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Cultural Evolution and the Evolution of Cultural Information

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Abstract
Cultural evolution is normally framed in informational terms. However, it is not clear whether this is an adequate way to model cultural evolutionary phenomena and what, precisely, "information" is supposed to mean in this context. Would cultural evolutionary theory benefit from a well-developed theory of cultural information? The prevailing sentiment is that, in contradistinction to biology, informational language should be used nontechnically in this context for descriptive, but not explanatory, purposes. Against this view, this article makes the case for the need to take a proper biology-based "informational turn" in the cultural evolutionary sciences. I argue that the current vague use of informational language misses out on the potential benefits for advancing understanding of phenomena that information-theoretic reasoning has provided in other sciences, especially genetics. In particular, by emphasizing the informational aspects of cultural evolutionary processes, this approach can clarify some conceptual and methodological problems that have plagued cultural evolutionary theory since its inception, including (1) how to determine the channel conditions of cultural information flow, (2) the nature and scope of cultural information, and (3) how to quantify trends of cultural cumulation. More generally, theories of cultural evolution will be incomplete until the mechanisms underlying cultural processes are better understood and integrated into the explanations. This article explores the adequacy of an information-theoretic framework to accomplish these purposes.

Keywords Analogy · Biological information · Cultural evolution · Cultural information · Genetic processes · Social learning

Introduction

The need for a naturalistic framework to address questions concerning the role of culture in human evolution, the process of cultural descent with modification, the relationship between culture and the genome, as well as culture in nonhuman animals, propelled a theoretical redirection towards a biology-based scientific approach to cultural evolution in the last four decades (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Dawkins 1989; Durham 1991; Sperber 1996; Odling-Smee et al. 2003; Mesoudi et al. 2006; Mesoudi 2011).

This field came to be known as cultural evolutionary theory (CET), and although it consists of multiple approaches including dual-inheritance theory, epidemiology of representations, niche construction, and memetics, which differ from each other in some important respects, it is based on the view that culture changes through time analogously to the way that organisms evolve genetically, and that both evolutionary processes interact causally. Hence, it is thought, cultural change can be productively studied by applying formal Darwinian models and concepts borrowed from or inspired by the biological sciences—effectively extending and adjusting the evolutionary framework to cover a nongenetic inheritance mechanism (Richerson and Boyd 2005; Mesoudi et al. 2006; Whiten et al. 2011).

One area that cultural evolutionists have borrowed from is the rich informational terminology widely used in the biological sciences, particularly in genetics. Cultural phenomena, including cultural processes such as inheritance, cumulation, diffusion, replication, and complexification, as well as their products such as knowledge, traditions, mental representations, artifacts, and so on, are normally couched in informational terms. For example, culture tends to be defined as *information*, which plays an analogous role to *genotype*; is *transmitted* through a social *channel*, which parallels the *genetic channel*; is *encoded* in and *decoded*

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from certain substrata such as artifacts and brains; and can be *redundant*, *stored*, *retrieved*, *programmed*, and *processed*.

This prompts questions such as: What role is this informational vocabulary playing in CET? What is cultural information and how does it evolve? Is this an adequate way of conceptualizing cultural evolution? Interestingly, researchers do not normally elaborate on their choice to employ informational terminology in their work, leaving it unclear whether its use is justified. Furthermore, despite being a popular concept, there are but few attempts to define “cultural information”—quite unlike the case of “biological information” (Griffiths and Stotz 2013).

The underdeveloped status of informational language is warranted if the theoretical role that it is supposed to play in CET is merely heuristic. That is, if it merely helps to describe various cultural evolutionary phenomena, but that no further theorization is required. In fact, these takes have been endorsed by some cultural evolutionists and philosophers (e.g., Richerson and Boyd 2005; Mesoudi et al. 2006; Lewens 2015).

The aim of this article is to argue for the need to take an informational approach in the study of cultural evolution that draws on the information-theoretic resources of evolutionary biology and genetics. On the one hand, I criticize the current mere heuristic use of informational language in CET. As I will argue, this use not only misses out on the potential benefits for advancing understanding of phenomena that informational thinking has provided in genetics and evolutionary biology,[1] but it is perniciously ambiguous for the science since it overlooks important differences between the dynamics of cultural and biological evolution. On the other hand, by emphasizing the informational aspects of cultural evolutionary processes, this article puts forward theoretical and conceptual developments towards building a more robust framework that can help to profitably bridge evolutionary biology, the scientific study of biological information processing, and cultural evolutionary sciences.

After an analysis of the current use of informational talk in CET (the second section), I undermine arguments put forward by critics suggesting that a theory of cultural information is untenable (section three). Subsequently, in the fourth section, I discuss some theoretical challenges that have plagued CET since its inception and that can be elucidated by a proper biology-inspired informational approach to cultural phenomena, specifically, that it is not clear how to model cultural inheritance and how to differentiate cultural from noncultural information. Finally, I put forward some promissory analytical considerations for the quantitative study of cumulative cultural evolution.

The Current Use of Informational Language in CET

Informational terminology is normally used in CET for two purposes: (1) to define culture and (2) to describe cultural evolutionary processes such as cultural inheritance (e.g., Boyd and Richerson 1985; Tomasello et al. 1993; Laland et al. 2000; Odling-Smee et al. 2003; Richerson and Boyd 2005; Mesoudi et al. 2006; Sperber and Cladière 2008; Mesoudi 2011. For philosophical analyses see Ramsey 2013; Lewens 2015; Driscoll 2017). Certainly, the immediately pressing question here has to do with the rationale for couching cultural evolutionary phenomena in informational terms, especially since other alternatives exist such as describing them in behavioral terms (e.g., Cavalli-Sforza and Feldman 1981; Jablonka and Lamb 2005).[2] It has been suggested that information talk comes naturally from studying paradigmatic cases of information processes, such as the transmission of knowledge and changes in mental states (Lewens 2015, pp. 55–57). However, this section demonstrates that, in reality, the motivations of cultural evolutionists for using informational vocabulary in their work depend on the approach taken, but generally these are in the spirit of drawing analogies with evolutionary biology and genetics.

