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# Why Did Memetics Fail? Comparative Case Study<sup>1</sup>

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*Although the theory of memetics appeared highly promising at the beginning, it is no longer considered a scientific theory among contemporary evolutionary scholars. This study aims to compare the genealogy of memetics with the historically more successful gene-culture coevolution theory. This comparison is made in order to determine the constraints that emerged during the internal development of the memetics theory that could bias memeticists to work on the ontology of meme units as opposed to hypotheses testing, which was adopted by the gene-culture scholars. I trace this problem back to the diachronic development of memetics to its origin in the gene-centered anti-group-selectionist argument of George C. Williams and Richard Dawkins. The strict adoption of this argument predisposed memeticists with the a priori idea that there is no evolution without discrete units of selection, which in turn, made them dependent on the principal separation of biological and memetic fitness. This separation thus prevented memeticists from accepting an adaptationist view of culture which, on the contrary, allowed gene-culture theorists to attract more scientists to test the hypotheses, creating the historical success of the gene-culture coevolution theory.*

## **1. Introduction**

Since the second half of the nineteenth century scholars have attempted to explain cultural patterns by using the evolutionary framework. In fact, the

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first cultural evolutionists introduced their conceptions before Darwin published *The Descent of Man and Selection in Relation to Sex* ([1871] 2009). Nevertheless, they only accepted from Darwin's work that which fit their progressivist understanding of cultural evolution and, therefore, misinterpreted his theory of natural selection (Kundt 2015). The massive revival of utilizing the truly Darwinian paradigm in the study of culture began in the 1950s (e.g., White et al. 1959) and culminated with the last chapter of Edward O. Wilson's *Sociobiology* (1975) in the 1970s, when the Darwinian paradigm in the study of culture became an established scientific field. Wilson mainly developed his views on human culture in his book *On Human Nature* (1978) where he argued that human behavior and culture are a result of the same evolutionary processes as animal behavior and that we can, as a result, study these processes by applying the same methods employed in animal studies.

Sociobiology later branched into sub-disciplines, such as evolutionary psychology (e.g., Tooby and Cosmides 1989) and human behavioral ecology (e.g., Cronk 1991). However, before that separation, two other approaches to the evolutionary study of culture, which were inspired by sociobiology and anchored in Darwinism, emerged in the 1970s. The first of these approaches was memetics (Dawkins 2006) and the second was the "dual-inheritance theory" (Boyd and Richerson 1976), later called gene-culture coevolution theory (GCCE) (Henrich 2016). Both theories came into being during the 1970s; both understood culture as being subject to evolutionary dynamics and being reducible to some cultural units, namely memes (Dawkins 2006) or cultural variants (Richerson and Boyd 2005). Also, both wanted to overcome the shortcomings of sociobiology by focusing on the question of whether culture affects behavior in a way that is irreducible to biology (Blackmore 1999; Boyd and Richerson 1982).

However, from their beginnings the theories proved to be different in crucial aspects and, later, the proponents of the respected theories even argued with each other (Blackmore 2016; Boyd and Richerson 2000). The fundamental difference between both theories was anchored in their approaches to the concepts of "units of selection" (Lewontin 1970). While memeticists considered culture to be reducible to gene-like units of cultural selection, which they called "memes" and according to memeticists, often spread at the expense of human fitness, GCCE theorists did not work with discrete units but rather with cultural traits in general. Moreover, GCCE scholars understood the human ability for cultural transmission to be an adaptation and focused on the potential adaptive values that cultural traits might have for their bearers (Boyd and Richerson 1995).

Approximately 40 years after the intellectual onset of GCCE and memetics, it could be concluded that memetics is the approach that failed whereas

GCCE is generally accepted among many evolutionary scientists. The development of a memetic framework was followed by many logical, theoretical, and empirical objections (Atran 2001; Bloch 2000; Boyd and Richerson 2000; Coyne 1999; Kundt 2015; Kuper 2000; Sperber 2000; Uhlř and Stella 2012), but there are also more objective indicators of memetics failure. First, currently only two well-known scholars could be identified as active memeticists (Blackmore 2016; Dennett 2017). Also, Edmonds (2005) shows that between 1986 and 2004, only 41 articles used the word “memetics” indexed in the database Web of Science. Second, memeticists themselves have realized that memetics is no longer considered a serious scientific theory. This can be illustrated in the case of Kate Distin, the author of the 2005 book *The Selfish Meme*, who wrote another book about cultural evolution in 2011 and titled it *Cultural Evolution*. She used the word meme only in references and in the appendix where she explains why she abandoned the concept of the meme. She did so because the word is, according to her, a considerable limitation and most people would not accept it if she would have used it (Distin 2011). The *Journal of Memetics* is the third indicator. It existed from 1997 to 2005 and during those eight years, only 41 original studies and four commemorative studies were published. The journal was discontinued in 2004 “due to a lack of quality submissions” (Edmonds 2005). In the commemorative issue of the *Journal of Memetics* Edmonds (2005) admitted that the science of memes lost the competition with other evolutionary accounts.

This brief list illustrates that memetics is no longer a “mainstream” scientific theory, raising a simple but non-trivial question: Why? Before proceeding to developing the question into more detail, the general framework for understanding the concept of science in which the whole analysis will be performed must be laid down. I follow the theory of Popper who claimed that the purpose of his falsification concept is “to select the one [theory] which is by comparison the fittest, by exposing them all to the fiercest struggle for survival” (Popper 2002, p. 20). Also, I understand science as a cultural institution where scientists decide what is and what is not corroborated or falsified. Thus, I agree with Hull (1990), and Toulmin (1972) that science is like an evolutionary arena where scientific concepts and theories compete for acceptance by the scientific community. Hence, the historical success of a theory could be measured by the number of scientists who work with it and accept it. (Note that under no circumstances does this framework propose that it can reveal an objective quality of science).

The question I asked seems to be very general and easy to answer: Because the theory was wrong. After all, several studies revealed logical inconsistencies in memetics. However, given the framework for understanding the development of science, the question needs to proceed with thorough

explanation of the crucial pitfall. One simple logic of natural selection operates at the core of memetics. It is based on the idea that humans developed the ability to transmit information via a second, non-genetical channel, namely the social or cultural learning that is conceptually separated from biological fitness. The information transmitted through this channel is subject to variation (random errors during transmission or interpretation of that information, and intentional changes) and competition (humans have only limited memory) and therefore not all information could survive, resulting in the process that I call memetic<sup>2</sup> selection. This logic affords formulating an at least partly adaptationist perspective on memetic evolution wherein some memes' survival depends most on their contribution to the biological fitness of the bearer, yet the mainstream memeticists refused this view and the majority of hypotheses that they proposed (e.g., memetic evolution of religious traditions) were based on decoupling the link between biological and memetic fitness. Memes, according to those authors, can propagate themselves despite being non-adaptive or even maladaptive for the bearer (Blackmore 1999; Brodie 2009; Dawkins 1993). As I will show later, it was the adaptationist perspective that allowed GCCE scholars to formulate testable predictions and hence succeed on the market of scientific theories. Thus, the question should be laid down with a crucial clause: Why were memeticists unable to rebuild the parts of their theory to meet the requirements of the scientific community even though the very general and flexible memetic logic would allow it? The fact that memetics had the theoretical potential to go the same way or to team up with GCCE may be illustrated on the recent blog post from Blackmore's (2019) personal website. The text is about the recent meeting of the *MemeLab*, which group people interested in memetics who had regular meetings from 1998 to 2001 and then again, albeit sporadically, from 2006. The last report reports about the meeting held August 17 and 18, 2019 where GCCE and memetics was discussed and Blackmore admitted the possibility that they are actually the same theories.<sup>3</sup>

This study aims to determine whether there could have been any constraints that emerged during the diachronic development of the memetic theory that could have impacted the way memeticists worked. However, many factors impact the success of scientific theories, for example, on the one

2. I am probably alone in using this term, but it is necessary for distinguishing between three possible levels of selection. Thus, I am using the concept of memetic selection to refer to the natural selection operating on memes as units of cultural information. Throughout this article, I will use also the term biological and genetical selection to refer to natural selection operating on genes.

