By Peter J. Richerson
Peter J. Richerson is Distinguished Professor Emeritus at the University of California Davis. He is coauthor with Robert Boyd of Culture and the Evolutionary Process, and Not By Genes Alone: How Culture Transformed Human Evolution.

SYMPOSIUM ON THE QUESTION “HOW IS CULTURE BIOLOGICAL?" ~ Six Essays and Discussions: Essay # 4, by Peter J. Richerson, "Culture Is an ACTIVE Part of Biology"

Published: APRIL 29, 2010

Abstract

In human biology, it is not possible to distinguish phenomena owing to genes from those owing to culture. Culture is part of human biology. Once we grasp this fact, tools for the synthesis of the genetic and cultural aspects of our humanity leap to hand. The similarities of genes and culture as inheritance systems means that it is easy to build theory in which they interact. Culture is not autonomous but is a powerful component in human evolution. The gene-culture conception of human life frees us from the false monotheisms of superorganicism and genetic reductionism.

Responses by Joseph Carroll and Diana Kornbrot
Rejoinder by Peter J. Richerson

****

Peter J. Richerson
Culture is an *Active* Part of Human Biology

Many pioneering social scientists in the first part of the 20th Century, such as the anthropologist A.L. Kroeber, advocated the view that the cultural aspects of human behavior were superorganic. As he put it in his textbook “[T]here are certain properties of culture—such as transmissibility, high variability, cumulativeness, value standards, influence on individuals—which it is difficult to explain or see much significance in, strictly in terms of the organic composition of personalities and individuals” (Kroeber, 1948: p. 63). Most scholars working in the in the social sciences and humanities today still place little credence in understanding human behavior by studying our “biology.” It would be like trying to analyze a play by worrying whether the stage is formed with wood or marble. You have to have a stage to put on a play, but beyond a few technical requirements the stage is *not* the play. It is as if biology and society and culture operated in different galaxies whose only interactions were a few photons of light that make their way across the billion light years between them. This trickle of photons might be of some interest to a few astronomers but the vast majority of scholars in both galaxies can safely ignore them.

The superorganic conception is, frankly, nuts. Two considerations, one substantive, the other methodological, require that we relegate the superorganic concept to the scholarly graveyard where phlogiston and natural theology lie. The substantive consideration is that humans can't be neatly dissected into the organic and the superorganic. The products of genes and the products of culture are most wonderfully entangled in concrete human life. Take art styles. These seem quite remote from biological considerations at first glance, nearly pure products of the superorganic. You need the eye to see them of course, but beyond that how does biology intrude? The answer is that art does evolutionary work on genes and culture. Art styles are often characteristic of groups, part of what makes belonging to a particular group salient and meaningful (Logan & Schmittou, 1998). Symbolically marked groups in turn tend to reduce the flow of ideas between them, helping refine local cultural adaptations (McElreath, Boyd, & Richerson, 2003). The human innate fascination with artistic productions, and the compulsion to produce them, probably evolved because of this social function. Sometimes symbolically marked groups are highly endogamous, which has genetic consequences. The endogamy that accompanies caste in India has had a strong effect on the genetic structure of the Indian population (Reich, Thangaraj, Patterson, Price, & Singh, 2009). To take a quite different example, psychologists Nisbett and Cohen (1996) conducted elegant experiments on the tendency of men from the Southern US to be angered by insults. Mild laboratory insults provoked increases in testosterone and cortisol in Southern but not Northern men in these experiments. A cultural institution, the Southern culture of honor, works its behavioral effects via the ancient hormonal fight and flight pathway. Nisbett and Cohen review evidence on how these differences are built into Southerners emotional machinery during socialization. No crack actually exists in human biology which can be exploited to split apart phenomena owing to genes from those owing to culture.

The methodological consideration is that if we think of culture as part of human biology, tools for the synthesis of the genetic and cultural aspects of our humanity leap to hand. For example, culture is like genes in many ways. Kroeber himself (1948: 60-69) pointed out the similarity and differences of genes and culture as systems of inheritance while insisting that the differences justified superorganicism. Actually the similarities and differences are the point of entry for the theory of gene-culture coevolution. The similarities of genes and culture as inheritance systems means that it is easy to build theory in which they interact. Furthermore evolutionary theory as regards genes is very well developed. We can borrow from it concepts and methods to apply to studying cultural evolution. In the early and mid 20th Century social sciences almost entirely ignored the Darwinian approach to evolution, as Kroeber among others had wrongly lobbied that they should. There was and still is a lot of catching up work to be done.[1] In the past 30 years much work on cultural evolution has been based on this approach (Cavalli-Sforza & Feldman, 1981; Richerson & Boyd, 2005). The mathematical formalisms of population genetics have been modified to study the properties of cultural evolution. Once we have a common theoretical framework it also becomes possible to study the basic properties of gene-culture coevolution. Among other things, this theory suggests that the original adaptive advantage of culture from the genetic fitness point of view is that can rapidly evolve elaborate cumulative adaptations to spatially and temporally varying environments. Humans constitute a dramatic cultural adaptive radiation that has spread all over the world using based on a staggering diversity of subsistence systems and social organization. Using the gene-culture coevolution approach it has been possible to make progress on problems such as the origin of human language (Tomasello, 2008) a system whose on radiation parallels the ones based on subsistence and social organization. The errors of the superorganicists left an abundance of low hanging fruit that could have been picked decades before. Children should have seen it!

This program of work has been described as reductionist by some of its most influential practitioners. And many of its critics agree and consider it a point against the program. Lumsden and Wilson (1981), argued that genes evolve to manage culture through epigenetic rules. They called the process by which epigenetic rules evolve to manage culture "the complete coevolutionary circuit." They used their famous leash metaphor capture the idea that culture is a well controlled domesticate in service of the interests of genes. Many human evolutionists share this picture of how genetic and cultural evolution relate to one another. For example Joseph Carroll (n.d.) writes:

Ideas and cultural practices can be disseminated and perpetuated only by activating psychological responses that affect behavior. Those psychological responses are themselves constrained by dispositions that have evolved through natural selection. Memes could thus not be "autonomous" in the way that genes are autonomous. Ideas and cultural practices are secondary and subordinate, causally, to the proximate mechanisms produced by natural selection.

