AHR Roundtable
Coevolutionary History

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COEVOLUTION HAS BEEN ONE OF THE most important processes in history. Yet despite its ability to lead to new interpretations of well-studied events, it has also been one of the least appreciated. Its low profile is due partly to the disciplinary divide between human history and natural science, partly to historians' reliance on sources that did not recognize it, and partly to the ease with which one can take its products for granted.[1] But look at some of its effects. By ushering in the Agricultural Revolution, it was responsible for the transition from prehistory to history (traditionally defined). It was the primary means of increasing physical power for almost all of history. It helped spark, and sustained, the Industrial Revolution. It helped human numbers to soar from 954 million to 7.1 billion in the past two hundred years. It was re-

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[1] Elsewhere, I have encouraged historians and evolutionary biologists to join forces in a research program known as evolutionary history. Edmund Russell, *Evolutionary History: Uniting History and Biology to Understand Life on Earth* (New York, 2011); Russell, "Evolutionary History: Prospectus for a New Field," *Environmental History* 8, no. 2 (2003): 204–228; Russell, "Introduction: The Garden in the Machine: Toward an Evolutionary History of Technology," in Susan R. Schrepfer and Philip Scranton, eds., *Industrializing Organisms: Introducing Evolutionary History* (New York, 2004), 1–16. One of several examples of an earlier use of evolutionary ideas in history is J. R. McNeill, *Something New under the Sun: An Environmental History of the Twentieth-Century World* (New York, 2000), xxii–xxiv. As research programs, evolutionary and coevolutionary history can contribute to any field that studies interactions among human and non-human populations, such as environmental history, agricultural history, food history, animal history, and medical history. See Donald Worster, "Historians and Nature," *American Scholar*, Spring 2010, http://theamericanscholar.org/historians-and-nature/; Christian W. Simon, "Evolutionary History: Trends in Contemporary History of the Historiography of Environment," *Storia della Storiografia* 47, no. 1 (2005): 90–112; Sam White, "From Globalized Pig Breeds to Capitalist Pigs: A Study in Animal Cultures and Evolutionary History," *Environmental History* 16, no. 1 (2011): 94–120; Christophe Bonneuil and François Hochereau, "Gouverner le 'progrès génétique,'" *Annales: Histoire, Sciences sociales* 63, no. 6 (2008): 1305–1340; Schrepfer and Scranton, *Industrializing Organisms*. Biologists, too, have urged a synthesis of their discipline and history. They have embraced the idea of cultural evolution as a bridge and explicitly rejected genetic determinism. Paul R. Ehrlich and Anne H. Ehrlich, *The Dominant Animal: Human Evolution and the Environment* (Washington, D.C., 2008).

sponsible for the food people ate, the way they made their living, the diseases they suffered, and the technology they developed. Not a trivial list of accomplishments.[2]

Coevolution is the process in which populations of different species evolve repeatedly in response to each other. The key ideas are reciprocity and continual change. Population A leads population B to evolve, the new version of population B leads population A to evolve, the new version of population A leads population B to evolve again, and so on through time. The idea of coevolution was first developed to explain why flowers seemed perfectly designed for the specific species of insects that pollinated them. Most likely, the traits of populations of plants and the traits of populations of their insect pollinators changed repeatedly in response to each other. Other examples of coevolution include fleet predators and prey (when one became faster, the other had to become faster, too, to survive) and the development of leguminous plants with nitrogen-fixing bacteria that inhabit their roots.[3]

Historians would have nothing to study without coevolution, because human beings probably would not exist. We might think of our bodies as entirely human, but it would be more accurate to think of them as porous ecosystems swarming with bacteria, fungi, protozoa, and viruses. Symbionts in our guts, hair, skin, and mouths help us survive by digesting food and protecting us from disease. They make up 90 percent of the cells in our bodies. Human cells are larger than bacterial and fungal cells, so our bodies are more human than not when it comes to volume, but our bodies are more bacterial than human when it comes to numbers. We have a lot to learn about human microbiota, the extent of which has only recently been documented, but evidence suggests that coevolution has adapted us to our microbiota and vice versa.[4] (For more on this topic, see Julia Adeney Thomas's essay in this roundtable.)

Coevolution in history occurred when populations of people and of non-human species repeatedly shaped each other's traits over time. Coevolution is an evolutionary process, and the idea that people can prompt evolution is unfamiliar to many scholars outside biology, so it is important to clarify the meaning of evolution before returning to coevolution. A popular definition equates evolution with the development of new species over millions of years through natural selection. If accurate, this definition would disqualify people as evolutionary actors. Few of us can identify a species that people created. Our species could not affect other species over millions

[2] Massimo Livi-Bacci, *A Concise History of World Population*, trans. Carl Ipsen, 5th ed. (Oxford, 2012), 25.

[3] Paul R. Ehrlich and Peter H. Raven, "Butterflies and Plants: A Study in Coevolution," *Evolution* 18, no. 4 (1964): 586–608; Douglas J. Futuyma and Montgomery Slatkin, *Coevolution* (Sunderland, Mass., 1983). The concept of coevolution has also been used to study the mutual shaping of genes and culture within human populations. See William H. Durham, *Coevolution: Genes, Culture, and Human Diversity* (Stanford, Calif., 1991). Coevolution may involve populations of three or more species, but, for simplicity's sake, this essay focuses on pairs of populations.