3. "Is memetics the same as conventional cultural evolution theory (which is now growing fast), or different? If they are the same, I might as well give up on memetics! And are there testable predictions that would discriminate between them?" (Blackmore 2019).

hand, the logical coherence and correctness of their theoretical assumptions (for the review of these theoretical obstacles see Kundt 2015), on the other hand, external factors such as the political and ideological environment in which the theories are developed, as in the case of Lysenkoism (some of these external factors surrounding the first reception of memetics are discussed in Burman 2012). Therefore, it is necessary to note that this study admits all these factors to be of potential relevance in the case of memetics failure but focuses solely on one particular factor, which is the genealogical constraints occurring during the internal development of the theory. Thus, the present study is also a micro history—a case study<sup>4</sup>—that shows how the contextual factors which are not external nor strictly internal influence the way scientific theory changes and, in this case, even degenerate. I subscribe this way of doing historiography under the conception of “a philosophical history of science” (e.g., Burman 2017; de Freitas Araujo 2017).

My answer and the sketch of argument in this article goes as follows: Although the theoretical core of memetics was flexible enough to formulate different approaches, mainstream memeticists aimed to defend the position that a substantial part of human culture is decoupled from the reproductive fitness of the culture bearers. In doing so, memeticists needed to work out a clear ontology of memes to make memes equally as strong as concepts as genes, which is how the crucial part of the memetic research program was formulated and many self-proclaimed memeticists were theoretically committed to developing meme ontology. This could be illustrated by pointing out two parts of the memetic theory: While the majority of self-proclaimed memeticists have agreed upon the basic theoretical assumptions such as “culture as replicators” or “memetic transmission” (see the particular sections of this paper), when dealing with the question “what are memes?”, scholars formulated their own memetic ontologies achieving only a little consensus among the memeticists. On the contrary, GCCE theorists did not argue with each other about the empirically tricky questions such as ontology and, instead, developed a framework that allowed them to model and then test hypotheses about the dynamics of gene-culture coevolution. The analysis of the context of the origins reveals that the commitment toward the meme ontology and meme “selfishness” is the consequence of the way memetics originated in the heart of Dawkins’ defense of Williams’ anti group-selectionists arguments. On the other hand, GCCE emerged as a package of formal models examining the adaptive value of learning without any conceptual but only empirical commitments. The following sections elaborate on this argument, first introducing the two compared disciplines and later comparing the main differences leading to failure/success thereof.

4. The concept of “case study” is understood in the same way as in Burian 2001.

## 2. Memetics

The single term “memetics” provides a false notion that there is some unified theory of memetics. However, this is not the case. Rather, the concept of “memetics” and “memeticists” should be understood as emic terms that refer to how scholars themselves understand their own work and scientific identities.<sup>5</sup> Popular and controversial auras surrounding the meme concept during its beginning could contribute to the shared identity of those who called themselves “memeticists” even though that they were often lonely thinkers and the memetic framework has never been promoted to a research program or at least a research line. There was a broader circle of “memeticists” around the *Journal of Memetics* and tighter around Blackmore’s *Meme-Lab* but, overall, students of prominent “memeticists” rarely inherited the teachers’ theoretical heritage.

Thus, for the comparison it is necessary to remove the quotation marks from the words “memeticists” and “memetics” by defining what I refer to when using them. By memeticists I mean all authors who meet a first and then at least a second or third of the following assumptions: 1) explicitly endorsing Dawkins’ memetic legacy; 2) using the term meme with some explanatory strength for cultural dynamics; 3) publishing in the *Journal of Memetics*. There are also other potential indicators of being a memeticist. For instance, Susan Blackmore runs a webpage where she maintains a list of memeticists including lesser known scholars like Nicholas Rose, Paul Marsden, and Hans Cees-Speel. Nevertheless, this list is subjective, and it is probably the result of a very narrow relationship between people around the *MemeLab*. Another possibility is to use mutual citations as an indicator of being a memeticist; however, this would cast limitations on who to include in the analysis. For example, Dennett in his 2017 book does not cite Distin’s (2005), Jan’s (2007) or Aunger’s (2002) work. In other words, the memetic citation patterns probably do not create a community and, at the same time, the parameters that define what type of citation pattern counts as memetic would be necessarily subjective.

With the outlined understanding of who memeticists are, the memetics could be seen, in my view, as a “core-periphery” research project. The core memetic logic, which is accepted by all, was introduced above. The “periphery” term refers to very broad theoretical and philosophical areas that are derived from the core and flexible enough to afford a variety of positions in inter-memetics

5. I understand the term scientific identity in the way that sociologists do (Berger and Luckmann 1967). Scientists construct their scientific identities during interactions with their environment, that is through their connection with other scientists, journals where they publish, conferences that they attend and articles that they read. However, these constructed identities are perceived as reality by individual researchers.

discussions. The core memetics contains the conception of replication and the basics of memetic transmission. On the other hand, more detailed insights into the question how individual memeticists understood the key forces in the memetic evolution and the discussion about meme ontology produced substantial amount of disagreement and resulted variation within the theoretical framework.

### 2.1. The Core of Memetics – Replication and the Logic of Memetic Selection

Replicator can be understood as a general type of entity—while gene is seen as a biological replicator, meme is a cultural one (Distin 2005). That is, the gene is the unit of biological selection (for the concept of units of selection see Lewontin 1970), and analogically, meme should play the same role in the memetic evolution of culture. Natural selection, according to the general assumption, occurs when there is heritage (transmission), variation (mutation), and competition (resource-limited environment). The majority of memeticists agree that memes transmit through a type of social learning or, more specifically, imitation (Blackmore 1998; Jan 2007; Lynch 1991). Transmission by social learning necessarily involves random errors but, as opposed to genetic transmission, also intentional variation, which occurs when people intentionally change the content of memes. However, this is not a conceptual problem for calling the process natural selection, since, according to Distin (2005), the conscious human changes in meme content are blind to what is the best strategy in a particular environment. Competition among memes is created and facilitated by space limits in human memory which memes compete for. Memes are successful when they attract the attention of people and stay in their memory long enough to start and complete another transmission process.

Since meme is another autonomous replicator, it is not principally dependent on biological evolution. This means that not all of the evolved cultural features (memes or their co-adapted complexes, namely memeplexes) must necessarily function as adaptations increasing the reproductive fitness of their bearers. Memes primarily increase their fitness whereas increasing the fitness of their bearers (humans) is only one of many possible ways to do so.

The outstanding question is what makes memes successful? The core memetics proposes that memes compete for human attention and a place in human memory. In this case, the success of memes is determined mainly by human psychology. Cognitive evolutionary scientists have identified several themes and subjects that are very successful in attracting our attention and based on these findings, Brodie says that memes could be successful because they can “push one or more of these four buttons—anger, fear,

hunger, and lust” (Brodie 2009, p. 76). Another feature of memes, which is dependent only on their content and which makes them successful, is the so-called “evangelism.” These are memes or memplexes containing an instruction for spreading (Dawkins 1993). However, memes can also travel in other memplexes without contributing to the success of the whole memplex (Brodie 2009). This conceptual separation of biological and memetic fitness, according to memeticists, opens up a new area for explanatory possibilities. The most significant contribution of memetics lies, according to its prominent advocate Blackmore, in the fact that it can explain cultural maladaptations, i.e., traits that decrease the reproductive fitness of its bearers, e.g., religion (Blackmore 1999; Dawkins 2007).

## 2.2. The Periphery of Memetics – Who (Mainly) Benefits and Where Memes Are?

However, some memeticists, though not many, argued that memes could also contribute to the reproductive fitness of their bearers to promote memetic fitness (Delius 1991). For example, Gottsch (2001) published a paper in *Journal of Memetics* where he proposed a framework for understanding successful transmission of “theistic” memes based on the idea, that those memes, compared to alternatives, contribute to the reproductive fitness of their bearers. Blackmore (1999) argued, that memes provided their bearers with reproductive advantages at the beginning of the memetic evolution but later, when the whole cognitive apparatus simplifying transmitting and receiving memes evolved in humans, memes broke the imaginary chain that made them subordinated to genes. From that time, memes were predominantly increasing memetic fitness and often creating biological maladaptations such as ideologies and religions that are attractive for human cognition but with negative consequences for human fitness. In Blackmore’s (1999) view, this process was also facilitated by runaway dynamics of sexual selection. The view of religion (and other cultural phenomena) as cultural trait with maladaptive effects on human genetic fitness was also proposed by Dennett (2006), Dawkins (1993) and Brodie (2009).<sup>6</sup>

Though the interpretation of the conceptual separation of genetic and memetic fitness produced some discrepancies between memeticists, much higher variation in ideas was produced in the field of meme ontology. In other words, memeticists have never agreed upon the question where/what memes are. Wilkins (1999) differentiates between two basic camps: identifying those

6. Note that GCCE does not a priori oppose the claim that some cultural variants may be maladaptive (at least in some socio-ecologies; see Richerson and Boyd 2001). The difference is that the mainstream memeticists made this the central claim of their theoretical framework without enough empirical evidence.



who put memes into the brain or mind as “pro-head” memeticists while those who put memes outside the mind as “anti-head.” I will use this categorization to describe the two basic camps. However, even inside these camps, researchers did not fully agree upon the precise definitions.

