FORUM ON THEORY IN ANTHROPOLOGY

Is Human Culture Cumulative?

Krist Vaesen and Wybo Houkes

It has been claimed that a unique feature of human culture is that it accumulates beneficial modifications over time. On the basis of a couple of methodological considerations, we here argue that, perhaps surprisingly, there is insufficient evidence for a proper test of this claim. And we indicate what further research would be needed to firmly establish the cumulativeness of human culture.

Cumulative cultural evolution (CCE) is widely regarded as a hallmark of our species (Boyd and Richerson 1996; Dean et al. 2014; Hill, Barton, and Hurtado 2009; Mesoudi 2011; Tomasello, Kruger, and Ratner 1993). A population exhibits CCE if its individuals, across generations, gradually improve their behavior through social transmission of beneficial modifications to the transmitted behaviors (Mesoudi and Thornton 2018). Over time, CCE results in cultural traits that could not be invented by a single individual (Dean et al. 2014; Richerson and Boyd 2005; Tennie, Call, and Tomasello 2009).

It is fairly evident that human populations have been able to improve at least some of their behavior through CCE, especially if one restricts oneself, as most of the relevant literature appears to do, to behaviors in the technological domain and relevant measures of improvement in this domain. Even a quick glance at the historical transitions in, say, lithic technologies, extant foragers' hunting gear, and modern combustion engines suffices to suggest that, indeed, CCE has allowed humans to increase the efficiency or effectiveness of traits. And the Apollo missions indeed seem to demonstrate that humans can "increase the *complexity* of their technology and knowledge over many episodes of social transmission, by building on the developments of their predecessors" (Dean et al. 2014:285; emphasis added).

Cultural evolutionists, however, often endorse a much stronger claim, namely, that CCE is a unique and characteristic feature of human culture (see, e.g., Dean et al. 2014; Lewis and Laland 2012; Tennie, Call, and Tomasello 2009).[1] They infer this from an alleged difference between humans and nonhuman animals: whereas CCE is rarely found in nonhuman animals, it is—or so the argument goes—pervasive in our species. As Richerson and Boyd (2005) write: "One thing is fairly clear: only humans show much evidence of *cumulative* cultural evolution. . . . Humans can add one innovation after another to a tradition until the results resemble organs of extreme perfection, like the eye. . . . In nonhuman animals, the evidence for cumulative cultural evolution is scanty and controversial" (107; emphasis in the original).

Boyd and Richerson are certainly right that it requires much evidence to substantiate the claim that CCE is a unique and characteristic feature of human culture. But is it, as they contend, fairly clear that there is much such evidence? Perhaps because contemporary industrialized societies abound with anecdotic evidence, researchers have been quick to accept the cumulative nature of human culture and have largely focused their efforts on examining nonhuman animal culture (see, e.g., the bias toward nonhumans in reviews of the comparative evidence in Dean et al. 2014; Tennie, Caldwell, and Dean 2018; Tennie, Call, and Tomasello 2009). A lack of generally accepted successes in establishing CCE in nonhuman animals would then seem to substantiate the idea that CCE is unique to humans.

Below, we argue, though, that properly establishing the propensity of human culture to accumulate beneficial modifications over time requires more and different kinds of evidence than are currently available: the few relevant extant data sets do not suffice for a proper test. Finally, we sketch what future research would need to do to secure a firmer empirical grounding for cumulative culture in humans and for the claim that this is a unique and distinctive feature of our species.

1. See, e.g., in Tennie, Call, and Tomasello (2009), "Human culture, in contrast [to nonhuman culture], has the distinctive characteristic that it accumulates modifications over time" (2045), in Lewis and Laland (2012), "But human culture appears unique in that it is cumulative, i.e. human cultural traits increase in diversity and complexity over time" (2171), and in Dean et al. (2014), "Human culture is clearly cumulative, with innovations being built upon the knowledge of previous generations and ideas from different disciplines and populations combined to formulate new traditions and technologies" (287).

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A Proper Test of Cumulative Culture

If cumulativeness is to qualify as a general characteristic of human culture (see the quotes in 1n), it is not enough to show that some human cultural behaviors result from CCE; rather, one must show that a large fraction of such behaviors result from CCE. Consider the following analogue. Bipedalism is, at least among primates, a uniquely and distinctively human trait. This is so because bipedalism is shared by most members of our species (and not by most members of other primate species); it is a statistical regularity characteristic of our species (but not of other primate species) that a majority of its members walk upright. In a similar vein, cumulativeness is a unique propensity of human culture only to the extent that most human cultural traits are brought about by CCE.

How should one substantiate such a characteristic statistical regularity? In an ideal scenario, one would start from established lines of descent of cultural traits. Consider figure 1*A*, which represents a phylogenetic tree that reconstructs the cultural-evolutionary relationships between five cultural traits (a–e). The number associated with each trait represents the value that the trait has with respect to a variable, *z*, which might denote the efficiency, effectiveness, or complexity of the trait (or any other dimension that traits can improve in). Among the four evolutionary transitions, three exhibit increases in *z* (a→b, a→c, b→d), and only one exhibits a decrease in *z* (b→e).

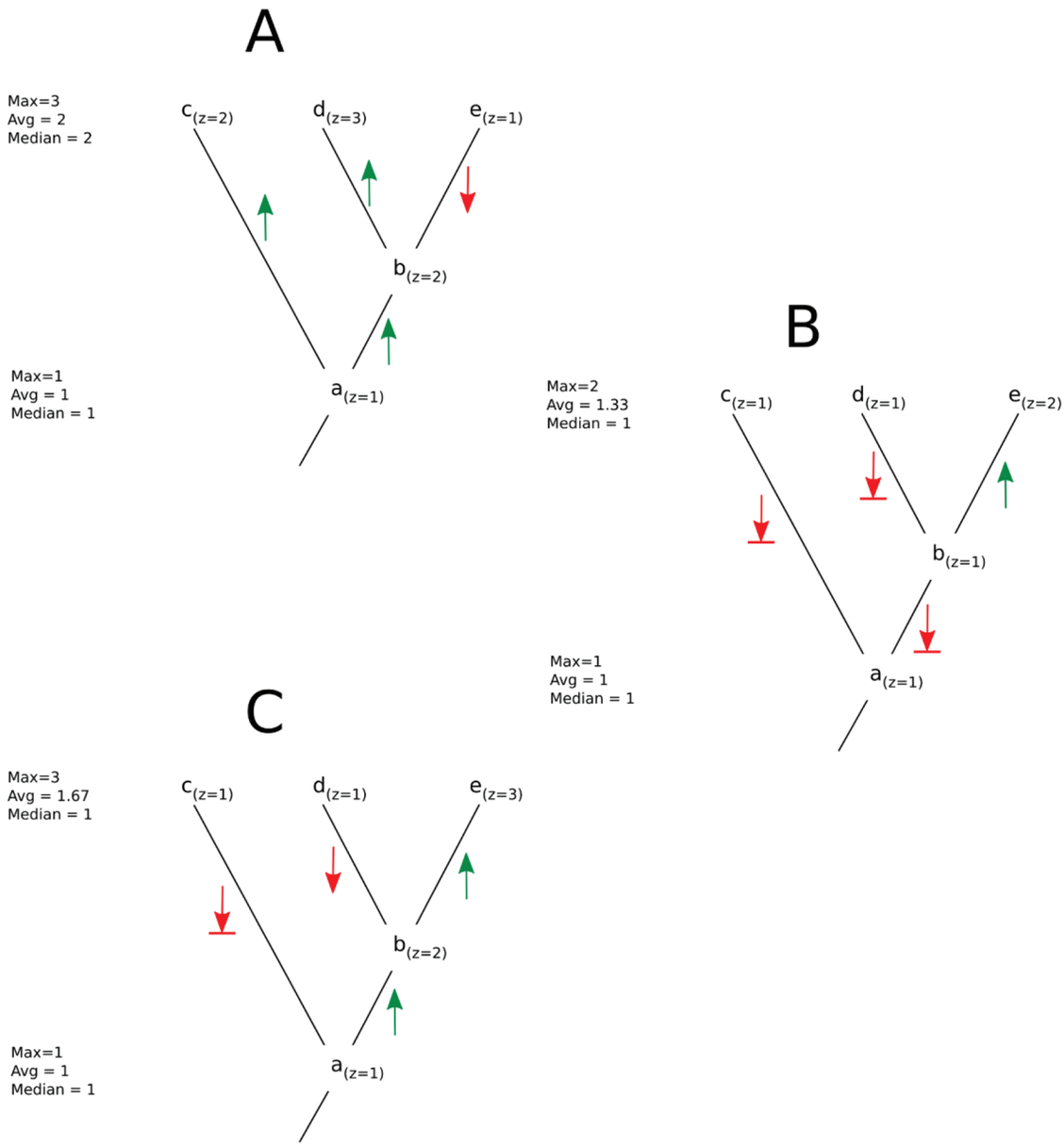

Figure 1. Phylogenetic reconstructions illustrating the inadequacy of maximum (max) and average (avg) values and the adequacy of median values for establishing cumulative culture. z = the efficiency, effectiveness, or complexity of a trait.

The reconstruction thus suggests that cumulation happens more often than not and thus that human culture (or at least the cultural domain represented by the phylogeny) has the general propensity to accumulate beneficial modifications over time.

Yet reconstructions are rarely as clear-cut as the one in figure 1*A*. Suppose one knows the *z* values of some original trait (e.g., an Oldowan stone tool) and of a set of traits that plausibly derive from it (e.g., Acheulean stone tools) but not the precise evolutionary relationships between the original and the derived traits. In such a scenario, one would not be able to determine the frequency of increases and decreases in *z*. Comparing the average and maximum *z* values of the two diachronic samples also would not tell us whether cultural evolution is mostly cumulative. The reason, originally stated for the biological domain (Gould 1996; McShea 1991, 1994), is that, whenever there is a lower bound to *z*, evolution will produce increases in the average and maximum value of *z*, even if such increases happen only rarely. To illustrate this, consider figure 1*B*. Let node a represent a one-component tool (e.g., an Oldowan flake), and let the tool's *z* value refer to its complexity, which is given by the tool's number of components (viz., one). Complexity thus has a lower bound: one cannot produce a tool with fewer than one component. Figure 1*B* shows that a single instance of cumulation—namely, the evolution of one two-component tool from one one-component tool, or transition b→e—already suffices to increase the average and maximum complexity of the later generation of tools. Accordingly, a unilinear sequence of the tools diagnostic for various Lower Paleolithic industries—say, a sequence from Oldowan flakes to Early Acheulean hand axes to Late Acheulean hand axes, as the one developed by Stout (2011; see also Muller, Clarkson, and Shipton 2017)—does not establish that human culture is characteristically cumulative,[2] for such a sequence involves only maximally complex traits and ignores developments in simpler technologies, including various developments in flaked technologies.[3]

Moreover, given that there is a lower bound to *z*, even a simple random walk (i.e., a sequence of transitions in which complexity decreases are as likely as complexity increases) can produce higher average and maximum values over time (Fisher 1986). This is illustrated by figure 1*C*. In this reconstruction, the maximum and average *z* values increase, although there are as many upward as downward (or, given the lower bound, stable) transitions.

2. We do not mean to imply that Stout (2011) or Muller, Clarkson, and Shipton (2017) endorse the view that cultural evolution is unilinear. We merely want to point out that they do present unilinear sequences and that such sequences are unsuited for testing whether human cultural evolution is cumulative.

3. The same applies if cumulation were to be expressed in terms of effectiveness or efficiency. E.g., for a hunting spear, the lower bound would be zero; one cannot produce a spear that allows one to make fewer than zero kills. Given this lower bound, the effectiveness and efficiency of spears will increase even if cumulation is rare.

In view of the foregoing, Gould (1996) suggests that median values are a more reliable proxy for the cumulative character of evolution than averages and maximum values. Figure 1 confirms this: median *z* values increase in case *z* increases more often than not (fig. 1*A*) and remain constant otherwise (fig. 1*B*, 1*C*).

In sum, to properly test whether human culture is distinctively cumulative, one should ideally determine the frequency of episodes of cumulation in established cultural phylogenies or networks. If this proves unfeasible—for example, because cultural evolution is highly reticulate and methods required for producing unambiguous rooted networks do not yet exist (Morrison 2011)—one should instead track the median *z* values across diachronic samples that can reasonably be assumed to be related by descent. Note that no such assumption can be made concerning traits that come from highly different domains. So it is pointless to refer to the vast difference in effectiveness or efficiency between contemporary and prehistoric modes of transport or to the vast difference in complexity between, say, the Apollo missions and the earliest stone tools. Such a comparison involves traits that are, in any but the broadest possible sense, unrelated through lines of descent, and if there is no plausible chain of episodes of social transmission, there cannot be a credible history of the accumulation of beneficial modifications.

On a final note, given that cumulativeness is said to be a defining characteristic of human culture in general, a proper test requires a global and high-resolution sample that is representative of all of the cultural-evolutionary processes that have taken place in our species. This implies, among other things, that it should not be biased toward data that pertain to certain historical eras or cultural groups or toward data that, by their mere format, suggest cumulation (e.g., unilinear sequences).

The Evidence

As argued above, proper evidence for the cumulativeness of human culture consists, minimally, in increasing median values of a variable denoting the efficiency, effectiveness, or complexity of cultural traits across diachronic samples that can reasonably be assumed to be related by descent and that are, overall, representative of all the cultural-evolutionary processes in our species. Seen in this light, it is notable that a considerable portion of the studies that have been invoked in support of the cumulativeness of human culture (e.g., Dean et al. [2014], Mesoudi [2011], and Kempe, Lycett, and Mesoudi [2014] invoke, respectively, Basalla [1988], de Solla Price [1963], and Hodgkin [2005]) in fact provide evidence only for episodes of social transmission.[4] That is, while these studies illustrate that

4. Additional evidence for this claim may be derived from the well-documented continuities between lithic technologies (e.g., from Lomekwian to Oldowan, from Oldowan to Acheulean, and from Acheulean to Middle Paleolithic), where innovations in the preceding period were built on in the consecutive period. See, e.g., Delagnes and Roche (2005), Nonaka, Bril, and

technologies develop by exposure to previous inventions (cultural evolution), they contain no information on efficiency, effectiveness, or complexity and thus do not substantiate the directionality of change (CCE).

