From cultural traditions to cumulative culture: parameterizing the differences between human and nonhuman culture

Marius Kempe [a], Stephen J. Lycett [b], Alex Mesoudi [a,*]

[a] Department of Anthropology and Centre for the Coevolution of Biology and Culture, Durham University, Dawson Building, South Road, Durham DH1 3LE, UK
[b] Department of Anthropology, University at Buffalo, SUNY, 380 MFAC-Ellicott Complex, New York 4261-0005, USA

HIGHLIGHTS

- Many species show cultural traditions, group-specific socially-learned behaviours.
- Only humans have cumulative culture, where traits are modified over generations.
- We construct and analyse models of both cultural traditions and cumulative culture.
- Cultural traditions emerge under a range of parameters, explaining their prevalence.
- Cumulative culture requires accurate social learning and multiple demonstrators.

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ABSTRACT

Diverse species exhibit cultural traditions, i.e. population-specific profiles of socially learned traits, from songbird dialects to primate tool-use behaviours. However, only humans appear to possess cumulative culture, in which cultural traits increase in complexity over successive generations. Theoretically, it is currently unclear what factors give rise to these phenomena, and consequently why cultural traditions are found in several species but cumulative culture in only one. Here, we address this by constructing and analysing cultural evolutionary models of both phenomena that replicate empirically attestable levels of cultural variation and complexity in chimpanzees and humans. In our model of cultural traditions (Model 1), we find that realistic cultural variation between populations can be maintained even when individuals in different populations invent the same traits and migration between populations is frequent, and under a range of levels of social learning accuracy. This lends support to claims that putative cultural traditions are indeed cultural (rather than genetic) in origin, and suggests that cultural traditions should be widespread in species capable of social learning. Our model of cumulative culture (Model 2) indicates that both the accuracy of social learning and the number of cultural demonstrators interact to determine the complexity of a trait that can be maintained in a population. Combining these models (Model 3) creates two qualitatively distinct regimes in which there are either a few, simple traits, or many, complex traits. We suggest that these regimes correspond to nonhuman and human cultures, respectively. The rarity of cumulative culture in nature may result from this interaction between social learning accuracy and number of demonstrators.

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1. Introduction

Many animal species exhibit *social learning*, i.e. the acquisition of information from conspecifics through learning (Galef and Laland, 2005); examples include the transmission of food preferences in rats (Laland and Plotkin, 1990), shoaling routes and nest site locations in fish (Helfman and Schultz, 1984), and foraging locations in bees and ants (Leadbeater and Chittka, 2007). Some of these species show cultural differences in the 'trait-profiles' of different populations, termed *cultural traditions* (Fragaszy and Perry, 2003). Examples include differences in the song dialects of different bird populations (Catchpole and Slater, 1995) and in the presence or absence of various tool-use and gestural behaviours in different populations of chimpanzees (Lycett et al., 2007; Whiten et al., 1999), orangutans (van Schaik et al., 2003) and capuchins (Perry et al., 2003). Humans, however, as well as exhibiting social learning and cultural traditions, appear to be the only species to unambiguously also have *cumulative culture*, where cultural traits are preserved and modified over successive generations resulting in a 'ratcheting up' of the complexity or efficiency of those traits

(Boyd and Richerson, 1996; Dean et al., 2013; Enquist et al., 2011; Tomasello, 1999). A common criterion for cumulative culture is that cultural traits become too complex for a single individual to invent in their lifetime. Whereas this does not appear to apply to any non-human cultural traits, such as chimpanzee nut-cracking, birdsong dialects or fish shoaling routes (although for possible reports in chimpanzees see Boesch et al., 2009; Sanz et al., 2010), such traits are commonplace in human cultural endeavours such as technology, science, and mathematics (Basalla, 1988; May, 1966; Oswalt, 1976; Price, 1963; Wilder, 1968). It is highly unlikely that string theory, smartphones and space travel, for example, lie within the inventive capacities of a single individual. Even so-called 'simple' early human technologies, such as certain types of stone tools, show evidence of having accumulated in complexity over multiple generations (Lycett and von Cramon-Taubadel, 2013; Roche, 2005; Simão, 2002). This cumulative culture, it is argued, has been instrumental in allowing our species to invade and inhabit virtually every terrestrial environment on the planet, while our closest primate relatives remain highly restricted in range and number (Boyd et al., 2011; Hill et al., 2009).

Our aim here is to construct simple models to identify the potential factors responsible for both the emergence and mainte-nance of cultural traditions, and for the shift from cultural traditions to cumulative culture that appears to be a hallmark of our species. Models are particularly useful here given the difficulty of directly studying such phenomena. Comparative studies have begun to address the underlying cognitive abilities that allow humans and other great ape species to solve simple cumulative-like tasks (Dean et al., 2012). However, comparative studies are limited because (i) only a single extant species (Homo sapiens) has cumulative culture, thus providing limited data points to test causal hypotheses, and (ii) the acquisition of cumulative cultural traits in humans typically takes many years and is thus not amenable to experimental investigation. Archaeological evidence can be used to indicate the emergence of cumulative culture in the Homo lineage (d'Errico and Stringer, 2011; Roche, 2005). However, the archaeological record provides only indirect evidence of the cognitive or demographic changes that might be associated with these phenomena.

