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REVIEW

Cultural evolution: A review of theoretical challenges

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Abstract

The rapid growth of cultural evolutionary science, its expansion into numerous fields, its use of diverse methods, and several conceptual problems have outpaced corollary developments in theory and philosophy of science. This has led to concern, exemplified in results from a recent survey conducted with members of the Cultural Evolution Society, that the field lacks 'knowledge synthesis', is poorly supported by 'theory', has an ambiguous relation to biological evolution and uses key terms (e.g. 'culture', 'social learning', 'cumulative culture') in ways that hamper operationalization in models, experiments and field studies. Although numerous review papers in the field represent and categorize its empirical findings, the field's theoretical challenges receive less critical attention even though challenges of a theoretical or conceptual nature underlie most of the problems identified by Cultural Evolution Society members. Guided by the heterogeneous 'grand challenges' emergent in this survey, this paper restates those challenges and adopts an organizational style requisite to discussion of them. The paper's goal is to contribute to increasing conceptual clarity and theoretical discernment around the most pressing challenges facing the field of cultural evolutionary science. It will be of most interest to cultural evolutionary scientists, theoreticians, philosophers of science and interdisciplinary researchers.

Keywords: cultural evolution; gene–culture co-evolution; theory; methods; philosophy of science

1. Introduction

The growing attraction of cultural evolutionary science stems from the fact that cultural evolutionary processes operate in ways that can be described as 'descent with modification'. Such processes, like language, exhibit dynamics similar to biological evolutionary processes. This paper serves the research community as a review of theoretical challenges (with occasional suggestions) in cultural evolutionary science across four domains: conceptual challenges; methodological issues, including modelling, experimentation and field studies; topical challenges; and implications and applications. In the remainder of this section, we define terms and restate survey results conducted by the Cultural Evolution Society, results which we use to motivate the rest of the discussion.

The term 'cultural evolutionary science' (abbreviated 'CES') refers to an interdisciplinary field of inquiry using an array of scientific methods to study culture and the interactions between cultural and biological evolutionary processes. Contents of cultural evolutionary science include observation statements, methodological commitments, presuppositions about varieties of statistical tests, and more. 'Cultural evolutionary theory' ('CET') refers to the subset of cultural evolutionary science composing laws, generalizations and hypotheses, and their derivations and entailments. The events, processes and objects in the world that physically and mentally instantiate the transmission and evolution of culture across persons, populations and generations we refer to simply as 'cultural evolution' or 'cultural evolutionary processes'.

Numerous reviews of CES have been written. Creanza et al. (2017) review CES results broadly relevant for demography and genetics. Legare (2017) reviews adaptations for teaching and imitation and their cultural representation. Mesoudi (2016) makes a broad review of findings in CES. Singh et al. (2021) review CES findings that, per the title, go 'beyond social learning'. Smith (2020) reviews theory and findings about cultural group selection. Tamariz (2017) focuses on cultural language evolution. Whiten (2019) reviews experimental findings pertaining to culture in non-animals. Smolla et al. (2021) focus on underappreciated features of cultural evolution. However, these papers have not attempted to diagnose theoretical problems in CES whose varied instantiations animate the discussion below. This is no criticism since the aims of these other review papers are mainly to summarize recent empirical results (usually within one sub-area of CES) and identify potential hypotheses for further testing. The present contribution is instead a critical review of the needs and challenges facing the body of theory accompanying CES, which we refer to as cultural evolutionary theory.

An efficient means for researchers concerned with CET to contribute to improvements in the field is to take account of and respond to the most pressing stated challenges facing the field. As a result, the present critical review of theoretical needs takes its cue from results of a recent survey of the membership of the Cultural Evolution Society about the field's 'grand challenges' (Brewer et al., 2017). Published results of this survey detail two varied sets of challenges. The first set was drawn from semantic analysis of topics directly from survey results. (Subsequent references to 'survey results' are to this paper.) Its most pressing challenge, revealed to be about twice as important as the next topic, was with 'knowledge synthesis'. The authors state that this topic relates 'primarily to issues of theoretical integration and speaks to the idea that while many behavioural scientists and humanities scholars see culture as a defining feature of humankind, different subfields rarely read each other's work or build interdisciplinary research programmes to explore how human cultures differ from those of other animals' (Brewer et al., 2017: 1). Additional topics of appreciable concern in the first set of results were topics labelled 'culture definition', 'theory', 'shared language' across the disciplines, 'pro-sociality' and 'cultural transmission'.

The second set of 'grand challenges' were produced by co-authors of the report following their reflection on the first set of results and the clustered relations amongst those results. In the second set are:

(C1) understanding 'social adaptation' and what drives it;
(C2) understanding 'the role of cultural evolution in the context of organic evolution' in light of the fact that 'culture is strongly influenced by biology';
(C3) overcoming problems involved in 'modelling culture as a complex adaptive system';
(C4) 'identifying processes of transmission and accumulation of cultural traits' to reach 'consensus on the mechanisms underlying' mathematical models of cultural evolution;
(C5) 'integrating methods, data, and results across disciplines', which is reported to necessitate 'shared conceptual references and vocabulary';
(C6) creating 'organizational and funding structures';
(C7) 'identifying cultural evolutionary processes that address significant social, economic, and political problems' including 'climate change'; and
(C8) 'educating policymakers' and developing a public understanding of results of cultural evolutionary research (Brewer et al., 2017: 3).

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One problem is symptomatic of several of these challenges.

Often CES research teams identify a concept representing some coarse-grained phenomenon; the concept is operationalized for use in modelling, laboratory experiments and/or field studies; corresponding empirical research is conducted and intriguing results are found. Often this occurs without a definition or formal analysis of (i.e. without providing a set of necessary and sufficient conditions to govern) the concept. (See Lewens 2020; we thank Tim Lewens for crystallizing this problem for us.) Tokens of this type of what we will call the 'general problem' not infrequently issue in enigmatic results, methodological challenges, misinterpretation or miscommunication. The presence of this general problem is unsurprising to those who believe that even the term 'cultural evolution' is 'confused' because it is 'being used to indicate both a phenomenon – culture changing through time – and an approach to study it' (Micheletti et al., 2022: 667). Echoes of this general problem lurk behind problems of 'knowledge synthesis' and 'theory', and concerns with definitions of 'culture', 'cumulative culture' and 'social learning', as well as challenges (C1)–(C5).

The primary goal of this paper is to contribute to improving future research in CES by increasing the conceptual clarity and theoretical discernment around several of the most pressing challenges facing CES as revealed by these survey results. These challenges range widely and frequently overlap, which informs the paper's eclectic organization. Section 2 opens with some case studies to establish the utility of a focus on theoretical issues. Section 3 reviews germane developments in the philosophy of science. Section 4 focuses attention on methods challenges in CES, especially on issues of integration as found in (C5). Section 5 discusses two topical issues, culture in human and non-human animals and the nature of 'selection' in linguistics. Taking a cue from (C7) and (C8), Section 6 discusses challenges facing application of CES to policy, with attention to climate change.

2. Case studies in the value of theory and conceptual analysis for CES

To motivate the utility of critical discussion of the field's theoretical challenges, we lead with three abbreviated case studies. Each represents one area in which survey results have pointed to a 'grand challenge'. Each case study anticipates a subsequent section of the paper.

