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Introduction

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Objectives of the Forum

Over the past forty years, the field of cultural evolution has grown from a handful of theorists using concepts and formal tools from population biology to model cultural change to a much larger and more diverse scholarly enterprise. This diversity has contributed valuable insights but it has also generated challenges for integration and comparison. This Ernst Strüngmann Forum provided an opportunity to bring together a cross section of active scholars representing this diversity to consider the present state of the field and to outline outstanding problems and future directions. Given our involvement at past Forums, we felt that this venue would best help us accomplish this task.

Briefly stated, the Forum offers scientists the opportunity to retreat and scrutinize the state of their fields. There are no lectures or presentations; instead, the entire time is spent in discussion. Previously held perspectives are subjected to debate and “gaps in knowledge” emerge; ways of “filling these gaps” are collectively sought, thereby defining possible directions for future research. The essence of these multifaceted discussions is then captured in book form for the purpose of expanding discussion even further.

In this introductory chapter, we wish to provide background to the overarching issues as well as to the specific discussions of this Forum. One of our most important objectives was to assess the extent to which studies of cultural evolution cohere as a common field of investigation. Contributors to this book, and to the field more generally, come from an exceedingly large number of conventional disciplines in the natural sciences, social sciences, and humanities—each of which has its own distinct methodologies and traditional subject matter preoccupations. In an effort to find common ground, Herbert Gintis (2007) has proposed gene–culture coevolution (i.e., cultural evolution plus the biological evolution that affects, or is affected by, cultural evolution) as one of a handful of concepts that can contribute to the unification of the disciplines that study humans, much as biological evolution is one of the major synthetic principles for biology. If this concept is correct, then participants in a highly interdisciplinary group such as the one we assembled—united by little else

than an interest in cultural evolution or something that is highly relevant to it—as well as those who will read this volume should find that such differences primarily reflect a comfortable division of labor rather than incommensurable perspectives which form no part of a larger project.

The Forum did give most of the participants a strong sense of being engaged in a common project. This book allows us to share some of the excitement of the Forum with the other members of the cultural evolution community and interested observers. We found the discussions at the Forum to be both positive and productive, a comparative rarity in our experience at interdisciplinary conferences, and hope that they will provoke further discussions throughout the human sciences.

Why the Four Sections

The basic argument in this book is that many aspects of human endeavor can be better understood by adopting a cultural evolutionary perspective, including the topics upon which the Forum concentrated: social systems, technology, language, and religion. We recognize that other broad subject matters, or different ways of dividing the subject matter, could have been used, but limitations in the number of participants precluded further broadening, and many people do think of themselves as specializing in one of these four areas.

Despite the rapid growth of the field of cultural evolution, especially over the last two decades, the number of practitioners and the amount of time they have had to work are still small relative to the size of the problems. The field still feels very young, even if the oldest contributors are quite gray! For example, much of the most sophisticated modeling of culture has been rather generic. The models specify the abstract structure of the inheritance system (vertical, oblique, or horizontal transmission) and a set of forces that drive cultural change (innovation, biased transmission, natural selection on cultural variation, random drift), which are often applied to narrow cases (dairying and adult lactase secretion, the demographic transition). The Forum considered whether intermediate levels of generality hold promise: Do models of the evolution of social organization, technology, language, and religion have interesting similarities but also differences? Can we hope for empirical generalizations at this level of abstraction? These four domains, of course, are not at all isolated from one another in real life; however, the field will benefit from a more systematically organized theoretical and empirical effort, not least because the traditional disciplines are so organized.

In the long run, the cultural evolution project will not fulfill its promise until every student of human behavior feels comfortable using cultural evolution as one of their tools, much as biologists are comfortable with organic evolution. The common problem is change over time in systems where the past influences the present. As Darwin noted, the phrase “descent with modification” fits the

evolution of societies, technologies, and languages as well as biological organisms. Still, how do we know that something is the product of an evolutionary process? We expect to observe tree-like phylogenetic relationships across both cultural and biological domains, but culture often produces more heavily reticulated phylogenies. To address such reticulation, methods have been developed (Gray et al., this volume), as have methods to incorporate geographical information and fit explicit evolutionary models to historical and geographical patterns simultaneously (Bouckaert et al. 2012).

Evolutionists in the broadest sense must thus confront problems of the complexity and diversity of the systems they study and of historical contingency. If Gintis's principles of unification are correct, then the history versus science dichotomy is an illusion, as is argued elsewhere (Boyd and Richerson 1992). Biologists have become rather humble about what they are able to know in the face of the complexity, diversity, and historical contingency of the systems they study, even as they exploit every trick they can devise to finesse these problems (e.g., Burnham and Anderson 2002). This change should comfort humanists who have legitimately complained about the arrogant reductionism of many scientists from earlier generations. Indeed, cultural evolutionists have been in the forefront in bringing cultural diversity to the attention of psychologists, who all too often assume that they can tap "human nature" in the laboratory using university undergraduates as research participants (Henrich et al. 2010b).

What Is Cultural Evolution?

If we define culture as the ideas, skills, attitudes, and norms that people acquire by teaching, imitation, and/or other kinds of learning from other people, cultural evolution is fundamentally just the change of culture over time. The authors of this book have a view of cultural change that is based on concepts and methods pioneered by Darwin in the nineteenth century. In this conception, culture constitutes of an inheritance system; variant ideas, skills, and so forth that are transmitted by (usually) more experienced to less experienced individuals. Societies are a population of individuals that we can characterize in terms of the frequency of the cultural variants individuals express in the population at any point in time. As time progresses, many factors impinge upon the population to change the frequency of cultural variants expressed in the population. For example, someone in the population may either invent or acquire from another society a new and better skill of economic importance, such as a new way to make string and rope that is faster than the currently common technique and results in stronger cordage. This new skill will tend to increase in the population, perhaps because (a) users can sell more cordage than competitors and use the resulting proceeds to rear larger families, who perpetuate the new technique, and also because (b) unrelated individuals

become aware of the new skill and its success and imitate those who have this skill. To study cultural evolution formally from this perspective means that we must set up an analytical accounting system to keep track of the increase or decrease in the frequency of cultural variants in order to try to establish the causes of the frequency changes (Cavalli-Sforza and Feldman 1981). The concrete reasons for cultural changes in particular populations are almost endlessly complex and diverse. To achieve some generalizable knowledge, we impose a taxonomy that collects the diverse concrete reasons into classes with similar dynamic properties (Henrich and McElreath 2003). The impact of a skill on the size of family one can raise is attributed to “natural selection.” The processes of selectively imitating people who display a successful variant are attributed to “biased transmission” or “cultural selection.” Biases, in turn, come in many varieties. A new form of speech, for example, might be acquired from someone we consider prestigious or charismatic.