Dual-inheritance and niche construction theorists normally adopt Richerson and Boyd’s conceptualization of culture as “information capable of affecting individuals’ behavior that they acquire from other members of their species through teaching, imitation, and other forms of social transmission” (Richerson and Boyd 2005, p. 5).[3] There are at least three motivations for taking this informational view of culture. Firstly, a central claim of these approaches is that culture is a second inheritance system in which information flows to produce adaptive phenotypes to changing environments (Boyd and Richerson 1985; Durham 1991; Whiten 2017). Even though the cultural and genetic inheritance

[1] Not everybody agrees that information talk has played a positive role in biological explanations. Some classic criticisms are Sarkar (1996) and Griffiths (2001). See Griffiths and Stotz (2013) and Godfrey-Smith and Sterelny (2016) for reviews of the controversies.

[2] Defining culture at the phenotypic level does not necessarily exclude the possibility of using informational terminology for other descriptive purposes within the same conceptual framework. For instance, even though Cavalli-Sforza and Feldman define culture as “the total pattern of human behavior and its products embodied in thought, speech, action and artefacts” (1981, p. 3), they nevertheless define relationships between cultural individuals in terms of transmission and flow of information.

[3] It is important to bear in mind that it is in the context of Darwinian approaches to cultural evolution where “culture as information” is proposed to be a useful conceptualization—i.e., whether this definition is applicable outside of CET does not concern cultural evolutionists, nor this article.

systems have some structural differences, cultural evolutionists argue that, nevertheless, both have important functional similarities as they evolved for the transmission, storage, and handling of inherited information. Mesoudi, for example, mentions that

> whereas genetic information is stored in sequences of DNA base pairs, culturally transmitted information is stored in the brain as patterns of neural connections (albeit in a way that neuroscientists are only beginning to understand), as well as in extrasomatic codes such as written language, binary computer code, and musical notation. And whereas genetic information is expressed as proteins and ultimately physical structures such as limbs and eyes, culturally acquired information is expressed in the form of behavior, speech, artifacts, and institutions. (Mesoudi 2011, p. 3; see also Kronfeldner 2021)

Importantly, this is consistent with the view that the major transitions of evolution—culture being the most recent one—consist in changes in the way information is obtained, stored, and transmitted (Maynard Smith and Szathmáry 1995).

A second motivation is to be able to identify culture with information and not with the expression of it, as this allows patterns of trait expression to be explained in terms of cultural causes in the same way that geneticists can explain some phenotypic differences in terms of genetic differences (Richerson and Boyd 2005; Mesoudi 2011; Ramsey 2013). For instance, Boyd and Richerson submit that, "two individuals with identical sets of culturally acquired dispositions may behave quite differently in different environments. Thus, by our definition, the relationship between culture and behavior is similar to the relationship between genotype and phenotype in noncultural organisms" (Boyd and Richerson, 1985, p. 36). In other words, what individuals actually inherit from others is encoded cultural information, not the behaviors, cognitive states, or other phenotypes that result from this information. Niche construction theorists agree with this view, but stress that for cultural information to be evolutionarily relevant, it should allow organisms to construct their niche and modify the selection forces inherited to subsequent generations (Laland et al. 2000; Odling-Smee et al. 2003; Sterelny 2012).

Finally, cultural evolution is also described in informational terms to achieve conceptual symmetry with evolutionary biology and genetics since, as is well known, there is an extensive use of information talk in these sciences (Maynard Smith and Szathmáry 1995; Maynard Smith 2000; Griffiths and Stotz 2013). As mentioned previously, CET was advanced as a research program that explores the advantages of using models, operationalizations, hypotheses, and methods of evolutionary biology to explain cultural change. This import of theoretical resources between the two disciplines can be eased if their explananda are described in similar terms. For instance, Boyd and Richerson mention that,

> The main reason we are interested in using the inheritance system analogy is practical. To the extent that the transmission of culture and the transmission of genes are similar processes, we can borrow the well-developed conceptual categories and formal machinery of Darwinian biology to analyze problems. (Boyd and Richerson 1985, p. 31)

The conceptual mirroring between cultural and biological evolutionary theory can be seen more explicitly in the work of memeticists. A central feature of meme theory is a commitment to the view that just as biological evolution needs replicating genes to operate, cultural evolution requires analogous replicating informational units that remain relatively stable, called "memes" (Dawkins 1989; Dennet 1995; Aunger 2000). Memeticists argue that cultural evolution occurs when there is a change in meme frequencies in the meme pool over successive generations, and a science of cultural evolution should focus on keeping track of the fate of memes and the selection forces affecting their distributions. Importantly, even though memeticists make use of information talk in their work to define memes and explain cultural dynamics, achieving conceptual symmetry with evolutionary biology, their focus is at the level of information-bearing entities, not on cultural information per se (Blackmore 1999).