2.1. Conceptual challenges

Conceptual challenges are typically problems of definitional scope. The importance of establishing clear definitions of terms is obvious from survey results that lament the field's lack of 'shared conceptual references and vocabulary' and its need to find 'common language' (Brewer et al., 2017: 3). Meanings of 'copying', 'imitation' and 'social learning' are used equivocally across CES, impeding consistent operationalization in experiments. An influential formal model of cultural transmission purports to show that 'environmental learning' does not, but 'social learning' does, produce the 'empirical 'S-shaped' cumulative adoption curves that dominate the diffusion of innovations literature' (Henrich, 2001: 992). (The term 'S-shaped curve' refers to a sigmoid curve plotting data about the adoption of innovations characterized by, first, lengthy, laboured growth of early adopters followed by a quick increase in adoption, creating a high slope, and concluded by a slowly increasing phase with low slope and many adopters.) Tim Lewens argues (2015: 114–118) that this model treats its concepts of 'environmental learning' and 'social learning' as mutually exclusive. Henrich's definition of 'environmental learning' reads: 'individuals acquire and evaluate payoff-relevant information about alternative behavioural options by action and interaction in their local social, economic and ecological environments' (Henrich, 2001: 992). As defined, the meaning of 'environmental learning' overlaps with the meaning of 'social learning'. That is, the two are not independently defined. This entails that 'environmental learning' could *also* be modelled to yield S-shaped curves. This appears inconsistent with Henrich's conclusions from the model.

If the definitions of 'social learning' and 'environmental learning' are not retooled, subsequent modelling and experimentation using these definitions are unlikely to overcome challenge (C3).

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This conceptual misstep appears to inform pointed empirical criticisms of the model's explanation (Henrich, 2004) of the contraction of the Tasmanian toolkit (Read, 2011; Vaesen et al., 2016a, b; Henrich et al., 2016). This preliminarily demonstrates the value of critical philosophical attention on definitions in CES; see Section 3 below.

2.2. Methods

'Cumulative cultural evolution', a topic of significant concern in survey results pertaining to the dynamics of cultural systems (Brewer et al., 2017: 2), refers to a process in which traditions are modified and improved over time with a performance capacity that is beyond what an individual could generate on her own. This marks a *necessary condition* for a process to represent cumulative culture, a necessary condition widely repeated amongst experimentalists. For example, in their experimental attempt to understand what they call 'cumulative culture', Derex et al. (2013) repeat this condition in their first paragraph by writing that cumulative culture is that which 'no individual could have invented alone' (p. 389). This necessary condition on cumulative culture was first articulated by Boyd and Richerson (1996: 80), who wrote that for a process to be properly cumulative, it must lead human cultures to 'accumulate changes over many generations, resulting in culturally transmitted behaviors *that no single human individual could invent on his own*' (Boyd & Richerson, 1996: 80; our italics). Thus, to test whether a *cumulative* effect has been obtained, an experiment must at minimum compare how a solitary individual and a diffusion chain fare on the same task using equivalent time resources (Miton & Charbonneau, 2018: 3).

Study of cumulative culture is done through a variety of methods including modelling, field studies, experiments and more, but this issues in a challenge of creating necessary and sufficient conditions (see (C5) at Brewer et al., 2017: 3) that are clear, consistent and integrated across methods. According to Miton and Charbonneau (2018), this is yet to happen in the study of cumulative culture. Specifically, a crucial difference emerged between theory-based analysis of the cumulative culture concept, in which the necessary condition was identified, and its operationalization in experiments and models. The necessary condition stated above is infrequently operationalized in experiments. And when it is (as in Derex et al., 2014; Mesoudi, 2011), it risks misleading readers. Suppose a solitary individual and a group in a diffusion chain are each given one hour to complete the same task, and suppose that the group completes the task faster. Is the necessary condition met by this operationalization? No. Miton and Charbonneau (2018: 3) argue that this is 'insufficient to warrant the conclusion that observed differences in performance are the results of a genuinely cumulative process' because these control conditions cannot distinguish between *performance capacity* (evidence of cumulative culture) and its confound of *improvement speed*. This is because participants might have their individual skill development accelerated by learning in a social context (improvement speed), and complete a puzzle, even though social collaboration across generations is unnecessary (performance capacity) for completion of the puzzle (Miton & Charbonneau, 2018: 3). Section 4 includes discussion of challenges (C3), (C4) and (C5) pertaining to three common methods in CES research, modelling, experimentation and field studies.

2.3. Topical challenges

Sub-disciplines within CES face messy challenges when researchers port coarse-grained focal concepts from one subfield to another. In the Cultural Evolution Society survey (Brewer et al., 2017: 1–2), the challenge of synthesizing knowledge across diverse research areas was rated as the field's most pressing concern. Consider the status of a prominent CES explanation of 'cooperation', which says that cooperation within groups emerged because of psycho-social consequences of belief in punitive gods (Johnson, 2005; Norenzayan, 2013). This causal claim was supported by diverse studies ranging from anthropological databases that identified statistical relations between a culture's adoption of a moralistic high god and markers of cooperation (Roes & Raymond, 2003) to economic games

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experiments that showed priming with religious concepts raised offers to strangers (Shariff & Norenzayan, 2007), and from cognitive science of religion research on minimally counterintuitive ideas (Norenzayan et al., 2006, although see Purzycki & Willard, 2016) to psychological studies of agent-based teleological thinking (Kelemen, 1999).

Yet CES-inspired study of religion and cooperation can succumb to the aforementioned challenges. As part of a wider problem in the social sciences, religious priming studies have suffered from multiple failures to replicate (e.g. Gomes & McCullough, 2015; Miyatake & Higuchi, 2017). While cross-cultural experimental evidence bolsters the supernatural punishment–cooperation relationship (Lang et al., 2019), the purported causal relation between supernatural punishment and social complexity (an index of broader cooperation) remains unclear (Watts et al., 2015) and more basic conceptual concerns about presumed psychological mechanisms linger (Schloss & Murray, 2011). Echoing our 'general problem', critics argue that the concept of 'cooperation' at work in models and experiments about effects of belief in supernatural punishment on cooperation often equivocates because within-group parochiality is confused with cooperation between non-kin (Galen, 2016).

Critics might argue that research on this topic is consistent with scientific progress owing to its self-correcting nature, and as a result, the community does not require theory-driven re-evaluation of the subfield but more detail-oriented diligence. While we could be incorrect, it seems that focus on prosaic aspects of CES research can camouflage hurdles still thwarting progress. Most hypotheses tested in this subfield were not logical derivatives from a principled theory in part because the concept of a 'high god' lacks adequate formality and consistency across operationalizations. Some advocates define the term 'high gods' as 'gods who cared about cooperative – and harmony – enhancing behavior' (Shariff, Norenzayan, & Henrich, 2010: 124); others defined 'high gods' as deities specifically responsible for creating reality, and who may or may not be 'specifically supportive of human morality' (Swanson, 1960). Confusions of this type put researchers' ability to falsify causal hypotheses about religious beliefs and cooperation at risk since, if a correlation was not discovered in a dataset, the former circular definition warrants the inference that the dataset represented a 'low' not a 'high' god (Nichols et al. (2020: 4), and see Table 1 in that paper for similar logical problems in this subfield; see Lightner et al. (2023), on the empirical implications of these conflations). Below, Section 5 analyses theoretical difficulties as found in the topical areas of non-human culture and language.

2.4. Implications and applications

There are many appreciable consequences of CES findings for public policy, social change, well-being and research ethics. Aside from a few exceptions (e.g. Wilson, 2011) these implications have not been thoroughly studied. Section 5 seeks to open this area with discussion of one application (about norms) and one implication (about human uniqueness).

These case studies provide ample justification for the value of theoretical and philosophical attention given to major challenges to CES. To improve the conceptual clarity and theoretical discernment in ongoing CES research, and because it may be unfamiliar to readers, we next encapsulate extant philosophy of science research devoted to challenges voiced in the survey results above.

