Cultural Evolution: Accomplishments and Future Prospects

Peter J. Richerson and Robert Boyd

Edward Wilson (1998) recently popularized William Whewell's nineteenth-century idea of "consilience." The idea was a favorite of Darwin's. It holds that seemingly disparate phenomena in the world are in fact connected. Nuclear physics is "remote" scientifically from the social sciences, yet nuclear reactions in the sun are the most important source of energy on earth, nuclear decay in the earth's interior drives seafloor spreading which in turn shapes terrestrial ecology, and nuclear weapons profoundly altered the shape of international politics in the twentieth century. Nothing is in principle irrelevant to the study of the human species--not nuclear reactions, not anything. Evolutionary theories apply to highly consilient phenomena.

Consilience appealed to Whewell, Darwin, and Wilson because the concept suggests that scientific theories have the desirable epistemological property of, on the one hand, explaining many things economically if they are correct, and, on the other, being horribly vulnerable to ambush from every direction if wrong. In this chapter, we argue that culture and cultural evolution are also consilient phenomena, and that the Darwinian theory of cultural evolution can take systematic advantage of the epistemological strengths of consilience. (In this volume, see Melissa Brown's Introduction for a definition of culture in terms of ideas acquired from others, and her and Roy D'Andrade's chapters for an analysis of some of the complexities that this definition causes. For more on the theory of cultural evolution, see Marcus Feldman's and Joseph Henrich's chapters).

We wish to sketch the outlines of how the theory of cultural evolution can--and in some measure already does--underpin a vibrant empirical science. We will build our case on examples of theoretical and empirical investigations, which, in the spirit of consilience, range quite widely. Most of these examples consist of studies done by social scientists who would not consider themselves Darwinian evolutionary scientists. In fact, some might quite resent the sobriquet! From the point of view of Darwinians, anything bearing on the processes by which culture changes as a function of time and circumstance is a contribution to the project. Social scientists and historians certainly observe and comment upon such changes and upon the myriad consilient things that play a role in such change. What we can hope to do is convince such scientists that all the Darwinian perspective means to do is to draw together the many threads that, for lack of a proper theory, seem like unrelated domains of investigation. The Darwinian approach simply offers a set of tools designed to analyze the puzzles presented by a special sort of change over time--change involving populations with inheritance systems such as genes or culture. We can also expect to discover gaps and weaknesses in the present corpus of social-science investigations, areas where little or no good work evolutionary has yet been done.

We divide the totality of evolutionary studies into five broad realms: logical coherence, investigations of proximate mechanisms, microevolutionary studies, macroevolutionary studies, and patterns of adaptation and maladaptation. To make the discussion more concrete, we will focus on studies that could cause us to doubt that culture is uniquely important in the human species. By this we mean the proposition introduced by Edward Tylor (1871) and especially integral to the foundations of anthropology, that a great deal of variation in human behavior is acquired from others by teaching and imitation. Much of this variation is expressed in differences between societies, although not a little exists between individuals within societies, along the lines of gender, age, social role, occupational specialization, and the like. These cultural differences have arisen by processes of cultural evolution that are crudely similar to organic evolution, though by no means identical. By contrast, Tylor and his successors argue, the biological differences between human individuals--especially the average biological differences between major subdivisions of the species--are small in comparison with the cultural differences. In modern language, the idea is that humans have both a genetic and cultural inheritance system, and that most of the differences between humans, particularly the differences between groups of humans, are cultural rather than genetic.

We have found it difficult to determine if any contemporary scholars actually doubt that culture is important in humans (see also D'Andrade, this volume). Some scholars, such as Tooby and Cosmides (1992) and Pinker (2002) argue that the standard picture of culture is typically wedded to an oversimplified blank-slate psychology, and that the direct effects of the environment on behavior may be underestimated. Some behavioral geneticists (e.g., Rushton 2000; Herrnstein and Murray 1994) seem to be arguing that genetic differences between major human groups are more important than the pure culture hypothesis allows. The economists' rational-choice theory, if taken literally, holds that perfectly rational actors with no information constraints adjust their behavior to the prevailing environment instantaneously and autonomously. This theory may cause economists to suspect that the role of culture relative to individual decision making is overemphasized by Tylorians. Because of its theoretical sophistication, rational-choice theory has been widely adopted as a theoretical foundation by other social scientists (e.g. Ostrom 1998; McCay 2002), who usually incorporate the culture concept or something like it into their formulation, using terms such as "bounded" or "situated" rational choice. Similarly, human behavioral ecologists (e.g. many of those represented in Smith and Winterhalder 1992), whose theories often formally amount to rational choice in light of fitness maximizing goals, are generally quite willing to believe that culture is proximally responsible for most behavioral adaptations. Arthur Wolf (this volume) notes that behavior is affected by social and ecological factors as well as culture, and that the former can easily be mistaken for the latter. His critique notwithstanding, we think that cultural evolutionists are quite sophisticated about the relationship between social organization and culture (see, e.g., Henrich, this volume).

Although hardly anyone seems to disagree with the importance of culture in humans, we think the exercise of systematically laying out the evidence to support the qualitative position we have outlined is useful. No one explicitly acknowledges how various and powerful the evidence is! Framing the case in terms of an evolutionarily based taxonomy highlights the contributions that cultural evolutionary analysis has made and is prepared to make to a science of culture. Ultimately, we seek quantitative, mechanistic answers to the questions of the contributions of genes, culture, and environment to human behavior. On this score, real ignorance and legitimate controversy litter the landscape we survey. Yet, across this huge field of scientific endeavor, we see prospects for progress everywhere.

Logical Consistency

Logical consistency is the proper domain of formal theoretical models. We do not emphasize this realm in this essay, but a brief characterization of its importance is in order. For an elementary treatment of cultural evolutionary models, see Richerson and Boyd (1992). For advanced treatments, see Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985). See also the chapters by Feldman and by Aoki et al. in this volume.