Such views neglect two important features of culture that make it no way*autonomous* but do make it as *powerful* a part of the human evolutionary equation as genes (Richerson & Boyd, 2005). First, cultural evolution is fast and is likely to play an important creative role in genetic evolution. Culture evolves quickly because we use epigenetic rules, and *culturally* transmitted preferences, to invent and chose among cultural variants, whereas genes are restricted to random mutation and natural selection to cause change. It might seem plausible that fast-evolving culture should mainly just protect genes from selection by contrivances like shelters to protect us from the full impact of weather extremes and medicines to treat diseases. Some of this surely goes on, but cultural adventuring also frequently leads to strong selection on the genes that must play many supporting roles in the cultural changes. Cultural adaptations guided in no small part by epigenetic rules will lead humans into new environments where selection will fall on genes. For example, the skeletons of the first modern humans to invade ice age Europe indicate that they were tall, lean Africans, poorly adapted morphologically to the periglacial environments that then prevailed there. They must first have adapted to the cold by making good clothing, sophisticated shelters, and efficient hearths. Later, their bodies became shorter-limbed and stouter to reduce heat loss in the cold climate. Recently, geneticists have developed methods to estimate what genes show signs of recent selection (Sabeti et al., 2006). An especially large number of genes seem to have come under selection in the Holocene as human life was transformed by the cultural evolution of agricultural subsistence systems (Hawks, Wang, Cochran, Harpending, & Woyzis, 2007). The functions of most of these genes are unknown, but a few are well understood adaptations to a new diet rich in plant calories and to the epidemic diseases that evolved to attack denser agricultural populations. Examples include an increase in the copy number of the amylase, a starch digesting enzyme, in agricultural people compared to living arctic hunters with little starch in their historic diet. Many genes for resistance to malaria have evolved in the tropical and subtropical peoples exposed to this family of diseases, which became epidemic when human populations exploded with agricultural subsistence.

Second, consider Ernst Mayr's distinction between ultimate and proximate causes alluded to in the quote above from Carroll's essay. Ultimate causes derive from the history of selection for form and function. *Why* do humans walk upright? Because selection favored a bipedal gait and free hands in our lineage. Proximate causes are the means by which form and function are accomplished. *How* do humans walk upright? The form of our hips, legs, spine and skull are arranged to make efficient striding walking and running possible in our species. Many students of human evolution have argued, like Carroll, Lumsden, and Wilson, that culture is like individual learning, a proximal mechanism for accomplishing genetically evolved functions like avoiding competition by exploiting new habitats. The problem with assigning only a proximal causal role to culture is that culture creates heritable variation. Universal Darwinists, beginning with Donald Campbell's (1965) pioneering ideas, have observed that if culture creates patterns of heritable variation, we can expect that natural selection will act on that variation.

One interesting possibility for selection on culture acting as a major *ultimate*cause in human evolution is our unusual social psychology. Consider how humans differ from other apes and most other animals. We are comparatively docile, are prone form attachments to groups, act altruistically to ingroup members, and use language to formulate and propagate social rules most of us are inclined to obey. A plausible explanation for this oddly prosocial psychology is what Boyd and I call the "tribal social instincts hypothesis" (Richerson & Boyd, 1999). We suppose that tribal scale group selection *acting on cultural variation* in the past has led to the evolution of an innate social psychology adapted to living in tribes. The fact that cultural evolution is relatively fast and that the exchange of ideas is often inhibited by linguistic and other symbolic boundaries means that considerable cultural variation can build up between groups, much more than in the case of genes (Bell, Richerson, & McElreath, 2009). Many evolutionists hold that group selection is implausible because appreciable genetic variation cannot build up between human groups. Selective forces on genes are weak relative to the tendency of migration to erode between group differences. The data for human groups reviewed by Bell et al. suggest this is true for genes in humans but that cultural variation averages at least an order of magnitude greater. In fact, key differences between competing human groups are often social institutions that include strong disincentives for deviating from the norms of the institution. Cultural group selection often seems to involve such institutions (Kelly, 1985), for which differences between the groups are practically categorical. Group selection on cultural variation can thus be a quite strong process. We imagine that some time in our evolutionary, as culture came to play an important adaptive role in our ancestors, selection on cultural variation at the group level began, perhaps at first merely in extended kin groups, to favor simple social norms. These norms would have made these groups slightly more cooperative. Group members who were innately prepared to follow the rules would be rewarded and those that resisted punished. Thus, social selection on human innate psychology slightly favored slightly more affiliative dispositions. Then slightly more prosocial customs could evolve. After repeated rounds of such coevolution humans became capable of living in rather large complex societies. Human social psychology was completely remodeled. The *ultimate* cause of some of our *genetic* predispositions is, this argument holds, selection acting on *culture*.

Now, Lumsden and Wilson's leash metaphor is not so apt. Better to think of a team of horses. The gene-culture team is firmly harnessed together and jointly pulls the human evolutionary coach. No question of *independence* of genes or culture from each other. Every movement by one member of the team is felt by the other. The cultural horse is intrinsically faster and smarter and tends to act as the team leader. But alone her ability to pull the coach is strictly limited. The coach can move any distance only if the genetic horse is healthy and somehow induced to pull in the direction the cultural horse wants to go, which he may often not. His needs have to be well attended to if the team is going to function properly. If the team metaphor is apt, separate sciences of human genes and human society would make as much sense as separate sciences of the left and right horses in teams. Culture is a large part of what human brains and human hands are ultimately evolved to accomplish. Culture is in turn adapted feed the bodies that support brains and hands and to organize them into societies. Culture cannot be reduced to genetics but neither can you cut genes out of the team if you want to understand either proximate or ultimate questions about human life.