3. Developments in the philosophy of science for cultural evolution

The contemporary field of cultural evolutionary science has its formal origins in the work of Luigi Luca Cavalli-Sforza and Marcus Feldman (1973) and Marcus Feldman and Cavalli-Sforza (1976). Borrowing modelling strategies from population genetics and epidemiology, they identified analogies between biological and cultural evolution and transmission, exploring culture as a distinct form of inheritance. Subsequent generations of researchers have fleshed out this modelling approach, developing it further in multiple directions and identifying new explanatory projects – opportunistically borrowing tools from evolutionary biology, quantitative and cultural sociology, anthropology and cognitive psychology, among others. As a result, even the foundational status of formal mathematical

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models has not led to anything like a single, paradigmatic approach in CET. Instead, the field's development reflects its eclectic opportunism, leaving a vibrant patchwork of loosely related approaches vulnerable to the aforementioned challenges, as well as to explicitly theoretical problems not mentioned in survey results but raised in recent philosophy of science.

In the first wave of theoretical and philosophy of science work on cultural evolution, applications to culture of the Modern Synthesis in biology were developed (see Griesemer, 1988; Hull, 1988; Wimsatt, 1999). A second wave emerged at the end of the twentieth century. While continuing to involve reapplication of tools from biology to culture (e.g. see Skyrms, 2014 on evolutionary game theory), in this period additional effort was placed on analysis of competing theoretical frameworks for CET (see Sterelny, 2017), understanding conditions for culture in non-human animals (e.g. Ramsey et al., 2007; Sterelny, 2009) and evaluating the special character of cultural evolutionary explanations (e.g. Godfrey-Smith, 2012). Currently, a third wave of theoretical work in CET is starting to swell (see e.g. Lewens, 2015) in response to the emergence of problems for CES without precursors in biology. Theoreticians and philosophers of science are now elaborating methods specific to CET, including modelling, experimentation and field studies, observing operational challenges in each that follow from the use of concepts like 'culture' and 'cumulative culture' (Buskell, 2022; Sterelny, 2021; Vaesen & Houkes, 2021), 'prestige bias' (Chellappoo, 2021) and 'cultural attractors' (Driscoll, 2011; Buskell, 2017). We contextualize then highlight three sets of philosophical problems that, in effect, we seek to add to the list of grand challenges facing the field.

First, CES sources generally deny the claim, originally by Dawkins (1989) about 'memes', that cultural transmission is replicative (Lewens & Buskell, 2023; see Henrich et al., 2008 & Sperber, 2000; Dennett, 2017 is an exception). Nonetheless, many CES researchers appeal to 'high-fidelity copying' to explain complexity and diversity in human culture. Befitting the early growth of a new scientific endeavour, we generally welcome explanatory pluralisms (Charbonneau, 2020), yet in this case it represents a theoretical problem for the field. In biology, since genotype to phenotype mapping exists, and since transmission occurs from genotype to genotype, a principled 'grain' of description exists to guide the scientific study of transmission. This is absent in culture. The following example illustrates the 'grain' problem, which can be considered an example of the general problem noted above. 'Suppose Andrew sings a line from a song, and Tim attempts to copy him: does "high fidelity" learning require Tim to reproduce the same melody, must he sing in the same key, must he sing with the same words, and the same emotional emphases?' (Lewens & Buskell, 2023: section 6.2). If Tim sings with different words, in a dissimilar key, or with new accompaniment, under what conditions is it appropriate to reason that he has 'copied' Andrew? The specific means by which CES researchers measure fidelity or copying often lead to incompatible and incommensurable results, challenging the idea that fidelity would be a general, natural property of human cultural learning, let alone a causal one (Charbonneau & Bourrat, 2021).

Second, the advent of CES practised in broad spatiotemporal frames includes projects that consolidate historical and cross-cultural data in large databases (Slingerland et al., 2020), efforts in evolutionary archaeology and cognitive archaeology (Killin & Pain, 2023), and in cultural macroevolution more generally (Gray & Watts, 2017). While surveyed members of the Cultural Evolution Society regard the definition of 'culture' as a vexed but important problem (see Driscoll, 2017; Ramsey & De Block, 2015), a corollary often goes unnoticed, viz. that individuating cultures is distinct from the problem of defining 'culture' *simpliciter*. So what are 'cultures' or 'cultural groups' and how should they be individuated? Are cultures natural kinds? The latter metaphysical question is not idle: many working in political philosophy have long alleged that talking about 'cultural groups' is erroneously essentialist (Patten, 2014). If we wish to avoid essentialist characterizations of specific 'cultures', then how can cultural groups be taxonomized in modelling or experimentation? Related, how do various elements of cultures, for instance, texts and material technologies, relate to one another (Buskell et al., 2019)?

Third is a set of issues emerging from the role of values in science, including epistemic values, absent from survey results. 'Epistemic values' is a term referring to normative traits of theories or methods themselves. Different methods and theories implicitly prioritize some values or purposes

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over others. For example, experimental collider physics prioritizes certainty over generalizability owing to its endorsement of a 5σ criterion of statistical significance. Cultural evolutionary science tends to emphasize the epistemic value of generalizability in part because of its origins in modelling. Generalizability can motivate the development of thin, abstract and largely ahistorical theories (Fracchia & Lewontin, 1999). Epistemic values of CES in turn support characterizations of human cognition that are automatic and 'kinetic' (Lewens, 2015), a term used to refer to the population modelling approach to cultural evolution as akin to treating individuals as undifferentiated molecules familiar from the kinetic theory of gasses, and thus, far easier to formally model. Extant, 'thin' characterizations of cognition can pose a special problem in CES because they may misrepresent actual enculturation and transmission of cognitive contents, and also because they may feed narratives about culture and cultural change according to which individuals, perhaps especially in non-Western cultures (Wolf, 2005; Chellappoo, 2022a), lack agency. Generally, what are the proper roles of personal and sub-personal processes in formal explanations of cultural transmission? This question gets to the heart of differences between the CES frameworks of cultural attractor theory and of population modelling (see Buskell, 2019). Is it appropriate for 'population-thinking' models to minimize agency by emphasizing roles of copying and imitation while neglecting to model roles of coercion or institutions (Boyd & Richerson, 1985)? Does 'cultural attractor theory' (Sperber, 1996) in contrast attribute to agents too much capacity to modify cultural items while transmitting them? Increased efforts to integrate modelling with subtler accounts of encultured human cognition and transmission, in which they are sometimes rational, effortful and culturally inflected, will probably improve the field.

Finally, current research in philosophy of science points to the promise of bootstrapping CES and CET research into a *philosophy of nature*, i.e. formulating an 'overall picture of the natural world that science […] seems to be giving us' (Godfrey-Smith, 2001: 284). Important contributions include Kim Sterelny's (2012, 2021) work aimed at outlining the natural history of human beings and their hominin ancestors, and work making sense of the striking increase in technological complexity of hominins (Pain & Brown, 2021). This marks a promising shift that some have described in terms of movement from a constrained form of behavioural innovation to one that is 'open-ended' (Borg et al., 2022; Charbonneau, 2015), perhaps in a way analogous to the open-ended possibilities afforded by genetic recombination (Charbonneau, 2016).