Lastly, epidemiology of representations theory is an approach that focuses mainly on the role of cognitive processes in the cultural acquisition, transmission, and diffusion of mental representations (Sperber 1996; Atran 1998). In this view, cultural traits are not replicated in an event of cultural transmission but reconstructed and transformed according to human universal cognitive dispositions. In their epidemiological explanations of mental states, these researchers make relatively moderate use of informational terminology, and their motivation is to provide a Darwinian approach to cultural evolution rooted in cognitive psychology, communication, and a population-level epidemiology of mental representations (Cladieré et al. 2014). Accordingly, although some researchers are sympathetic to the use of information talk in other approaches (Sperber and Cladière 2008), they disagree in identifying cultural phenomena exclusively with information. For instance, Morin asks, "*Can traditions be identified with the information that is passed on when they are transmitted? No, not always*. Just because cultural transmission involves an exchange of ideas does not mean that traditions themselves are the ideas that their proliferation relies on" (Morin 2011, p. 49; italics in original. See also Sperber and Cladière 2008).

A few other researchers have advanced slightly more detailed definitions. Richerson and Boyd clarify that, "by *information* we mean any kind of mental state, conscious or not, that is acquired or modified by social learning and affects behavior" (Richerson and Boyd 2005, p. 5; italics in original). However, this proposal has been subjected to analysis by a handful of philosophers of biology with negative results. Driscoll (2017, pp. 43–44) considers that the notion of "information" is disposable when it is equated with mental states since these are phenotypes. Ramsey (2013) agrees with Driscoll that information should not be identified with phenotype and argues that cultural information can be distinguished by what it flows through and what it affects. Lewens (2015, pp. 45–47), for his part, thinks that Richerson and Boyd are not providing an account of cultural information whatsoever, but a statement about its main stratum (i.e., the brain).

In summary, informational language is widely used in cultural evolutionary sciences for different reasons that depend on the approach taken, but only to describe cultural phenomena in an ambiguous and nontechnical way. Consequently, in contradistinction to evolutionary biology and genetics, the information-theoretic foundations of the evolutionary study of cultural phenomena are underdeveloped. Interestingly, investigators in this field seem to pay scant attention to the matter while the research keeps thriving. For some, this suggests that despite its underdeveloped status, or maybe because of it, informational language nonetheless plays a valuable epistemic role that does not require further theorizing. In the following sections, I offer arguments that undermine this line of reasoning and show the advantages of developing a more rigorous informational approach to the study of cultural evolution.

Cultural Information Theory and its Discontents

Some researchers think that the development of a theory of cultural information inspired by biological theory is the wrong call. The reasons advanced are fundamental in the sense that they have to do with the tenability of such an approach. Specifically, critics suggest that there is currently insufficient knowledge about the physical underpinning of cultural informational processes, that information talk is causally inert, and that cultural information operates differently than biological information. Although this article does not intend to suggest that explaining cultural evolutionary processes in terms of information is without its difficulties, in this section, I argue that these are not the ones put forward by critics so far.

Lack of Empirical Grounding

One of the main worries about an informational approach to cultural evolution is our current limited understanding of the biochemical, neural, and other physical mechanisms underpinning cultural inheritance (Rendell et al. 2011). In fact, how cultural information is acquired, stored, and inherited to the next generations and how it gets translated into adaptive phenotypes remain one of the grand challenges of cultural evolutionary science (Brewer et al. 2017). Since it is not clear whether there is a cultural analogue to biological information carried by DNA, some researchers have speculated that we can only wait for the "cultural equivalents of Watson and Crick making key discoveries concerning how information is stored in the brain, expressed as behaviour, and transmitted to other brains" (Mesoudi 2011, p. 116).

However, it is important to bear in mind that the limited understanding of the physical mechanisms enabling cultural inheritance and storage does not impede the articulation of theoretical models. Furthermore, one of the lessons that can be retrieved from the history of genetics and the discovery of the genetic code is that, rather than being a deterrent, the lack of empirical grounding can be stimulated by theoretical developments (Mayr 1982, pp. 633–828; Kay 2000; Cobb 2015). Therefore, in order to make progress along this line, it is important to recognize that what informational models and concepts can provide will certainly be incomplete and somewhat idealized. Nevertheless, they can play important explanatory roles that help in the generation of new approaches, operationalizations, and hypotheses that may pave the way towards a more complete model of cultural evolution.

Information has no Causal Power

Another criticism that has been put forward against appeals to information in CET is that information does not play any causal role either in developmental or evolutionary processes, calling into question its explanatory import. Sperber and Claidière, for instance, posit that, "information is an abstract relational property. It is not something that, in and of itself, has causes or effects. Rather, it is a property that material items may possess in virtue of their causal connections" (Sperber and Claidière 2008, p. 284). In the same vein, Driscoll advances a slightly more categorical claim. According to her, "cultural information as such cannot cause behavior, changes in the environment, and so on, as most cultural evolutionary explanations suggest it can" (Driscoll 2017, p. 44).

To see that these worries are misplaced, let us consider how scientists understand the idea that genetic information causes amino acid sequences. Broadly speaking, it is understood that genetic information is intrinsic in the molecular and coding processes responsible for gene expression and inheritance; and hence, that it is part of the "causal history" of amino acid sequences and development (Crick 1970; Godfrey-Smith 2000; Stegmann 2016). This does not imply that genetic information alone produces amino acid sequences. As argued by Maynard Smith, "certainly, a gene requires the translating machinery of a cell—ribosomes, tRNA's, etc.—but this does not invalidate the analogy: a computer program needs a computer before it can do anything" (Maynard Smith 2000, p. 187). In molecular genetics, the notion that genetic information plays a causal role in determining amino acid sequences has proved valuable for generating explanations. Similarly, for explanatory purposes, cultural information should be understood as intrinsic in the physical processes of cultural inheritance and part of the causal history of artifacts, rituals, technology, and other cultural phenotypes.