The gene-culture conception of human life frees us from the false monotheisms of superorganicism and genetic reductionism. People in this theory actually are what they seem to be to the unaided eye, culture and genes all stirred together in a wonderful systemic mix. The novelist, poet, and painter depict lovely youths displaying hints of attractive secondary sexual characters that in real life lead to the gritty genetic work of sexual reproduction. Yet, they give us not (usually) pornographic stories, verses and drawings but ones more or less chastefully couched in the courtship conventions of a particular time and particular place. Anthropologists teach us that courtship and marriage are usually cultural productions. Human reproduction is in no small measure a community matter, embedded in the social reproduction of a cultural group as well as genetic reproduction of a population. Hence humans often construct corporate kinship systems at some variance with biological kinship. On the other hand, claims that superorganic concepts of kinship have completely freedom to toy with genetic imperatives meet with rather devastating facts (Silk, 1980). Great art is often the product and symbol of cultural groups as in the monumental art of civilizations. Yet, many a stonemason has attracted a wife and supported a family making high art. The low arts sometimes serve quite raw genetic ends, for example, the use of cosmetics to improve upon nature and lure a mate. Food is just fuel for metabolism from the gene's eye point of view. Yet the "food is fuel" concept doesn't begin to do justice to human cookery. Elaborate ceremonial meals are the canvas of human social life. From Mom's Sunday dinners to State Banquets there is hardly a social alliance that is not celebrated with a meal. Think of your favorite historical novel or biography. The genes' business of courtship, reproduction and child rearing takes place embedded in great cultural events, wars, revolutions, colonial expansions, businesses or political parties rising and falling, monumental buildings being constructed, and the like.

To boil it down to sacred dictum: *you humanists shall worship two jealous gods, genes and culture*. The two gods have a long, tight history of intimate moments, some loving, some fractious. If one were to die, so would the other, just as no human can live without a culture or without a genome. If you play favorites, the neglected one will surely spoil your hypothesis or your novel!

References

Bell, A. V., Richerson, P. J., & McElreath, R. (2009). Culture rather than genes provides greater scope for the evolutuon of large-scale human prosociality.*Proceedings of the National Academy of Sciences USA, 106*(42), 17671-17674.

Campbell, D. T. (1965). Variation and selective retention in socio-cultural evolution. In H. R. Barringer, G. I. Blanksten & R. W. Mack (Eds.), *Social Change in Developing Areas: A Reinterpretation of Evolutionary Theory* (1965 ed., pp. 19-49). Cambridge, MA: Schenkman Publishing Company.

Carroll, J. (n.d.). Evolutionary culture theory. *manuscript*.

Cavalli-Sforza, L. L., & Feldman, M. W. (1981). *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton, NJ: Princeton University Press.

Hawks, J., Wang, E. T., Cochran, G. M., Harpending, H. C., & Woyzis, R. K. (2007). Recent acceleration of human adaptive evolution. *Proceedings of the National Academy of Sciences USA, 104*(52), 20753-20758.
Kelly, R. C. (1985). *The Nuer Conquest: The Structure and Development of an Expansionist System*. Ann Arbor: University of Michigan Press.
Kroeber, A. L. (1948). *Anthropology: Culture Patterns and Processes* (New ed.). New York: Harcourt, Brace & World.
Logan, M. H., & Schmittou, D. A. (1998). The uniqueness of Crow art: A glimpse into the history of an embattled people. *Montana: The Magazine of Western History*(summer), 58-71.
Lumsden, C. J., & Wilson, E. O. (1981). *Genes, Mind, and Culture: The Coevolutionary Process*. Cambridge, MA: Harvard University Press.
McElreath, R., Boyd, R., & Richerson, P. J. (2003). Shared norms and the evolution of ethnic markers. *Current Anthropology, 44*, 122-129.
Nisbett, R. E., & Cohen, D. (1996). *Culture of Honor: The Psychology of Violence in the South*. Boulder, CO: Westview Press.
Reich, D. E., Thangaraj, K., Patterson, N. J., Price, A., & Singh, L. (2009). Reconstructing Indian population history. *Nature, 461*, 489-494.
Richerson, P. J., & Boyd, R. (1999). Complex societies – The evolutionary origins of a crude superorganism. *Human Nature-an Interdisciplinary Biosocial Perspective, 10*(3), 253-289.
Richerson, P. J., & Boyd, R. (2005). *Not By Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.
Sabeti, P. C., Schaffner, S. F., Fry, B., Lohmueller, J., Varilly, P., Shamovsky, O., et al. (2006). Positive natural selection in the human lineage. *Science*, *312*, 1615-1620 + Supplementary Material online.
Silk, J. B. (1980). Adoption and Kinship in Oceania. *American Anthropologist: . 82*(4), 799-820.
Tomasello, M. (2008). *The Origins of Human Communication*. Cambridge MA: MIT Press.

****

RESPONSES to Peter J. Richerson

1. Joseph Carroll's Response to Pete Richerson

Pete Richerson makes a case for the relative autonomy of "memes." To give a wider context for the difference he adumbrates between his own views and those exemplified by Lumsden and Wilson, me, and other proponents of "gene-culture co-evolution," I'll cite here a passage from a symposium debate on cultural evolution. I wrote an article titled "An Evolutionary Paradigm for Literary Study." The article, responses from thirty-five scholars, and my rejoinder were published in the journal *Style* (vol. 42, numbers one and two, 2008). The passage below is from my rejoinder to the responses.

Richerson and Boyd develop arguments both for gene-culture co-evolution and for cultural evolution, but they identify no significant cultural structure that is not constrained by evolved dispositions. Their views on gene-culture co-evolution are widely shared by other evolutionary theorists. Their arguments for "cultural evolution" remain more speculative and controversial [2]. . . .

We should by no means neglect group-level processes. The common lexicon, to take an obvious example, contains the collective and shared intelligence of untold generations, a wealth of "knowledge" that could not possibly be generated in the life of any individual or even any succession of individuals. Culture extends the imaginative life of each of us far beyond the boundaries of individual experience, and in that crucial respect, it separates us from the other animals, even those animals that are capable of empathy for the other animals with which they come directly into contact. Even so, in taking due heed of the collective cultural mind, we need to be careful not to make the simple mistake of supposing that Dawkins' notion of memes offers the best available way of thinking about culture. Dawkins' notion is catchy in part because of the term itself, selected, for that purpose, with all the shrewd care an advertising executive gives to the selection of words in a jingle. At a deeper level, the notion of "memes" is catchy because it appeals to our natural cognitive disposition to handle difficult theoretical issues by thinking in analogies. Genes vary and are selected and inherited. So then might also "memes," we think, and in so thinking are led down many a blind alley shrouded in mist.