Only a few existing data sets comprise diachronic samples from cultural lineages that indicate changes, within the lineages, of complexity (Lindenfors et al. 2015; Moore et al. 2009; Neamtiu, Xie, and Chen 2013; Perreault et al. 2013; Stout 2011; Strumsky, Lobo, and van der Leeuw 2012). However, as we have detailed elsewhere (Vaesen and Houkes 2017), these data sets do not constitute a representative sample of human cultural evolution. For one thing, they pertain only to technology and, even within this restriction, only to four technological domains (viz., stone technologies, cooking recipes, software, patents), three of which come from what Henrich, Heine, and Norenzayan (2010) have called Western, educated, industrialized, rich, and democratic (WEIRD) societies. Furthermore, half of the studies present low-resolution (viz., unilinear) sequences that, by their format, are biased toward complexification. Furthermore, for two of four domains, the results are ambiguous with respect to complexification (Vaesen and Houkes 2017, table 2): some data sets for the domain point to increasing, others to decreasing complexity. Given the above, the claim that human cultural evolution generally leads to more complex traits cannot be said to be sufficiently supported (or discredited) by credible evidence.

Alternatively, support may be sought for the claim that cultural evolution generally produces more efficient or more effective traits. Researchers have attempted to mimic cultural-evolutionary processes in the laboratory by means of experiments in which one human participant acts as demonstrator for a second participant, who acts as a demonstrator for a third, and so forth. Some of these so-called transmission chain experiments suggest that cultural evolution can lead to cumulative improvements in effectiveness (Caldwell and Millen 2010*a*, 2010*b*; Fay et al. 2019) and efficiency (Flynn 2008). Yet all were performed on WEIRD subjects. Furthermore, the studies by Caldwell and Millen (2010*a*, 2010*b*) suggest that CCE occurs in some conditions but not in others. More specifically, the occurrence of CCE was found to be contingent on the size of the group of demonstrators (Caldwell and Millen 2010*b*; Fay et al. 2019) and on the predictability of payoffs (Caldwell and Millen 2010*a*; note that Flynn [2008] did not control for these factors). Given these contingencies and given these researchers' own warning against extrapolation of their experimental results to real phenomena (Caldwell and Millen 2010*b*:317; Fay et al. 2019:6729), it remains an open question whether CCE is a general characteristic of human culture.

Another study that pertains to effectiveness and efficiency and that uses historical data from WEIRD and non-WEIRD societies is a study by Morris (2013). It suggests that, since 14 kya, human culture has shown an upward trend in per capita energy capture, where this encompasses the full range of energy (food, fuel, raw materials) extracted from the environment. This might be taken as evidence that human culture is characterized by cumulative improvements in effectiveness or efficiency (viz., gradual increases in per capita energy capture), although it should be noted that no conclusion to this effect is drawn in the study itself. But, however extensive Morris's data set may be, it features two unilinear sequences, one for the Western and one for the Eastern world, represented at each stage by the technologically most advanced societies of their time. The Western sequence, for instance, starts in 14,000 BCE with Late Ice Age foraging societies in southwest Asia and leads, in broad outline, via agriculturalists and archaic states in Mesopotamia and Mediterranean societies from early and late classical antiquity, to contemporary Euro-American societies. The data for this sequence may well point to an increase in energy capture over time, but it is doubtful whether the stages it comprises are linked by descent, and a proper test of the human uniqueness of cumulative culture would moreover need to include data from (parallel) sequences that pertain to societies that are less reliant on technologies (e.g., foraging and pastoralist societies in Mesopotamia or foraging, food-producing, and pastoralist societies in Africa). Finally, an error margin of $\pm 20\%$ is used in the study (Morris 2013:106), which seems reasonable given the uncertainties and assumptions involved. Yet this entails that the evidence is compatible with the claim that per capita energy capture remained virtually constant before ~10 kya. Thus, insofar as Morris's data establish cumulation at all, they do so only for a tiny fraction of human culture. In sum, the claim that human cultural evolution is generally cumulative is, at present, not sufficiently supported by credible evidence.

Suggestions and Discussion

Our methodological considerations are not meant to establish when there would be a sufficiently robust and diverse evidential basis for the claim that human cultural evolution is generally cumulative. Rather, they identify several shortcomings of the current body of evidence, as well as pathways for improvement.

One shortcoming of the current body of evidence is its low resolution and its consequent failure to be representative of the cultural-evolutionary processes that have taken place in our species. To ascertain that cumulation is a species-specific rather than a WEIRD feature of cultural evolution, future research would need a strong focus on studying non-WEIRD societies (past and present). Furthermore, it would need to develop reconstructions that are not unilinear. In line with what was indicated above, such reconstructions are feasible. By way of illustration, in a study by de la Peña and Wadley (2017), the authors analyzed all lithic artifacts from several stratigraphic layers at Sibidu Cave (South Africa) and determined for each assemblage the median complexity, namely, the median number of procedural units in the production of the artifacts. The samples were broader than those implied in unilinear reconstructions: they included various types of cores, retouched blanks,

Rein (2010), Shipton (2016), and Wilkins, Pollarolo, and Kuman (2010). We thank an anonymous reviewer for directing us to this literature.

blanks without retouch, and chips. Furthermore, rather than tracking the lines of descent of individual artifacts or artifact types, the study assumed stratigraphic layers to correspond to consecutive stages of evolution in the domain of stone technologies. Interestingly, the younger post–Howiesons Poort assemblages were found to be less complex than the older Howiesons Poort assemblages. Admittedly, high-resolution studies such as the one by de la Peña and Wadley demand large time and resource investments. But until such investments have been made, we at least recommend that researchers acknowledge and indicate in their writings the uncertainties that accrue to claims regarding the cumulative character of human culture.

A complementary way to improve the representativeness of the current evidential base is to include data sets pertaining to nontechnological domains (e.g., oral traditions, ritualistic behaviors, stylistic features of artifacts). Without such data, ongoing discussions about cumulative human culture are in fact more restricted in scope; namely, they concern cumulative technology.

Where these pathways would improve direct evidential support for the claim that human culture is cumulative, one might also seek more indirect support. As said at the outset, CCE is taken to result in cultural traits that could not be invented by a single individual (Dean et al. 2014; Richerson and Boyd 2005; Tennie, Call, and Tomasello 2009). Thus, establishing that a trait is beyond the capacity of individual humans to invent alone (Reindl et al. 2017; Tennie, Caldwell, and Dean 2018) might be taken as indirect evidence for the operation of CCE. Leaving aside the difficulties in properly implementing an individual inventability test, such as finding suitably "naive" individuals, positive results could provide a valuable addition to current evidence regarding human cultural evolution. However, some of our previous methodological considerations apply with equal force: the tests should pertain to a sufficiently broad range of cultural traits (e.g., technological and nontechnological, WEIRD and non-WEIRD) to be representative of all human cultural-evolutionary processes. Moreover, care should be taken in interpreting results: individual inventability tests per se cannot reveal directionality of change in cultural traits. For example, suppose that we were to discover that it is beyond an individual's ability to invent a Late Acheulean hand ax. That finding would suggest that Late Acheulean hand axes are products of cultural evolution, namely, that Late Acheulean toolmakers built on innovations of earlier periods (i.e., Early Acheulean hand axes). However, the finding is insufficient to justify claims concerning gradual improvement (CCE): the refinement of hand axes over time might very well not have had anything to do with increases in effectiveness or efficiency but rather with changes in stylistic traditions (Beyene et al. 2013; Lycett and Gowlett 2008).

Our methodological considerations also have repercussions for claims regarding the uniqueness of CCE to our species. As we have argued, there is insufficient evidence to conclude that human cultural evolution is generally cumulative—although there certainly are uncontroversial cases showing our capacity for CCE. Thus, given the current state of evidence regarding human cultural evolution, one generally accepted example for a nonhuman species would suffice to discredit the claim that the capacity for CCE is uniquely human.

On a final note, human cultural evolution could still be found to be unique, even if it would not be distinctively, uniquely cumulative. Perhaps, as in biological evolution, the real change in cultural evolution concerns increases in the total diversity of traits (Shea 2011). Or perhaps human culture is special in the simple sense that it governs so much of our behavior.

Comments

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Human Culture Is Cumulative, but Cumulative Cultural Evolution Will Not Be Evident in All Contexts

We agree wholeheartedly with Vaesen and Houkes's view that research on human culture would benefit hugely from having more real-world data sets analyzed for conclusive evidence of cumulative cultural evolution (CCE) in action. However, we take issue with their argument in several ways. First, we dispute their representation of the prevailing view in this field; they have constructed a straw man argument in relation to the distinctiveness of human culture. Second, we disagree with the conjectures extrapolated from this misconstrued account. Third, we question the focus on complexity, which we consider a poor metric of the presence or otherwise of CCE. Finally, we highlight the challenges of implementing the proposed analyses. We suspect that the dearth of evidence is attributable to the substantial difficulties associated with generating it, rather than failure to appreciate its merit.

Vaesen and Houkes misinterpret the statements of those advocating a view of CCE as "a unique and characteristic feature of human culture" with their assertion that "cumulativeness is a unique propensity of human culture only to the extent that most human cultural traits are brought about by CCE" and their analogy with human bipedalism. This conclusion does not follow from claims regarding the distinctiveness of human CCE. Should an analogy be needed, we would instead compare the human propensity for CCE to a cheetah's ability to run at 70 miles per hour. This characteristic sets cheetahs apart from other animals (many of which can run, just not at this speed) and has significant fitness consequences. Nonetheless, we do not expect to see this displayed in a large proportion of a cheetah's locomotion.

Our own view is that what is distinctive about human culture is the (relatively) broad range of contexts within which CCE

occurs. This more modest claim also provides a constructive starting point for further investigation targeted at understanding the extent and limits of CCE in humans and nonhumans. Our recent work (Wilks et al. 2021) has shown that for some populations (in this case, young children), the "ratchet effect," considered a hallmark of CCE, may be apparent only in limited cognitively unchallenging contexts, while for others (older children), the effect is less restricted.

Vaesen and Houkes acknowledge that attempts have been made to test for evidence of CCE in the technological domain but extrapolate from their inference regarding the predominance of CCE in human culture that this should also encompass nontechnological domains, including "oral traditions, ritualistic behaviors, stylistic features of artifacts." However, it would be a flawed endeavor to subject data sets from very different cultural domains to the same standards of evidence. We should not expect to see CCE manifested as a unitary phenomenon (or at least as a phenomenon that can be quantified and evaluated in a unitary fashion) across domains. The reason that researchers have focused almost exclusively on technological traditions is that it is somewhat more straightforward to demonstrate an accumulation of beneficial modifications within this domain. Assuming that the intended function of an artifact is known, it may be possible to formulate a relatively objective measure of its effectiveness, independent of historical and geographical context, enabling conclusions about whether functionality has improved over time.

However, for symbolic conventions, even if one can identify a measurable function, that functionality will be necessarily context dependent. The more arbitrary relationship between form and function means that a sign that has high functionality in one context (e.g., the word "dreich" in Scotland) may have almost none when used in a community that does not share the convention (e.g., see Caldwell and Smith 2012 for an experimental demonstration). Such traits cannot be assigned a context-independent value, rendering it virtually impossible to establish whether later variants represent "improvements" of their precursors.

We also question the focus on complexity as a metric for CCE, which we believe to be misguided and potentially misleading. While increasing complexity can be an outcome of the accumulation of beneficial modifications (i.e., where that complexity brings improved functionality), this is far from inevitable. Indeed, since ease of learning and production also represent benefits, functionless complexity is in fact expected to decrease under CCE (e.g., see Tamariz and Kirby 2015). We suggest that using direct measures of functionality may be the only valid approach to establishing evidence for CCE. Although such an approach is not without its own limitations, we cannot see how other measures can be used as universal proxies for the accumulation of beneficial modifications.

Finally, although we share the enthusiasm for a stronger historical evidence base, it is important not to underestimate the likely difficulties of achieving this. For example, our suggestion regarding functionality depends on being able to establish the goal of those using the trait. As experimentalists ourselves, we have the luxury of being able to dictate this, in that we give participants explicit instructions and a clearly defined task (e.g., Caldwell and Millen 2008). However, measurement and comparison cannot be achieved in such a clean manner for real-world cultural traits. Interestingly, one real-world data set that arguably achieves this goal of demonstrating increasing trait functionality over generations of social transmission comes from nonhumans. Jesmer et al. (2018) studied the migratory behavior of translocated bighorn sheep and moose and concluded that it had taken multiple generations for the introduced populations to develop migratory patterns as effective as those of historically resident populations, synchronizing movement with the availability of high-quality forage. In this case, it is a reasonable assumption that maximizing resource exploitation is desirable and that migration patterns function largely to achieve this. Later generations therefore appeared to have benefited from the accumulated experience of their predecessors.

We stand by the consensus view that human culture is distinctive, despite neither seeing CCE as completely unique to humans nor having any expectation that it will be obvious in all or even most human cultural traits. We agree that more evidence is needed to move the field forward, but the interesting questions are when, where, and how CCE manifests itself. We hope that researchers rise to the challenge laid down in this stimulating forum article.

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I must admit that the article by Vaesen and Houkes has challenged my unquestioned assumptions about cumulative cultural evolution, which is a human trait that I had previously taken for granted. After reading their paper, I concur with them, following the different lines of reasoning highlighted in their article, that there is still not enough evidence to affirm, roundly, that cumulative cultural evolution is a fact for humans.

I was delighted to read that archaeology is taken as a fundamental line of evidence in this debate and, moreover, that they vindicate nonpartial data sets or studies. Indeed, these should be obvious key factors to consider. As an archaeologist, my comments on their article largely advise caution from an archaeological perspective and, tacitly, from an anthropological perspective.

One of the initial points in the article states that most of the literature on this debate revolves around the domain of technology. They later propose that "a complementary way to improve the representativeness" would be to include other nontechnological domains, such as oral traditions or ritualistic behaviors. I could not agree more with this suggestion

for future research, although it is important to bear in mind that none of the abovementioned domains can be isolated. In particular, technology cannot be understood without other domains such as symbolism. As highlighted by Simondon (1958), there is no technology without symbolic meaning.