### 2.3. “Pro-Head” Ontology of Memes

The first inceptions of the pro-head ontology can be traced back to Dawkins (1982a) who considered human behavior to be the result of memes’ phenotypic effects. This idea was particularly expanded by Delius who proposed that memes are units of information stored in the physical and chemical structures of memory—in the “synaptic constellations” (Delius 1991, p. 83). However, he argued that memes are not themselves neural constellations but instead just meanings stored in them. The meaning and thus the function of the meme could be the same even when it is stored in different constellations (Delius 1991). This argument can be illustrated by the metaphor: The same information, for example, a song, can be carried on vinyl or a CD (compact disk).

A similar position is held by Aunger and Lynch. Aunger (2002) claimed that a meme is a neuronal arrangement of one or more neurons into nodes. He argued that “They [memes] are, in fact, electrical things—propensities to fire—tied to the special type of cells called neurons (but are not the neurons themselves)” (Aunger 2002, p. 196–197). In other words, memes are extremely short states of mind. Lynch (1998) created his own terminology of mnemons that he defined as abstract memory forms such as ideas, attitudes or habits. Only mnemons that enter the mind as copies of other mnemons and not situations themselves, are memes. For example, when an earthquake erupts, many people have the mnemon of it, but it is derived from the earthquake, and hence it is heteroderivative mnemon, not a meme (Lynch 1991). However, when the earthquake is in the evening news and the reporter talks about it, the mnemon of the earthquake becomes homoderivative, and thus it is a meme. Finally, to fully illustrate the variance in the memetic ontology of pro-head scholars I briefly mention Distin’s view. She considers memes to be mental representations with a phenotypical effect outside the mind. She views memes to be information inside the brain whereas behavior and physical objects are its phenotypes, which natural selection operates on (Distin 2005).

### 2.4. “Anti-Head” Ontology of Memes

While the first group of memeticists puts memes into the brain or mind, the second group puts memes outside of the human body. For example, Benzon (1996) considers memes to be the whole of physical culture, such as pots, knives, written words, radios, songs, and paintings. Ideas, desires,

and emotions behind these physical entities are then analogous to the phenotype (Benzon 1996). Similarly, Gatherer (1998) argues that memetics should be anchored mainly in the methodology of population thinking that can count material objects. This is not possible with the pro-head approach focused on mental representations as mathematical tools are of no use in this case. The second reason to put memes outside of the brain, according to Gatherer, is one of the pitfalls of the former approach: namely, that it is not able to explain why memes are spreading. The reasoning is that we cannot distinguish between copying and other forms of transmission. As a consequence of these problems, he places memes outside of the brain.

The last anti-head memeticist introduced is Sterelny (2006). Overall, Sterelny is skeptical about the possibility of explaining the cultural dynamics from the perspective of memes but should he admit their usage in the cultural realm at all, he would place them into human-made artifacts. He introduces two reasons for this proposition. The first reason is that the information does not copy itself; rather, it is re-constructed again through innate or acquired cognitive modules of the human mind/brain. The second reason is that when we place memes into the mind it is not clear what memes should compete with as there is no useful memetic analogy to the alleles which are, in biology, particular forms of individual genes (e.g., the gene for an eye color can have an allele for green or for blue eyes). According to Sterelny (2006), if we think about memes as artifacts, the problem is easier to solve. For example, different spears compete for the tool status, which is how the variant is spread among the population of spears that are actually created and used.

## 2.5. Other Approaches

It may appear puzzling that I did not include Blackmore and Dennett in these two categories of meme ontology. This is because, in my interpretation, neither of these two leading memeticists fits the criteria for the “pro-head” and “anti-head” distinction introduced above, which adds extra variation within the memetic periphery area.

Blackmore does not address the meme ontology. She argues that Darwin himself did not have a gene unit at his disposal, and yet he was able to formulate the theory of natural selection. Thus, she defines a meme as anything that could be passed on by imitation and then she focuses on applying the memetic logic to certain cultural phenomena. Moreover, she prefers to use the term memplexes instead of simple meme terms when she describes the real-world memetic dynamics, and this allows her to avoid the problem with the question of where a particular meme begins and where it ends. Memplexes are groups of mutually co-adapted memes that occur together as one package since this has proven to be more successfully

transmitted compared to other memes (or memplexes) in the population of memes (Blackmore 1999). This logic recalls the application of a group selection approach on the level of memes even though memeticists did not label this process as “memetic group selection”. However, in general, memeticists did not develop the concept of group selection in more detail or, following Dawkins (2006), were even opposed to it, which will be discussed later in the article.

In Dennett’s case, it is difficult to decide where he places the memes. On the one hand, he talks about a new entity—a person—created when memes furnished and re-structuralized human brains (Dennett 1995). On the other hand, he names pictures, books, words, and tools as meme vehicles. However, when we follow the gene analogy—the vehicles containing the replicators that created them—it follows that memes are embodied in artifacts. In his latest advocacy of memetics, he explicitly claims, that “The theory I am [Dennett is] defending declares, non-metaphorically and literally and without caveat, that words are memes that can be pronounced” (Dennett 2017, p. 224). In an answer to another objection, he adds that memes are not only words but also their written codes, ways of making arrows, axes, cooking, music, dancing and other traditions (Dennett 2017). Based on these assumptions, we can categorize him as both “pro-head” and “anti-head” ontology.

Finally, there were also other discussions where memeticists did not achieve mutual agreement. Some of them were more than less conceptually linked to the debate about ontology, namely the debate about proper memetic analogies of concepts widely used in genetics such as “genotype” (memotype)/phenotype distinctions (e.g., Benzon 1996; Distin 2005; Rose 1998) or memetic alleles (e.g., Dennett 2017; Distin 2005; Sterelny 2006). Another discussion carried in *Journal of Memetics* was connected to the transmission of memes and the extent to which only imitation (Blackmore 1998) or also other forms of social learning (Laland and Reader 1999) are at play.

### 3. Gene-Culture Coevolution Theory

The term “gene-culture coevolution theory” also evokes the appearance of one synthetic framework and although it definitely went through some debates and significant changes during its development, it can be said that it represents a much more complete account of the evolution of human culture and nature than memetics. For example, I am using “GCCE” (gene-culture coevolution) rather than DIT (dual-inheritance theory) or simply cultural evolution. While DIT is used by Boyd and Richerson (1976), in my view, it no longer reflects the scope of the theory. It is because during twentieth century, the formal models presented mainly by Richerson and Boyd described only the way biology designed human ability to learn

and imitate as well as the dynamics of multiple types of cultural transmission. However, today the crucial aspect of the theory is the feedback loop between culture and genes which is responsible for countless of human genetical adaptations (Henrich 2016). Cultural evolution, on the other hand, is too broad a concept and it would lead to conceptual confusion when comparing with memetics. Thus, by GCCE I mean the early work of Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) on populational thinking about cultural evolution and the further work that built on those models, for example, recent experimental, cross-cultural and ethno-historical examinations of the basic psychological and cognitive assumptions and advanced hypotheses such as *cultural group selection* (Richerson et al. 2016), *tribal instincts* (Richerson, Boyd, and Henrich 2003), and *moralizing gods* (Norenzayan et al. 2016). I understand the models of adaptive value of social learning and basic models of transmission biases as the core of the theory that stands in opposition to the memetics' focus on replicators, and the additional GCCE hypotheses and different methodological perspectives as the more flexible part during the diachronic theoretical development. However, unlike memetics, GCCE's two parts are highly consistent with each other, and also the variety of approaches within the second part of GCCE development coherently contributes to a mutual consensus. At the sociological level, GCCE shows the coherence also at the level of relationships between scientists. We can draw the imaginary line from Richerson and Boyd through Henrich to Muthukrishna while the institutional stability of the approach is established by multiple big projects (e.g., PULOTU, Database of Religious History) and recently by an official organization called *Cultural Evolution Society*.<sup>7</sup>

### 3.1. Culture without Replicators

GCCE does not consider replication to be the central assumption of the evolutionary theory but works with a more general term—heredity (Richerson and Boyd 2005). Consequently, GCCE proponents conclude that there is no natural selection of cultural units assumed by memetics. Instead, natural selection operates primarily on behavioral phenotypes created by genetic and cultural transmission, and their interactions with environmental conditions. This is why the theory was originally called the “dual-inheritance theory” (Boyd and Richerson 1976): cultural species individuals are understood as entities subject to two systems of inheritance. The first system is the inheritance of biological traits and the second is the inheritance of cultural traits. However, proponents of GCCE do not posit a priori separation of cultural and genetical natural selection.

