

# Fidelity and the Emergence of Stable and Cumulative Sociotechnical Systems

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## ABSTRACT

The stability of behavior across generations is a definitional feature of culture that is typically seen as an effect of high cultural transmission fidelity. With some recent exceptions, however, formal models have rarely been brought to bear on this problem. Using an evolutionary *quasispecies* model, I here explore the connection between fidelity and the emergence of stable complex sociotechnical organization. I find that fidelity determines the “bandwidth” of cultural transmission under selection, but that the process is highly unstable and that high transmission fidelity in itself does not provide stability. This means that to explain *stability* we must look to other factors that can scaffold the transmission process and prevent crashes. It is suggested that by lowering the rate of transmission errors *and* providing robustness against the effects of errors—which is the main stabilizing factor that we identify—the evolution of sophisticated pedagogical adaptations made the unique human type of generative and flexible culture possible.

## SECTION 1: INTRODUCTION

Few probably lie awake at night wondering why early hominins never constructed tall cultural edifices like those that we see around us today. The reason why this did not happen is all too obvious—you need a big brain for that. This obvious answer is most likely also accurate—in one way or the other—but it might be instructive to nevertheless push the question further in an attempt to specify more exactly what causes what in cultural evolution. Why, for example, would cultural evolution require sophisticated cognition to be cumulative when biological evolution obviously does not? There can be little doubt that the *particular type* of culture that humans have accumulated would not be possible without cognitive capabilities on par with our’s, but could we not imagine some other type of equally complex culture based on a much less advanced cognitive apparatus? Perhaps something more like the genetically transmitted—but socially maintained nevertheless—culture-like behavior of social insects.

The retort in the next step must be that blind biological evolution required—and had—much more time on its hands. If we consider the full scope of natural history, that is surely true. But on closer inspection, the difference in pace has not been as striking as one might think. The archaeologically recorded depth of hominin culture is around 2.6 Ma (Semaw et al. 2003). But Great-Ape-like hominoids have been around since at least the middle Miocene (ca. 12 Ma; see Moyà-Solà and Alba et al. 2009), so the type of culture that we see among extant Great Apes could be on the order of 10 Ma old; simpler animal culture could of course be much older yet<sup>1</sup>. Ten Ma is also the order of time over which most major phyla arose—from a very humble starting point—during the Cambrian Explosion from ca. 543 Ma (see Erwin and Valentine 2013). Under the right conditions it seems that intelligence is not at all a requirement for

rapid evolutionary generation and accumulation of exquisitely adapted complex structure.

Granted that a hypothetical *H. habilis* or chimpanzee high culture would look very different than a human high culture, it still seems that the reason why no such thing has ever accumulated is not as obvious as it might seem. There is a channel of inheritance, there is variation and there is selection. So why is there so little cumulativity in animal culture? Why is there much more cumulativity in hominin culture? Why did human culture suddenly “explode”?

Andersson (2011) argues that important clues can be found in theory that was developed for understanding the first steps following the emergence of the original biological channel of inheritance. The new cultural channel of inheritance—like its genetic counterpart—would initially lack any structures ensuring high transmission fidelity. This is known to severely constrain how much information that can be retained in a population (e.g., Domingo et al 2012; Eigen and Schuster 1977; Schuster 1986; Szathmari and Maynard-Smith 1997). Culture would also presumably face constraints and paradoxes similar to those that faced early life (such as Eigen’s paradox; Eigen 1971)<sup>2</sup> That is, limited cumulativity would block the evolution of the very structures that were needed for cumulativity.

So the argument by Andersson (2011) is that retention is as important as invention when it comes to understanding the tempo and mode of cultural evolution. Today, whether we look at narrative or formal theorizing about cultural evolution, the focus however lies firmly on the *creative* side of the evolutionary process. What were the hominins capable of inventing? When did hominins gain the cognitive capability to invent more complex tools and practices?

The idea that capability for invention is the only credible constraint on cultural evolution is pervasive and well entrenched. Retention is (with few exceptions, see e.g.,

Henrich 2004) tacitly assumed to be a passive and automatic consequence of cultural transmission and positive selection—there is no perceived need for explaining why something that was adaptive would stably remain in place across generations.

Understanding why retention has received so little attention, and what we stand to gain from changing this state of affairs, requires a brief historical analysis. Cultural evolution is today conceptualized in close analogy with neo-Darwinian theories of organic evolution—be it formally, such as in so-called dual-inheritance theory (following, e.g., Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981), or less formally in narrative argumentation more widely dispersed throughout the literature. But this theoretical package comes not only with useful and well-established general concepts and models of evolution but also with an assortment of methodological and empirical idiosyncrasies from biology and from the history of scientific disciplines. Some are more salient and readily identifiable, such as that variation in culture is goal-directed, whereas it is strictly blind in biology. Others are more subtle, but not necessarily thereby any less important. The treatment of retention and fidelity is an example of precisely that.<sup>3</sup>

Retention is well recognized as a salient problem in evolutionary systems with low transmission fidelity in biology—such as proto-biological RNA replicators or viruses—where it has been studied using so-called *quasispecies models* (e.g., Domingo et al 2012; Eigen and Schuster 1977; Schuster 1986; Szathmary and Maynard-Smith 1997). The main difference between a quasispecies model and the “species models” that we are used to from population genetics, and that have been widely used in the study of cultural evolution in the dual-inheritance tradition, is that quasispecies models do not treat functional units (i.e., genes, habits, ideas, etc.) as atomic but as consisting of sequences of components (i.e., base pairs in the case of genes). These are replicated individually but need to make it across *together* in order to preserve the overall functionality. The main point of such a model formulation is to be able to investigate the effects of variable transmission fidelity.

In population genetics, by contrast, the concept of transmission errors lacks any meaning. If genes, ideas, representations and so on get selected they are simply transmitted to the next generation, and thereby these models tacitly assume perfect transmission fidelity. This is not problematic for the typical purposes of population genetics since—unknown at the time of the formulation of the theory<sup>4</sup>—DNA replication in higher life forms is exceedingly faithful (e.g., Drake and Charlesworth 1998). A tiny error probability per base pair raised to the power of any reasonable size of a gene is still a quite tiny probability. That is however no longer the case if the error rate is not minuscule, such as in the evolution of RNA molecules, viruses and—as argued by Andersson (2011)—culture.

Quasispecies models show us that if transmission error rates are *not* minuscule, a host of important evolutionary phenomena come to make themselves known. The essence of this group of phenomena is that transmission fidelity

becomes a strong limitation on how much information an evolutionary system can maintain over time. This brings out two factors that evade us completely if we stick with population genetics models or the narrative logic of the neo-Darwinian tradition—transmission fidelity and the complexity/size of the functional units. Andersson (2011) outlines and briefly discusses some potential effects on human evolutionary history that become visible when these factors are taken into account.

In this paper I will focus on the question of the cultural and physiological adaptations that we should expect to see if indeed fidelity and complexity has played such a role. In biological systems we clearly see such adaptations. DNA replication has a very high fidelity because of the presence of highly evolved structures and mechanisms for error correction (e.g., Kunkel and Bebenek 2000), and without these structures, biological evolution would not be possible. If fidelity rather than inventive capability has limited cultural cumulativeness, then we must suspect that mechanisms for increasing, allocating, and maintaining transmission fidelity must have played a central role also in cultural evolution.

Such an inquiry is important and timely not least because fidelity has started to attract more attention over the past years. Today the argument for how fidelity contributes to cultural stability (and thereby cumulative evolution), however, tends to be loosely conceptualized and problematized; such as by referring to fidelity as being “sufficiently high” (e.g., Goldman-Neuman and Hovers 2012; Henrich and Boyd 2002; Tennie et al 2009; Tomasello 1991; Whiten et al. 2009). We agree with Claidiere and Sperber (2010) that loosely referring to fidelity in transmission mechanisms is not enough. There is a lack of formal explorations and this, in turn, is holding back more detailed empirical interpretations of fidelity, retention, and their roles in the evolutionary process. But there does exist a recent incipient literature that the present contribution joins. Lately a small number of different modeling studies investigating various aspects of the role of fidelity in more detail have been presented. For example (Enquist et al. 2010) find that fidelity strongly affects the longevity of traditions and Lewis and Laland (2012) find that high fidelity is crucial for cultural cumulativeness.