Human minds aren't well adapted to thinking through the consequences of linked population-level processes. Although critics of mathematical models often recoil at their simplicity, simple models are an effective prosthesis for a brain that is rather poor at following intricate quantitative causal pathways. Model builders are often quite surprised at their own results, even when their intuitions are well-schooled by related models. The strategy of using simple models to study complex phenomena is well developed in many scientific disciplines, and should hardly be controversial (Richerson and Boyd 1987). We think of simple models as tactical reductionism, something entirely different from supposing that real human behavior is simple enough to be accurately described by such models. The models are just tools to help us think a little harder about complex problems. ***Not*** using these tools condemns the theorist to rely entirely upon verbal arguments and intuitions that are difficult to check for logical consistency, especially when phenomena obey quantitative rather than categorical causal rules.

Population-genetics<->style models of cultural evolution are well enough advanced to demonstrate that they can play exactly the same role in studies of cultural evolution as in studies of organic evolution. One of the most important properties of models is that they are not constrained much by disciplinary history or by empirical difficulties. The logical exercise of making a complete evolutionary model, even a very simple one, typically forces the modeler to cut across traditional disciplines. The simplest sorts of recursion equation models of cultural evolution incorporate some sort of model of individual psychology and some sort of model of a population. Typically, the results of such models depend both upon the properties of individuals and upon the properties of the populations they make up. Psychologists study individuals, whereas cultural populations tend to fall under the disciplines of anthropology and sociology. The models show how the findings of each discipline are relevant to the other. Social scientists have had great difficulty theorizing about the relationship between individuals and societies; sociologists refer to the "macro-micro problem" (J. Alexander et al. 1987). When they start with considerations of individuals, sociologists find it hard to drive the properties of societies; when they start with "social facts," they find it hard to make a place for individuals. The evolutionist's recursion equation formalism that integrates over individuals within a generation and then iterates over time does what sociologists have otherwise found it hard to do.

Although the amount of modeling done to date is small relative to the immense complexity of the problems of cultural evolution, the diversity of problems tackled is certainly adequate to demonstrate the power of the technique. Studies range from the analysis of specific empirical cases to quite broad analyses of the general function of the cultural system (Aoki 2001). The very fact that such models can be made and that they behave in close accord with empirical cases may not seem like much, except that people have confidently asserted otherwise. Gregory Bateson (1972: 346<->63) and David Hull (in Lamarck 1984: xl<->lxvi) argue that systems with inheritance of acquired variation would be dysfunctional if they existed. This is not true; models linking learning to social transmission are easy to make and have quite interesting properties (Boyd and Richerson 1989). On the other hand, Bateson and Hull point to features of a system for the inheritance of acquired variation that is indeed dysfunctional under certain circumstances; more on this point below. To take another topical example, many people argue that unless culture comes in discrete units like genes, cultural evolution on the Darwinian plan is impossible (Weingart et al. 1997). Actually, models show that Darwinian evolution is compatible with unitless cultural variation (Boyd and Richerson 1985: 70<->79). Furthermore, near-perfect replication after the fashion of genes is not necessary to create patterns of heritable variation that respond to Darwinian evolutionary forces (Henrich and Boyd 2002).

The formal models thus demonstrate that culture *can* exist and have all the basic properties claimed for it by proponents of its importance.

Proximal Mechanisms

If culture is important in humans, we must have a psychology that is adapted to acquiring information from other individuals by teaching or imitation. Classic experiments by Bandura and Walters (1963) and Rosenthal and Zimmerman (1978) showed that children are very rapid and accurate imitators, and that they use sophisticated rules to bias their imitations of people with different characteristics.

More recently, psychologists have begun to dissect these skills in greater detail. Developmental linguistics is perhaps the most advanced field in this regard. Tomasello (1999a, reviews evidence that human caregivers and children engage in a rather complex behavior called *joint attention*. Joint attention develops at around one year of age, and Tomasello infers that it is an innate capacity. Children follow the gaze of adults and gestures such as pointing. They can readily discern the focus of an adult's attention, which makes it easy for them to associate words with specific objects. Bloom (2000) discusses the many skills and strategies such as joint attention that children deploy to learn new words. Some of these are no doubt ancient and not at all specific to language learning. Babies already have an object-recognition system built into their visual system. Spelke (1994) shows that infants use rules such as *cohesion* to classify their visual experience into conceptions of objects: pieces that move together are taken to be objects Thus, if an experimenter shows an infant a simple cartoon of a bicycle and rider appearing together on one side of screen, and reappearing still together on the other side of the screen, the infant will treat the combination of bicycle and rider as a single object. If after several repetitions of this pattern, the bicycle and rider suddenly reappear separately, the infant reacts with surprise, and quickly learns that people and bicycles are separate objects. Later, toddlers realize that the parts of people and bicycles do not move entirely together and that arms and wheels are semi-separate parts of people and bicycles. Native Americans are said to have mistaken Spanish cavalrymen for centaur-like humanoid beasts, suggesting that coherence has a powerful influence even in adult cognition. Presumably all animals with good vision and reasonably advanced cognition use such strategies. Other tricks seem more directly tied to speech. For example in *fast mapping*, children use simple clues to deduce part of the meaning of a novel word. For example, if asked to bring the chromium tray when the choices are a blue tray (a color word the child already knows) and an olive one (a color word unknown to the child), children will assume that "chromium" refers not only to a color, because that is the only salient difference between the trays, but also specifically to olive. They retain this theory about "chromium" for some time on the basis of a single trial. The very rapid buildup of vocabulary in middle childhood probably depends crucially on such economical heuristic guesses of the meaning of new words. Presumably, similar skills underlie the imitation of motor skills (e.g., tying knots) and the learning of social rules and customs.