7. See the websites for individual projects: PULOTU (<https://pulotu.shh.mpg.de>), DRH (<https://religiondatabase.org/landing/>), and Cultural Evolution Society (<https://culturalevolutionsociety.org>).

In other words, whereas memetics understands natural memetic selection as operating on memes (that is, on units of cultural replication with their own reproduction fitness) and separated from natural selection acting on genes, natural selection in the GCCE framework operates on cultural variants (as memetic selection does) but also on individuals or groups. As a result, cultural and genetic variants that generated relatively less adaptive phenotypes (behavior) do not proceed to next generations. Therefore, the conceptual distinction of cultural and genetical selection would create a false dichotomy within GCCE. Two independent definitions of natural selection cannot be derived as there are no two types of different replicators in the GCCE framework. Genetic selection and “memetic” selection are two sides of one coin—single concept of natural selection—and there is no reason to treat them separately.

### 3.2. Evolutionary Dynamics within the GCCE Framework

Cultural transmission differs from genetic transmission in several aspects, which makes natural selection only one of several forces active in cultural evolution. First, cultural information is transmitted by people from the mind to the mind. Therefore, human psychology is a crucial factor that affects what information will be transmitted and in what direction.

Cavalli-Sforza first suggested that while genes are transmitted only vertically from parents to offspring, other types of transmission are present in cultural transmission, for example, from older to younger individuals who are not descendants of the older, between individuals within one generation, or by a combination of these two channels. The first combination is a “many-to-one” transmission, in which many others influence one individual. This transmission is essentially social pressure preserving cultural traits in the population. The second type is a “one-to-many” transmission, in which many individuals learn from one single individual. This is extremely important because due to this process, cultural transmission becomes much faster than genetic transmission and can very quickly stabilize a cultural trait within the population (Cavalli-Sforza 1986).

The concept of many-to-one transmission has developed into models of conformist and prestige biases sometimes known as context biases. The fundamental postulate is that in a population where individuals learn from random individuals, it is unlikely for any adaptive trait to be retained and stabilized. Therefore, Henrich and his colleagues argued that natural selection favors those individuals who are subject to a particular type of prejudice consisting of learning the most common traits among the population (Henrich and Boyd 1998) or the traits of most successful individuals (Henrich and Gil-White 2001). These learning biases reduce cultural variation within the group and allow learners to learn the most likely adaptive traits for the given conditions. After the introduction of the methods of

experimental psychology into the previously mainly modeling framework of GCCE, these two types of preferential transmission have begun to be tested in a laboratory environment. If participants had the information about the success of a model, they imitated those who were more successful. When the models had the same success on average, the participants imitated a more common strategy (McElreath et al. 2008).

Similar developmental pattern of theoretical considerations and later empirical examinations with variety of methods could be found in the research on other types of evolutionary forces such as content biases (Mesoudi 2016; Mesoudi, Whiten, and Dunbar 2006; for non-GCCE approach called cognitive attraction see Sperber 1996) or cultural drifts and dynamics behind reduction of cultural complexity (Drexler et al. 2013; Henrich 2004b; Muthukrishna et al. 2013).

### 3.3. Cultural Group Selection (CGS)

Contrary to memeticists, GCCE theorists explicitly proposed the cultural form of group selection as one of the fundamental contributions of GCCE to evolutionary sciences (Richerson et al. 2016). They employed CGS to answer specific standing puzzles about human behavior such as large-scale anonymous cooperation. The traditional concept of group selection (Wynne-Edwards 1962) proposed that altruistic behavior, which appears to be disadvantageous to individuals, is the result of selection between groups of individuals. Groups consisting of individuals who behave altruistically will be favored at the expense of those groups in which individuals behave selfishly, even if some forms of altruistic behavior are disadvantageous to the individuals themselves. Williams (1966, 1992) rejected this argument because it would assume that animal groups contain sufficient genetic variation and almost zero migration, and that group extinction rates are frequent enough (sometimes more frequent than the death rates of individuals) for selection among groups (inter-group selection) to overcome selection within groups (intra-group selection). According to Williams (1966), these conditions are just not fulfilled in reality, except for the occasional exceptions.

However, GCCE theorists emphasize the role of culture in the process of group selection (Henrich 2004a; Richerson and Boyd 2005), which provides them with a strong argument against Williams. First, the groups are protected by cultural boundaries and thus maintain high intragroup homogeneity and intergroup variation, even in the case of high migration rates (Richerson and Boyd 2008). Second, individuals from one group can imitate individuals from a more successful group (Boyd and Richerson 2002). Third, the extinction of the group does not require the physical death of all its members. Instead, they may be absorbed by a more successful

group or the better cultural variant may attract more migrants from neighbors who recognize that the group is more successful than their own (Boyd and Richerson 2010). In other words, points two and three indicate that cultural transmission accelerates the frequency of group extinction. As a result, the cultural version of group selection fits Williams' criteria. Moreover, Soltis, Boyd, and Richerson (1995) tested their CGS hypothesis with data from Papua New Guinea, investigating how often culturally defined groups become extinct and whether the cultural variation between groups affects the survival rates of these groups for long enough so that CGS could operate on these groups. They calculated that CGS operates within the range of 500 to 1000 years and thus provides the required empirical support for the CGS hypothesis.

### 3.4. Coevolution of Culture and Genes

While it was argued in the previous paragraphs that genes together with the process of natural selection shape culture, GCCE proponents argue that culture may also impact gene frequencies. Cumulative cultural evolution creates a stable environment, which in turn, applies selective pressure on individuals and favors those who can better exploit the opportunities that culture brings about. The most common example of the coevolution of genes and culture is the spread of the gene that controls the production of the lactase enzyme, which allows its bearer to break down lactose, milk, and sugar. In most cases, lactose intolerance begins at around the age of five. The ingestion of milk may then cause serious health issues. However, the majority of European and American population is lactose tolerant after the age of five (they developed lactase persistence). According to the logic of coevolution of culture and genes, the reason is that this particular gene spreads together with the cultural trait of animal domestication. The sooner cattle farming is adopted in a specific world region, the higher the distribution of the lactose-digesting gene is found within its population. The reason is that mutants who were able to benefit from the high availability and nutritional value of milk, even after reaching five years of age, had an advantage over those who could not (Henrich 2016; for more comprehensive review see Gerbault et al. 2011).

One of the most critical hypotheses based on the concepts of CGS and the coevolution of genes and culture is the "tribal social instincts hypothesis" (Richerson et al. 2003). This hypothesis serves to explain human cooperation in large anonymous groups. The argument is that CGS first created cultural social institutions that were maintained by social sanctions. This means that if the individual does not follow the standards of the institution, the rest of the group will often restrict his/her access to essential resources or ostracize this individual. The existence of these standards gives the group

an advantage because it reduces intragroup conflict and minimalizes defection. Social institutions then create a new selective environment that favors individuals with the psychology that allows them to live more easily within these norms. People who have, for example, emotions of shame, guilt, empathy, ethnic identity, and hatred (Gintis et al. 2003) are better prepared to obey social norms within a given group and are less often subject to social punishment or ostracism. Therefore, individuals with these emotions are more likely to survive long enough and to be successful in the reproduction market in such a norm-structured society (Boyd and Richerson 2008).