[4] Fredrik Bäckhed, Ruth E. Ley, Justin L. Sonnenburg, Daniel A. Peterson, and Jeffrey I. Gordon, "Host-Bacterial Mutualism in the Human Intestine," *Science* 307 (March 25, 2005): 1915–1920; Jian Xu et al., "Evolution of Symbiotic Bacteria in the Distal Human Intestine," *PLoS Biology* 5, no. 7 (2007): 1574–1586; Amber Benezra, Joseph DeStefano, and Jeffrey I. Gordon, "Anthropology of Microbes," *Proceedings of the National Academy of Sciences* 109, no. 17 (2012): 6378–6381; Hachung Chung et al., "Gut Immune Maturation Depends on Colonization with a Host-Specific Microbiota," *Cell* 149, no. 7 (2012): 1578–1593; Human Microbiome Project Consortium, "Structure, Function and Diversity of the Healthy Human Microbiome," *Nature* 486 (June 14, 2012): 207–214; Tanya Yatsunenko et al., "Human Gut Microbiome Viewed across Age and Geography," ibid., 222–227; Manimozhiyan Arumugam et al., "Enterotypes of the Human Gut Microbiome," *Nature* 473 (May 12, 2011): 174–180.

of years because *Homo sapiens* developed perhaps 195,000 years ago. If "nature" refers to the non-human world, then natural selection would seem to exclude human actions. The problem with the popular definition is that it is too narrow. All development of new species over millions of years through natural selection is evolution, but not all evolution is development of new species over millions of years through natural selection.[5]

Biologists define "evolution" as change in the frequency of inherited traits in populations over generations. This definition contrasts with the popular definition in at least six ways. First, the entities that evolve are populations, not necessarily entire species. Populations consist of members of a species that live in a given place and usually do not interbreed with members of other populations. Sometimes all populations of a species evolve, in which case the species evolves, but local populations can evolve without affecting other populations of the same species. Second, any degree of change qualifies as evolution. Sometimes changes are so radical that populations become new species, but most evolution involves smaller changes within populations. All changes in the frequency of inherited traits of populations over generations are evolution, even if those changes are temporary and later reversed. Third, the time required for evolution is only two generations, not a specific or large number of years. Species with short generation times, such as bacteria, can evolve in hours. Fourth, natural selection and evolution are different processes. Natural selection is a mechanism that leads to evolution. It is the differential survival of *individuals* due to differences in traits. Selection acts *within* generations. Fifth, evolution does not require natural selection; there are other evolutionary mechanisms as well. Sixth, evolution is defined by a pattern (change in inherited traits), not by the cause of the pattern. People are as capable as any other species of affecting evolution.[6]

An example from Africa shows how evolution can take place in historical time as a result of human action. In some populations of elephants, the frequency of an inherited trait (tusklessness) increased over the twentieth century. Two mechanisms other than natural selection (if taken to exclude human actions) were responsible. One was human selection. Poachers killed elephants for their tusks, which they sold into an international ivory market. Poachers had no reason to kill tuskless individuals, which survived and reproduced at a higher rate than tusked individuals. Another mechanism probably was *drift*, which means differences in reproduction rates of individuals due to chance. Once elephant populations became small, tuskless individuals apparently reproduced more often than tusked individuals by chance, which led tusklessness to increase even in the absence of poaching.[7]

[5] The popular view of evolution described here emerged in individual conversations with scholars, questions at conferences and seminars, and comments by manuscript reviewers.

[6] Eric R. Pianka, *Evolutionary Ecology*, 6th ed. (San Francisco, 2000); Brian Charlesworth and Deborah Charlesworth, *Evolution: A Very Short Introduction* (Oxford, 2003), 5–6; Douglas J. Futuyma, *Evolutionary Biology*, 3rd ed. (Sunderland, Mass., 1998), glossary. For examples of evolution in the wild, see Peter R. Grant, *Ecology and Evolution of Darwin's Finches* (Princeton, N.J., 1999); B. Rosemary Grant and Peter R. Grant, *Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of the Galápagos* (Chicago, 1989). For an accessible overview of research on contemporary evolution in Darwin's finches, see Jonathan Weiner, *The Beak of the Finch: A Story of Evolution in Our Time* (New York, 1994).

[7] Eve Abe, "Tusklessness amongst the Queen Elizabeth National Park Elephants, Uganda," *Pachyderm* 22 (1996): 46–47; H. Jachmann, P. S. M. Berry, and H. Imae, "Tusklessness in African Elephants:

In addition to situating evolution in (not outside of) history, this example illustrates the need for historians and biologists to join forces to understand the way life has changed over time. The traditional tools of historians do an excellent job of explaining the social factors that led to selection for tusklessness. Art historians can explain the development and appeal of ivory carving, economic historians can analyze the development of the international ivory trade, political historians can explain why some African countries lacked the capacity or desire to enforce laws against elephant hunting, and social and economic historians can analyze the enduring poverty that created a strong incentive for poaching. But the traditional tools of history cannot explain why killing tusked elephants encouraged tusklessness over generations. The tools of biology can. Genetics explains how elephants inherited tusklessness from their parents. Evolutionary biology explains why tusks evolved (they aided survival and reproduction) and why they became less common (hunting made the risks of tusk-bearing outweigh the benefits). Reducing populations to a few individuals increased the odds that chance differences in reproduction would affect the frequency of traits in populations.

Another example illustrates the life-and-death consequences of coevolution in historical time. The earth sustains more than 7 billion people today only because of coevolution that resulted in highly productive domestic plants and animals and people who knew how to tend them. But coevolution also has sent millions to their graves. The end of one of the earth's great killers, malaria, hove into sight after World War II when new insecticides (to kill malaria-carrying mosquitoes) and drugs (to kill malaria plasmodia) became common. The worldwide malaria-eradication project made stunning progress until mosquitoes and plasmodia evolved resistance to insecticides and drugs. The end of malaria receded back over the horizon, and the World Health Organization abandoned the eradication project. By 2000, about 2 million people were dying yearly of malaria, and the disease infected 300–500 million more. Between these poles of life and death lie thousands of other examples of coevolution that changed the lives of human beings, and the lives of members of non-human species, in ways large and small.[8]

Human beings have affected the evolution of populations of other species through many mechanisms. Charles Darwin named two of them. *Unconscious selection* is the process in which people affect the traits of populations without intending to do so, usually by helping individuals with certain traits survive more often than those with other traits. (Unconscious selection by people served as Darwin's model for natural selection in the wild.) Selecting for tusklessness is an example. *Methodical selection* is the process in which people affect the traits of populations intentionally through selective mating or by limiting reproduction to favored indi-

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A Future Trend," *African Journal of Ecology* 33 (1995): 230–235; Anna M. Whitehouse, "Tusklessness in the Elephant Population of the Addo Elephant National Park, South Africa," *Journal of the Zoological Society of London* 257, no. 2 (2002): 249–254.

