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Why does human culture increase exponentially?

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ABSTRACT

Historical records show that culture can increase exponentially in time, e.g., in number of poems, musical works, scientific discoveries. We model how human capacities for creativity and cultural transmission may make such an increase possible, suggesting that: (1) creativity played a major role at the origin of human culture and for its accumulation throughout history, because cultural transmission cannot, on its own, generate exponentially increasing amounts of culture; (2) exponential increase in amount of culture can only occur if creativity is positively influenced by culture. The evolution of cultural transmission is often considered the main genetic bottleneck for the origin of culture, because natural selection cannot favor cultural transmission without any culture to transmit. Our models suggest that an increase in individual creativity may have been the first step toward human culture, because in a population of creative individuals there may be enough non-genetic information to favor the evolution of cultural transmission.

1. Introduction

Culture, in terms of traditions passed from one generation to the next, is not limited to humans (Levebre and Palameta, 1988; Whiten et al., 1999; Avital and Jablonka, 2001; Laland and Hoppit, 2003), yet human culture is unique in many respects. A striking aspect of humans is their ability to shape and accumulate cultural information over generations, to an extent that could not be achieved by a single generation (Sahlins, 1960; Boyd and Richerson, 1996; Tomasello, 1999). That is, human culture is *cumulative*. Animal traditions, in contrast, are almost invariably so simple that they could have been established within a single generation, i.e., invented by one individual and then transmitted to others (Tomasello et al., 1993; Boyd and Richerson, 1996). We use here a very broad definition of culture, including anything that can be influenced by cultural transmission (Rogers, 1988), such as actions or rules for action, ideas, values and artifacts.

Human culture, indeed, is cumulative in more than one respect. One is the *efficiency* with which tasks are performed or goals are obtained. Culture accumulates in this sense when the efficiency at a given task increases over generations. For example, agriculture can be improved to increase yield, a knife to be a better tool, a physical theory to better describe the world. Another aspect of culture is its *amount*, which can be measured, for instance, by the number of countable items within a cultural domain, e.g., tool types, mathematical theorems, poems. Accumulation in this sense thus refers to an increase in the number of cultural items. Efficiency and amount are distinct aspects of culture, yet they are not wholly unrelated. For example, increasing the number of tool types allows specialization for particular tasks. Culture can also accumulate in terms of increasing *complexity*, as seen for instance in social organization (Quigley, 1979; Tainter, 1988).

We consider here accumulation in terms of the amount of culture. Our choice is motivated by a lack of theory in this area (see below) and the impressive data on growing amounts of culture in human history. Lehman (1947) provides the most comprehensive study, considering the accumulation in philosophy, mathematics, chemistry, geology, genetics, botany, entomology, economics and political science, education, literature, and music, in periods between 1200 and 1925 AD. Lehman consulted chronologies, dictionaries and encyclopedias about these fields and counted how many contributions (inventions, discoveries, etc.) were recorded each year. He considered, for instance, 49 histories of education, more than 50 histories of philosophy, 51 lists of significant books collated in Dickinson (1925), 15 books on Opera, eight books on music. Graphing such data, he discovered a ubiquitous pattern

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Table 1
Accumulation rate of contributions to various subjects

Subject	Time period	Accumulation rate (yr^{-1})	Goodness of exponential fit (r^2)
Philosophy	1275–1875 AD	0.009	0.99
Geolology	1500–1900 AD	0.015	0.99
Genetics	1675–1900 AD	0.022	0.99
Pathology	1225–1875 AD	0.009	1.00
Education	1350–1850 AD	0.008	1.00
Mathematics 1	1450–1900 AD	0.011	1.00
Mathematics 2	1450–1900 AD	0.012	1.00
Chemistry	1550–1900 AD	0.020	0.99
Medicine and hygiene	1275–1875 AD	0.008	1.00
Economy and political science	1525–1875 AD	0.013	0.99
"Best books"	1525–1875 AD	0.012	0.99
Entomology	1600–1900 AD	0.018	0.99
Botany	1600–1900 AD	0.016	0.98
Grand opera	1700–1900 AD	0.034	0.98
Orchestral and symphonic music	1725–1875 AD	0.021	0.99
Important scientific and technical discoveries	1100–1900 AD	0.010	0.99
Categories of stone tools	1.8–0.0225 MYa	2.16×10^{-6}	0.93

Original data from Lehman (1947), except for "Important scientific and technological discoveries" (Darmstaeder and Dubois Reymond, 1904) and "Categories of stone tools" (Isaac, 1972; Durham, 1991). Mathematics 1 and 2 refer to two histories of mathematics analyzed by Lehman (1947). "Best books" refer to the list of notable books compiled by Dickinson (1925). Data are plotted in Figs. 1 and 2. The accumulation rate is the value of k that yields the best fit of $e^{k(t-t_0)}$ to the data. Goodness of fit is measured by Pearson's r^2 (proportion of explained variance).