Memes possess no internal replicative mechanism, and no one has yet been able to identify structural principles for memes that would approximate to the sharply demarcated molecular structure of genes. Moreover, genes and organisms are tightly locked into functional interdependence. The organization of physiological processes in organisms displays a deep systemic coherence regulated by astonishingly complex genetic interactions. Specific genes are functionally organized to replicate organisms of a specific type, and specific types of organisms are functionally organized to replicate specific genes. The relation between memes and human organisms constitutes no such functionally integrated structure in a replicative process. Specific ideas and cultural practices (memes) might or might not contribute to the inclusive fitness of individual human organisms, but human organisms are not functionally organized to replicate specific memes. Throughout its life, an individual human organism retains the same genetic makeup but can undergo many profound changes in ideas and cultural practices. In these various ways, then, genes and memes display fundamental structural differences. As a result, using the analogy between genes and memes as a general heuristic for thinking about culture is almost certain to lure theorists into problematic speculation (*Style*, 42 [2008]: 320-21).

****

In this current essay, Pete objects to “assigning only a proximal causal role to culture.” In my understanding, “ultimate” cause in evolution refers not to phylogeny (“the history of selection for form and function”) but rather to inclusive fitness. Proximal causes do refer to what Tinbergen would call mechanisms that have evolved to produce fitness. Culture would be a proximal cause, as would, for instance, male dispositions for selecting healthy female mates, female dispositions for selecting males with resources, and fight/flight reactions designed to avoid danger or resist predation.

Theorists of gene-culture co-evolution acknowledge that culture can have major causal effects on form and function, as, for instance, cooking has done. Cooking is a cultural technology but has fundamentally altered the hominid gut and brain. Culture and genes have co-evolved, each influencing the other, with culture (cooking) producing a bigger brain, and the bigger brain producing yet more culture.

Genes can replicate without cultural carriers, as indeed they do in most species, from bacteria up through most mammals. Cultural practices or “memes,” in contrast, cannot survive independently of genetic carriers. Cultural practices can no doubt function for short periods in ways that contravene fitness (the replication of genes)—Richerson and Boyd make much of one such instance in*Not by Genes Alone*—but a cultural practice that contravened inclusive fitness over generations, within a closed population, would ultimately be self-eliminating. By destroying its carrier, it would destroy itself. Celibate utopian communities offer a simple and striking example. Unless their membership is constantly replenished from outside the community, they necessarily expire within a single generation (barring, of course, the sort of cheating that eventuates in miraculous Virgin Births).

2. Diana Kornbrot’s Response to Pete Richerson

Richerson argues compellingly against the super organism view of culture. It is also unarguable that culture effects biology in the sense that infant mortality and life expectancy co vary with culture.

However Richerson argues for some much stronger claims. Firstly he argues that genes and culture co-evolve. The evidence for this claim in its strong form is weak. I know of no evidence that babies who are adopted from a gene pool of one culture to a parent of another are any more or less successful than babies raised in the culture of their gene pool. On the contrary, it appears that the human species is homogenous relative to other species. Differences in mathematical, musical, literary or leadership talents within any human race far outstrip any differences between sub-populations [races or identifiable gene pools]. On the other hand, the co-evolution of genes for adult milk digestion and cattle herding in Eurasian populations is, of course, a widely cited example of co-evolution. What other examples exist? What evidence exists to support the claim that different cultures [however defined] are associated with different gene pools for social or cognitive traits?

The second strong claim is that cultural evolution is faster than genetic evolution. Again the evidence is controversial. Farming took an awful long time to get adopted, while sickle cell genes against malaria may have quite quickly reached equilibrium proportions. As far as I know there are NO genes that reliably distinguish current human populations from those that lived 35k years ago. Just as there are NO cultural societal organisations that have totally disappeared. Is evolution simply acquiring new genes or cultural modes; or is it the complete take over by some new gene [e.g. for language] or cultural mode [e.g. agriculture]? What is the evidence that cultural evolution is *always* faster?

****

REJOINDER
by Peter J. Richerson

Response to Joe Carroll's Critique

I tried to anticipate Joe's argument by explicitly disavowing the idea that culture is "autonomous." Neither culture nor genes is autonomous. They are inextricably linked in the development of human behavior. Their evolution is intimately intertwined by gene-culture coevolution. Joe correctly points out that human culture can't survive without genes. But neither can *human* genes exist without culture! Humans are completely dependent upon their cultures to teach them how earn a living, conduct their social life, speak their language, and so many other things. For a considerable stretch of the evolution of our lineage, perhaps going back to the first stone tool traditions, human adaptations have depended crucially on culture.

In our 2005 book we invited readers to imagine they were plunked down in the Sonoran Desert of southern Arizona with six months of supplies and a mission to call up their inner hunter-gather in order to make a living when the six months were up. We reckon that no one could learn enough to survive as a hunter-gatherer in an unfamiliar environment on their own. If instructed by knowledgeable natives, you might survive, but even then, six months is not much time to pick up the lore of the desert. Hilliard Kaplan, Kim Hill and their colleagues have assembled data from hunting and gathering societies that show that young humans need about 20 years to learn enough to begin to have a net positive contribution to their subsistence economy and about 30 years to reach their peak of productivity (Gurven et al., 2006, Kaplan et al., 2000). The 1860-1 Burke-Wills expedition explored inland Australia from north to south west of the Great Dividing Range. Half way home, the expedition ran out of supplies. They turned to the natives for assistance and were taught to extract starch from a local plant, nardoo, that the natives used as a staple. Unfortunately Burke and Wills either did not learn the whole recipe or chose to leave out some critical step. Many plant staples have to be carefully detoxified to make them edible. In this case, the nardoo plant contained a vitamin B1 antagonist. Burke and Wills died lingering deaths due to beri-beri trying to live on a plant the natives happily used in quantity with proper detoxification. A third member of the expedition survived after the natives took him in.

The crux of the issue can be most easily seen by going back to Darwinian fundamentals. Selection doesn't act directly on genes, it acts on phenotypes. The evolutionary *response* to selection is a product of the phenotypic effect of selection times the additive heritable variance of the phenotypic trait. Note that this way of expressing how selection acts is true by definition. It is a mathematical expression of Darwin's original formulation. Darwin's own ideas about inheritance were rudimentary to say the least. Darwin got as far as he did because genes are not necessary for the action of selection. They are merely one way to generate heritable variation. Culture is another way of generating heritable variation. Joe's rhetoric notwithstanding, this is not a matter of analogy at all.

