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Cultural Evolution: Overview

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Abstract

This article provides an overview of the field of cultural evolution, in which cultural change is studied as a Darwinian evolutionary process. Although a fringe interest just 20 years ago, cultural evolution is now a major area of interdisciplinary study. This article outlines the key tenets of cultural evolution theory, describes the main methods used, and highlights outstanding debates and issues that are currently being investigated in the field.

The study of cultural evolution is one of the fastest growing fields in the social and behavioral sciences. In the 1970s and 1980s, cultural evolution was studied by just a handful of scholars at the fringes of traditional disciplines such as anthropology, psychology, and biology. From such small beginnings has spawned a major area of contemporary research. As Figure 1 shows, the number of journal articles selfdescribing their subject matter as 'cultural evolution' has increased from less than 10 per year in the 1970s and 1980s to well over 100 per year at present. The study of cultural evolution is also unusual in its interdisciplinarity: cultural evolution researchers have an equal chance of having backgrounds in anthropology, archaeology, psychology, biology, economics, and linguistics, and inroads have recently been made into other fields such as history and neuroscience. This article provides an overview of the main theoretical tenets of cultural evolution theory, the primary methods used, the topics studied, and the current controversies within the field, supplementing more detailed articles elsewhere in this volume.

What Is Cultural Evolution?

The answer to this question hinges, naturally, on what one means by both 'culture' and 'evolution.' Although 'culture' has been defined in numerous ways across the social and behavioral sciences (Baldwin et al., 2006), cultural evolution researchers adopt a broad definition along the lines of the following:

Culture is information that is acquired from other individuals via social transmission mechanisms such as imitation, teaching, or language. (Mesoudi, 2011; pp. 2–3)

This may include beliefs, knowledge, attitudes, skills, preferences, words and grammatical rules, and social norms; essentially, anything that is learned from another individual. Culture can be contrasted with information that is acquired genetically, in the form of parentally inherited sequences of DNA, as well as information that is generated *de novo* by a single individual in isolation, with no social transmission. There is no requirement in this definition that culture be restricted to humans; indeed, many cultural evolution researchers study the cultural capacities of nonhuman species in order to illuminate the evolutionary origins of human cultural evolution (*see* Social Learning and Culture in Nonhuman Organisms). It is also possible for culturally transmitted information to be stored exo-somatically, in external storage devices such as books or computer disks, as well as in brains.

'Evolution' has similarly been defined in various ways during the history of biology (see Evolution, History of), although Darwin's conceptualization in The Origin of Species (Darwin, 1859) is commonly accepted as the foundational definition within biology. Darwin's theory of evolution comprised three key principles, each of which is necessary for evolution to occur (Lewontin, 1970). There must be (1) variation within a population of entities; (2) competition for survival or reproduction of those entities, for example, due to finite resources; and (3) inheritance of the characteristics of those entities, such that offspring resemble parents more than expected by chance. Darwin demonstrated that these principles applied to populations of organisms. The same principles can be documented for human culture (Mesoudi et al., 2004): (1) there is abundant variation in cultural traits, such as the almost 7000 languages spoken, the 7.7 million technological patents issued, or the 10000 religious beliefs held in the world today; (2) there is inevitable competition between those traits for memory space, as no one could plausibly speak 7000 languages, understand or use 7.7 million patents, or subscribe to just two different religions at the same time; and (3) cultural traits are reliably passed on to other individuals, as people acquire the languages they speak, the technology they use, the religious beliefs they hold, and so on from other people via social learning. This basic idea that human culture comprises an evolutionary process that fulfills Darwin's definition in Origin should be relatively uncontroversial and obvious, and indeed soon after Darwin wrote Origin, he himself noted that the same principles apply to cultural change, primarily linguistic change:

The formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel ... The survival or preservation of certain favoured words in the struggle for existence is natural selection. (Darwin, 1871; pp. 90–91)

Two important points should be made here. First, this Darwinian notion of cultural evolution is quite different from



Figure 1 The number of publications with 'cultural evolution' listed as a keyword, 1970–2011. Source: Web of Science.

the theories of social or cultural evolution that were common in anthropology during the late nineteenth century, such as those of Tylor (1871) or Morgan (1877). These theories proposed that entire societies proceed through fixed stages of increasing complexity (e.g., from 'savagery' to 'barbarism' to 'civilization'). These progressive theories are Spencerian, not Darwinian (see Evolution, History of). The notion that evolution involves the inevitable progression of species along fixed stages of increasing complexity was long ago shown to be an invalid model of biological evolution (it describes the development of a single organism, not the evolution of a population), and contemporary theories of cultural evolution similarly make no assumptions about the progression of entire societies along developmental stages, focusing instead on how variation changes within populations, as did Darwin (Mesoudi, 2011).