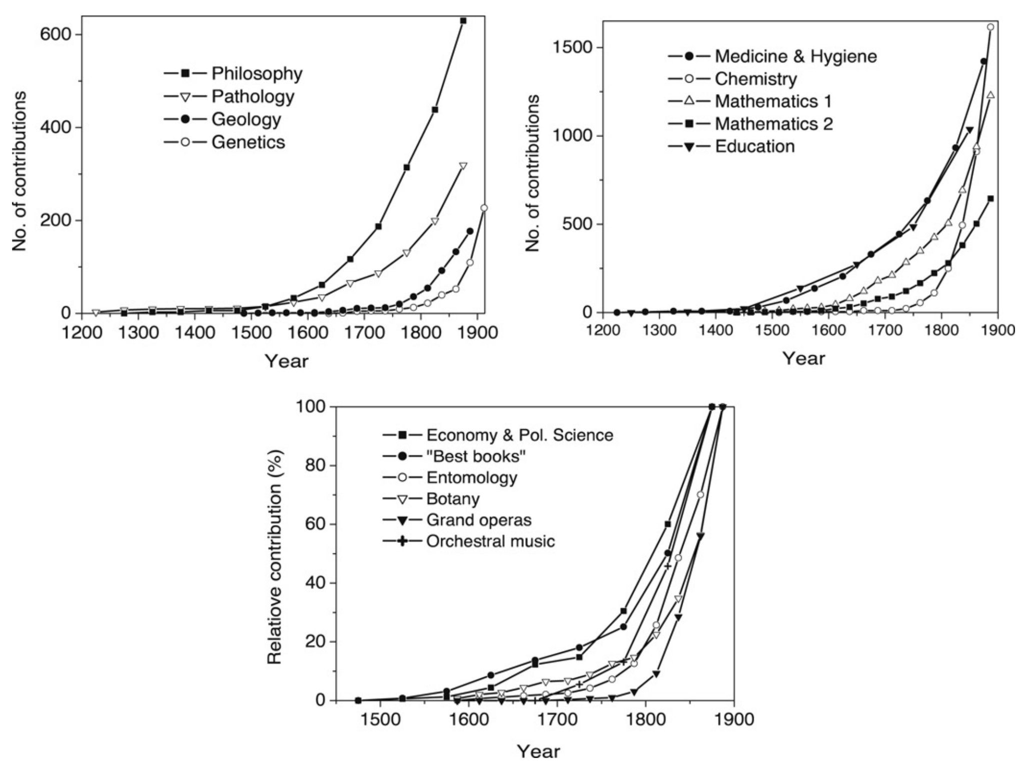

Fig. 1. Examples of exponential increase in the amount of culture compiled by Lehman (1947) consulting chronologies, dictionaries and encyclopedias about various disciplines. The top panels plot the number of contributions recorded in successive time periods of 25 or 50 years. The bottom panel plots the number of contributions as a percentage of the number recorded in the last available time period (there are no count data for these disciplines in Lehman, 1947). The curve "Best books" refers to the lists of notable books by Dickinson (1925). See also Table 1.

of accumulation, described with extreme precision by a simple exponential curve (Fig. 1, Table 1). Fig. 2 shows further examples; Ogburn (1950) and Purcell (1982) provide yet more.

Note that Lehman *analyzed* data that had been *collected* in most cases by experts and historians in the considered fields, usually for encyclopedic or documentation purposes. Data collection thus happened years or decades before Lehman's analysis and without connection to any research hypothesis on cultural accumulation. Lehman usually counted all contributions mentioned in his sources, but sometimes he applied a mild filter such as counting only contributions mentioned by at least 3 sources (out 49 original sources on education) or at least 5 sources (out of 20 on economics and political science).

The most robust feature of the data Figs. 1 and 2 is the pattern of exponential increase. This is the empirical phenomenon we seek to explain. We are not concerned with the exact number of contributions recorded in each field, which may vary according to one's criteria. For instance, of the two histories of mathematics consulted by Lehman, Cajori (1922) reports 1229 contributions between 1400 and 1900 AD, while Bell (1940) reports only 645. Yet in both cases Lehman found an almost perfect agreement in the *pattern* of increase: exponential growth at a rate of 1.1%–1.2% per year. Thus an inevitable degree of arbitrariness in defining a

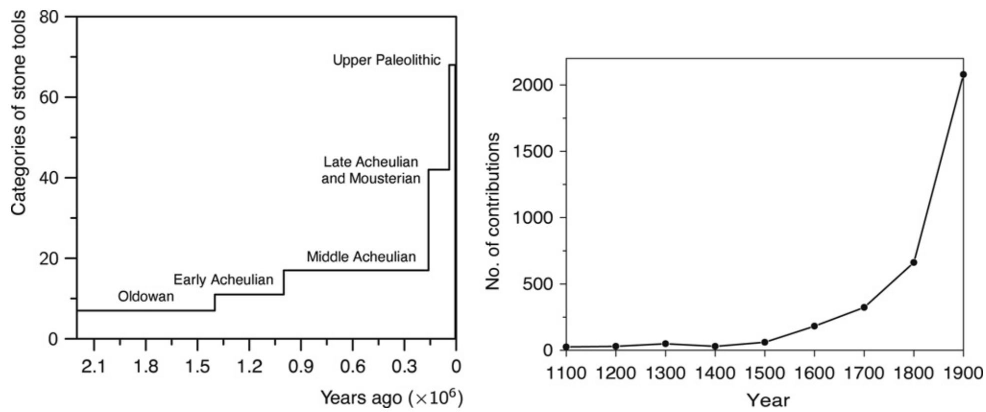

Fig. 2. Left: Exponential increase in the number of stone tool categories during hominid evolution, according to Isaac (1972). Although these data most likely reflect a mix of cultural and genetic evolution, it is interesting to note that the pattern of increase is exponential as for the data relative to shorter time scales (Fig. 1), where the effects of genetic evolution are probably unimportant. Right: Exponential increase in the number of scientific discoveries between 1100 and 1900 A.D., according to Darmstaeder and Dubois Reymond (1904). See also Table 1.

"contribution" seems relatively unimportant to the overall pattern of growth.

In this paper, we first develop simple formal models to clarify how creativity and cultural transmission may cause the amount of culture to increase or decrease, with a special focus on exponential increase. Second, we explore the conditions under which cultural capacities related to the creation and transmission of culture may evolve by genetic evolution, cultural evolution and gene-culture co-evolution. Lastly, we use our results to discuss the origin and uniqueness of human cumulative culture.

Before presenting our models we clarify two points and, in the next section, briefly summarize theories of cumulative culture. The first point is that, of course, cultural evolution may also lead to a decrease in the efficiency, amount and complexity of culture (Sahlins, 1960; Tainter, 1988; Diamond, 2005; Henrich, 2004). A striking historical example, perhaps the cultural equivalent of biological mass extinction, is the loss in mathematical, scientific and technical knowledge at the end of the Greek era (Russo, 2004). Elements of culture may also stay practically unchanged for shorter or longer periods (e.g., subsistence technology) or change without increasing or decreasing in efficiency, amount or complexity (many examples can be found in language evolution). Our models do highlight some conditions for equilibrium and decrease in the amount of culture, yet our main focus is the important fact that culture *can* accumulate rapidly.