Cultural Information and Teleofunctionality

Finally, it has also been suggested that cultural information does not operate like biological information, and that this invalidates the option of profitably using the causal-informational framework and reasoning of genetics and evolutionary biology to shed some light on cultural evolutionary phenomena.

In particular, it has been observed that, for genetic information to flow, it requires the teleofunctions of the genome that have evolved gradually by natural selection for the storage and transmission of information (Maynard Smith 2000; Bergstrom and Rosvall 2011; Shea 2013). However, in the case of cultural information, researchers have pointed out that some of its features contradict teleofunctional theory (Sterelny 2012; Lewens 2015). Specifically, if it is taken into account that cultural information also flows through the environment, then we are faced with some important complications.

As hypothesised by Sterelny (2012), it is plausible that in the evolutionary history of human culture, there was a primitive stage in which the behavior of humans was guided indirectly by previous generations through the environmental changes they caused before individuals were capable of social learning and imitation. Put differently, there was probably flow of cultural information before the biological adaptations for cultural learning emerged. For example, hammering is a skill that initially may have been passed down through generations without teaching by simply making hammers available. This shows, according to critics, that teleofunctional properties are not an imperative for the flow of cultural information, as they are for the flow of genetic information.

The problem with these observations is that they are not exclusive to cultural evolution. In fact, in molecular evolutionary history, it is also plausible that there was a stage that preceded the appearance of special adaptations for genetic inheritance. For instance, "metabolism first" hypotheses of the origin of life suggest that metabolic processes emerged spontaneously and predated the functional traits for genetic replication (e.g., Kauffman 1993; Vasas et al. 2012). Because genetic replication is proposed to be possible only as a posterior addition into the metabolic system, this hypothesis suggests that there was transmission or flow of (non-DNA) genetic information before the adaptations for genetic replication emerged. The important point to notice is that Sterelny's hypothesis does not disprove the adequacy of teleofunctional theory to account for cultural information more than the "metabolism first" hypotheses of biogenesis disprove its adequacy to account for genetic information. In other words, biological and cultural information can be viewed from a teleofunctional perspective with the same degree of coherence.

Towards an Informational Turn in CET: Theoretical Challenges

A point that this article takes seriously is that the utilization of informational models and concepts has played an important role in the efforts to unify developmental and evolutionary biological phenomena within the same theoretical framework (Maynard Smith and Szathmáry 1995; Hoffmeyer 1996; Maynard Smith 2000; Barbieri 2003; Yockey 2005). Moreover, this article also acknowledges that CET is no longer the premature research program of the 1980s in which a robust conceptual toolbox was a less important resource. Especially since the turn of the 21st century, cultural evolutionary studies have become a burgeoning and increasingly mature field for interdisciplinary research (Mesoudi 2011, 2017; Richerson and Christiansen 2013). However, CET has not fully taken an informational turn in the sense that an integral use of informational models and technical concepts in the production of explanations is lacking. Consequently, despite the fact that informational discourse is commonplace in CET, the work done in cultural evolution has remained disconnected from the scientific study of biological information processing, signaling, and informational approaches to biological evolution.

The previous section demonstrated that some of the most common arguments advanced so far against the tenability of a more precise and technical informational approach in the context of cultural evolution have important limitations. In contrast, the aim of this and the following sections is to take some steps towards a biology-based informational turn in CET. I identify some conceptual and methodological challenges that have afflicted this research program since its inception and that can be elucidated by highlighting the informational aspects of cultural evolution by drawing analogies with genetic and other evolutionary processes. Moreover, I also point out promising and, currently, unexplored lines of research that a theory of cultural information could open.

Modelling Cultural Transmission

A tangible difficulty of using a technical concept in a non-technical way, just as cultural evolutionists do with "information," is that it is hard to strip it away from its original techno-theoretical implications. It was in communication sciences where the concept first gained its operational grip, particularly thanks to the work of Shannon (1948; see also Shannon and Weaver 1949). Shannon was concerned with solving what he called an "engineer's problem," namely, to reduce uncertainty in a communication event in order to faithfully reproduce an encoded message sent through a channel to a receiver. To achieve this feat, he devised a mathematical theory of communication grounded on the differential probabilistic values of communication events measured algorithmically independently of their semantic content.

Some important features of cultural evolutionary dynamics that seem to be adequately captured by informational terminology are its transmissibility and uncertainty-reducing effects. According to information theory, information can be transmitted from one physical entity to another, forming an information system. Furthermore, this transmission of information minimizes the uncertainty about which outcome or event will happen. Normally, it is assumed that the transmission of information occurs between a sender and receiver through a channel (Shannon 1948). In communication technologies, two devices—such as phones or computers—can play the role of senders and receivers, whereas cables or electromagnetic waves can play the role of channels. The uncertainty reduced by an information transmission event concerns the message received out of many possibilities. In genetics, it has been argued that genes have an informational relationship with the amino acids they code for, that is, that genetic informational input plays the functional role of specifying one outcome out of many (Godfrey-Smith 2000; Stegmann 2016). Moreover, genes also have an informational relationship with the next generations whose development they aid in regulating (Bergstrom and Rosvall 2011; Shea 2013). However, it is not obvious how to model an event of cultural transmission, and various options are plausible according to the different approaches available in CET (Fig. 1).