My second comment on their article refers to the remarks about the way in which cumulative cultural evolution is valued through increased efficiency or effectiveness, or complexity. The way we measure efficiency is culturally biased, depending on what we weigh as important for efficiency. Is efficiency the amount of useful work performed with a given technology? In the Cambridge dictionary, efficiency is defined as "the good use of time and energy in a way that does not waste any" (http://dictionary.cambridge.org/dictionary/english/efficiency). However, the adoption or rejection of a technology (and its success in the long term), in many societies, results from cultural values and social relations (Lemonnier 2002) rather than from inherent benefits understood from a cost-benefit modern and Western perspective. To put it bluntly, a technological choice might seem highly inefficient economically but highly beneficial sociologically (and indeed beneficial from an adaptive perspective). It can be difficult for a researcher to discern which factors influenced the technological choices—whether they were economical (in terms of cost and benefits) or were, rather, sociological. Since the Late Pleistocene, there have been abundant technological examples that serve a purpose beyond what might be considered what we see as efficient today. This could be aligned with the warning that the authors give urging scholars to broaden their search for data outside Western, educated, industrialized, rich, and democratic societies (Henrich, Heine, and Norenzayan 2010). However, even in modern society today, there are abundant examples in the anthropological record of technological choices that may be highly technologically inefficient but are beneficial in other domains. Some examples that I can quickly think of include baby hair bands for hairless babies and Japanese *kaizōsha* motorbikes or Bōsōzoku cars.

Finally, when we look at the archaeological record, we must always remember that the evidence that we find is always a partial version of what it was. Therefore, the evolutionary conclusions that we might derive from the archaeological record should be taken with extreme caution, even when we look strictly at the technological domain (usually the stone tools). From a technological perspective, in the past there was surely a great variety of wood and botanical tools that have very seldom been preserved (see some exceptions here: Rios-Garaizar et al. 2018; Wadley et al. 2020). Moreover, it is possible that certain time periods have accumulated archaeological evidence that is more conspicuously complex (from the modern archaeologist's perspective) than others. A good example is the African Middle Stone Age archaeological record (Wadley 2015). It seems that the Howiesons Poort and the Still Bay are extraordinary technological traditions with abundant examples of technological and symbolic complexity, such as the engraving of ostrich eggshell containers, the appearance of engraved ocher, formal bone tool technology, compound adhesives for hafting, and a great variability in hunting techniques (for a synthesis of these technological traditions, see de la Peña 2020; Henshilwood 2011). However, the apparently unusual and exceptional evidence of the Still Bay or the Howiesons Poort might merely be an archaeological illusion, as we have not been aware of other clues of the rest of the Middle Stone Age in the archaeological record. As a result, outside those two abovementioned technological traditions, the Middle Stone Age might (artificially) seem to be monotonous. I hope that these three archaeological remarks are useful for the future debate between cultural evolutionist specialists and philosophers on cumulative cultural evolution.

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Not Necessarily Additive, Linear, or Beneficial

Cultural evolution (CE) is by now an established fact. There is also a wide consensus that human CE is cumulative (cumulative CE [CCE]). Vaesen and Houkes challenge this consensus, hinting at missing evidence for cumulativeness. In a recent discussion, we (Haidle and Schlaudt 2020, 2021) argued that, quite the contrary, all CE—human and nonhuman—should be considered cumulative. Such a divergence in opinion is noteworthy, demonstrating considerable disagreement on basic ideas and fundamental premises.

It seems that Vaesen and Houkes's criticism is based on three implicit interconnected assumptions: (1) that cultural traits (i.e., behavioral patterns and tools) are autonomous units that can be studied and assessed independent of their context, (2) that such traits can be characterized by single factors and their effects (corresponding to the variable z in the paper, denoting "effectiveness, efficiency, or complexity"), and (3) that cumulative evolution, consisting in successive modifications of this factor, is by definition constrained to beneficial effects. In short, Vaesen and Houkes seem to identify CCE with the ratchet effect (Tennie, Call, and Tomasello 2009).

We do not accept these premises. First, we advocate an "ecological" approach (based on Gibson 1979; Köhler 1926; von Uexküll 1921; Vygotsky and Luria 1993), according to which tools and behavioral patterns have to be studied in their respective contexts. A tool has a "backward" matching the skills and resources necessary for obtaining or producing it, a "synchronous" matching the technical and cognitive requirements of its use, and a "forward" matching the resources it makes accessible to the user. Vaesen and Houkes state, for example, that a one-component tool cannot be less complex, which is true if you consider only the object, independent of its context. According to the ecological approach, however, an unmodified

hammerstone, a modified hook tool, an Oldowan flake tool, and a wooden spear—all single-component tools—differ significantly in their processes of acquisition, manufacture, use, and resulting options and thus in the complexity expressed by the problem-solution distance (Haidle 2010, 2012; Lombard, Haidle, and Högberg 2019). To "improve the representativeness of the current evidential base" as Vaesen and Houkes demand, a less restricted view of cultural traits and technology than that of Vaesen and Houkes is required.

Second, we consider cultural traits multifactorial. A tool and the associated behavior, for example, represent an understanding of the combination of material, form, function, technology of production, technology of use, and general problem-solution concept (Haidle and Bräuer 2011). Thus, and contrary to premise 2, the evolution of a cultural trait should be assessed as a multifactorial process. An invention can affect one or several of these factors simultaneously; an evolutionary sequence of inventions can first affect factor a, then c, then e, then b, then a again, and so on. These changes can have different effects on the requirements and outcomes.

Third, consequently, we see a fundamental problem in the connotation of a change as unambiguously "beneficial" as it relates to an increase in complexity, efficiency, or effectiveness (Haidle 2019). While a modification can be beneficial on one axis, for example, the higher availability of raw material, it can prove problematic on another axis, for example, less durability in use, and neutral on a third axis, for example, length of the cutting edge. What can be perceived by some, focusing on factor a, as an increase in efficiency, can be valued by others, regarding factor b, as less efficient. And a cultural trait can become more efficient by introducing a shortcut that reduces complexity. Consequently, CE must not be considered as taking place in one-dimensional space, that is, along a line (of increasing complexity and growing usefulness). CE unfolds in a multidimensional space. It thus might be compared to mountaineering rather than to climbing up a ladder or ratcheting in a single direction (Haidle et al. 2015:51; Lombard 2012). In this scenario, cultural traits anchor populations within their respective evolutionary trajectories and fitness landscapes, and while it is always possible to increase cultural complexity, it is equally possible to revert to seemingly simpler options (Lombard 2016). Thus, in the mountaineering analogue, different paths, each with multiple perspectives, can be explored, and sometimes moving backward proves helpful (e.g., simplification of tools).

The expectation should be that modifications of cultural traits result in diverse effects depending on perspective, if we take into account the plurality of the relevant dimensions. What is more, such variation need not come along with an increase in one of the variables; that is, CCE need not be cumulative in the additive sense described above. A case in point is the repurposing or exaptation of cultural traits (Gould and Vrba 1982), the importance of which has become more and more clear in recent research (e.g., de Beaune 2004; d'Errico et al. 2018; Schlaudt 2020). Cases of exaptation fall in the category of CCE because exaptation (1) draws on preexisting cultural resources and (2) brings about something new. Thus, although exaptations are cumulative innovations, they do not necessarily come along with an increase of complexity, effectiveness, or efficiency.

In this sense, speaking of CCE might be misleading. It tends to identify CCE with or reduce it to the ratchet effect. Instead, we see as crucial to CCE that each invention draws on preexisting cultural resources and therefore can be explained by them (de Beaune 2004). The concept of "path dependence" would lend itself to this if it did not connote the individualistic approach of economics, which we consider at odds with our ecological approach. Not only do inventions have to be approved by the community to become innovations, but also they are produced by individuals who (1) are inherently social and (2) draw on cultural and thus socially inherited resources. All inventions thus go beyond the capacity of individual humans to invent alone, and in this sense, they are cumulative, but they are not additive, linear, and beneficial in the sense of Vaesen and Houkes. This suggests simply refraining from speaking of CCE and accepting that all CE is inherently cumulative in the way described above.

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What Is Cumulative Culture, and How Should It Be Tested?

I agree with the general point made by Vaesen and Houkes: we need more fine-grained, quantitative, cross-cultural data regarding human cumulative cultural evolution (CCE), which tracks the effectiveness or efficiency of a socially learned trait over successive generations within cultural lineages. However, I take issue with some of their specific points. Vaesen and Houkes seem to set the evidential bar so high for CCE that it is unreachable and define CCE in ways that do not always match the literature.

First, Vaesen and Houkes argue that "if cumulativeness is to qualify as a general characteristic of human culture (see the quotes in 1n), it is not enough to show that some human cultural behaviors result from CCE; rather, one must show that a large fraction of such behaviors result from CCE." I do not fully understand what is meant by "a general characteristic," but I do not know of any such claim in the literature. None of the quotes in their footnote make any claims about how much of human culture must be cumulative. They simply assert that human culture exhibits the property of being cumulative in at least some instances. As Vaesen and Houkes point out, technology is the best and most often cited example of a domain that is cumulative. Yet much of human culture is clearly noncumulative. Cultural traits such as pottery decorations, choices of pet breeds, and first names exhibit dynamics consistent with neutral drift (Bentley, Hahn, and Shennan 2004; although see

Kandler and Crema 2019), which by definition is noncumulative. Convergence on intuitive, cognitively attractive representations such as bloodletting (Miton, Claidière, and Mercier 2015) is also a common form of non-CCE. In this, cultural evolution is really no different from genetic evolution, which may sometimes be cumulative, producing complex adaptations such as eyes, but is often characterized by drift. We should not expect more from cultural evolution than we do from genetic evolution.

Consequently, to demand that "a proper test" of CCE requires data that are "representative of all of the cultural-evolutionary processes that have taken place in our species" surely sets the bar unnecessarily high. There is no reason to expect that all cultural-evolutionary processes in our species should be cumulative, only those in which selection pressures favor increasing effectiveness or efficiency.

Second, Vaesen and Houkes discount evidence because it comes from Western, educated, industrialized, rich, and democratic (WEIRD) samples (e.g., dismissing experiments because "all were performed on WEIRD subjects"). I am all for diversifying samples beyond WEIRD countries (Mesoudi et al. 2015, 2016). But that does not mean that we can discount evidence because it comes from WEIRD samples. WEIRD people are people too. Vaesen and Houkes seem to imply that CCE must be demonstrated in every society worldwide before we can accept it as a valid concept—surely far too high a bar for an idea that emerged in the late 1990s. Most examples of CCE in the literature do indeed involve historical trajectories or samples from WEIRD countries, probably because written historical records are more readily available and experiments more feasible in such societies. However, Henrich (2015) and Boyd (2018) provide examples of complex technologies and customs found in hunter-gatherer and other small-scale societies that seem to exceed individual learning and are therefore suggestive of CCE. No doubt, future empirical research will provide better evidence across more diverse contexts, but dismissing research on WEIRD people altogether seems unreasonable.

Third, Vaesen and Houkes ignore recent evidence regarding nonhuman CCE. While many authors have indeed claimed that CCE is unique to humans, others have claimed to have shown CCE in nonhuman species. Sasaki and Biro (2017) showed how homing pigeons improve the efficiency of their route over successive generations as a result of repeated social learning. This exactly fits Vaesen and Houkes's definition of CCE, requiring "individuals, across generations, [to] gradually improve their behavior through social transmission of beneficial modifications." By their own definition, then, it has already been demonstrated that CCE is not unique to humans. Mesoudi and Thornton (2018) argued that the concept of CCE should be unpacked: we described the repeated improvement of a socially learned trait as the "core criterion" for CCE and identified several "extended criteria" that may be what distinguish human CCE from that of other species.

Fourth, Vaesen and Houkes do not present any alternatives to CCE for the technological and sociopolitical complexity that our species has produced. Are such complex traits instead the product of individual learning (e.g., the "improvisational intelligence" of Pinker [2010])? Or genetically encoded responses "evoked" by different environments (Tooby and Cosmides 1992)? Scientific progress requires testing between alternative explanations.

Fifth, Vaesen and Houkes criticize experiments for finding that "CCE occurs in some conditions but not in others." Yet this is not a problem. Models demonstrate how cultural complexity can be lost under various conditions (e.g., small population sizes; Henrich 2004) or plateau because of learning costs (Mesoudi 2011). Contrary to nineteenth-century unilinear social evolutionism, the modern concept of CCE does not predict inevitable and unidirectional cultural change. The accumulation of cultural modifications, just like the accumulation of genetic modifications, is reversible and subject to demographic and other constraints.

Finally, the examples that Vaesen and Houkes provide from the literature are somewhat limited. Vaesen and Houkes are correct that Morris (2013) conflates multiple cultural lineages and uses coarse-grained data subject to substantial error. But several other studies that track increases in effectiveness or efficiency within specific cultural lineages also exist: Nia et al. (2015) showed that violins gradually improved in acoustic conductance over several centuries, Miu et al. (2018) showed how solutions to math problems improved within a programming community via successive bouts of copying and innovating, and several studies have traced the evolution of increasingly energy-efficient bicycle designs (Lake and Venti 2009; Minetti, Pinkerton, and Zamparo 2001; Van Nierop, Blankendaal, and Overbeeke 1997). To return to my initial point: more such evidence is definitely needed and from more diverse sources and samples. But let us not ignore or dismiss the evidence that does exist or make requirements (e.g., that all human culture is cumulative or that CCE should be unidirectional) that are not warranted by theory.

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The Ongoing Search for the Origins of Cumulative Culture

I first wish to thank Vaesen and Houkes for their concise and thought-provoking article. They seek to question the perceived orthodoxy that cumulative cultural evolution is inherent to humans and that cultural evolution in humans is inherently cumulative. In doing so, they argue that this topic requires more and different lines of evidence to test it properly. This is a welcome challenge to archaeologists and one that will no doubt engender a robust and valuable debate.

The question of whether cumulative culture is present in nonhumans is one that I will leave to the behavioral ecologists and evolutionary anthropologists better suited to address such questions. Instead, the portion of this paper I wish to examine is the evidentiary threshold they set for ascribing cumulativeness to human culture: "Proper evidence for the cumulativeness of human culture consists, minimally, in increasing median values of a variable denoting the efficiency, effectiveness, or complexity of cultural traits across diachronic samples that can reasonably be assumed to be related by descent and that are, overall, representative of all the cultural-evolutionary processes in our species."