The second point to be clarified regards the relationship between culture and genetic fitness, or biological adaptiveness. Above we have defined the efficiency, amount and complexity of culture without reference to biological adaptation. The reason is that, in principle, these characteristics can vary independently of the adaptive value of cultural traits. For instance, we may have, say, very good tools (efficiency), very many tools (amount) and very complex tools (complexity) to pursue both adaptive and maladaptive ends. Adopting fitness-neutral definitions we do not deny that culture can highly increase genetic fitness, as testified by the impressive ecological success of humans. We will return to this point below, when we study the genetic evolution of capacities for culture.

2. Overview of ideas about cumulative culture

There are many hypotheses about the origin and evolution of human culture (e.g. Cavalli-Sforza and Feldman (1981), Galtung and Inayatullah (1997), Durham (2001), Laland and Brown (2002) and Carneiro (2003)), and some explicitly consider cumulative culture. Boyd and Richerson (1985, 1989, 1995, 1996) show that cultural evolution can increase the efficiency of culture if errors in transmission generate random variation in a cultural trait, and if selective imitation allows individuals to preferentially acquire more efficient traits. This work considers the efficiency of a single cultural trait and thus does not explain the exponential increase in the amount of culture. We will highlight below some differences in modeling amount vs. efficiency of culture. Changes in the amount of culture are considered in the model by Henrich (2004) about the loss of material culture among Tasmanians. This model shows how population size and mechanisms of social learning can interact in such a way that larger populations are able to maintain larger amounts of culture. It is not directly concerned about how the amount of culture changes in time but contains some ideas about the link between individual capacities and the amount of culture that a population can maintain (see Section 5).

Turning to verbal models, Basalla (1988) considers both the efficiency and the amount of culture in a theory of technological evolution that has several similarities with genetic evolution: innovations are continuously generated based on existing technologies, and individuals choose among them with a tendency to select the most efficient ones. Just like genetic evolution, the process is not assumed to be deterministic (i.e., to improve at every step) but is nevertheless expected to produce in the long run an increase in both the efficiency and number of technologies. This theory, however, does not make predictions about the time course of accumulation. The most developed theory of accelerating cultural accumulation is probably that of Ogburn (1950), (see also Ogburn and Nimkoff, 1958), based on a dynamical view in which elements of culture may be gained and lost, with accumulation resulting when gains outnumber losses. Ogburn notes that innovations are often generated by combining existing technologies in new ways. Thus the number of innovations per generation is predicted to increase with the amount of culture, because more culture means more raw material on which innovations can build. In the following we will explore this idea formally, together with other processes that may cause an increase or decrease in the amount of culture.

3. The logic of cultural accumulation

In this section we study the conditions under which culture accumulates over generations. We lump all processes that affect culture into just two subprocesses: one that creates culture and another that destroys it. The first process represents the result of individual or cooperative activities in creating new culture, while the latter describes the accuracy, or lack thereof, of the social transmission of culture. Our aim is to link these processes to the

Table 2
Definition of mathematical symbols

Symbol	Definition	Equation
x	Amount of culture at time t	(1)
$\dot{x}$	Rate of change (derivative) of x, $\dot{x} = dx/dt$	(1)
λ	Culture is lost at rate λx	(1)
x_0	Initial value of x	(2)
γ	Culture increases at rate γ (independent of x)	(3)
$\bar{\gamma}$	Culture-independent creativity of single individual	(13)
$c(\bar{\gamma})$	Cost of $\bar{\gamma}$	(13)
$F(\bar{\gamma})$	Fitness of $\bar{\gamma}$	(13)
ϵ	Genetic evolution causes γ to increase at rate ϵ	(15)
δ	Culture increases at rate δx (depends on x)	(18)
$\bar{\delta}$	Culture-dependent creativity of single individual	(21)
$C(\bar{\delta})$	Cost of $\bar{\delta}$	(21)

All quantities are ≥ 0, except for $\dot{x}$ which can also be negative. A quantity is usually defined in the text just before the equation when it is first used.

cultural capacities of individuals, especially capacities for cultural transmission and creativity, and derive long term predictions by analyzing the balance between creation and destruction of culture.

Table 2 summarizes our mathematical notation. The amount of culture, x, is the main quantity of interest. It can be thought as the number of traits that are shared among individuals, i.e., that have reached a non-negligible part of a population. It would be desirable to provide a more detailed description of culture by characterizing, e.g., how many individuals have each trait, whether there exist correlations between traits, and so on. A theory of cultural accumulation at this level of detail is, unfortunately, beyond what can be attempted today. Our models are an effort to investigate cultural accumulation at the population level (similarly to macro-economical models or physical theories such as thermodynamics that do not consider molecular behavior) and should be understood as a first step rather than a complete theory.

3.1. *Cultural transmission alone cannot maintain large amounts of culture*

The successful transmission of culture between generations depends on many factors (Cavalli-Sforza and Feldman, 1981; Richerson and Boyd, 2005). First, the older generation must make information available to the younger one. Exposure of young to culture may occur by simple observation of the elder, but can be greatly enhanced by such activities as demonstrations or teaching. Second, the younger generation must have the ability to acquire culture (social learning). Third, the young must accurately remember acquired information to transmit it further. Processes within a generation, so-called horizontal transmission, can also modify culture. Here we are not concerned with the specific processes that enable culture to be passed from one generation to the next. Our main point is rather that, unless transmission processes are so precise that nothing is ever lost, cultural transmission inevitably results in some loss of culture. For instance, of many important books of the past only a few fragments, or just the title, have arrived to us. Most, if not all, elements of culture can be lost in this way, e.g., the proof of a mathematical theorem and how to prepare a medicine or process a food.