The second important point is that while both genetic evolution and cultural evolution are Darwinian processes, they are not identical. As made clear by the founders of contemporary cultural evolution research (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981), the underlying mechanisms of cultural evolution may be very different from the mechanisms of genetic evolution. For example, while genetic mutation is blind with respect to fitness, cultural innovations may be guided by purposeful agents; while genetic inheritance is particulate (i.e., it involves the high-fidelity transmission of discrete units of inheritance), cultural inheritance may be of much lower fidelity and involve the blending of multiple, continuously varying traits. None of these differences invalidate a Darwinian theory of evolution; there are still mutation and inheritance, even if they are not blind or particulate - they just mean that it must be modeled and understood differently. The failure to appreciate these differences was one of the pitfalls of memetics (Aunger, 2000a), which did, for example, require particulate inheritance of gene-like units of inheritance (memes), and which never properly took off as a scientific discipline, perhaps because of this insistence.

Cultural Microevolution

In the 1970s and 1980s, two pairs of researchers laid the foundations for the contemporary study of cultural evolution. Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) constructed mathematical models of cultural evolution using techniques drawn from population genetics (see Cultural Evolution: Theory and Models). Their models of cultural evolution were Darwinian, in that they assumed variation in a set of cultural traits and modeled various processes that act to change this variation over time as these traits are transmitted from individual to individual. Yet they also successfully incorporated the differences between genetic evolution and cultural evolution noted above, such as incorporating blending inheritance or guided (rather than blind) variation. Because these models are concerned with the processes that transform variation within populations, such models can be described as concerning cultural microevolution.

The aim of these models is to identify the population-level signatures of different microevolutionary processes. For example, models suggest that vertically transmitted traits, which are passed from parent to offspring just like genes, will change slower than horizontally transmitted traits, which are passed between unrelated members of the same generation (Cavalli-Sforza and Feldman, 1981), a prediction supported in subsequent empirical research (Hewlett and Cavalli-Sforza, 1986). In another example, Henrich (2001) modeled the diffusion of a novel technological innovation through a society via different transmission biases. Conformist transmission, in which individuals preferentially adopt the most common trait in the population, was shown to generate S-shaped diffusion curves, whereas individual trial-and-error learning generated r-shaped curves. Given that most innovations exhibit S-shaped dynamics (see Evolution: Diffusion of Innovations), Henrich (2001) concluded that conformist transmission is the most plausible process responsible for the spread of novel technological innovations.

Cultural Macroevolution

In parallel to these mathematical models of cultural microevolution, another group of researchers has used analytical methods borrowed from evolutionary biology to study *cultural macroevolution*, which refers to large-scale, long-term patterns of cultural change at or above the level of the society. These methods, originally designed to reconstruct the evolutionary history of biological species (*see* Comparative Method in Evolutionary Studies), have been used to reconstruct the evolutionary history of cultural traits such as languages (*see* Evolution and Language: Phylogenetic Analyses; see also Pagel, 2009), written manuscripts (Howe et al., 2001), technological artifacts such as stone tools (*see* Evolution, Technology of; see also Lipo et al., 2006), and behavioral practices such as cattle keeping and rules of wealth inheritance (Holden and Mace, 2003).