Burke and Willis had a lethal cultural variant for nardoo processing. The natives had evolved a processing procedure that allowed them to eat it. The natives' procedure may well have been shaped in part by natural selection. Over the years, families with inadequate procedures for detoxifying nardoo would have tended to suffer from beri-beri and hence from selection against their procedure. During dearths in which nardoo was a particularly important staple, families with adequate procedures would have done well, and those with poor ones poorly. Over many generations, native peoples all around the world have come to have pretty well adapted procedures to exploit tricky resources like nardoo. Now, cultural evolution is not entirely dependent on natural selection. Ailing families taken in by a successful family during a dearth might have modified their nardoo detoxification procedure to resemble that of their successful hosts. "Imitate the successful" is a useful general rule for biasing cultural transmission, one that turns up in the laboratory and in the field (McElreath et al., 2008). But just because we have genetically (or culturally) specified transmission biases does not automatically mean that selection is absent. In cultural evolution, as in genetic evolution, realized change is the net result of the interaction of several forces acting simultaneously. Just as ordinary selection, sexual selection, mutation, and drift might all act to a measurable degree on a genetic locus, so too can selection and transmission biases both act on cultural variation.

I don't much care for the term "meme" for the same reason that Joe dislikes it. It implies a close analogy between genes and cultural variants. It also tends to imply that an inheritance system has to be quite gene-like to count as an entity that can behave in Darwinian ways. None of these things is necessarily true (Henrich et al., 2008). The "gene" itself is rather mythologized in discussions like this one. The fact is that most phenotypic traits upon which

selection falls are not “genetic” in any simple sense, resembling simplified 20th Century textbook treatments. In the age of genomics, such accounts need substantial revision. In some cases, such as the famous sickle cell gene that provides protection against falciparum malaria when heterozygous, the connection is simple enough. But most genes act on phenotype in concert with many other genes in complex developmental and regulatory circuits, circuits that modern developmental biologists are just beginning to understand. The modern field of “evo-devo” has grown up to get at the way in which developmental processes connect genes to phenotypes, and how developmental processes influence the evolutionary processes. One of the latest stories is that “epigenetic” variation seems to be transmitted from one generation to the next (Jablonka and Raz, 2009). Epigenetic variation in the first instance is the changes in gene expression that permit different cells in the body to behave very differently. Thus, your liver cells and brain cells have the same basic DNA they both acquire from their ancestral fertilized egg. But during development many differences arise between cell lineages in which genes are actually active, and how active. These differences result in highly specialized nerve cells and liver cells (both composed of a number of subtypes). The epigenetic system is open to environmental influences so that development can adjust on the fly in the face of environmental contingencies. The genes in the egg and the sperm contain epigenetic markers that quite possibly may turn out to constitute a rather large system for the inheritance of acquired variation. The 21st Century genomics revolution has put back into play some of the dogmas of 20th Century genetics as well as making the “gene” a very complex and multi-faceted entity.
Joe’s point that the cultural inheritance system is messy and poorly understood is fair enough, but his implication that the genetic system is neat and well understood is a victim of the genomics revolution. I have recently spent some time educating myself regarding its evolutionary implications, and, believe me, it will make your head spin! The genetic system is extremely messy. One thing that mystifies me is the seeming fact that both regulatory and structural genes seem to be extensively reused for different purposes in different tissues. This would seem to be a recipe for making evolution impossible. A mutation that is favored for its function in one tissue at one time seems likely to have random effects in other tissues and other times. Most random changes would presumably be dysfunctional, as mutations usually are. If so, a gene responding to selection for one function would be counter-selected for many other functions. Natural selection simply bogs down in the complexity of it all! We know that selection does work from studying evolution at the phenotypic level, but it is still not clear how genes are organized to create the additive heritable variation the selection requires. Joe’s picture of specific genes functionally organized to replicate organisms of a specific type, and these specific organisms to replicate specific genes, is misleading.

All that said, at least some examples of cultural transmission are tolerably well understood and are rather textbook-gene-like in their coding precision. Take word learning.

Developmental linguists have taught us a lot about how kids learn the meanings of words (Bloom, 2000). In this case developmental linguists have described in some detail the mechanism by which the meaning of words is rather faithfully replicated from one generation to the next. As regards common words known by most adult speakers of a language, differences between speakers in the meaning of words is modest. Words like "finger", "dog," and "bachelor" are a lot like conserved genes; within a given language, the root meanings of these words are essentially the same for a large majority speakers. Many genes are duplicated, and the duplicates often take on new functions. So it is with words. They can take on additional meanings. Thus "finger" in colloquial American English has the meaning "rude gesture with the middle finger." Speakers who command both variant meanings will not have much trouble deciding which is correct in a given sentence. As with genes, variation exists at all level. Individuals have minor variations in the speech that linguists call "idiolects". Then there are dialects, languages, language families. The processes of language change are tolerably well understood by sociolinguists and historical linguists. Historical linguistics differs from most other realms of culture in that historical linguists were already pretty sophisticated evolutionists in the late 18th Century. Unabridged dictionaries for some languages long ago described the evolution of every word in a language. Had people interested in other domains of culture embraced evolutionary thinking as long ago as historical linguists, our conversation here might have seemed unsophisticated in 1900.

An interesting side note. Noam Chomsky once argued that the syntax of languages are rather tightly controlled by complex innate genetic language acquisition device, the "principles and parameters" model that many of us know from Steven Pinker's book the *Language Instinct*. This position has been abandoned by Chomsky and most of its former protagonists. Linguists like Michael Tomasello, in his recent book *Origins of Human Communication*, have built a case for a much stronger cultural component than was commonly imagined 20 years ago.