Previous models have examined either the evolutionary origin of social learning (Aoki et al., 2005; Boyd and Richerson, 1985; Enquist et al., 2007; Rogers, 1988), or the number of independent (non-cumulative) traits in a single population (Enquist et al., 2010; Lehmann et al., 2011; Strimling et al., 2009), or the dynamics of cumulative culture in a single population (Mesoudi, 2011; Pradhan et al., 2012) or at a macroscopic level that does not permit the study of demographic factors such as population size or migration (Enquist et al., 2011; Lewis and Laland, 2012). While all of these models have generated useful inferences about cultural dynamics, none have directly addressed the emergence and maintenance of between-group cultural traditions, which requires the simulation of multiple populations, and none have sought to explain the transi-tion from non-cumulative traditions to cumulative culture. Here we attempt to fill this gap by first modelling cultural traditions and explicitly comparing our model output to empirical data on non-human primate traditions. We then present a model of cumulative culture that builds on previous individual-based models of non-cumulative culture. Finally, we combine these models, finding that the emergence of cumulative culture most likely occurred through the interaction of the accuracy of social learning and the number of demonstrators from whom individuals copy.

2. Model 1: Cultural traditions

We take as our starting point a model constructed by Strimling et al. (2009), in which independent (i.e. non-cumulative) cultural traits are acquired by individuals in a single population. To this we add multiple populations and migration between those popula-tions, in order to permit the emergence of between-population cultural traditions. In their model, Strimling et al. showed how the number of different traits found in the population and the number of traits known by each individual increased as a function of population size, individuals' social learning accuracy, and indivi-duals' innovativeness. We are therefore interested in whether, and if so how, cultural traditions are also shaped by these factors, in addition to the novel factor of migration. As in Strimling et al.'s original model, we make several simplifying assumptions, such as that cultural traits have identical cultural fitness and have no effect on biological fitness, and that individuals do not vary in their social learning accuracy or innovativeness. While these assump-tions are most likely unrealistic and deserve scrutiny in future research, these tactical simplifications allow us to focus on the aforementioned key factors that have been the subject of previous research (population size, social learning accuracy and individual innovativeness) in this new multi-group context.

Strimling et al.'s (2009) model contains three stages. First, one of the N individuals in the population is picked at random, dies, and is replaced by a naive individual. Second, the naive individual picks one other individual at random and independently learns every trait that individual knows with probability a per trait (where $0 < a < 1$). Third, the individual invents a random number of new traits with expectation μ. (Note that social learning and innovation are therefore modelled as separate processes; for simplicity, Strimling et al. assumed that social learning cannot itself give rise to new traits through inferential copying errors.) To this we add a fourth stage, in which the individual migrates to another population with probability $m/2$ (where $0 \leq m \leq 2$). There are p such populations in the metapopulation, and the individual is equally likely to migrate to any of the $p-1$ other populations. When the individual migrates, it swaps population memberships with a randomly chosen member of its target population, so that the size of each population remains constant. Because each migration event involves two individuals and the target popula-tion is picked at random, the expected number of individuals who migrate away from any given population in one timestep is $(m/2)+(m/2)(p-1)/(p-1)=m$; this is why m is halved above.

In order to model multiple populations of such learners, we must also decide which traits individuals invent. Strimling et al. (2009) do not specify this, assuming only that individuals always invent traits that are currently unknown in the population. Lehmann et al. (2011), using a similar model, assume that there are a very large number of traits, tending towards infinity, and individuals invent a random trait chosen from this set. This strikes us as unrealistic, particularly for foraging or gestural behaviours that are constrained by the affordances of the objects and food types found in a species' habitat, and motor constraints on the possible gestures or calls that can be produced. Thus, we assume instead that there are infinitely many traits which are invented in a fixed sequence that is the same in all populations. We use the simplest possible sequence, in which traits are labelled by the natural numbers and invented in the order 1, 2, 3, etc. Individuals always invent the first trait in the sequence that is not currently known by any individual in their population. For example, if traits 1, 2, 4 and 5 are present in the population, then a naïve individual will first invent trait 3, rather than trait 6. This represents an idealized situation in which individuals' physical and cognitive predispositions and the nature of their physical and social envir-onments create a clear ranking in the "obviousness" of traits; for example, tool techniques for foraging easily-visible food resources may be invented before techniques for foraging hard-to-find foods, and foraging technologies in general may be invented before social or symbolic behaviours that are less important for survival. While
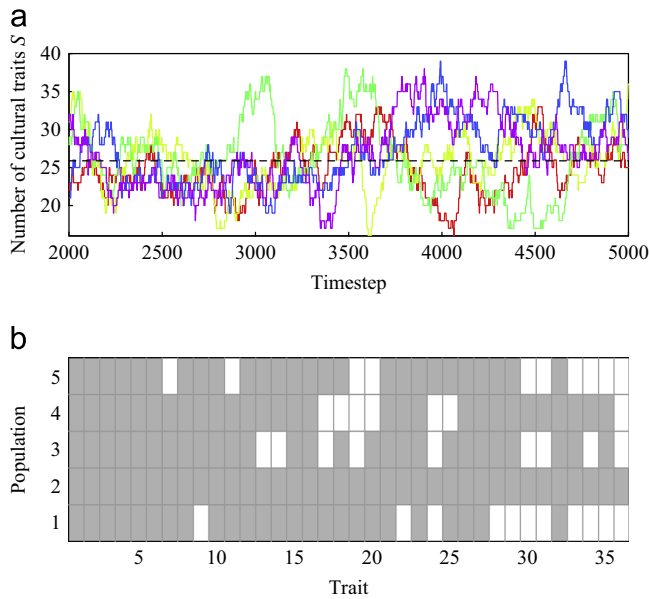
Fig. 1. One simulation of the cultural differences model. (a) Time series of the number of traits S known in each population. The initial part of the simulation is not shown. The dashed line shows the exact expected value derived by Strimling et al. (2009), Eq. (3). (b) Trait-profiles of each population at the end of the simulation, with grey cells marking the presence of a given trait in a given population and white cells marking its absence. The average similarity $\bar{s}$ between the populations is 0.71. Parameter values: $N=100$, $a=0.9$, $\mu=0.1$, $m=0$, $p=5$.