Even good evolutionists sometimes speak of evolutionary “forces,” such as natural selection and biased transmission, as if they were similar to gravity. As an analogy, this usage is harmless enough, but it certainly should not be taken literally. The force of gravity is a deep, universal physical law. Evolutionary forces are the outcome of diverse processes which interact to influence survival and reproduction. They have enough in common to permit a relatively small set of mathematical models, with roughly similar structure, to fit the data. Under closer examination, however, evolutionary forces have none of the universality and tidiness of the inverse square law and the universal gravitational constant. The “forces” usage often troubles humanists, who usually want to stick close to the details of particular cases of cultural variation and cultural change. Past attempts to formulate laws of history have had a checkered record, to say the least (Popper 1947). However, thoughtful evolutionists are well aware of the differences between concrete instances of genetic or cultural evolution and the abstraction involved in synthetic analyses based on the estimation of evolutionary forces (Turchin, this volume; Nitecki and Nitecki 1992). Even if reasonably robust findings emerge from our collective efforts, they are unlikely to fit any particular case perfectly.

The Investigation of Cultural Evolution: A Brief History

Humans have almost always had neighbors that spoke different languages or dialects, and many societies were aware that different societies preceded them. Hunter-gatherers living in the Great Basin in the nineteenth century, for example, were aware that the rock art in the area was made by inhabitants who they believed were not their own ancestors. The earliest systematic study of human differences and change was pioneered by historian-ethnographers in Greece (Herodotus, 484–420 BCE) and China (Sima Qian, 145–86 BCE) (Martin 2009). The writing of proper histories and ethnography, using methods

designed to produce accurate treatments of other societies and the past, as opposed to myths with negligible attention to veracity, were relatively rare until the last couple of centuries (Brown 1988). Historical scholarship in the West exploded in the late eighteenth century, marked by Edward Gibbon's *History of the Decline and Fall of Rome* (1782). Ethnographic investigations also began to boom as expeditions of discovery became more professionalized, with scientific societies nominating naturalists to serve on them (Sorrenson 1996).

From the late eighteenth century to the middle of the nineteenth century, the field of historical linguistics (comparative philology) flowered into the first truly sophisticated cultural evolutionary research program (Müller 1862/2010; Hock and Joseph 2009). Not only did linguists notice the fairly remote connections between languages, such as those of northern India and Western Europe (Jones 1786/2013), they mapped the pattern of descent with modification of the Indo-European and Semitic languages in some detail, partly using ancient texts from dead languages as historical anchor points. As pointed out by Müller, linguists aspired to develop a theoretically sophisticated causal account of the mechanisms that drive linguistic change and diversification.

Darwin's contributions to the study of evolution were revolutionary. He is remembered primarily as a biologist, but his ideas about biological heredity were very rudimentary. In the preface to the second edition of the *Descent of Man* (Darwin 1874), he insisted that the effects of use and disuse were heritable and spoke of "inherited habits." Further, when discussing the evolution of human societies, he used such terms as "customs," "education," "laws," and "public opinion." In the chapter, "On the Races of Man" (Darwin 1874), he demolished the argument that a race could be considered a species, thus countering the main plank of nineteenth-century "scientific" racism used to justify slavery and other abuses of non-European peoples. He cited Edward Tylor (1871), the pioneering anthropologist who was the first to define "culture" in the way we use it here, to support his argument that differences between the races were due much more to traditions and customs than to organic differences. Darwin made a tolerably good start on a theory of cultural evolution.

It is possible to read Darwin as using cultural transmission as his model of biological inheritance. This would be quite understandable. The process of cultural transmission is partly quite accessible to natural-historical observation, whereas genes must be studied using the careful phenomenological experiments of the Mendelians. Genes only became truly "visible" once DNA was discovered to be the genetic basis of the gene, and in the last decade, gene sequencing has become so inexpensive that biologists can routinely observe genes directly. Darwin's (1877) detailed observations of one of his children's early development made him quite cognizant of the power of imitation and teaching to transmit culture. He might have intuited that an inheritance system which did not conserve acquired variations would waste the efforts that parents put into individual learning and other forms of phenotypic adaptation. Human life, as we know it, would be unimaginable without a cultural inheritance

system passing on the knowledge acquired by parents and other adults to children. Wouldn't the inheritance of acquired variation be part of the organic system of inheritance as well? In any event, in 1869 Darwin proposed a theory of organic inheritance called "pangenesis"; this involved all the cells of the body casting off "gemmales," which were collected in the gonads and incorporated into gametes as the hereditary substance responsible for the development of offspring organisms. If an organ had been modified to adapt to the organism's environment, modified gemmules would be produced to reproduce the acquired variation (Darwin 1869:374–405). Twentieth-century biology marked this theory as Darwin's greatest mistake (Ridley 2009). Ironically, in that important respect, Darwin's theory of evolution was a better fit to human culture than to genes, yet Darwin is generally thought of as a biologist whose ideas about human evolution are generally thought to be mistaken.¹