It is refreshing to see cumulative culture being defined so clearly and strictly when elsewhere the term can be used loosely. For instance, in a comprehensive review of the literature, Mesoudi and Thornton (2018, table S1) found 36 definitions, which were as diverse as they were plentiful. Vaesen and Houkes's definition is comparably rigorous and well suited for strict hypothesis testing. My only concern is that it may be too high a bar for the vagaries of the archaeological record. Unfortunately, truly long-term diachronic samples that are related by descent and that preserve the full suite of human behaviors are few and far between in archaeology. I certainly second their praise of studies like that by de la Peña and Wadley (2017), in which the complexity of diachronically and culturally linked lithic assemblages was examined. Moreover, Vaesen and Houkes's call for more diverse lines of evidence, including oral traditions, ritual behaviors, and stylistic elements, is a valuable one. However, archaeological data are inherently biased and fragmentary, and this is increasingly the case the further back in time we look. We certainly wish for the types of evidence suggested by Vaesen and Houkes and even strive for them. My only concern is that such a high evidentiary standard a priori precludes almost all of prehistory from the possibility of cumulative cultural evolution. Despite this, it may be the case that cumulative culture, as defined here, is absent in prehistory.

Vaesen and Houkes are certainly right to question the supposed ubiquity of cumulative culture in humans. There is a tendency in the literature to conflate high-fidelity cultural transmission with cumulative culture. I agree with the authors that the first does not imply the latter. For instance, high-fidelity social transmission has been demonstrated in the Oldowan (Stout et al. 2019) and the Acheulean (Shipton 2019) but on a scale too infrequent to be classified as cumulative culture.

Take the hand ax, for instance. Vaesen and Houkes state that an inexperienced individual alone is unable to make a later Acheulean hand ax. Ask any nonknapper to make a hand ax, and this will be self-evident (e.g., Shipton 2020). If prehistoric knappers were not constantly reinventing the hand ax from scratch, then some form of cultural evolution and social transmission was likely involved (however, see the compelling argument for an alternative hypothesis laid out by Tennie et al. [2016, 2017]). Additionally, while the Acheulean is sometimes considered a period of technological stasis, a number of innovations did occur. Later Acheulean hand axes often possess features that are absent from earlier ones. These innovations include edge trimming, platform preparation, the introduction of softer organic hammers, and longer reduction sequences involving a more codified succession of strikes and rotations (Chazan 2015; Sharon and Goren-Inbar 1999; Shipton 2016, 2018; Stout et al. 2014). So while the general shape and style of hand axes were relatively stable throughout the Acheulean, multiple innovations appear to have accrued throughout this time. However, these innovations accrued over more than a million years, and the knappers who introduced these innovations were almost certainly separated by a great deal of time and space. As Vaesen and Houkes rightly point out, this transmission is not necessarily or innately cumulative.

I thus welcome the authors' call for new and better lines of evidence in the search for the origins of cumulative culture. But before the possibility of its presence in prehistory can be dismissed entirely, we need an agreement on definitions as well as suitable evidence for testable hypotheses. To ascribe cumulative culture to prehistoric humans, Vaesen and Houkes wish to see most cultural traits accruing beneficial innovations most of the time. But I am concerned that such a tendency for cumulative culture is likely almost impossible to discern in the archaeological record. Whether this is evidence of absence or an absence of evidence remains to be seen. A testable hypothesis for which archaeologists have at least a chance to find supporting evidence is whether humans have the capacity for cumulative culture. Humans do not need to be continuously displaying cumulative cultural evolution for it to be an underlying and innate part of their cultural, behavioral, and cognitive repertoire. As Vaesen and Houkes point out, there are isolated and uncontroversial instances of humans displaying a capacity for cumulative culture. Perhaps a way forward beyond this definitional impasse is by focusing not on whether human culture is generally cumulative but rather on identifying more instances when we display the capacity for cumulative culture.

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We Are All Capable of Cumulative Cultural Evolution, but We Do Not Need to Use It All the Time

Vaesen and Houkes provide a new perspective on claims that cumulative cultural evolution (CCE) is a defining characteristic

of humans. They argue that, contrary to the broadly accepted notion that humans exhibit CCE, a granular view of typical methodological approaches to studying CCE has limitations, thus prohibiting a sound test of this claim. Here, we, as developmental and comparative experimental psychologists, reflect on some points that they raise.

Vaesen and Houkes argue that the field of CCE relies too heavily on data from the technological domain. Many cultural traits are hidden or abstract; therefore, studying the use and evolution of physical tools is valuable in terms of historical, experimental, and comparative perspectives and allows us to empirically quantify mechanisms underpinning CCE. Our own examination of the use of novel artifacts such as puzzle boxes allows us to study, in real time and across diverse age groups and species, candidate mechanisms supporting CCE. These include social learning strategies, imitation, innovation, cooperation, and prosocial behavior. Science is itself a cumulative process, with subsequent scientists building on previous evidence, a process that naturally hones emphasis on the same area and has done so very effectively within technological research. We believe that this research domain would not have developed such a deep, interdisciplinary, and robust theoretical and experimental base had scientists not taken this approach. Indeed, we note that Vaesen and Houkes focus on technological examples when critiquing applied methodologies and suggesting future approaches.

We agree and welcome the call for the study of more varied phenomena. Indeed, there is a vibrant and growing body of work examining CCE across diverse domains, including social norms, folktales and urban legends, cooking, language, mathematics, religion, and rituals—which is of course not a comprehensive list (see, e.g., Acerbi, Kendal, and Tehrani 2017; Lindenfors et al. 2015; Norenzayan et al. 2014; Savage 2019; Stubbersfield, Flynn, and Tehrani 2017; Subiaul et al. 2016). These lines of work have developed sophisticated methods of observing, coding, and analyzing complex behavior. Accordingly, they provide substantial insights regarding how nontechnical behavior has evolved in ways analogous to and different from technological CCE, as the references cited conclude.

A valuable call to move research beyond Western, educated, industrialized, rich, and democratic samples has rightly taken hold recently, and the authors add their voice to this. We strongly support this call and those who have been making it within the field of cultural evolution (e.g., Kline, Shamsudheen, and Broesch 2018) and within the broader study of human psychology (Henrich, Heine, and Norenzayan 2010; Nielsen et al. 2017). Developmental psychology in particular has embraced cross-cultural research. There is a growing corpus of developmental research documenting cultural variation and continuity in the expression of the building blocks of CCE imitation and innovation, advancing our understanding of the ontogeny of CCE (Legare and Nielsen 2015; Neldner et al. 2020; Rawlings et al. 2019; Van Leeuwen et al. 2018). Such cross-cultural research is crucial for improving our understanding of our capacity to flexibly adapt cultural learning to diverse ontogenetic environments. We further highlight the need to develop testable hypotheses to explain cultural consistency and variation. For example, exposure to formal education has been hypothesized as a potential factor in shaping the development of innovation and imitation (Neldner et al. 2019). The globalization of formal education offers a unique opportunity to test this hypothesis and to provide insight into specific sociocultural predictors of CCE.

A key issue raised in the article concerned claims that CCE is a "unique and characteristic feature of human culture." The authors argue, "It is not enough to show that some human cultural behaviors result from CCE; rather, one must show that a large fraction of such behaviors result from CCE." We agree that as academic researchers we must consider our terms carefully and avoid generalized terms based on the outcome of a given experiment using a specific demographic sample. However, we question why a large proportion of cultural behavior should result from CCE, as CCE underpins the changes in culture, not the acquisition and transmission of culture. This is not to suggest that all humans are not capable of innovation. One look at the internet's endless supply of "life hacks," for instance, demonstrates humans' abilities to innovate and transmit in everyday life. Yet we also conform to our cultural norms and conventions most of the time, thus allowing a streamlined societal functioning. We thus argue that the universal human capacity for CCE rather than the volume of CCE behaviors is a more appropriate point of reference.

We also question the practicality—and therefore the utility—of the solution presented by the authors. To meet their criterion for CCE, "a proper test requires a global and high-resolution sample that is representative of all of the cultural-evolutionary processes that have taken place in our species." Meeting this requirement seems logistically impossible and thus has little value as a platform for future research. Similarly, the authors referred to cumulative culture as a process that produces traits that cannot be invented by a single individual within their lifetime. Although this is a commonly used criterion to attribute a given output as a product of cumulative culture, it is increasingly recognized that this is logistically impossible to test experimentally and thus has little utility as a diagnostic criterion (Mesoudi and Thornton 2018; Miton and Charbonneau 2018). Accordingly, we suggest that the authors propose a more feasible test of CCE to allow scientific knowledge accumulation on the subject.

As a final note, we turn to the reader and ask, if we step back and reflect on our environment—our transport, language, medicines, culinary practices, and so on—is it difficult not to think that our species holds something distinct, compared with other species, that allows rapid cultural and technological advances? Thus, it is not difficult to theorize from our everyday world that humans have a distinct cumulative culture process that needs to be understood at both a holistic and a granular level.

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Hunter-Gatherer Societies Innovate and Adapt; They Do Not Accumulate Complexity

Vaesen and Houkes have delivered a timely paper pushing back against the assumption that cumulative culture is pervasive across human societies. There are two problems with the widespread use of the phrase cumulative culture that are contradicted by the Paleolithic record of deep time cultural change. First is the low bar often set for cumulative culture, which simply equates it to high-fidelity social transmission; second is the lack of evidence for cumulative culture in multimillennial records of *Homo sapiens* hunter-gatherer societies.

Cumulative culture is sometimes defined as high-fidelity social transmission, such that ever-increasing cultural complexity is an inevitable consequence of reliable transmission, as any innovations are rarely lost. However, Paleolithic prehistory belies this equation. High-fidelity transmission is evident in the Lower Paleolithic from at least the onset of the Acheulean (Shipton 2010, 2019), if not the preceding Oldowan (Stout et al. 2019), but the growth of technological complexity was slow enough that different hominin species were making the same distinctive complex artifact types across the entire 1.5-million-year duration of the Acheulean. While there were occasional incremental improvements in knapping techniques during the Acheulean (Stout et al. 2014), rates of innovation were so low that on timescales of less than hundreds of thousands of years, complexity looks more like random walks than progressive increases (Shipton 2018). One of probably several additional ingredients required for cumulative culture is an increase in the capacity for innovation (Shipton and Nielsen 2015).

Middle Paleolithic Levallois technology was an innovation that arose through the generative recombination of concepts used in Acheulean biface knapping (Shipton et al. 2013). The dearth of Levallois technology in East Asia, where previously there was a dearth of biface technology (Movius 1949), supports the hypothesis that Levallois built on Acheulean technological foundations in a way that might be described as cumulative. However, broader behavioral change at the Lower to Middle Paleolithic transition (e.g., Brooks et al. 2018) suggests that the technological change may reflect a new cognitive mode rather than cumulative culture. The pioneering modern knappers who were the first to recreate prehistoric technologies also showed that Levallois technological complexity is not beyond the capacity of a single individual to acquire from scratch. In contrast to the Acheulean to Middle Paleolithic transition, it is not clear whether Upper Paleolithic prismatic blade technology directly built on Middle Paleolithic Levallois knapping (Kuhn 2003), and it does not appear to be any more complex (Muller, Clarkson, and Shipton 2017).

In addition to the case of Sibudu Cave cited by Vaesen and Houkes, I offer further examples that suggest that the Upper Paleolithic and Later Stone Age cultural complexity of *H. sapiens* hunter-gatherers cannot be described as cumulative. Panga ya Saidi on the East African coast preserves a record of repeated *H. sapiens* hunter-gatherer occupation across the major climatic fluctuations of the past 80,000 years (Shipton et al. 2018). Here, technological innovations such as backing and prismatic blade technology emerged at different points in the sequence as adaptations to particular environmental circumstances. Early backed crescents, for example, are associated with drier environments and large bovid remains (Roberts et al. 2020), probably in part because of the role of these armatures in bringing down large prey. However, when bovid prey size decreased, backed crescents were entirely abandoned for tens of thousands of years before being reintroduced in the terminal Pleistocene. Innovation, abandonment, and reinvention also characterize the use of Levallois and prismatic blade technology at the site. Looking beyond stone tools, there are similar stories: carved osseous artifacts and a variety of shell bead types featured at various times, but these came and went rather than accumulating (d'Errico et al. 2020). The site of Madjedbebe in northern Australia presents a parallel case whereby different stone artifact technologies appeared and disappeared across the 65,000-year sequence, and rather than accumulating complexity, the most complex stone tool type, the ground-stone ax, is found at the beginning of the sequence (Clarkson et al. 2017).

Hunter-gatherer occupation records spanning ~48,000 to 5,000 years ago occur on the tropical islands of both Sri Lanka and Timor at the sites of Fa Hien Lena and Asitau Kuru, respectively. Throughout these sequences, there is consistency in faunal exploitation patterns, with monkeys and squirrels favored at Fa Hien Lena (Wedage et al. 2019*a*) and fish and shellfish at Asitau Kuru (O'Connor, Ono, and Clarkson 2011). Likewise, there is strong continuity in stone toolmaking traditions at both sites with, for example, bipolar knapping of quartz to produce backed crescents throughout the Fa Hien Lena sequence (Wedage et al. 2019*b*) and large chert flakes used as discoidal cores to produce small flakes with prepared platforms throughout the Asitau Kuru sequence (Shipton et al. 2019). In neither case does a prolonged continuity of traditions appear to have given rise to a progressive increase in complexity. Aside from the lithic technology, elaborate carved bone arrowheads and shell beads are found from the beginning of occupation at Fa Hien Lena (Langley et al. 2020), and shell beads and red pigment crayons occur in the early occupation phases at Asitau Kuru (Langley and O'Connor 2016, 2018).

Cumulative culture is not an inevitable consequence of high-fidelity transmission: deep time records of hunter-gatherer material cultures do not show progressive increases in complexity. Instead, hunter-gatherers persist with the same effective cultural adaptations for tens of thousands of years. Innovations occur in response to external factors such as environmental change,

but these do not typically lead to an increase in complexity, with technologies likely to be abandoned and replaced when circumstances change again. A case might be made for Epipaleolithic and Neolithic societies having had cumulative culture, but there we are generally talking about expanding populations, and the growth in complexity is a function of the size of the society. It may not have been until the invention of writing that human cultures could be said to be truly cumulative.

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What Is "Cumulative" Evolution?

Vaesen and Houkes usefully highlight conceptual difficulties with the idea of "cumulative cultural evolution" (CCE) that warrant consideration even beyond the empirical critique they provide. As Vaesen and Houkes imply, the idea of CCE is so intuitively appealing to Western, educated, industrialized, rich, and democratic scientists socialized in a culture of progressivism that very little evidence beyond a passing reference to, for example, the Apollo missions is typically required to justify its validity and importance. But progress is a very dangerous concept in evolutionary theory (Ruse 1996) and a problematic criterion (cf. Mesoudi and Thornton 2018) on which to define CCE as something distinct from "regular" or "noncumulative" cultural evolution. What does it actually mean to call an evolutionary process, cultural or otherwise, cumulative?