[8] R. S. Phillips, "Current Status of Malaria and Potential for Control," *Clinical Microbiology Reviews* 14, no. 1 (2001): 208–226; Jean-François Trape, "The Public Health Impact of Chloroquine Resistance in Africa," *American Journal of Tropical Medicine and Hygiene* 64, no. 1–2 (2001): 12–17; J. A. Nájera, "Malaria Control: Achievements, Problems and Strategies," *Parassitologia* 43, no. 1–2 (2001): 1–89; Stephen R. Palumbi, *Evolution Explosion: How Humans Cause Rapid Evolutionary Change* (New York, 2001), 137–138; Peter B. Bloland, *Drug Resistance in Malaria* (Geneva, 2001), 2.

viduals. Plant and animal breeding are examples. A third mechanism is drift, in which the frequency of traits in a population changes as a result of chance differences in reproduction of individuals with those traits. Recently, a fourth means, *genetic engineering*, has provided a powerful way to modify the traits of populations, including by moving genes from one kingdom to another. Frogs, tobacco plants, and monkeys now glow in the dark or under ultraviolet light thanks to genes from fireflies and jellyfish, and tobacco and lettuce plants manufacture insulin thanks to the insertion of a human gene. The pervasive impact of human beings on evolution has led an evolutionary biologist to suggest that we are living amidst an anthropogenic "evolution explosion." By changing environments around the world—so much so that scholars have suggested that we live in a new geological era, the Anthropocene—people have changed the conditions in which virtually all organisms evolve.[9]

Anthropogenic evolution led to coevolution when changes in traits of non-human populations circled back to change traits of human populations. A dramatic recent example is the coevolution of human populations with genetically engineered organisms that manufacture medicines. The U.S. Food and Drug Administration first approved the use of a product of genetic engineering, insulin from genetically modified bacteria, in the early 1980s. Genetic engineers had changed a trait of a bacterial population, and this new trait in a bacterial population circled back to change the frequency of diabetes symptoms in a human population. The same can be said about symptoms of other human diseases that have declined due to coevolution with genetically engineered, non-human populations. By 2009, the U.S. Food and Drug Administration and the European Medicines Agency had approved the use of 151 products of genetic engineering. Forty-five of them came from populations of a single species of bacteria, *Escherichia coli*, so human populations were coevolving with at least 45 genetically distinct populations of *E. coli*. Other products have come from genetically modified populations of yeast, an insect, and mammals.[10]

Historians have long recognized that the Agricultural Revolution was the most important revolution in history. The development of agriculture led to settled populations, large social groups (towns, cities, states, empires), hierarchical social structures, occupational specialists outside agriculture (including the scribes who invented writing), growing populations, and increased crowd disease (picked up from domestic animals). The Agricultural Revolution laid the foundation for nearly ev-

[9] Charles Darwin, *The Variation of Animals and Plants under Domestication*, 2 vols. (Baltimore, 1998), 2: 176–178; Darwin, *The Origin of Species by Means of Natural Selection; or, The Preservation of Favoured Races in the Struggle for Life*, 6th ed. (London, 1872), 102; Palumbi, *Evolution Explosion*; David W. Ow et al., "Transient and Stable Expression of the Firefly Luciferase Gene in Plant Cells and Transgenic Plants," *Science* 234 (November 14, 1986): 856–859; Diane Boyhan and Henry Daniell, "Low-Cost Production of Proinsulin in Tobacco and Lettuce Chloroplasts for Injectable or Oral Delivery of Functional Insulin and C-Peptide," *Plant Biotechnology Journal* 9, no. 5 (2011): 585–598; Erika Sasaki et al., "Generation of Transgenic Non-Human Primates with Germline Transmission," *Nature* 459 (May 28, 2009): 523–528; Will Steffen, Paul J. Crutzen, and John R. McNeill, "The Anthropocene: Are Humans Now Overwhelming the Great Forces of Nature?," *Ambio* 36, no. 8 (2007): 614–621.

[10] Neus Ferrer-Miralles, Joan Domingo-Espín, José Luis Corchero, Esther Vázquez, and Antonio Villaverde, "Microbial Factories for Recombinant Pharmaceuticals," *Microbial Cell Factories* 8, no. 1 (2009): 17.

erything historians have studied, and historians traditionally have used one of its byproducts (the invention of writing) to mark the end of prehistory and the beginning of history.[11]

Historians (and other scholars) have credited the Agricultural Revolution to domestication, making it one of the most important processes in history. Most definitions of the word "domesticate" resemble Webster's: "to adapt (an animal or plant) to life in intimate association with and to the advantage of humans." This definition has several key features, most of them implicit. First, domestication is an evolutionary process (adaptation). Domestication requires changes in traits of populations to suit them to a human environment. Second, domestication changes non-human organisms. The definition does not preclude human change, but neither does it require it. Third, the benefits of domestication flow to people. The definition does not preclude benefits to non-human organisms, but neither does it require it. Fourth, domestication might be a one-time event. The definition does not preclude continual change after domestication, but neither does it require it. Fifth, the emphasis on one-way impacts makes it easy to assume that people initiated the process. Explicitly or implicitly, historians have used "domesticate and domestication" in ways consistent with these meanings. Studies often describe domestication as a one-way, and implicitly one-time, process that people initiated and controlled thousands of years ago.[12]

