Research

Transmission fidelity is the key to the build-up of cumulative culture

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Many animals have socially transmitted behavioural traditions, but human culture appears unique in that it is cumulative, i.e. human cultural traits increase in diversity and complexity over time. It is often suggested that high-fidelity cultural transmission is necessary for cumulative culture to occur through refinement, a process known as 'ratcheting', but this hypothesis has never been formally evaluated. We discuss processes of information transmission and loss of traits from a cognitive viewpoint alongside other cultural processes of *novel invention* (generation of entirely new traits), *modification* (refinement of existing traits) and *combination* (bringing together two established traits to generate a new trait). We develop a simple cultural transmission model that does not assume major evolutionary changes (e.g. in brain architecture) and show that small changes in the fidelity with which information is passed between individuals can lead to cumulative culture. In comparison, modification and combination have a lesser influence on, and novel invention appears unimportant to, the ratcheting process. Our findings support the idea that high-fidelity transmission is the key driver of human cumulative culture, and that progress in cumulative culture depends more on trait combination than novel invention or trait modification.

Keywords: cumulative culture; technology; social learning; innovation; tradition; complexity

1. INTRODUCTION

Humans possess a complex cumulative culture manifest in the presence of knowledge, artefacts and technology, and complex cultural institutions. These traits are not typically produced in a single step, but are produced by small, incremental changes over time, with refinements of existing knowledge and technology, a process known as 'ratcheting' [1]. Culture, or at least simple socially transmitted behavioural traditions are documented in other animals, for example, milk-bottle opening in birds [2,3], sweet potato washing in macaques [4], pine cone stripping in black rats [5] and bird song dialects [6]. Multiple socially transmitted behaviour patterns have been recorded for many primate species, including capuchin monkeys [7] and orangutans [8]. However, besides humans, chimpanzees possess the most documented behavioural traditions, including tool use, grooming and courtship behaviour [9]. Thirty-nine traditions have been identified as habitual or customary in some populations, but absent in others, but with (the authors claim) no obvious ecological explanation for their absence [9].

Claims have been made for cumulative culture in chimpanzees, through their use of multiple tools to accomplish a task (e.g. combining hammers and anvils to crack nuts; [10]), and also in New Caledonian crows (which in some regions manufacture complex stepped tools that may be viewed as an advance on unstepped tools [11]). However, the evidence for cumulative culture in other animals is limited, circumstantial and strongly contested [1,12–14]. For instance, in the chimpanzee and crow examples, it is difficult to rule out the possibility that the more complex tools could have been invented by a single individual anew. Such cases are markedly different from human culture, where, for instance, we possess technology of mind-blowing complexity, that no individual could possibly invent for themselves, and that can have been generated only through the repeated refinement of pre-existing technology over thousands of years. Thus, relative to other animals, the capability for cumulative culture must either be regarded as unique to, or massively enhanced in, humans.

The archaeological record of hominin material culture is currently traced back at least to stone tool manufacture by *Homo habilis* 2.5 Mya, and to the use of flake tools by australopithecines dated to 3.39 Mya [15,16]. This Oldowan (mode 1) technology is thought to have consisted of basic stone flakes, used for butchering carcasses and extracting meat and bone marrow [15]. Even these tools, which are not simple to produce, requiring an understanding of appropriate materials, the appropriate point of impact and angle of strike, and so forth [15], can be viewed as an advance on the use of stone hammers by non-human primates. By 1.8 Mya Acheulian (mode 2) technology, associated with *Homo erectus* or *Homo ergaster*, consisted of hand axes that

were particularly well-suited to butchery of large animals, and also possessed a symmetry, thought possibly to be indicative of an understanding of aesthetics [15,17]. These systematically manufactured tools, which require considerable skill to produce and are an undoubted advance on Oldowan technology, together with the appearance of hominins outside Africa, evidence for systematic hunting, and use of fire, lead many archaeologists to the view that the erectines benefitted strongly from cumulative cultural knowledge [15]. By around 300 kya, in various archaic *Homo* species, there is evidence of wooden spears with grooves possibly for flint flakes [18], possibly fire hardened spears (see Movius [19]) and big game hunting [15]. There is evidence from around the same time of dwellings complete with hearths (see James [20] for a review of fire use by hominids), indicating further examples of the combination of traits in a cumulative fashion. The Mousterian (mode 3) technology, commonly associated with *Homo neanderthalensis* from 200 to 36 kya, but also with early *Homo sapiens* from 160 kya, marks a further advance in lithic technology, with a complex procedure of core preparation, and a variety of tool types manufactured from the same stone [21]. African Middle Stone Age sites, dated (approx. 65–90 kya), provide some of the earliest evidence of abstract art, blade tools, barbed bone harpoon points and marine shell personal ornaments [22]. This era provides further evidence of composite tool use, such as hafting implements from 40 kya [23] and awls (see Hayden [24]) probably used in the production of sewn clothing. Sometime between 35 and 45 kya, there is a change in the archaeological records of our species, associated with more elaborate and standardized tool kits (blades, chisels, scrapers, points, knives, drills, borers, throwing sticks, needles); tools made from antler, ivory, and bone; raw materials transported over long distances; construction of elaborate shelters; creation of art and ornaments, ritualized burials, etc. Further increases in technological complexity appear with the advent of agriculture, and with the industrial revolution [25,26], with human culture continuing relentlessly to grow in intricacy and diversity, culminating in the mind-boggling technological complexity of today's satellites and particle accelerators.