To start at the ground floor, both cultural and biological evolution "can be described as systems of inherited variation that change over time in response to processes such as selection, migration, and drift" (Mesoudi 2017:7853). Seeing as inheritance and change over time are already included, the only thing that the modifier cumulative adds to cultural evolution is to stipulate that the change must be an "improvement." As it turns out, however, improvement is a slippery concept. For it to be anything other than an arbitrary preference, it needs to be grounded on some ultimate criterion such as genetic or cultural fitness (even if these are invariably represented by proxy measures; Mesoudi and Thornton 2018). But we already have a word for evolutionary change that increases fitness: adaptation (Reeve and Sherman 1993).

Increasing complexity (itself hard to adequately define and measure) is another frequently mentioned characteristic of cumulative culture. But increasing complexity is just a particular form of adaptive response that, as Vaesen and Houkes argue, may be idiosyncratic to technology (see also Derex and Mesoudi 2020) or certain cultural contexts. Evolutionary biologists study the evolution of exquisitely complex adaptive systems without feeling the need to demarcate a special form of cumulative biological evolution; it is not clear that use of this term (e.g., Stout et al. 2019) adds anything to the study of cultural evolution apart from implicit progressivist assumptions.

Vaesen and Houkes attempt to resolve this underlying confusion by equating CCE with the biological concept of persistent evolutionary trends (McShea 1994). They then make a convincing case that there is little empirical evidence that human cultural evolution is broadly characterized by such trends. However, it is not entirely clear that this is the key issue. The CCE concept originated in an attempt to identify what is special about human culture and cognition, with the proposed answer being the existence of uniquely cultural learning mechanisms that enable high-fidelity social reproduction (Tomasello, Kruger, and Ratner 1993). It is this capacity for cultural inheritance that allows human traditions to have deep "histories" in a way that animal traditions do not (Tomasello, Kruger, and Ratner 1993). But inherited variation is a prerequisite for any kind of evolution, not a special cumulative feature associated with persistent trends. Similarly, the population-level processes proposed to support the unique cultural adaptive capacity of humans (Boyd, Richerson, and Henrich 2011) are features of cultural evolution in general, not of some special cumulative or directional mode of change.

The real issue is thus not the frequency with which persistent trends emerge over human cultural evolution but rather the kinds of traits that can evolve at all. If a cultural trait cannot be inherited, whether because of limitations on social (Tennie, Call, and Tomasello 2009) or individual (Osiurak and Reynaud 2019; Whiten, Horner, and Marshall-Pescini 2003) learning, it cannot evolve in any direction. Conversely, when conditions for evolution are met, Vaesen and Houkes point out that maximum and average trait values will tend to increase even in the absence of persistent trends within lineages. So the real question of interest is what happened over human evolution to repeatedly expand the range (and, yes, complexity; Stout 2011) of cultural traits that can be inherited. Rather than arguing for or against the crossing of a CCE Rubicon, after which the march of progress dominated, we should focus our efforts on understanding this complex and contingent evolutionary history (Stout 2018; Stout and Hecht 2017).

A key part of this project will be to better define the units and scope of analysis. Vaesen and Houkes base part of their critique on the assumption that cultural trait complexity can be quantified in a straightforward way. For example, "One cannot produce a tool with fewer than one component." But what about the complexity of the processes by which that one component is produced and used, the social and material demands of learning these techniques (Pargeter, Khreisheh, and Stout 2019), or the possibility that methods were developed to accomplish the same goals with a different tool or no tool at all? As Vaesen and Houkes point out, technology may provide a favorable context for studying cultural evolution, but it is still not a simple phenomenon. The prevailing "technological systems" approach to technology studies, for example, identifies a technology as an integrated system of hardware, people, skills, knowledge, social relations, and institutions (Dusek 2006; Hughes 1987). To properly study the

cultural evolution of technology, we will need to address this more holistic technological niche (Stout and Hecht 2017), including the inheritance of material infrastructure (Pradhan, Tennie, and van Schaik 2012) and social arrangements (Derex and Mesoudi 2020; Powers, van Schaik, and Lehmann 2016) as well as interactions between technologies (Kolodny, Creanza, and Feldman 2015).

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Humans (but Not Other Apes) Frequently Cumulate Know-How

Some (including me) might read Vaesen and Houkes's title—"Is Human Culture Cumulative?"—as boldly asking whether human culture has ever been cumulative. Such questions are welcome, and I was even prepared to read a claim that human culture never cumulates.[5] Vaesen and Houkes, however, quickly concede—and I agree—that human culture can be cumulative and then move to alternative target questions regarding the extent and importance of this cumulation in humans. Below I formulate my interpretation, concretization, and clarification of their alternative questions and my answers—sometimes falling in contrast to Vaesen and Houkes.

How ecologically important is human cumulative culture (HCC)? The "Paris school" (Sterelny 2017) questions the HCC-centric view, de-emphasizing its importance. But the "California school" (Sterelny 2017) and others have argued consistently—and convincingly—that human distribution and survival across earth depend on HCC (e.g., Richerson and Boyd 2006). HCC therefore is ecologically important and frequently so. Some even argue that HCC is responsible not only for many human products (e.g., tools) but also for our cultural processes (such as know-how copying mechanisms; cf. Heyes 2018; see also Tennie 2019*a*).[6]

How evolutionarily important is HCC? This importance arguably first depends on the answer to another question, namely, when HCC first solidified in our lineage. The temporality of this still remains unclear, though two accounts have recently argued for a late onset (the adaptation-based account by Corbey et al. [2016] and the Baldwin effect and socially mediated reinnovation account by Tennie [2019*a*, 2019*b*] and Tennie et al. [2016, 2017]). Yet, given the likely high ecological relevance of HCC today (see above), we may reasonably suspect that HCC has been very important in our evolution (at some points in time).

How important is HCC as a differentiator between humans and other species? There is, of course, no a priori reason to believe that humans must be differentiated from other species at all. However, there are certain phenomena (e.g., our language or our persistent presence across earth despite our biological ill preparedness) that suggest differentiation on some level or at least to some degree (Tennie, Call, and Tomasello 2009). However, the search for specific differentiators should always be carried out in an attempt to then study these differentiators—which is my group's aim—and never to somehow use them to prove "human superiority."[7]

For various reasons (see Tennie, Hopper, and van Schaik 2021; Tennie et al. 2020), my lab uses a specialized, condensed definition of HCC. We argue that an important aspect of HCC is that it can consist of cumulative cultural know-how—to the point of copying-dependent know-how (Bandini et al. 2020; Tennie et al. 2017). This requires at base the skill of copying know-how. A human-specialized definition (based on know-how copying) is useful in the current context, as, if we find even this special type of cumulative culture in other species, then HCC cannot be a universal differentiator.

Empirically, certain nonhuman species do copy know-how—even copying-dependent know-how (e.g., some animal songs, such as lyrebird song).[8] This alone shows that even know-how copying fails as a differentiator between humans and all other species. At first sight, one potential remaining differentiation could be based on the added criteria of efficiency and complexity.[9] However, it is reasonable to assume that know-how copying increases the complexity of at least some animal song cases. It might even render some animal songs more efficient over time—in the songs' effects on others (Tennie, Caldwell, and Dean 2018).[10]

Yet, phylogenetically, it is most informative to look for evidence of HCC in our closest living relatives—other apes. However, wild ape cultures are best explained by a lack of know-how copying (Acerbi, Snyder, and Tennie 2020; Motes-Rodrigo and Tennie, forthcoming). Experimental work likewise shows that apes do not spontaneously copy copying-dependent know-how (e.g., Clay and Tennie 2017; review in

5. Note that I use "cumulate" rather than "accumulate," as accumulation has been defined instead as increases in the number of traits (Dean et al. 2014).

6. Many but not all products are culturally dependent in this way (Reindl et al. 2016, as already cited by Vaesen and Houkes)—but we have now also shown this cross-culturally (i.e., just as was called for by Vaesen and Houkes; see Neldner et al. 2020).

7. I am writing this as a general comment—it is therefore not meant as a critique of Vaesen and Houkes.

8. Vaesen and Houkes depict us as claiming that humans are unique in having cumulative culture: "that CCE is a unique and characteristic feature of human culture (see, e.g., . . . Tennie, Call, and Tomasello 2009)." The 2009 paper was focused on apes, but in any case, our stance is that some other animals have cumulative culture. E.g., in Tennie, Caldwell, and Dean (2018), we wrote, "Some nonhuman animals are capable of copying what they could not have invented on their own. Such cases are suggestive of cumulative culture."

9. It remains debated whether cumulative culture should require these criteria (Tennie, Caldwell, and Dean 2018).

10. We once planned to empirically test this, but other things got in the way.

Tennie, Hopper, and van Schaik 2021). Maybe most importantly, apes simply do not need to copy their know-how from each other because, empirically, they proved perfectly able to individually and spontaneously reinnovate this know-how in the absence of any opportunities for know-how copying (e.g., review in Bandini and Tennie 2020; Tennie, Hopper, and van Schaik 2021). Indeed, even if humans "instill" know-how copying into apes (as an "alien skill" via human training and human enculturation), these skills are quickly lost across one or two ape generations (Tennie 2019*a*). All of this does point to a real difference—at least between ape and human cultures. Only the latter is frequently based on know-how copying. It also again points to an onset—among apes—of frequently know-how copying–based cumulative culture in our lineage, that is, after the split from the last common ancestor (Tennie 2019*a*, 2019*b*; Tennie et al. 2016, 2017).

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Reply

We wish to start with a disclaimer. We received invaluable feedback from no fewer than 19 commentators, and our rejoinder cannot address all the issues that they raised. Moreover, although we acknowledge that most of their comments warrant specific in-depth discussion, for purposes of readability, we have chosen not to structure our response as a series of rejoinders to such individual comments. Rather, our strategy is to elaborate on two interrelated general themes that emerge from the commentaries and to make an attempt at a constructive synthesis of what may be concluded about these themes in light of the entire forum discussion (target article and comments). The first theme pertains to the types of views that could or should be pursued under the heading of "cumulative cultural evolution" (CCE). The second concerns the types of evidence that are needed to substantiate these views.

Concerning the first theme, our aim in our target article was to test a view that we claimed to be commonly endorsed in the relevant literature. In this view—let us call it "generalized CCE"—it is a characteristic feature of human culture (in general) that it accumulates beneficial modifications over time. We noted that, for this feature to be genuinely characteristic of human culture and thus for generalized CCE to hold, "It is not enough to show that some human cultural behaviors result from CCE; rather, one must show that a large fraction of such behaviors result from CCE."

Many commentators pointed out that generalized CCE—which, to emphasize, we reconstructed on the basis of the literature and do not endorse ourselves—is a misrepresentation (also see below) of the received wisdom among researchers. We address this charge of misrepresentation below. But before that, it should be noted that the commentaries in fact reveal that there simply is no received wisdom about the most salient characteristics of CCE or about the features of CCE that deserve scientific interest and study, for our commentators mention or endorse at least seven alternatives to the view that our target article engaged with (i.e., generalized CCE):

1. Human culture exhibits the property of being cumulative in at least some instances (Mesoudi).
2. Humans have a capacity for cumulative culture (Muller; Rawlings, Flynn, and Wood; and Stout).
3. Human culture is unique in that CCE occurs in a broad range of contexts (Caldwell et al.).
4. CCE occurs only in those domains in which selection pressures favor increasing effectiveness or efficiency (Mesoudi).
5. Human culture became truly cumulative only some 5,000 years ago (Shipton).
6. Human culture is cumulative in the sense that it exhibits cumulation in know-how (not necessarily in finished products; Tennie).
7. All human and nonhuman cultural evolution is cumulative (Haidle and Schlaudt).

This diversity of opinions is not problematic in itself. Arguably, many established fields of inquiry exhibit even higher levels of disagreement on central claims. In fact, we regard it as an important result of the current forum discussion (target article and comments) that hypotheses about CCE and the divergence between them have been made explicit, more so, we have the impression, than is customary in the CCE literature. Indeed, the lack of a single unambiguously stated and widely endorsed view or hypothesis in the literature was our reason to reconstruct such a claim in the first place.

By way of illustration, consider the review paper by Dean et al. (2014) to which we referred in our article. Just in the abstract of their paper, Dean et al. make minimally three different claims about CCE: generalized CCE,[11] generalized CCE but restricted to technology,[12] and a "threshold view" (Vaesen and Houkes 2017), according to which CCE leads to the development of traits far more complex than one individual could invent alone.[13]

11. "Human culture [in general] . . . is unambiguously cumulative" (Dean et al. 2014:284), where cumulative culture is defined as "the modification, over multiple transmission episodes, of cultural traits . . . resulting in an *increase in the complexity or efficiency of those traits*" (287; emphasis added).

12. "Human cumulative culture combines high-fidelity transmission of cultural knowledge with beneficial modifications to generate a 'ratcheting' in technological complexity [general increase in complexity]" (Dean et al. 2014:284).

13. "Human cumulative culture . . . [leads] to the development of traits far more complex than one individual could invent alone" (Dean et al. 2014:284).

Dean et al. (2014) are primarily concerned with reviewing the available evidence for CCE. Differentiating claims would be unnecessary if they would be supported by the same evidence or perhaps if they would all be supported by similar evidence. However, in Vaesen and Houkes (2017), we pointed out that much of the evidence discussed by Dean et al. (2014) in fact supports yet another claim, the more modest claim that technological innovations just build on the knowledge of previous generations (cultural evolution), without such processes leading to directional change (CCE).

In any case, the study by Dean et al. does support, in contrast to what some commentators suggest, the contention in our target article that "it has been claimed [not by all authors all the time] that a unique feature of human culture is that it accumulates beneficial modifications over time." And our references to studies by Tennie, Call, and Tomasello (2009) and by Lewis and Laland (2012) suggest that this is a "commonly endorsed" (albeit not by all authors all the time) view.

Still, generalized CCE is not the only claim that has been repeatedly endorsed in the literature. So why select this claim as the focus of our target article rather than, say, the threshold view? The reason is related to the second theme of our rejoinder: the types of evidence that are needed to corroborate claims about CCE. In table 1, we have made an attempt at classifying the abovementioned CCE claims according to how high they set the evidential bar (low, intermediate, and high). As can be seen there, we agree with some of our commentators (Caldwell et al., Mesoudi, Muller, and Rawlings, Flynn, and Wood) that the bar of generalized CCE is at the high end.