Culture, via gene-culture coevolution, plays an important role in genetic evolution in humans via two mechanisms, one a special case of the other. The general mechanism is called the Baldwin Effect after the late 19th Century psychologist James Mark Baldwin (1896). Baldwin was concerned to revise Darwin's picture of inheritance in light of the emerging consensus around August Weismann's theory of the separation of the germ line from the soma. Even before the rediscovery of genes around 1900, Darwin's espousal of the inheritance of acquired variation was in trouble among biologists of the day. If inheritance passed down only through germ line cells, the mechanics of the inheritance of acquired variation looked problematical to Weismann and other biologists. Baldwin elaborated a mechanism by which acquired variation could generate selection pressure without the need for literal transmission of acquired variation. Take a case such as the introduction of a species to a new continent. In genetic terms, the introduced population might well be quite ill adapted to the new environment. But smart animals could use individual learning to adapt to the new environment well enough to survive and reproduce. Heritable variation in the survivors would now be exposed to selection, and the population's organic inheritance—now we'd say the population's genes—would begin to change. The individual learning system would tend to guide the adaptive process in detail. If the population happened to learn that a certain fruit was edible, genetic specializations to recognize, process, and digest that fruit might lead it to specialize on that fruit. The cultural transmission of adaptations put the Baldwin Effect on steroids. The human ability to create complex cultural adaptations has led human populations to occupy some extremely rough places given our ancestry as a tropical ape. Finely tailored clothing, seaworthy skin boats and a considerable number of other culturally transmitted technological and social adaptations allowed Inuit and Inupiat peoples to live above the Arctic Circle. Geneticists have already documented many adaptations to the far-flung environments into which people dispersed and to the diverse subsistence systems we have deployed in doing so. For example, humans that live in cold environments evolve stocky physiques, including Neandertals and many modern people such as those that live in the Arctic, Himalayas, and Andes. Without cultural adaptations as a bridge, humans would simply never have made it to frigid environments in the first place. This version of gene-culture coevolution is not very controversial I think.

The specific idea that cultural variation can respond directly to selection, and then influence genes by the Baldwin Effect, is harder for many people to swallow. I reiterate that entertaining this idea is just to walk down Darwin's straight and narrow path. It all boils down to heritable variation for fitness. Richard Dawkins followed this path in the *Selfish Gene* where he introduced the concept of memes. One of the problems with the meme concept as it evolved is that users of the term focused far too heavily on the selfish potential of memes. But I think it is near to undeniable that cultural variants are sometimes selected to become selfish pathogens along the lines that Dawkins suggested. Since some cultural variants can spread rapidly among people, as in the case of fads, they rather resemble the life cycle of a viral or bacterial pathogen. Many phenomena, such as heroin epidemics, appear to be examples of cultural pathogens. My colleagues and I have devoted a lot of effort to dissecting the modern demographic transition to low, often below replacement, fertility in many countries (Newson et al., 2007), but this is only the tip of the iceberg. Any parent who sends their kids to school observes that the come home with colds, flus and bad habits. The extremes of carefully crafted cultural isolation practiced by the North American Anabaptists is testimony to how hard it is to keep modern ideas out of a subculture. Just having a pronatalist ideology helps only marginally.

Joe is quite correct to point out that if selfish memes were all that human culture did, the system would go extinct. The selfish meme enthusiasts can't be entirely correct. Clearly cultural traditions are often highly adaptive in the inclusive fitness maximizing sense. The example of the adaptive technology of the Arctic peoples can be replicated endlessly.

Cultural ecologists, archaeologists, geographers, and economic historians have documented a very large number of traditional subsistence systems ingeniously adapted to demanding environments. Last year I had the opportunity to take an informal field trip over the Atlas Mountains to the edge of the Sahara. The modest rivers flowing out of the mountains supported immense date groves. In the understory of the palms many other crops were being grown—wheat maize, alfalfa, henna, melons, grapes, okra. The irrigation water pumped from shallow wells was so salty that white crusts were often visible on the soil surface where evaporation caused it to precipitate. Salt is the arid land irrigator's potentially mortal enemy. Even tolerant crops like dates have their limits. The Berber farmers of Morocco are managing well in the face of the challenge of limited, salty water. Everywhere I've had a chance to observe traditional subsistence farmers, they look like they are doing a competent job. Subsistence farmers often lead tough lives, and ones who use poor practices are liable to have fewer offspring than those who use good ones. The trick is that, in addition to selection, individuals have some control over the culture they acquire, unlike the genetic case. That is what typically makes cultural evolution so much swifter than genetic evolution. At least in the world of mathematical models, using decision rules like "imitate the successful" cause the rapid evolution of cultural adaptations. This rule, and others that we have investigated theoretically, are empirically very well grounded in empirical studies of the diffusion of innovations, the study of dialect microevolution, and similar literatures. The cultural system could prevent the spread of most pathologies by conservatively limiting cultural transmission to the parent child pathway, shadowing the transmission of genes. The price to be paid would be the inability to use epigenetic rules like "imitate the successful" to acquire useful ideas. There is a tradeoff, and the models suggest that you can easily be too conservative. If other people take risks in using decision rules to ferret out the latest techniques in salt management, and pest control, and the latest varieties of crops, you are liable to be outcompeted. The risk of picking up a bad habit, like the risk of importing a crop pest while trying out a new cultivar, is just a risk you take in this culture business. Selection on genes for decision rules has likely shaved this tradeoff as finely as possible!

I think Joe misunderstands ultimate causality. Anchoring the concept to inclusive fitness, rather than to effects on selection on heritable variation, is not all that secure. In the case of genes, accounting for all the costs and benefits of altruistic acts is hard in most realistic cases. For example, the fact that kin stick together makes kin altruism possible, yet that will also tend to make kin competitors. In some simple models, these two effects balance and the kin altruism effect evaporates (Taylor, 1992). Analysis deriving from kin selection is thus highly model bound (Taylor and Grafen, 2010). In the case of culture, the analog of kinship is very hard to estimate. Having two parents with equal genetic contribution makes the calculation of relatedness easy. In cultural transmission, one, two, a few, or many people in your social network are possible sources of culture. People may use different parts of their network for different cultural domains. No one has proposed a way to estimate cultural relatedness in the face of such problems. But if we ground our analysis in heritable variation and selection directly we only depend on the canonical formula describing selection. The evidence, reviewed in Rob Boyd's and my (2005) book, is that plenty of heritable variation exists at the group level to support cultural group selection (see also Bell et al., 2009). If selection has played on such variation, and if it exists, selection will almost surely have done so, then the ultimate explanation for a pattern of behavior like human cooperation would be selection acting on culture directly and on genes indirectly via gene-culture coevolution.