4. Methods: Models, experiments and field studies

In this section, we discuss challenges pertaining to three common methods in CES. Giant strides have been made in the refinement and sophistication of these scientific techniques in recent decades. The body of local theory tethered to a single method is used to warrant choices in modelling (e.g. about framework or scale), in experimentation (e.g. about deriving from theory a hypothesis for testing) and in field studies (e.g. about operationalizing 'social learning' in archaeological contexts). The local theoretical reflection on decision-making about model type, parameterization and more, is rich and growing richer. This type of 'method-specific' theory is distinct from and narrower in scope than the cross-disciplinary theory essential for improving knowledge integration and meeting other needs of the CES research community. For example, even though an agent-based model might be exquisitely motivated on its own terms, there are rarely to be found theoretical tools that provide a principled structure for how the results of such a model are to be validated using data or results from experiments or field studies, even when those methods are used to explore ostensibly similar research questions.

4.1. Models in cultural evolution

As cultural evolution developed into a scientific field, innovative mathematical and computational techniques were devised to represent intricate features of cultural processes (Kandler et al., 2012). Broadly speaking, three important modelling frameworks have helped to improve our theoretical

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understanding of evolutionary processes. The first framework is composed of *gene–culture coevolution models*, which assume a continuous, bidirectional interaction between genes and culture (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985). Next are *cultural neutral models*, which assume that all variants are equally likely to be adopted, and attempt to understand cultural evolution in the absence of selective forces by assuming that changes in cultural variants are due solely to random drift and innovation (Bentley et al., 2004; Blythe, 2012; Reali & Griffiths, 2009). Finally, the *cultural selection* framework assumes that some variants spread more rapidly than others, making evolution a process that is not neutral, but subject to biases (e.g. systematic cognitive and transmission patterns deviating from rationality) or selection pressures (e.g. environmental factors that affect fitness of variants) (Boyd & Richerson, 1985; Hagen & Hammerstein, 2006; Henrich & McElreath, 2007; Vale et al., 2017).

While modelling frameworks make distinctive assumptions about the nature of cultural processes, these frameworks can each be instantiated at either of two common scales. Regarding the scale used to model cultural evolution, researchers in the field have distinguished between two general classes (Van Dyke Parunak et al., 1998; Kandler et al., 2012). The first is composed of *micro-scale models*, which aim to simulate how individual units in a system behave and interact with one another. The best-known type of micro-scale model is the agent-based model, which consists of a system composed of a set of autonomous units called agents, which simulates the decision-making, behaviour and interactions of agents to understand how patterns emerge at the population level. Such models have been used to study segregation dynamics (Schelling, 1971), the emergence of cooperation (Axelrod & Hamilton, 1981), the evolution of language (Centola et al., 2007; Kirby et al., 2014) and network dynamics (Segovia-Martín et al., 2020), and to adjudicate between competing explanations for biocultural phenomena like footbinding (Chowdhury et al., 2022).

The second class is composed of *macro-scale models*, which attempt to capture the overall behaviour of the system. Macro-scale models may consist of ordinary or partial differential equations that contain one or more functions with their derivatives. In this context, the functions represent quantities (e.g. populations A and B), the derivatives define their rates of change and the equation defines the relationship between both variables. These models have been used to study topics such as language competition (Abrams & Strogatz, 2003), political competition (Misra, 2012), the evolution of religiosity (Rowthorn, 2011), the distribution of cultural traits (Manrubia & Zanette, 2002) and innovation (Kandler & Laland, 2009), among other social issues (see Brown, 2007). Other macro-models, such as phylogenetic or statistical inference models, are oriented to encompass the broader evolutionary relationships between organisms and groups using existing experimental, historical and archaeological data (Turchin et al., 2012).

An appreciable challenge facing the use of modelling to draw substantive inferences about actual cultural processes is that varied costs involved in selection of a framework and a scale for analysis often limit the inferential range of the model's results. Micro-scale models allow more control over the properties of individual entities in the system, generally at the expense of higher computational cost and greater complexity of formalization, which limits their reproducibility and generalizability. Macro-scale models, on the other hand, allow greater control over population variables and the evaluation and formalization of the dynamical system, although at the cost of a lack of control over the individual entities of the system. From these two types of models emerged a general theoretical concern over how to integrate their results.

Of very special consideration in models of cultural evolution is the development of techniques to represent multivariate causal interactions between phenomena at both micro- and macro-levels, e.g. the 'ratchet effect' (Tennie et al., 2009), often regarded as indispensable for explaining cumulative cultural evolution. Recent formal developments enabling the combination of micro- and macro-models are allowing modellers to meet this need and, consequently, they will stimulate high-quality research in CES and assist in overcoming challenge (C3). Micro- and macro-models can be combined by building adaptive dynamics models or with multilevel selection models where both events at the individual level generate effects at the group level and events at the group level affect the individual properties of the

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system (Mullon & Lehmann, 2017; Fishwick, 1995; McElreath & Henrich, 2007; Waring et al., 2017; Segovia-Martin & Tamariz, 2021). This represents the future of modelling in cultural evolution, but it is not itself without challenges.

Despite numerous advantages, joint micro-macro models are now confronting novel theoretical problems. These include reconciling the role of individual-level behaviours with aggregate-level phenomena; addressing emergent properties that cannot be explained by the actions of individual agents alone; accounting for feedback loops between the micro- and macro-levels; and specifying the content, behavioural influence and population-level effects of 'regulatory traits', i.e. traits governing cultural transmission of other traits (Acerbi et al., 2014). Given their content, progress on these problems would benefit from formal analyses of concepts like *collective action*, *coercion* and *institutions,* which would facilitate operationalization in models.

4.2. Experiments in cultural evolution

Challenge (C3) focuses on the need to overcome several problems facing the effort to model culture as a complex, adaptive system. In their report of survey results, authors wisely distinguish this from a corollary challenge, (C4), which involves the need to develop an evidential bridge between modelling results and research on the psycho-social mechanisms instantiating cultural transmission in the world. Given the ascendant place of modelling in CES, validating models against data from experiments and field studies has remained a persistent challenge. This challenge for CES typically has one of four points of inception: (i) a lack of data, making validation unfeasible; (ii) a conceptual gulf between model and empirical data; (iii) limitations of the model's ability to properly describe new, previously unseen data; and (iv) a lack of parallelism between model mechanisms and actual mechanisms, making models of little use in capturing the causal interactions between real evolutionary processes (see Weisberg, 2007, on assignment, scope and fidelity). Mechanisms for cultural evolution like social learning biases have of course been proposed (Boyd & Richerson, 1985), modelled (Denton et al., 2020) and experimented upon (Efferson et al., 2008). Yet CES nonetheless faces several problems integrating theory and modelling with experimentation often owing to the absence of a set of criteria for a measurable outcome that is commensurable across methods.

Take, for example, research that frames lab- and field-based experiments (see Mesoudi & Whiten, 2008 and Tamariz, 2017 for reviews). Cultural transmission has been a focus of laboratory experiments, many of which examine whether or not some of the postulated learning biases exist. Other studies pit multiple learning biases against each other to assess which are more powerful explanations of cultural retention and transmission. While some experiments focus on biased social learning, including, among others, content- (e.g. Boyer & Ramble, 2001; Broesch et al., 2014) and prestige-biased cultural transmission (e.g. Jiménez & Mesoudi, 2019) in the retention and recall of stimuli, others utilize sequential transmission chains to examine ostensibly unique properties of human cultural evolution such as cumulative evolution and problem-solving (e.g. Caldwell & Millen, 2008; Jiménez & Mesoudi, 2020). In step with the classic experiments of Bartlett (1932), many of these studies follow the logic and structure of 'telephone', a game that exploits distortion of information across chains of multiple learner-teachers. Other experiments stress communication and group coordination through actively and collectively aligning individual behaviours, such as drumming and movement, and examining downstream behaviour (e.g. Tunçgenç & Cohen, 2016; Wood et al., 2018). Aptly, but unsystematically, the range of participants' agency varies significantly across cultural transmission experiments. This also applies to studies of cultural evolution in non-human animals, where a variety of evidence stemming from controlled experiments and anchored in social learning models has been observed (Whiten, 2019).