This might make why we chose to focus on this particular claim seem all the more puzzling. However, we worked on the implicit assumption—made explicit here—that there is great scientific merit in stating and pursuing empirically demanding hypotheses. Conversely, it is worthwhile to highlight bold claims that have been made and review whether they have been or even can be substantiated. Our focus on generalized CCE should be seen against this background. Our piece shows that this particular hypothesis currently has insufficient empirical support. What is more, the methodological challenges that it poses in collecting sufficient supporting evidence are such that generalized CCE is probably unknowable. Indeed, as de la Peña and Muller suggest, the archaeological evidence might very well be too fragmentary and poorly preserved to allow us to discern a generalized pattern of CCE in prehistory. And, indeed, as Caldwell et al., Mesoudi, and Rawlings, Flynn, and Wood indicate, collecting the kind of contemporary evidence that generalized CCE requires is nothing but a logistical nightmare. To be sure, that generalized CCE is insufficiently supported or unknowable is a negative result. Yet we regard this as a contribution to the field: for it to make progress, it is good to identify which claims that we know remain unknowable have been endorsed so that research efforts may be focused on substantiating those claims that are within reach. Note that what we have just said about generalized CCE also applies to the five other claims that we labeled high (i.e., claims 6–9 and 11), for all these claims demand enormous global data sets that, logistically, are virtually impossible to build and that, in part, would need to pertain to archaeologically poorly documented phenomena. Accordingly, we suggest that the field might want to focus on more modest and evidentially less demanding claims or at least clearly differentiate those from high claims that will remain speculative.

This does not mean that the evidential bar should be brought all the way down, though. Claims that we labeled low are, in our opinion, empirically too undemanding or trivial to deserve (extensive) scientific study. Indeed, observations of our everyday world (e.g., increasing efficiency of at least some combustion engines, improvements in the performance of computers, the Apollo missions, and the Large Hadron Collider) or existing histories of technologies (e.g., Lindenfors et al. 2015; Moore et al. 2009; Neamtiu, Xie, and Chen 2013; Perreault et al. 2013; Stout 2011; Strumsky, Lobo, and van der Leeuw 2012) suffice to substantiate the following low claims: that human culture is cumulative in at least some instances (claim 1 in table 1), that humans have a capacity for human culture (claim 2 in table 1), and that some technologies have become so complex that they could not have been invented by one individual alone (claim 3 in table 1). Hence, we started our piece by acknowledging that "it is fairly evident that human populations have been able to improve at least some of their behavior through CCE," referring to the contemporary observations and historical records mentioned above. Again, by taking this in stride, we assume that the field should have higher aspirations, which is not to say that the research that the commentators invoke in support of claims 1–3 is trivial. Yet we submit that it should be used in support of more ambitious claims than the low ones for which they are enlisted now.

Combining these conclusions on high and low claims, we conclude that, from the 11 claims in table 1, only two turn out to be scientifically worthy of pursuit (viz., the intermediate claims, 4 and 5). These claims strike a proper balance between informativeness, knowability, and scientific effort. Note that we do not claim that our list is exhaustive in this respect: there may be more hypotheses than those included in table 1 that also strike such a balance. Consider, for instance, some commentators' other criticisms of generalized CCE, as follows: (i) Caldwell et al., de la Peña, and Haidle and Schlaudt find fault with treating cultural traits as relatively independent units, (ii) Caldwell et al. and Stout do not consider complexity a meaningful measure of cumulation, (iii) Haidle and Schlaudt take issue with assessing cumulation in a unifactorial way, (iv) Tennie takes issue with focusing on finished artifacts rather than on the underlying know-how, and (v) de la Peña, Muller, and Shipton take issue with the demands that generalized CCE puts on the fragmentary and poorly preserved prehistoric archaeological record. These objections to generalized CCE may help us to formulate (new) hypotheses that are informative, knowable, and worthy of scientific study. Following i, one might express claims 4 and 5 in terms of cultural systems rather than individual traits, following iii, one might assess cumulation in a

Table 1. The various claims and hypotheses that have emerged from the current forum discussion, the evidence required to substantiate them, and an assessment of the height of the evidential bar they set

Claim or hypothesis (reference[s])	Required evidence	Evidential bar
1. Human culture is cumulative in at least some instances (Mesoudi)	Evidence that some cultural traits are produced by CCE	Low
2. Humans have a capacity for cumulative culture (Muller; Rawlings, Flynn, and Wood; Stout)	Evidence that some cultural traits are produced by CCE	Low
3. CCE leads to traits far more complex than one individual could invent alone (Dean et al. 2014)	Evidence that some cultural traits cannot be invented by one individual	Low
4. Human culture is unique in that CCE occurs in a broad range of contexts (Caldwell et al.)	Evidence in humans that cultural traits in several domains are produced by CCE and evidence that nonhuman animal culture does not exhibit the same trend	Intermediate
5. Technological innovations develop by modifying earlier technologies (i.e., cultural evolution rather than CCE; Dean et al. 2014)	Evidence from a sample representative of all technologies showing that these technologies resulted from descent with modification	Intermediate
6. CCE occurs only in those domains in which selection pressures favor increases in effectiveness or efficiency (Mesoudi)	Evidence that distinguishes selectively neutral from selectively nonneutral cultural traits; evidence from a sample representative of both types of traits showing that the former did not result from CCE but the latter did	High
7. Human culture became truly cumulative only some 5,000 years ago (Shipton)	Evidence from a sample representative of all pre-5,000 traits and from a sample representative of all post-5,000 traits showing that the former did not result from CCE but the latter did	High
8. Human culture is cumulative in the sense that it exhibits cumulation in know-how (not necessarily in finished products; Tennie)	Evidence from a sample representative of all cultural traits showing that they resulted from the accumulation of (often poorly documented) know-how	High
9. It is a unique and characteristic feature of human technologies that they accumulate beneficial modifications over time (generalized CCE restricted to technology; Dean et al. 2014)	Evidence from a sample representative of all technologies showing that a large fraction of them resulted from CCE	High
10. It is a unique and characteristic feature of human culture (in general) that it accumulates beneficial modifications over time (generalized CCE; Dean et al. 2014)	Evidence from a sample representative of all cultural traits showing that a large fraction of them resulted from CCE	High
11. All human and nonhuman cultural evolution is cumulative (Haidle and Schlaudt)	Evidence from a sample representative of all human and nonhuman cultural traits showing that they all resulted from CCE	High

Note. CCE = cumulative cultural evolution.

multifactorial way, following iv, one might need to restrict one's hypotheses to the past 5,000 years of human evolution, following v, it might be worthwhile to decrease the evidential burden of claim 8 and study developments only in human know-how, and any combination of the above.

As an aside, we are very sympathetic to these criticisms of generalized CCE—a view that we, to reiterate, do not endorse ourselves but rather have critically reviewed for its empirical support. Our own thoughts about cultural evolution align with the ideas that cultural traits should be studied in relation to other cultural and noncultural phenomena, that complexity and unifactorial measures of cumulation are misguided, that one might need to restrict the study of CCE to developments after 5,000 years ago, and that CCE scholars tend to be overly concerned with finished artifacts rather than with design or use plans.

Let us sum up the main results of this forum discussion. There appears to be no unanimity among researchers about the most salient characteristics of CCE or about the features of CCE that deserve scientific interest and study. We have also seen that the different CCE claims that are mentioned in the forum discussion and the literature demand different types of evidential support and vary according to the height of the evidential bar they set. Finally, we have illustrated the fruitfulness of differentiating claims in terms of their evidential demandingness: this differentiation allows one to separate the pursuit-worthy "wheat" (viz., intermediate claims) from the commonsensical or unknowable "chaff" (viz., low and high claims) and thus to bring focus to the various research efforts in CCE research.

On a final note, our rejoinder should not be read as a plea for consensus. There are plenty of interesting hypotheses about CCE that are worthy of pursuit, and, as the philosophy of science teaches us, such diversity is not or only rarely (e.g., in urgent science) to be given up for consensus. Yet, for a field to advance, it is necessary not to waste resources on hypotheses that are not in

need of further substantiation or on hypotheses that are scientifically impossible to corroborate. We sincerely thank our commentators for helping us in making these important points.

—Krist Vaesen and Wybo Houkes

References Cited

Acerbi, Alberto, Jeremy Kendal, and Jamshid J. Tehrani. 2017. Cultural complexity and demography: the case of folktales. *Evolution and Human Behavior* 38(4):474–480, https://doi.org/10.1016/j.evolhumbehav.2017.03.005. [BR/EGF/LAW]

Acerbi, Alberto, William Daniel Snyder, and Claudio Tennie. 2020. Ape cultures do not require behavior copying. *bioRxiv* 2020.03.25.008177. [CT]

Bandini, Elisa, Alba Motes-Rodrigo, Matthew P. Steele, Christian Rutz, and Claudio Tennie. 2020. Examining the mechanisms underlying the acquisition of animal tool behaviour. *Biology Letters* 16:20200122. [CT]

Bandini, Elisa, and Claudio Tennie. 2020. Exploring the role of individual learning in animal tool-use. *PeerJ* 8:e9877. [CT]

Basalla, George. 1988. *The evolution of technology*. Cambridge: Cambridge University Press.

Bentley, R. Alexander, Matthew W. Hahn, and Stephen J. Shennan. 2004. Random drift and culture change. *Proceedings of the Royal Society B* 271(1547): 1443–1450. [AM]

Beyene, Yonas, Shigehiro Katoh, Giday WoldeGabriel, William K. Hart, Kozo Uto, Masafumi Sudo, Megumi Kondo, et al. 2013. The characteristics and chronology of the earliest Acheulean at Konso, Ethiopia. *Proceedings of the National Academy of Sciences of the USA* 110(5):1584–1591.

Boyd, Robert. 2018. *A different kind of animal: how culture transformed our species*. Princeton, NJ: Princeton University Press. [AM]

Boyd, Robert, and Peter J. Richerson. 1996. Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy* 88:77–93.

Boyd, Robert, Peter J. Richerson, and Joseph Henrich. 2011. The cultural niche: why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences of the USA* 108(suppl. 2):10918–10925. [DS]

Brooks, Alison S., John E. Yellen, Richard Potts, Anna K. Behrensmeyer, Alan L. Deino, David E. Leslie, Stanley H. Ambrose, Jeffrey R. Ferguson, Francesco d'Errico, and Andrew M. Zipkin. 2018. Long-distance stone transport and pigment use in the earliest Middle Stone Age. *Science* 360(6384):90–94. [CS]

Caldwell, Christine A., and Ailsa E. Millen. 2008. Experimental models for testing hypotheses about cumulative cultural evolution. *Evolution and Human Behavior* 29(3):165–171. [CAC/ER/DK/KHB/CEHW/MA/SBK/GM]

———. 2010*a*. Conservatism in laboratory microsocieties: unpredictable payoffs accentuate group-specific traditions. *Evolution and Human Behavior* 31(2): 123–130.

———. 2010*b*. Human cumulative culture in the laboratory: effects of (micro) population size. *Learning and Behavior* 38:310–318.

Caldwell, Christine A., and Kenny Smith. 2012. Cultural evolution and perpetuation of arbitrary communicative conventions in experimental microsocieties. *PLoS ONE* 7(8):e43807. [CAC/ER/DK/KHB/CEHW/MA/SBK/GM]

Chazan, Michael. 2015. Technological trends in the Acheulean of Wonderwerk Cave, South Africa. *African Archaeological Review* 32(4):701–728. [AM]

Clarkson, Chris, Zenobia Jacobs, Ben Marwick, Richard Fullagar, Lynley Wallis, Mike Smith, Richard G. Roberts, Elspeth Hayes, Kelsey Lowe, and Xavier Carah. 2017. Human occupation of northern Australia by 65,000 years ago. *Nature* 547(7663):306–310. [CS]

Clay, Zanna, and Claudio Tennie. 2017. Is overimitation a uniquely human phenomenon? insights from human children as compared to bonobos. *Child Development* 89(5):1535–1544. [CT]

Corbey, Raymond, Adam Jagich, Krist Vaesen, and Mark Collard. 2016. The Acheulean handaxe: more like a bird's song than a Beatles' tune? *Evolutionary Anthropology* 25(1):6–19. [CT]

Dean, Lewis G., Gill L. Vale, Kevin N. Laland, Emma Flynn, and Rachel L. Kendal. 2014. Human cumulative culture: a comparative perspective. *Biological Reviews of the Cambridge Philosophical Society* 89(2):284–301.

de Beaune, Sophie Archambault. 2004. The invention of technology: prehistory and cognition. *Current Anthropology* 45(2):139–162, https://doi.org/10.1086/381045. [MNH/OS]

Delagnes, Anne, and Hélène Roche. 2005. Late Pliocene hominid knapping skills: the case of Lokalalei 2C, West Turkana, Kenya. *Journal of Human Evolution* 48(5):435–472.

de la Peña, Paloma. 2020. Howiesons Poort. In *Oxford research encyclopedia of anthropology*. Oxford: Oxford University Press. https://oxfordre.com/anthropology/view/10.1093/acrefore/9780190854584.001.0001/acrefore-9780190854584-e-34. [PdlP]

de la Peña, Paloma, and Lyn Wadley. 2017. Technological variability at Sibudu Cave: the end of Howiesons Poort and reduced mobility strategies after 62,000 years ago. *PLoS ONE* 12(10):e0185845.

Derex, Maxime, and Alex Mesoudi. 2020. Cumulative cultural evolution within evolving population structures. *Trends in Cognitive Sciences* 24(8):654–667. [DS]

d'Errico, Francesco, Luc Doyon, Ivan Colagé, Alain Queffelec, Emma Le Vraux, Giacomo Giacobini, Bernard Vandermeersch, and Bruno Maureille. 2018. From number sense to number symbols: an archaeological perspective. *Philosophical Transactions of the Royal Society B* 373:20160518, https://doi.org/10.1098/rstb.2016.0518. [MNH/OS]

d'Errico, Francesco, Africa Pitarch Marti, Ceri Shipton, Emma Le Vraux, Emmanuel Ndiema, Steven Goldstein, Michael D. Petraglia, and Nicole Boivin. 2020. Trajectories of Middle to Later Stone Age cultural innovation in eastern Africa: personal ornaments, bone artifacts and ocher from Panga ya Saidi, Kenya. *Journal of Human Evolution* 141:102737. [CS]

de Solla Price, Derek J. 1963. *Little science, big science*. New York: Columbia University Press.