One aim of these studies is simply to reconstruct the most likely historical scenario that gave rise to contemporary variation in a trait, in terms of which language, technology, and practice emerged earlier and what came later. However, such methods can go beyond mere historical reconstruction and address specific hypotheses concerning why particular cultural traits successfully spread. For example, Holden and Mace (2003) showed that the adoption of cattle led to the switch from matrilineal (mother-to-daughter) to patrilineal (fatherto-son) wealth inheritance, rather than vice versa (inheritance rules influencing the adoption of cattle). Gray and Atkinson (2003) showed that Indo-European languages most likely hitchhiked along with early Anatolian farmers rather than being spread later by nonfarming Kurgan horsemen. A longstanding issue in these analyses is the extent to which cultural macroevolution constitutes a branching process of phylogenetic divergence, thus resembling the evolution of animal species, versus one in which traits readily transfer between lineages, thus resembling the evolution of many bacteria and plant species, in which horizontal gene transfer causes lineages to blend (see Cultural Evolution: Phylogeny versus Reticulation).

Methods

As noted in section Cultural Microevolution, the earliest cultural evolution research primarily involved the construction of mathematical models (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981), and this is still a vibrant area of research (e.g., Boyd and Richerson, 2005; Enquist et al., 2011; Lewis and Laland, 2012; Aoki et al., 2011; Bentley et al., 2004; Mesoudi and Lycett, 2009). Increasingly, the predictions of these models are being tested empirically both in the field and in the lab. The first ethnographic field study to explicitly test the predictions of cultural evolutionary models in a small-scale society was Hewlett and Cavalli-Sforza (1986), and ethnographic methods have continued to be used primarily to determine how cultural traits are transmitted through smallscale social networks (e.g., Aunger, 2000b; Reyes-Garcia et al., 2009; Henrich and Henrich, 2010). More recently, lab experiments have been used to examine, under more controlled conditions, how and when people learn the solutions

to semirealistic artificial tasks from other members of small groups (Mesoudi and O'Brien, 2008; McElreath et al., 2005; Toelch et al., 2008; Efferson et al., 2008).

The phylogenetic methods discussed in section Cultural Macroevolution were first applied to cultural datasets by Mace and Pagel (1994), and have since been applied to datasets from linguistics (Pagel, 2009), anthropology (Lipo et al., 2006; Mace et al., 2005), and archaeology (O'Brien et al., 2001; Lycett, 2009). Again, these methods have been supplemented with ethnographic studies of cultural transmission, for example to measure the extent of cross-lineage blending (Tehrani and Collard, 2009), as well as lab experiments (Spencer et al., 2004). In the latter study, artificial manuscripts were passed along a known phylogeny, and then phylogenetic methods were used to reconstruct the simulated phylogeny, in order to test the validity of those methods.

As can be seen by this brief overview, there is an encouraging interplay in the cultural evolution literature between formal models, lab experiments, ethnographic field studies, and phylogenetic reconstruction of historical data. This is the sign of a healthy science, as theoretical models generate predictions that are then tested empirically, with the results of those empirical tests fed back into the models, which generates new predictions to be tested, and so on.

Current Topics and Issues

Domain-Specific versus Content-Free Biases

One ongoing debate concerns the relative importance of domain-specific 'content biases' versus content-independent 'context biases.' The former are emphasized by cognitive anthropologists (e.g., Sperber, 1996; Atran, 2001) who argue that the spread of cultural representations can be predicted from an understanding of the biologically evolved cognitive structure of the brain. This creates 'cognitive attractors' (Sperber, 1996) that bias cultural change toward intrinsically appealing ideas. For example, it is argued that the kinds of supernatural beliefs that are most likely to spread are those that are 'minimally counterintuitive' (Norenzayan et al., 2006), meaning that they violate some of our intuitions but not excessively so, such as ghosts that violate our folk physics by passing through walls but that obey our folk psychology by exhibiting memory and a desire for revenge. In contrast, other researchers (Henrich and Boyd, 2002; Richerson and Boyd, 2005) place more emphasis on content-free transmission biases, such as conformist transmission (copy whatever is most common in your society) or prestige bias (copy whatever the most prestigious member of your society does). This latter camp argues that many cultural adaptations, from canoes to computers, are too complex and novel to have domain-specific cognitive attractors dedicated to them, and are instead the result of chance innovations spreading via content-independent transmission biases (Boyd et al., 2011a). A similar debate is occurring in linguistics between Chomskian nativists who emphasize language-specific cognitive processes and cultural evolution researchers (e.g., Kirby et al., 2007) who emphasize general properties of cultural transmission (see Evolution and Language: Cultural Transmission).