Much of the behavioural experimental work that falls under the rubric of cultural evolution assesses the magnitude and scope of cooperation that is unique to our species. By measuring individual decisions in allocating money and other resources, experiments in cross-cultural behavioural economics suggest that culture and cultural institutions play a significant role in promoting more cooperative

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strategies (Pisor et al., 2020) or, less appreciated in CES, in *reducing* cooperation (cf. Akbari et al., 2019). Studies that deploy the same experimental game but have culturally salient treatment conditions show that when made culturally relevant, salient beliefs and values can alter the course of interpersonal behaviour (Cronk, 2007; Gerkey, 2013; Lightner et al., 2017). In such experiments, the outcome variable is cooperation, not whatever cultural information that is purportedly inducing it, and certainly not the transmission of such cultural information. Yet some paradigms have exploited such experiments, and rather than using beliefs and cultural framings to predict behaviour, some have reversed this structure and examined how game outcomes can predictably shift the content and structure of extant beliefs (Purzycki et al., 2020). Neither of these experimental paradigms directly speaks to transmission, however; one seeks to explain the evolution of cooperation and the other seeks to explain the evolution of beliefs as responses to threats to cooperation.

While the ultimate theory that motivates such studies posits that cultural norms can co-evolve with problems of cooperation, there remains a notable deficit in just how little of this work specifically attends to cultural transmission and the co-variation between cooperation and tradition. Experiments about variability of dynamics in transmission across cultures are infrequently motivated by integration with cross-cultural psychology and so, albeit with exceptions (e.g. Mesoudi et al., 2014, which found significant cross-cultural variation in the adoption rate of success-based social copying), they generally do not motivate or test explicit hypotheses about cultural differences in transmission. Many such studies might assess the cultural mechanisms that promote or reduce cooperation but do nothing in the way of accounting for the diffusion or maintenance of such beliefs. In other words, while we might see co-varying effects of cultural information and behaviour in the lab, and while this might make certain explanations or theories more plausible, it remains unclear what this has to do with the evolution and persistence of the cultural part of the dynamics. Are particular cultural strains prevalent *because* they promote (or reduce) cooperation? Do the social benefits of cooperation contribute to the prevalence and maintenance of particular cultural mechanisms? Such questions are ripe for serious experimental treatment, and returning to challenge (C4), the results of such experiments are expected to inform representations of subtle, varied causal interactions in future micro–macro models.

4.3. Field studies

Field studies fall into various kinds. *Ethological* field studies concern cultural performances beyond our species. *Archaeological and palaeoanthropological* excavations provide insight into the deep past and into the emergence of cultural evolution of hominins from australopithecines and different *Homo* species up to anatomically modern humans. *Anthropological* field studies, often separated into cultural anthropology and evolutionary anthropology, examine social and material interactions in present-day human groups and societies and their cultural products. Although these three fields differ markedly in the nature and acquisition of their basic data as well as in their theoretical presuppositions, they share important commonalities. Key features of all three approaches are: adoption of long-term data collection methods and analysis; attention to facts about the material, ecological and behavioural contexts of cultural behaviours; and interest in identifying a potential variety of contributing elements. Field studies in CES aim to gain a broad overview of cultural performances and their environmental conditions, and to examine the differences between distinct social and ecological settings in order to increase understanding of the historical and biological circumstances of cultural evolution. Field studies in CES incorporate fuzzy evidence about multi-faceted entanglements between agents, environments and behaviours, captured with a variety of data types ranging from anecdotal reports to behaviour coding to structured research protocols, within which meaningful patterns of relations and development can be detected.

Field studies have played and will continue to play the most prominent role in CES responses to challenge (C8), which encompass the need to convince policymakers of the need to conserve animal cultures. Until the second half of the twentieth century, culture had only been ascribed to humans.

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Since the expansion of the definition of culture to make it applicable to non-human animals (McGrew, 1992), and subsequent studies on behavioural traditions in chimpanzees (Whiten et al., 1999), which combined field research from several groups in search of differences of occurrences of behaviour across sites under similar environmental conditions, ethological field studies with cultural evolutionary scope have been on the rise. The variety of animal species examined as well as evidence of performances with basic cultural features have markedly increased. Ethological research has produced studies on the pace of animal innovations, as found in seasonal changes in songs of humpback whales (Schulze et al., 2022), on cultural transmission in the manufacture of tools, as in New Caledonian crows (Hunt & Gray, 2003), and on the adoption of new behavioural elements from resident individuals when they must adapt to new habitats after dispersal, as in male orangutans (Mörchen et al., 2023). The current state of the field suggests that there is a variety of basic cultural performances in a wide array of animal orders from invertebrates to birds and mammals (Whiten, 2021) and that the number of (unspecified) cases of 'culture' is underestimated (Schuppli & Van Schaik, 2019).

In contrast to field studies on animal behaviour and ethnography, which include direct observations of performances, primary data from archaeological field studies provide only indirect insights into past human behaviour through trace material evidence. Performances, and thus also group-specific patterns and their development, must be inferred from finds via multiple analytical steps before interpretation (Perrault, 2019). The chronological frame of archaeological field studies spans more than 3 million years. Research focused on distinct spans of time within this epochal stretch has enabled data collection from the material record to respond to quite different questions about cultural evolutionary processes. Inspired by behavioural studies on animals, evolutionary archaeological research focusing on an *early* phase up to 500,000 years ago (Shennan, 2008) is dominated by the distinction of primate and hominin cultural capacities (Tennie et al., 2017), long-lasting technical traditions and convergent evolution in technologies (O'Brien et al., 2018), and the development of simple stages of communication and cooperation (Gärdenfors & Högberg, 2017). For a *middle* phase between 500,000 and 100,000 years ago, the research focus shifts to the study of evidence for the increasing complexity of technical expressions (Lombard & Haidle, 2012) and the necessity of advanced forms of cultural transmission (Stolarczyk & Schmidt, 2018), group structures and the advent of ritual behaviour (Dapschauskas et al., 2022). In a *late* phase from 100,000 years on, relations of techno-complexes and social systems as well as the development of group identities (Vanhaeren & d'Errico, 2006) and belief systems become increasingly important. The analysis of spatial, material and social networks and their dynamics (Mills, 2017) aligns with other anthropological approaches to questions about the biocultural evolution of our species.

Ethnographic field studies are a major means for collecting data within cultural anthropological research. Although the method of participant-observation has well-known limitations (Howell, 2018), this is not the only tool in the anthropological tool kit. Complementing participant-observation are long-term and open-ended participatory methods that allow for individuals within the studied population to speak for themselves. Alongside these are tools like qualitative and structured interviews, genealogy and network analyses (Beer & König, 2020; Seligmann & Estes, 2020). Ethnology, the comparative study of peoples, represents another approach to answering canonical CES-inspired questions under the field study umbrella. Although ethnology has also long been subject to critique, it has never been absent from anthropological research (Schnegg, 2014). More recently, comparative methods have become supercharged by the increased accumulation and availability of cross-cultural data together with rigorous comparative methods (Fox & Gingrich, 2002). Such methods are now applied to a broad anthropological domain, expanded by inclusion of urban settings, the digital world and specific groups (e.g. professional, religious, gender) within larger communities. With a growing interest in the universality of human rights (Nagengast, 1997), relations of performance and cognition (Antweiler, 2016), and the origins and evolution of broader concepts such as religion and morality (Purzycki et al., 2018), more universal perspectives have been taken.