I proceed in an exploratory way and discover that although fidelity strongly controls the “bandwidth” of cultural transmission, cultural transmission is still highly prone to crashes. This suggests a need for another set of functions, besides fidelity, to also stabilize the process—a particular type of robustness against the effects of errors. These transmission-modifying functions we see as being provided (besides a host of other and better known functions) by what we refer to collectively as *pedagogical adaptations*<sup>5</sup>, connecting thereby to an emerging body of work on the importance of pedagogy in cultural evolution (see, e.g., Csibra and Gergely 2009, 2011; Dean et al 2012; Gergely and Csibra 2006; Lehmann et al 2011; Sterelny 2011; Tehrani and Riede 2008; Tennie et al 2009; Thornton and Raihani 2008; Tomasello 1991).

## SECTION 2: WHAT IS A COMPLEX SOCIOTECHNICAL SYSTEM?

The model that I will use is based on three main assumptions about “cultural traits” that need to be argued and delimited to be correctly understood: (1) complexity affords key adaptive functionality; (2) the function of cultural traits is sensitive to change; and, (3) complex cultural traits are harder to transmit than simpler traits. But I will begin by specifying what I mean by complexity and by that also what I mean by concepts like traits and fidelity.

Let us for these purposes conceptualize cultural traits as hierarchical sociotechnical systems of nested components (see, e.g., Arthur 2011; Simon 1996; Wimsatt and Griesemer 2007); this conceptualization is also inherent to the idea of combining and re-combining cultural traits which has lately begun to be explored also in paleoanthropology (see, e.g., Lewis and Laland 2012). By referring to “socio-technical systems,” I wish to emphasize the entangled and heterogenous nature of cultural systems—they contain social as well as technological (or artifactual) components and these are not separable in the general case; e.g., a tool makes no sense without methods for using it and without identified attributions of functionality.

We may frame such an approach in two statements as follows:

1. Cultural traits can be recursively decomposed into systems of smaller components.
2. Components of such systems are functionally linked and cannot change independently.

Saying that cultural traits can be recursively decomposed into systems of subcomponents (see, e.g., Arthur 2009; Sanden and Hillman 2011; Simon 1996) means that a cultural trait could then be defined on any level in this hierarchy—from an entire culture down to its smallest components. We will therefore speak of traits as being more high- or low-level to indicate approximate vertical position in this hierarchy. What these components would be differs from case to case—the components of a belief may be a narrative containing a system of mutually supporting sub-beliefs that may be similarly unpacked; a tool on the other hand may contain both material elements and the skills needed to combine them and so on recursively. We say that a cultural trait is *complex* to the extent that it relies upon a large system of components and inter-linkages if we unpack it recursively like this. This amounts basically to a Kolmogorov type of complexity measure (e.g., Li and Vitanyi 2008), or “structural complexity” (e.g., Erdi 2008), or simply “complicatedness.”

It is well to note some consequences of this hierarchical view of culture and its components. A high-level trait may *rely on* a highly complex hierarchy of component traits, but its own manifestation is not necessarily—or even likely—very complex on that account, for example, a javelin thrown with accuracy at the right moment, or an arrowhead with a specific imposed form. A more everyday example would be a smartphone—despite the tremendous complexity of its organization all the way down to the molecular level, including the skills and tools that go into de-

signing and manufacturing it, it is still simple enough on its functional level that an infant can master it. So when we speak of “complex traits” we primarily mean traits that rely on a tall and wide hierarchy of sub-traits, not traits whose *manifestations* are complex. What sets the manifested complex trait *itself* apart from the simple trait—as I will discuss shortly—is more that the former is less arbitrary than the latter. Complexity is *behind* the complex trait; it may or may not be evident *in* it.

With this background, we must suspect that complex traits have a larger target area for mistakes in cultural transmission. Moreover, since sub-traits are interlinked, changes in one component tend to cascade throughout such systems with results that are potentially catastrophic to high-level functionality (see, e.g., Wimsatt 1999; Wimsatt and Griesemer 2007). How sensitive traits are to changes in the underlying trait hierarchy, of course, varies greatly both within and between traits<sup>6</sup>.

What I will argue is that many traits are indeed highly resilient to errors and omissions, but that this is not a robustness that cultural traits enjoy automatically. They need to be organized and scaffolded to be robust. The presence in hominin societies of sophisticated and costly pedagogical institutions and cognitive capabilities indicate that there are strong and important problems inherent to the transmission of cultural traits that warrant the maintenance of such cultural and biological adaptations.

We may now revisit assumptions 2 and 3 at the beginning of this section. **Complex cultural traits are harder to transmit than simpler traits:** Generally speaking, the components of a trait must make it across *together* in transmission, and this means that the fidelity of a trait will be the *product* of the fidelity of its components. Half a skill (like half a gene) does not imply half a functionality. The transmission fidelity of a trait will therefore tend to decrease *exponentially* as a function of its complexity.

**The function of cultural traits is sensitive to change:** The function of a trait will often be highly sensitive to change in the hierarchy of traits that it relies upon, be it in the form of errors in transmission, omissions, or supposed improvements, or indeed any type of changes. A small change can destroy a complex trait as easily as it can destroy a simple trait.

## SECTION 3: COMPLEXITY AND FITNESS

Obviously, making a cultural trait more complex does not by itself improve function, nor does improving function necessarily require making the trait more complex. In fact, the opposite is frequently true. But generally speaking you can do more with more and sometimes you *need* more. It is, for example, hard to see how rabbit hunting could be made as simple as, say, picking up turtles. The point is neither that a turtle picking skill would benefit from becoming more complex, nor that rabbit hunting in itself is “more fit” than turtle picking because it is more complex. The point is that complexity is key to two highly abstract, but no less important, affordances—flexibility and specialization. For hominins to effectively hunt rabbits, a certain degree of

strategic and technological complexity is needed, so if this complexity is unattainable, then so is the ecological specialization of targeting rabbits. In short, complexity enables. In summary, we can see that the argument that “complexity affords key adaptive functionality” works especially well when we consider cultural traits on a high level of organization, e.g., entire systems of tools and behaviors rather than singular tools or behaviors.

To the extent that increased trait complexity affords specialization and otherwise unattainable adaptive functionality, that means that complexity should in many cases have a tendency to increase. This tendency is central to the model that I will be using here. In terms of actual processes, the issue of *how* complexity would grow can be described from the point of view of innovation studies and developmental psychology as a consequence of human—and presumably hominin—inventiveness in the face of opportunities and problems that appear as cultural traits are being exercised. As a trait is being used in its area of application, opportunities for changing it come to be revealed in its “zone of proximal development” (Vygotsky 1978) or “zone of latent solutions” (Tennie et al 2009). One important modality of change is expansion by adding new components *within* the trait’s organization, causing it to swell in a “sandwiched” fashion (Lane 2005), while combining traits, as modeled by Lewis and Laland (2012) represents another. This dynamic has also been described as a tendency for innovation to cascade (see, e.g., Lane 2011; Schiffer 2005).

#### SECTION 4: TRANSMISSION FIDELITY FOR COMPLEX CULTURAL TRAITS

By fidelity I will mean quite generically the likelihood of cultural traits to make it across in transmission without functionally consequential errors being introduced. It would really be more accurate to speak of “maladaptive change” rather than “error” since traits are sensitive also to changes that cannot be properly labeled as errors. But to simplify the terminology (and avoid lengthy definitions) I will retain the term “error”.

Exactly what goes into the fidelity concept depends on which level of this hierarchical organization that the trait and its transmission resides. I see fidelity as a functionality of a range of processes across many levels of organization, and involving both social and material (sites, artifacts, etc.; see, e.g., Clark and Chalmers 1998; Menary 2010) channels. In other words, it covers, but is not limited to, fidelity in microlevel social interactions, which is the context in which the term is most frequently used (on the level of exchanges between individuals, see, e.g., Eerkens and Lipo 2005; Whiten et al. 2009). Pedagogical adaptations and institutions involving learning, teaching, apprenticeship, imitation, emulation, and language have, for example, been cited as sources of high fidelity (e.g., Csibra and Gergely 2009, 2011; Dean et al. 2012; Gergely and Csibra 2006; Lehmann et al 2011; Sterelny 2011; Tehrani and Riede 2008; Tennie et al. 2009; Thornton and Raihani 2008; Tomasello 1991) and they act across many such different levels. I also will argue that such pedagogical adaptations and institutions have

other important effects on cultural transmission than that of increasing transmission fidelity.