If lossy transmission is the only process that modifies the amount of culture, and if what is lost is never reinvented, it is easy to see that all cultural traits will eventually be lost. This argument may be formalized as follows. Let x be the expected amount of culture at a given time, and $\dot{x}$ its rate of change (formally, its time derivative, $\dot{x} = dx/dt$). As observed earlier, measures of the amount of culture can be defined operationally referring to countable items of culture (Fig. 2). We define a loss rate λ as the rate at which culture elements are lost ($\lambda > 0$) and we assume that each element is lost or preserved independently of the others. The resulting formal model is:

$$\dot{x} = -\lambda x. \tag{1}$$

This corresponds to the simple case in which cultural traits are lost independently of each other and have an expected lifetime of $1/\lambda$. By standard techniques, the solution of Eq. (1) is

$$x(t) = x_0 e^{-\lambda t} \tag{2}$$

where x_0 is the amount of culture present at time $t = 0$. Eq. (2) predicts that all culture is eventually lost (Fig. 3), and thus confirms our verbal argument above: cultural capacities related to transmission (teaching, social learning, memory, etc.) can, on their own, explain neither the accumulation of culture nor its long-term maintenance.

We emphasize that we do not believe that all transmission errors cause loss of culture: they can also cause its transformation. Such errors may increase the efficiency of a cultural trait by sometimes generating new, and sometimes more efficient, variants (Boyd and Richerson, 1985, 1996; Richerson and Boyd, 2005). Here, however, we consider the main effect of transmission to be loss of cultural traits rather than their modification. The reason is that we consider the number of traits rather than their efficiency. When considering very many traits, it is realistic to assume that some traits are sometimes lost (see examples above). Moreover, we argue in Section 4.3 that the creation of culture by transmission errors seems insufficient, by itself, to cause an exponential increase in the amount of culture.

3.2. *Creativity alone cannot lead to cumulative culture*

We consider now a model in which individuals can create culture, but cannot transmit it between generations. The latter assumption means that the lifetime of a cultural element coincides with the lifetime of its bearers. If we take as our unit of time the average expected lifetime of individuals, we can represent this assumption by a loss rate of $\lambda = 1$ in Eq. (1). Let γ be the amount of culture that is, on average, created in a time equal to the average lifetime of individuals. The dynamics of culture is then:

$$\dot{x} = -x + \gamma. \tag{3}$$

The solution of Eq. (3) is:

$$x(t) = \gamma + (x_0 - \gamma)e^{-t}. \tag{4}$$

Thus, independent of the initial amount of culture, only an amount γ can be maintained (Fig. 3). In other words, there is no accumulation of information beyond what individuals can invent within a generation (either on their own or in collaborative activities).

3.3. *Cultural transmission and creativity combined allow the accumulation of large amounts of culture*

We now consider cultural transmission and creativity together. We can combine Eq. (1) with Eq. (3) and get:

$$\dot{x} = -\lambda x + \gamma \tag{5}$$

whose solution with initial condition x_0 is:

$$x(t) = \frac{\gamma}{\lambda} + \left(x_0 - \frac{\gamma}{\lambda}\right) e^{-\lambda t}. \tag{6}$$

According to this equation, an equilibrium amount of culture is reached in the long run:

$$\lim_{t\to\infty} x(t) = \frac{\gamma}{\lambda}. \tag{7}$$

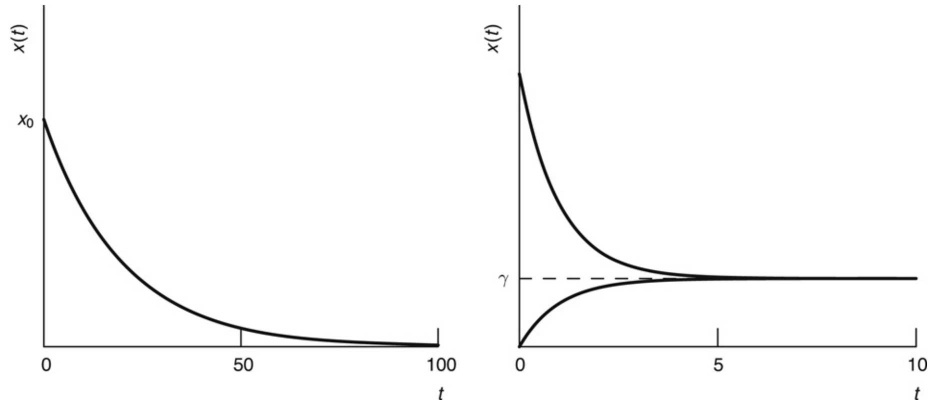

Fig. 3. Left: Decrease in culture due to imperfect cultural transmission (Eq. (2) with $x_0 = 1$ and $\lambda = 0.05$). Right: If creativity is the only driving force, culture rapidly reaches an equilibrium value corresponding to what is created in each generation (Eq. (4) with $\gamma = 1$ and either $x_0 = 0$ or $x_0 = 4$).

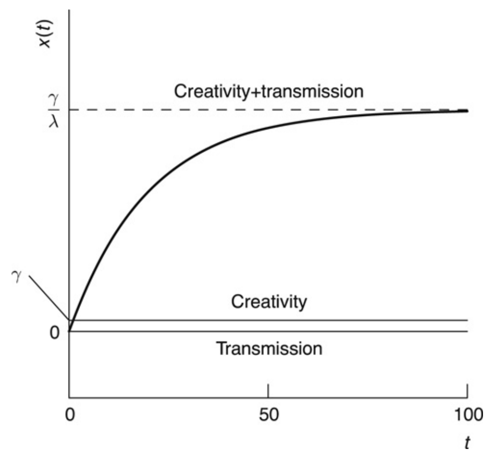

Fig. 4. Accumulation of culture due to creativity and cultural transmission combined (Eq. (6) with $\lambda = 0.05$, $\gamma = 1$, $x_0 = 0$).

The equilibrium amount of culture increases if either the accuracy of cultural transmission or creativity increase. If cultural transmission is accurate (small λ), much more information can be maintained than could be produced within a single generation (Fig. 4. For instance, if cultural information is created at the rate of one unit per generation (i.e., $\gamma = 1$), and is lost at a rate of 0.05 ($\lambda = 0.05$), then 20 units of information can be maintained (the average lifetime of a cultural trait is $1/\lambda = 20$).

Although this model can support substantial accumulation of culture, the time course of x is negatively rather than positively accelerated (compare, e.g., Figs. 1 and 4). The only case in which x grows without bound concerns perfect transmission, $\lambda = 0$. In this case Eq. (6) is not valid and the solution of Eq. (5) is rather $x(t) = x_0 + \gamma t$. This represents an unlimited increase in the amount of culture, but much slower than the empirical pattern of exponential increase.