In the last half of the nineteenth century, Darwin's ideas on cultural evolution had a major impact on important thinkers in psychology and economics, where historical scholarship has been conducted at a high standard (for psychology, see Richards 1987). A considerable number of late nineteenth- and early twentieth-century psychologists were highly evolutionary in their approach to animal and human behavior, including George Romanes, William James, Conwy Lloyd Morgan, Henry F. Osborn, and James Mark Baldwin. Herbert Spencer's influence was large alongside Darwin's, about whose theory of natural selection Spencer was skeptical. Even Alfred Wallace thought that natural selection could not explain the human mind. These scholars were preoccupied with understanding the nature of heredity, the primary processes driving evolution, and the fundamental differences, if any, between human minds and behavior and those of other animals. Prior to the rediscovery of Mendel's principles, everyone's understanding of heredity remained primitive. Darwin's endorsement of the inheritance of acquired variation and Spencer's exclusive dependence on it became controversial with the rise of August Weismann's arguments about the separation of the germ line and the soma early in the embryonic development of most animals. Baldwin particularly struggled to reconcile Darwin's argument for the inheritance of acquired variation with Weismann's doctrine. Eventually he arrived at something like our contemporary understanding of the main issues. He proposed that there were two systems of heredity: organic heredity, which obeyed Weismann's doctrine, and social heredity, particularly important in humans, which does not. He also proposed a form of selection,

¹ Darwin may yet be vindicated regarding the inheritance of acquired variation. The development of multicellular organisms depends upon up-regulating and down-regulating genes so as to specialize cell lines for their highly divergent functions. Once specialized, the operational "transcriptome" of each cell type is transmitted to daughter cells in that line by means of various "epigenetic" mechanisms. Recent work on epigenetic inheritance suggests that some modified phenotypes may be transmitted across generations, even in obligate sexually reproducing organisms (Grossniklaus et al. 2013), and may greatly influence evolution (Laland et al. 2011; Jablonka 2013).

“organic selection,” to explain the appearance of the inheritance of acquired variation in organic traits. Developed independently by Morgan and Osborn, it became more popularly known as the Baldwin Effect. The idea is that phenotypic adaptation would keep a population from extinction under changed conditions while selection did its work, and phenotypic adaptations would often foreshadow the direction that selection on the Weismannian hereditary material would take. Hence, human cognitive power could influence evolution by a Lamarckian process that is underpinned by social heredity, via the organic selection process operating on germ line heredity that mimicked the inheritance of acquired variation mechanism, without actually depending on it.

Geoffrey Hodgson (2004) provides a thoughtful, detailed analysis of late nineteenth-century ideas about cultural evolution and related topics, centered on the institutional economist Thorstein Veblen, whose creative work took place between 1898 and 1909. Veblen was much influenced by Darwinian psychologists, who are the focus of Richards’ (1987) book. His most important contribution was to articulate the concept of institutions—culturally transmitted systems of rules that structure human social life. Like Baldwin, Veblen struggled to understand the relationship between the biological heredity that we share with other organisms and the cultural system that is more or less unique to humans. He insisted that it was important to understand the causal mechanisms, analogous to natural selection, that drive cultural evolution; however, his work on the subject was unsystematic in Hodgson’s estimation. Veblen did imagine that innate predispositions, specifically what he called an “instinct for workmanship,” might influence technological evolution (Cordes 2005). This concept clearly foreshadows the notion of epigenetic rules, cultural selection, and biased transmission that figure in the late twentieth-century revival of Darwinian theories of cultural evolution. The instinct for workmanship motivated humans to search for elegant functional technological designs that efficiently serve basic human needs. The instinct would motivate the careful production of artifacts, attempts on the part of craftspeople to improve them, and the borrowing of better designs from others.

Given the number, prestige, sophistication, and diversity of Darwin’s early twentieth-century followers in the human sciences, one might have thought that the legacy of the *Descent of Man* was secure. Instead, just as Darwinian ideas began to be combined with genetics to form one of the theoretical foundations in biology (Provine 1971), the equally productive ideas of Darwin and his followers regarding cultural evolution, and the link between organic and cultural inheritance in humans, went into a half-century near-total eclipse (Richerson and Boyd 2001). The reasons for this eclipse have not been well told except in the special cases of psychology and institutional economics. Chance may have played a role. Both Baldwin’s and Veblen’s careers were damaged at their peak by sexual scandals, according to Richards (1987) and Hodgson (2004). Many of the emerging social scientists were keen to distinguish themselves from biology and to downplay the significance of biology for sciences of human

behavior. For example, the influential early French sociologist Gabriel Tarde (1903) excluded biological considerations in his pioneering study of the “laws of imitation.” Hodgson (1993) described how the greater prestige of physics compared to biology caused economists to look to physics for models of scientific rigor rather than biology, as this discipline began to professionalize around the turn of the twentieth century. The prestige of Darwin’s own ideas about evolution reached a minimum around that time, inhibiting the social science pioneers from using him for inspiration, much less authority (Bowler 1983). When Darwinism began to emerge from its eclipse with R. A. Fisher’s (1918) paper, which showed how natural selection could be reconciled with the genetic theory of inheritance, it emerged as a contribution to biology (Provine 1971, chapter 5); the contributions of Darwin and late nineteenth-century Darwinians to the study of human behavior were largely forgotten.

The theory of evolution which did inform many of the early twentieth-century social scientists derived from Spencer rather than Darwin. Ideas of progressive evolution stemming from Spencer were popular, often under the misleading label “Social Darwinism.” Spencer’s main idea was that the same principle of evolution underlay cosmological, geological, biological, and human behavioral change. The principle was that all structures progress from simple, undifferentiated homogeneity to complex, differentiated heterogeneity (Spencer 1862). Physicists will recognize Spencer’s principle as the Second Law of Thermodynamics—*backward*. Robert Carneiro (1967) outlined Spencer’s impact on twentieth-century social science (see also Freeman et al. 1974). Richard Hofstadter (1945) wrote a famous critique of Social Darwinism which was, in turn, the subject of a sharp countercritique (Bannister 1979).