## SECTION 5: THE MODEL

### SECTION 5.1: OVERVIEW

The model stylistically depicts an age-structured population of agents in possession of culturally transmitted traits that convey variable adaptive advantages. These traits could be anything from a tool to a hunting strategy to an entire role of an individual in a society. Younger agents are associated with older agents to engage in a process of learning that may or may not be successful. The selection of role-models to which younger agents become associated is based on the quality of the possessed trait variant and is best described as success- or prestige biased (see, e.g., Henrich and McElreath 2003).

The probability of successfully transmitting a trait is modeled as a component-level transmission fidelity raised to the power of the complexity of the trait. We thereby say that to retain the function of a trait, all components must make it across (see Section 2). Relaxing that assumption has important effects, but those are among the effects that we want to investigate, so we will begin from this ideal starting point and exploratorily extend the model.

Selection acts directly on complexity in the model. As I have argued, this does not mean that I assume that complexity *in itself* conveys fitness but rather that complexity provides affordances that are necessary to achieve some generally adaptive results, namely specialization and flexibility (see Section 3). Adaptive change exploiting such affordances is modeled as random increases in the complexity of traits. This corresponds to the agent holding the trait in question performing an invention (e.g., addition or combination) that increases its complexity and results in an increase in the utility that is derived. Other types of adaptive change are not modeled.

The main difference between this model and the original model by Andersson (2011) is that I here explore the impact of population size and articulate the model further by introducing a number of additional parameters. In the original model, variants were identified as the cultural systems of entire groups, so in order to go more into the details of the transmission process I here move from a demographical meta-population to populations of role models and learners within single groups.

### SECTION 5.2: MORE FORMALLY

The model simulates the evolution of a single trait *quasispecies* (see Section 1) where fitness

$$F(T) = C(T)^\epsilon, \quad (1)$$

is a function of the complexity  $C(T)$  of trait variants and a parameter  $\epsilon$  (elitism) that controls the strength of the selection pressure for more complex traits. With  $\epsilon \rightarrow 0$ ,  $F$  converges to unity (complexity brings no opportunities and is therefore not selected for), and as  $\epsilon$  increases, traits with

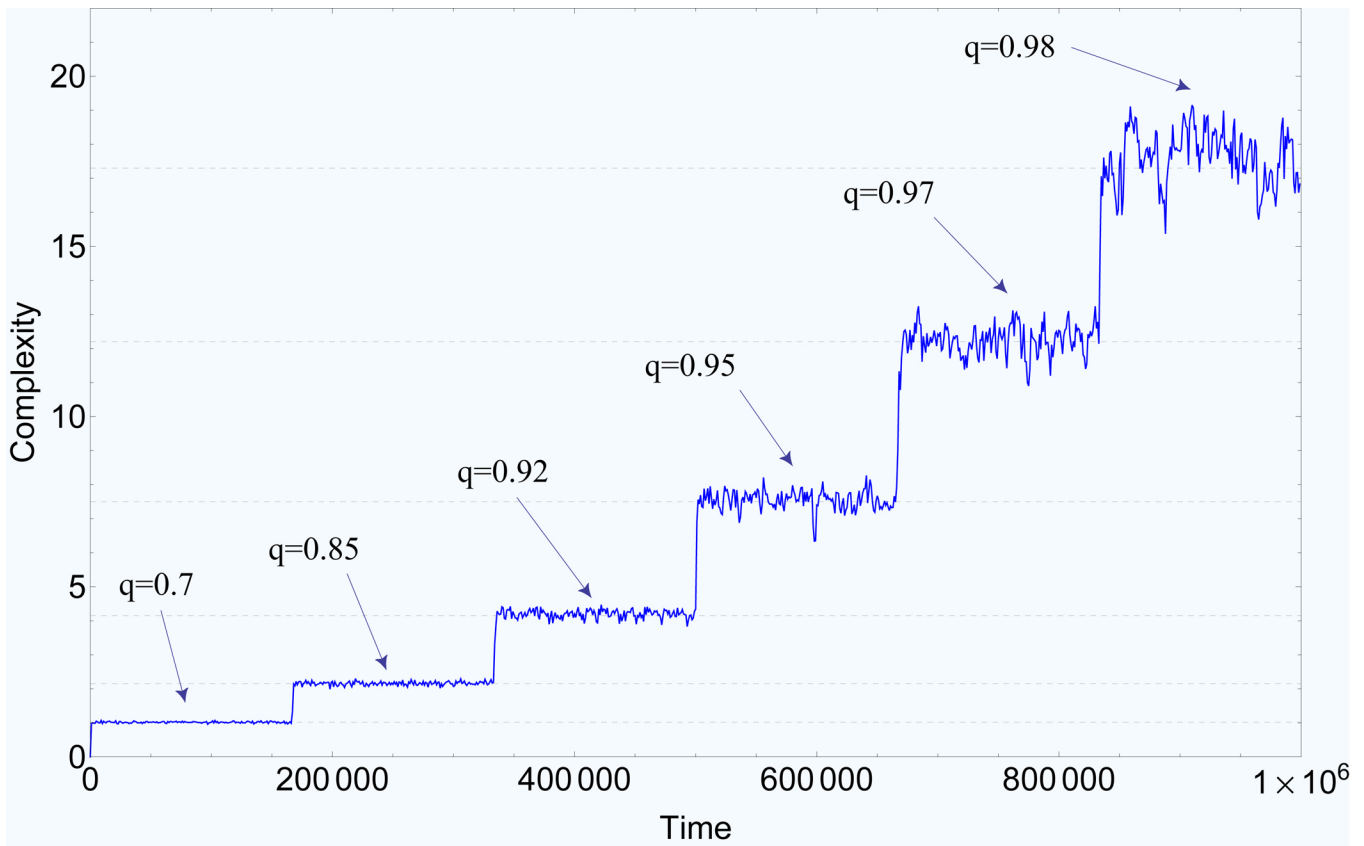


Figure 1. Above we see a time evolution of average complexity as the fidelity parameter  $q$  is taken through six steps, each yielding a corresponding jump in the average trait size present in the population. Model parameters:  $N=100$ ,  $\varepsilon=2$ ,  $\sigma=0.05$ .

higher complexity will dominate more and more.

The model implements a population of  $N$  agents, where each agent  $A$  is in possession of a trait variant  $T(A)$ . At each time step a turnover fraction  $\tau$  of the population, selected with a probability linearly dependent on their age, is replaced by new agents, keeping the population at a constant size.

Selection of “role models” from which new agents’ traits are adopted is success-biased with the probability of selecting an agent being proportional to the fitness value of its trait

$$p(A) = \frac{F(T(A))}{\sum_i^N F(T(A_i))}. \quad (2)$$

Upon having selected a role model  $A_{teacher}$ , the new agent  $A_{new}$  is encultured by adopting the trait  $T(A_{new}) = T(A_{teacher})$  subject to a per-component fidelity,  $q$ , such that with probability<sup>8</sup>

$$p(T) = 1 - q^{C(T)} \quad (3)$$

the agent fails to learn the trait, which is then lost to that agent. Finally, at a rate  $\lambda$  a successful learner increases or decreases the complexity of the the trait  $C(T)$  by one unit

with equal probability.<sup>9</sup> The parameters  $\lambda$  and  $\tau$  are fixed throughout at  $\lambda = 0.1$  and  $\tau = 0.05$ . Varying either (within reasonable bounds) will only have the effect of compressing or expanding the temporal pattern.