this situation is clearly idealized, it is more realistic than assuming random draws from a large set of traits, and it is simple enough to analyse. Note that, as in Strimling et al. and Lehmann et al.'s models, these traits are not cumulative; later traits do not build on earlier traits, and an individual can socially learn any set of traits irrespective of the traits' position in the sequence. A trait may also be lost from the population and later re-invented without affecting any other traits.

Fig. 1 shows the time course and end result of one simulation of the model, at this point with no migration (i.e. $m=0$). In this and all subsequent simulations we ran the model until the values of the various measurements (e.g. number of traits) had clearly reached a stable value and were performing random walks around that value. Fig. 1(a) shows that the number of different traits known in each population, called S by Strimling et al., hovers around the expected value they derived in their Equation 3, providing a replication of their model and confirming the validity of ours. Fig. 1(b) shows the trait-profiles present in each population at the end of the simulation. Intuitively, one expects that if all populations invent the same traits in the same order, different populations will have identical trait profiles. However, the trait-profiles in Fig. 1(b) clearly show variation between populations. To quantify this variation we define s, the cultural similarity between two populations, in the same way as Enquist et al. (2011) $s = (|X \cap Y|)/(|X \cup Y|)$, where X is the set of traits known in the first population and Y is the set known in the second. Thus, s is the proportion of all traits known in either population that are known in both populations. To compare more than two populations we define $\bar{s}$ as the mean similarity between every possible combination of populations in a metapopulation.

Fig. 2 shows how the mean similarity between populations $\bar{s}$ increases with population size N (in a decelerating fashion) and accuracy of social learning a (in an accelerating fashion). Fig. 2 (c) shows how $\bar{s}$ varies across the parameter space created by N and a, demonstrating that no realistic parameter values generate complete inter-population homogeneity. The reason that the assumption of a fixed sequence of traits does not lead to complete
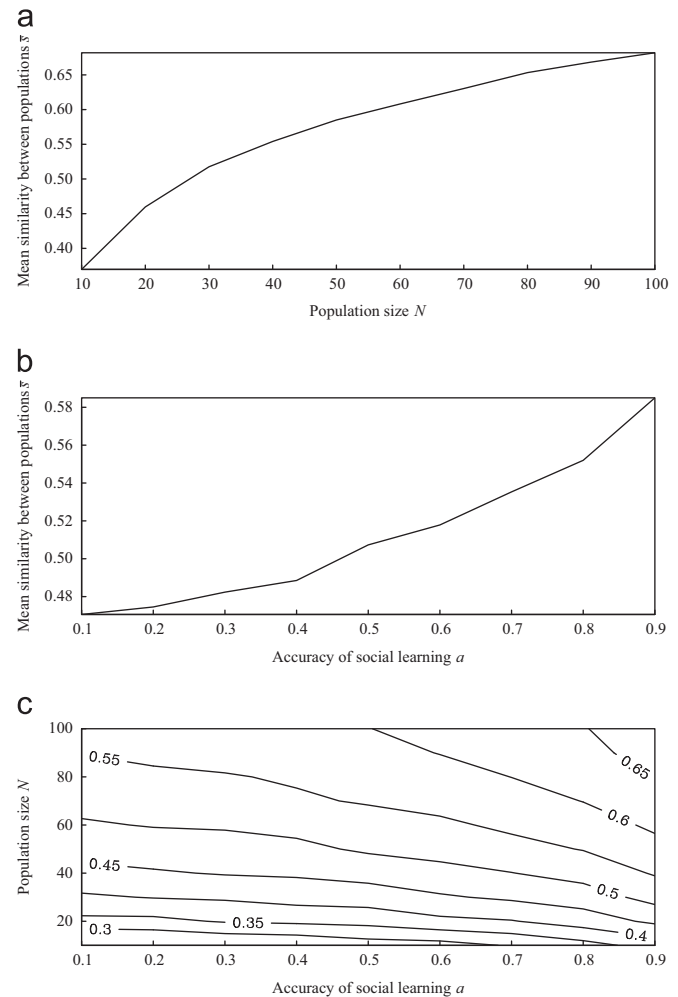