Perhaps the most sophisticated twentieth-century evolutionist in the Spencerian tradition was Julian Steward (1955), who critiqued the simple unilinear theories derived from Spencer, suggesting that societies progressed lockstep through an invariant succession of stages of complexity. Steward was an ethnographer of very wide experience and even wider reading. He knew that trajectories of change in social complexity and the like were highly variable. He also knew that the correlation between the complexity of such features as technology and social organization was imperfect. Thus he focused his analysis of evolution on what he called the “culture core,” which comprised technology and the aspects of other features of culture directly related to the mobilization of technology to provide human subsistence. He described how societies that used hunting and gathering technology varied greatly in the details of their social organization, depending on the exact nature of the resources that are hunted and gathered. Hunting small game and gathering dispersed plant resources favored very simple but highly flexible family-level organization, whereas large herding game typically led to cooperation between many families, and thus more complex social organization. Steward’s culture core framework was a sort of commonsense adaptationism overlaying a concept of progressive change. In this it resembled the sociological functionalists (e.g.,

Lenski and Lenski 1982). None of these thinkers were preoccupied with the micro-mechanistic foundations of evolution in the way Darwin and his followers were. There is no doubt, however, that progressivist human evolutionists were onto *something*. The overall trend toward greater complexity of human societies in the Holocene is unmistakable. Paleoanthropologists, especially in the late twentieth century, documented this trend far back in the history of our lineage (Klein 2009). In evolutionary biology, the issue of progress has been vexatious, going right back to Darwin's ambivalence about it (Nitecki 1988).

A revival of a Darwinian approach to cultural evolution began rather modestly in the 1950s when Armen Alchian (1950) suggested that profit-maximizing firms might emerge from natural selection on random variation between competing firms rather than because firm managers consciously chose profit-maximizing strategies. Alchian's paper, in turn, led to the lively field of evolutionary economics, whose single most important classic was Richard Nelson and Sidney Winter's (1982) book: *An Evolutionary Theory of Economic Change*. A few years later, neurophysiologist Ralph Gerard, mathematical psychologist Anatol Rapoport, and anthropologist Clyde Kluckhohn teamed up during a yearlong interdisciplinary meeting at the Center for Advanced Study in the Behavioral Sciences in Stanford to write a rather sophisticated programmatic essay describing how cultural evolution might be studied using the concepts and methods of evolutionary biology (Gerard et al. 1956). This paper influenced several of the contributors to the next wave of cultural evolution work, including Cavalli-Sforza and Feldman (1973), Durham (1982), and Richerson (1977).

In psychology, the key figure in reintroducing Darwinian theory was Donald Campbell (1960, 1965, 1975). In the first of these papers, Campbell argued that creative thought might consist of an intrapsychic process of "blind variation and selective retention" analogous to natural selection, an idea later developed by Gerald Edelman (1987). In his 1965 essay, Campbell developed the concept of "vicarious selectors," genetically evolved mental devices that evolved under natural selection to shape human learning and bias social learning in adaptive directions. This concept, though not Campbell's term, influenced all subsequent Darwinian approaches to cultural evolution. The essay also argued that cultural inheritance would evolve much as genes do, except for the role that vicarious selectors play alongside blind variation and natural selection. The 1975 paper described how genetic and cultural evolution could come into conflict and how the micro-mechanistic Darwinian approach to cultural evolution differed from the neo-Spencerian progressive approaches. These three papers were highly cited and widely influential. Other early contributors to the emerging field included Ruyle (1973), Cloak (1975), and Pulliam and Dunford (1980).

In child development, also in the late 1950s and early 1960s, Albert Bandura began publishing his extremely influential studies of social learning in children (e.g., Bandura and Walters 1963). This work established the critical importance

of imitation in the acquisition of human behavior and led, in due course, to a reasonably sophisticated understanding of the capacity for culture acquisition in humans. At the same time, Lev Vygotsky's (1978) neglected cultural-historical approach to child development began to have a major impact on the field. Important modern work in this field includes Tomasello (1999), Whiten and Custance (1996), Carey and Spelke (1994), Bloom (2000), and Harris and Koenig (2006).

Another relevant field is the diffusion of innovations, which traces back to Tarde's work in sociology and to the diffusionist school in anthropology. Because the diffusion of modern innovations is so important to economic growth, the phenomenon attracted the attention of economists and applied economists in the 1940s and 1950s (e.g., Griliches 1957). By the early 1970s, around 1,500 reasonably detailed studies of the phenomenon were known. Everett Rogers and Floyd Shoemaker (1971) did a pioneering meta-analysis of these data and teased out a number of robust strategies which people exposed to innovations used to decide whether or not to adopt them. Robert Boyd and Peter Richerson (1985) derived their taxonomy of bias forces from Rogers and Shoemaker's analysis and studied mathematical models of several of the processes they described. Much subsequent modeling and empirical work has been based on this foundation (e.g., Henrich and McElreath 2003).

Language evolution did not experience the same eclipse in the twentieth century as did other human sciences fields. Explicit theoretical discussions on the evolution of language in the hominid lineage remained largely outside the academic discourse, in part because of the ban on such discussions imposed by the influential Société Linguistique de Paris in 1866. Nonetheless, historical and descriptive linguistics continued to document the histories of language families around the world and their resultant linguistic diversity (for a review, see Evans, this volume). In addition, several innovative research programs in linguistics emerged in the latter part of the twentieth century in parallel to the other fields discussed above. William Labov (1963) initiated a program of detailed micro-mechanistic studies of sound changes (dialect evolution) that eventually produced a rather detailed account of the evolutionary pressures on sound change from within languages and from the external social environment (Labov 1994, 2001). Similarly detailed studies of languages in contact showed how linguistic innovations could flow between speech communities (Thomason and Kaufman 1988). Historical linguists also discovered that function words and morphemes could evolve by the shortening and conventionalizing of constructions using referential words, outlining how grammar evolves by "grammaticalization" (Traugott 1980; Hopper and Traugott 2003).