## SECTION 6: RESULTS AND EXPLORATIONS

### SECTION 6.1: THE BASIC MODEL

The relationship between transmission fidelity  $q$  and the complexity that can be maintained was investigated by Andersson (2011) and that relationship also applies in this formulation. This is shown in Figure 1, where a time evolution is subjected to periodical increases in  $q$ , bringing it through a series of transitions; the parameter  $\sigma$  used in Figures 1 and 2) will be introduced shortly. As soon as transmission fidelity increases, the pressure for more complex traits will promptly push the sizes of traits in the population up to a new equilibrium level (the “Glass Ceiling”) where too large variants are culled by the exponentially increasing error rate and smaller variants are eliminated by positive selection favoring longer traits.

“Cultural memory capacity” as a function of transmission fidelity (i.e., the level of the Glass Ceiling), was determined by Andersson (2011) analytically as

$$N_c = -\frac{1}{\ln q}, \quad (4)$$

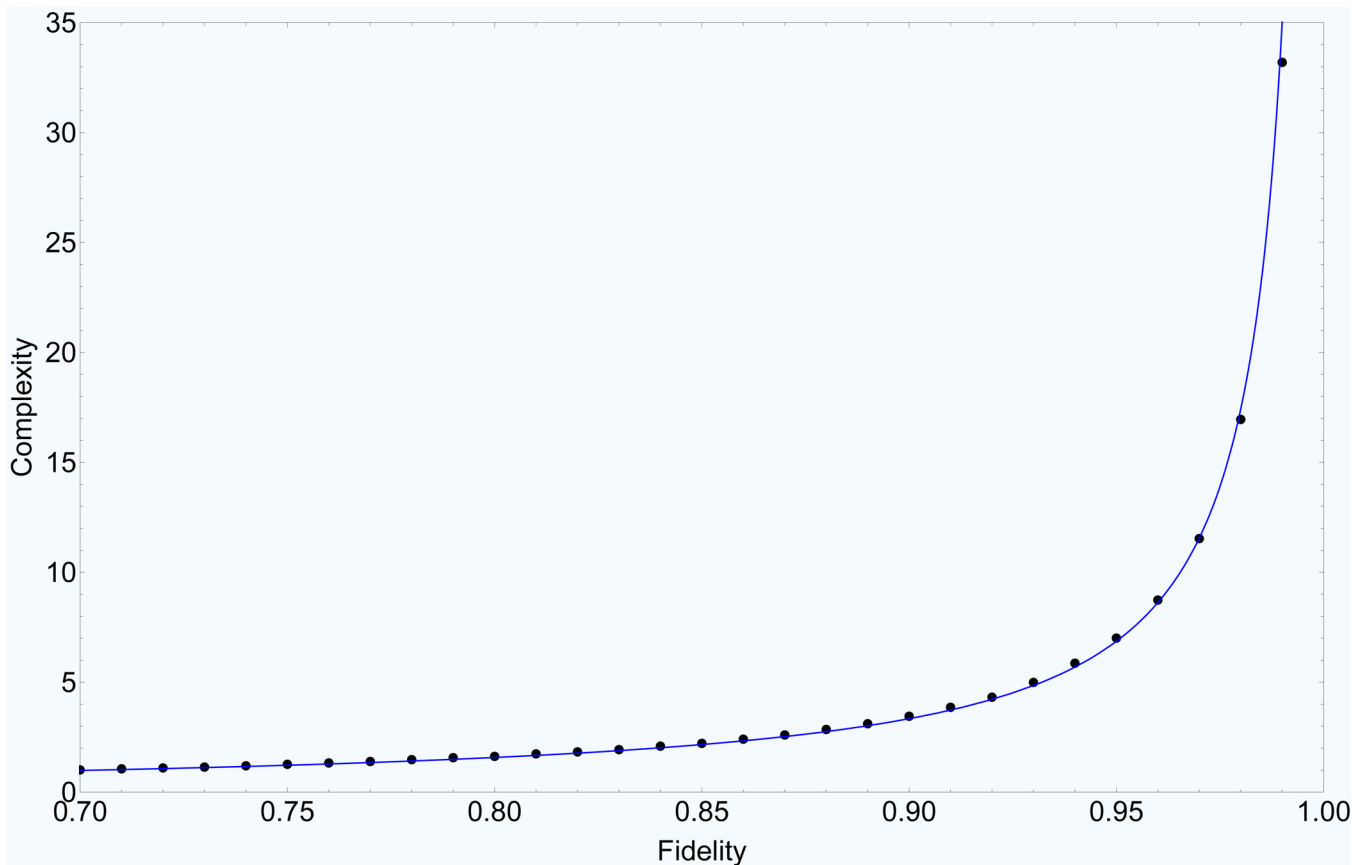


Figure 2. Plotted above is equilibrium average complexity as a function of transmission fidelity. Dots represent data from runs of the model and the line represents the analytical model (Equation 4) from Andersson (2011). The scale factor used to fit the curve was 0.359. Model parameters:  $N=200$ ,  $\varepsilon=1$ .

with  $N_c$  denoting the critical trait size; i.e., the complexity beyond which the population is not capable of retaining traits over time at a given value of  $q$ . As can be seen in Figure 2, the analytical model predicts the behavior also of the model used here down to a scale factor.

The commanding effect of replication fidelity on the amount of complexity that can be maintained stands firm, but the present model also reveals a much richer story that did not emerge from the model used by Andersson (2011). Figure 3 shows us that the balance seen in Figure 1 between transmission failure and selection by no means obtains automatically. In Figure 4, I look more closely at these dynamics and it is revealed that maximum and minimum complexity in the trait population follow each other very closely. The minimum and maximum complexity curves outline the distribution of complexity within the population as it evolves, and we can see that it is driven well past the Glass Ceiling level by selection. But above the Glass Ceiling level, the competitive advantage of traits no longer compensate for losses due to errors, so the “reservoir” of individuals that possess a functional version of the trait, and that can serve as role models, decreases. The crash occurs when the size of this reservoir fluctuates to zero.<sup>10</sup> This also applies if complexity gets increased only exceedingly rarely (using very low values of  $\lambda$ ); it only takes a longer time to reach the Glass Ceiling.

In Figure 3, we see that the more strongly that complexity is selected for, the more unstable the cultural memory becomes.<sup>11</sup> In other words, while there must be a pressure for higher trait complexity if complex traits are to accumulate in the first place, the stronger that pressure gets, the more forcefully will the population of traits be pushed against the Glass Ceiling from below. This increases the likelihood that the whole population will simultaneously find itself in the critical region.

## SECTION 6.2: STABILIZING A CUMULATIVE CULTURE

The Glass Ceiling effect tells us that fidelity imposes a critical level of complexity beyond which traits will not be stable. But it does not tell us how trait populations would avoid being driven past that point by selection. The main lesson so far is that a high transmission fidelity in itself does not help, and this means that we must look to other circumstances and mechanisms to explain what could prevent trait populations from crashing. To begin exploring this question, let us briefly consider how different types of traits may interact with this Glass Ceiling effect.

In Section 3, I compared rabbits and turtles to argue that certain resources demand a high degree of trait complexity for effective harvesting. But once a particular resource is efficiently harvested (e.g., to the carrying capacity

