and controversial continuation of the long history of evolution and society.

Of course, all this can be taken too far. We must keep in mind that evolutionary theory might provide an explanation for society, but it cannot provide a justification. Evolution also cannot provide an epistemic justification for ethical theory, for example, despite the numerous attempts to do so. "Is" cannot lead to "ought." Evolution cannot tell us how societies ought to behave, except insofar as it follows that societies must accept evolutionary theory as good science if they agree to accept science at all.

BIBLIOGRAPHY

Ackert, L. 2007. The "cycle of life" in ecology: Sergei Vinogradskii's soil microbiology, 1885–1940. *Journal of the History of Biology* 40: 109–145.

Adams, M. B. 1994. *The Evolution of Theodosius Dobzhansky: Essays on His Life and Thought in Russia and America.* Princeton, NJ: Princeton University Press.

Bowler, P. J. 1983. *The Eclipse of Darwinism: Anti–Darwinian Evolution Theories in the Decades around 1900.* Baltimore: Johns Hopkins University Press.

Boyd, R., and P. J. Richerson. 1985. *Culture and the Evolutionary Process.* Chicago: University of Chicago Press.

Brandon, R. N., and R. M. Burian. 1984. *Genes, Organisms, Populations: Controversies over the Units of Selection.* Cambridge, MA: MIT Press.

Browne, J. 1995. *Charles Darwin: Voyaging.* New York: Knopf.

———. 2003. *Charles Darwin: The Power of Place.* Princeton, NJ: Princeton University Press.

Dawkins, R. 1976. *The Selfish Gene.* Oxford: Oxford University Press.

———. 1982. *The Extended Phenotype: The Gene as the Unit of Selection.* New York: W. H. Freeman.

Degler, C. 1992. *In Search of Human Nature: The Decline and Revival of Darwinism in American Social Thought.* New York: Oxford University Press.

Desmond, A. J. 1997. *Huxley: From Devil's Disciple to Evolution's High Priest.* Reading, MA: Addison-Wesley.

Desmond, A. J., and J. R. Moore. 1991. *Darwin.* New York: Warner Books.

Diamond, J. M. 1992. *The Third Chimpanzee: The Evolution and Future of the Human Animal.* New York: HarperCollins.

Eldredge, M., and S. J. Gould. 1972. Punctuated equilibria: An alternative to phyletic gradualism. In T. J. M. Schopf, ed., *Models in Paleobiology,* 82–115. San Francisco: Freeman, Cooper.

Falconer, D. S. 1989. *Introduction to Quantitative Genetics.* New York: Longman.

Galton, F. 1869. *Hereditary Genius: An Inquiry into Its Laws and Consequences.* London: Macmillan.

Hall, B. K. 1998. *Evolutionary Developmental Biology.* London: Chapman and Hall.

Hamilton, W. D. 1964. The genetical evolution of social behaviour, I. *Journal of Theoretical Biology* 7: 1–16; The genetical evolution of social behaviour, II. *Journal of Theoretical Biology* 7: 17–52.

Hodge, M. J. S., and G. Radick. 2003. *The Cambridge Companion to Darwin.* Cambridge: Cambridge University Press.

Hofbauer, J., and K. Sigmund. 1998. *Evolutionary Games and Population Dynamics.* Cambridge: Cambridge University Press.

Hofstadter, R. 1959. *Social Darwinism in American Thought.* New York: G. Braziller.

Holland, J. H. 1995. *Hidden Order: How Adaptation Builds Complexity.* Reading, MA: Addison-Wesley.

Hull, D. 1973. *Darwin and His Critics: The Reception of Darwin's Theory of Evolution by the Scientific Community.* Cambridge, MA: Harvard University Press.

Huxley, J. 1942. *Evolution: The Modern Synthesis.* London: Allen and Unwin.

Kevles, D. J. 1985. *In the Name of Eugenics: Genetics and the Uses of Human Heredity.* New York: Knopf.