Firstly, drawing on dual-inheritance theory and epidemiology of representations theory (Cavalli-Sforza and Feldman 1981; Durham 1991; Sperber 1996; Richerson and Boyd 2005; Mesoudi 2011), one option is to construe generations of cultural organisms as the senders and receivers of cultural information, while social learning and imitation constitute the "cultural channel." Although this assumption is probably the most intuitive one, a problem becomes apparent when we apply a more rigorous genetics-based informational reading to it. Unlike the central dogma of molecular biology in which genes have an asymmetric informational relationship with phenotypes, there is a sense in which it could be said that cultural phenotypes, such as artifacts and the environment, can have an informational relationship with cultural organisms. That is, there could be a bidirectional flow of information between cultural phenotype and cultural genotype.

Take a house as a toy model. It can be argued that the structure of a house stores cultural information because it has been shaped in accordance with certain traditions, beliefs, skills, values, and so on, that pertain to the cultural repertoire of a population. This cultural information reduces uncertainty about the kind of everyday life behaviors that will be performed by its occupants, as well as their beliefs about the private and the public, personal relationships, lifestyle, social organization, aesthetic preferences, and so on. Because the human occupants learn or receive the cultural information from the house, then it may seem adequate to construe the latter as a sender of cultural information too.[4]

Another way to model cultural transmission events is based on memetics (Dawkins 1989; Dennet 1995; Blackmore 1999). Challenging the idea that humans are at the extremes of a sender-channel-receiver scheme, memeticists have proposed that memes use humans as vehicles for their own "selfish" replication interests:

> Just as genes propagate themselves in the gene pool by leaping from body to body via sperms or eggs, so memes propagate themselves in the meme pool by leaping from brain to brain via a process which, in the broad sense, can be called imitation. (Dawkins 1989, p. 192)

To take the meme's eye view entails a reconfiguration of the conventional understanding of the structure of a cultural transmission system in which humans are now seen as channels, exploited by memes in order to achieve the successful replication of themselves. Of course, the main worry about this perspective is that it diminishes the active role that humans play in cultural evolutionary dynamics.

Finally, an alternative model uses niche construction theory as a starting point (Laland et al. 2000; Laland et al. 2001; Odling-Smee et al. 2003; Sterelny 2012). This theory builds on the fact that organisms interact with their environments in

[4] Given the tremendous impact that human culturally driven behavior has had on planet Earth, it is likely that these sorts of cases are rather common and may include the flora and fauna.