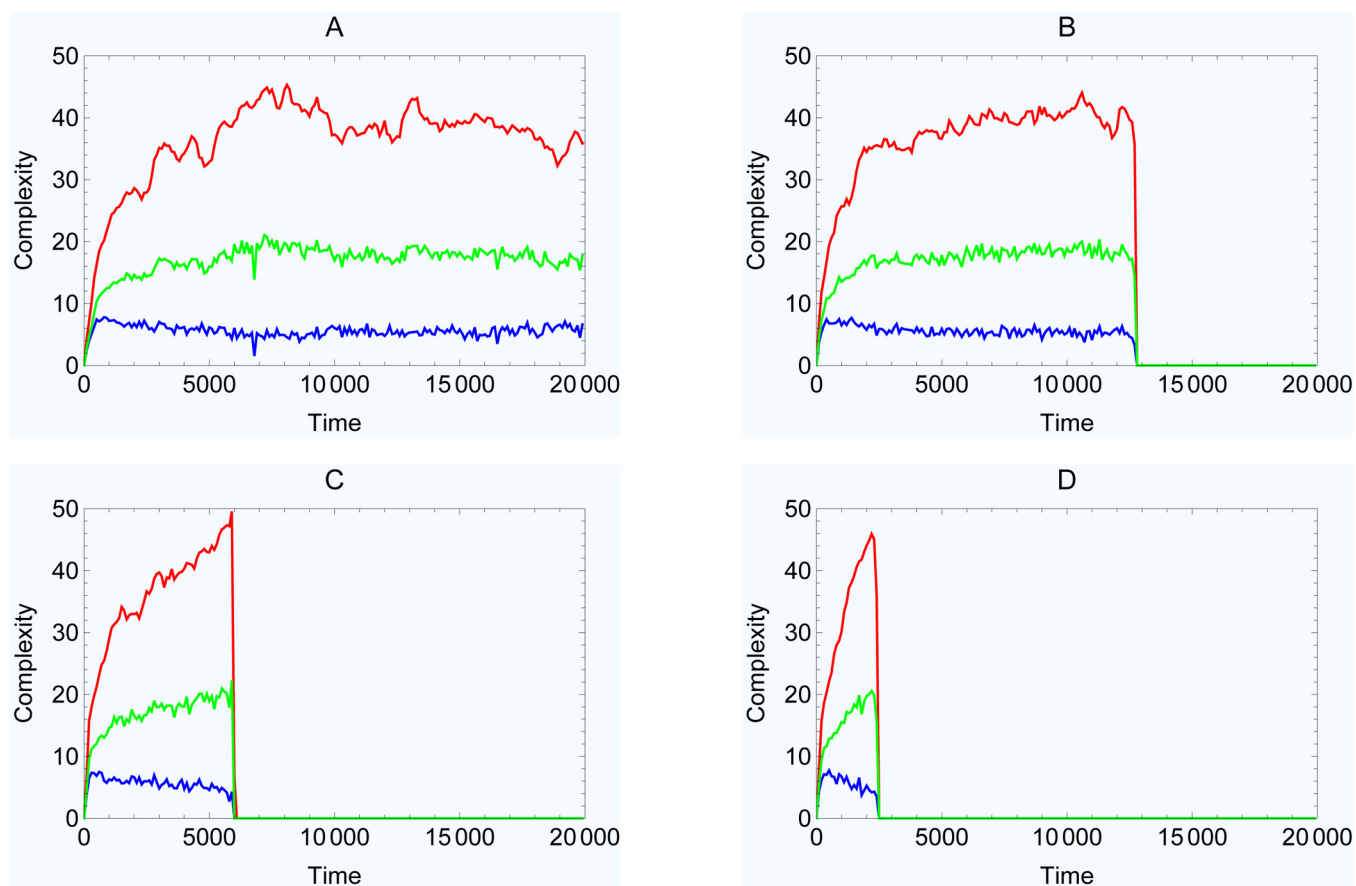


Figure 3. Figures A-D show time evolutions of complexity over 20,000 iterations. Elitism values  $\epsilon$  of 3, 5, 8 and 12 are used respectively. The red (top) lines show maximum fitness, the blue (bottom) lines shows the average fitness over the whole population, the green (middle) lines shows the average fitness of the role models selected for transmission. The idea is to outline how the distribution of the complexity of trait populations evolves over time. Model parameters:  $N=100$ ,  $q=0.95$ .

of the resource) the adaptive affordances brought about by increasing the complexity of the trait further will rapidly dry up. For certain resources this will happen sooner and in others later. For turtle and berry picking it probably happens quite quickly while for rabbit and large game hunting additional complexity is likely to keep paying off for quite some time.

Given a certain level of the Glass Ceiling, we can see traits falling into two categories (Figure 5): (i) those where the adaptive affordances of additional complexity run out safely before the Glass Ceiling; and, (ii) those where they do not. What we have been modeling are those that fall into the latter category.

We believe that traits in category (ii) are particularly important in hominin societies. Not only will more innovation paths forward be opened up by increasing cognitive capability in hominins (see, e.g., Read and van der Leeuw 2008), there is also a type of basic and generative traits that appear to be characteristic of hominin culture. These act as components in wide ranges of high-level traits and are highly recombinatorial. A prime example of this is modified lithic technology, which lends itself to exceptionally wide uses, such as cutting, scraping, and piercing (Davidson and McGrew 2005). Apart from affording the potential

to branch out into many types of more specialized tools, lithic tools may also be used for fashioning (and from the early Middle Palaeolithic/Middle Stone Age become part of, see, e.g., Mazza et al. 2006; Rots and Van Peer 2006; Rots et al. 2011)<sup>12</sup> secondary implements, providing a tremendous leverage on their range of uses and on their propensity for generating open-ended trait systems.

Just as important in this respect may be the rarity of suitable lithic raw material, as evidenced by its conscious transportation (e.g., Braun et al 2008; Stout et al. 2010) already in the Oldowan; see also Goldman-Neuman and Hovers (2012) who also link an increase in the complexity of technological organization during the Oldowan to higher transmission fidelity. Even without diversifying or specializing function there was a consistent potential for increasing economic efficiency through the entire production chain, from raw material procurement to tool use—higher quality raw material, caching of raw materials and tools, exchange, sharing, trade, control over the shapes of produced flakes, retouch of worn tools to renew or change properties, and so on (for a review of how lithic technological organization is currently viewed, see Andrefsky 2009). While far from all individual traits in hominin culture would fall into category (ii), hominin culture as a whole seems to be