This difference in emphasis has led to some spirited debate (Claidiere and Sperber, 2007; Henrich et al., 2008), but the two positions are not mutually exclusive. Some traits, such as food preferences, are likely to be highly influenced by biologically evolved cognitive biases due to the direct biological relevance of their content; others, such as recent and complex technologies, are unlikely to have dedicated cognitive biases and so result from a more content-free, populational process.

The Origin of Cumulative Cultural Evolution

Many species exhibit social transmission (Galef and Laland, 2005), and several exhibit regional traditions in tool use or foraging behavior that appear to have spread culturally (Whiten et al., 1999; Lycett et al., 2007). No other species, however, appears to have the capacity for cumulative cultural evolution (CCE), whereby modifications are built up over successive generations such that a single individual could never have invented it alone (think of quantum physics or a computer tablet). An outstanding question is why only humans have CCE. Some have argued that only humans possess cultural transmission mechanisms of high enough fidelity to support CCE, such as imitation (Lewis and Laland, 2012; Tennie and Over, 2012). Other evidence suggests that our species' capacity for collaboration and cooperation is key (Dean et al., 2012; see also next section). An alternative hypothesis is that there was no cognitive change associated with the emergence of CCE, and instead it was the result of larger population sizes and densities that made the loss of complex cultural traits less likely (Powell et al., 2009). Further comparative studies with nonhuman species, and archaeological study of the origin of complex cultural traits, will shed light on this.

The Evolution of Human Cooperation

Several cultural evolution researchers have drawn a link between our species' unusual capacity for CCE (see previous section) and our similarly unusual capacity to cooperate with nonkin (see Human Cooperation, Evolution of; Kin Selection). Whereas other primate species direct help only to close relatives (Jensen et al., 2007), humans frequently help nonkin in situations in which they are unlikely to get any personal return or increase their genetic fitness. Boyd, Richerson, and others (Boyd and Richerson, 1985; Gintis et al., 2003; Boyd et al., 2011b) have argued that a process of cultural group selection has occurred in humans, in which selection has acted on culturally homogeneous (but not necessarily genetically homogeneous) groups to favor groupbeneficial traits. This remains a contentious hypothesis given the controversy surrounding group selection within biology (West et al., 2011), and one that is receiving increasing empirical attention (Lamba and Mace, 2011; Mathew and Boyd, 2011).

Culture-Driven Genetic Change

The field of gene-culture coevolution (*see* Gene-Culture Coevolution) has explored, mostly theoretically, the extent to which cultural evolution might interact with genetic

evolution (Laland et al., 2010). The conclusion of many of these models is that cultural evolution can often drive genetic evolution to new equilibria that it would not have reached in the absence of culture. For example, the cultural invention of dairy farming led to the spread in some populations of lactose tolerance alleles, due to the fitness benefits of drinking milk in adulthood (Itan et al., 2009). Similarly, sickle cell genes likely spread because they confer resistance to malaria, a disease that spread when agricultural methods created ideal conditions for mosquitoes to breed (Durham, 1991). The extent to which cultural evolution has shaped the human genome, and whether this extends beyond physiological changes in response to the agricultural revolution, are empirical questions that will be addressed as gene-sequencing technology advances.

The Neural Basis of Cultural Transmission

Genetics was revolutionized by Watson and Crick's discovery of the molecular basis of genetic inheritance. An equivalent understanding of the molecular basis of cultural evolution would concern how information is stored neurally in brains, and how that neural information is transmitted from one brain to another. Current understanding of how the brain works is not yet able to provide the answer to this question. One potentially promising line of enquiry involves mirror neurons, cells that fire both when an individual observes a specific action (e.g., a particular hand grip) and when the individual observes another individual doing that same action (Rizzolatti and Craighero, 2004), potentially providing a cellular basis for imitation (Iacoboni et al., 1999). However, how this translates into the transmission of, say, tool-making skills remains unclear (Stout, 2011). As neuroimaging technology improves, a better understanding of the neurological basis of cultural transmission will hopefully emerge.