"Coevolution" offers a better way of thinking about domestication and history. Crediting the Agricultural Revolution to domestication, as usually understood, is partly correct. People did change the traits of plant and animal populations in ways that benefited human beings thousands of years ago. This process was necessary for the Agricultural Revolution, but it was not sufficient. The traits of human populations also had to change during domestication, making the process bidirectional. It is probably more accurate to think of domestication as a relationship between populations of two species, rather than as a state into which one puts the other. As Bruce Smith put it, "The establishment of such a new and sustained pattern of interaction . . . is clearly the independent variable or component in the causal chain—the behavioral relationship *is* domestication." For agriculture to thrive and spread, human and non-human populations had to continue to coevolve right up to the present. The process has not been glamorous or well recognized, but it has been essential.[13]

[11] Robin W. Winks, *World Civilization: A Brief History*, 2nd ed. (Lanham, Md., 1993), 20; Steven Wallech et al., *World History: A Concise Thematic Analysis*, 2nd ed., 2 vols. (Hoboken, N.J., 2013), 1: 5; Jared Diamond, *Guns, Germs, and Steel: The Fates of Human Societies* (New York, 1999); Donald Worster, "Transformations of the Earth: Toward an Agroecological Perspective in History," *Journal of American History* 76, no. 4 (March 1990): 1087–1106; for a challenge to the traditional definition of history, see Daniel Lord Smail, *On Deep History and the Brain* (Berkeley, Calif., 2008), Introduction, chaps. 1–2.

[12] For summaries of common views of historians, I looked to textbooks of world history. An example of a description emphasizing human initiation and control of domestication comes from Robin Winks: "The earliest history of agriculture is that of the slow process of finding and selecting suitable wild grains [and] remaining long enough in one location to cultivate them"; *World Civilization*, 20. Wallech et al. describe something similar for animals: "To domesticate members of any wild species of animal, a human first had to tame the individual animal and then successfully breed it in captivity"; *World History*, 1: 15. Some evolutionary biologists emphasize one-way impacts, too. David P. Mindell says, "Humans created dogs from wolves. Wolves have been our partners, but, as with all domestications, we have driven the process"; Mindell, *The Evolving World: Evolution in Everyday Life* (Cambridge, Mass., 2006), 56.

[13] Some historians have emphasized the reciprocal nature of obligations created by domestication.

Authors often attribute domestication to methodical selection, but unconscious selection seems likely to have played an important, even primary, role. People acting for short-term gain could, in the long run, have modified the traits of non-human and human populations enough to result in domestication. One of the best tests of this hypothesis came in experiments by the Russian geneticist Dmitry K. Belyaev. He domesticated foxes by selecting for only one trait, tameness, which he defined as willingness to approach human beings. After twenty generations, 35 percent of the foxes showed behaviors we associate with dogs. They ran to people, licked their faces, responded to pet names, and wagged their tails. It is easy to imagine that people and wolves domesticated each other by a similar process. Wolves willing to approach hunter-gatherer camps may have scavenged more food than their skittish relatives, giving them an advantage in survival and reproduction, which eventually might have led to domestic wolf populations (dogs). One of the unexpected findings from Belyaev's experiments was that selection for tameness could also produce physical traits seen in domestic animals. Many tame foxes had traits found in dogs, such as black and white fur and droopy ears. If we need further proof that domestication could develop unconsciously, we need only look to the animal world. Ants have coevolved domestic relationships with fungi and insects (aphids and other species of ants), and no one has credited them with advanced cognition.[14]

A coevolutionary approach addresses two other flaws in the traditional definition of domestication. One is the assumption that people initiated the process. We could just as easily assume that non-human populations initiated the process. Take the example of wolf domestication via camp followers. Certain wolf behaviors could have elicited and rewarded certain human behaviors. Wolves near human camps could have warned of approaching enemies (human and animal) and transported fresh meat (their own muscles) to new campsites, where people could slaughter them as needed. These behaviors could have encouraged human groups to keep wolves nearby by feeding them waste or surplus food. We can say similar things about plants. Yes, people probably helped maize to develop from teosinte by selectively harvesting unusually large heads. But it would be equally accurate to say that teosinte began the process by producing unusually large heads, which encouraged human beings to selectively harvest and plant them. Rather than forcing us to choose one partner or the other as initiator, as the common understanding of domestication does, coevolution enables us to focus on the actions of both partners in evolving a relationship.

Wallech et al. write, "At the heart of domestication is a special relationship between organisms from two different species that requires both to maintain a long and productive association with one another: symbiosis"; *World History*, 1: 14. Bruce D. Smith, "Documenting Domesticated Plants in the Archaeological Record," in Melinda A. Zeder, Daniel G. Bradley, Eve Emshwiller, and Bruce D. Smith, eds., *Documenting Domestication: New Genetic And Archaeological Paradigms* (Berkeley, Calif., 2006), 15–24, here 17, emphasis in the original.

[14] L. N. Trut, "Experimental Studies of Early Canid Domestication," in A. Ruvinsky and J. Sampson, eds., *The Genetics of the Dog* (New York, 2001), 15–41; A. B. Munkacsi, J. J. Pan, P. Villesen, U. G. Mueller, M. Blackwell, and D. J. McLaughlin, "Convergent Coevolution in the Domestication of Coral Mushrooms by Fungus-Growing Ants," *Proceedings of the Royal Society of London B* 271, no. 1550 (2004): 1777–1782; Bernhard Stadler and Anthony F. G. Dixon, "Ecology and Evolution of Aphid-Ant Interactions," *Annual Review of Ecology, Evolution, and Systematics* 36, no. 1 (2005): 345–372; Ulrich G. Mueller, Stephen A. Rehner, and Ted R. Schultz, "The Evolution of Agriculture in Ants," *Science* 281 (September 25, 1998): 2034–2038.