4. The evolution of cultural capacities

In the models above the parameters λ and γ were fixed, but in reality the capacities for cultural transmission and creativity can evolve. To study what patterns of cultural accumulation may result from the coevolution of culture and cultural capacities, we consider here the genetic evolution of creativity and cultural transmission as well as gene-culture coevolution of these capacities.

4.1. Evolution of cultural transmission cannot produce exponential accumulation of culture

The genetic evolution of cultural transmission is a complex problem with both mechanistic aspects (what cognitive mechanisms underlie cultural transmission; Tomasello et al., 1993; Tomasello, 1999; Heyes and Galef, 1996) and functional ones (whether natural selection does, under given circumstances, favor cultural transmission; Boyd and Richerson, 1996). Additionally, cultural evolution has produced innovations such as literacy and schooling that have improved our capacity to transmit culture. In this paper, however, we are not concerned with how and why cultural transmission evolved, but only with the effect of cultural transmission on cultural accumulation. That is, we ask whether an exponential increase in amount of culture can be caused by a change of cultural transmission over time.

In our model, an improvement in cultural transmission corresponds to a decrease in the loss rate λ. Any such decrease leads to an increase in the amount of culture that can be maintained, Eq. (7), provided that culture is continuously created ($\gamma > 0$). The first question we ask is thus whether it is possible to replace the constant λ in Eq. (5) with a time varying function $\lambda(t)$ so that x increases exponentially over a given time period. The second question is whether such a time varying function can plausibly reflect improvements in transmission caused by genetic or cultural evolution. To answer these questions we start from the defining property of exponential increase, i.e., that the rate of increase in x is proportional to x itself:

$$\dot{x} = kx \tag{8}$$

with $k > 0$. Using this expression in Eq. (5) and allowing λ to be a function of time we find

$$\lambda(t) = \frac{\gamma}{x(t)} - k. \tag{9}$$

Thus if λ follows this time course, x will increase exponentially at rate k. There are, however, several reasons why this account is untenable. First, Eq. (9) does not have any justification other than producing the desired result. Second, Eq. (9) predicts that λ will eventually reach zero, after which accumulation will no longer be exponential, but simply linear. Third, fitting the model to the data reveals that cultural accumulation is simply too fast to be plausibly driven by changes in cultural transmission. To see this let us consider an exponential accumulation between times t_1 and t_2 and let x_i and λ_i be the amount of culture and loss rate at t_i ($i = 1, 2$). Recall that we are studying the hypothesis that an exponential increase of culture is driven by changes in λ, so that

γ is constant. Hence, given that Eq. (9) must hold for both pairs (x_1, t_1) and (x_2, t_2), we can solve for γ and write:

$$(\lambda_1 + k)x_1 = \gamma = (\lambda_2 + k)x_2. \tag{10}$$

We can now write λ_1 as a function of λ_2 and observed quantities:

$$\lambda_1 = \frac{x_2}{x_1}\lambda_2 + \left(\frac{x_2}{x_1} - 1\right)k. \tag{11}$$

This formula can be applied to estimate the change in λ that is required to support an exponential increase in x between t_1 and t_2. Consider for instance the field of education in Fig. 1. Together with medicine, this is the discipline that, according to Lehman (1947), has grown at the slowest rate, $k = 0.008\ \text{yr}^{-1}$ (Table 1). Suppose, for the sake of the argument, that cultural transmission at time t_2 is perfect, $\lambda_2 = 0$. Lehman's data indicate that the amount of culture within education has increased about 1000-fold in the recorded period, i.e., $x_2/x_1 \simeq 1000$. Using these values in Eq. (11) we get

$$\lambda_1 \simeq 1000 \times 0.008\ \text{yr}^{-1} \simeq 8\ \text{yr}^{-1}. \tag{12}$$

This would mean that at $t_1 = 1250$ AD a contribution to education would have had an average lifetime of just 1/8 years, i.e., about six weeks. Another problem with this account is the enormous level of creativity implied. From Eq. (10) we see that γ would be estimated to be of the same order of magnitude as λ_1 (because $x_1 \simeq 1$ and k is very small), i.e., in 1250 AD important innovations in the field of education would arise at the rate of about one every six weeks, only to be forgotten at an almost equal rate. The assumption of perfect transmission in 1850 AD ($\lambda_2 = 0$) is not crucial for these conclusions: the results would be even more paradoxical assuming $\lambda_2 > 0$, because this would increase the estimates of both λ_1 and γ (Eqs. (10) and (11)). An application of the model to longer time periods seems equally untenable. Fitting the model to the stone tool data in Fig. 2, for instance, yields $\gamma \simeq 7000\ \text{yr}^{-1}$, meaning the invention of a new stone tool design every about 7000 years, or more than 100 designs just in the Oldowan period. Not only does this seem unreasonable: it also requires Oldowan tool makers (e.g., *Homo habilis*) to be as creative as Paleolithic tool makers (*Homo sapiens*).

We conclude that the hypothesis that culture is created at a fixed rate and lost at a rate that decreases with time cannot explain the observed patterns of exponential increase in amount of culture. The argument is the same regardless of whether improvements in cultural transmission occur by genetic or cultural evolution.

4.2. Genetic evolution of creativity may lead to accumulation of culture at a constant rate

In this section we ask whether the genetic evolution of individual capacities to create culture can account for an exponential increase in amount of culture. In general, a genetically determined cultural capacity may evolve if it is favored by natural selection, i.e. if it benefits individual survival and reproduction or other aspects of genetic fitness (Grafen, 1991; Houston and McNamara, 1999). So far we have not considered individual fitness, but this becomes necessary if we want to study genetic evolution. In practice, we need to calculate the fitness of an individual with creativity $\bar{\gamma}$ in a population characterized by an amount of culture x (we write $\bar{\gamma}$ rather than γ as above to distinguish individual creativity from the creativity of the whole population). Let us assume for simplicity that an individual's genetic fitness is always increased by acquiring a larger amount of culture; we will comment on this assumption in the Discussion. If all culture is adaptive, an individual's fitness can be written as the sum of three terms:

(1) The amount of culture that the individual acquires through cultural transmission. This is equal to $(1 - \lambda)x$, i.e., the current amount of culture minus what is lost owing to imperfect transmission.
(2) The amount of culture the individual can create on its own, $\bar{\gamma}$.
(3) A cost paid for the capacity of creativity, written $c(\bar{\gamma})$. We assume that higher creativity comes at a higher cost because of, for instance, greater requirements in terms of memory or learning mechanisms.