The early 1990s saw a resurgence of scientific interest in language evolution, following the publication of the landmark paper by Pinker and Bloom (1990) on the role of natural selection in the evolutionary emergence of human language. Theoretical considerations were quickly complemented by formal models of language evolution. Whereas initial computational models focused

on the biological evolution of language-specific mechanisms (e.g., Hurford 1989), recent years have seen a shift toward cultural evolution as the primary explanation for the emergence of linguistic structure (Christiansen and Kirby 2003; see also Jäger et al. 2009; Steels 1997). Much of this theorizing came in response to the emerging evidence that social learning plays a much stronger role in language acquisition than the heavily innatist proposals of the early generative grammar period envisioned (contrast Pinker 1994 with Tomasello 2005 and Hurford 2011).

The study of cultural evolution has had a largely conflictual relationship with the most highly visible evolutionary approach to human behavior, human sociobiology. The human sociobiology program was tentatively launched by an important paper by Richard Alexander (1974) and the last chapter in Edward O. Wilson's (1975) treatise on sociobiology, followed shortly by book-length evolutionary treatments of human behavior (Alexander 1979; Lumsden and Wilson 1981). This work was considered a political abomination by many on the left, who (mistakenly) associated evolution with right-wing ideology, as well as by many social scientists who could not imagine how biologists could make any useful contribution to the social sciences (Segerstråle 2000). At the same time, a small number of anthropologists and psychologists embraced the sociobiological turn because they were skeptical of the atheoretical, if not antitheoretical, use of cultural “explanations” in their fields (Chagnon and Irons 1979; Sperber 1984; Tooby and Cosmides 1989). The cultural evolutionists, specifically the dual inheritance theory version of Richerson and Boyd (1976), envisioned from the beginning a much more active role for cultural evolutionary processes than did the original founders of sociobiology or the pioneers of the descendant fields, human behavioral ecology and evolutionary psychology. Indeed, the cultural evolution field owes much more to the other influences described above than to human sociobiology, although it must be said that the temperature of debates with human behavioral ecologists, evolutionary psychologists, and others has diminished in recent years as the empirical importance of cultural evolutionary processes has come to be more widely appreciated, especially by younger scholars.

The history of the last two decades or so in the field of cultural evolution is embodied in the various chapters of this book. To say more at this stage would begin to reiterate their contents.

Common Themes across the Four Areas

One of our major objectives in this book is to explore the commonalities of the evolutionary processes between the four designated areas: the structure of human groups, technology and science, language, and religion. Although each of these areas has attracted the attention of many disciplines, the specific disciplines that have contributed to the study of cultural evolution vary. This

is to be expected since the substance of the phenomena which they cover is distinctively different. For example, variation in the details of social organization and technology is perhaps more likely to have consequences for survival and reproduction than variation in the details of language and religion. Much of the variation in the latter, with its highly symbolic phenomena, is adaptively neutral. Different words for “cat” and different rituals for invoking the favor of the gods may matter less for survival and reproduction of users than the species of a tree used to make a bow or the manner in which warriors are recruited, trained, and led. Nevertheless, for the most part, cultural evolution does share important commonalities across different domains.

Gene–Culture Coevolution

In our species, genetic evolution and cultural evolution are inextricably linked. Our bodies are adapted to acquire and use culture, and our cultures are adapted to help our genes perpetuate themselves. The deep entangling of the cultural and genetic evolutionary subsystems, each complex enough in its own right, poses many hard problems in each of the areas we considered (as well as in others). Possibly, the evolution of an innate social psychology, which was predisposed to follow norms and institutions, coevolved with culture-generated social selection (Jordan et al., this volume). Language evolution likely involved gene–culture coevolution—a process that is perhaps still active today (Levinson and Dediu, this volume; Evans, this volume). The issue has not entirely been resolved. Not a few evolutionists adhere to a strongly gene-centric view of even human evolution (Laland et al. 2011). Not a few humanists and humanistically oriented scientists take a dim view of introducing considerations of genes into the study of culture (e.g., Fracchia and Lewontin 2005).

Use of Mathematical Models

Mathematical models have played a key role in the development of our field, as illustrated by the above-mentioned pioneering work in modeling (see also Turchin, this volume), and they will continue to play an important role (e.g., Chater et al. 2009; Henrich and Boyd 2008; Bowles and Gintis 2011). Perhaps the most innovative new use of models is as a data analytic tool. Advances in computing power have made it practical to use maximum likelihood and Bayesian inference methods to fit competing causal models directly to data (e.g., Leonardi et al. 2012; McElreath et al. 2008).

Experimental Methods

Evolution is a population-level process, as evolutionists are wont to say. Experiments that are logically and ethically feasible may seem too small in scale to be very informative. However, many questions are difficult to answer

without some sort of controlled experiment. Experiments are a little like mathematical models: they are simplified caricatures of a real large-scale process, but they can give us nice insights into the workings of components of the process. Robert Jacobs and Donald Campbell (1961) reported the first laboratory-scale experiment on cultural transmission and evolution in a laboratory microsociety. A handful of experiments were subsequently done, including a very ambitious series of experiments on the evolution of leadership by Chester Insko et al. (1983). Recently, laboratory microsociety experiments have been used to study the evolution of in-group favoritism (Efferson et al. 2008a), cumulative cultural evolution of technology (Caldwell and Millen 2008; see also other papers in that issue), the use of social-learning strategies by individuals (Mesoudi 2011b), and the evolution of language (Scott-Phillips and Kirby 2010). Other sorts of experiments are used to test functional hypotheses about the impact of cultural beliefs on behavior such as religious beliefs on helping behavior (e.g., Laurin et al. 2012; reviewed by Norenzayan et al., this volume).