Another flaw is the assumption that only people benefited from domestication. They did, but so did the domesticated organisms that people helped to survive and spread.[15]

It might seem surprising that changes in the frequency of behaviors in human populations can be described as evolution—that is, changes in the frequency of inherited traits. Many of us are accustomed to thinking of traits as physical features. But behaviors are traits of individuals and populations, too, and they can be just as essential for survival and reproduction: think feeding and mating. Even if we recognize behaviors as traits, it might be hard to see how they could evolve, because evolution requires inheritance of traits. We know that genes provide a means of inheriting physical traits. Are behavioral traits also genetic? Some behaviors, such as the beating of hearts and breathing, are largely under the control of genes (though we can consciously affect both if we wish). Other behaviors have no clear genetic basis (beyond creating the ability to perform the behavior). We can cheer for a new football team when we move to a new city, but genes cannot explain the new behavior. Genes stay the same throughout one's lifetime.

The answer to this conundrum lies in recognizing that many species, including people, have at least two means of inheritance: genes and culture. Scholars have used "culture" to mean many things. Anthropologists and other scholars use it to mean ideas about how to do things. "Instructions," "recipes," "practices," "rules," "traditions," "customs," and "guidelines" mean roughly the same thing. They all refer to instructions for behaviors (or instructions for interpreting the meaning of the behaviors of others, including their words). The key point is that culture and genes both transmit instructions for traits (physical or behavioral), so behaviors grounded in culture can evolve. Cultural inheritance resembles genetic inheritance in several ways. It carries instructions for traits from parents to offspring. Instructions for a trait may come in multiple versions (alleles). Some traits might result from a single instruction, but others result from the combination of multiple instructions. Instructions might be copied faithfully, or copying may introduce changes. Culture also differs from genes. Culture passes among non-relatives and backward in generations (from offspring to parents). Culture is learned, so it can change multiple times within an individual's lifetime, which enables cultural traits to evolve more rapidly than genetic traits. (This learning may be conscious, as in schooling, or it may be unconscious, as when we accidentally memorize an advertising jingle.) Culture can be stored outside bodies (for example, in a book), as well as in bodies (brains). People have no monopoly on culture. In many species, parents teach their offspring how to hunt (among other things).[16]

Human and non-human populations coevolved under agriculture in at least four

[15] Stephen Budiansky, *The Covenant of the Wild: Why Animals Chose Domestication* (New York, 1992).

[16] Recent research has suggested a third form of inheritance, epigenetics, in which individuals inherit acquired traits without changing the underlying DNA. Durham, *Coevolution*; Robert Boyd and Peter J. Richerson, *Not by Genes Alone: How Culture Transformed Human Evolution* (Chicago, 2005); Boyd and Richerson, *The Origin and Evolution of Cultures* (New York, 2005); L. L. Cavalli-Sforza and M. W. Feldman, *Cultural Transmission and Evolution: A Quantitative Approach* (Princeton, N.J., 1981); Eric J. Richards, "Inherited Epigenetic Variation—Revisiting Soft Inheritance," *Nature Reviews Genetics* 7 (2006): 395–401. My aim in defining "culture" is to clarify its meaning in this essay, not to suggest that this definition is superior to, or should replace, others.

ways. First, and probably most commonly, human populations changed culturally, and non-human populations changed genetically. People changed their own behavior (by planting seeds, for example) and selected for genetic traits they valued in other organisms (such as large heads of grain).[17] Second, human and non-human populations both changed genetically. As plants and animals evolved in ways that increased the production of certain foods, such as starch and milk, the frequency of genes that helped people digest those foods increased.[18] Third, people evolved genetically, and populations of other species evolved culturally. As human populations evolved adult tolerance of lactose in milk, dairy animals learned to stand still while milking, and to walk from fields to barns in the evening.[19] Fourth, human and non-human populations both evolved culturally. People learned to milk cows and feed them in barns, and cows learned to be milked.

Another advantage of a coevolutionary framework for agriculture (the list keeps growing) is its emphasis on continual change. The first domesticated plants and animals would have had low yields, so farmers had to continue selecting for desired traits to increase production. Pests of plants and animals would exploit agricultural populations, so farmers had to develop strains that resisted them. Pests would evolve ways to circumvent a given strain's defenses, forcing farmers to introduce new strains, and so on in a never-ending coevolutionary race. Spreading crops and animals to new regions demanded adaptation to new climates, soils, and foods.[20]

One of coevolution's less-appreciated impacts on history has been its contribution to power. Historians in many fields use the term "power," often without defining it.

[17] Diamond, *Guns, Germs, and Steel*, 120.

[18] Sarah A. Tishkoff et al., "Convergent Adaptation of Human Lactase Persistence in Africa and Europe," *Nature Genetics* 39, no. 1 (2007): 31–40; J. Burger, M. Kircher, B. Bramanti, W. Haak, and M. G. Thomas, "Absence of the Lactase-Persistence-Associated Allele in Early Neolithic Europeans," *Proceedings of the National Academy of Sciences of the United States of America* 104, no. 10 (2007): 3736–3741; Todd Bersaglieri et al., "Genetic Signatures of Strong Recent Positive Selection at the Lactase Gene," *American Journal of Human Genetics* 74, no. 6 (2004): 1111–1120; Nabil Sabri Enattah et al., "Independent Introduction of Two Lactase-Persistence Alleles into Human Populations Reflects Different History of Adaptation to Milk Culture," *American Journal of Human Genetics* 82, no. 1 (2008): 57–72; F. Imtiaz et al., "The T/G 13915 Variant Upstream of the Lactase Gene (LCT) Is the Founder Allele of Lactase Persistence in an Urban Saudi Population," *Journal of Medical Genetics* 44, no. 10 (2007): e89; Sean Myles et al., "Genetic Evidence in Support of a Shared Eurasian–North African Dairying Origin," *Human Genetics* 117, no. 1 (2005): 34–42; Nabil Sabri Enattah et al., "Evidence of Still-Ongoing Convergence Evolution of the Lactase Persistence T-13910 Alleles in Humans," *American Journal of Human Genetics* 81, no. 3 (2007): 615–625; Kevin N. Laland, John Odling-Smee, and Sean Myles, "How Culture Shaped the Human Genome: Bringing Genetics and the Human Sciences Together," *Nature Reviews Genetics* 11 (2010): 137–148.