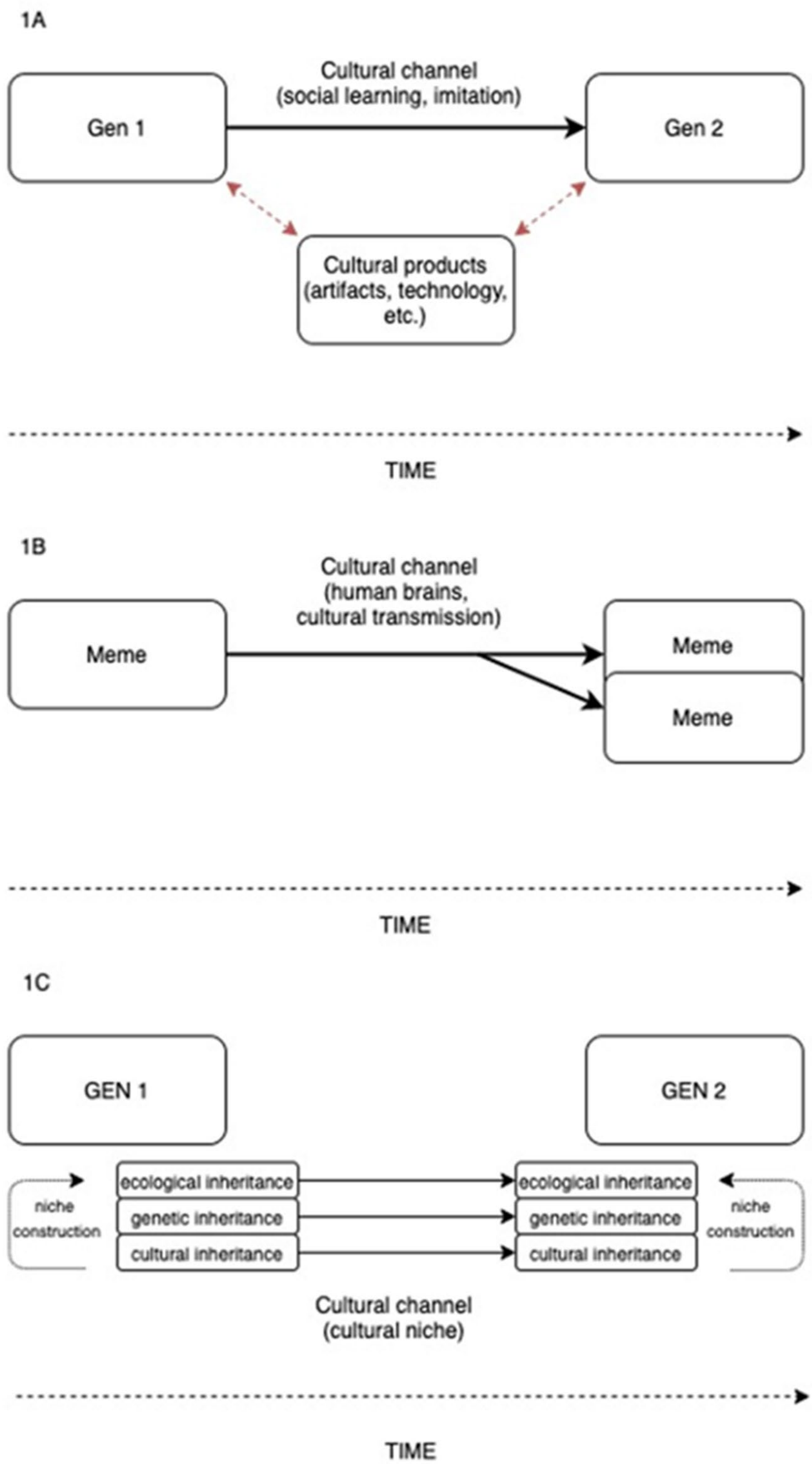

Fig. 1 **a** Model of cultural transmission assumed by dual-inheritance and epidemiology of representations theorists. Generation 2 of cultural organisms receives cultural information and cues from Generation 1 through social learning and imitation (the cultural channel). The active informational role of cultural products such as artifacts is ambiguously modelled. **b** An event of meme replication. Memes use human brains and social learning as channel conditions to achieve replication. **c** Cultural niche construction. Individuals of Generation 2 inherit genes and a culturally constructed niche from individuals of Generation 1. (adapted from Laland et al. 2000, p. 134)

multiple ways, modifying the selection pressures in a process called "niche construction." According to this view, culture is an additional mechanism that some species have evolved for constructing their niche, in which "culturally modified selection pressures are now regarded not as unique, but simply as part of a more general legacy of modified natural selection pressures bequeathed by human ancestors to their descendants" (Laland et al. 2000, p. 137). The relevant corollary of this approach is that the cultural information stored in the "cultural niche" is also viewed as part of this legacy from previous generations. Therefore, cultural phenotypes like houses—which are part of the cultural niche—do not have an informational relationship with the cultural repertoire of organisms; instead, cultural organisms have an informational relationship with other organisms through the cultural niche.

An issue that arises here is that these different ways of modelling the structure and dynamics of cultural transmission might be reflecting the assumptions of the approach taken and the research question pursued rather than the objective reality of cultural inheritance. However, the channel/sender distinction should be a fact, not an interest-relative decision. Importantly, parallel problems of ambiguity are virtually absent in molecular genetics (however, see Griffiths 2001), and some positive criteria for modelling cultural information transmission can be derived from it.

Channel/Sender Distinction and Natural Selection

In genetics, the channel conditions and the sender are not specified by the interests of researchers, but by the evolutionary process of natural selection. The structure of DNA has important characteristics that makes it easy to replicate and store information in great quantities within a confined space. The genome, by itself, cannot do much work. In fact, it requires the molecular processes of transcription and translation to decode the information and assemble proteins. These molecular mechanisms have evolved to bear coding capacities for the transmission of information through the processes of gene expression and genetic inheritance, and this compellingly indicates that they evolved to be the channel conditions of biological reproduction and development (Bergstrom and Rosvall 2011). Similarly, in order to model cultural transmission objectively, the framework should be determined not by the observer's interests, but by the evolutionary history of human capacities for cultural learning. Indeed, the evidence gathered so far indicates that humans have evolved a set of behavioral and cognitive adaptations including natural pedagogy, imitation, emulation, teaching, and others, for the storage, handling, and transmission of cultural information (e.g., Csibra and György 2011; Rendell et al. 2011; Hoppit and Laland 2013), suggesting that they play the meta-function of channel conditions for cultural inheritance between individuals. Effectively, this rules out the notion that the niche is a channel of cultural transmission since it has not evolved by natural selection to play that function. Likewise, this puts some pressure on memeticists to prove that human social brains evolved for the sole benefit of selfish meme replication, and that this is not a mere perspective.

The Role of Cultural Phenotypes

Cultural transmission is interesting in that some cultural phenotypes can have an active informational role with cultural genotypes, that is, a reversed situation of the central dogma in genetics. The models of cultural transmission based on a unidirectional information flow from senders to receivers fail to capture these dynamics because they construe artifacts and the culturally manipulated environment as passive receptacles of information. Cultural niche construction theory, however, seems to capture the bidirectional causal-informational relationship between organisms and the environment without diminishing the role of organisms as the senders and receivers of cultural information, as memetics does (Laland et al. 2000, 2001; Odling-Smee et al. 2003. Laland and O'Brien 2011). Nevertheless, there are currently some conceptual limitations in niche construction theory that need to be overcome to make headway with this project. Namely, because the theory is concerned first and foremost with the selection pressures modified by organisms, it potentially puts cultural traits whose high frequency might not be associated with fitness (i.e., nonadaptations) out of the scope. Indeed, a salient effect of cultural systems is that fitness-neutral cultural information can be sustained and even propagated due to several causes, including the existence of different pathways of cultural transmission (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985) and cognitive mechanisms underlying an epidemiology of representations in a population (Sperber 1996).

The Nature and Scope of Cultural Information

Besides accurately modelling the structure and dynamics of cultural inheritance, there is the pending issue of figuring out what, precisely, makes cultural information cultural. This endeavor is relevant because behavior, and other phenotypes, are also affected by noncultural "kinds" of information that can potentially flow through the same social channels. For instance, there is de novo information that individuals can generate through trial-and-error tactics, as well as information that serves the purpose of ephemeral communication. Additionally, there is information that can be described as cognitively induced and that may appear cultural. For example, Miton et al. (2015) show that the success of the widespread medical procedure of bloodletting in Asia and the West throughout history is due to the way our cognitive apparatus works, and not exclusively to the transmission of cultural information over generations.