Field Studies of Microevolutionary Processes

In evolutionary biology, field studies aimed at estimating the strength of natural selection and other evolutionary forces are a classic method (Endler 1986) of directly studying microevolutionary processes. Historians, sociolinguists, and students of the diffusion of innovations conduct similar field projects, though they do not use quite the same theory-driven approach to quantification that evolutionary biologists do. Evolutionist anthropologists have pioneered applying the approach of field biologists to human field data, beginning with the work of Soltis et al. (1995) working with extant ethnographic data and that of Auger (1994) using purpose-collected field data. More ambitious long-term projects have begun to report early results (Bell 2013; Henrich and Henrich 2010). A larger number of field studies address particular evolutionary hypotheses without formally estimating the strength of forces (Mathew and Boyd 2011; Sosis and Bressler 2003; Norenzayan et al., this volume). Field studies by linguists have not only documented the astonishing diversity of linguistic structures, they have also illuminated the mechanisms that drive change (Evans, this volume). Games devised by experimental economists have been used as tools for mapping cultural diversity with respect to prosocial propensities (e.g., Henrich et al. 2006; Herrmann et al. 2008).

Critical Importance of Development

The individual-level process of development is the place where genetic and cultural inheritance systems interact most vigorously. Claims about the developmental process have thus figured importantly in the debates between more gene-centric (e.g., Tooby and Cosmides 1992; Pinker 1994) and more culturally oriented (Tomasello 1999; Richerson and Boyd 2005) conceptions

of how the human evolutionary process works. The developmental process is formidably complex, and much has been proven to happen in the first few months of life. Even as the human brain is still quite undeveloped, infants are active observers of other's behavior, capable of exercising attention biases (e.g., Kinzler et al. 2011). Children's tendencies to learn socially from others that are like them culturally are the foundation for the generation of so much between-group cultural variation in our species (Haun and Over, this volume). Fortunately, developmentalists have devised methods to infer what judgments are being made, even by preverbal infants. For example, eye gaze and attention patterns betray an infant's interests and choices (Carey 2009; Boysson-Bardies 1999). Developmentalists study a wide variety of subject domains, including science and religion (e.g., Harris and Koenig 2006), language (e.g., Bloom 2000), social norms (e.g., Chudek and Henrich 2011), and motor skills (e.g., Whiten et al. 2009). Comparative work shows that human children have a powerful imitative system compared to even highly intelligent apes and monkeys (Dean et al. 2012), and human adults are well adapted to support the social learning of children (Csibra and Gergely 2011). The evidence accumulated since the 1990s amounts to a rather devastating refutation of the highly gene-centric cognitive modules view of development (Sterelny 2012), the original inspiration for which was Chomsky's failed principles and parameters approach to language learning. Lieven (this volume) reviews the evidence that at very young ages infants are already highly sensitive to the particularities of the language they are learning. Combined with the development of such devices as shared attention, which also operates in other cultural domains, the powerful imitative capacity of children is sufficient for them to acquire very diverse languages without having an elaborate innate dedicated language-learning system. As discussed further by Lieven et al. in the Appendix of this volume, developmental processes are likely to have a key impact on cultural evolution across a variety of domains.

Accounting for Macroevolutionary Events and Trends

Many of the most interesting evolutionary questions involve large-scale trends and events in human evolution. Gintis and van Schaik (this volume) outline the basic pattern of hominin social evolution over the last few million years. Why did complex cumulative culture evolve so recently, despite the fact that it has made us an extraordinarily successful species (see Boyd et al., this volume)? Why did brain size and cultural sophistication in our lineage increase progressively over the Pleistocene? When and why did our distinctive societies with high rates of cooperation between nonkin arise? Why do we institutionalize cooperation between relatives and long-term partners when the familiar evolutionary mechanisms of inclusive fitness and reciprocity would seem to explain such cooperation without the need to invoke cultural mechanisms (Mathew et al., this volume)? When did something like the modern capacity for language

evolve? Why did anatomically modern people disperse out of Africa around 60 KYA when our species is perhaps 100 thousand years older? What was and is the role of religion in the simpler societies of the Pleistocene and transitional societies of the Holocene (Bulbulia et al., this volume; Guthrie 2005)? Why did human populations evolve agriculture, states and their distinctive religions, and industrial production in the Holocene (see chapters by Turchin, Slingerland et al., Norenzayan et al., and Bulbulia et al., this volume)? Why do Holocene societies have boom and bust dynamics?

The concepts and tools of cultural evolution and gene–culture coevolution have devoted substantial attention to these topics (e.g., Steele and Shennan 2009). Innovations in both empirical methods and in modeling and model-fitting data analysis are driving a considerable increase in the sophistication of archaeology and historical reconstructions (e.g., Collard et al. 2010; Turchin and Nefedov 2009). The quest is for synthetic long time span, high-resolution quantitative records constructed from the short qualitative records that are directly available from historians and archaeologists, often using clever proxies for unmeasured variables like population density. Given such time series, we can hope to find informative fits of modestly complex evolutionary models. Gene sequencing techniques are producing a cornucopia of data on human genetic diversity (and some excellent sequences from subfossil DNA). This data produces evidence of past selection and past demography of humans, our parasites, and domesticates. As methods improve, there is hope that genetic data can supplement the sparse conventional paleoanthropological record, especially for things like language and social dispositions which fossilize poorly, by finding evidence for genetic responses to gene–culture coevolution (Pinhasi et al. 2012; Richerson et al. 2010).

Major Ongoing Problems to Solve

For most of the problems reviewed thus far, the field of cultural evolution might be characterized as at the end of the beginning. For these questions we can point to sound methodological approaches and a decent body of findings that are likely to hold up reasonably well to future scrutiny. Here, we want to highlight problems where we are closer to the beginning of the beginning.