[19] J. Rushen, A. M. B. de Passillé, and L. Munksgaard, "Fear of People by Cows and Effects on Milk Yield, Behavior, and Heart Rate at Milking," *Journal of Dairy Science* 82, no. 4 (1999): 720–727.

[20] Alan L. Olmstead and Paul W. Rhode, "Biological Innovation and Productivity Growth in the Antebellum Cotton Economy," *Journal of Economic History* 68, no. 4 (2008): 1123–1171; Olmstead and Rhode, "Biological Innovation in American Wheat Production: Science, Policy, and Environmental Adaptation," in Schrepfer and Scranton, *Industrializing Organisms*, 43–83; Olmstead and Rhode, *Creating Abundance: Biological Innovation and American Agricultural Development* (New York, 2008); Smith, "Documenting Domesticated Plants in the Archaeological Record"; Melinda A. Zeder, "Archaeological Approaches to Documenting Animal Domestication," in Zeder, Bradley, Emshwiller, and Smith, *Documenting Domestication*, 171–180; J. O. Ware, "Plant Breeding and the Cotton Industry," in *Yearbook of Agriculture 1936* (Washington, D.C., 1936), 657–744.

Two senses are important: physical power and social power. Physicists define physical power as the rate at which energy is put to work. Units for measuring power include horsepower and watts. This definition guides our attention to two key items: devices that convert energy to work (engines), and the sources of energy. It is important to study physical power not only for its own sake, but also because it has contributed to social power (here meaning roughly getting other people to do what one wants). Social power might have multiple sources, such as access to knowledge, but nothing social happens without some physical action, at minimum by human bodies. Multiplying one's physical power also leads to social power, as military and political leaders have long known.[21]

Until the mid-twentieth century—that is, for almost all of history, however defined—most people relied on muscles as the primary devices for converting energy to work. Many people in rural Asia, Africa, and Latin America still do today. Nothing highlights the importance of muscles more than the units of power that pioneers of the Industrial Revolution chose to use: horsepower. The developers of steam engines needed to explain to potential buyers how much work their devices could do, so they measured output in terms of their competition. In their markets, the dominant engines were horses, so steam entrepreneurs defined one horsepower as the weight a horse could lift or pull a certain distance in a certain time. This unit enabled buyers to compare the cost of doing the same work with equine muscles or with steam engines.[22]

Coevolution was responsible for developing both animal engines and the energy sources that fueled them. Coevolution shaped the bodies, temperaments, and culture of animals to make them useful in harness. Workhorses and racehorses both lived in Britain in the eighteenth century, but strong, heavy, patient workhorses looked and behaved very differently from fleet, lithe, and flighty racehorses. In comparing their engines to horses, steam entrepreneurs were not comparing them to racehorses, but to animal engines designed for the same purpose (lifting or pulling weight). The fuel for animal engines came largely from products of human-plant coevolution, such as oats and parts of plants unfit for human food. Fuel also could come from wild plants, such as grasses. One of the virtues of animal engines was their ability to use flex fuels: domestic and wild plants. Bullocks in India lived on crop byproducts such as rice straw, mustard oil cakes, and chopped banana leaves, and on plants growing along roadsides and canals.[23]

Horses and other draft animals were not the only muscular engines. The first, and always essential, engines of history were human muscles. People sometimes used their own muscles to do work, and sometimes they persuaded, paid, or forced other

[21] This section builds on ideas in Edmund Russell et al., "The Nature of Power: Synthesizing the History of Technology and Environmental History," *Technology and Culture* 52, no. 2 (2011): 246–259; for basic concepts of energy and power, see Vaclav Smil, *Energy in World History* (Boulder, Colo., 1994), 1–14. In this essay, I am using "social power" in the instrumental sense of Max Weber when he wrote, "In general, we understand by 'power' the chance of a man or of a number of men to realize their own will in a communal action even against the resistance of others who are participating in the action." Women should be included in this definition. Weber, *From Max Weber: Essays in Sociology*, trans. H. H. Gerth and C. Wright Mills (New York, 1946), 180. I am defining the term to clarify its usage in the essay, not to suggest that this definition is superior to, or should supplant, others (which are numerous).

[22] Smil, *Energy in World History*, 6, 94, 225.