#### 4. Comparison

When we compare the diachronic development and basic conceptual apparatus of both theories on a very general level, several clear differences are striking. These are coherence, adaptationist view of culture, cultural group selection, ontology and diachronic development. However, the question is whether and how these differences contributed to the memetic failure. I argue, that the crucial aspect of coherence was predominantly adaptationist approach to culture taken by GCCE scholars which was impacted by the context of the origin as mathematical models of human ability to learn socially. Also, the later development proved to benefit from the adaptationist perspective because the adaptationist models allowed to derive and test numerous predictions. The environment around GCCE that was not loaded by gene-centered and anti-group-selectionist ideology allowed the formulation of an hypothesis of cultural group selection which in turn helped with developing projects around *moralizing gods* and *tribal instincts hypotheses* in interaction with culture-gene coevolution. Contrary, memeticists found themselves struggling with meme ontology as they needed to meet the requirements of the memetic ideological heritage.

The difference in the level of the theory's inner coherence is striking. On the one hand, GCCE shows high levels of mutual consensus between the first (Boyd and Richerson), second (Henrich) and third (Muthukrishna) generation of researchers while two recent generations built on the concepts and findings of the first generation. On the other hand, memetics resembles a partially connected network of lonely thinkers. The fragmentation of memetics is clearly evident from the example of ontology which was, from the beginning, project with very dubious point since the ontological claims lacked either the semantical structure of testable propositions or the tests were impossible to perform with the actual technological equipment (Coyne 1999). The lack of aspiration for being tested explicitly was admitted by Dennett when he attempted to immunize memetics by claiming that it stands on behalf of scientific approach to



culture.<sup>8</sup> For self-proclaimed memeticists, it was subjectively crucial to work on meme ontology if they wanted to further develop the theory. After all, finding a structure that carries memetic information would legitimize the postulation of the second memetic replication system in the same sense that finding a physical gene has legitimized evolutionary biology. If there is a second replication system, it must be anchored somewhere, otherwise the natural memetic selection does not have anything on which to operate. The same factor also led memeticists to develop analogies to other concepts from genetic evolution such as memetic “genotypes” (memotypes)/phenotypes or memetic alleles. However, above I showed that the logic of memetic selection did not automatically assume empirical separation of genetic and memetic fitness and the core memetic logic allowed for genetically adaptive understanding of memes and memplexes. The question that now needs to be investigated and answered is what constraints within the development of the theory committed the majority of memeticists to work on ontology and to adhere to the non-adaptive, virus-like approach to culture (Blackmore 1999; Brodie 2009; Dawkins 1993; Dennett 1995; Lynch 1996). In answering the question, I will proceed to compare the context of the origins of both theories.

Memetics originated as a single chapter in one book (Dawkins 2006, chap. 11). One of the primary aims of *The Selfish Gene* was to popularize and develop Williams’ (1966) arguments for a gene-centered view in evolutionary biology. Williams argued that the ultimate unit of selection in biology is a gene; not an individual and not a group of individuals. Dawkins (2006) developed Williams’ (1966) approach in such a way as to make the concept of evolution more general. He argued that genes are replicators and that replicators are substrate-independent entities that transfer information. To clarify his argument, he introduced an example of another possible replicator, namely the memes. The function of that chapter was originally not to introduce a full theory nor had he an ambition to do it. Dawkins’ chapter on memetics was rather a pedagogical tool that had to help readers to understand the logic of replicators. Burman (2012) argues that with this in mind it is no surprise that it took approximately one decade for the meme concept to become famous and that this success is thanks to Dennett, and Hofstadter transferred Dawkins’ original pedagogical argument to the new context of serious mind investigations all reprinted in a popular edited collection without any explanation (Hofstadter and Dennett 1982).

8. “It might be, for example, that, although the processes of cultural transmission of ideas are truly Darwinian phenomena, for various reasons they resist being captured in a Darwinian science, so we will have to settle for the ‘merely philosophical’ realizations we can glean from this, and leave science to tackle other projects” (Dennett 1995, p. 346).

Modern biology is built on the concept of a gene that is considered to be the replicator. The gene-centered approach to biological evolution, currently the only feasible paradigm in biology, cannot consider evolution without genes or gene-like units. The context of the origins of the gene-centered evolutionary theory and the authority of Williams and Dawkins made it imperative to search for the units of cultural selection. Scholars who understood themselves as memeticists had to accept another part of the memetic researcher identity, namely the rest of Dawkins-Williams argumentation. Replicator-centered view of evolution and the idea of culture as an entirely natural (evolutionary) phenomenon together constructed the identity of the memeticist. Thus, memeticists inherited a fascinating idea of cultural evolution but also the commitment to replicators. The idea of cultural replicator, however, was not a properly built scientific concept but only a popular analogy and the process of developing the concept and the physical unit of the gene was entirely different from the process of developing a meme and its ontology, leading to the scientific success of the former but not the latter concept.

In the case of the gene-centered evolutionary theory, there was first the work of Gregor Mendel on pea crossing and then the independent theory of natural selection which were later, after many conflicts between Mendelians, embryologists, statisticians, paleontologists, and other biologists, fused into the modern evolutionary synthesis (Sapp 2015). Subsequently and independent of the development of the evolutionary theory, molecular biologists identified the genetic information in the physical structure of DNA (Watson and Crick 1953). Thus, when Dawkins made his generalization from a gene to a replicator, he already knew that there is an exact physical ontology of the gene. However, when he introduced the abstract concept of a replicator into the study of culture, memeticists had no previous work analogous to the work of Watson and Crick at their disposal. What they had was limited to a highly speculative argument about a substrate-independent replicator. They posited the existence of a meme and then tried to ontologically capture memes in the same way as genes were ontologically captured by Watson and Crick (1953). This obsession was due to the argumentation from which memetics emerged, namely that there can be no adequate theory of evolution using natural selection without the units of replication.

The diachronic development of the meme ontology may be reconstructed as follows: first, there was an ontology of the gene (DNA); second, Dawkins made an inference from gene to a general replicator; subsequently, he inferred from a replicator to a meme. Thus, the “hunt” for the ontology of memes commenced. The process of the emergence of meme ontology was precisely opposite that of the process of the emergence of gene concept.

On the other hand, GCCE diachronic genealogy is akin to evolutionary biology. It began as the package of formal mathematical models exploring

the adaptive value of the organism's ability to have a culture through the lens of populational thinking. Authors of GCCE explicitly stated that in populational thinking they were inspired by Darwin. Although this statement, moreover when proposed retrospectively (Richerson and Boyd 2001), could represent the need for having big father founders to legitimize the existence of system of ideas that scientific theory definitely is, it also shows how authors themselves perceived their theory. They did not understand it as a new paradigm unifying all social sciences like some of memeticists (Brodie 2009; Gatherer 1997; Lynch 1996), but they linked their ideas and approaches to Darwin and also Campbell (Richerson and Boyd 2001) who did not have the concept of units of selection at their disposal. Boyd and Richerson developed their ideas from the beginning as a systematic theory for understanding cultural change not by first publishing the overall framework, but with small pieces of formal evidence (Boyd and Richerson 1976, 1983, 1995, 1996). Their first book on GCCE was, rather than popular introduction of the whole theory, another set of formal models (Boyd and Richerson 1985). In their second book, they admitted that they were not interested in the question of ontology and that they worked with phenotypical depictions of cultural traits similar to the way behavioral ecology works with behavioral traits without saying anything about the genes (Richerson and Boyd 2005). Contrary to memeticists, GCCE scholars were committed to an adaptationist perspective that is present within evolutionary ecology and protected from being primed by the replicator-based style of thinking, opening up the possibility of uniting scientists from various disciplines under one theoretical umbrella and dealing with the subsequent empirical challenges.