Fig. 2. The effect of (a) the population size N, (b) the accuracy of social learning a, and (c) both, on the mean similarity between populations $\bar{s}$. Panel (c) shows the value of $\bar{s}$ on a contour plot in an analogous way to a geographical map showing the height of a mountain at various points in space. All panels show the value found after 2000 timesteps, averaged over 1500 simulations with parameter values $\mu=0.1$, $p=5$, and $m=0$; in (a) $a=0.9$ and in (b) $N=50$.

inter-population homogeneity is trait loss due to imperfect social learning. We show in the Appendix that in the absence of migration, the probability that a trait will spread beyond its inventor is $(a)/(1+a)$. Since a must be less than 1, this probability is always less than 1/2. In other words, most newly invented traits die out with their inventor, even with high fidelity cultural transmission. This feature of the model accords reasonably with evidence on chimpanzee (*P. t. schweinfurhii*) inventions documented at Mahale, Tanzania, where approximately 43% of innovations documented over a 30-year period did not spread (Nishida et al., 2009). In the model, this frequent loss of traits is balanced by the re-invention of traits that have been lost, and this dynamic creates the moderate (and realistic) dissimilarity between population trait-profiles.

We now analyse the effects of migration. Fig. 3 shows how the mean number of different traits known in a population $\bar{S}$ and the mean similarity between populations $\bar{s}$ both increase with m. We show values from simulations with m ranging from 0 (no migration) to 0.5 (half of all individuals migrate); the latter may be realistic in both chimpanzees, where one sex typically disperses (Hiraiwa-Hasegawa et al., 1984), and humans, where there is frequent migration of both sexes (Hill et al., 2011). As expected, migration makes populations more similar in their trait-profiles,

but even frequent migration does not completely homogenize them. Migration also increases the total number of traits known, because migrants can bring traits that have not been invented in the target population; this resembles the beneficial effect of migration on accumulation found by Powell et al. (2009), but not as pronounced. A possible empirical example of this is the introduction of ant-fishing into the Kasekela chimpanzee (*P. t. schweinfurthii*) community by a female immigrant from the Mitumba community at Gombe, Tanzania (O'Malley et al., 2012).

To compare the results shown in Fig. 3(b) with empirical data, we calculated the values of $\bar{s}$ from data reported on chimpanzees (*Pan troglodytes*) (Whiten et al., 1999) and orangutans (*Pongo*

pygmaeus) (van Schaik et al., 2003), ignoring all comparisons involving traits thought to be absent for ecological reasons or insufficient observation. The values of $\bar{s}$ were approximately 0.46 and 0.32, respectively. Note that these values probably underestimate the true values, because these studies only included traits that the investigators suspected *a priori* might vary between populations. With this in mind, Figs. 2(c) and 3 show that the model produces realistic between-population variability.

3. Model 2: Cumulative culture

We now construct and analyse a model of cumulative culture in a single population, before adding the assumption of multiple populations in the following section. For our cumulative culture model, we take as our starting point Enquist et al's. (2010) model which expanded Strimling et al.'s (2009) model to include multiple demonstrators. Hence our model has two parameters: a, the accuracy of social learning (as before), and n, the number of cultural models (where in Model 1, as well as in previous models of cumulative culture such as Mesoudi (2011), $n=1$, but which in Model 2 can vary). As in Model 1, both parameters are assumed to be constant across all individuals. The population consists of N individuals, and as above, in each time step a randomly chosen individual dies and is replaced by a naive individual. The individual then randomly picks n other individuals from the population to be its cultural demonstrators. The individual attempts to learn the trait from each of the n demonstrators in turn. Whether this learning is successful depends on whether or not the demonstrators carry the trait and on a. Finally, after attempting to learn socially from all n demonstrators, the individual innovates with probability μ.

The trait has an infinite number of complexity levels. Learning any given level is dependent on having learned all previous levels. The levels represent cumulative improvements that can be made to the basic, level 1 trait. Thus, they may roughly correspond to Oswalt's (1976) "techno-units," or to successive modifications to a technology or social practice; plausible definitions and examples of different levels are given by Pradhan et al. (2012). In our model, individuals learn these levels as follows: for each demonstrator, the individual learns the first level of the trait that it does not already know with probability a, and moves on to the next level if successful, which it again learns with probability a, and so on. Thus the probability of a naive individual learning a given level l
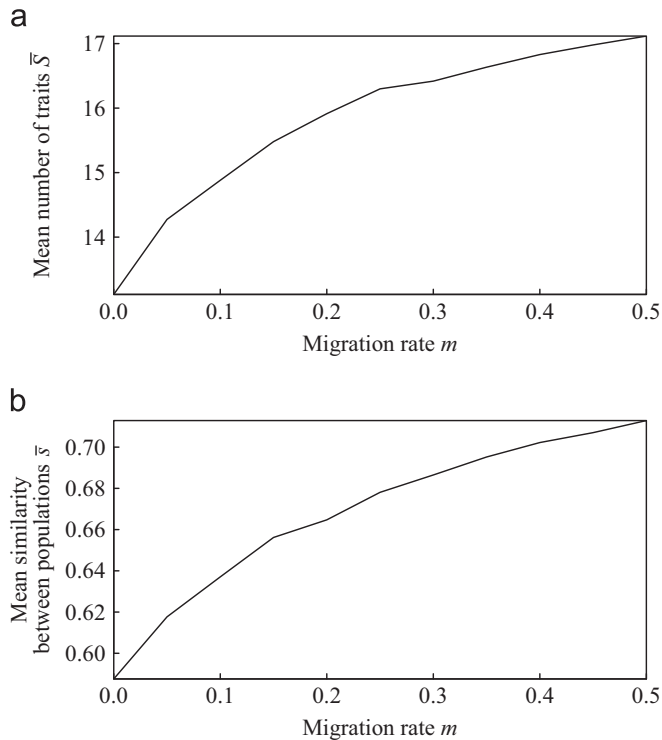