[23] Ibid., 6, 39–49.

people to work for them.[24] (Social and physical power reinforced each other when some people benefited from the work of others.) In all these cases, human muscles were engines that converted food energy to useful work. After the Agricultural Revolution, most of the food energy that fueled human muscles came from domestic plants, especially those that stored energy in carbohydrates, such as wheat, rice, maize, and potatoes. Some domestic plants, most notably nuts and seeds, supplied muscle fuel in the form of fats. In wealthier societies, fat from domestic animals also fueled human muscles. The energy in animal fat derived from plants, both domestic and wild. Coevolution was responsible for developing the domestic plants that supplied fuel to human muscles both directly (plant food) and indirectly (animal fat). It was also responsible for the domestic animals that turned domestic and wild plants into fat that fueled human muscles.[25]

The coevolution that led to draft animals multiplied human power both directly and indirectly. Animal muscles multiplied human power directly by virtue of numbers (one person could control the work of many animals) and of strength (one ox could haul a bigger block of stone than a person could). It took between a hundred and two hundred hours for a peasant to prepare a hectare of land for planting using a hoe, and a little more than thirty hours to do so with a single ox drawing a plow. Domestic animals multiplied human power indirectly by increasing yields of domestic plants, thereby supplying more food energy for people and for animals. They did this both with their muscles—by pulling plows, for example, which helped farmers raise more crops, and by lifting irrigation water from wells—and with their guts, by turning fodder into manure, the primary fertilizer for fields before synthetic fertilizers in the twentieth century. Manure production depended on coevolution of domestic animals with non-human species that, unlike the pests mentioned above, benefited animals (making them mutualists). Ruminants (cattle, sheep, goats) could not break down cellulose themselves. Billions of microbes (bacteria, protozoa) in their digestive tracts did it for them.[26]

Animal power was crucial not just for agriculture, but for the activities studied by other fields of history. To mention just a few examples, domestic animals lifted, via ropes and pulleys, the stones that built the great cathedrals of Europe (history of art, architecture, and religion), carried goods along the Silk Road (economic history), hauled soldiers and weapons into battle (military history), and enhanced the mobility and cultural complexity of hunters on the Great Plains of North America (Native American and social history).[27]

Coevolution was one of the most, possibly *the* most, important means of technological invention and development in history. Artifacts that people use to do human work are tools, and all tools are technologies. Every time human groups coevolved domestic relationships with new populations, they invented new types of tools. And every time they adapted a plant or animal to a particular place or use, they further developed the tool. We easily recognize mechanical invention and de-

[24] Alan Mikhail, "Unleashing the Beast: Animals, Energy, and the Economy of Labor in Ottoman Egypt," *American Historical Review* 118, no. 2 (April 2013): 317–348.

[25] Smil, *Energy in World History*, chap. 3.

[26] Ibid., 40–49; Brian Donahue, *The Great Meadow: Farmers and the Land in Colonial Concord* (New Haven, Conn., 2007).

[27] Smil, *Energy in World History*, chap. 4.

velopment in history, and we readily credit these processes with transforming the world during and after the Industrial Revolution. But many of us are not accustomed to seeing the world-transforming power of biological invention and development.[28]

In addition to making the Agricultural Revolution possible, coevolution played a key role in the Industrial Revolution. This idea runs counter to a dominant narrative of industrialization in which machinery replaced biology as the driving force in history. In fact, coevolution made the Industrial Revolution possible in at least three ways. These contributions were not sufficient for industrialization, but they were necessary.

First, coevolution enabled inventors to work. England, where the Industrial Revolution was born, was a nation of tinkerers who invented machinery, such as steam engines and cotton-spinning machines, that helped transform the world. The mechanics owed their ability to focus on invention and development to farmers who produced more food than they needed themselves. The productivity of farmers derived from their coevolution with domestic plants and animals. This may seem like an obvious point, and it is, but it is a mistake to take the obvious for granted. If we want to explain how automobiles work, we know that we need to talk about the role of gasoline in supplying the energy that turns the engine. It would be good to develop a similar habit and consider the role of food in supplying the energy that occupational specialists and social systems need to function.

Second, coevolution supported the Industrial Revolution by powering the bodies of workers. Most of the research on energy in the Industrial Revolution has focused on waterpower (especially in the early years) and the burning of coal, and for good reason. These energy sources fueled the machines essential for industrialization. Often overlooked, however, was an equally essential source of energy: food. All the coal in the world would have been useless without workers to operate the machines that ran on coal. The leaders of the Industrial Revolution recognized this fact. England could not grow enough food to support its workers, so industrialists helped lead the fight to reform the Corn Laws and liberalize grain imports. One source that England turned to for imports was the United States. The productivity of American farmers depended partly on fertile soils and partly on coevolution that adapted European wheat varieties to American conditions, increased yields, and maintained yields despite coevolution with pests that otherwise would have sent yields plummeting. When pests and pathogens circumvented the defenses of a wheat variety, farmers adapted culturally by substituting another.[29]

Third, coevolution produced cotton with traits suited to mechanization. Coevolution was important for food, but it was also important for fiber. Mechanization of cotton textiles has long been considered a breakthrough in the Industrial Revolution. The first stage of mechanization developed machines to spin cotton into thread. (The

[28] Schrepfer and Scranton, *Industrializing Organisms*.

[29] Thomas Finger is writing a dissertation at the University of Virginia on the importance of American grain for the British Industrial Revolution. His findings, which I draw on here, are summarized in Russell et al., "The Nature of Power"; Olmstead and Rhode, "Biological Innovation in American Wheat Production."

second stage developed machines to weave cotton thread into cloth.) The earliest domesticated cottons, circa 5,000 years ago, apparently grew fibers too short to spin into thread at all, much less by machine. Bolls may have been collected for use as stuffing (e.g., in mattresses). Human selection probably lengthened fiber enough for spinning, first by hand and then by machine. Amerindians and South Asians carried out this selection, and cotton did not grow in England, which throws new light on the invention of spinning machines. English inventors did not mechanize the cotton industry purely because of their own ingenuity. They used their ingenuity to respond to an opportunity created for them by coevolution between cotton populations and human populations elsewhere. The coevolution began 5,000 years earlier and continued with development of extra-long fiber and adaptation of cotton populations to the West Indies (another source of British imports).[30]