Summing these contributions we can write the fitness, $F(\bar{\gamma})$, of an individual with creativity equal to $\bar{\gamma}$ as

$$F(\bar{\gamma}) = (1 - \lambda)x + \bar{\gamma} - c(\bar{\gamma}). \tag{13}$$

An increase in $\bar{\gamma}$ will be favored by natural selection if its benefits exceed its costs. Formally, this is equivalent to the condition

$$c'(\bar{\gamma}) < 1 \tag{14}$$

where $c'(\bar{\gamma})$ is the derivative of the cost function $c(\bar{\gamma})$. What is important about this condition is that it does not depend on x, the current amount of culture. Thus higher individual creativity is favored even when the population as a whole does not have culture. Indeed, the intensity selection for individual creativity is higher when there is little culture, because when x is large the first term in Eq. (13) will tend to dilute fitness differences due to differences in creativity.

As long as natural selection for larger creativity exists, a simple assumption is that the genes will respond with a steady increase in creativity. This can be derived from standard quantitative genetics models, given that genetic variation for creativity continues to exist and that creativity is the result of additive genetic effects at many loci (in other words, we assume that the response to selection is a constant proportion of the selection differential, and that heritability does not change; Falconer, 1981). We make these assumptions because they represent a favorable case for cultural accumulation and thus allow us to establish an upper bound to the possible contribution of the genetic evolution of creativity to cultural accumulation. Going back to the population level, we can thus assume that the creativity of the population increases linearly with time:

$$\gamma(t) = \gamma + \epsilon t. \tag{15}$$

The dynamics for x thus becomes

$$\dot{x} = -\lambda x + \gamma + \epsilon t. \tag{16}$$

The solution of this equation is

$$x(t) = \frac{a}{\lambda} + \left(x_0 - \frac{a}{\lambda}\right)e^{-\lambda t} + \frac{\epsilon}{\lambda}t \tag{17}$$

where $a = \gamma - \epsilon/\lambda$. If we compare this equation with Eq. (6), which describes cultural accumulation under constant creativity, we see that the main difference lies in the last term, which increases with time at a constant rate of ϵ/λ. Thus natural selection acting on individual creativity may lead to the accumulation of culture at a constant rate, but not to accelerating accumulation.

4.3. Cultural evolution of creativity may lead to accelerating accumulation of culture

We now modify our model with the assumption that creativity may be enhanced by cultural evolution. For instance, culture may improve our cognitive or practical skills (Ong, 1982; Tomasello, 1999), as demonstrated by observations of the improved performance of the human cortex in response to experiences, including training and education (Tomasello, 1999; Deacon, 1997), and by findings such as the fast rise in IQ scores in the 20th century (Flynn, 1987). Our creativity may also benefit from innovations such as

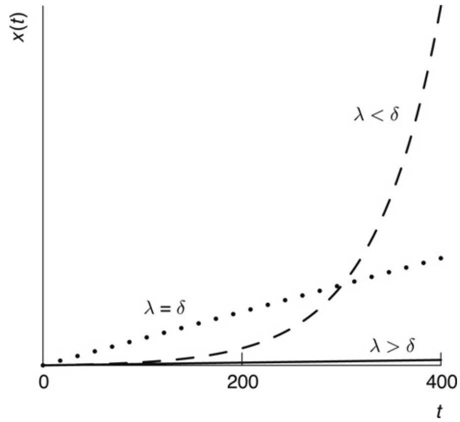

Fig. 5. Accumulation of culture following different hypotheses on the relationship between loss of culture, λ, and culture dependent creativity, δ (Eq. (19)). According to the relative magnitude of λ and δ, there are three qualitatively different outcomes: (1) an equilibrium amount of culture ($\lambda > \delta$, solid line); (2) a linear increase in amount of culture ($\lambda = \delta$, dotted line); (3) an exponential increase in amount of culture ($\lambda < \delta$, dashed line).

literacy, thinking techniques (e.g., logic and mathematics), technologies (e.g., computers). As noted in the Introduction, culture may also increase creativity by providing more raw material for innovations (Ogburn, 1950). The latter seems especially relevant when new cultural items must necessarily build on existing ones, e.g., a new mathematical theorem building on preexisting results.

There are many other cultural factors that may influence creativity, such as division of labor, cooperation and other sociocultural variables, but their analysis is beyond our present scope. Here we assume simply that creativity be a linear function of the amount of culture:

$$\gamma(x) = \gamma + \delta x \tag{18}$$

where the parameter δ measures how much an increase in amount of culture increases creativity ($\delta > 0$). The dynamics for x is now:

$$\dot{x} = -(\lambda - \delta)x + \gamma. \tag{19}$$

Note that the value of x in this equation and in the preceding one is the amount of culture that has accumulated up to the present time. Thus it depends, implicitly, on λ as well as on other model parameters. This means that the rate at which new culture is generated depends on the efficiency of social transmission, reflecting the observation that culture-dependent creativity can only operate on culture that has been preserved in the population.

Eq. (19) is formally identical to Eq. (5), with $\lambda - \delta$ replacing λ. If $\lambda \neq \delta$, the solution is

$$x(t) = \frac{\gamma}{\lambda - \delta} + \left(x_0 - \frac{\gamma}{\lambda - \delta}\right) e^{-(\lambda-\delta)t}. \tag{20}$$

The long term prediction depends here on whether λ is larger or smaller than δ. If $\lambda > \delta$ creativity generated by culture has an effect analogous to reducing λ in Eq. (6), that is an equilibrium level of culture is reached, equal to $\gamma/(\lambda - \delta)$. This value is larger than what could be reached in the case of fixed γ, but the amount of culture is nevertheless bounded. If $\lambda < \delta$, however, the outcome is dramatically different: culture accumulates exponentially, without bound. The reason is simply that culture is generated at a higher rate than it is lost. The case $\lambda = \delta$ is not ruled by Eq. (20) but rather by $x(t) = x_0 + \gamma t$. This means that culture accumulates without bound, but at a constant rate. The three cases are illustrated in Fig. 5.