Fig. 3. The effect of the migration rate m on (a) the mean number of different traits across all populations $\bar{S}$ and (b) the mean similarity between populations $\bar{s}$. Both panels show the value found after 2000 timesteps, averaged over 2000 simulations with parameter values $N=50$, $a=0.9$, $\mu=0.1$, and $p=5$.
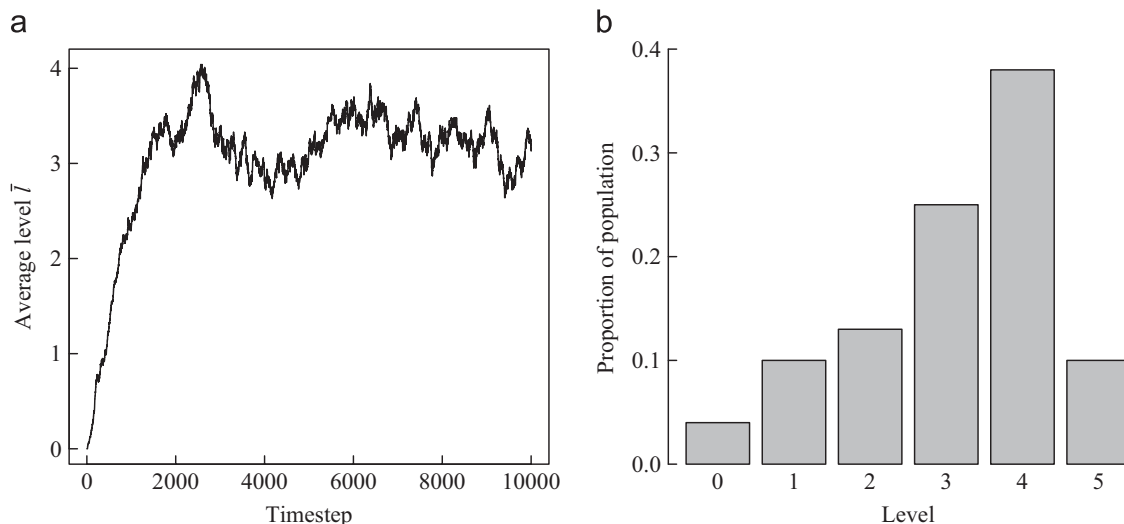

Fig. 4. One simulation of the cumulative culture model. (a) Time series of the mean level $\bar{l}$ known in the population. (b) The distribution of levels in the population at the end of the simulation. Parameter values: $N=100$, $a=0.7$, $n=3$, $\mu=0.1$.

from a demonstrator who knows at least l levels of the trait is a^l. After social learning, each individual has a probability μ of improving its knowledge of the trait by one level through innovation.

We are interested in understanding how $\bar{l}$, the mean level of cultural complexity that a population maintains, depends on the accuracy of social learning a, the number of cultural models n, and the innovativeness μ. In each simulation of the model the population begins completely unknowledgeable. Fig. 4 shows the time course and end result of one simulation of the model. In Fig. 4(a) we see that the mean level of the trait in the population initially rises and then stabilizes; Fig. 4(b) shows the resulting distribution of levels amongst the individuals of the population.

Fig. 5 shows the effects of a and n on the mean level $\bar{l}$ of the trait that is maintained in the population. The mean level $\bar{l}$ increases linearly with n (Fig. 5(a)), and non-linearly with a (Fig. 5(b)). When varying the innovativeness μ in simulations, we found that increasing μ from 0.1 to 1 increases $\bar{l}$ by ≈ 3 regardless of the values of the other parameters; thus, the effects of a and n are much stronger than the effect of μ. This replicates previous modelling results that innovation is far less important for cumulative culture than is social learning accuracy (Lewis and Laland, 2012) or number of demonstrators (Enquist et al., 2010).

Fig. 5(c) shows how $\bar{l}$ varies across the parameter space created by a and n. Enquist et al. (2010) showed that only if $an > 1$ could the trait be stably maintained in the population through social learning in their model. Since the trait in their model corresponds to the basic level 1 trait of ours, this result clearly applies here too. Much of the parameter space features realistic levels of accumulation; compare the values of $\bar{l}$ shown in Fig. 5(c) to the mean techno-unit values of 3–7 found by an empirical analysis of the complexity of marine foraging technology in a number of Oceanic human populations (Kline and Boyd, 2010). However, there are clearly many different combinations of a and n that will maintain a given mean level $\bar{l}$ in the population; thus, observing a given level of accumulation in a population does not allow us to completely identify the values of a and n for that population.