A coevolutionary approach helps explain the location and timing of English mechanization in ways that other explanations have not. Historians have credited mechanization to English cultural traits, such as tinkering with machinery, protection of private property, and industriousness, but they have a hard time using this hypothesis to explain why the breakthrough inventions came at a specific time (the eighteenth century) in a small corner of the island (Lancashire). These cultural traits presumably were common in other parts of the British Isles, too. We can resolve this puzzle if we think of cotton fiber not as a fungible commodity, as economic historians are wont to do, but as the product of populations with different traits. Cotton fiber came from different species in the Old World and the New World. Old World cottons grew shorter fibers than New World cottons. Length was critical because it affected the strength of thread. Short fibers twisted into weak thread. Long fibers twisted into strong thread. Deft fingers might spin short fibers into (weak) thread adequate for hand weaving, but machines broke short-fibered thread too often for it to be profitable to spin, much less to weave. So long as England relied on imports of short-fibered cotton from the Old World, it failed to mechanize spinning.[31]

Long-fibered cotton from the New World surged into Lancashire in the eighteenth century, which partly explains the location and timing of mechanization. Slave ships brought cotton from the New World to Liverpool as part of the triangular trade, and Liverpool supplied the surrounding region of Lancashire. (The port of London imported cotton mainly from the Old World, and the regions surrounding London did not invent the breakthrough spinning machines.) New World cotton cost much more than Old World cotton, but factory owners bought it because they had no choice. In another example of coevolution, the United States became a major supplier only after adapting a population of a Mexican species to grow in upland areas across the South. India, Egypt, and other regions of the world became important industrial suppliers only after they replaced Old World species with populations of New World species that they adapted to local conditions. The textile industry succeeded only because populations of farmers and of cottons continued to coevolve.[32]

This example shows how novel encounters between populations with complementary traits can lead to radical change in history. In this case, the encounter in-

[30] Russell, *Evolutionary History*, chap. 9.
[31] Ibid.
[32] Ibid.

volved a human population in England with certain cultural traits (e.g., inventiveness, profit motive, private property, industriousness) and a cotton population with certain genetic traits (e.g., long fiber). Complementarity was a matter of chance. Long fiber coevolved in the Americas and happened to suit the English economic environment. Mechanical inventiveness and other cultural traits evolved in England (among other places) and happened to suit long-fibered cotton. Each population's traits were necessary but insufficient for mechanization. If inventiveness had been sufficient, England would have mechanized spinning using Old World cottons. If long fiber had been sufficient, spinning machines would have originated in the New World. The new combination of a human population with certain cultural traits and cotton populations with certain genetic traits created an opportunity (not a necessity) to invent machines that helped transform the world.

The story of cotton mechanization highlights the complex, contingent nature of coevolutionary history. It is not reductionist or deterministic, as some historians might fear from an approach that draws on natural science. By stressing culture, it highlights the value of historical topics and methods. By pointing out the importance of non-human populations, it leads to a more complex understanding of causation and consequences than approaches that limit explanations to human actions. By emphasizing variation among and within populations, it highlights the particularity that historians treasure. By examining chance encounters between populations and unconscious selection, it is more contingent than approaches that credit historical change to human intentionality alone.

A CONSTRUCTION METAPHOR HELPS SUM UP the significance of coevolution for history (traditionally defined). The fields of human endeavor, such as economics and politics, are the rooms of a house. The house stands only because it rests on a foundation (agriculture) that has lasted for thousands of years. The stones in the foundation are coevolved relationships between populations of people and populations of domestic plants, animals, and microorganisms. When people wanted to expand the house's footprint (migrate elsewhere), they cut more stones (coevolved with new domesticates and adapted current domesticates to new conditions) to build a wider foundation. As food producers became more efficient, they freed up other people to take up other trades and build the rooms of the house (politicians, religious leaders, artists, and so on). Agriculture created the specialists who built the first story of the house, which has lasted about 12,000 years, as well as the specialists who built the second floor (industrialists) over the past couple of centuries or so. The rooms and inhabitants multiplied.

The metaphor can be extended to describing why anthropogenic evolution has been easy to overlook in history. As the house added rooms and stories, inhabitants began to spend more and more time inside their own rooms. Servants delivered food to the rooms, and many inhabitants never visited the basement, so they had little idea of the house's foundation (coevolution of human and non-human populations). If they ventured out, they often visited neighboring rooms on the same floor. Political and military leaders, for example, often met for drinks. It became easy to take the foundation for granted and to think that the rooms stood because of what people inside the rooms did. When inhabitants of rooms wrote reports and memoirs, they described their rooms. If we rely on their records to write history, we stay inside their rooms. If we step outside, it becomes easier to see that historical change is inseparable from changes in populations of non-human species.[33] Coevolutionary history is not disciplinary imperialism by natural science. It is a bridge that enables historians and biologists to coevolve by exchanging ideas that enrich both fields. Historians who cross the bridge will find, in my experience, biologists who welcome our knowledge and approaches.[34]

By capitalizing on the strengths of history and biology, coevolutionary history can prompt new questions and answers. We can start by asking about patterns. Have social divisions among human populations— along race, class, and gender lines, for example—created differences in traits of populations of other species? Have differences in traits of non-human populations circled back to shape the way human populations have interacted with each other? Have different economic systems shaped populations of a non-human species in different but predictable ways? Have deliberate changes in non-human populations circled back to shape human populations in unintended ways? Have non-human populations developed new traits accidentally that prompted cultural or genetic change in human populations? Have these new traits empowered or disempowered weaker social groups? If we find any of these patterns, we can move on to the two most interesting questions, why and how. Some of the answers are sure to surprise us.

[33] Donald Worster, "Appendix: Doing Environmental History," in Worster, ed., *The Ends of the Earth: Perspectives on Modern Environmental History* (New York, 1988), 289–307.

[34] R. Lee Lyman, "Paleozoology in the Service of Conservation Biology," *Evolutionary Anthropology: Issues, News, and Reviews* 15, no. 1 (2006): 11–19.

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