Moreover, it is also becoming important to model the semantic features of cultural information. For a long time, anthropologists have observed that much of human culture contains shared meaning, which is encoded in the form of language and other symbols. In the context of evolutionary studies, recent ground-breaking cross-comparative analyses of different animal cultural systems have spurred the need to understand this encoded semantic cultural information. On the one hand, it has been proposed that human cultural transmission is a high-fidelity mechanism and that its level of fidelity is unparalleled in the rest of the animal kingdom (Tomasello 1999; Richerson and Boyd 2005). On the other hand, there are reasons to think that "there is no consensual understanding of what cultural fidelity amounts to, [l] et alone any principled way to operationalize the concept" (Charbonneau 2019, p. 2). In other words, the required workable theoretical framework and methodology for identifying, deciphering, and collating semantic content is lacking in CET, bringing into question the soundness of transmission fidelity claims.

Even though operationalizing cultural information is important, it is also difficult because there is currently no satisfactory understanding of the neurophysiological mechanisms enabling cultural learning. However, some ways to circumvent this difficulty have been proposed. Boyd and Richerson suggest focusing on the observable properties that cultural information shares with biological information. Specifically, they argue that both kinds of information share

> the property that energetically minor causes have energetically major effects. For example, DNA, which represents a small fraction of the biomass of an organism, control the energetically major features of metabolism and phenotype. Similarly, culture is cheaply acquired information, encoded in memory, that is capable of producing major phenotypic effects. (Boyd and Richerson 1985, p. 35)

Although Boyd and Richerson's proposal has merits, it is subject to counterexamples. For instance, take social norms about inactions (e.g., "do not eat pork" or "do not shake hands") whose outcomes, by definition, require no energy whatsoever. Likewise, Lewens (2015, pp. 47–48) talks about cases in which this criterion reverses, such as the information stored in the structure of churches (an energetically major cause) about the kind of rituals performed within it (an energetically minor effect).

Other researchers have proposed focusing not on the properties of cultural information per se, but on its relationship with behavior (Mesoudi 2011; Ramsey 2013). According to Ramsey (2013, p. 466), information is cultural if, in addition to being acquired from other individuals, it "flows through and brings about the reproduction of, and a lasting change in, the behavioral trait." These restrictions effectively single out cultural information from other sources. For instance, short-lived communicative information is ruled out since it does not produce a lasting change in a behavioral trait. However, although linking cultural information with behavior is an important epistemic goal of CET, it is not clear whether the assumption that cultural information brings about the reproduction of behaviors only is warranted. The reproduction of cultural artifacts and the existence of social norms about inactions are cases that seem to challenge this view.

Biologists have not had to go through similar great pains to parsimoniously interpret and demarcate genetic information from other sources of information in order to guarantee the explanatory adequacy of their models. The reason, in part, is that the key justification for speaking of biological information and biological codes in genetics is the isomorphism between the transcription/translation processes of gene expression and the encoding/decoding processes in communication technologies. It is the particular arrangements of nucleotides in genes that determine the production of particular amino acid sequences that form proteins, and, in this sense, it is said that genes have a meaningful informational relationship with amino acids. Without these informational and coding properties of genes, the use of information talk in genetics would be explanatorily less powerful as causality is enough to account for noncoding copying mechanisms (Godfrey-Smith 2000). Cultural evolutionists have attempted to draw direct analogies with genetics and evolutionary biology to justify their approach. However, their work does not consider whether all the mechanisms of social learning are analogous to genetic processes. In fact, on one side of the spectrum, the mechanisms of social learning that involve the use of symbolic elements such as linguistic instruction seem to be more amenable to an informational approach as it resembles genetic processes. However, social learning occurring merely by observational imitation, and its variations (Hoppit and Laland 2013, pp. 62–104), might not require an informational framework as it could be accounted for as cases of phenotype-phenotype copying—analogous to nongenetic mechanisms of replication such as enzymatic sample-base copying (see also Jablonka and Lamb 2005). At best, this is still an open question, but it highlights the need for theoretical enquiries into the nature of cultural information.

Cumulative Culture and the Quantification of Cultural Information

Another area of CET that may benefit from a biology-inspired informational approach is the quantitative studies of cultural cumulation. Considered the hallmark of human culture, cultural cumulation is normally defined as the capacity for incremental modifications of the cultural repertoire to build upon over successive generations, whose products surpass individual inventiveness (Boyd and Richerson 1985, 1996; Tennie et al. 2009; Dean et al., 2014; Mesoudi and Thornton 2018). Effectively, over the last fifteen years, quantitative models based on population biology have been brought to the fore in CET for the purpose, among others, of studying the mechanisms, drives, and constraints of cultural cumulation.

A challenge that cultural evolutionists have had to face is how to adequately operationalize cultural cumulation. More precisely, it has been necessary to provide definitions and characterizations of the phenomenon in a way that allows one to measure it. For example, cultural evolutionists using mathematical models and computer simulations tend to approach cultural cumulation by focusing on its abstract effects such as the increase of average fitness, average skill, and level of transmission fidelity of a skill (Henrich 2004; Powell et al. 2009; Kobayashi and Aoki 2012). In contrast, cultural evolutionists doing field work and statistical analyses of ethnographic data tend to measure cultural cumulation in a way that is more amenable to their empirical approach, such as by counting the number of cultural traits (i.e., cultural complexity), as well as the number of types of cultural traits (i.e., cultural diversity) (Collard et al. 2011, 2012; Fogarty et al. 2017).

Interestingly, even though there are currently various operationalizations of cultural cumulation in use (Mesoudi and Thornton 2018), there are none based on cultural information. This is relevant for the following reason: if cultural phenomena are defined in informational terms, but cultural cumulation is defined and operationalized in noninformational terms, and no additional rationale about how these two concepts may be related is offered, this immediately suggests conceptual dissonance. For instance, can we deduce the rates of accumulation of cultural information by measuring the increase of average cultural fitness? Is cultural complexification positively correlated with increase of cultural information in all cases? Does the number of cultural traits give us an accurate approximation of the amount of cultural information in a population? These and similar questions have not yielded formal answers yet, only guesses based on intuition.