Conclusions

Cultural evolution provides a rich set of theories and methods for studying cultural change, encompassing the subject matter of several traditional academic disciplines. It provides rigorous, scientific tools for linking individual-level cultural transmission dynamics to population-level patterns of cultural change and variation, solving the 'micro-macro' problem that has beset the social sciences in the past. Previously, I have suggested that just as evolutionary theory served to synthesize the biological sciences in the 1930s and 1940s within an overarching 'evolutionary synthesis' (Huxley, 1942), so too evolutionary theory can synthesize the social sciences (Mesoudi, 2011; Mesoudi et al., 2006). 'Macroevolutionary' disciplines, such as archaeology, comparative sociology, macroeconomics, history, and historical linguistics, would be united with 'microevolutionary' disciplines, such as ethnography, psychology, microsociology, microeconomics, and sociolinguistics, with the historical and comparative patterns identified by the former explained in terms of the individuallevel mechanisms studied by the latter. The recent spread of cultural evolutionary theory to disciplines such as history (see Turchin, 2003), economics (*see* Evolutionary Economics), and archaeology suggests that such a synthesis is, in principle, possible.

Our species' ability to adapt culturally to new environments via cultural evolution, rather than genetically via natural selection as seen in other species, is likely responsible for our rapid colonization of virtually every terrestrial environment on the planet. Many of those environments have now been transformed beyond recognition by our ongoing cultural evolution, both for the better (e.g., the eradication of diseases by medical knowledge and technology) and for the worse (e.g., atmospheric pollution from the processing of fossil fuels). An interesting possibility is whether our increasing understanding of cultural evolution might help to encourage the former and discourage the latter.

See also: Comparative Method in Evolutionary Studies; Cultural Evolution: Phylogeny versus Reticulation; Cultural Evolution: Theory and Models; Evolution and Language: Overview; Evolution and Language: Phylogenetic Analyses; Evolution, History of; Evolution: Diffusion of Innovations; Evolutionary Economics; Evolutionary Epistemology; Gene– Culture Coevolution; Human Cooperation, Evolution of; Kin Selection; Social Learning and Culture in Nonhuman Organisms; Technology, Evolution of.

Bibliography

- Aoki, K., Lehmann, L., Feldman, M.W., 2011. Rates of cultural change and patterns of cultural accumulation in stochastic models of social transmission. Theoretical Population Biology 79, 192–202.
- Atran, S., 2001. The trouble with memes: inference versus imitation in cultural creation. Human Nature 12, 351–381.
- Aunger, R. (Ed.), 2000a. Darwinizing Culture. Oxford University Press, Oxford.
- Aunger, R., 2000b. The life history of culture learning in a face-to-face society. Ethos 28, 1–38.
- Baldwin, J.R., Faulkner, S.L., Hecht, M.L., Lindsley, S.L., 2006. Redefining Culture: Perspectives across Disciplines. Lawrence Erlbaum, Mahwah, NJ.
- Bentley, R.A., Hahn, M.W., Shennan, S.J., 2004. Random drift and culture change. Proceedings of the Royal Society B 271, 1443–1450.
- Boyd, R., Richerson, P.J., 1985. Culture and the Evolutionary Process. University of Chicago Press, Chicago, IL.
- Boyd, R., Richerson, P.J., 2005. The Origin and Evolution of Cultures. Oxford University Press. Oxford.
- Boyd, R., Richerson, P.J., Henrich, J., 2011a. The cultural niche: why social learning is essential for human adaptation. Proceedings of the National Academy of Sciences 108, 10918–10925.
- Boyd, R., Richerson, P.J., Henrich, J., 2011b. Rapid cultural adaptation can facilitate the evolution of large-scale cooperation. Behavioral Ecology and Sociobiology 65, 431–444.
- Cavalli-Sforza, L.L., Feldman, M.W., 1981. Cultural Transmission and Evolution. Princeton University Press, Princeton.
- Claidiere, N., Sperber, D., 2007. The role of attraction in cultural evolution. Journal of Cognition and Culture 7, 89–111.
- Darwin, C., 1859/1968. The Origin of Species. Penguin, London.
- Darwin, C., 1871/2003. The Descent of Man. Gibson Square, London.
- Dean, L.G., Kendal, R.L., Schapiro, S.J., Thierry, B., Laland, K.N., 2012. Identification of the social and cognitive processes underlying human cumulative culture. Science 335, 1114–1118.
- Durham, W.H., 1991. Coevolution: Genes, Culture, and Human Diversity. Stanford University Press, Stanford.
- Efferson, C., Lalive, R., Richerson, P.J., McElreath, R., Lubell, M., 2008. Conformists and mavericks: the empirics of frequency-dependent cultural transmission. Evolution and Human Behavior 29, 56–64.