Note that my claims about adaptationist and ontology commitments do not represent evaluative propositions. The logic underlying these claims results from the theoretical assumption presented in the introduction. The quantity of scientists working with the theory "creates" its success and working with the theory in most cases means to test it. Thus, although it is not clear whether the adaptationist paradigm is objectively better for evolutionary sciences than, for example, the "by-product" paradigm (Gould and Lewontin 1979), the approach that allows for more predictions will attract more empirical scientists.<sup>9</sup> Following this logic, to make the core of the theory general enough allows for an increase in the number of scientists working with it. However, one also has to ensure that the interdisciplinarity will not split the

9. In a recent article, Muthukrishna and Henrich (2019) argue that the current crisis in psychology is caused by lack of proper formal general theory with clear predictions rather than by poor methodology. According to their subsequent argumentation, GCCE is one of the examples of such a needed theory.

theory, which, in comparison with GCCE, happened to memetics when diverse educational backgrounds divided memeticists in their thoughts on meme ontology. The adaptationist (yet not entirely adaptationist; see Richerson and Boyd 2001) orientation of GCCE more likely connected the theory with measurable reality, which in turn, precluded GCCE researchers from speculation-driven splitting up. What benefits can we assign to adaptationist perspective on culture in GCCE?

First, adaptationism enabled researchers to formulate more detailed predictions about cultural variability, behavior, and its impact on biological fitness. Inversely, the focus on decoupling memetic fitness from the biological fitness means, for instance, that cultural practices should spread independently of ecological factors and thus the status of its hypotheses is similar to the null hypotheses (Linguist 2016).

Second, it allowed formulating the coevolutionary aspect of the theory with clear-cut predictions about variation in gene frequencies in world populations (e.g., Chiao and Blizinsky 2010). Memeticists also introduced a hypothesis that could be called coevolutionary, such as the hypotheses of big brains (Blackmore 1999). According to this hypothesis, once memes appeared, they applied selective pressure on genes to create better imitators and thus bigger brains. This process, possibly influenced by the runaway acceleration of sexual selection, eliminated those individuals who were not good at imitation, even though the memes which they imitated could be disconnected entirely from the individual reproductive fitness. This logic is also applied in other memetic hypotheses as well, for example, the explanation of language (Blackmore 1999; Vaneechoutte and Skoyles 1998) or consciousness (Dennett 1991). However, similar to the argument in the previous paragraph, due to the decoupled memetic and biological fitness, it is not clear under which ecological circumstances should the meme-gene coevolution occur and how to test it.

Third, the adaptationist view of culture enabled GCCE researchers to build on the robust functionalist tradition in anthropology that dates back to Durkheim (2011) as well as on more recent ecological anthropology (Rappaport 1968) and human behavioral ecology (Cronk 1991) projects. In contrast, memetics was supposed to be a “new science” (Brodie 2009) and a new scientific paradigm (Lynch 1996) built on older less-known French sociology (Marsden 2000) that detached itself from well-established disciplines such as more traditional functional and cultural anthropology (Douglas 1966; Rappaport 1979) and behavioral ecology (Cronk 1991).

Finally, the adaptationist view enabled theorists to also develop the concept of CGS, which in turn, led to GCCE theories of human ultrasociality (Boyd and Richerson 2009; Richerson and Boyd 1998; Richerson et al. 2003; Tomasello 2009; Turchin 2016). On the contrary, the pioneer of

memetics Dawkins (1982b, 2006) explicitly built on the ideas of Williams (1966) who argued against group selection in biology. Thus, one would expect that memeticists did not utilize any ideas of the contemporary group—today called multi-level—selectionists (Wilson and Sober 1989; Wilson et al. 2008). However, this was not the case. They utilized group selection logic exactly when they theorized about memplexes because they understood memplexes as groups of memes ideally spreading as units (Blackmore 1999). Therefore, ideologies and religious doctrines could be understood as “memetic group adaptations.” This *prima facie* confusion arises due to the differences in the concept of natural selection. There is just one concept of natural selection in the GCCE framework whereas there are two separate concepts of natural selection in the memetic framework with each of these operating separately on different replicators. Memeticists then focused on the selection operating on cultural units where, as we could see, they employed the logic of group selection. However, they did not have the necessary theoretical apparatus to develop the CGS concept in the same way as GCCE, namely, to grasp theoretical “memetic group selection” as operating on groups of people. Therefore, their anti-group-selectionist theoretical heritage of the argument (Dawkins 2006; Williams 1966) from which memetics emerged prevented them from using the concept of group selection in the same way as the proponents of GCCE did. This also prevented them from even using the term in the memetic realm although they worked with the very same logic when dealing with memplexes.

## 5. Conclusion

Two theories of cultural evolution were analyzed and compared in this study, namely memetics and culture-gene coevolution theory. The goal of this comparison was to unmask the causes of the historical failure of memetics. I compared both theories on the theoretical level and also on the level of their diachronic development. The conclusion is that the failure of memetics lies in its overly constrained origins in gene-centered argumentation in evolutionary biology and in Dawkins’ authority that pre-determined all the scholars who wanted to work within the framework of memetics to preoccupy themselves with the strict separation of memetic and genetic fitness and with the ontology of memes, as opposed to the formulation of empirically testable hypotheses. Compared to GCCE, this, in turn, made memetics less attractive to empirically oriented scientists.

Nevertheless, it would be naive to consider my explanation to be the only one. I see two possible additional factors that are, in my view, complementary to the approach taken in this study. First, Burman (2012) found the connection between the fast and sudden spread of memetics during the late 1980s and 1990s and the rise of individualistic ideologies in the USA

and Great Britain. We can speculatively extend this link to our question and ask whether these ideologies could not shield memetics against the concepts of adaptiveness and cultural group selection. The second possible factor is the way memetics was publicized and disseminated, namely very often in popular books without peer reviews and open scientific discussion (e.g., Brodie 2009; Tyler 2011).

Finally, I consider this study to be only an attempt at explaining why memetics is no longer in the mainstream in the study of the evolution of human culture. Here, I also stress the notion from the Introduction that this work should be understood as an attempt to do micro history case study of modern science rather than a final analysis. I see three possible ways of future research arising from it. The first is to examine the precise similarities and differences in the development of the gene and meme concepts, which would require an extensive study of the history of biological disciplines in the first half of the twentieth century. The second is to focus more on the sociological aspects and ask whether there were any external factors impacting the gradual rejection of memetics, such as the number of more senior researchers among memeticists, the number of grants awarded, and therefore the amount of money that was available to them, or the analysis of the arguments of Dennett and Dawkins in their public debates to determine whether they used memetics as an ideological anti-theistic tool. Finally, following recent debates on the intersection between history and philosophy of science (e.g., Arabatzis and Schickore 2012; Araujo 2017), this micro-historical analysis should be framed within a broader picture of how scientific theories evolve, change and “die.”

## References

- Arabatzis, Theodore and Jutta Schickore. 2012. “Introduction: Ways of Integrating History and Philosophy of Science.” *Perspectives on Science* 20(4): 395–408.
- Araujo, Saulo Freitas. 2017. “Toward a Philosophical History of Psychology: An Alternative Path for the Future.” *Theory and Psychology* 27(1): 87–107.
- Atran, Scott. 2001. “Trouble with Memes: Inference versus Imitation in Cultural Creation.” *Human Nature* 12(4): 351–381.
- Aunger, Robert. 2002. *The Electric Meme: A New Theory of How We Think*. New York: Free Press.
- Benzon, William. 1996. “Culture as an Evolutionary Arena.” *Journal of Social and Evolutionary Systems* 19(4): 321–362.
- Berger, Thomas L. and Thomas Luckmann. 1967. *The Social Construction of Reality: A Treatise in the Sociology of Knowledge*. London: Penguin Books.
- Blackmore, Susan. 1998. “Imitation and the Definition of a Meme.” *Journal of Memetics* 2. [http://cfpm.org/jom-emit/1998/vol2/blackmore\\_s.html](http://cfpm.org/jom-emit/1998/vol2/blackmore_s.html)