Baum (1994: 105, and personal communication) argues that humans differ from other animals in our high degree of sensitivity to social reinforcement. Interacting in a friendly way with other people is pleasurable, and being subject to verbal abuse, complaints, and the cold shoulder are quite unpleasant. Our responsiveness to social reinforcement makes humans relatively easy to teach. Some human skills are far too complex to learn by simple imitation. Polanich (1995) analyzed the case of diffusion of coiled basket construction from Yokuts to Mono peoples in the Southern Sierra region of California. Mono weavers by tradition made baskets by the twining technique. In coiled baskets, the main structural element of the basket spirals outwards from the center; in twined baskets the main structural elements radiate from the center like the spokes of a wheel. To learn the difficult Yokuts technique, Mono weavers had to work side by side with an experienced coiler and learn each stitch through careful demonstration and instructional feedback. Yokuts and Mono basket weavers became intimate enough friends for the student-teacher bond to become established, and thus for coiling to be transmitted to the Mono students. By contrast the decorative designs on baskets diffused much more easily because twiners could easily represent coiler's decorative patterns in twined baskets and vice versa. Henrich and Gil-White (2001) argue that human prestige systems are substantially built on the basis of rewards that imitators and learners provide to people they take to have superior knowledge in one domain or another.

Although many animals have rudimentary capacities for social learning (Heyes and Galef 1996), humans are much more adept imitators and teachers than any species yet tested. Two independent research groups working at Yerkes Primate Center compared young children and adult human-reared chimpanzees on the same imitation tasks (Tomasello 1996; Whiten and Custance 1996). In these studies, children of three and four were considerably more accurate imitators than chimpanzees, although chimpanzees are in turn known to be better imitators than most other species. Similarly, anecdotal accounts of chimpanzees reared by humans as though they were children report that although chimpanzees respond to social reinforcement, they do so much less than children (Hayes 1951; Temerlin 1975).

Some doubt does remain about the precise gap between humans and chimpanzees as regards social learning. Boesch (this volume) notes that field researchers observe a considerable variety of what appear to be cultural behaviors in chimpanzees and other apes, more than sometimes seems consistent with controlled laboratory studies of social learning. The observations may be misleading, the experiments may contain artifacts, or much information may pass to young apes via relatively simple systems of social learning. Experimental evidence for more sophisticated social cognition in chimpanzees continues to be found in the laboratory (Hare et al. 2001). Nevertheless, we think it implausible that what Darwin called the "great gap" between living humans and our closest relatives will ever be closed. The sheer quantity of information that humans acquire by social learning outdistances that of our relatives by perhaps a couple of orders of magnitude.

Much work remains before we understand human social learning in detail. We and others have constructed mathematical models based on plausible assumptions about the social learning strategies that people might use. For example, theory suggests that people should use conformity to the majority under a wide variety of circumstances (Henrich and Boyd, 1998). Recently, we have begun an experimental program to dissect the way people (mostly undergraduate students volunteers, but also non-Western adults) deploy social learning strategies in laboratory tasks (McElreath et al., 2005, Efferson et al., 2007). This program is in its infancy, but it has already turned up surprises. Individual variation in strategies used is high and our participants often use less social learning and less conformity than would be optimal in the tasks they are given to solve.

Microevolution

At the heart of Darwinism is the close study of evolutionary processes on the generation-to-generation time scale, which is susceptible to precise observation and controlled experiment What is the prevailing rate of change of gene frequencies, and why are they changing? Weiner's (1994) description of Peter and Rosemary Grant's famous study of the microevolution of the beaks of Galapagos finches is an accessible introduction to the genre.

Most cultural change is relatively gradual, and is apparently the result of modest innovations spreading by diffusion from their point of origin to other places. Cultural evolution is a population phenomenon. Individuals invent, and observe the behavior of others. Imitation by discriminating observers selectively retains and spreads innovations. Innovations accumulate and gradually build to complex technology and social organization. Darwin described such patterns of change as descent with modification. The theoretical and empirical tools designed by evolutionary biologists to study genes are well suited to describing cultural evolution, given suitable modification.

Anyone interested in human history is a student of cultural evolution. What Darwinians bring to the table is a commitment to quantitative study of the processes of cultural evolution. In order to gain leverage to compare across cases, Darwinians seek a taxonomy of forces that affect evolution. We (Boyd and Richerson 1985) favor a taxonomy that distinguishes three forces that are highly analogous to their counterparts in organic evolution: *random variation*, *drift*, and *natural selection*. In addition to these are what we call the decision-making forces, which others call cultural selection (Cavalli-Sforza and Feldman 1981; see also Feldman, this volume). The decision-making forces can in turn be broken down into the effects of individual learning--*guided variation*--and the effects of biased choices of cultural parents or of the traits they carry--*biased transmission*. Biases depend upon the decision rules the learner or teacher uses, so several distinctive types exist, even at a rather general level. If the science of cultural evolution evolves as that of organic evolution has, new forces will be discovered and old ones will be subdivided.

A study by Hewlett and Cavalli-Sforza (1986) on the transmission of hunting techniques by Aka Pygmies in the Congo illustrates the basic strategy of microevolutionary analysis. When asked how they had learned their hunting techniques, Aka men almost always answered that they learned them from their fathers and other male relatives with whom they hunted. The exception was the making and use of highly effective crossbows. Most men had learned this technique from one of the few men who had acquired their knowledge from outsiders. In fact, most other hunting techniques were long extant in the band and were known to all adult males. Fathers normally taught their sons to hunt. Although the lack of variety in hunting techniques resulted in a conservative pattern of vertical transmission for the most part, the Aka ability to use other modes of transmission and to employ biases is evident in the spread of the crossbow.