4. Model 3: Combined model

Here we combine our two models to ask under what conditions cultural traditions become cumulative. Imagine that each trait in Model 1 comes in the infinite number of levels described in Model 2, and that instead of choosing only one cultural demonstrator, naive individuals choose n cultural demonstrators, learn from them, and then both invent new traits and improve existing ones. The structure of the traits and trait levels in this model is shown in Fig. 6. As illustrated in the figure, the difference between traits and trait levels is that 'traits' measure the quantity of cultural traits and 'trait level' measures their complexity. The combined model then simulates the dynamics of independent cumulative traits within and between populations that interact by migration. To fully analyse this combined model, a choice must be made as to how cumulative traits are improved; whether, for example, there is a fixed expected number of improvements per individual, or whether more knowledgeable individuals make on average more improvements. Unfortunately there is little empirical evidence on this question.

Without deciding this one way or another, we can still make useful statements about the combined model. Consider the expected number of different traits S in a population. If $n=1$, Strimling et al. (2009) derived an analytical approximation for S, which shows that, for realistic but high values of these parameters, say $N=100$, $a=0.9$, and $\mu=0.5$, then $S \approx 133$ traits. On the other hand, if $n > 1$ no analytical approximation for S is known, but we can approximate S by following Strimling et al. and noting that
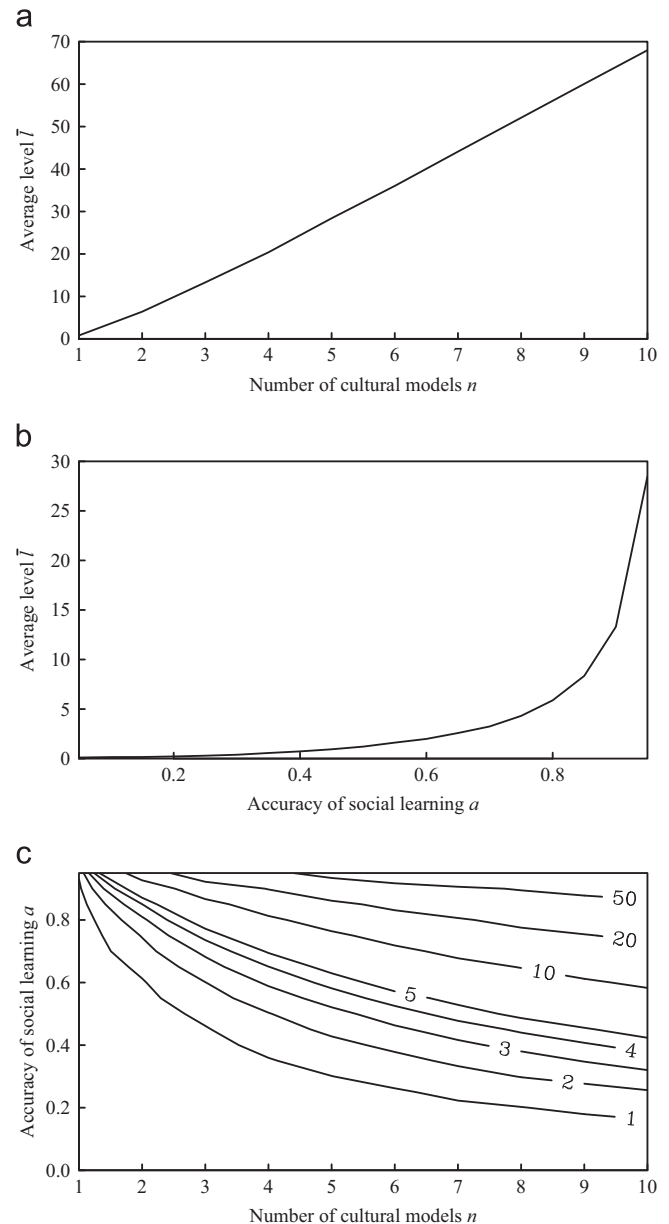

Fig. 5. The effect of (a) the number of cultural models n, (b) the accuracy of social learning a, and (c) both, on the mean trait level $\bar{l}$ maintained in the population. All panels show the value found after 10,000 timesteps, averaged over 20 simulations, with $N=100$ and $\mu=0.1$; in (a) $a=0.9$ and in (b) $n=3$.

$S=\mu NT$, where T is the expected lifetime, in generations, of a newly invented trait. We conducted simulations that showed that even for very small values of the parameters which satisfy the criterion $an > 1$, say $N=30$, $a=0.65$, and $n=2$, then $T \approx 100$, and T increases very rapidly with increases in the parameters. Assuming additionally a low value for innovativeness, e.g. $\mu=0.1$, then $S \approx 300$ traits (Fig. 7) and rises very quickly into the thousands and tens of thousands of traits with increases in the parameters. Moreover, the condition $an > 1$ is also the condition for cumulative culture to arise, as noted above.