It remains a challenge to explain why this explosion in cultural complexity is present only in humans [13,27,28]. A number of distinct hypotheses have been proposed concerning the cognitive capabilities, or social conditions, thought to be necessary for cumulative culture [29]. These explanations include a hypothesized critical dependency of cumulative culture on teaching, language or imitation [1,12], features of social structure that mitigate against the spread of superior solutions, including scrounging, the tendency of dominants to monopolize resources or a lack of attention to low-status inventors [20–32], and very large social networks that may enhance cultural diversity and promote cumulative culture [33]. Tomasello [1,12,34] has argued that it is the high fidelity with which information is passed between humans, through our use of accurate imitation, language and teaching, that has uniquely led to cultural ratcheting. Galef [13,35], Heyes [14] and Whiten & Erdal [36] put forward related arguments, while Dawkins [37]

emphasizes the importance of fidelity to effective replicators. However, although it is obvious that humans have the cognitive abilities to engage in high-fidelity information transmission and possess a massively complex and cumulative culture, there has been no formal theoretical investigation of whether the hypothesized link between the two is correct.

It has previously been shown, through the use of mathematical models, that high-fidelity cultural transmission can greatly increase both the longevity of cultural traits within a group, and the number of independent cultural traits within a population [38]. Trait longevity increased exponentially with transmission fidelity, such that a small increase in the accuracy with which information was transmitted resulted in a big difference in how long the cultural trait remained in the population, and as a result to far larger numbers of cultural traits in the population. On the basis of these findings, Enquist *et al.* [38] put forward a verbal argument that the increased existence times of accurately transmitted cultural traits could result in more opportunity for modifications or combinations to occur, and thus could lead to the cultural ratcheting described by Tomasello [1,12]. The reasoning is that animals are unlikely to refine cultural traits if the traits do not exist for long, which is frequently the case for non-human traditions, which are probably largely reliant on low-fidelity transmission mechanisms; conversely, long-lasting culture allows such refinement, while lots of cultural traits create the opportunities for cross-fertilization and combination [38]. Enquist *et al.* speculate that improvements in transmission accuracy, afforded by the evolution of high-resolution motor imitation, teaching and scaffolding and/or language and verbal instruction, might plausibly explain the emergence of cumulative culture in our lineage. Consistent with this hypothesis, it has recently been shown that socio-cognitive processes such as teaching, verbal instruction and imitation, enable children to develop cumulative solutions to a sequential problem [29]. An objective of this paper is to determine, through use of simulation, whether this speculative argument is correct.

Given the established positive relationship between transmission fidelity and trait longevity [38], which we expand on in the electronic supplementary material, in this paper, we explore the effects of high-fidelity cultural transmission on cumulative culture by manipulating trait longevity in a simulation model. By systematically changing the rate at which traits are lost from the population, we explore the hypothesis that cognitive changes that result in higher fidelity transmission can lead to cumulative culture such as is found in humans.

Cumulative culture cannot develop through retention of traits alone; other processes besides trait loss potentially affect its evolution. These include the rate at which new traits are invented from scratch (henceforth 'novel invention'), an increase in which has been shown to increase the number of independent cultural traits held by an individual and a population [39]. Also of potential significance is the rate at which established traits are refined or improved (henceforth 'modification') or brought together into complex composites (henceforth 'combination') [40–42]. Novel invention, modification and combination are all forms

of innovation. While cognitive requirements for the different forms of innovation could be very different, innovation rate itself (encompassing all of these) has been used as a naturalistic measure of cognition [43]. Although these processes have been considered separately in models exploring the build-up of numbers of cultural traits [39,40,44–46], or of trait complexity [40], there has been little general consideration of how these processes affect cumulative culture, nor how they interact, nor of their relative importance.

We constructed a simple mathematical model in which we manipulated the rates of novel invention, modification, combination and loss of cultural traits, to explore the primary factors affecting the build-up of cumulative culture. The model assumes that the propensity to engage in particular creative (or transmission) processes may change without massive evolutionary leaps in cognitive architecture. Although we consider cognitive advances that affect the abilities of animals to engage in novel invention, modification, combination and loss of cultural traits, the simple model illustrates the effect on cumulative culture of small changes in the different rates at which these processes occur without having to make specific assumptions about the underlying processes.

2. METHODS

(a) *Fidelity, longevity and trait loss*

A positive exponential relationship between transmission fidelity and longevity of cultural traits was established by Enquist *et al.* [38]. Using a similar set of assumptions, we present a mathematical analysis that leads to this result (see electronic supplementary material). Electronic supplementary material, figure A1*a* shows this result, and figure A1*b* illustrates that the loss rate decreases monotonically with fidelity.

With this in place, we now ignore the underlying individual-level processes of transmission and population dynamics (including population size). Instead, we use loss rate as a proxy for the long-term effects of fidelity. This is equivalent to assuming two time-scales at which processes are acting, a concept that is further explored in Godfrey-Smith [47]. At the shorter time-scale, there are interactions between individuals where information is passed through social learning, and increasingly accurate (high-fidelity) transmission leads to increasing trait longevity, i.e. micro-evolutionary processes (*sensu* Godfrey-Smith [47]). We explore the relationship between loss and cumulative culture, as well as the impact of novel invention, modification and combination, at the longer macro-evolutionary time-scale (*sensu* Godfrey-Smith [47]) through a simulation model.