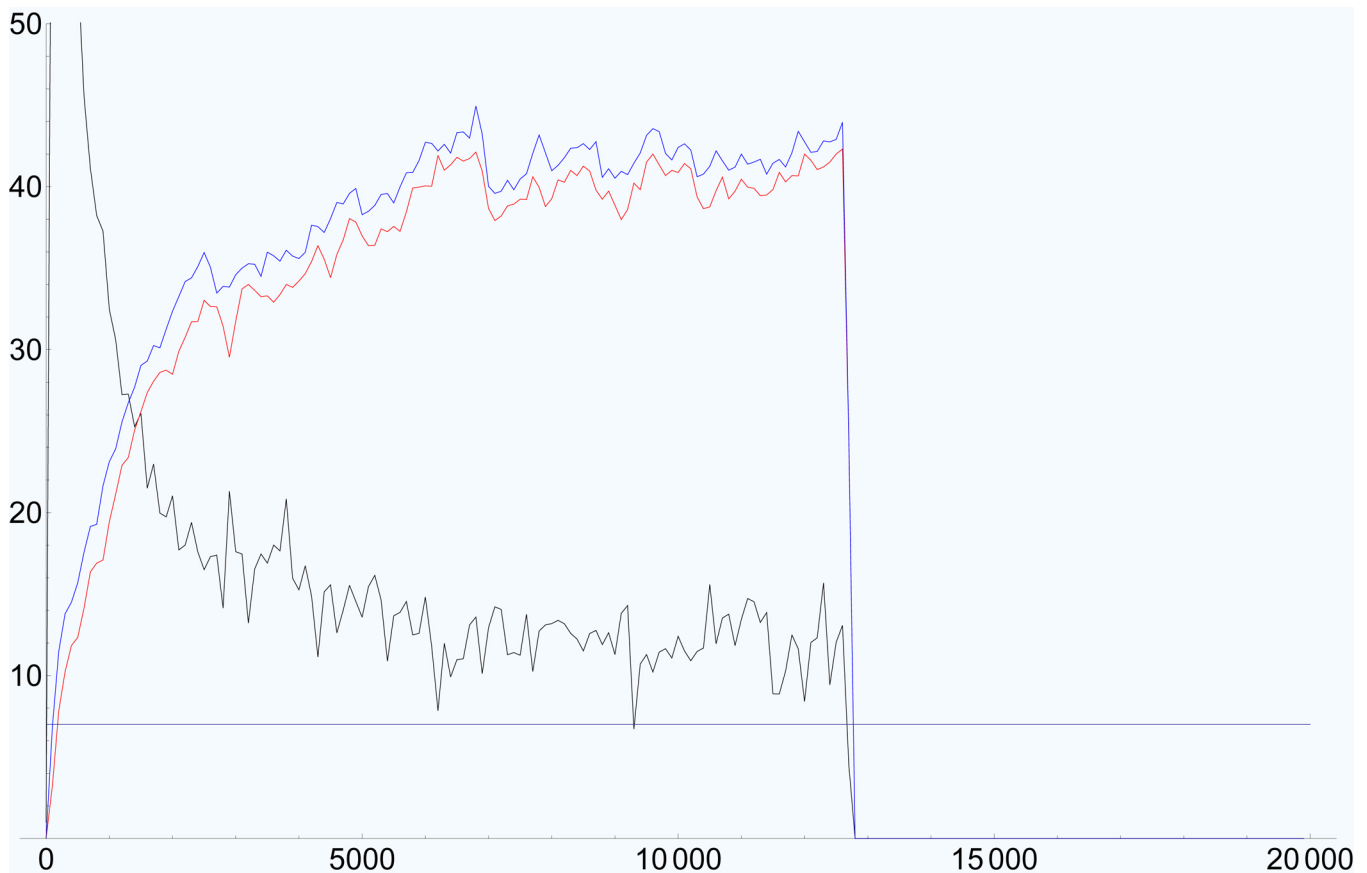


Figure 4. The horizontal line shows the approximate theoretical level of the Glass Ceiling, computed using Equation 4 with the scaling factor used in Figure 2. The blue line (top at crash) shows the time evolution of the maximum complexity and the red line (middle) shows minimum complexity. The black line (bottom) shows the number of individuals that possess a functional trait and that are thereby able to serve as role models. Model parameters:  $N=100$ ,  $q=0.95$ .

quite open-ended and to more or less perpetually fall into category (ii).

So stability would be ensured automatically for traits falling into category (i), while for those in category (ii) we would need something more. A plausible candidate would be mechanisms ensuring what we might call “trait robustness under transmission”—that imperfect learning leads to simpler but still functional versions of the trait rather than to a complete loss of function. A specific mechanism in human cultural transmission that provides this type of learning is what Thornton and Raihani (2008) refer to as “progressive learning” whereby tasks are structured to become progressively more demanding in a logical sequence such that the next step builds upon and extends what has already been mastered (see also, e.g., Greenfield et al. 2000; Stout 2005). The utility and complexity of the skill increases gradually as the transmission process unfolds and apprentices are made useful long before they have achieved full mastery of their skills (e.g., Bock 2002; MacDonald 2007; Shennan and Steele 1999). The risk of turning out apprentices that cannot transmit the trait further at all—as would be the case in our base model—is thereby minimized. But making the most out of each apprentice will of course also have an economic and much more direct value. What I sug-

gest here is that a less obvious by-effect of also stabilizing transmission would be of crucial importance for the evolution of hominin culture.

We are not in a position to answer the question of to what extent these pedagogical strategies can be argued to apply also to cultural transmission in other species. But it does appear reasonable to suspect that unless we are speaking of very simple cases, pedagogical strategies probably require quite a deal of cognitive and psychological adaptation. In human culture, such a pedagogical system is highly developed, is widely seen as having deep roots in the past, and has been suggested as a defining feature of hominin culture that has co-evolved with cognitive and psychological adaptations (Csibra and Gergely 2009, 2011; Gergely and Csibra 2006; Sterelny 2011; Tehrani and Riede 2008; Thornton and Raihani 2008).

Species that lack the ability to maintain complex pedagogical institutions may therefore be limited to maintaining traits that fall into their category (i). Moreover, just as it is conceivable that cognitive capabilities can serve to make traits more generative (i.e., more likely to fall into category ii; see also Read and van der Leeuw 2008), it is also conceivable that cognition could be adapted to *keep* traits in category (i). Tennie et al. (2009) identify the emulation of



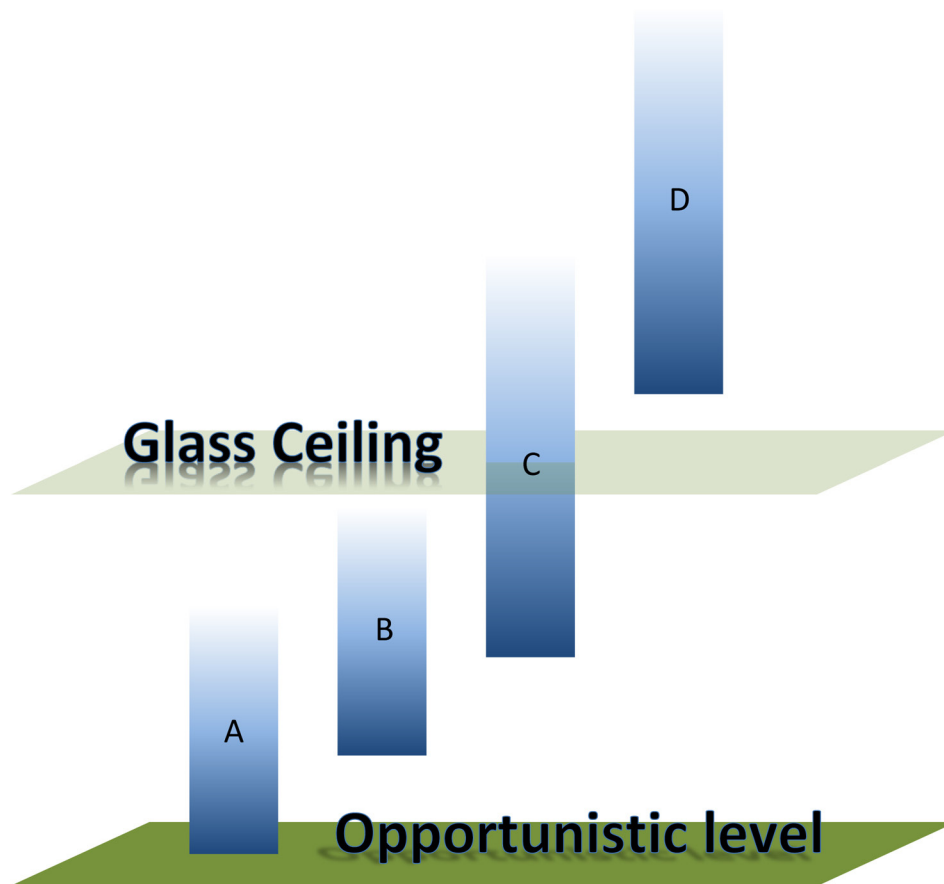


Figure 5. Four hypothetical traits are illustrated in relation to the Glass Ceiling and an “opportunistic level,” meaning that no trait must be culturally carried to enable the strategy. Color gradient corresponds to pressure for higher complexity. A is a trait that is available as an opportunistic strategy but that can be improved by the development of a culturally carried trait that would belong to category (i) since the pressure for complexity abates before the Glass Ceiling level. B is a strategy that is not opportunistically available but that is also in category (i). C is a category (ii) trait. D represents a trait that is currently unattainable as its minimum effective complexity is above the level of the Glass Ceiling.

outcomes (rather than imitation of process) that chimpanzees frequently employ for learning as having precisely the effect of limiting cumulativity (see also Dean et al. 2012) by limiting the potential for transmitting trait components whose causal role may not be immediately obvious. Horner and Whiten (2005) furthermore show that this seems not to be due to an *inability* to imitate—chimpanzees preferentially choose to emulate outcomes unless a lack of information leaves imitation of an observed process as the only option; see also Whiten et al. (2009).

I will not take up space with graphs from an implementation of category (i) traits. The results are precisely what could be expected and what was explained just above—traits are stabilized if the pressure for complexity abates before the Glass Ceiling. But in order to investigate what happens when pedagogy is applied to deal with category (ii) traits we will introduce a new parameter  $\sigma$  to the model by which we control the probability that an error (Equation 3) will yield a simpler variant rather than a lost trait. This is implemented in the following way—every time an error occurs, the outcome will be a simpler variant with probability

$p = \sigma$  and a lost trait with probability  $p = 1 - \sigma$ . We thus obtain the original model when  $\sigma = 0$ .

As we see in Figure 6, this mechanism appears to be powerful as a way of achieving stability. Notably, increasing the selection pressure for more complexity no longer strongly affects stability (compare the  $\epsilon$  value with the values used in Figure 3). We also see that in the parameter regimes that we have used so far this simplification effect does not even have to be very strong. What is important is the persistent presence of less complex versions that persistently keep the population partly below that Glass Ceiling. As the rate of error explodes past the Glass Ceiling, so will also the production of those simpler traits resulting from imperfect learning, leading to a quite robust self-regulation of category (ii) traits.