Only a handful of microevolutionary studies have yet been designed deliberately by Darwinians to study cultural evolution (Aunger, 1994, Joseph Henrich, personal communication), but many studies designed for other purposes give a good picture of cultural microevolution in domains where social scientists have in effect reinvented Darwinism. An early and very self-consciously population-based approach is Foster's classic 1960 study of the effect of the Spanish Conquest upon Latin American culture. Latin Americans acquired a small sample of Iberian cultures, partly because immigrants were few and from selected areas, partly because church and state authorities deliberately biased the culture carried over to the New World (see Durham, this volume, on "imposition"), partly because the Native Americans were selective in what they borrowed, and partly because Spanish settlers selectively adopted Native American items. Scholars have conducted more than a thousand studies of the diffusion of innovations, predominantly technical innovations (Rogers 1995; Rogers and Shoemaker 1971). These studies usually use questionnaires and are designed much like Hewlett and Cavalli-Sforza's Aka study. They provide much useful evidence on the role of decision-making forces in cultural evolution. The study of language microevolution is also a well-developed field (Guy and Labov 1996; Labov 2001; Deutscher, 2005). Dialect evolution is particularly well studied. Change is often appreciable on the generation-to-generation time scale; it is studied by sampling the speech of people of different ages. A number of forces have a significant role in driving language evolution, but many of them are prestige biases of one form or another. For example, speakers of stigmatized dialects often exaggerate (hypercorrect) features of the prestige dialect that they cannot manage to master exactly. When hypercorrecters are numerous relative speakers of the prestige dialect, hypercorrection actually drives the evolution of the target dialect. Local prestige is often the most potent force. Typically, the most advanced speakers of a changing dialect are upper-working-class or lower-middle-class women with high prestige in their communities. Because dialect is not normally altered after puberty, the inference is that popular pre-pubertal girls from the middling classes are the main drivers of language evolution. Language mavens, know it and weep!

A powerful method for studying cultural microevolution is to compare two communities derived from the same parent community, using quasi-experimental designs. Walter Goldschmidt designed such a study in East Africa, from which Robert Edgerton (1971) produced the most synthetic analysis. Goldschmidt chose four societies, each of which had some communities in the humid highlands specialized in horticulture, and some communities in the arid Rift Valley specialized in raising livestock. The exact degree and timing of the separation of the communities within a tribe was not known, but was surely not very great--perhaps a few generations. Because settled farming and migratory cattle-raising have huge implications for social organization as well as subsistence, communities at either extreme should be under strongly divergent evolutionary pressures. In fact, much more of the variation in the data Edgerton collected could be explained by common tribal affiliation than by economic mode. However, in a significant minority of cases the effect of economy was significant. Often the tribe X economic-mode interaction effect was also large; even when horticultural and herding communities were diverging, they were not necessarily converging on other communities with the same economic system. Goldschmidt and Edgerton's study demonstrates both that culture has significant "inertia" and that strong evolutionary pressures lead to quite measurable change in a few generations. These are the same general microevolutionary features we find in the case of organic evolution and this design deserves much more widespread use to understand cultural evolution than it has received (McElreath 2004).

Two related questions about cultural evolutionary process are quite controversial. Most people seem to have the intuition that most directional cultural evolution is due to decision-making processes and that natural selection (on cultural variation) has little if any part to play. We think, to the contrary, that the microevolutionary evidence for the operation of natural selection is actually rather compelling. For example, Hout et al. (2001) conducted a careful and thorough analysis of the effects of fertility and of conversion on the growth of conservative Protestant denominations relative to mainline ones in the United States. Although decision-based movements between conservative and mainline denominations explain some of the difference, three quarters of the increase in conservatives was attributable to higher birthrates between 1903 and 1973, at which time conservative and mainline birthrates converged.

The second controversial question is whether group selection can play a role in human evolution. Darwin (1874: 178<->79) clearly thought that humans group selected. Several prominent modern Darwinians (Hamilton 1975; E. Wilson 1975: 561<->62; Eibl-Eibesfeldt 1982; R. Alexander 1987: 169) have also given serious consideration to group selection as a force in the special case of human ultra-sociality. They are impressed, as we are, by the organization of human populations into units that engage in sustained, lethal combat with other groups, not to mention other forms of cooperation. The trouble with a genetic group-selection hypothesis is our mating system. We do not build up concentrations of intra-demic relatedness, as do social insects, and few demic boundaries are without considerable intermarriage. By contrast, theoretical models show that group selection is a more plausible process if the variation selected is cultural (Boyd and Richerson 1982; Avital and Jablonka 2000). For example, if migrants are resocialized when they enter new groups, especially if their cultural variants are discriminated against by conformist transmission, then cultural group selection requires only the social, not the physical, extinction of groups. Soltis et al. (1995) reviewed the ethnography of warfare in simple societies in Highland New Guinea. The patterns of group extinction and new group formation in these cases conform well to the assumptions of the Boyd and Richerson (1982) model. The strength of group selection in Highland New Guinea was strong enough to cause the spread, in about 1,000 years, of a favorable new social institution through a region composed of many populations. Cases of group selection by demic expansion are quite well described, for example the spread of the Southern Sudanese Nuer at the expense of the Dinka (Kelly 1985); the expansion of the Marind-anim at the expense of their neighbors by means of large, well-organized head-hunting raids (including the capture and incorporation of women and children) at the expense of their neighbors (Knauft 1993: chap. 8); and the Spanish conquest of Latin America (Foster 1960).

Everyone agrees that human behavior is very diverse. To the extent that this variation is genetic, patterns of microevolution should conform to genetic patterns. To the extent that it is a direct product of individual interactions with environments, we should not see any microevolution of the Darwinian descent-with-modification sort at all. In fact, patterns of microevolution betraying the peculiar mix of decision-making, chance, and selection that culture theorists model are commonly observed. The diffusion of linguistic and technical innovations by biased horizontal and oblique transmission are fundamental to explaining these phenomena. Group selection on cultural variation is viewed with suspicion by many evolutionary social scientists, but we believe that this is the result of a prejudice acquired from the study of evolutionary biology, where the general case against group selection is more plausible.