(b) *The model*

The model considers how traits are gained and lost across the entire population, and how aspects of cultural change affect cultural evolution [40]. We build on the modelling framework developed by Enquist *et al.* [40], which focuses on the cultural traits present in a population, rather than considering the specific traits held by individuals, or individual-level processes. This allows us to look at the cultural development of a population based on general cultural rates, and explore

the complex dependencies between cultural processes, allowing us to go beyond the simple accumulation of a single one-dimensional improvement or of multiple unrefined traits (see [40]).

As a starting point, we assume that there are a fixed number of traits that can appear within a cultural group through novel inventions, independently of any other traits within the culture. We call these novel inventions 'cultural seed-traits' after [40], and for simplicity assume that there are up to 10 of these in a population. It is challenging to determine a realistic value for this parameter, but 10 suffice to allow us to explore the emergence of cumulative culture. Further analyses established that increasing the number of seed traits leads to qualitatively similar results (see electronic supplementary material, figures A11–A21), suggesting that this is not of primary importance.

A brief outline of the simulation model is given here, with full details in the electronic supplementary material. To begin, the cultural group is initialized with two cultural seed traits drawn at random. The next event that takes place can be one of four options. The first possibility is that a new trait from the set of seed traits is acquired by the group through novel invention, which occurs with probability ρ_1. The second possibility is that two of the cultural traits present in the group are combined to produce a new cultural trait, which occurs with probability ρ_2. The third possibility is that one of the traits present in the group is modified or refined in some way to produce a new variant of the trait, which occurs with probability ρ_3. The final possibility is that one of the traits present in the group is lost, which occurs with probability ρ_4.

Once an event has taken place, the culture of the group is updated (augmented with a new trait, or a lost trait removed) and the next event takes place, with the process repeated for 5000 events. A predecessor trait is not necessarily lost from the population and can undergo separate modifications leading to several variants. Cultural traits can thus evolve by modification in both a linear stepwise manner and also through differentiation, where a single trait might give rise to more than one new element [40]. We assume that all traits present in the population can be refined or combined with all other traits present, with the exception that composite traits that have any seed-trait components in common cannot be combined.

We carried out two types of simulation, the first in which the four events were constrained such that $\rho_1 + \rho_2 + \rho_3 + \rho_4 = 1$. In this case, one of these four events must happen at the next time step, which corresponds to the assumption that the time between events is variable. This analysis allowed us to avoid any assumptions about underlying demographic rates (births, deaths, migrations) and to interpret the results in several ways with respect to time. Additionally, this approach is computationally simple and therefore allowed exploration of many parameter sets (see electronic supplementary material, table A1). Loss rate ranged from 0.2 to 0.7 in increments of 0.1; the remaining parameters were varied in increments of 0.1, with no parameter allowed to be zero (as we were particularly interested in how the processes interact and not in the effects of major evolutionary changes that bring forth

Table 1. Definitions of properties of culture.

property	description
trait	any seed trait, combination of seed traits, modification of a seed trait or modification of a combination of seed traits
trait complexity	the number of steps required to produce the trait (number of seed traits it contains + number of modifications it contains)
lineage	any group of traits made up of the same seed traits (irrespective of modifications)
lineage complexity	the number of seed traits required to make up a lineage

the processes). For each parameter set, 10 independent replicate cultural groups were simulated. In the second set of simulations, rates varied independently, allowing additional analysis of parameter interactions, but the approach was more computationally expensive and so was limited to exploring more course parameter space. As the results of the second approach broadly agreed with our first, further details and results are given in the electronic supplementary material for completeness, and only the simpler case is presented in the main text.

(c) *Trait utility*
We assume that each cultural seed has a utility representing its usefulness to the user. We further assume that the probability that a particular trait is lost is inversely proportional to the trait's utility relative to the utilities of the other traits present. On average, less-useful traits will be lost before more-useful traits. This assumption is consistent with the application of learning biases, such as a tendency for individuals to copy the most successful individuals, or to copy in proportion to the demonstrator's payoff [41,48,49], for which there is considerable empirical evidence in both humans and other animals [50–53]. Godfrey-Smith [47] discusses models that make similar assumptions about the lifetime of cultural variants ('differential mortality'), as well as 'differential fertility' in cultural traits.

Here, cultural seed traits were initialized with utilities drawn from a random uniform distribution (from 0.75 to 1). The utility of a new trait formed by combination of traits was determined by adding some small random amount (normally distributed with mean zero and s.d. of 0.1) to the largest of the utilities of the two traits. Combination traits were therefore close in utility to the 'best' trait from which they were made up, but with slightly better or worse utility. The utility of new traits produced by a refinement was that of the trait chosen for modification plus some random noise (distributed as before); therefore modifications did not always represent improvements. Utilities of traits were not bounded as utilities have no absolute meaning, but give a measure of relative usefulness. Later, we show that successive improvements lead to utilities well above unity.