Dusek, Val. 2006. *Philosophy of technology: an introduction*. Malden, MA: Blackwell. [DS]

Fay, Nicolas, Naomi De Kleine, Bradley Walker, and Christine A. Caldwell. 2019. Increasing population size can inhibit cumulative cultural evolution. *Proceedings of the National Academy of Sciences of the USA* 116(14):6726–6731.

Fisher, D. C. 1986. Progress in organismal design. In *Dahlem Konferenzen 1986*. D. M. Raup and D. Jablonski, eds. Pp. 99–117. Berlin: Springer.

Flynn, Emma. 2008. Investigating children as cultural magnets: do young children transmit redundant information along diffusion chains? *Philosophical Transactions of the Royal Society B* 363:3541–3551.

Gibson, James J. 1979. *The ecological approach to visual perception*. Boston: Houghton Mifflin. [MNH/OS]

Gould, Stephen Jay. 1996. *Full house*. New York: Harmony.

Gould, Stephen Jay, and Elisabeth S. Vrba. 1982. Exaptation: a missing term in the science of form. *Paleobiology* 8(1):4–15, https://www.jstor.org/stable/2400563. [MNH/OS]

Haidle, Miriam Noël. 2010. Working-memory capacity and the evolution of modern cognitive capacities: implications from animal and early human tool use. *Current Anthropology* 51(suppl. 1):S149–S166, https://doi.org/10.1086/650295. [MNH/OS]

———. 2012. *How to think tools? a comparison of cognitive aspects in tool behavior of animals and during human evolution*. Tübingen, Germany: TOBIAS-lib. http://hdl.handle.net/10900/49627. [MNH/OS]

———. 2019. The origin of cumulative culture: not a single-trait event, but multifactorial processes. In *Squeezing minds from stones*. Karenleigh A. Overmann and Frederick L. Coolidge, eds. Pp. 128–148. New York: Oxford University Press. [MNH/OS]

Haidle, Miriam Noël, Michael Bolus, Mark Collard, Nicholas J. Conard, Duilio Garofoli, Marlize Lombard, April Nowell, Claudio Tennie, and Andrew Whiten. 2015. The nature of culture: an eight-grade model for the evolution and expansion of cultural capacities in hominins and other animals. *Journal of Anthropological Sciences* 93:43–70. [MNH/OS]

Haidle, Miriam Noël, and Jürgen Bräuer. 2011. From brainwave to tradition: how to detect innovations in tool behaviour. In *Innovation and the evolution of human behavior*. Special issue, *PaleoAnthropology* 2011:144–153, https://doi.org/10.4207/PA.2011.ART48. [MNH/OS]

Haidle, Miriam Noël, and Oliver Schlaudt. 2020. Where does cumulative culture begin? a plea for a sociologically informed perspective. *Biological Theory* 15(3):161–174, https://doi.org/10.1007/s13752-020-00351-w. [MNH/OS]

———. 2021. Taking the historical-social dimension seriously: a reply to Bandini et al. *Biological Theory*. Forthcoming. https://doi.org/10.1007/s13752-021-00375-w. [MNH/OS]

Henrich, Joseph. 2004. Demography and cultural evolution. *American Antiquity* 69(2):197–214. [AM]

———. 2015. *The secret of our success*. Princeton, NJ: Princeton University Press. [AM]

Henrich, Joseph, Steven J. Heine, and Ara Norenzayan. 2010. The weirdest people in the world? *Behavioral and Brain Sciences* 33(2/3):61–83, https://doi.org/10.1017/S0140525X0999152X.

Henshilwood, Christopher S. 2011. Late Pleistocene techno-traditions in southern Africa: a review of the Still Bay and Howiesons Poort, c. 75–59 ka. *Journal of World Prehistory* 25(3/4):205–237. [PdlP]

Heyes, Cecilia. 2018. *Cognitive gadgets: the cultural evolution of thinking*. Cambridge, MA: Harvard University Press. [CT]

Hill, Kim, Michael Barton, and A. Magdalena Hurtado. 2009. The emergence of human uniqueness: characters underlying behavioral modernity. *Evolutionary Anthropology* 18(5):187–200.

Hodgkin, Luke Howard. 2005. *A history of mathematics*. Oxford: Oxford University Press.

Hughes, Thomas P. 1987. The evolution of large technological systems. In *The social construction of technological systems: new directions in the sociology and history of technology*. Wiebe E. Bijker, Thomas P. Hughes, and Trevor Pinch, eds. Pp. 45–76. Cambridge, MA: MIT Press. [DS]

Jesmer, Brett R., Jerod A. Merkle, Jacob R. Goheen, Ellen O. Aikens, Jeffrey L. Beck, Alyson B. Courtemanch, Mark A. Hurley, et al. 2018. Is ungulate migration culturally transmitted? evidence of social learning from translocated animals. *Science* 361(6406):1023–1025. [CAC/ER/DK/KHB/CEHW/MA/SBK/GM]

Kandler, Anne, and Enrico R. Crema. 2019. Analysing cultural frequency data: neutral theory and beyond. In *Handbook of evolutionary research in archaeology*. Anna Marie Prentiss, ed. Pp. 83–108. Cham, Switzerland: Springer. [AM]

Kempe, Marius, Stephen J. Lycett, and Alex Mesoudi. 2014. From cultural traditions to cumulative culture: parameterizing the differences between human and nonhuman culture. *Journal of Theoretical Biology* 359:29–36.

Kline, Michelle A., Rubeenya Shamsudheen, and Tanya Broesch. 2018. Variation is the universal: making cultural evolution work in developmental psychology. *Philosophical Transactions of the Royal Society B* 373(1743): 20170059, https://doi.org/10.1098/rstb.2017.0059. [BR/EGF/LAW]

Köhler, Wolfgang. 1926. *The mentality of apes*. New York: Harcourt Brace. [MNH/OS]

Kolodny, Oren, Nicole Creanza, and Marcus W. Feldman. 2015. Evolution in leaps: the punctuated accumulation and loss of cultural innovations. *Proceedings of the National Academy of Sciences of the USA* 112(49):E6762–E6769. [DS]

Kuhn, Steven L. 2003. In what sense is the Levantine Initial Upper Paleolithic a "transitional" industry? In *The chronology of the Aurignacian and of the transitional technocomplexes: dating, stratigraphies, cultural implications*. João Zilhão and Francesco d'Errico, eds. Pp. 61–70. Lisbon: Instituto Português de Arqueologia. [CS]

Lake, M. W., and J. Venti. 2009. Quantitative analysis of macroevolutionary patterning in technological evolution: bicycle design from 1800 to 2000. In *Pattern and process in cultural evolution*. Stephen J. Shennan, ed. Pp. 147–174. Berkeley: University of California Press. [AM]

Langley, Michelle C., Noel Amano, Oshan Wedage, Siran Deraniyagala, M. M. Pathmalal, Nimal Perera, Nicole Boivin, Michael D. Petraglia, and Patrick Roberts. 2020. Bows and arrows and complex symbolic displays 48,000 years ago in the South Asian tropics. *Science Advances* 6(24): eaba3831. [CS]

Langley, Michelle C., and Susan O'Connor. 2016. An enduring shell artefact tradition from Timor-Leste: *Oliva* bead production from the Pleistocene to Late Holocene at Jerimalai, Lene Hara, and Matja Kuru 1 and 2. *PLoS ONE* 11(8):e0161071. [CS]

———. 2018. 40,000 years of ochre utilization in Timor-Leste: powders, prehensile traces, and body painting. In *Personal ornaments in early prehistory*. Special issue, *PaleoAnthropology* 2019:82–104. [CS]

Legare, Cristine H., and Mark Nielsen. 2015. Imitation and innovation: the dual engines of cultural learning. *Trends in Cognitive Sciences* 19(11):688–699. [BR/EGF/LAW]

Lemonnier, Pierre. 2002. *Technological choices: transformation in material culture since the Neolithic*. Abingdon, UK: Routledge. [PdlP]

Lewis, Hannah M., and Kevin N. Laland. 2012. Transmission fidelity is the key to the build-up of cumulative culture. *Philosophical Transactions of the Royal Society B* 367(1599):2171–2180.

Lindenfors, Patrik, Ida Envall, Sven Isaksson, and Magnus Enquist. 2015. An empirical study of cultural evolution: the development of European cooking from medieval to modern times. *Cliodynamics* 6(2):115–129, https://doi.org/10.21237/C7CLIO6225072.

Lombard, Marlize. 2012. Thinking through the Middle Stone Age of sub-Saharan Africa. *Quaternary International* 270:140–155, https://doi.org/10.1016/j.quaint.2012.02.033. [MNH/OS]

———. 2016. Mountaineering or ratcheting? Stone Age hunting weapons as proxy for the evolution of human technological, behavioral and cognitive flexibility. In *The nature of culture: based on an interdisciplinary symposium "The Nature of Culture," Tübingen, Germany*. Miriam Noël Haidle, Nicholas J. Conard, and Michael Bolus, eds. Pp. 135–146. Dordrecht, Netherlands: Springer. [MNH/OS]

Lombard, Marlize, Miriam Noël Haidle, and Anders Högberg. 2019. Cognition: from capuchin rock pounding to Lomekwian flake production. *Cambridge Archaeological Journal* 29(2):201–231, https://doi.org/10.1017/S0959774318000550. [MNH/OS]

Lycett, Stephen J., and John A. J. Gowlett. 2008. On questions surrounding the Acheulean "tradition." *World Archaeology* 40(3):295–315.

McShea, Daniel W. 1991. Complexity and evolution: what everybody knows. *Biology and Philosophy* 6:303–324.

———. 1994. Mechanisms of large-scale evolutionary trends. *Evolution* 48(6): 1747–1763.

Mesoudi, Alex. 2011. Variable cultural acquisition costs constrain cumulative cultural evolution. *PLoS ONE* 6(3):e18239.

———. 2017. Pursuing Darwin's curious parallel: prospects for a science of cultural evolution. *Proceedings of the National Academy of Sciences of the USA* 114(30):7853–7860. [DS]

Mesoudi, Alex, Lei Chang, Sasha R. X. Dall, and Alex Thornton. 2016. The evolution of individual and cultural variation in social learning. *Trends in Ecology and Evolution* 31(3):215–225. [AM]

Mesoudi, Alex, Lei Chang, Keelin Murray, and Hui Jing Lu. 2015. Higher frequency of social learning in China than in the West shows cultural variation in the dynamics of cultural evolution. *Proceedings of the Royal Society B* 282(1798):20142209. [AM]

Mesoudi, Alex, and Alex Thornton. 2018. What is cumulative cultural evolution? *Proceedings of the Royal Society B* 285(1880):20180712.

Minetti, Alberto E., John Pinkerton, and Paola Zamparo. 2001. From bipedalism to bicyclism: evolution in energetics and biomechanics of historic bicycles. *Proceedings of the Royal Society B* 268(1474):1351–1360. [AM]

Miton, Helena, and Matthieu Charbonneau. 2018. Cumulative culture in the laboratory: methodological and theoretical challenges. *Proceedings of the Royal Society B* 285(1879):20180677, https://doi.org/10.1098/rspb.2018.0677. [BR/EGF/LAW]

Miton, Helena, Nicolas Claidière, and Hugo Mercier. 2015. Universal cognitive mechanisms explain the cultural success of bloodletting. *Evolution and Human Behavior* 36(4):303–312. [AM]

Miu, Elena, Ned Gulley, Kevin N. Laland, and Luke Rendell. 2018. Innovation and cumulative culture through tweaks and leaps in online programming contests. *Nature Communications* 9(1):2321. [AM]

Moore, M. W., T. Sutikna, M. M. Jatmiko, and A. Brumm. 2009. Continuities in stone flaking technology at Liang Bua, Flores, Indonesia. *Journal of Human Evolution* 57(5):503–526.

Morris, Ian. 2013. *The measure of civilization: how social development decides the fate of nations*. Princeton, NJ: Princeton University Press.

Morrison, David A. 2011. *Introduction to phylogenetic networks*. Uppsala: RJR Productions.

Motes-Rodrigo, Alba, and Claudio Tennie. Forthcoming. Locally restricted behaviors: in search of potential great ape culture dependent traits. *Biological Reviews*. [CT]

Movius, Hallam L. 1949. Lower Paleolithic archaeology in southern Asia and the Far East. In *Early man in the Far East*. William W. Howells, ed. Pp. 17–82. Detroit: American Association of Physical Anthropologists. [CS]

Muller, Antoine, Chris Clarkson, and Ceri Shipton. 2017. Measuring behavioural and cognitive complexity in lithic technology throughout human evolution. *Journal of Anthropological Archaeology* 48:166–180.

Neamtiu, Iulian, Guowu Xie, and Jianbo Chen. 2013. Towards a better understanding of software evolution: an empirical study on open-source software. *Journal of Software: Evolution and Process* 25:193–218.