Kimura, M. 1983. *The Neutral Theory of Molecular Evolution.* New York: Cambridge University Press.

Kohn, D., and M. J. Kottler. 1985. *The Darwinian Heritage.* Princeton, NJ: Princeton University Press.

Kuper, A. 1994. *The Chosen Primate: Human Nature and Cultural Diversity.* Cambridge, MA: Harvard University Press.

Lightman, B. 2007. *Victorian Popularizers of Science: Designing Nature for New Audiences.* Chicago: University of Chicago Press.

Margulis, L. 1981. *Symbiosis in Cell Evolution: Life and Its Environment on the Early Earth.* San Francisco: W. H. Freeman.

Maynard Smith, J. 1982. *Evolution and the Theory of Games.* Cambridge: Cambridge University Press.

Maynard Smith, J., R. M. Burian, et al. 1985. Developmental constraints and evolution. *Quarterly Review of Biology* 60: 265–287.

Maynard Smith, J., and E. Szathmáry. 1995. *The Major Transitions in Evolution.* Oxford: W. H. Freeman.

Mayr, E. 1982. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance.* Cambridge, MA: Belknap Press of Harvard University Press.

Mayr, E., and W. B. Provine. 1980. *The Evolutionary Synthesis: Perspectives on the Unification of Biology.* Cambridge, MA: Harvard University Press.

Mocek, R. 2002. *Biologie und soziale Befreiung: Zur Geschichte des Biologismus und der Rassenhygiene in der Arbeiterbewegung.* Frankfurt am Main: Lang.

Paul, D. B. 1995. *Controlling Human Heredity, 1865 to the Present.* Atlantic Highlands, NJ: Humanities Press.

Portmann, A. 1951. *Biologische Fragmente zu einer Lehre vom Menschen.* Basel: B. Schwabe.

Przibram, H. 1904. *Einleitung in die experimentelle Morphologie der Tiere.* Leipzig: Franz Deuticke.

Raff, R. A. 1996. *The Shape of Life: Genes, Development, and the Evolution of Animal Form.* Chicago: University of Chicago Press.

Rechenberg, I. 1973. *Evolutionsstrategie: Optimierung technischer Systeme nach Prinzipien der biologischen Evolution.* Stuttgart–Bad Cannstatt: Frommann-Holzboog.

Richards, R. J. 2002. *The Romantic Conception of Life: Science and Philosophy in the Age of Goethe.* Chicago: University of Chicago Press.

Ruse, M. 1979. *The Darwinian Revolution: Science Red in Tooth and Claw.* Chicago: University of Chicago Press.

———. 1996. *Monad to Man: The Concept of Progress in Evolutionary Biology.* Cambridge, MA: Harvard University Press.
———. 2003. *Darwin and Design: Does Evolution Have a Purpose?* Cambridge, MA: Harvard University Press.
Semon, R. 1908. *Die Mneme als erhaltendes Prinzip im Wechsel des organischen Geschehens.* Leipzig: Engelmann.
Smocovitis, V. B. 1996. *Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology.* Princeton, NJ: Princeton University Press.
Sober, E., and D. S. Wilson. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior.* Cambridge, MA: Harvard University Press.
Todes, D. P. 1989. *Darwin without Malthus: The Struggle for Existence in Russian Evolutionary Thought.* New York: Oxford University Press.
Wassersug, R. J., and M. R. Rose. 1984. A reader's guide and retrospective to the 1982 Darwin centennial. *Quarterly Review of Biology* 59, no. 4: 417–437.
Weismann, A. 1892. *Das Keimplasma: Eine Theorie der Vererbung.* Jena: Fischer.
Wilson, E. O. 1975. *Sociobiology: The New Synthesis.* Cambridge, MA: Belknap Press of Harvard University Press.
Ziegler, H. E. 1918. *Die Vererbungslehre in der Biologie und in der Soziologie.* Jena: G. Fischer.