Understanding the Epigenetic and Neurobiological Systems that Underpin Culture

Aunger (2002) made a brave attempt to provide a neurobiological foundation for human culture. Since then, Rizzolatti (2005) hypothesized that a mirror neuron system homologous to that detected in macaques using single electrode techniques plus associated regulatory circuits, might produce the human capacity for imitation. Support for this hypothesis is confounded by the number

of areas in the human brain that show mirror-like activity in fMRI studies (Molenberghs et al. 2012). The complexity of the human brain circuitry together with limitations of imaging techniques leave us with a very incomplete understanding of the neurobiology of the culture capacity (Stout, this volume). Whitehouse (this volume) proposes a landscape model for the roles of genes, culture, and environment on epigenetic processes. Several quite basic features of the cumulative cultural system are poorly understood (Boyd et al., this volume). While the highly gene-centric cognitive picture of human evolution seems precluded by developmental studies, which clearly identify a powerful early developing capacity or capacities to acquire information by imitation and teaching, the detailed division of labor between innate-cognitive structures and cultural transmission remains quite controversial. Slingerland et al. (this volume) argue that a number of key cognitive structures underpin the phenomenon of religion, whereas Harris and Koenig (2006) imply that simple trust in the testimony of adults can explain many of the mysteries of religious belief. On the other hand, the “core cognition” proposal of Carey (2009), consistent with Harris’ proposal, has been criticized as being too innatist by developmental systems enthusiasts (Spencer et al. 2009).

Epigenetics introduces another level of complexity to understanding the mechanistic basis of culture capacities. Provençal et al. (2012) found a large number of changes in the methylome of the prefrontal cortex of macaques reared with mothers present versus only a peer present, and methylation patterns are only one component of the epigenetic system. In humans we might imagine that the epigenetic system is a vehicle for massive cultural influences on gene expression, but it could also be a vehicle for massive contingent epigenetic effects on factors which bias culture acquisition. Further, the possibility that some epigenetic changes can be transmitted to offspring leads to the possibility that transgenerational epigenetic transmission can be confounded with culture and that this represents still another pathway by which genes and culture can influence one another (Jablonka 2013; Daxinger and Whitelaw 2012).

Moving beyond Proof-of-Concept Examples of Gene–Culture Coevolution

Genome-wide scans, which search for genes that have come under strong selection in humans recently enough to leave internal evidence in the genome, have apparently uncovered many such genes (e.g., Sabeti et al. 2002; Hawks et al. 2007). We commented above on the promise of studying gene–culture coevolution by using possible responses to such coevolution in combination with the paleoanthropological record to understand better how our species evolved. However, present evidence for gene–culture coevolution still rests on a few classic cases, such as the evolution of lactase persistence in dairy-ing peoples and the evolution of hemoglobin polymorphisms in malarial areas. So far, the

difficulty of discovering the functional significance of the alleles that have apparently been under selection leaves most of the new examples tantalizing but enigmatic. The putative “language gene” *FOXP2* provides a cautionary tale in this regard (Coop et al. 2008; Fisher and Scharff 2009). Similarly, as regards religion, our understanding of the linkages between genetic and cultural components is still primitive (Norenzayan et al., this volume). Without methodological breakthroughs, the promise of genomic studies will remain the prisoner of slow and expensive retail functional biology.

Understanding the Diversity of Micro Processes

Laboratory studies of the strategies individuals use to acquire information from others has revealed a surprising amount of individual variation and much use of suboptimal strategies (Efferson et al. 2008b; McElreath et al. 2008; Mesoudi 2011b). Limited simulation studies conducted thus far suggest that diverse social-learning strategies will persist at equilibrium (Whitehead 2007). There is every reason to think that substantial cross-cultural variation exists in social-learning strategies (Bettinger and Eerkens 1997; Shennan, this volume). For example, just in the last few centuries, the principles of scientific reasoning and the social organization of systemic criticism, which constitute the scientific enterprise, arguably created a novel cultural system institutionalizing new forces that shape an unprecedented form of cumulative cultural evolution (McCauley, this volume). The fact that scientific institutions and the coupling of science to technical innovation are so successful, yet so recent, gives rise to the worry that science as a cultural system may be fragile (Mesoudi et al., this volume). Cross-cultural variation in the use of language as a device for socialization has been documented but not well explored, nor has justice been done to the contribution of peer interactions on the evolution of language during childhood (Lieven, this volume). We are at the very beginning of the effort to understand the diversity within and between cultural systems.

Using History and Living Diversity as a Natural Laboratory for Studies of Cultural Evolution

The use of phylogenetic methods to study cultural evolution is well advanced. However, as mentioned above, empirical methods have advanced to the point where we can use model fitting and model selection methods to try to infer directly the underlying process that drove a particular evolutionary trajectory (Itan et al. 2009; Bouckaert et al. 2012; Turchin and Nefedov 2009). Human documentary history is quite rich, and the human fossil and archaeological records are rather rich. The cornucopia of genetic data that is currently flowing from ever cheaper sequencing technology not only makes this data available, it is pushing developments in bioinformatics which can also be applied to cultural data. Constructing quantitative time series using these data and

comparing the fits of alternative models to the data promises a revolution in our understanding of cultural evolution; however, the issues involved are not trivial (Shennan, this volume). Even in linguistics, one of the most sophisticated fields in cultural evolution to use diversity as a natural laboratory, Evans (this volume) identifies no less than seven major challenges. Gray et al. (this volume) highlight three outstanding questions in the evolution of language that can be addressed with computational phylogenetic methods, and Dedić et al. (this volume) formulate a number of challenges facing future research into the cultural evolution of language.