(d) *Measures of cumulative culture*
We propose several measures of cumulative culture (definitions given in table 1): number of traits, mean trait complexity, number of lineages, mean lineage complexity, maximum lineage complexity, mean number of seed traits in each trait, mean number of modifications in each trait and mean, minimum and

maximum utility. Together, these complexity and utility measures enable us to describe the cumulative nature of the cultures (see [54]), which we distinguish from the build-up of a large number of simple traits. We measured all properties after each event throughout the simulations. To obtain a single representative value for each replicate cultural group, we measured the average (mean) value of each property over the final 1000 events. We also measured the maximum and minimum number of traits and lineages over the final 1000 events. Finally, a principal component analysis (PCA) was carried out on the measured time-averaged properties of the cultural groups. This allowed us to extract a single composite measure of the cumulative nature of the cultural groups from the many measured properties

3. RESULTS
(a) *Principal component analysis*
We consider the first principal component (PC1), which explained 67.3 per cent of the variance in the data and which was significantly positively correlated with all properties except minimum utility, with which it was significantly negatively correlated (see electronic supplementary material, table A2; figure 1). Overall, a high PC1 value indicates a more complex cumulative culture with more traits, more lineages, more complex traits and lineages, with some very high-utility traits present and a high average trait utility.

A linear regression of PC1 against each rate was carried out separately (owing to non-independence of rate parameters). For novel-invention rate (ρ_1), the regression had a coefficient of -0.17 (not significant, $p = 0.6$). For combination rate (ρ_2), the regression had a coefficient of 4.3 ($p < 0.001$, $r^2 = 0.3$). For modification rate (ρ_3), the regression had a coefficient of 2.6 ($p < 0.001$, $r^2 = 0.1$), but the relationship is unlikely to be linear (figure 1). Finally, for loss rate (ρ_4), the regression had a coefficient of -6.7 ($p < 0.001$, $r^2 = 0.75$). (d.f. $= 559$, leading to small p-values for the significant regressions.) These analyses suggest that loss is likely to be the most important factor affecting cumulative culture, and novel invention the least important factor, a finding confirmed by the second analysis in which the parameter rates are varied independently.

(i) *The effects of novel invention, combination, modification and loss*
These patterns are repeated when we consider each measure separately. The distributions of several component measures of cumulative culture are shown in figures 2 and 3 for increasing values of the rates ρ_1
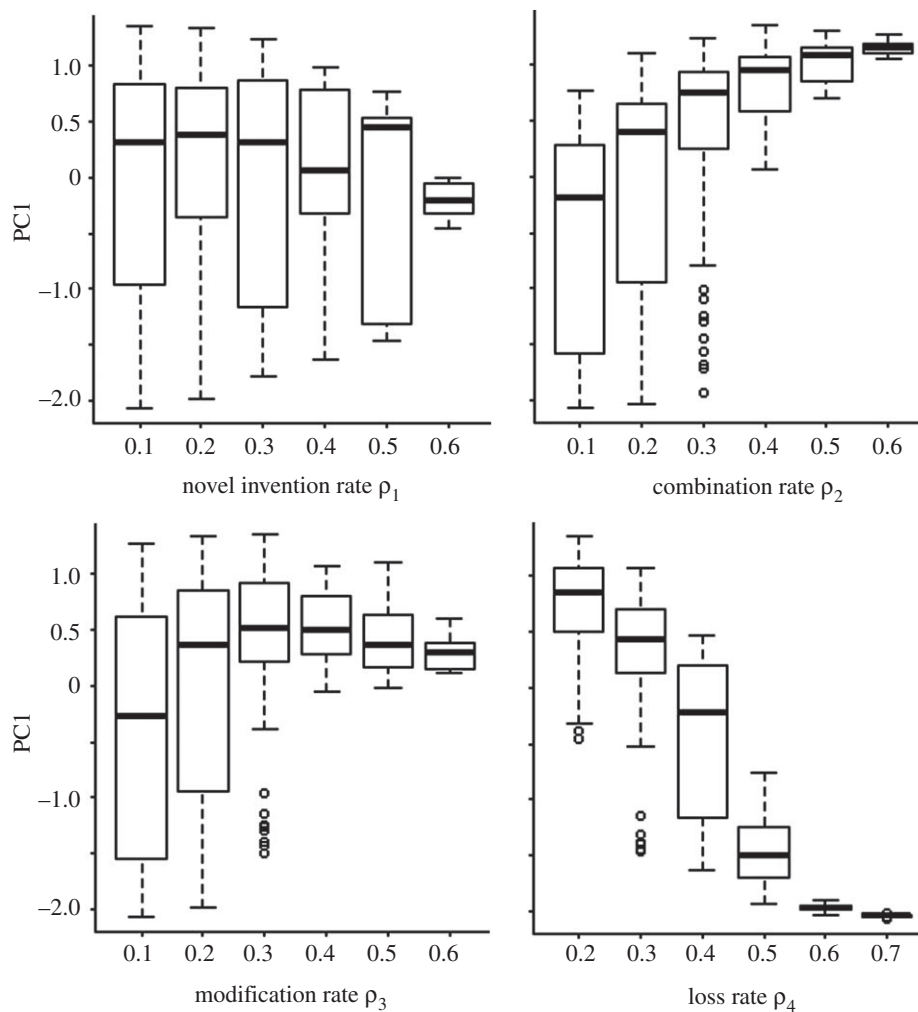
Figure 1. The distributions of PC1 scores for increasing values of the rate parameters of the model. Data are pooled across all values of the other parameters. Each parameter combination was simulated 10 times, resulting in different numbers of replicates per individual parameter value (see electronic supplementary material, table A1).

to ρ_4. For loss rates greater than 0.5, some measures fall below unity, indicating periods when there is no socially transmitted culture.