Some of Joe's humanistic colleagues say things about culture that make me feel like I'm being "led down many a blind alley shrouded in mist." Joe seems convinced that the contemporary humanist critique of a science of culture is correct and therefore we have to relate everything to genes if we are to avoid the confusion and error. My contention is that culture and cultural evolution are as amenable to mathematical analysis and critical empirical investigation as genes. To my way of thinking, culture is anything but a misty alley. Culture is hard heritable variation on the ground. It sometimes throws its weight around in the coevolutionary equation. If you think culture misty, imagine something like this: You are an Anglo-American in hiding in an Arab country during anti-American riots organized by jihadis. You have two old friends offering to help you cross through the jihadi checkpoint between your temporary hiding place and the airport, where flights for refugees are taking people like you home. You are certain that neither is insincere about wanting to get you through the checkpoint. One is a long time expat Anglo-American, a convert to Islam, a fluent Arabic speaker, and rather knowledgeable of, and somewhat sympathetic to, the jihadis' cause. The other is a person whose parents came from the Arab country who has returned for a tourist visit. He has the right skin tone, but speaks broken Arabic, has no local knowledge, and little appreciation or sympathy for the jihadis' cause. Life or death decision. Who is the best bet to get you to the airport?

References

Baldwin, James Mark. 1896. A new factor in evolution. *American Naturalist*30:441-457, 536-554.

Bell, Adrian V., Richerson, Peter J., and McElreath, Richard. 2009. Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proceeding of the National Academy of Sciences USA* 106:17671-17674.

Bloom, Paul. 2000. *How Children Learn the Meanings of Words*. Cambridge, MA: MIT Press.

Gurven, Michael, Kaplan, Hillard, and Gutierrez, Maguin. 2006. How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span. *Journal of Human Evolution* 51:454-470.

Henrich, Joseph, Boyd, Robert, and Richerson, Peter J. 2008. Five misundertandings about cultural evolution. *Human Nature* 19:119-137.

Jablonka, Eva, and Raz, Gal. 2009. Transgenerational epigenetic inheritance: prevalence mechanisms, and implications for the study of heredity and evolution.*Quarterly Review of Biology* 84:131-176.

Kaplan, H., Hill, K., Lancaster, J., and Hurtado, A. M. 2000. A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology* 9:156-185.

McElreath, Richard, Bell, Adrian V., Efferson, Charles, Lubell, Mark, Richerson, Peter J., and Waring, Timothy. 2008. Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. *Philosophical Transactions of the Royal Society B* 363:3515-3528.

Newson, Lesley, Postmes, Tom, Lea, S.E.G., Webley, Paul M., Richerson, Peter J., and McElreath, Richard. 2007. Influences on communication about reproduction: The cultural evolution of low fertility. *Evolution & Human Behavior* 28:199-210.

Richerson, Peter J., and Boyd, Robert. 2005. *Not By Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.

Taylor, Peter D. 1992. Inclusive fitness in a homogeneous environment.*Proceedings of the Royal Society of London B* 249:299-302.

Taylor, Peter D., and Grafen, A. 2010. Relatedness with different interaction configurations. *Journal of Theoretical Biology* 262:391-397.

Response to Diana Kornbrot's critique

Most of the gene-culture coevolution that my colleagues and I think drove the evolution of our species is ancient and relevant to the whole species. These cases have nothing to do with differences between living cultures. For example, in a series of papers and books, we have argued that both theoretical models and much evidence support the idea that humans were subject to group selection on cultural variation at the level of tribes (e.g. Bell et al., 2009, Boyd and Richerson, 1982, Boyd and Richerson, 2008, Henrich, 2004, Soltis et al., 1995). As the human capacity for culture evolved deep in the Pleistocene, at some point it became rich enough to allow the elaboration of primitive social institutions. A number of features of cultural variation allow it to support more variation between groups that can genetic variation. As primitive institutions came under selection to enlarge the scope of cooperation beyond what could be supported by kin selection, behaving according to cooperative rules would have enjoyed social support and behavior not consistent with prevailing rules would have been sanctioned. Genotypes that couldn't conform to cultural norms would decline in frequency and ones that could would increase. Over repeated rounds of such coevolution, the social psychology of evolving hominins became capable of large scale cooperation with non kin. At least some other authors have found this hypothesis plausible (e.g. Fehr and Fischbacher, 2003). Almost everyone who has thought about language evolution imagines that as culture capacities arose, some simple form of symbolic language became transmitted culturally. To the extent that language was useful, individuals who could learn and use a more complex language would have been favored by selection. Repeated rounds of gene-culture coevolution would have eventually led to modern language capabilities (e.g. Pinker and Bloom, 1990, Tomasello, 2008). The idea that tool traditions exerted coevolutionary pressure on human brain size is one I heard in my 1st year anthropology class (Washburn, 1959).

As I mentioned in my essay, recent genomic studies suggest that a fairly large number of genes underwent selection in the wake of the evolution of agriculture in the middle and early Holocene (see the Sabeti et al. and Hawks et al. references my original essay). These include the case of adult lactase secretion in dairying populations, as Kornbrot mentions. Other examples include many hemoglobin polymorphisms that are protective against malaria, amylase (starch digesting enzyme) copy number increase in agricultural populations. It is still early days in the genomics revolution. So far, large scale statistical scans of sequence data for genes under selection has turned up many more candidates. But the function of the selected variants of the bulk of these genes remains to be worked out. While one has to be careful at this stage, the evidence for a strong coevolutionary response to the evolution of agriculture is fairly strong (Laland et al., 2010). The genomic evidence for more ancient coevolution is still scanty but also promising (Richerson and Boyd, 2010). For example, pale skin evolved multiple times by slightly different molecular mechanisms as human populations moved from the tropics to temperate and subarctic conditions (Jablonski, 2010). Protection of the skin from UV damage is a priority in the tropics, favoring heavily pigmented skin. Vitamin D photosynthesis is a problem in low sunlight environments, favoring lightly pigmented skin.

The recently evolved genetic differences between human populations should not be exaggerated. We are still a single species and all living populations share a recent African ancestry. As Kornbrot says, the total amount of genetic variation in humans is relatively modest compared to most other mammals including chimpanzees. By contrast, our cultural variation is enormously greater than in any other species. Most of the genetic variation between human populations owes to drift experienced in multiple founder effects as humans spread out of Africa about 60,000 years ago (Lawson Handley et al., 2007). Still, the importance of the genes that adapt us to the many environments we inhabit, to the diets made possible by agriculture, and to the diseases made possible by agriculture, is by no means trivial. The historian Crosby (1986) noted that European expansion 900-1900 CE was mainly successful in regions with climates similar to Europe where our familiar plants and animals could thrive. European expansion was especially easy in the New World, Australia, and New Zealand where the native peoples were highly susceptible to diseases introduced by Europeans. The expansion into regions with serious diseases to which Europeans were susceptible, especially the Old World tropics, was quite unsuccessful. Given modern medicine, nutritional knowledge, good shelter and clothing, and the money to buy medicines and imported goods, it is possible for immigrants and adoptees to move into any environment. Before these things were available, long distance movement was dangerous.