Contributions of evolutionary anthropology (EA) and its sister, human behavioural ecology (HBE) (differences between which are left aside here) prize coherence with other methods of knowledge

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discovery and prioritize theoretical relations to natural selection. Unlike some areas of evolutionary science, work in EA and HBE generally avoids optimality assumptions that often characterize evolutionary psychology (about this see Fessler et al., 2016: 1030). The frameworks of EA and HBE occupy an unusually high-traffic crossroads within CES and, to extend the analogy, these crossroads are located near wide bridges traversing the waters between cultural and biological evolution. Despite their pluralistic use of methods and their ecumenical approach to research questions, EA and HBE are unified by the assumption, put roughly, that concepts from evolutionary biology have considerable utility in explanations of gene–culture co-evolutionary phenomena. Evolutionary anthropologists might study modifications of the hip, pelvis and spine revealed in the hominin archaeological record (Lovejoy, 2005a, b), or information about ancestral pathogen loads across regions in relation to present-day, culturally variable social psychological traits (Fincher et al., 2008; Faulkner et al., 2004). Modifications of the hominin body plan supporting bipedality, and cross-cultural variation in social-psychological factors in relation to pathogen load, are hypothesized to result, in the end, from their consequences on biological fitness. The ready explanatory pluralism of HBE and EA has probably contributed to their nuanced awareness of evolutionary trade-offs at play across human life history, e.g. between current and future reproduction and quantity and quality of offspring (Hill & Kaplan, 1999); their attention to both uniformity and difference between primate 'proto-shame' and human shame systems (Fessler, 2007); and their pleasing, simultaneous concern with multiple dimensions of a single scientific explanation, dimensions such as physical realization, causation and phylogeny, which are often treated autonomously elsewhere in CES.

Working with results of field studies in the context of findings from elsewhere in CES makes a special contribution to challenges about knowledge synthesis and interdisciplinary integration (C5). This is not least because it is in the form of field studies that the bulk of research on non-human culture occurs. Operationalizing the culture concept across archaeology, biological anthropology and ethology, and applying it to behaviourally modern humans, earlier humans and non-humans, each requires improvements to this common but coarse-grained concept. Without more unanimity on the culture concept, survey results suggest that 'siloing' will continue (on the problems of disciplinary 'siloing' see Brewer et al., 2017: 2). Perhaps, for example, a law-like systematicity links the roles that social learning plays in the transmission of behavioural traits within different animal species and within hominin groups, but the underlying theory and methods issues have yet to be adequately resolved to support law-like cross-species generalizations about necessary conditions for the ontogeny of culture.

5. Unresolved theoretical issues in specific areas of cultural evolutionary science

In this section we focus on theoretical challenges faced in two core areas of CES: culture in other animals, and languages as culturally evolving systems. Our goal is just to show, with specific examples, that many unanswered or poorly framed scientific questions in cultural evolution would benefit from attention to theory.

5.1. Culture in other animals

The existence of behavioural traditions passing (not necessarily replicating) between generations through social learning in animals – a working characterization of 'culture' – is now uncontroversial. As a result, questions of interest to researchers have moved to focus on the mechanisms that support cultural transmission in animals, and questions about the methods with which animal cultures are studied. Answers to these questions can tell us whether human forms of culture – not least cumulative culture – are likely to be found in the animal kingdom.

Historically, animal cultures have been studied via the 'method of exclusion' (Whiten et al., 1999; later refined by Langergraber et al., 2011). This identifies behavioural patterns as cultural when they differ between geographically diverse groups of the same species. If genetic differences between these

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groups can be ruled out (e.g. because of inter-group migration), and behavioural differences cannot be attributed to local ecological conditions, then behavioural patterns are likely to be products of social learning – and so are indicative of variant cultural traditions. While influential, this method has been criticized as insufficiently informative, and as resting on a conceptual problem, specifically a false dichotomy between nature and culture (Rogoff, 2003). First, it probably undercounts culture, where behaviours are universal (and so do not differ between populations) but are nonetheless socially learned. Second, it gives no insight into the kinds of social learning mechanisms that support cultural transmission (Sterelny, 2009; Acerbi et al., 2022). This criticism is important because some higher fidelity social learning processes, such as imitation (aka 'process copying' Buskell & Tennie, 2022, or 'know-how copying' Tennie, 2023), are thought to play an important (if not always necessary) role in the emergence of cumulative culture (Tennie et al., 2009; Moore, 2013). These may be missing in other species, or too inconsequential to produce and maintain similar cultures.

Tennie and colleagues have developed a series of paradigms designed to test whether putatively cultural behaviours in our nearest relatives, the great apes, are a product of imitation. Early paradigms established that chimpanzees do not acquire behaviours whose transmission requires high-fidelity transmission chains (Tennie et al., 2009). More recent studies show that many great ape behaviours can be explained as products of serial reinvention (often through trial-and-error learning) (e.g. Bandini et al., 2021). Since naïve apes spontaneously reinvent these behaviours when left alone with the necessary apparatus, they cannot depend on social learning. Tennie and colleagues call these behaviours 'latent solutions'. They do not deny that some forms of social learning support the transmission of great ape behaviours (Tennie et al., 2020). However, they argue that great apes do not copy new forms of 'know-how' from peers. Rather, for the most part, great ape social learning occurs because features of the environment are made salient through the actions of others. On this account, the presence of others in a learning environment is conceived of as a 'probabilistic difference maker' (Scarantino, 2015): a non-essential but nonetheless causally significant factor. It may facilitate the acquisition of behaviours without being essential for their development.

While it should now be uncontroversial that great apes do not, in their natural habitat, engage in high-fidelity know-how copying, the finding that great apes can learn to imitate (e.g. Pope et al., 2017) raises the question of whether their *lack* of imitation is itself a product of their developmental environment, and so potentially a culturally evolved 'cognitive gadget' (Heyes, 2018). Nonetheless, even trained apes seem unable to retain cultural inventions over successive generations (Tennie, 2019). This means that chimpanzees must often reinvent their ancestors' technologies in ways that human communities need not, and explains why cumulative culture is rare, at best, in great ape communities. Tentative reports of cumulative culture in whales and monkeys suggest that further empirical research is needed to determine whether and how animal cultures can gain in complexity over time. Theoretical research specifying what would constitute evidence of cumulative culture (and how 'acultural' explanations from natural selection would be ruled out) must precede or at least accompany additional field studies. A valuable contribution by theoreticians here would be to assist in fixing the social and cognitive conditions that are necessary and sufficient for cumulative culture, and by developing hypotheses about the kinds of mechanistic changes that support the development of higher fidelity social learning in non-human animals (Berio & Moore, 2023).

A final question asks whether non-human animals, and especially apes, are capable of understanding norms. Norm cognition is taken to be a prerequisite of many of our culturally evolved social institutions (e.g. institutions of justice). While some are sceptical that norm cognition is present in great apes (Schlingloff & Moore, 2017), others have argued that this scepticism is driven by an intellectualized account of the cognition required for normativity, suggesting a need for minimal models of norm cognition (Westra & Andrews, 2022). A further obstacle remains for investigating norm cognition in animals. The best method for identifying norms is through third party enforcement of perceived norm violations – and this is strikingly absent from great apes (Schlingloff & Moore, 2017). The theoretical formulation of alternative methods for identifying normative behaviours would thus constitute a valuable contribution to the field.