(ii) *Build-up of culture through time*
In electronic supplementary material, figures A2–A10 (and A13–A21 for 20 seed traits), the progression of cultures is plotted against the number of events that have occurred as a proxy for time. The number of events need not map linearly to time. If instead the number of events per unit time increases with the number of traits (e.g. because there are more traits to lose or from which to create new traits [40]), then a simple mapping of number of events to time can lead to an exponential increase in the number of traits (figure 4*b*), or an asymptotic increase (figure 4*a*) depending upon the parameters even when culture is cumulative (i.e. when loss rate is less than 0.5). (Mapping: number of events occurring in time t to $t + \Delta t$ is given by the number of traits at time t divided by some constant, taken to be 4 for illustration, and multiplied by Δt.)

4. DISCUSSION
Our results are quite clear in establishing an important role for the fidelity of social transmission

in the development of cumulative culture, supporting the argument that cognitive mechanisms (for instance, teaching, language, imitation) that make high-fidelity cultural transmission possible may be necessary for cumulative culture [1,12,29,33]. It had previously been shown [38], and we have confirmed (see electronic supplementary material, figure A1), that increasing the fidelity of cultural transmission leads to exponential growth in trait longevity, and how this translates into reduced trait loss. Our study also supports the argument that large population sizes facilitate cumulative knowledge gain [33]: as populations get larger, for example in Enquist *et al.* [38], we see an increasingly rapid growth in trait longevity with increasing fidelity, and a corresponding reduction in the probability of trait loss. However, no previous study had compared the relative importance of trait loss, novel invention, modification and combination with cumulative culture. Our study establishes that the trait loss rate (our proxy for fidelity) is by far the most important factor affecting cumulative culture.

The results of our simulation model strongly imply that transmission fidelity is the key factor affecting the appearance of cumulative culture. It is only when the trait loss rate is at or less than 0.5 that cumulative culture can develop, implying that there may be a
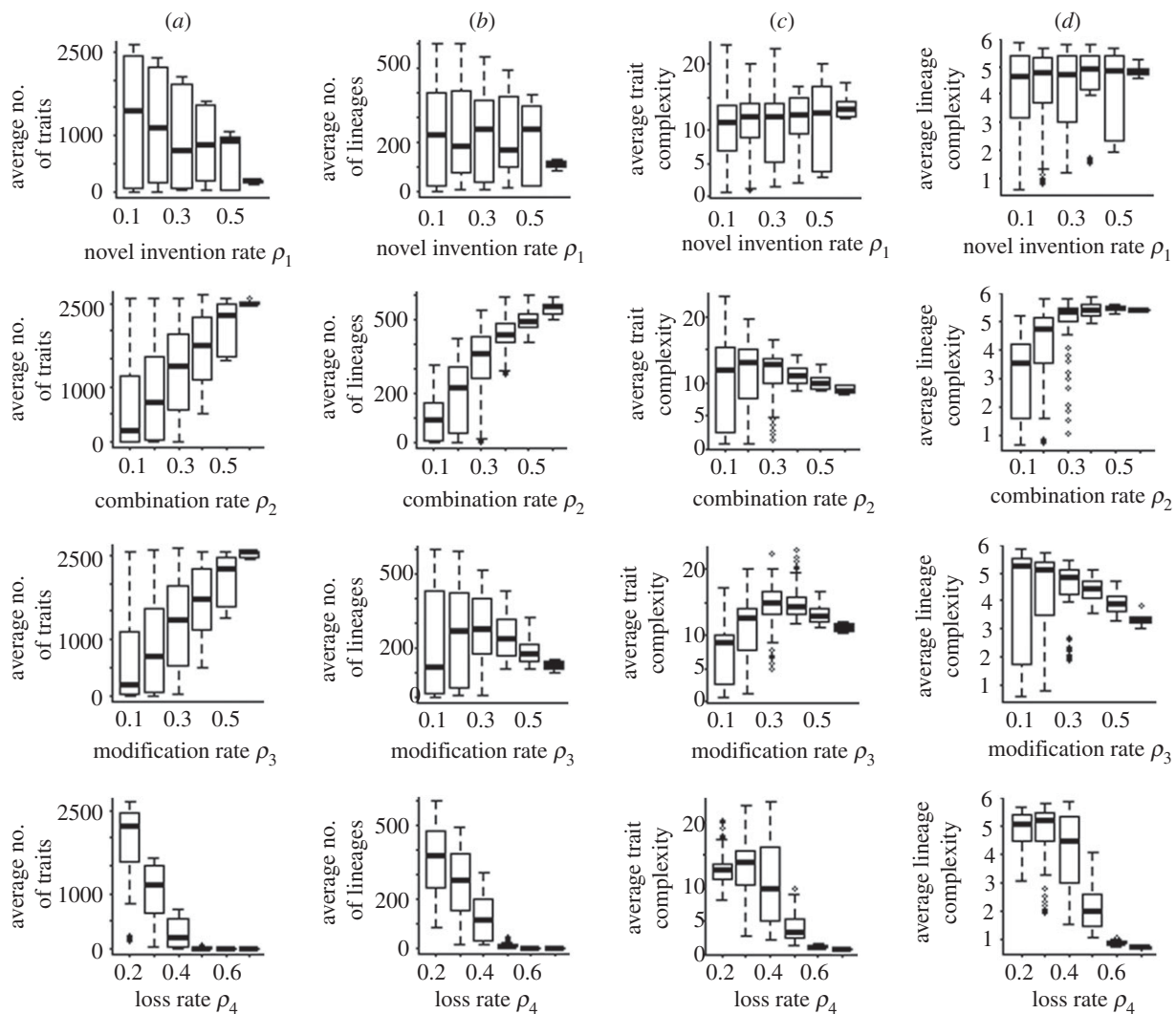
Figure 2. The distributions of the time-averaged: (*a*) number of cultural traits within the population, (*b*) number of lineages within the population, (*c*) mean trait complexity and (*d*) mean lineage complexity. Time averages (means) calculated for each cultural group across the final 1000 events.