- Blackmore, Susan. 1999. *The Meme Machine*. Oxford: Oxford University Press.
- Blackmore, Susan. 2016. "Memes and the Evolution of Religion: We Need Memetics, Too." *Behavioral and Brain Sciences* 39. <https://doi.org/10.1017/S0140525X15000357>
- Blackmore, Susan. 2019. Personal website. <https://www.susanblackmore.uk/memetics/memelab/>. Accessed 7 December 2019.
- Bloch, Marc. 2000. A Well-Disposed Social Anthropologist's Problems with Memes. Pp. 189–204 in *Darwinizing Culture: The Status of Memetics as a Science*. Edited by R. Aunger. Oxford: Oxford University Press.
- Boyd, Robert and Peter J. Richerson. 1976. "A Simple Dual Inheritance Model of the Conflict between Social and Biological Evolution." *Zygon* 11(3): 254–262.
- Boyd, Robert and Peter J. Richerson. 1982. "Cultural Transmission and the Evolution of Cooperative Behavior." *Human Ecology* 10(3): 325–51.
- Boyd, Robert and Peter J. Richerson. 1983. "Commentary: Why Is Culture Adaptive?" *The Quarterly Review of Biology* 58: 209–214.
- Boyd, Robert and Peter J. Richerson. 1985. *Culture and the Evolutionary Process*. Chicago: The University of Chicago Press.
- Boyd, Robert and Peter J. Richerson. 1995. "Why Does Culture Increase Human Adaptability?" *Ethology and Sociobiology* 16: 125–143.
- Boyd, Robert and Peter J. Richerson. 1996. "Why Culture Is Common, but Cultural Evolution Is Rare." *Proceedings of the British Academy* 88: 77–93.
- Boyd, Robert and Peter J. Richerson. 2000. Memes: Universal Acid or a Better Mousetrap? Pp. 143–162 in *Darwinizing Culture: The Status of Memetics as a Science*. Edited by R. Aunger. Oxford: Oxford University Press.
- Boyd, Robert and Peter J. Richerson. 2002. "Group Beneficial Norms Can Spread Rapidly in a Structured Population." *Journal of Theoretical Biology* 215: 287–296.
- Boyd, Robert and Peter J. Richerson. 2008. "Gene–Culture Coevolution and the Evolution of Social Institutions." Pp. 305–324 in *Better than conscious? Decision Making, The Human Mind, and Implications for Institutions*. Edited by C. Engel and W. Singer. Cambridge, Mass.: MIT Press.
- Boyd, Robert and Peter J. Richerson. 2009. "Culture and the Evolution of Human Cooperation." *Philosophical Transactions of the Royal Society B: Biological Sciences* 364: 3281–3288.
- Boyd, Robert and Peter J. Richerson. 2010. "Transmission Coupling Mechanisms: Cultural Group Selection." *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3787–3795.

- Brodie, Richard. 2009. *Virus of the Mind: The New Science of the Meme*. Carlsbad: Hay House.
- Burian, Richard M. 2001. "The Dilemma of Case Studies Resolved: The Virtues of Using Case Studies in the History and Philosophy of Science." *Perspectives on Science* 9(4): 383–404.
- Burman, Jeremy Trevelyan. 2012. "The Misunderstanding of Memes: Biography of an Unscientific Object 1976–1999." *Perspectives on Science* 20(1): 75–104.
- Burman, Jeremy Trevelyan. 2017. "Philosophical Histories Can Be Contextual without Being Sociological: Comment on Araujo's Historiography." *Theory and Psychology* 27(1): 117–25.
- Cavalli-Sforza, Luigi L. 1986. "Cultural Evolution." *American Zoologist* 26(3): 845–855.
- Cavalli-Sforza, Luigi L. and Marcus W. Feldman. 1981. *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton: Princeton University Press.
- Chiao, Joan Y. and Katherine D. Blizinsky. 2010. "Culture-Gene Coevolution of Individualism/collectivism and the Serotonin Transporter Gene." *Proceedings of the Royal Society B: Biological Sciences* 277: 529–537.
- Coyne, Jerry A. 1999. "The Self-Centred Meme." *Nature* 398: 767–68.
- Cronk, Lee. 1991. "Human Behavioral Ecology." *Annual Review of Anthropology* 20(1): 25–53.
- Darwin, Charles. (1871) 2009. *The Descent of Man and Selection in Relation to Sex*. Cambridge: Cambridge University Press.
- Dawkins, Richard. 1982a. *The Extended Phenotype: The Long Reach of the Gene*. Oxford: Oxford University Press.
- Dawkins, Richard. 1982b. Replicators and Vehicles. Pp. 45–64 in *Current Problems in Sociobiology*. Cambridge: Cambridge University Press.
- Dawkins, Richard. 1993. Viruses of the Mind. Pp. 13–27 in *Dennett and His Critics: Demystifying Mind*. Edited by B. Dahlbom. Malden, Mass.: Blackwell Publishers.
- Dawkins, Richard. 2006. *The Selfish Gene*. Oxford: Oxford University Press.
- Dawkins, Richard. 2007. *The God Delusion*. London: Black Swan.
- Delius, D. J. 1991. The Nature of Culture. Pp. 75–99 in *The Tinbergen Legacy*. Edited by R. Dawkins and T. R. Halliday. London: Chapman & Hall.
- Dennett, Daniel C. 1991. *Consciousness Explained*. Boston: Little, Brown and Company.
- Dennett, Daniel C. 1995. *Darwin's Dangerous Idea: Evolution and the Meanings of Life*. London: Penguin Books.
- Dennett, Daniel C. 2006. *Breaking the Spell: Religion as a Natural Phenomenon*. New York: Penguin Books.



- Dennett, Daniel C. 2017. *From Bacteria to Bach and Back: The Evolution of Minds*. New York, London: W. W. Norton & Company.
- Derex, Maxime, Marie-Pauline Beugin, Bernard Godelle, and Michel Raymond. 2013. "Experimental Evidence for the Influence of Group Size on Cultural Complexity." *Nature* 503: 389–391.
- Distin, Kate. 2005. *The Selfish Meme*. Cambridge: Cambridge University Press.
- Distin, Kate. 2011. *Cultural Evolution*. Cambridge: Cambridge University Press.
- Douglas, Marry. 1966. *Purity and Danger: An Analysis of the Concepts of Pollution and Taboo*. London: Routledge.
- DRH website. <https://religiondatabase.org/landing/>. Accessed 7 December 2019.
- Durkheim, Émile. 2011. *The Elementary Forms of Religious Life*. Oxford: Oxford University Press.
- Edmonds, B. 2005. "The Revealed Poverty of the Gene-Meme Analogy – Why Memetics per Se Has Failed to Produce Substantive Results." *Journal of Memetics* 9.
- Gatherer, Derek. 1997. "Macromemetics: Towards a Framework for the Re-Unification of Philosophy." *Journal of Memetics* 1.
- Gatherer, Derek. 1998. "Why the Thought Contagion Metaphor Is Retarding the Progress of Memetics." *Journal of Memetics* 2.
- Gerbault, P., A. Liebert, Y. Itan, A. Powell, M. Currat, J. Burger, D. M. Swallow, and M. G. Thomas. 2011. "Evolution of Lactase Persistence: An Example of Human Niche Construction." *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 863–877.
- Gintis, Herbert, Samuel Bowles, Robert Boyd, and Ernst Fehr. 2003. "Explaining Altruistic Behavior in Humans." *Evolution and Human Behavior* 24(3): 153–172.
- Gottsch, J. D. 2001. "Mutation, Selection, and Vertical Transmission of Theistic Memes in Religious Canons." *Journal of Memetics* 5.
- Gould, Stephen Jay, and Richard C. Lewontin. 1979. "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme." *Proceedings of the Royal Society of London, Series B* 205(1161): 581–598.
- Henrich, Joe, and Robert Boyd. 1998. "The Evolution of Conformist Transmission and the Emergence of Between-Group Differences." *Evolution and Human Behavior* 19: 215–241.
- Henrich, Joseph. 2004a. "Cultural Group Selection, Coevolutionary Processes and Large-Scale Cooperation." *Journal of Economic Behavior and Organization* 53: 3–35.
- Henrich, Joseph. 2004b. "Demography and Cultural Evolution: How Adaptive Cultural Processes Can Produce Maladaptive Losses: The Tasmanian Case." *American Antiquity* 69(2): 197–214.