5. Discussion

Our models give results that mimic the phenomena of between-population cultural traditions and cumulative culture in
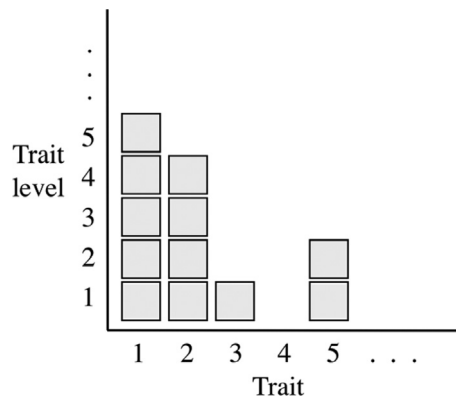
Fig. 6. A schematic illustration of the structure of the traits and trait levels for one hypothetical individual in the combined Model 3. In this example, the individual knows trait number 1 to level 5, trait number 2 to level 4, trait number 3 only at the first level, does not know trait number 4, and knows trait number 5 to level 2.
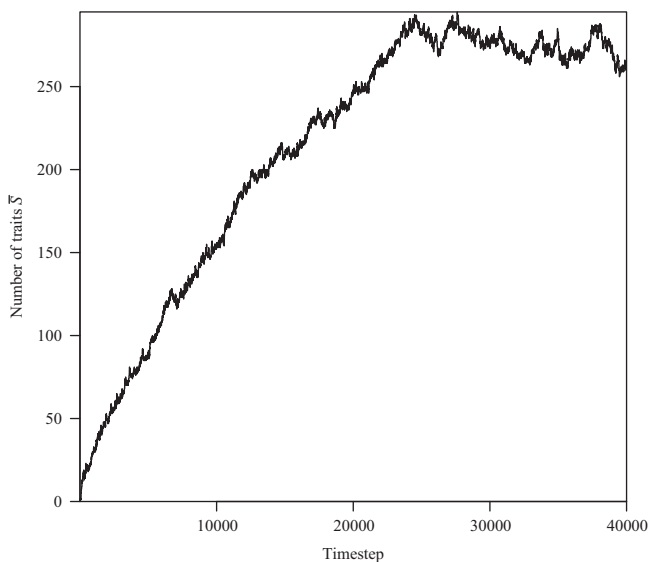

Fig. 7. The number of traits known in the population in one simulation of the combined model. Parameter values: $N=30$, $n=2$, $a=0.7$, $\mu=0.1$, $m=0$, $p=1$.

reasonably realistic ways. In our model of cultural traditions (Model 1) we find that realistic differences between populations are maintained despite assuming that all individuals invent the same traits in the same order, individuals learn from only a single demonstrator, and despite frequent migration between populations. This occurs because traits die out with non-negligible frequency, and most traits do not spread beyond their inventor. In our model of cumulative culture (Model 2), we find that the accuracy of social learning and the number of cultural demonstrators interact to determine the cumulative level of a trait that a population can stably maintain, and that portions of the parameter space feature realistic levels of accumulation.

Results from Model 1 show that it is surprisingly easy to generate realistic cultural traditions, defined as moderately dissimilar trait profiles in different populations linked by migration, in contrast to the lack of spread of any cultural traits (the absence of culture), or the homogenization of all populations to an identical trait profile (the absence of traditions). Inter-population similarity increases with social learning accuracy, population size and migration rate, but traditions reliably emerge at broad ranges of values of these parameters rather than a specific range. Even assuming very inaccurate social learning (e.g. $a=0.1$), as is often claimed to characterize non-human social learning, we still obtain

values of inter-population similarity that match those found empirically, at realistic population sizes and migration rates (Fig. 2). In general, Model 1 is in line with analyses indicating that behavioural traditions in non-human primates are cultural rather than genetic (Lycett et al., 2007; 2010), and in fact suggests that stable cultural traditions may be more widespread in nature than currently thought. Indeed, since the landmark paper by Whiten et al. (1999), more and more cultural traditions have been identified in diverse species as researchers have begun to look for such patterns (Laland and Galef, 2009). Furthermore, the time series in Fig. 1(a) imply that phenomena such as chimpanzee cultures have inherent historical dimensions (Lycett, 2010), which have begun to be investigated using archaeological (Haslam et al., 2009) and phylogenetic (Lycett et al., 2010) methods. On the grounds of phylogenetic homology, we might also therefore expect traditions in prehistoric hominins to have displayed similar historical dynamics (Kuhn, 2004; Lycett, 2013).

Results from Model 2 imply that cumulative culture is more difficult to generate: note the large parameter space in Fig. 5 (c) where accumulation does not occur (i.e. $\bar{l}=1$). Cumulative culture requires some combination of high fidelity social learning and multiple demonstrators, replicating the findings of previous macroscopic (Henrich, 2004; Lewis and Laland, 2012) and non-cumulative (Enquist et al., 2010) models. The relative unimportance of individuals' innovativeness is supported by comparative work showing that humans appear to possess unusually high-fidelity social learning, and are roughly comparable in their individual learning abilities, compared to other great apes (Dean et al., 2012; Herrmann et al., 2007). This reinforces arguments that humans inhabit a 'cultural niche' (Boyd et al., 2011), characterized by faithful social learning rather than particularly enhanced individual cognitive abilities.

The dependence of cumulative culture on two different factors may help to explain its rarity in nature. Our analysis of the combined Model 3 reinforced this further, showing that social learning accuracy and number of demonstrators interact to generate two qualitative regimes dictating both number of traits and trait complexity. When $an < 1$, the number of traits known in the population is relatively low and there is no cumulative culture. When $an > 1$, many traits are known in the population and there can be cumulative culture. To our knowledge, this is the first time this link between trait number and trait complexity has been drawn. It seems plausible that these regimes correspond qualitatively to nonhuman and human cultures, respectively: human culture is not only cumulative, as noted in the Introduction, but also has a huge number of both cumulative and non-cumulative traits (see Mesoudi et al., 2004 for estimations of the magnitude of human cultural variation).