minimum threshold level of transmission fidelity necessary for cumulative knowledge gain. At 0.5, cumulative culture is possible to some limited extent, but there is a large jump in the cumulative nature of the culture (as represented by utility, complexity and number of traits and lineages) as the loss rate is reduced to 0.4 (figures 1 and 2). As loss rate is decreased further, it seemingly becomes impossible for cumulative culture *not* to develop (figures 1 and 2) provided that some level of combination and/or modification is possible. We also found that loss rate has the largest coefficient of the individual regressions relating the various cultural rates to the measure of cumulative culture (extracted by PCA). In the individual regression, loss rate explains 75 per cent of the variance in this measure, compared with 30 per cent explained by combination when considered independently, and less for the other processes.

The earlier-mentioned findings draw from the constrained analysis, where we consider the relative loss rate relative to the other, creative processes. In this analysis, the three other (creative) processes occur with probability $1 - \rho_4$; so it might be argued that the cumulative nature of the culture could equally be due to an increase in overall creativity. However, the results of the simulations where the parameters were allowed to vary independently (see electronic supplementary material) confirm that loss rate is genuinely the most important of the rates rather than an artefact. The four strongest effects in a linear regression analysis of the rates against a measure of cumulative culture were all either interactions that included loss rate or the loss rate alone. Thus, the independent parameter simulations strongly support our finding that loss rate is the most important factor in determining the cumulative nature of culture.

These observations support the argument, made most forcefully by Tomasello [1,12,33], that the apparent absence of cumulative culture in other species results directly from their reliance on low-fidelity copying mechanisms (e.g. local enhancement) rather than the high-fidelity processes observed in humans (e.g. teaching, verbal instruction, accurate imitation). Teaching is rare in other animals, and is restricted to single traits rather than applied broadly across multiple tasks and domains, as in humans [55]. Not only do other animals not possess language, but cases where communication is also applied to enhance the fidelity of information transmission (e.g. through signalling, or
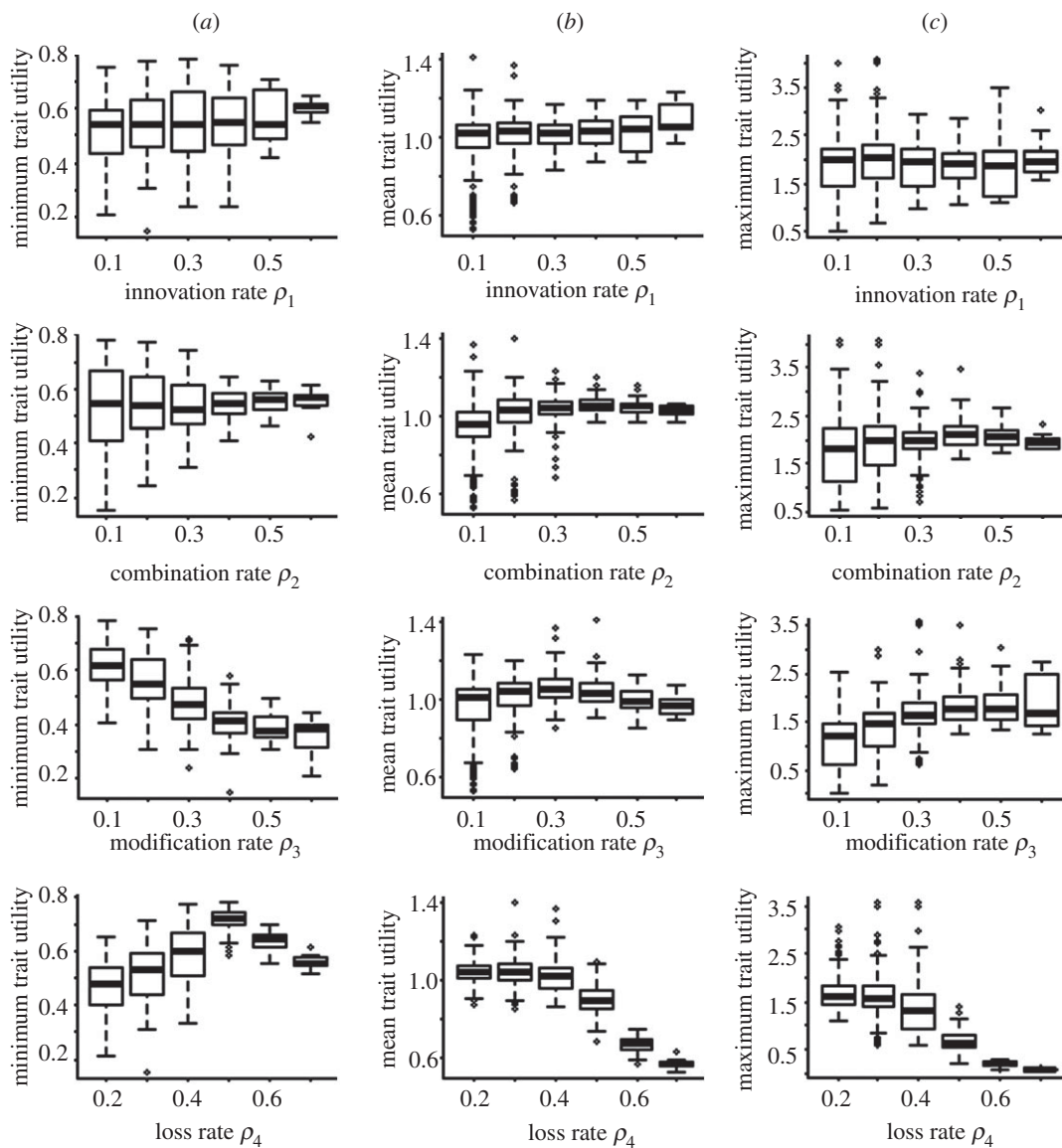
Figure 3. The distribution of the time-averaged: (*a*) minimum trait utility, (*b*) mean trait utility and (*c*) maximum trait utility. Time averages (means) calculated for each cultural group across the final 1000 events.