Macroevolution

Understanding what regulates the rate of evolution in different times and places is one of the main tasks of macroevolutionary studies. The large scale and comparative evidence suggest that cultural evolutionary theory, and the coevolution of genes in response to novel culturally constructed environments, have important roles to play in understanding the major events in human evolution. In favorable cases, detailed archaeological sequences can be investigated directly by fitting microevolutionary models. Bettinger and Eerkens have applied microevolutionary models to the analysis of stone point evolution in the Great Basin of North America, finding contrasting evolutionary dynamics in different times and places Bettinger and Eerkens, 1997; Eerkens and Lippo2005; see also Shennan and Wilkinson, 2001). Improved statistical techniques based on fitting models representing different hypotheses directly to data make this approach promising (Burnham and Anderson, 2002).

Two approaches to the study of macroevolution are more common than direct model fitting because they cope well with the sparse data normally available about deep historical events. One is to use comparative evidence from different species or different major cultural groups to try to understand how large-scale differences have arisen. The second is to closely examine major transitions and long-time-scale trajectories of species or societies, in an effort to disentangle the causal processes involved. Precise reconstructions of the past are seldom possible, but some things are well documented in the archaeological, paleoanthropological, and paleoenvironmental records.

The simplest and best-documented evidence is the rate of change of cultural (and gross biological) features of past populations. For example, the existence of decision-making forces in cultural evolution makes the cultural evolutionary process rather more rapid than ordinary genetic evolution. At least in the case of adaptive biases, these forces will act additively with each other and with natural selection to speed cultural evolution in adaptive directions. Rates of evolution of artifacts vary dramatically over the course of hominid evolution. Only in the late Pleistocene does cultural evolution become so rapid as to create temporally and spatially localized cultures that bear a strong resemblance to ethnographically known hunter-gatherers (Donald 1991; Klein 1999). Evidently, the cultural evolutionary system became fully modernized less than 250,000 years ago, perhaps as recently as 50,000 years ago (McBrearty and Brooks 2000).

At least one of the innovations that made the complex, rapidly evolving culture of modern humans possible is the ability to form social bonds with strangers, even across ethnic divides. The case of the exceedingly simple material culture of the Aboriginal Tasmanians is an interesting test of how large a culture area must be to maintain complex culture. Tasmania was isolated from Australia by the flooding of the Bass Strait in the early Holocene. Tasmanians started with a toolkit as complex as those anywhere else in Australia, but by the time of European contact, they had the simplest toolkit ever collected by European explorers (Diamond 1978). Henrich (2004) gives an ingenious model of the loss. If the transmission of complex culture is fairly error-prone, transmission itself will result in selective degradation of more complex items in the repertoire. Rare, highly skilled craftspeople will tend to reinvent the otherwise degrading cutting edge of a technology. The 4,000 people on Tasmania likely included too few such experts to maintain a toolkit of ordinary complexity. If Henrich's hypothesis is correct, many more were necessary, and we do know that cross-cultural trade and other contacts linked peoples together across vast distances during the late Pleistocene, but probably not earlier (Klein 1999: 470<->71, 544<->45). In Upper Paleolithic Europe, Moderns moved desirable raw materials hundreds of kilometers, compared with tens of kilometers for Neanderthals, and the settlement density of Moderns was greater as well. Gravettian Venus figurines were distributed over most of Europe. To judge from the size of their brains, Neanderthals were as intelligent as Moderns at the individual level, but if they lacked the social "instincts" to maintain wide-ranging social contacts, the complexity of their toolkit would have been limited by the "Tasmanian effect," as seems to be the case. Also consistent with the Tasmanian effect is the progressive increase in the complexity of toolkits and other aspects of culture in the last 10,000 years. Agriculture boosted population densities, transport technology was transformed by the use of inanimate and animate energy sources, and writing and mathematics substantially relieved memory limitations. In the last few centuries, innovations such as cheap printing, mass education, science, and industrial espionage have further revolutionized the number of experts available to each individual.

Recent discoveries of the nature of paleoclimates are revolutionizing our understanding of the environmental stage within which human macroevolution took place (Vrba et al. 1995; Potts 1996; Alley 2000; Richerson and Boyd 2000; Calvin 2002;). During the Plio-Pleistocene eras the Earth's climates have changed dramatically and often very abruptly. Ice cores taken in Greenland in the late 1980s record proxies indicating climates with huge variation on time scales of a millennium or less during the last glacial--much more than during the preceding 11,500 years. Several similarly detailed core records from temperate and tropical latitudes, taken from anoxic lake and ocean sediments, show that very similar fluctuations occurred at these latitudes as well (e.g. Martrat et al., 2004). High-resolution data for the rest of the Plio-Pleistocene will likely be produced in the next few years, for example, from the sediments of Lake Malawi (Scholz 2005).

Already, some of the climate patterns are extremely suggestive of influences on cultural evolution. The transition from highly variable glacial to much more tranquil Holocene climates was quite abrupt, and coincides with the broadening of human diets to include high-processingcost plant foods (Richerson et al. 2001). Many human populations began an evolutionary trajectory that sooner or later led to agricultural production. All but one of the known sequences start in the Holocene. The exception is the Natufian and neighboring cultures of the Near East. These cultures flourished in the B<sla>olling-Aller<sla>od period of warm, calm climates just before the last cold, variable period (the Younger Dryas) that ended with the beginning of the Holocene. The Natufian plant-rich system substantially decayed during the Younger Dryas, but with the return of warm calm climates, the earliest domestications began almost immediately in the Fertile Crescent.