We have mentioned in Section 3.1 that some errors in transmission can create a new trait rather than cause the loss of a trait. If the new trait replaces the old one, the amount of culture does not change—such errors need not be taken into account here. If both the old and the new trait are retained in the population, however, then transmission errors can contribute to an increase in the amount of culture. Can such "creative errors" be the main driving force behind exponential increase in amount of culture? Assuming a constant probability of transmission error per trait, the number of traits that transmission errors can generate is proportional to the number of traits that exist. Creative errors are then, in our framework, a form of culture dependent creativity. The problem of generating exponential increase in amount of culture by creative mistakes is that this mechanism makes contrasting demands on cultural transmission. The condition to generate an exponential increase in amount of culture is $\lambda < \delta$ which would mean that more traits should be generated by transmission errors than the traits that are lost, also due to transmission errors. A large δ would mean that transmission is sloppy enough that many variant traits are generated, but a small λ would mean that transmission is good enough that very few traits are lost.

4.4. Genetic evolution of culture dependent creativity depends on culture

If culture dependent creativity underlies the evolution of exponentially increasing cumulative culture, we need to understand the conditions under which culture dependent creativity may be favored by natural selection. An individual with a capacity of $\bar{\delta}$ for culture dependent creativity will be able to create an amount $\bar{\delta}x$ of culture in addition to what can be learned from others or created by culture independent creativity. Under the assumption that all culture is adaptive (see above), the individual would enjoy a fitness gain of $\bar{\delta}x$. If $C(\bar{\delta})$ is the cost of culture dependent creativity, reasoning as above one can show that natural selection favors an increase in $\bar{\delta}$ if

$$C'(\bar{\delta}) < x. \tag{21}$$

There are two important points to make about this condition. First, it depends on x, the current amount of culture, while the corresponding condition for $\bar{\gamma}$ is independent of x (Eq. (14)). Second, the condition, is more difficult to fulfill when x is small. This translates the intuition that the ability to create new culture based on existing culture is useful only if there is some culture to build on (Boyd and Richerson, 1996).

In conclusion, when the amount of culture is small natural selection favors capacities for creativity that do not depend on culture ($\bar{\gamma}$), but as x grows natural selection increasingly favors creativity that exploits existing culture ($\bar{\delta}$). At this point, changes in x (through cultural evolution) and $\bar{\delta}$ (through genetic evolution) reinforce each other, that is the increase in one of these variables results in a stronger selection for the other to increase as well. This kind of gene-culture coevolution agrees with the classic idea that a positive feedback may develop between the cultural and genetic evolution of cultural capacities (Dobzhansky, 1962; Wilson, 1975).

5. Discussion

Our results highlight the importance of both creativity and cultural transmission for cumulative culture. Their roles are somewhat different: improved cultural transmission reduces the loss of culture, but only creativity can produce new culture. Recent discussions of human cultural evolution have mainly focused on cultural transmission (Boyd and Richerson, 1985; Heyes and Galef, 1996; Tomasello et al., 1993; Cavalli-Sforza and Feldman, 1981), and a stronger emphasis on creativity may be important for our understanding of both the origin of culture and patterns of cultural growth and decline.

5.1. Bottlenecks in the origin of culture

The origin of human culture offers an evolutionary puzzle because extensive cultural capacities are confined to humans and do not seem to evolve easily in animals. Boyd and Richerson (1985, 1996) have thus argued that the evolution of human-like culture is subject to some significant bottlenecks. In particular, they suggest that capacities for cultural transmission are unlikely to be favored by natural selection unless some culture exist, at the same time that the maintenance of culture requires such capacities. A similar bottleneck appears in our models, because an individual's gain in fitness due to acquired culture is small when the amount of culture is small (see, e.g., the first term in Eq. (13)). Our results suggest, however, that the evolution of individual creativity can facilitate the evolution of cultural transmission. The key observation is that, for cultural transmission to be favored, it is not necessary that the information that can be transmitted has itself a cultural origin, in the sense of having been previously transmitted between generations. An alternative is that non-genetic information be continuously created by creative individuals. Such information would die with its bearers, but if individuals are creative enough there will always be some information that others could benefit from learning. This result, we stress, derives from the fact that we have not separated non-genetic information according to its origin (created in the present generation vs. inherited from the previous one). According to this scenario, the first bottleneck to be overcome in the evolution of cumulative culture may be the evolution of enough creativity to maintain a substantial amount of non-genetic information, rather than the evolution of cultural transmission in the absence of culture.

5.2. The transition to accelerating cultural accumulation and the uniqueness of human culture

Our analyses prompt us to modify somewhat the claim that cumulative culture is unique to humans, because both creativity and cultural transmission seem necessary to maintain *any* amount of culture. Thus even animal cultures may have a limited potential for growth. In many songbirds, for instance, the young learn their song from the father and other males, and it is common to find local dialects maintained as traditions (Catchpole and Slater, 1995). It is possible that the number of song elements in such dialects be in a dynamic equilibrium between creation and loss of elements, and that starting from scratch we would see an increase in the number of song elements up to the equilibrium value. A dynamical equilibrium scenario may also apply to some parts of human culture, for instance the number of person names in use at any given time, or size of the basic vocabulary in a language (not including technical terms).