referential communication) are seemingly very infrequent [56]. Finally, while evidence for both contextual and production imitation has been reported in chimpanzees and some birds [57–59], comparative studies imply that imitation is quicker, more accurate and more complete in humans compared with other animals [60,61]. If it is indeed the case that other animals typically copy with low-fidelity, then the learning mechanisms that they deploy will not be capable of supporting cumulative culture. Consistent with this reasoning, a recent study [29] has shown that the achievement of higher levels in a sequential problem-solving task was associated with socio-cognitive processes, including verbal instruction and imitation, in human children but not chimpanzees or capuchin monkeys. We note that there currently exist no data specifying transmission fidelity for different social-learning mechanisms, nor estimating typical rates of social transmission fidelity in different species.

Assuming a low loss rate, the exact nature of the culture that develops is highly dependent on the relative rates of the other processes. This is clear from the large spread of values for all properties, the PC1 scores of the cultures generated with low loss rates (figures 1 and 2), and the exponential increase in culture for some parameter combinations but not others (figure 4). An exponential increase in culture (number of traits and complexity) is often observed in humans (reviewed in [54]) and this has previously been explained by allowing the rate of creativity (rate at which new traits are created in time) to increase as the number of traits increases [54]. However, our results establish that the type of creativity is critically important, and that some forms of creativity, such as high levels of novel invention relative to combination and modification, generate an asymptote in both complexity and number of traits, rather than the exponential increase seen when combination and modification rates are comparatively high (figure 4).

In terms of the creative processes, we found that relative combination rate had the greatest effect, and novel invention the least effect, on cumulative culture. Considered alone, combination explains 30 per cent of the variance in the PCA that describes the cumulative
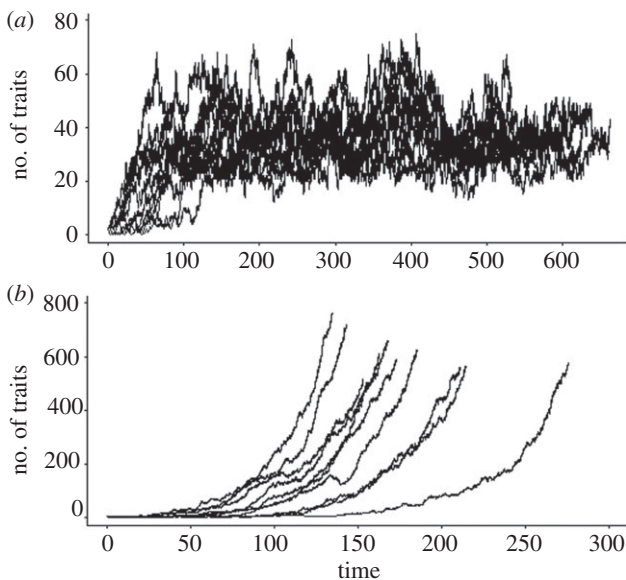
Figure 4. Growth in the number of traits for parameters (*a*) $\rho_1 = 0.3$, $\rho_2 = 0.1$, $\rho_3 = 0.2$, $\rho_4 = 0.4$, (*b*) $\rho_1 = 0.1$, $\rho_2 = 0.2$, $\rho_3 = 0.3$, $\rho_4 = 0.4$, with time rescaled to reflect increasing number of events with an increasing number of traits. Ten independent replicate cultural groups are shown.

nature of the culture, with novel invention having a non-significant effect, both of which are supported by considering the individual properties shown in figure 2. These observations are consistent with the argument that trait combination is a, indeed probably *the*, major source of human innovation [62], and imply that progress in cumulative culture is more reliant on combination than on either novel invention or modification. The finding that novel invention turns out not to be so important is consistent with studies of human innovation, which find that innovation or discovery is often the result of chance, combination and incremental refinement rather than 'genius' [63]. Indeed, scholars of the history of technology criticize the 'myth of the heroic inventor' [64], a 'myth' that in our terms would attribute progress in cumulative culture to novel invention.