The climate change across the Pleistocene-Holocene boundary proves to be much more complex than a poleward shift of isotherms. Last glacial climates were lower in CO_2, on average much drier, and much more variable on time scales from decades to millennia than than Holocene climates. In the Near East, the time required for societies to progress from an initial domestication to substantial reliance on crop plants was three or four thousand years (and, of course, increases in agricultural productivity continue right up to the present). Moves in the direction of agriculture all involved focusing on a handful of key proto-domesticate species that rewarded investments in labor and skill to collect (later, cultivate) and process. Considerable shifts in other aspects of subsistence followed from sedentary life, and from the nutritional implications of eating large amounts of one or two species of plants inevitably lacking in critical amino acids, vitamins, and minerals. In a world in which year-to-year climate variation probably exacerbated the risks of depending heavily upon one or two plants and in which environments were changing very rapidly relative to the cultural macroevolutionary time scale, the evolution of a complex, productive, but risk-prone subsistence strategy seems quite unlikely. By contrast, the demographic time scale is considerably shorter than the cultural evolutionary time scale. Populations can double each generation under favorable circumstances, and they probably did grow substantially at favorable times and places in Pleistocene, only to be cut back by climate deterioration. Had agriculture been merely a response to population pressure (M. Cohen 1977), people would have presumably shifted in and out of agriculture in the highly variable ice-age climates as good times for this subsistence system alternated with hard times.

The rapidly improving climate record is important not only for identifying environmental drivers of human evolution, but also for isolating other factors that regulate the long-term rate of cultural evolution. In the Holocene, societies everywhere in the world intensified their focus on plant resources, albeit at very different rates. The progress to agriculture, and to the spinoff effects of agriculture such as political sophistication, was most rapid in western Asia and China, but much slower in some other places. In Australia no societies practiced agriculture, and only few did in western North America. The different regions of the world in the Holocene provide a useful natural experiment to test hypotheses about the rate-limiting processes affecting cultural evolution. Diamond (1997) takes on this project. He and others have proposed more than a half-dozen major types of explanations for the regulation of rates of cultural evolution (Richerson and Boyd 2001b).

The macroevolutionary record is highly consistent with culture playing a dominant role in human behavioral variation. On one hand, cultural evolution is distinctly less rate-limited than genetic evolution. The rates of behavioral evolution of modern humans are dramatic by the standards of genetic evolution. Given decision-making systems that have an adaptive tendency, humans can run up social and technological adaptations to variable environments much more quickly than could be accomplished by the evolution of new instincts and new anatomy. The success of modern humans in mastering the highly variable last glacial environment, in the course of the Out of Africa II migration, is testimony to the power of rapid adaptation to new environments. On the other hand, cultural evolution is very far from instantaneous. It follows the pattern of descent with modification familiar from genetic evolution. Holocene climates have varied very little, and for the past 11,500 years human societies have exhibited a progressive trend toward larger and more complex societies. This trend has run at different speeds in different parts of the world, but setbacks, perhaps sometimes in response to environmental changes, have been of modest depth and duration relative to advances. The telling fact, we believe, is that no other species in the last few hundred thousand years has had a macroevolutionary pattern at all similar to ours despite being subject to the same powerful climatic forces.

Patterns of Adaptation and Maladaptation

Darwinians are often happy to be called adaptationists, and critics of Darwinism are often suspicious of adaptive explanations. We think that these stereotypes, to whatever extent they are true, are unfortunate. Adaptation is clearly important, especially in the human case. We are the Earth's dominant organism; perhaps no single species in the history of the earth has ever been such a stunning adaptive success. On the other hand, people do many things that certainly do not appear to be adaptive. Perhaps because our adaptation is so dominating, we have more scope for doing ridiculous things than do species hedged in by tough competitors and dangerous predators.

Adaptations and maladaptations are interesting in their own right, but both are also interesting as clues to how evolutionary processes work (Boesch, this volume). In this regard, maladaptations are typically more revealing than adaptations. Adaptations are over-determined. Genes are selected to favor them. The cultural system is evolved to favor adaptations by the action of decision-making forces as well as by selection (Durham 1991). Individual learning favors adaptive behavior via reinforcement. Maladaptations, on the other hand, often arise through the operation of a more limited set of processes. Because clearly maladaptive behaviors are relatively rare, they are more likely to have arisen by one process, and hence to give direct insight into that process (see also Durham, this volume).

The social sciences have always had functionalist schools, and the recent rise of Darwinian social science has added evolutionary psychology (Barkow et al. 1992) and human behavioral ecology (Smith and Winterhalder 1992; Barrett et al. 2002) to this list. Humans have two closely related adaptive syndromes: technology and social organization (the two are related at least in the apparent need for large social networks to maintain complex technical adaptations using an error-prone cultural transmission system, as seen in the Tasmanian Effect). Both illustrate well the overdetermination of adaptation. Take social organization. People live in societies unusually large for a primate, and cooperate, or at least coordinate, with unusually distant relatives. Evolutionists have offered many explanations for human cooperation, including indirect reciprocity (R. Alexander 1987), group selection on genes (Hamilton 1975), sexually selected display (Smith and Bliege Bird 2000), innate algorithms for detecting rule violators

(Cosmides and Tooby 1989), Machiavellian intelligence (Whiten and Byrne 1988), reputation effects (Nowak and Sigmund 1998), and the cultural group-selection process we describe above. None of these proposals can easily be ruled out. Likely many, if not all, play a role in the evolution of our social systems. Our own view, which combines the results of models with the broad empirical patterns, is rather baroque (Richerson and Boyd 2001a**).** We do think that the data do very strongly rule in a major role for cultural evolutionary processes, but perhaps the same can be said for competing explanations. A great many interesting if difficult puzzles lie in the problem of dissecting human adaptive systems.