Generally speaking, the use of different measures to study a certain phenomenon is considered a good scientific practice if these converge into similar results (i.e., if they show "convergent validity"). The reason is because convergent results reliably indicate that the different measurements used are effectively measuring the same thing (Campbell and Fiske 1959). However, this has not been the case in the quantitative studies of cultural cumulation. Particularly in research on the drives and constraints of cumulative rates, the use of different measures to test hypotheses has tended to produce divergent results (Collard et al. 2013; Querbes et al. 2014; Vaesen et al. 2016). To mention one example, research using abstract operationalizations that fit mathematical and simulation models tend to find positive correlations between population size and the cumulation or complexification of culture (Henrich 2004; Powell et al. 2009), whereas research using operationalizations adequate for field work and statistical analyses of historical records tend to find no correlation between these same two variables (Collard et al. 2005; Querbes et al. 2014; Vaesen et al. 2016; Read and Andersson 2019).

The disconnection between cultural cumulation and cultural information is also reflected in the widespread tendency to take the evolution of technology as a paradigmatic case of cultural cumulation (Read and Andersson 2019; Buskell 2020). The problem is that not all cultural knowledge, ideas, traditions, beliefs, and so on, are materialized into technological implements and artifacts. Furthermore, no compelling reason has been advanced for assuming that the complexity of an artifact reflects the complexity of its underlying cultural information. This seems to suggest that cultural evolutionists might take for granted that an increase of cultural cumulation at the phenotypic level is positively correlated with an increase of cultural information. However, the work done on the evolution of biological complexity that uses information theory might offer some insights into the veracity of this assumption (Kimura 1961; Maynard Smith and Szathmáry 1995; Adami et al. 2000; Adami 2012).

What matters for the purposes of this article is to understand the reasons why some biologists prefer to focus on genetic information to study the evolution of biological complexity and not, say, functional or morphological complexity. Soon after the discovery that DNA is the hereditary material of organisms and the repository of genes, it was speculated that highly complex organisms possess large genomes, i.e., that they have a high C-value. However, it was soon found that simple organisms also have big genomes, called the "C-value paradox" (Thomas 1971). A reformulation was consequently advanced: highly complex organisms do not only have more genes of any kind, but more protein-coding genes, i.e., a high G-value. The era of genomic sequencing soon debunked this idea by showing that species like Pinot Noir grapes possess significantly more protein-coding genes than humans, sometimes called the "G-value paradox" (Hahn and Wray 2002).

These paradoxes have revealed that there is no reason to expect that phenotypic complexity should be positively correlated with genotypic complexity in a simple manner such as by the number of genes in the genome. A new approach to measuring trends of complexification in evolutionary history based on information was therefore proposed. One of the first biologists to produce major results along this line was Kimura (1961), whose research determined that genetic information accumulates at a rate of 0.29 bits per generation in the genome (see also Yockey 2005). Moreover, informational concepts and models have also been used to determine organisms' adaptive histories to their niches (Adami 2012) and explain natural selection as an optimizing power in evolution (Maynard Smith and Szathmáry 1995; Barbieri 2003; Jablonka and Szathmáry 1995), among other purposes. The fact that CET has not taken advantage of the models and insights of the work on the evolutionary trends of biological complexity compellingly indicates that there is a promising line of research waiting to take off.

Finally, in order to get a better understanding of the patterns of cultural cumulation over time, it is necessary to build a coherent conceptual framework on which operationalizations can be hinged, preventing the risk of a lack of convergent validity in quantitative studies of cultural cumulation. In particular, it would be profitable to base the operationalizations of cultural cumulation on a causal-informational framework to achieve conceptual congruency. Of course, it needs to be mentioned here that an "informational turn" in quantitative studies of cultural cumulation does not impede the use of non-informational operationalizations. However, if an informational framework has been established in CET as a standard to describe cultural phenomena in general, then it is important to explain the relationship that non-informational operationalizations of cultural cumulation hold with cultural information—a lesson that biologists learned already in the case of the relationship between measures of phenotypic complexity and genotypic complexity.

Conclusion

Research in cultural evolution aims at explaining cultural change by importing concepts, models, approaches, principles, methods, and other theoretical resources that are used by biologists to study biological evolution. As an inertial consequence of this naturalistic approach, there has been some enthusiasm about describing cultural phenomena in the language of information for various epistemic purposes. However, this article argued that, currently, this approach is insufficiently theoretically developed to provide either a robust basis to objectively model cultural information systems or a complete guidance for researchers to operationalize cultural cumulation. As a consequence, ambiguity permeates research, including the existence of competing models of cultural transmission and a lack of convergent validity in the quantitative studies of cultural cumulation.

On the positive side, this article argued that the project of developing a biology-based approach to cultural evolution is promising. However, this project cannot progress if the scientific study of biological information processing and the informational approaches to evolutionary biology are disconnected from the cultural evolutionary sciences. One way to bridge these areas of science involves highlighting the informational aspects of cultural evolutionary phenomena. In working towards this goal, I explored the implications of seeing cultural evolutionary phenomena under a causal-informational framework, particularly with regards to the cultural genotype/phenotype distinction, the channel conditions from which cultural information is transmitted to a receiver, and the uncertainty-reducing properties of cultural processes. Of course, this article does not exhaust the different advantages that a more robust "informational turn" can bring to advancing understanding of cultural evolution, but it hopefully motivates the development of a line of research currently mostly understudied.

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Conflict of interest The author has no competing interests to declare that are relevant to the content of this article.

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