Comparing Figure 7 with Figure 4, we can see the effect of  $\sigma$  more in detail. The span of trait complexity in the population is much wider here, and, significantly, minimum trait complexity remains in the vicinity of the Glass Ceiling level throughout. This ensures that the reservoir of potential role models remains large enough that it is unlikely

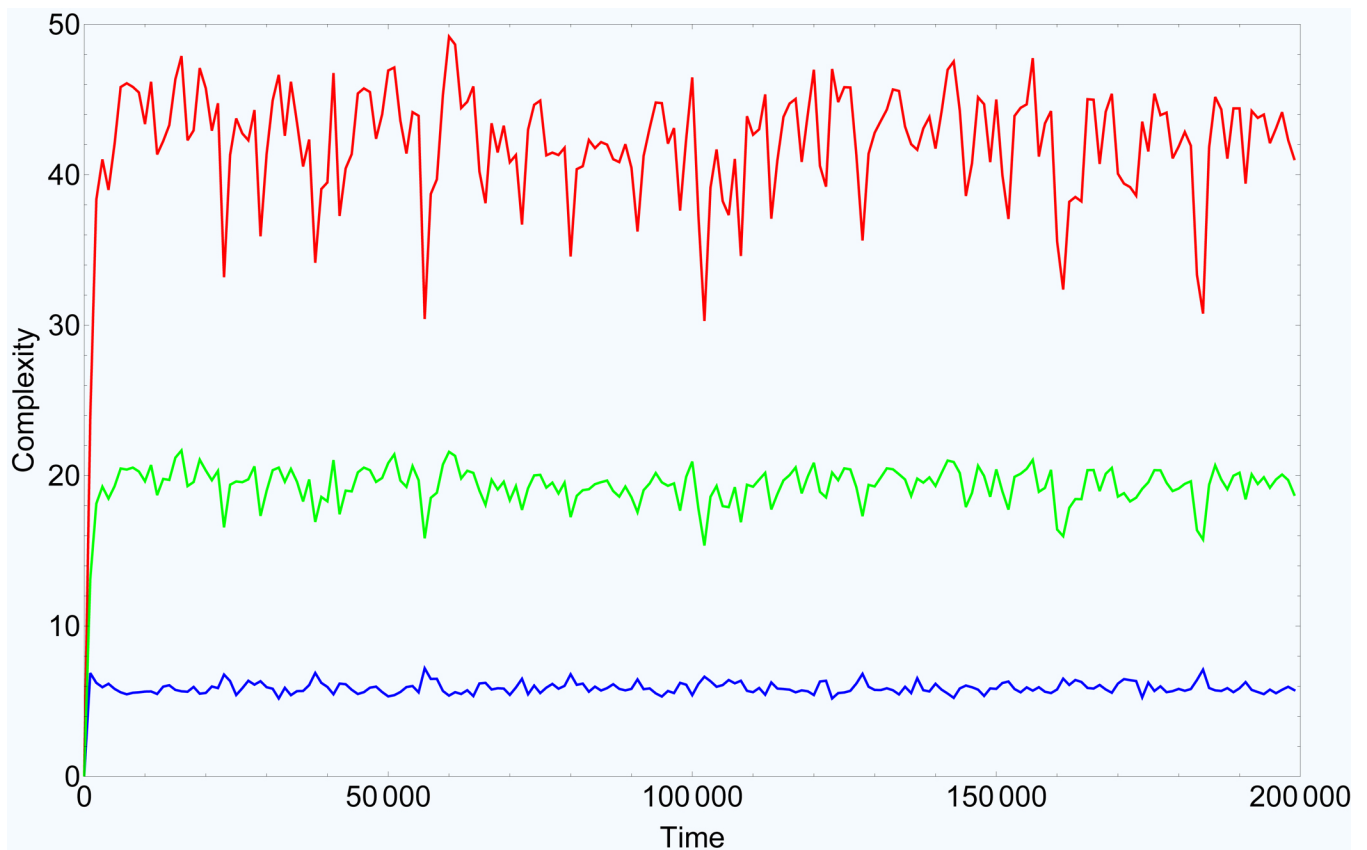


Figure 6. Shown above is a time evolution of complexity using imperfect learning. The red (top) graphs show maximum fitness, the blue (bottom) graph shows the average fitness over the whole population, the green (middle) graph shows the average fitness of the role models selected for transmission. Imperfect learning leads to traits of uniformly distributed random lengths between zero and the size of the trait whose copying was attempted. Model parameters:  $N=100$ ,  $q=0.95$ ,  $\varepsilon=12$ ,  $\sigma=0.05$ . Note that the time evolution in Figure 3 is only plotted over a tenth of the time shown here.

to fluctuate to zero. One can clearly see how excursions in complexity are mirrored by the size of this reservoir.

Besides fidelity, population size is a factor that has recently been implicated in the question of technological complexity in the literature, see, e.g., Henrich (2004); Kline and Boyd (2010); Powell et al. (2009, 2010). The main hypothesis in this literature is that larger populations are able to maintain more complex and highly adapted technology. This hypothesis has been subject to criticism by Read (2006, 2008, 2009, 2012) aimed both at the formulation of the models and at the empirical basis for making such a connection. As we see in Figure 8, population size also here has little effect on the complexity of strategies in the population. Although population size early on has a clear impact on average trait complexity, this effect rapidly diminishes as population size increases. But population size has another potentially important effect: it reduces the incidence of crashes (Figure 9). The mechanism is simple—the larger the trait population the lower the probability that the reservoir of potential role models will fluctuate to zero.

With very small populations, much higher demands are placed on pedagogical adaptations (such as apprenticeship institutions) to generate what would correspond to a high  $\sigma$  value (Figure 10). The mechanism is again simple—

what is important is that there are sustainable variants available at all time, so with a small population,  $\sigma$  must be higher for its stabilizing effect to kick in.

Very small trait populations could be a consequence of small groups but also of division-of-labor across larger groups, and both these conditions can be argued to have applied in important ways in the deep past. Pre-Upper-Paleolithic residential groups appear to have been very small. It was recently estimated by Vallverdú et al. (2010) that Neanderthal occupations held groups of only single digit sizes. Although these may have represented “task groups” connected over a larger area it still provides an indication that populations of cultural traits must have been quite small during the Middle Paleolithic and before<sup>13</sup>. Furthermore division-of-labor could also strongly reduce trait populations, so improvements in pedagogy might have been a precondition for the development of a diverse “gadget technology” in the Upper Paleolithic and Late Stone Age (Hayden 1981; Kuhn and Stiner 2001).