The case is not quite so dire in the case of technology. We have so far found no colleagues willing to dispute that the skills to make and use tools are products of cultural evolution. However, many people have the intuition that new technology is rapidly mobilized to exploit new opportunities or adaptive pressures. Boserup (1981) famously argued that agricultural innovation so closely tracks population growth that Malthusian worries about demographic crises are unfounded. If so, cultural change must rest on such powerful decision-making forces as to obviate any role for natural selection on cultural variation and to make the decision rules in individual heads much more interesting than the population-level properties of culture as a system of traditions evolving, like organisms, by a relatively gradual process. Stephen Pinker (2002) and other evolutionary psychologists sometimes seem to embrace a view like this, as do human behavioral ecologists when they pursue the phenotypic gambit. One might think that the slow but generally progressive trend toward more sophisticated technology during the Holocene compels one to take seriously the inertia of the cultural evolutionary system on time scales of millennia. Indeed, students of the evolution of technology typically stress how difficult a time inventors have had in developing such simple tools as paper clips and dinner forks (Petroski 1992). However, intuitions differ in this regard. A prominent human behavioral ecologist argued to one of us not long ago that environmental change since the Holocene-Pleistocene transition will likely turn out to explain the apparently progressive trajectory of cultural evolution over this span of time.

The typically shorter list of explanations for maladaptations often highlights the operation of evolutionary processes rather neatly. Perhaps the most important example is how asymmetries between two inheritance systems reveal the power of natural selection. The presence of genes on mitochondria that are transmitted only through the female line (or genes on y chromosomes only transmitted by males) can give rise to distorted sex ratios (Hamilton 1967). Mitochondria are transmitted only by females and y chromosomes only by males (in mammals). Mitochondrial genes sometimes arise that bias the sex ration in favor of females, and y chromosome genes sometimes arise that bias the sex ratio in favor of males. Human culture is not transmitted completely symmetrically to genes, and highly analogous effects may occur. Kumm et al. (1994) argue that male-biased sex ratios in China and India could result from selective killing of high-cost female neonates, because when the cost of carrying a fetus to term is high enough, selection will favor reduced investment in the disfavored sex, rather than a compensating increase in the number of the disfavored sex, as would occur according to a simple Fisherian argument. Actually, Skinner's (1997) huge Chinese census sample is consistent with the hypothesis that the Chinese sex ratio is shaped directly by cultural processes, with a Fisherian primary sex ratio of around 106. According to Skinner's (1997) family systems theory, the Chinese desire a family with a ratio of 2 boys to one girl, and actively shape family configurations to meet this goal.

Thus, in families with excess boys--say, two, three, or four boys and no girls--male infants will be at a progressively greater risk of infanticide as the family's sex ratio climbs beyond 2:1, just as girls are when it is below 2:1. In Skinner's large sample, rather rare family configurations are sufficiently numerous to test this hypothesis quite tightly. The data support the theory. Clearly some sort of cultural evolutionary process is acting here at variance to what selection on genes normally favors.

At least two cultural evolutionary mechanisms might lead to behavior that is maladaptive from the genetic point of view. First, prestige-biased cultural transmission is potentially prone to runaway dynamics, much as in models of sexual selection either as a pure runaway or as a handicap signaling superior cultural variants (Boyd and Richerson 1985: chap. 7). Melissa Brown's (1995) description of the necessity for Taiwanese to bind the feet of women in order for them to achieve full status as ethnic Chinese strongly suggests this mechanism, probably among other processes (see also Brown's epilogue to this volume). Only other women had the skills necessary to bind feet, and in immigrant communities on Taiwan, which were made up mostly of men, ethnically Chinese families felt that they were still savages for lack of this practice. Many of the symbolic differences between human communities, ranging from dialect to ritual, are plausibly the result of runaway or quality-signaling dynamics.

The second source of cultural maladaptations is an analog of microbial pathogens. Culture is, to a greater or lesser extent, transmitted obliquely and horizontally as well as vertically (see also Jones, this volume). Selection can in theory act upon obliquely and horizontally transmitted cultural variation, selecting for "pathological" behaviors that parasitize effort devoted to biological reproduction (and vertically transmitted culture) in favor of effort devoted to horizontal and oblique cultural reproduction (Richerson and Boyd 2005: chap. 5). For example, individuals who delay marriage in favor of continuing their educations have a higher likelihood of entering the professions, including the teaching professions. Evidence suggests also that children from small families tend to do better in school. The advent of mass education in the last couple of centuries has had the effect of making oblique transmission relatively more important than previously, giving greater scope for the process just described. Blake (1989) argues the case for small family size increasing educational attainment. Kasarda et al. (1986) detail the case for the tendency of educated women to acquire professional aspirations that conflict with their reproductive careers. The progressive decline in fertility over time in the developed West, and increasingly elsewhere, is due not so much to this conflict becoming more severe as it is to ever more women being exposed to education at a level that triggers career aspirations. Anabaptists are a rare example of a group in the developed world that takes very great care to inculcate traditional family roles for both men and women and very great care to limit children's exposure to modern prestige norms (Peter 1987; Kraybill and Olshan 1994). For example, Anabaptist groups usually restrict education to the first eight grades, and resort to parochial schools when public schools introduce movies and other forms of modern mass communication into their curriculum. Anabaptist reproductive rates remain high.

Oddly, the existence of maladaptive and neutral variation has been used to contest the Darwinian approach to social science (Sahlins 1976a, 1976b), when in fact explanations for maladaptations are the strongest arrows in our quiver! Special creation is a good account of adaptations, one that most pre-Darwinian scientists, including the youthful Darwin, subscribed to. Darwin's account was superior because it could account for maladaptation--individual variation, vestigial organs, uselessly exaggerated ornaments, and the like. To take a modern example, Hamilton's (1964) theory of inclusive fitness is basically a theory of why cooperation is drastically undersupplied relative to what would optimize fitness. A benevolent God could have designed a much more harmonious world. Interesting special cases such as human societies demonstrate the rule. Humans are a hugely successful species in large part because we can organize cooperation on a scale that no other vertebrate can accomplish. We are not especially good large-scale cooperators on an absolute scale (relative to an imaginary society of saints, say), but we are so much better than any close competitors that we succeed abundantly. Darwinians should take care not to appear to be naïve adaptationists in their quite legitimate enthusiasm for discovering exotic and interesting new adaptations.