That all cultures have a potential for growth does not imply that the uniqueness of human culture stems solely from quantitative differences in genetically determined cultural capacities. An alternative is that humans are unique in the extent to which culture can influence cultural capacities. Our analyses show that a cultural component of creativity may be crucial for generating an exponential increase in the amount of culture, and that such a capacity may set us apart from other animals. In our models, an exponential increase in culture occurs when culture dependent creativity more than compensates for the loss of culture caused by imperfect transmission, corresponding to $\delta > \lambda$ in Eq. (19). If $\delta < \lambda$, on the other hand, the amount of culture reaches an equilibrium value (Fig. 5). Thus the model suggests that two distinct mechanisms can contribute to a transition from equilibrium to exponential increase. The first mechanism is an increase in the capacity to elaborate on existing culture, so that δ becomes greater than λ (Fig. 6). The second mechanism is an increase in the fidelity of cultural transmission, whereby λ may fall below δ. Thus it would be wrong to conclude that the evolution of cultural transmission cannot play a role in the evolution of cumulative culture. However, our models suggest that improvements in cultural transmission may have a dramatic impact only in the presence of culture dependent creativity. Note that changes in δ and λ may arise from both genetic and cultural evolution. Schooling, for instance, may improve both cultural transmission and the capacity to elaborate on existing culture.

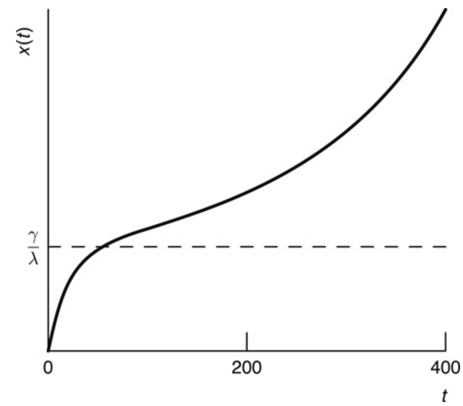

Fig. 6. Transition to accelerating cultural evolution caused by genetic evolution of cultural dependent creativity, assuming that the genes can always respond to natural selection for increased amounts of culture (cf. Eq. (15)). Cultural dynamics is given by Eq. (19), with δ starting from zero and increasing at a rate $\kappa = 0.0001$. The dashed line is the equilibrium level of culture corresponding to $\delta = 0$. Parameter values: $\lambda = 0.05$, $\gamma = 1$.

5.3. Growth, equilibrium and decline

Exponential increase in culture, of course, cannot continue forever as in our simple models. Some factor must ultimately either halt or reverse the increase of creativity, or increase the loss of culture. It is conceivable that different conditions (individual capacities, patterns of transmission, institutions, etc.) are associated with different "carrying capacities", that is with a maximum amount of culture that can be maintained, in analogy with standard models of population dynamics where each environment can support a maximum population size. Such a maximum level would depend on detailed assumptions on how culture dependent creativity and loss of culture depend on the amount of culture, and it is difficult to draw general conclusions (see Henrich, 2004; Ghirlanda and Enquist, 2007, for models that link the amount of culture and population size).

Our focus so far has been on accumulation, but our models also suggest how culture may be lost. For instance, we have used Eq. (6) to show how culture can accumulate from an initial value $x_0 = 0$ (Fig. 4). The same equation, however, predicts a loss of culture if the initial amount of culture is higher than the equilibrium level. A decrease in culture may also follow from changes in cultural capacities, for instance if γ decreases or if λ increases. Such changes may be caused, in reality, by a variety of events, for instance the deterioration of social conditions or institutions such as schools. A famous example of loss of culture is the case of Tasmanians, who lost many complex skills following their isolation from mainland Australia (Henrich, 2004), but there are many other equally interesting cases, e.g., the loss of scientific knowledge at the end of the Greek era (Russo, 2004). Our models suggest that these cases should be understood in terms of changes to capacities for preserving and/or creating culture, but are not detailed enough to describe specific cases. The latter can be the topic of future work, as outlined next.

5.4. Outlook

Our models can provide a basic understanding of what is required for an exponential increase in the amount of culture, but are a great simplification of cultural dynamics. They consider the creation and transmission of culture at the population level, without linking them explicitly to specific characteristics of individuals, to the structure of cultural information, and to social organization. To study how these variables affect cumulative culture more detailed models are required. We give here a few examples of important issues that may be investigated developing our models.

The first example concerns the actual basis of cultural capacities. Here we considered cultural transmission and creativity as separate capacities, whereas Tomasello (1999) suggests that they are both influenced by a genetically based capacity to understand others as intentional beings and Reader and Laland (2002) find that the incidence of innovation and social learning covary positively across primate species. We also considered selection on individual creativity as independent of selection on cultural transmission, while Boyd and Richerson (1985) have argued that these selective pressures may interact, because individuals who acquire information culturally may do so at the cost of individual creativity. Further research on these topics is needed to ascertain whether a significant increase in individual creativity can really favor the evolution of cultural transmission, as suggested above.

The second example concerns the interplay between culture and demography. Population growth between 1100 and 1900 AD has been approximately exponential at a rate of 0.003 yr^{-1} (McEvedy and Jones, 1978). This is less than half the growth rate of any of the disciplines surveyed by Lehman (1947) (see Table 1). Hence the increase in amount of culture is not simply a byproduct of the increase in population. That is, it cannot be explained by the hypothesis that each individual creates a fixed amount of culture. Explaining this pattern requires a more detailed model of how individuals create culture in interaction with others (Henrich, 2004; Ghirlanda and Enquist, 2007).

Lastly, a more refined model should revise our simplifying assumption that all culture is adaptive. We made this assumption because we are exploring what dynamical processes may underlie an exponential increase in the amount of culture. We are not studying the adaptive value of culture. The two issues are not unrelated, however, because the extent to which culture is adaptive can influence both its dynamics and the genetic evolution of cultural capacities. Hence, our assumption is not justified in general (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Richerson and Boyd, 2005). We have not considered this issue here because there is no theoretical understanding of what determines the proportion of adaptive and maladaptive culture. Existing models of the adaptive value of culture consider the efficiency of a single cultural trait (see above) rather than the adaptive value of culture as a whole. If culture can be genetically maladaptive the conditions for its emergence will be more restrictive than we have considered here, and it may not be possible to sustain long-term exponential growth. Preliminary results suggest that adaptive culture is more difficult to maintain than maladaptive culture, and that this might have imposed further constraints on the evolution of cultural transmission while promoting mechanisms to distinguish between adaptive and maladaptive culture (Henrich, 2004; Enquist and Ghirlanda, 2007).

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