Reducing the Gaps between the Natural Sciences, Social Sciences, and Humanities

In the nineteenth century, the arts and sciences were weakly organized. The great national academies covered all of the sciences. There were few professional positions for scholars; many practitioners were rich gentlemen and enthusiastic amateurs with broad interests. Darwin published on geology, zoology, botany, and anthropology and wrote an account of the Voyage of the Beagle for a popular audience. William Thompson, Lord Kelvin, worked as a theorist on electricity and thermodynamics, on engineering projects, such as the transatlantic telegraph, and on improvements to the mariner's compass. In his attempt to estimate the age of Earth, Kelvin's pioneering geophysical work brought him into conflict with Darwin and many geologists, who inferred a much greater age than the 10–20 million years Kelvin's calculation allowed. Many projects in history and historical linguistics were founded on serious methodological innovations, such as the comparative method. The eighteenth- and nineteenth-century project known as the Quest for the Historical Jesus (Bartley 1984) provides one example. What we normally think of as science-minded anthropologists often make use of such methods today (e.g., Wiessner and Tumu 1998; Currie et al. 2010a). As the history of the study of cultural evolution shows, the professionalization of the sciences and humanities around the turn of the twentieth century resulted in many more active, full-time, paid, specialist scholars who became organized into disciplines that tended to behave in a quasi-tribal fashion (Campbell 1979). The unity of the scholarly enterprise broke down. Even within the social sciences, disciplinary balkanization is a problem (Mesoudi et al., this volume), far more serious than in the much larger field of biology, where subdisciplinary boundaries are not taken all that seriously.

During the political upheavals of the 1960s and 1970s, critical theory and deconstructionism included the natural and social sciences in the analyses of how ethnocentrism, paternalism, and political power distorted the intellectual enterprise. Some natural and social scientists reacted quite defensively to these critiques, penning polemical counterarguments (e.g., Gross and Levitt 1997). Some of the frequently leveled critiques of evolutionary studies by the

humanistically inclined—for example, that evolutionary views are connected to conservative political ideologies—are demonstrably false (Tybur et al. 2007; Lyle and Smith 2012). Rants against reductionism and positivism sounded strange to those of us brought up on philosophers of biology arguing that these ideas were purely of historical interest. One of us (PJR) was a participant in a 1981 conference organized by Donald Campbell and Alex Rosenberg to explore what Campbell termed the concept of an “epistemologically relevant internalist sociology of science.” He was impressed by the young proponents of the internalist Strong Program in the Sociology of Science (e.g., Bloor 1971), whom he saw as pursuing a valuable, intimately ethnographic look at the micro-scale processes by which science worked. At the same time he had no doubt that the then conventional realist notion that science worked fairly well as an instrument for fallible but real discovery was essentially correct. In fact, he looked forward to the Strong Program contributing to the improvement in the functioning of science as a social system. In effect, Campbell was trying to stop the “Science Wars” before they started. He had no success with either the internalists or realists at the conference. It was clear that the internalists perceived themselves to be young innovators with no use for the “errors” of their elders, whereas the realists saw the internalists as making no useful contribution. At least one paper from each side was subsequently published, thus giving an impression of the passions with which each side pressed its case (Woolgar 1982; Gieryn 1982).

In our view, the “Science Wars” were based on willful ignorance on both sides and have done serious damage to scholarship in the four focal areas of this volume. As some of our participants have argued elsewhere (Slingerland 2008; N. Henrich and Henrich 2007; Boyd and Richerson 1992; Turchin 2008), as have others (Leijonhufvud 1997), “humanistic” and “scientific” methods each make distinctive and vital contributions to understanding the world. In essence, evolving systems are complex and diverse. They cannot be reduced to a single model, and even if they could be so reduced, the model would be far too complex to actually use. Much of our understanding of such systems is bound to remain semantic, qualitative, particularistic, incomplete, and open ended. On the other hand, the discipline of acquiring quantitative data and fitting formal models often yields great insights, albeit fallible insights on a narrow front. Mathematics and quantitative empirical methods are just mental prostheses invented to finesse the unaided mind’s weak powers of deduction and inability to estimate quantity accurately. Most scholars do not have serious problems deploying quantitative and qualitative methodologies opportunistically. We have never met a historian or archaeologist, no matter how “humanistic,” who objected to using radiometric dating in situations where it would be useful. Evolutionists, even the most “scientific” ones, are usually decent natural historians, historians, or ethnographers whose qualitative command of some segment of the world is essential to their science. We think that you have to don some sort ideological blinders to start a fight over which sort of tools

are more valuable. The world we all want to understand is fiendishly hard to comprehend. Why would any sensible scholar reject “on principle” any useful method to advance understanding?

Conclusion

The field of cultural evolution has grown rapidly over the last forty years, particularly as a self-conscious entity. This growth rests on deep foundations in the social sciences and humanities. It also has a solid foundation in behavioral biology, which unfortunately is not covered here in depth. Other animals turn out to have important systems for social learning analogous to human culture, and the last few decades have matured into a veritable golden age of studies of animal culture (Danchin et al. 2004; Whiten et al. 2011; see also Menzel and Fischer 2011). The first two-thirds of the twentieth century were a sharp hiatus in the study of cultural evolution from a Darwinian perspective. Since the mid-1960s, it has taken nearly a half century to make up for the neglect that the field suffered across most of the range of research topics covered in this book.

As evidenced by the chapters contained in each of the four topic areas, understanding human cultural evolution constitutes a similar but not identical problem. The issue of understanding the developmental support for cumulative culture is much the same. The same basic forces which shape evolutionary change work everywhere. For example, borrowing technology and words or grammatical constructions from another culture represent similar processes. Differences, however, are surely important. Few variant words or variant religious beliefs have the same direct impact on well-being as variant subsistence technology. Variant words and religious practices do play important roles in structuring social life and can certainly have an important indirect impact on health and welfare. We do not want to discount the diversity of cultural processes across domains within cultures nor across cultures nor in the historic and especially prehistoric past.

Given the inherent complexities, no publication short of a multivolume treatise could hope to do complete justice to the current field of cultural evolution. Nevertheless, this book provides a broad sample of the work that is ongoing by cultural evolutionists. We hope that you enjoy it as much as we enjoyed the Forum and the resulting editing.

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