- Enquist, M., Ghirlanda, S., Eriksson, K., 2011. Modelling the evolution and diversity of cumulative culture. Philosophical Transactions of the Royal Society B 366, 412–423.
- Galef, B.G., Laland, K.N., 2005. Social learning in animals: empirical studies and theoretical models. BioScience 55, 489–499.
- Gintis, H., Bowles, S., Boyd, R., Fehr, E., 2003. Explaining altruistic behavior in humans. Evolution and Human Behavior 24, 153–172.
- Gray, R.D., Atkinson, Q.D., 2003. Language-tree divergence times support the Anatolian theory of Indo-European origin. Nature 426, 435–439.
- Henrich, J., 2001. Cultural transmission and the diffusion of innovations. American Anthropologist 103, 992–1013.
- Henrich, J., Boyd, R., 2002. On modeling cognition and culture: why cultural evolution does not require replication of representations. Journal of Cognition and Culture 2, 87–112.
- Henrich, J., Boyd, R., Richerson, P.J., 2008. Five misunderstandings about cultural evolution. Human Nature 19, 119–137.
- Henrich, J., Henrich, N., 2010. The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. Proceedings of the Royal Society B 277, 3715–3724.
- Hewlett, B., Cavalli-Sforza, L.L., 1986. Cultural transmission among Aka pygmies. American Anthropologist 88, 922–934.
- Holden, C.J., Mace, R., 2003. Spread of cattle led to the loss of matrilineal descent in Africa: a coevolutionary analysis. Proceedings of the Royal Society B 270, 2425–2433.
- Howe, C.J., Barbrook, A.C., Spencer, M., Robinson, P., Bordalejo, B., Mooney, L.R., 2001. Manuscript evolution. Trends in Genetics 17, 147–152.
- Huxley, J.S., 1942. Evolution, the Modern Synthesis. Allen & Unwin, London.
- Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. Science 286, 2526–2528.
- Itan, Y., Powell, A., Beaumont, M.A., Burger, J., Thomas, M.G., 2009. The origins of lactase persistence in Europe. PLoS Computational Biology 5, e1000491.
- Jensen, K., Call, J., Tomasello, M., 2007. Chimpanzees are rational maximizers in an ultimatum game. Science 318, 107–109.
- Kirby, S., Dowman, M., Griffiths, T.L., 2007. Innateness and culture in the evolution of language. Proceedings of the National Academy of Sciences 104, 5241–5245.
- Laland, K.N., Odling-Smee, J., Myles, S., 2010. How culture shaped the human genome: bringing genetics and the human sciences together. Nature Reviews Genetics 11, 137–148.
- Lamba, S., Mace, R., 2011. Demography and ecology drive variation in cooperation across human populations. Proceedings of the National Academy of Sciences 108, 14426–14430.
- Lewis, H.M., Laland, K.N., 2012. Transmission fidelity is the key to the build-up of cumulative culture. Philosophical Transactions of the Royal Society B 367, 2171–2180.
- Lewontin, R.C., 1970. The units of selection. Annual Review of Ecology and Systematics 1, 1–18.
- Lipo, C.P., O'Brien, M.J., Collard, M., Shennan, S. (Eds.), 2006. Mapping Our Ancestors: Phylogenetic Approaches in Anthropology and Prehistory. Aldine, New York.
- Lycett, S.J., 2009. Understanding ancient hominin dispersals using artefactual data: a phylogeographic analysis of Acheulean handaxes. PLoS One 4, 1–6.
- Lycett, S.J., Collard, M., McGrew, W.C., 2007. Phylogenetic analyses of behavior support existence of culture among wild chimpanzees. Proceedings of the National Academy of Sciences 104, 17588.
- Mace, R., Holden, C., Shennan, S. (Eds.), 2005. The Evolution of Cultural Diversity: A Phylogenetic Approach. UCL Press, London.
- Mace, R., Pagel, M.D., 1994. The comparative method in anthropology. Current Anthropology 35, 549–564.
- Mathew, S., Boyd, R., 2011. Punishment sustains large-scale cooperation in prestate warfare. Proceedings of the National Academy of Sciences 108, 11375–11380.
- McElreath, R., Lubell, M., Richerson, P.J., Waring, T.M., Baum, W., Edsten, E., Efferson, C., Paciotti, B., 2005. Applying evolutionary models to the laboratory study of social learning. Evolution and Human Behavior 26, 483–508.
- Mesoudi, A., 2011. Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences. University of Chicago Press, Chicago, IL.
- Mesoudi, A., Lycett, S.J., 2009. Random copying, frequency-dependent copying and culture change. Evolution and Human Behavior 30, 41–48.
- Mesoudi, A., O'Brien, M.J., 2008. The cultural transmission of Great Basin projectile point technology I: an experimental simulation. American Antiquity 73, 3–28.
- Mesoudi, A., Whiten, A., Laland, K.N., 2004. Is human cultural evolution Darwinian? Evidence reviewed from the perspective of *The Origin of Species*. Evolution 58, 1–11.