Cultural maladaptations follow a familiar pattern. When elements of inheritance are transmitted asymmetrically, evolutionary conflicts of interest easily arise. The modern world, with its emphasis on mobility, exposure to formal education, and work outside the home has reduced the role of parents and other family members in enculturation relative to modern roles such as teachers, coworkers, supervisors. The mass media have become important sources of influence upon children and adults. These changes have made it much easier for maladaptive cultural elements, such as those favoring low fertility and wasteful consumption of prestige goods, to spread. Parents notice how children bring colds, flues, and bad habits home from school. Only groups like the Anabaptists that seal their culture off from the influences of modernity have resisted cultural changes like the demographic transition to small families (Newson et al., in press). We expect that many cases of evolved maladaptations will be discovered when the data are better explored. Take the prevalence of female-preferential relative to male-preferential infanticide in the ethnographic record. The human sexes have gendered subcultures, more extreme in some cultures than others. If the general theory is correct, such subcultures, especially when most highly differentiated, should lead to sex-ratio distortion. Given that males generally manage to dominate females politically and culturally, the result should be expressed as female-preferential infanticide, as in the case of the Chinese family system. The female subsystem should normally be coadapted to the dominant system by the process that Durham (this volume) terms *hegemony*. The case of Chinese women being proximally responsible for foot binding is an example of this process.

Conclusion

Critics of the Darwinian approach to cultural evolution typically make categorical arguments against it (Marks and Staski 1988; Sober 1991; Fracchia and Lewontin 1999; Lewontin 2005). Their argument boils down to the claim that because culture has some properties different from genes, borrowing concepts and methods from evolutionary biology to study culture is an error. We think that the evidence we have sketched here is perfectly sufficient to answer any such critics (see also Feldman, this volume). Recursion models are a comfortable formalism to capture cultural evolutionary processes, and related empirical techniques are equally apt. The critics are certainly right that cultural evolution differs in very important ways from genetic evolution, but these differences are easy to model. Indeed, the entire theoretical project initiated by Cavalli-Sforza and Feldman's (1973a, 1973b) pioneering papers has been to explore the *differences* between cultural and genetic evolution. If the two systems were the same, the theoretical project would be trivial!

Are culture and cultural evolution massively important in the human case? At least some evidence can be supplied in all five of our consilient domains--logical coherence, investigations of proximate mechanisms, microevolutionary studies, macroevolutionary studies, and patterns of adaptation and maladaptation. The math works. The psychology of humans appears to be designed to acquire and manage a cultural repertoire. No other known animal is nearly as well equipped as humans to do this. The microevolutionary foundations of the program find support. The macroevolutionary data rather clearly show that cultural evolution is gradual, but faster--sometimes much faster--than genetic evolution. Culture is pretty clearly an adaptation-generating system that arose in response to the onset of high-frequency climate change in the Pleistocene. It is prone to a characteristic suite of maladaptations that follow from its evolutionary properties.

Such a very general conclusion about the importance of culture seems to us to be as safe as scientific generalizations ever get. The importance of culture to human behavior is about as likely to be disproved as the inverse square law. That said, the work of understanding cultural evolution is in its infancy. Newton started a revolution in physics; he didn't end it. It wasn't until the 1930s that biologists finally concluded that Darwin's nineteenth-century picture of evolution, wedded to the genetic theory of inheritance, was basically correct. Rather than ending the field evolutionary biology, this realization set off its golden age. The same ought to be true for cultural evolution. Once we understand that cultural evolution is basically a Darwinian phenomenon, myriad questions spring to mind. Major gaps still exist in the modeling effort. For example, as far as we know, only one model exists in which cultural change is driven by a collective process (Roemer 2002). Boehm (1996), using simple societies as his examples, and Turner (1995: 16<->18) with complex societies in mind, both point to the fact that people use village meetings, committees, councils, legislative bodies, constitutional conventions, academies of sciences, and other such institutions to make collective decisions, many of which constitute or cause cultural change. As regards proximal mechanisms, no consensus yet exists even for language learning, where the most effort has been expended (Thomason 2001). Our knowledge of cultural variation is largely qualitative. No extant study of cultural microevolution yet meets standards that are routine in evolutionary biology. Descriptively, we know more about human macroevolution than about most other aspects of our evolution. In terms of understanding the processes that control the macroevolutionary record, however, we stand almost at the beginning of the field.

An interesting small problem in cultural evolution is why a Darwinian field did not emerge a century ago in social science as it did in biology. The mythical history, believed by many credulous social scientists, is that a Darwinian social science did emerge, but got entangled in genetic reductionism and racism, and suffered the deserved fate of extinction along with the horrific political regimes it patronized (Hofstadter 1945). Bannister (1979) pointed out the cartoonish nature of Hofstadter's analysis, which applied accurately to only a few Darwinians, such as Ernst Haeckel. More recently Richards (1987) focusing on psychology, and Hodgson (2004), looking at economics, have told a much different story. Darwin's own *Descent of Man* (1874) was much more sophisticated as regards culture than critics give it credit for being. Followers were active in the late nineteenth and early twentieth centuries. In psychology Mark Baldwin, and in economics Thorstein Veblen] successfully showed how the main problem in

Darwin's own thinking, the confounding of cultural and genetic inheritance, could easily be rectified. Neither Baldwin nor Veblen was a genetic reductionist in any sense nor a racist. Veblen is remembered mainly for his biting satire of consumer capitalism; he was much influenced by Marx. Both men made a number of other conceptual and methodological contributions. They were influential figures in their day, and yet they were, in the end, largely written out of the emerging social-science disciplines of their day. The reasons Richards and Hodgson give for their being ignored are contingent historical ones. For example, both men became entangled in sexual scandals that complicated their professional lives. In the small scientific community of the day, too few hands existed to pursue all reasonable paths, and, fateful choice by fateful choice, Darwinian social scientists lost effective proponents in every discipline, leaving the social sciences without a collection of essential tools to do their business. We must not let it happen again!

For references you must find the book; they are consolidated at the end.