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5.2. Languages as culturally evolving systems

Until not long ago, discussion of language 'evolution' was somewhat taboo. As recent as 1994, textbooks observed that 'Evolution … has become a "dirty word" in modern linguistic theory' (McMahon, 1994: 314). This is because through the twentieth century the nomenclature of evolution risked some allusion to outdated, often racist, views about how some languages – and by extension some social groups – might be 'more evolved' than others. It is now uncontroversial within linguistics that no language is inherently 'better' or 'more useful' than others. So, while vigilance must be maintained, the socio-political risks associated with evolutionary talk have begun to fade, and in the past 30 or so years evolutionary approaches to languages have grown dramatically in prominence (Tallerman & Gibson, 2011; Dediu & de Boer, 2016).

Today, the expression 'language evolution' is widely used to describe at least two distinct phenomena and one methodological advance. The two phenomena are: the biological process by which humans, and apparently only humans, became a 'language-ready' species; and the set of cultural – or 'cultural evolutionary' – processes by which relatively simple and unstructured systems become highly structured, and hence acquire some of the common, characteristic properties of languages, such as symbolism, compositionality and duality of patterning. The methodological advance is the application of phylogenetic tools, derived from population genetics, to study language history and language change. All three of these literatures are now very large, comprising thousands of papers each. Multiple past papers review, summarize and synthesize them (e.g. Mace & Holden, 2005; Tomasello & Call, 2019; Greenhill et al., 2020; Haspelmath, 2020; Roberts & Sneller, 2020; Scott-Phillips & Heintz, 2023; Scott-Phillips & Kirby, 2010). Here we focus on a philosophical issue arising from this growing influence of evolutionary thinking.

The challenge, put simply, is: what exactly does the evolutionary perspective bring that other approaches do not? The biology of language, language emergence and language change have all been important topics for language science for a long time, and a great deal of what has been uncovered by evolutionary approaches has previously been investigated and described in other terms. Research adopting an evolutionary perspective has enriched our understanding, provided new methods and added many new findings, but does it fundamentally alter our understanding of what the empirical phenomenon is and how it works?

One answer might be that a relatively faithful transposition of the Darwinian model – where variation, selection and inheritance combine to generate natural selection and hence the appearance of design in nature – is possible, and brings with it new insights, explanations and tools. With languages, there is something like variation (linguistic items vary enormously), there is something like selection (some items become more common than others) and there is something like inheritance (we learn from the previous generation). Some linguists indeed propose that linguistic items, of some sort or another, could be identified as units of selection closely analogous to genes (e.g. Croft, 2008; Ritt, 2004; Tamariz, 2019). However, deeper analysis raises difficult questions, and the issue is contentious: a decade ago, a group paper on language as a culturally evolving system observed that, 'Various scholars have proposed that concepts, cultural behaviors, or artifacts may function as replicators. It remains to be seen whether any, all, or some combination of these entities are reasonable candidates for cultural replicators' (Dediu et al., 2013: 314). The situation has not changed substantially since.

Another response to this question would be to adopt only specific parts of the Darwinian toolkit. That is, one could reduce the role of an analogy between variation in language and variation in genes while retaining other parts of Darwinism (Claidière et al., 2014). For instance, there might be scope for perspectives that adopt population thinking and some commitment to selectionism, but without the stronger commitment to replicators.

Languages are arguably the cultural domain *par excellence* for population thinking because languages are, more than any other cultural phenomena, especially amenable to 'atomization' – to being studied in terms of discrete items – and hence to identification and analysis of the types and their changing frequencies over time. As such, an emergent and pressing theoretical question is:

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how best can linguistic types and tokens be precisely identified to facilitate cultural evolutionary study and modelling? Constructionist approaches to grammar, which describe grammars as networks of form–function pairs (Goldberg, 2003; Hilpert, 2014, *inter alia*), may be especially suitable for this goal. However, because there is little research developing this idea, treating constructions as the targets of population thinking (partial exceptions are Kirby, 1999; Steels, 2016) remains necessary.

6. Implications and applications of CET

The authors of the Cultural Evolution Society's report of survey results stated that one grand challenge involves the identification and study of cultural evolutionary processes that address 'significant social, economic, and political problems' (Brewer et al. 2017: 3), challenge (C8), which explicitly mentions climate change as an example. A growing number of scientists have begun focusing on such practical implications of CES, often concerning the role of norms. We define 'norms' as the shared values and rules that are enforced within a group, and which we contrast with the individual values or preferences of members. Reward and punishment are the basic means by which political entities and groups exert control over their members, organize them into roles and maintain order. For instance, reliable enforcement of norms against harming others reduces mutual fear among group members, making it easier to live together and making it more likely that individuals will survive. Indeed, from the perspective of both genetic and cultural evolution, theorists converge on cooperation and coordination as the general function of norms. Thus, practical implications of CES on social, economic and political challenges often concern the importance of norms in social life, yet coarse-grained concepts like *norm* or *cooperation norm* fall into the general conceptual problem mentioned above. Although modellers and experimentalists often refer to 'norms', the precise conditions under which norms (let alone different types of norms) are psychologically instantiated have yet to be perspicaciously individuated.

Adopting one approach to human cooperation defended within CES (Boyd & Richerson, 2009), philosophers Sripada and Stich (2006) attempted to address this challenge with the development of a theory of norm psychology that distinguishes between *intrinsic* and *instrumental* psychological motivations to follow and enforce norms. Instrumental motives focus on gaining rewards and avoiding punishment, while intrinsic motives concern the rightness or wrongness of an act itself, independently of any punishment or reward. A desire to comply with the speed limit may be instrumentally motivated, as a desire to avoid being fined as punishment, or it may be intrinsically motivated, as a desire to avoid doing something wrong by putting others at risk. Both motives can occur simultaneously, but research suggests that these are distinct functional capacities, with distinct inputs and outputs, and distinct ontogenies. Intrinsic motivations to follow norms evolved specifically in response to the adaptive problems posed by norm enforcement (Chudek & Henrich, 2011), so they could only have evolved quite recently, presumably after cultural learning capacities became sophisticated enough to support the widespread sharing of enforcement practices. This is neither the history nor the function of the various instrumental motivations involved in norm compliance, such as desire for social status, fear of pain, concern for mating prospects, the role of self-interest, etc. With a formal analysis of norms in hand, CES researchers could better test implications hypothesized to follow from one or another type of norm.

Davis et al. (2018) opened up this research by studying the intrinsic–instrumental motivational distinction as it operates within the sustainability movement. They discovered that too little attention is paid to the potential of intrinsic motives, and suggested clear ways to test the strength and frequency of intrinsic motives, and subsequently, methods to increase intrinsic motivation. Similarly, Kline et al. (2018) use the same theoretical framework to examine group structure and organization by analysing the norms of groups, organizations and institutions involved in suppressing free riding in sustainability contexts. For this they introduce novel models of cultural multilevel selection that address the competing pressures operating at different levels or scales of social organization. These attempts to apply CET to sustainability concerns have met with some uptake among practitioners in civil engineering, who face problems of free riding addressed at multiple levels of government. Hydrologists modelling

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social-ecological systems have urged the adoption of a norm psychology framework informed by CES findings to address cooperation problems surrounding water scarcity and conservation (Yu et al., 2020).