We provide two words of caution to these findings. Firstly, when allowing the cultural rates to vary independently, the interaction between modification and combination has a greater effect on the cumulative nature of the culture than either rate alone, suggesting that it is the relative size of these processes that is important. This is further shown in figure 2, where the trade-off between modification and combination (in the main constrained simulations) results in a nonlinear relationship between average trait complexity and both of these rates. At high combination rate, one would expect more complex traits; however, in the constrained model this would correspond to low modification, which intuitively would lead to low trait complexity. Hence, the most complex traits occur at intermediate levels of these two rates. This highlights that for fixed rates of loss and novel invention, knowing either modification rate or combination rate without the other does not provide enough information to predict the nature of the culture that would develop. Also, in the independent analysis, modification rate has a larger

effect than combination rate on the cumulative nature of the culture. Secondly, our model does not allow complex, high-utility traits to be created from scratch, and therefore a 'heroic inventor' would not be possible. However, there is little empirical evidence that complex novel traits are created from scratch [64]. In sum, the analysis gives us little grounds for thinking that novel invention plays a central role in cumulative culture.

Our model allocates utilities to traits, which is a reflection of how useful or efficient they are. We assumed that (on average) less-useful traits were lost before more-useful traits, which to some degree filters maladaptive traits (those with low utilities) from the evolving cultures. This assumption is justified in the light of experimental evidence that humans, like other animals, have evolved psychological mechanisms, or forms of plasticity, that facilitate the preferential copying of successful individuals [41,48,50,65,66]. However, in spite of this bias, for some parameter combinations, we witness very low utilities among the least useful traits present (figure 3). This occurs at high loss rates owing to there being very few traits present in the culture; in fact there are often no traits, and therefore zero utility that reduces the mean. At high modification rates, but low loss rates, new modifications of traits are created often but are rarely lost, which generates diverse but low utility culture with no 'best approach' to anything being adopted by the population. Hence, at the low loss rates that would result from high-fidelity copying, a high modification rate could lead to maladaptive (low relative utility) traits being present within a culture. Interestingly, maladaptive cultural traits, which may become embedded in cumulative culture, are frequently observed in humans, often with devastating effects (reviewed in earlier studies [67,68]). Note, we do not suppose that the modification process is the driver behind the presence of maladaptive traits; rather it is the lack of loss of the traits that offers a mechanistic explanation.

Godfrey-Smith [47] notes that humans may employ intelligent copying where combinations and modifications are made during the copying procedure, resulting in less-useful traits being continuously abandoned. He goes on to suggest that too much intelligent copying could prevent the build-up of lineages of traits. Although this process confounds two or three of the processes in our model, our results agree with this to some extent, but we note that very high loss rates are required for this failure of cumulative culture to occur. (Other suggestions as to why cumulative culture sometimes does not occur are based on social structure: for instance, small population size [30–33]). In fact, the results of our model reveal that modification can buffer against loss: the number of lineages can increase with the modification rate and actually decrease with increases in the novel-invention rate (see electronic supplementary material: figure A5*a,e,h,j* corresponds to a single (intermediate) loss rate and a single combination rate). This is initially surprising because modification does not create lineages, whereas novel invention does (to the extent of introducing a new seed trait to the culture). However, the process of modification creates multiple copies (although modifications) of the same trait within a lineage. Multiple versions of the traits

within the lineages means that, at intermediate rates of loss, the loss of a trait is unlikely to result in the complete loss of a lineage. Conversely, to the extent that an increase in the rate of novel invention corresponds to a decrease in the relative modification rate, it can have a negative influence on the number of lineages.

5. CONCLUSIONS

Our simple model has shown that the loss rate and the relative rates of the different creative processes strongly affect whether cumulative culture can occur, as well as its richness and diversity. Cultural traits have to exist for long enough within the population for modifications to occur and to be combined with other traits in order for cumulative culture to develop, and that disproportionately large gains in trait longevity can occur if traits are passed more faithfully between individuals (see electronic supplementary material, figure A1 and [38]). This strongly supports Tomasello's argument that transmission fidelity is the key to cumulative culture, and that humans alone, through their language, teaching and imitation, possess the highly accurate transmission mechanisms necessary for extensive cumulative culture to develop [1,12]. A massive leap in the cumulative nature of the culture can occur once the rate of trait loss relative to the other processes falls below a critical threshold. Assuming that other processes are held equal, a change in the cognitive capabilities of a species that leads to increased transmission fidelity, would in turn lead to an increase in the length of time that traits exist within the culture of a population, corresponding to a decrease in the rate of trait loss, thereby creating conditions under which cumulative culture can emerge. Thus, without making specific assumptions about changes in cognitive or behavioural processes, we have shown that modest increases in the fidelity of transmission of cultural traits between individuals can lead to the development of cumulative culture.

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