- Henrich, Joseph. 2016. *The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter*. New York: Princeton University Press.
- Henrich, Joseph, and Francisco J. Gil-White. 2001. "The Evolution of Prestige: Freely Conferred Deference as a Mechanism for Enhancing the Benefits of Cultural Transmission." *Evolution and Human Behavior* 22: 165–196.
- Hofstadter, Douglas R., and Daniel C. Dennett, eds. 1982. *The Mind's I: Fantasies and Reflections on Self and Soul*. New York: Basic Books.
- Hull, David L. 1990. *Science as a Process: An Evolutionary Account of the Social and Conceptual Development of Science*. Aldershot: Ashgate.
- Jan, S. B. 2007. *The Memetics of Music: A Neo-Darwinian View of Musical Structure and Culture*. Aldershot: Ashgate.
- Kundt, Radek. 2015. *Contemporary Evolutionary Theories of Culture and the Study of Religion*. London: Bloomsbury Academic Press.
- Kuper, R. 2000. If Memes Are the Answer, What Is the Question? Pp. 175–188 in *Darwinizing Culture: The Status of Memetics as a Science*. Edited by R. Aunger. Oxford: Oxford University Press.
- Laland, Kevin N. and S. M. Reader. 1999. "Do Animals Have Memes?" *Journal of Memetics* 3.
- Lewontin, Richard C. 1970. "The Units of Selection." *Annual Review of Ecology and Systematics* 1: 1–18.
- Linguist, Stefan. 2016. "Which Evolutionary Model Best Explains the Culture of Honour?" *Biology and Philosophy* 31: 213–235.
- Lynch, Aaron. 1991. "Thought Contagion as Abstract Evolution." *Journal of Ideas* 2(1): 3–10.
- Lynch, Aaron. 1996. *Thought Contagion: How Belief Spreads through Society*. New York: Basic Books.
- Lynch, Aaron. 1998. "Units, Events and Dynamics in Memetic Evolution." *Journal of Memetics* 2.
- Marsden, Paul. 2000. "Forefathers of Memetics: Gabriel Tarde and the Laws of Imitation." *Journal of Memetics* 4.
- McElreath, R., A. V. Bell, C. Efferson, M. Lubell, P. J. Richerson, and T. Waring. 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: Biological Sciences* 363(1509): 3515–3528.
- Mesoudi, Alex. 2016. "Cultural Evolution: A Review of Theory, Findings and Controversies." *Evolutionary Biology* 43: 481–497.
- Mesoudi, Alex, Andrew Whiten, and Robin Dunbar. 2006. "A Bias for Social Information in Human Cultural Transmission." *British Journal of Psychology* 97: 405–423.

- Muthukrishna, Michael, and Joseph Henrich. 2019. "A Problem in Theory." *Nature Human Behaviour* 3: 221–229.
- Muthukrishna, Michael, Ben W. Shulman, Vlad Vasilescu, and Joseph Henrich. 2013. "Sociality Influences Cultural Complexity." *Proceedings of the Royal Society B: Biological Sciences* 281(1774): 1–8. <https://doi.org/10.1098/rspb.2013.2511>
- Norenzayan, Ara, Azim F. Shariff, Will M. Gervais, Aiyana K. Willard, Rita A. McNamara, Edward Slingerland, and Joseph Henrich. 2016. "The Cultural Evolution of Prosocial Religions." *Behavioral and Brain Sciences* 39: 1–65.
- Popper, Karl R. 2002. *The Logic of Scientific Discovery*. London: Routledge Classics.
- PULOTU website. <https://pulotu.shh.mpg.de>. Accessed 7 December 2019
- Rappaport, Roy A. 1968. *Pigs for the Ancestors: Ritual in the Ecology of a New Guinea People*. Connecticut: Yale University Press.
- Rappaport, Roy A. 1979. The Obvious Aspects of Ritual. Pp. 173–221 in *Ecology, Meaning and Religion*. Edited by R. Rappaport. Richmond, CA: North Atlantic Books.
- Richerson, Peter, Ryan Baldini, Adrian V. Bell, Kathryn Demps, Karl Frost, Vicken Hillis, Sarah Mathew, Emily K. Newton, Nicole Naar, Lesley Newson, Cody Ross, Paul E. Smaldino, Timothy M. Waring, and Matthew Zefferman. 2016. "Cultural Group Selection Plays an Essential Role in Explaining Human Cooperation: A Sketch of the Evidence." *Behavioral and Brain Sciences* 39: 1–68.
- Richerson, Peter J. and Robert Boyd. 1998. The Evolution of Human Ultra-Sociality. Pp. 71–96 in *Ideology, Warfare, and Indoctrinability: Evolutionary Perspectives*. Edited by I. Eibl-Eibesfeldt and F. K. Salter. New York: Berghahn Books.
- Richerson, Peter J. and Robert Boyd. 2001. "Built for Speed, Not for Comfort: Darwinian Theory and Human Culture." *History and Philosophy of the Life Sciences* 23: 425–65.
- Richerson, Peter J. and Robert Boyd. 2005. *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: The University of Chicago Press.
- Richerson, Peter J. and Robert Boyd. 2008. "Migration: An Engine for Social Change." *Nature* 456(7224): 877.
- Richerson, Peter J., Robert T. Boyd, and Joseph Henrich. 2003. Cultural Evolution of Human Cooperation. Pp. 359–388 in *Genetic and Cultural Evolution Of Cooperation*. Edited by P. Hammerstein. Cambridge: The MIT Press.
- Rose, Nicholas. 1998. "Controversies in Meme Theory." *Journal of Memetics* 2.

- Sapp, J. 2015. *Genesis: The Evolution of Biology*. Oxford: Oxford University Press.
- Soltis, Joseph, Robert Boyd, and Peter J. Richerson. 1995. "Can Group-Functional Behaviors Evolve by Cultural Group Selection? An Empirical Test." *Current Anthropology* 36(3): 473–494.
- Sperber, Dan. 1996. *Explaining Culture: A Naturalistic Approach*. Oxford: Blackwell Publishers.
- Sperber, Dan. 2000. An Objection to the Memetic Approach to Culture. Pp. 163–173 in *Darwinizing Culture: The Status of Memetics as a Science*. Edited by R. Aunger. Oxford: Oxford University Press.
- Sterelny, Kim. 2006. "The Evolution and Evolvability of Culture." *Mind and Language* 21(2): 137–165.
- Tomasello, Michael. 2009. *Why We Cooperate*. Cambridge, Mass.: The MIT Press.
- Tooby, John and Leda Cosmides. 1989. "Evolutionary Psychology and the Generation of Culture, Part I: Theoretical Considerations." *Ethology and Sociobiology* 10(1–3): 29–49.
- Toulmin, S. 1972. *Human Understanding*. Oxford: Clarendon Press.
- Turchin, Peter. 2016. *Ultrasociety: How 10,000 Years of War Made Humans the Greatest Cooperators on Earth*. Chaplin: Beresta Books.
- Tyler, Tim. 2011. *Memetics: Memes and the Science of Cultural Evolution*. CreateSpace (at author's own expense).
- Uhlř, Vilém and Marco Stella. 2012. "Who Needs Memetics? Possible Developments of the Meme Concept and Beyond." *Anthropologie* 50(1): 127–42.
- Vanechoutte, M. and J. R. Skoyles. 1998. "The Memetic Origin of Language: Modern Humans as Musical Primates." *Journal of Memetics* 2.
- Watson, J. D. and F. H. Crick. 1953. "Molecular Structure of Nucleic Acids." *Nature* 171(4356): 737–738.
- White, L. A., J. N. Spuhler, C. F. Hockett, H. F. Harlow, R. W. Gerard, M. D. Sahlins, and S. L. Washburn. 1959. *The Evolution of Man's Capacity for Culture*. Detroit: Wayne State University Press.
- Wilkins, J. 1999. "Memes Ain't (Just) in the Head." *Journal of Memetics* 3.
- Williams, G. C. 1966. *Adaptation and Natural Selection. A Critique of Some Current Evolutionary Thought*. New York: Princeton University Press.
- Williams, G. C. 1992. *Natural Selection: Domains, Levels, and Challenges*. New York: Oxford University Press.
- Wilson, David Sloan and Elliott Sober. 1989. "Reviving the Superorganism." *Journal of Theoretical Biology* 136: 337–56.
- Wilson, David Sloan, Mark Van Vugt, and Rick O'Gorman. 2008. "Multilevel Selection Theory and Major Evolutionary Transitions:

Implications for Psychological Science.” *Current Directions in Psychological Science* 17(1): 6–9.

Wilson, Edward O. 1975. *Sociobiology: The New Synthesis*. Cambridge: Harvard University Press.

Wilson, Edward O. 1978. *On Human Nature*. Boston: Harvard University Press.

Wynne-Edwards, V. C. 1962. *Animal Dispersion in Relation to Social Behaviour*. New York: Hafner Publishing Company.