The idea that culture normally evolves faster than genes is based on the important differences between genetic and cultural evolutionary processes. Culture evolves not only by random variation and selection but also by the non-random variation (learning, invention, and creative thought) and to using rules like “imitate the successful” to acquire cultural variants. Humans are embedded in social networks with many sources of new ideas besides parents. Apparently useful cultural variants, unlike genes, can spread rapidly from person to person following the links in such networks. Think of the cellular telephone’s phenomenal spread in recent years. Mathematical models suggest that rapid tracking of varying environments is what culture is an adaptation to do. The empirical evidence seems to support this idea. The heavy dependence of humans on culture evolved under the highly variable climate regime of the late Pleistocene. The evolution of agriculture may not seem terribly swift, but I’m impressed that in the 11,500 years of the Holocene human populations evolved myriad different socioeconomic systems adapted to nearly every terrestrial and near-shore aquatic habitat on earth, outside of Antarctica. Some human diets are almost entirely carnivorous while others are completely vegetarian. Many people today live in societies more complex than even the most complex social insect societies. Even Holocene hunter-gatherers were different from and much more diverse ecologically that their Middle and Late Paleolithic ancestors. I don’t know of any gene-based adaptive radiation that compares to that of Holocene humans in its rapid invasion of such a diversity of habitats using cultural adaptations.

Archaeologists and historians are unfortunately not much given to estimating rates of change so a direct comparison with typical genetic rates of change is not possible. Historical linguists have done much work along these lines, recently using methods borrowed directly from evolutionary biology (e.g. Gray et al., 2009). The time scale over which an inheritance system changes enough to erase its history is one index of the rate of evolution. Language trees for the Austronesian and Indo-European language families suggest that last common ancestors that spoke Proto-Austronesian and Proto-Indo-European lived about 5,500 years ago and 8,700 years age, respectively. Languages were almost certainly spoken tens of or even hundreds of thousands of years earlier than these dates. But languages change so rapidly that nearly every element becomes different over time scales of 5-10,000 years, wiping out the older history. The deeper history of languages cannot be reconstructed. Mitochondrial genomes are very fast evolving by genetic standards and are used to trace the history of human populations since the migration out of Africa about 60,000 years ago. Much deeper than that, the mitochondrial trace of history in our lineage ceases, but

Neandertal mitochondria are distinctively different from modern human ones, based on fossil DNA extracted from bones. The nuclear genes are useful for tracing historical relationships back towards the origins of life. Actually, ALL modern populations of people (except close neighbors) can easily be distinguished genetically from each other and from populations 35,000 years ago. Contrariwise, ALL information about cultural systems is wiped out on the time scale of 10,000 years or less, except what we can recover from the paleoanthropological record. It is true that under strong selection, important genetic changes can occur in a few generations. Cultural traits can surely change little on this time scale. So it is fair to say that there is no doubt some overlap in the rates of evolution of genes and culture.

References

Bell, Adrian V., Richerson, Peter J., and McElreath, Richard. 2009. Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proceeding of the National Academy of Sciences USA* 106:17671-17674.

Boyd, Robert, and Richerson, Peter J. 1982. Cultural transmission and the evolution of cooperative behavior. *Human Ecology* 10:325-351.

Boyd, Robert, and Richerson, Peter J. 2008. Gen-culture coevolution and the evolution of social institutions. In *Better Than Consciousness? Decision Making, the Human Mind, and Implications for Institutions*, eds. Christophe Engle and Wolf Singer, 305-323. Cambridge MA: MIT.

Crosby, Alfred W. 1986. *Ecological Imperialism: The Biological Expansion of Europe, 900-1900*: Studies in environment and history. Cambridge: Cambridge University Press.

Fehr, Ernst, and Fischbacher, Urs. 2003. The nature of human altruism. *Nature*425:785-791.

Gray, R. D., Drummond, A. J., and Greenhill, S. J. 2009. Language phylogenies reveal expansion pulses and pauses in Pacific settlement [January 23, 2009].*Science* 323:479-483.

Henrich, Joseph. 2004. Cultural group selection, coevolutionary processes and large-scale cooperation. A target article with commentary. *Journal of Economic Behavior and Organization* 53:3-143.

Jablonski, Nina. 2010. The skin that makes us human. *Proceedings of the National Academy of Sciences USA* This Special Issue.

Laland, Kevin N., Odling-Smee, John, and Myles, Sean. 2010. How culture shaped the human genome: bringing genetics and the human sciences together.*Nature Reviews Genetics* 11:137-148.

Lawson Handley, Lori J., Manica, Ardrea, Goudet, Jerome, and Balloux, Francois. 2007. Going the distance: Human population genetics in a clinal world.*Trends in Genetics* 23:432-
.

Pinker, S., and Bloom, P. 1990. Natural language and natural selection [1990].*Behavioral and Brain Sciences* 13:707-784.
Richerson, Peter J., and Boyd, Robert. 2010. Gene-culture coevolution in the age of genomics. *Proceedings National Academy of Science USA* In press.
Soltis, Joseph, Boyd, Robert, and Richerson, Peter J. 1995. Can group-functional behaviors evolve by cultural group election? An empirical test. *Current Anthropology* 36:473-494.
Tomasello, Michael. 2008. *Origins of Human Communication*: Jean Nicod Lectures. Cambridge MA: MIT Press.
Washburn, S.L. 1959. Speculations on the interrelations of the history of tools and biological evolution. *Human Biology* 31:21-31.

Notes

---

[1] Note that the shoe could have turned out to be on the other foot. Many late 19th and early 20th Century biologists also believed that Darwin's ideas were erroneous; Darwinian methods were not firmly the centerpiece of the theory of genetic evolution until the 1930s. Meanwhile the emerging social sciences had influential Darwinians until around 1900.
[2] For a taxonomic analysis of the theoretical options available within gene-culture co-evolution and cultural evolution, see Geoffrey M. Hodgson, "Taxonomizing the Relationship between Biology and Economics: A Very Long Engagement," *Journal of Bioeconomics* 9 (2007): 169-85.