Author's personal copy

Mesoudi, A., Whiten, A., Laland, K.N., 2006. Towards a unified science of cultural evolution. Behavioral and Brain Sciences 29, 329–383.

Morgan, L.H., 1877. Ancient Society. Henry Holt, New York.

- Norenzayan, A., Atran, S., Faulkner, J., Schaller, M., 2006. Memory and mystery: the cultural selection of minimally counterintuitive narratives. Cognitive Science 30, 531–553.
- O'Brien, M.J., Darwent, J., Lyman, R.L., 2001. Cladistics is useful for reconstructing archaeological phylogenies: Palaeoindian points from the Southeastern United States. Journal of Archaeological Science 28, 1115–1136.
- Pagel, M., 2009. Human language as a culturally transmitted replicator. Nature Reviews Genetics 10, 405–415.
- Powell, A., Shennan, S., Thomas, M.G., 2009. Late Pleistocene demography and the appearance of modern human behavior. Science 324, 1298–1301.
- Reyes-Garcia, V., Broesch, J., Calvet-Mir, L., Fuentes-Pelez, N., McDade, T.W., Parsa, S., Tanner, S., Huanca, T., Leonard, W.R., Martínez-Rodríguez, M.R., 2009. Cultural transmission of ethnobotanical knowledge and skills: an empirical analysis from an Amerindian society. Evolution and Human Behavior 30, 274–285.
- Richerson, P.J., Boyd, R., 2005. Not by Genes Alone. University of Chicago Press, Chicago. Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annual Review of Neuroscience 27, 169–192.
- Spencer, M., Davidson, E.A., Barbrook, A.C., Howe, C.J., 2004. Phylogenetics of artificial manuscripts. Journal of Theoretical Biology 227, 503–511.

- Sperber, D., 1996. Explaining Culture: A Naturalistic Approach. Oxford University Press, Oxford.
- Stout, D., 2011. Stone toolmaking and the evolution of human culture and cognition. Philosophical Transactions of the Royal Society B: Biological Sciences 366, 1050–1059.
- Tehrani, J.J., Collard, M., 2009. On the relationship between interindividual cultural transmission and population-level cultural diversity: a case study of weaving in Iranian tribal populations. Evolution and Human Behavior 30, 286–300.
- Tennie, C., Over, H., 2012. Cultural intelligence is key to explaining human tool use. Behavioral and Brain Sciences.
- Toelch, U., van Delft, M.J., Bruce, Donders, R., Meeus, M.T.H., Reader, S.M., 2008. Decreased environmental variability induces a bias for social information use in humans. Evolution and Human Behavior 30, 32–40.
- Turchin, P., 2003. Historical Dynamics: Why States Rise and Fall. Princeton University Press, Princeton, NJ.
- Tylor, E.B., 1871. Primitive Culture. John Murray, London.
- West, S.A., El Mouden, C., Gardner, A., 2011. Sixteen common misconceptions about the evolution of cooperation in humans. Evolution and Human Behavior.
- Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. Nature 399, 682–685.