We caution that the models we have presented contain many simplifying assumptions. We assumed that our parameters (e.g. innovativeness, social learning accuracy) operate identically across all individuals, whereas in reality these probably vary across individuals. The extent to which this individual variation is important, or just averages out at the population level, remains to be determined. More complex and realistic social learning biases are possible, such as copying successful individuals (Mesoudi, 2008) or conforming to the group majority (Henrich and Boyd, 1998). However, we note that adding such biases is not straightforward given the ambiguous and often conflicting evidence across non-human species for biases such as conformity (van Leeuwen and Haun, 2013). Moreover, we might expect in some cases that such biases will magnify our findings: conformity, for example, emphasises between-population variation (Henrich and Boyd, 1998), thus reinforcing our conclusion that cultural traditions should be commonplace. Another interesting question is whether our assumption in Model 2 that individuals copy *n*

demonstrators once per generation is reasonable. It is also possible that individuals may sample the same demonstrator(s) multiple times over their lifetime. Whether multiple learning trials, as well as (or instead of) access to multiple models, facilitates cumulative culture, and which of these is a more realistic assumption, remains to be explored.

The emergence of cumulative culture in human evolution is sometimes framed in terms of cognition vs. demography: was there some genetically-derived change in hominin cognition such that social learning became more accurate (e.g. via imitation or teaching) and which allowed cumulative culture to take off (Klein, 2009), or did cumulative culture emerge when populations became large enough to support increasing cultural complexity (Henrich, 2004; Powell et al., 2009)? Our models suggest that the answer to this question is unlikely to be one or the other, and the interaction between social learning accuracy and number of demonstrators is key. We also note that our (and other modellers') parameters do not necessarily neatly map onto 'cognition' and 'demography'. While it is possible that social learning accuracy improved through some genetically-based adaptation for imitation or theory of mind, it could equally have increased through purely cultural means. Examples of this in recent history might include the invention of writing or the printing press, which would have dramatically reduced errors in cultural transmission (see Mesoudi, 2011 for a cumulative culture model incorporating such cultural innovations). Some kind of prehistoric equivalent may have similarly driven increases in early hominin social learning accuracy, and hence cumulative culture. Similarly, an increase in the number of demonstrators may have depended straightforwardly on the overall population size. Alternatively, it may have required cognitive changes that allowed a shift from vertical uniparental cultural transmission to 'many-to-one' cultural transmission (Cavalli-Sforza and Feldman, 1981), independently of overall population size. Modelling alone cannot ultimately address such questions, but can guide comparative and archaeological study to begin to answer them.

In conclusion, we have presented a set of models that extend and combine previous theoretical findings concerning the emergence of cultural traditions and cumulative culture. Regarding the former, we find that empirically realistic patterns of cultural traditions are surprisingly easy to generate with minimal assumptions, supporting recent work suggesting that cultural traditions are widespread in nature. Regarding the latter, we reinforce previous findings that cumulative culture can only emerge through an interaction of social learning accuracy and number of demonstrators, and that these conditions favour both a rapid increase in the number and cumulative complexity of cultural traits. We suggest that this two-parameter threshold is why cumulative culture is restricted to just our own species.

Acknowledgements

Appendix

Imagine, in Strimling et al.'s model (i.e. with $m=0$), that a focal individual has just invented a new trait. In the next timestep, one of three things can happen: the trait can be lost because the individual dies, the trait can continue to be known only by the inventor, or another individual can learn the trait. Let us denote the probabilities of these three events by p_{lost}, p_{kept} and p_{copied}. The trait will be lost if the inventor is randomly picked to die; thus

$$P_{lost} = \frac{1}{N}$$

The trait will be learned by another individual if the inventor does not die, and the individual randomly picks the inventor to learn from, and is successful at learning; thus

$$P_{copied} = \left(1 - \frac{1}{N}\right)\left(\frac{1}{N-1}\right)a = \frac{a}{N}$$

Finally,

$$P_{kept} = 1 - P_{lost} - P_{copied} = 1 - \frac{1}{N} - \frac{a}{N} = \frac{N-a-1}{N}$$

What is the probability $P(t)$ that the trait is learnt by another individual for the first time exactly t timesteps after it was invented? For this to happen, the trait must continue to be known only by the inventor for $t-1$ timesteps, and must then be learnt by another individual on the tth. Thus

$$P(t) = P_{kept}^{t-1} P_{copied} = \left(\frac{N-a-1}{N}\right)^{t-1} \frac{a}{N}$$

Finally, what is the probability that the trait will ever spread beyond its inventor? This happens if $P(t)$ ever happens, i.e. with probability

$$\sum_{t=1}^{\infty} p(t) = \sum_{t=1}^{\infty} \left(\frac{N-a-1}{N}\right)^{t-1} \frac{a}{N}$$

Using the standard identity for infinite geometric series, this can be shown to be equal to

$$\frac{a}{1+a}.$$

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