The use of CET in sustainability science represents little more than proof of concept for the potential value of applying results in CES, and it is important not to dress old solutions up in the clothes of new theories (Chellappoo, 2022b). However, the case also illustrates a broader strategy of focusing theoretically perspicacious CES research upon norm-based social ills. For instance, as norms of democracy have come under threat from authoritarianism around the world (Norris & Inglehart, 2019), it has become salient that commitments to the rightness of democracy itself really matter. Without them, voters and officials often use their democratic powers to make governments less democratic or non-democratic. Addressing this problem requires the internalization of democratic norms, not instrumental reasons for following them. Another important form of intervention focuses on cases where conflicting norms exist in an equilibrium within a population. In such contexts changing the minds of a relatively small portion of the population can serve as a tipping point, initiating a cascade that quickly shifts the rest of the population to one side of the conflict (Andreoni et al., 2021). Against this background, Vogt et al. (2016) elegantly show how entertainment programming can be effective in shifting a few people's attitudes in one direction. In Sudan, they carefully embedded arguments against female genital cutting within a controlled series of telenovelas and found that viewers' attitudes toward uncut girls substantially improved. The demonstrably effective use of CES research to exploit mechanisms of cultural transmission to alter norms, and through them behaviour, augurs its own problems and might be received too optimistically (Wilson, 2011). This represents just one of several areas of CES in which knotty moral questions are rapidly arising, in this case about the role of CES in generating findings that allow political, corporate or military leaders to more effectively seed swiftly spreading, behaviour-altering cultural content through social and electronic media.

In addition to practical implications on individual attitudes and behaviours, cultural evolutionary processes have indelibly influenced human nature, for example by making human nature especially 'open-ended' (see Section 3 above), a continuing avenue for future CES and CET research (Hannon & Lewens, 2018; Ramsey, 2023). According to Kern and Moll (2017), the evolution of capacities for shared intentionality has transformed our species. Humans are the only species whose members have an awareness of themselves as embodying a unique, collectively structured form of life. The fact that culture accumulates over historical time has exerted remarkable effects on humans' understanding of self and other. There appears to be a sharp division between species whose culture 'ratchets up' in the way human culture does, and others, whose behavioural patterns are not preserved across generations. Importantly, with the dawn of cultural evolutionary processes, humans developed a consciousness of themselves as being part of a community whose members are interdependent in their learning (Moll & Kern, 2020; Moll, 2020). Bjorklund (2021) and other evo-devo scholars argue that what most drastically changed over the course of human evolution is our ontogeny, i.e. the processes by which we become mature individuals. We claim that hominin ontogeny was transformed such that children began to take a vested interest in their social learning and started to turn to adults as models and teachers. Adults, likewise, developed awareness of their role as teachers and authorities. Csibra and Gergely (2009, 2011) have discussed the evolution of a unique pedagogical communication system, whereby adults signal to learners their intent to transmit knowledge to them, and, in response, learners adopt a learning stance in which they assume the general relevance of what they are being shown or taught. Parents and their offspring thus not only became interdependent in unique ways but also developed an awareness of their interdependence and of their need to cooperate within a transmission system that serves to preserve lifeways that would otherwise disappear. This points to a possible constraint on cumulative cultural evolution worthy of further reflection: for culture to get preserved cross-generationally, there had to be a transformation in the cognitive apparatus and in the self-representation of the agents who are at once the 'movers' and 'recipients' of this process.

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7. Conclusion

Although our review is broad, the field of cultural evolution is broader still, and several key areas and pressing problems were not adequately discussed above. We conclude by emphasizing two problems lurking near the ungainly relationship between cultural and biological evolution voiced in challenge (C2).

Since genes are fundamental units of selection in biological evolution, improving the relation between cultural and biological evolution, and integrating results across fields of inquiry inclusive of biology (see (C4) above), may necessitate increasing use of genetics research in CES. Scientists in cultural genomics research have identified countless neuro-functional differences across descent groups relevant for emotion and cognition at the levels of individuals and groups (Han, 2017; Chen & Moyzis, 2018). A recent, thorough review of genetic contributions to 'moral performance' found allelic variation in polymorphic genes linked to culturally characterizable descent groups. Functions of these polymorphisms related to neurohormone support, prosocial behaviour and aggressive behaviour. These neurohormones included oxytocin (regulated via polymorphic genes OXTR and CD38), dopamine (via COMPT, DRD3 and DRD4), serotonin (via TPH2 and 5-HTTLPR) and testosterone (via AR) (Wang & Su, 2022). Many moral cautions and epistemological objections accompany the use of gene × culture data, as they should. This area has met with its share of methodological missteps. For example, Chiao and Blizinsky's (2010) remarkable finding of a strong statistical relation between the ratio of several distinct serotonin transporter polymorphisms distributed across descent groups with the position of specific groups on the individualism–collectivism spectrum led authors to explain the relationship as a case of culturally infused biological selection. This result was subsequently invalidated (Eisenberg & Hayes, 2011). Even so, many findings in this field appear well warranted. Indeed, the statistical relationship just mentioned was later largely vindicated by Chiao, Blizinsky and co-authors through retesting on a much larger sample inclusive of not only European and East Asian but also African samples (Mrazek et al., 2013). We surmise that growth in this subfield is hindered by uncertainty and possible moral hazards. Compared with fields like anthropology and zoology, whose leading academic organizations have published statements governing research ethics, as a nascent field, cultural evolution may be relatively unprepared to deal with moral challenges implicitly raised by gene × culture research. At least, problems of this kind did not register as concerns in the Cultural Evolution Society's survey results (Brewer et al., 2017).

We finally turn to multi-level selection. The Cultural Evolution Society survey report identifies the topic of 'theory' and 'integration' as two of the most pressing issues facing the field (Brewer et al., 2017: 2). This pair forcefully collides when it comes to the status of multi-level selection theory in CES and evolutionary psychology. Recent work in evolutionary psychology contends that individual-level punishment explains substantial amounts of human cooperation (Krasnow et al., 2015); that third-party punishment is shown to arise from defence of personal interests (Kraswow et al., 2016); and that the threat of targeted conspiratorial killing selected for groupishness (Wrangham, 2021). Unifying these results is their support of the conclusion that biological selection on individual human organisms leads to group-level norms as by-products. These findings raise sceptical questions about the status of multi-level, especially group-level, adaptations in explanations of cooperation. Group-functional traits like language and norms are considered mere by-products of individual-level factors in evolutionary psychology (Gangestad et al., 2006, underappreciated in CES despite its authoritative authorship). In CES, though, group-level 'traits' are often treated as products of cultural adaptation and explanatorily irreducible to individual-level biological adaptations (Richerson et al., 2016). Evidence for group-level adaptations has been provided by theory (Sober & Wilson, 2003), modelling (Richerson et al., 2016) and experiment (Shariff & Norenzayan, 2007), but it is contested.

The disputed status of group selection and problems consequent from the use of this and allied coarse-grained terms is a significant cause of the wide gap and lack of knowledge integration between CES and fields like theoretical biology and evolutionary psychology and biology. This is epitomized by Krasnow and Delton's (2016: e43) argument that CES lacks a theoretical core capable of generating unambiguous, falsifiable predictions, is overly dependent on modelling and offers merely retrodictive

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redescriptions of group-level traits as group adaptations. What developments could bring about a rapprochement between CES and the evolutionary human sciences? The study of evolutionary transitions in individuality holds prospects for more productive disagreement and engagement (see Carmel et al., 2023 and the issue of which it is a part). A more promising approach is likely to be creatively drawing and judiciously testing entailments of inclusive fitness theory to understand culture's role in cooperation – and biology's role in culture. (Of the 18,121 publications currently recorded in Web of Science as representing the 'topic' of 'cultural evolution', a mere 47 refer to 'inclusive fitness', suggesting untapped potential.) We suspect that, if the influence and authority of evolutionary anthropology and human behavioural ecology, pluralistic fields capable of a wide embrace, continue to grow within CES and CET, productive steps towards greater theoretical coherence with evolutionary sciences will follow.

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