Neldner, K., J. Redshaw, S. Murphy, K. Tomaselli, J. Davis, B. Dixson, and M. Nielsen. 2019. Creation across culture: children's tool innovation is influenced by cultural and developmental factors. *Developmental Psychology* 55(4):877–889, https://doi.org/10.1037/dev0000672. [BR/EGF/LAW]

Neldner, K., E. Reindl, C. Tennie, J. Grant, K. Tomaselli, and M. Nielsen. 2020. A cross-cultural investigation of young children's spontaneous

invention of tool use behaviours. *Royal Society Open Science* 7(5):192240, https://doi.org/10.1098/rsos.192240. [BR/EGF/LAW, CT]
Nia, Hadi T., Ankita D. Jain, Yuming Liu, Mohammad-Reza Alam, Roman Barnas, and Nicholas C. Makris. 2015. The evolution of air resonance power efficiency in the violin and its ancestors. *Proceedings of the Royal Society A* 471(2175):20140905. [AM]
Nielsen, Mark, Daniel Haun, Joscha Kärtner, and Cristine H. Legare. 2017. The persistent sampling bias in developmental psychology: a call to action. *Journal of Experimental Child Psychology* 162:31–38, https://doi.org/10.1016/j.jecp.2017.04.017. [BR/EGF/LAW]
Nonaka, Tetsushi, Blandine Bril, and Robert Rein. 2010. How do stone knappers predict and control the outcome of flaking? implications for understanding early stone tool technology. *Journal of Human Evolution* 59(2):155–167.
Norenzayan, Ara, Azim F. Shariff, Will M. Gervais, Aiyana K. Willard, Rita A. McNamara, Edward Slingerland, and Joseph Henrich. 2014. The cultural evolution of prosocial religions. *Behavioral and Brain Sciences* 39:E1, https://doi.org/10.1017/S0140525X14001356. [BR/EGF/LAW]
O'Connor, Sue, Rintaro Ono, and Chris Clarkson. 2011. Pelagic fishing at 42,000 years before the present and the maritime skills of modern humans. *Science* 334(6059):1117–1121. [CS]
Osiurak, François, and Emanuelle Reynaud. 2019. The elephant in the room: what matters cognitively in cumulative technological culture. *Behavioral and Brain Sciences* 43:1–57. [DS]
Pargeter, Justin, Nada Khreisheh, and Dietrich Stout. 2019. Understanding stone tool-making skill acquisition: experimental methods and evolutionary implications. *Journal of Human Evolution* 133:146–166. [DS]
Perreault, Charles, P. Jeffrey Brantingham, Steven L. Kuhn, Sarah Wurz, and Xing Gao. 2013. Measuring the complexity of lithic technology. *Current Anthropology* 54(suppl. 8):S397–S406.
Pinker, Steven. 2010. The cognitive niche. *Proceedings of the National Academy of Sciences of the USA* 107(suppl. 2):8993–8999. [AM]
Powers, Simon T., Carel P. van Schaik, and Laurent Lehmann. 2016. How institutions shaped the last major evolutionary transition to large-scale human societies. *Philosophical Transactions of the Royal Society B* 371(1687):20150098. [DS]
Pradhan, Gauri R., Claudio Tennie, and Carel P. van Schaik. 2012. Social organization and the evolution of cumulative technology in apes and hominins. *Journal of Human Evolution* 63(1):180–190. [DS]
Rawlings, Bruce, Natália Dutra, Cameron Turner, and Emma Flynn. 2019. Overimitation across development: the influence of individual and contextual factors. In *Conducting research in developmental psychology: a topical guide for research methods utilized across the lifespan*. Nancy Aaron Jones, Melannie Platt, Krystal D. Mize, and Jillian Hardin, eds. Pp. 26–39. New York: Routledge, https://doi.org/10.4324/9780429352065-2. [BR/EGF/LAW]
Reeve, Hudson Kern, and Paul W. Sherman. 1993. Adaptation and the goals of evolutionary research. *Quarterly Review of Biology* 68(1):1–32. [DS]
Reindl, E., I. A. Apperly, S. R. Beck, and C. Tennie. 2017. Young children copy cumulative technological design in the absence of action information. *Scientific Reports* 7:1788.
Reindl, E., S. R. Beck, I. A. Apperly, and C. Tennie. 2016. Young children spontaneously invent wild great apes' tool-use behaviors. *Proceedings of the Royal Society B* 283:1825. [CT]
Richerson, Peter J., and Robert Boyd. 2006. *Not by genes alone*. Chicago: University of Chicago Press.
Rios-Garaizar, Joseba, Oriol López-Bultó, Eneko Iriarte, Carlos Pérez-Garrido, Raquel Piqué, Arantza Aranburu, María José Iriarte-Chiapusso, et al. 2018. A Middle Palaeolithic wooden digging stick from Aranbaltza III, Spain. *PLoS ONE* 13(3):e0195044, https://doi.org/10.1371/journal.pone.0195044. [PdlP]
Roberts, Patrick, Mary Prendergast, Anneke Janzen, Ceri Shipton, James Blinkhorn, Jan Zech, Alison Crowther, et al. 2020. Late Pleistocene to Holocene human palaeoecology in the tropical environments of coastal eastern Africa. *Paleogeography, Paleoclimatology, Paleoecology* 537:109438. [CS]
Ruse, Michael. 1996. *Monad to man: the concept of progress in evolutionary biology*. Cambridge, MA: Harvard University Press. [DS]
Sasaki, Takao, and Dora Biro. 2017. Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications* 8:15049. [AM]
Savage, Patrick E. 2019. Cultural evolution of music. *Palgrave Communications* 5(1):1–12, https://doi.org/10.1057/s41599-019-0221-1. [BR/EGF/LAW]
Schlaudt, Oliver. 2020. Type and token in the prehistoric origins of numbers. *Cambridge Archaeological Journal* 30(4):629–646, https://doi.org/10.1017/S0959774320000165. [MNH/OS]
Sharon, Gonen, and Naama Goren-Inbar. 1999. Soft percussor use at the Gesher Benot Ya'aqov Acheulian site? *Mitekufat Haeven* 28:55–79. [AM]
Shea, John J. 2011. *Homo sapiens* is as *Homo sapiens* was. *Current Anthropology* 52(1):1–35.
Shipton, Ceri. 2010. Imitation and shared intentionality in the Acheulean. *Cambridge Archaeological Journal* 20(2):197–210. [CS]
———. 2016. Hierarchical organization in the Acheulean to Middle Palaeolithic transition at Bhimbetka, India. *Cambridge Archaeological Journal* 26(4):601–618.
———. 2018. Biface knapping skill in the East African Acheulean: progressive trends and random walks. *African Archaeological Review* 35:107–131. [AM, CS]
———. 2019. The evolution of social transmission in the Acheulean. In *Squeezing minds from stones*. Karenleigh Overmann and Frederick L. Coolidge, eds. Pp. 332–354. Oxford: Oxford University Press. [AM, CS]
———. 2020. The unity of Acheulean culture. In *Culture history and convergent evolution: vertebrate paleobiology and paleoanthropology*. Huw Groucutt, ed. Pp. 13–27. Cham, Switzerland: Springer. [AM]
Shipton, Ceri, Chris Clarkson, Jaganath N. Pal, Sacha C. Jones, Richard G. Roberts, Clair Harris, M. C. Gupta, Peter W. Ditchfield, and Michael D. Petraglia. 2013. Generativity, hierarchical action and recursion in the technology of the Acheulean to Middle Palaeolithic transition: a perspective from Patpara, the Son Valley, India. *Journal of Human Evolution* 65(2):93–108. [CS]
Shipton, Ceri, and Mark Nielsen. 2015. Before cumulative culture. *Human Nature* 26(3):331–345. [CS]
Shipton, Ceri, S. O'Connor, N. Jankowski, J. O'Connor-Veth, T. Maloney, S. Kealy, and C. Boulanger. 2019. A new 44,000-year sequence from Asitau Kuru (Jerimalai), Timor-Leste, indicates long-term continuity in human behaviour. *Archaeological and Anthropological Sciences* 11:5717–5741. [CS]
Shipton, Ceri, Patrick Roberts, Will Archer, Simon J. Armitage, Caesar Bita, James Blinkhorn, Colin Courtney-Mustaphi, et al. 2018. 78,000-year-old record of Middle and Later Stone Age innovation in an East African tropical forest. *Nature Communications* 9(1):1832. [CS]
Simondon, Gilbert. 1958. *Du mode d'existence des objets techniques*. Paris: Aubier. [PdlP]
Sterelny, Kim. 2017. Cultural evolution in California and Paris. *Studies in History and Philosophy of Science Part A* 100:42–50. [CT]
Stout, Dietrich. 2011. Stone toolmaking and the evolution of human culture and cognition. *Philosophical Transactions of the Royal Society B* 366(1567):1050–1059.
———. 2018. Human brain evolution: history or science? In *Rethinking human evolution*. Jeffrey H. Schwartz, ed. Pp. 297–318. Cambridge, MA: MIT Press. [DS]
Stout, Dietrich, Jan Apel, Julia Commander, and Mark Roberts. 2014. Late Acheulean technology and cognition at Boxgrove, UK. *Journal of Archaeological Science* 41:576–590. [AM, CS]
Stout, Dietrich, and Erin E. Hecht. 2017. Evolutionary neuroscience of cumulative culture. *Proceedings of the National Academy of Sciences of the USA* 114(30):7861–7868. [DS]
Stout, Dietrich, Michael J. Rogers, Adrian V. Jaeggi, and Sileshi Semaw. 2019. Archaeology and the origins of human cumulative culture: a case study from the earliest Oldowan at Gona, Ethiopia. *Current Anthropology* 60(3):309–340. [AM, CS, DS]
Strumsky, Deborah, José Lobo, and Sander van der Leeuw. 2012. Using patent technology codes to study technological change. *Economics of Innovation and New Technology* 21(3):267–286.
Stubbersfield, Joseph M., Emma G. Flynn, and Jamshid J. Tehrani. 2017. Cognitive evolution and the transmission of popular narratives: a literature review and application to urban legends. *Evolutionary Studies in Imaginative Culture* 1(1):121–135, https://doi.org/10.26613/esic.1.1.20. [BR/EGF/LAW]
Subiaul, Francys, Katherine Winters, Kathryn Krumpak, and Cynthia Core. 2016. Vocal overimitation in preschool-age children. *Journal of Experimental Child Psychology* 141:145–160, https://doi.org/10.1016/j.jecp.2015.08.010. [BR/EGF/LAW]
Tamariz, Mónica, and Simon Kirby. 2015. Culture: copying, compression, and conventionality. *Cognitive Science* 39(1):171–183, https://doi.org/10.1111/cogs.12144. [CAC/ER/DK/KHB/CEHW/MA/SBK/GM]
Tennie, Claudio. 2019*a*. Could non-human great apes also have cultural evolutionary psychology? *Behavioral and Brain Sciences* 42:e184. [CT]

———. 2019*b*. The zone of latent solution (ZLS) account remains the most parsimonious explanation for early stone tools. *Current Anthropology* 60:331–332. [CT]

Tennie, Claudio, Elisa Bandini, Carel P. van Schaik, and Lydia M. Hopper. 2020. The zone of latent solutions and its relevance to understanding ape cultures. *Biology and Philosophy* 35:55. [CT]

Tennie, Claudio, David R. Braun, L. S. Premo, and Shannon P. McPherron. 2016. The island test for cumulative culture in Paleolithic cultures. In *The nature of culture*. Miriam Nöel Haidle, Nicholas J. Conard, and Michael Bolus, eds. Pp. 121–133. Dordrecht, Netherlands: Springer. [AM, CT]

Tennie, Claudio, Christine A. Caldwell, and Lewis Dean. 2018. Culture, cumulative. In *The international encyclopedia of anthropology*. Hilary Callan, ed. New York: John Wiley & Sons.

Tennie, Claudio, Josep Call, and Michael Tomasello. 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B* 364(1528):2405–2415.

Tennie, Claudio, Lydia M. Hopper, and Carel P. van Schaik. 2021. On the origin of cumulative culture: consideration of the role of copying in culture-dependent traits and a reappraisal of the zone of latent solutions hypothesis. In *Chimpanzees in context: a comparative perspective on chimpanzee behavior, cognition, conservation, and welfare*. Stephen Ross and Lydia M. Hopper, eds. Pp. 428–453. Chicago: University of Chicago Press. [CT]

Tennie, Claudio, L. S. Premo, David R. Braun, and Shannon P. McPherron. 2017. Early stone tools and cultural transmission: resetting the null hypothesis. *Current Anthropology* 58(5):652–672. [AM, CT]

Tomasello, Michael, Ann C. Kruger, and Hilary H. Ratner. 1993. Cultural learning. *Behavioral and Brain Sciences* 16(3):495–552.

Tooby, John, and Leda Cosmides. 1992. The psychological foundations of culture. In *The adapted mind*. Jerome H. Barkow, Leda Cosmides, and John Tooby, eds. Pp. 19–136. London: Oxford University Press. [AM]

Vaesen, Krist, and Wybo Houkes. 2017. Complexity and technological evolution: what everybody knows? *Biology and Philosophy* 32(6):1245–1268.

Van Leeuwen, Edwin J. C., Emma Cohen, Emma Collier-Baker, Christian J. Rapold, Marie Schäfer, Sebastian Schütte, and Daniel B. M. Haun. 2018. The development of human social learning across seven societies. *Nature Communications* 9:2076, https://doi.org/10.1038/s41467-018-04468-2. [BR/EGF/LAW]

Van Nierop, O. A., A. C. M. Blankendaal, and C. J. Overbeeke. 1997. The evolution of the bicycle: a dynamic systems approach. *Journal of Design History* 10(3):253–267. [AM]

von Uexküll, Jacob. 1921. *Umwelt und innenwelt der tiere*. 2nd augmented and corrected edition. Berlin: Springer. [MNH/OS]

Vygotsky, Lev S., and Aleksandr R. Luria. 1993. *Studies on the history of behavior: ape, primitive, and child*. Hillsdale, NJ: Lawrence Earlbaum Associates. [MNH/OS]

Wadley, Lyn. 2015. Those marvellous millennia: the Middle Stone Age of southern Africa. *Azania: Archaeological Research in Africa* 50(2):155–226. [PdlP]

Wadley, Lyn, Irene Esteban, Paloma de la Peña, Marine Wojcieszak, Dominic Stratford, Sandra Lennox, Francesco d'Errico, et al. 2020. Fire and grass-bedding construction 200 thousand years ago at Border Cave, South Africa. *Science* 369(6505):863–866. [PdlP]

Wedage, Oshan, Noel Amano, Michelle C. Langley, Katerina Douka, James Blinkhorn, Alison Crowther, Siran Deraniyagala, Nikos Kourampas, Ian Simpson, and Nimal Perera. 2019*a*. Specialized rainforest hunting by *Homo sapiens* ~45,000 years ago. *Nature Communications* 10(1):1–8. [CS]

Wedage, Oshan, Andrea Picin, James Blinkhorn, Katerina Douka, Siran Deraniyagala, Nikos Kourampas, Nimal Perera, Ian Simpson, Nicole Boivin, and Michael Petraglia. 2019*b*. Microliths in the South Asian rainforest ~45-4 ka: new insights from Fa-Hien Lena Cave, Sri Lanka. *PLoS ONE* 14:e0222606. [CS]

Whiten, Andrew, Victoria Horner, and Sarah Marshall-Pescini. 2003. Cultural panthropology. *Evolutionary Anthropology: Issues, News, and Reviews* 12(2): 92–105. [DS]

Wilkins, J., L. Pollarolo, and K. Kuman. 2010. Prepared core reduction at the site of Kudu Koppie in northern South Africa: temporal patterns across the Earlier and Middle Stone Age boundary. *Journal of Archaeological Science* 37(6):1279–1292.

Wilks, Charlotte E. H., Eva Rafetseder, Elizabeth Renner, Mark Atkinson, and Christine A. Caldwell. 2021. Cognitive prerequisites for cumulative culture are context-dependent: children's potential for ratcheting depends on cue longevity. *Journal of Experimental Child Psychology* 204:105031. [CAC/ER/DK/KHB/CEHW/MA/SBK/GM]