## SECTION 7: SUMMARY AND DISCUSSION

### SECTION 7.1: SUMMARY

In this paper I have continued the investigation of an evo-

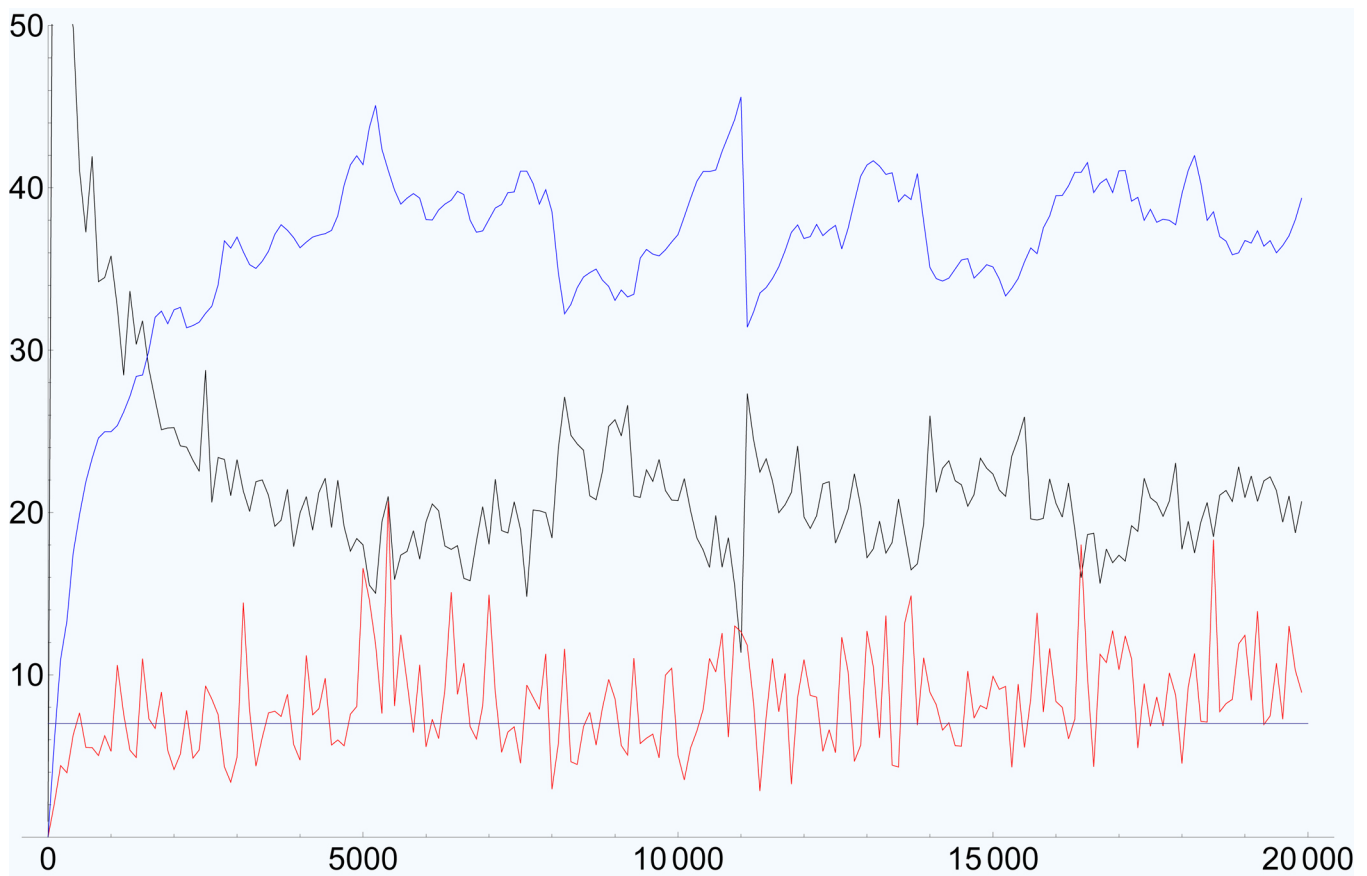


Figure 7. As in Figure 4, the horizontal line here shows the approximate theoretical level of the Glass Ceiling, computed using Equation 4 with the scaling factor used in Figure 2. The blue line (top at right) shows the time evolution of the maximum complexity and the red line (bottom) shows minimum complexity. The black line (middle) shows the number of individuals that possess a functional trait and that are thereby able to serve as role models. Model parameters:  $N=100$ ,  $q=0.95$ ,  $\sigma=0.05$ .

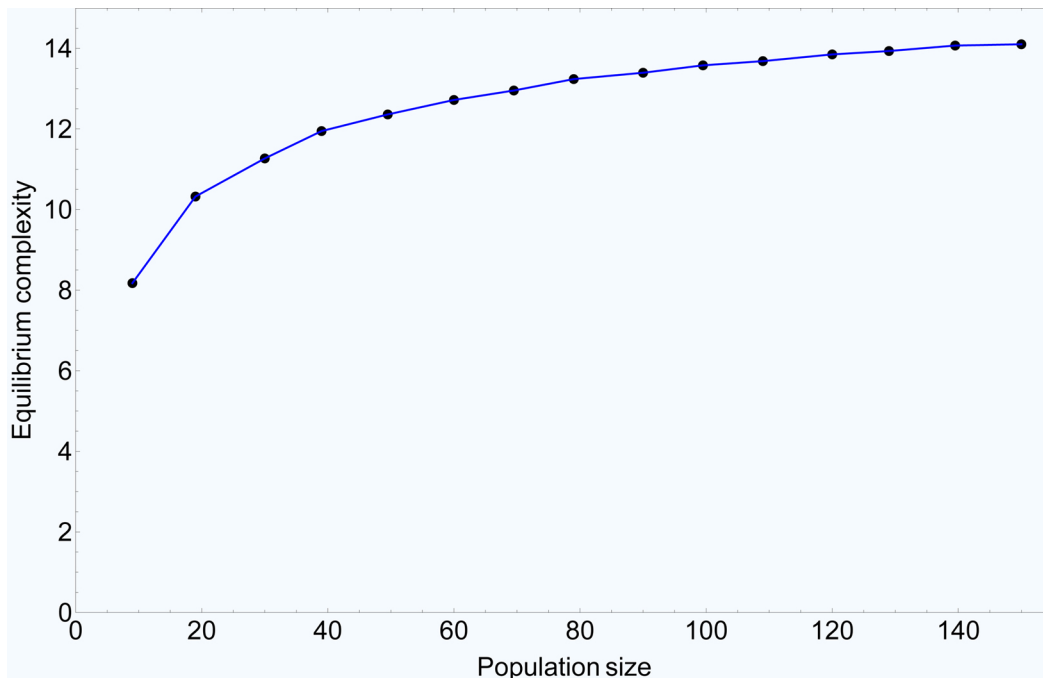


Figure 8. We here see average equilibrium complexity plotted as a function of population size. Model parameters:  $q=0.95$  and  $\varepsilon=5$ ,  $\sigma=0.75$ .

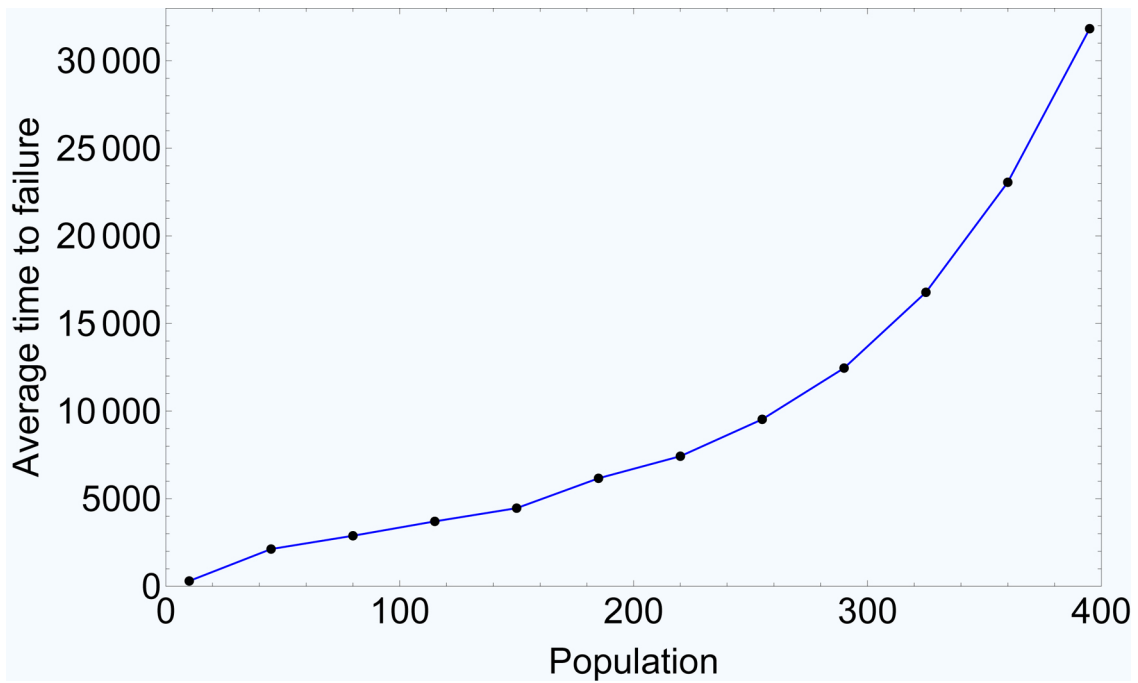


Figure 9. We here see average time to failure plotted as a function of population size. Model parameters:  $q=0.90$ ,  $\epsilon=5$ , and  $\sigma=0$ .

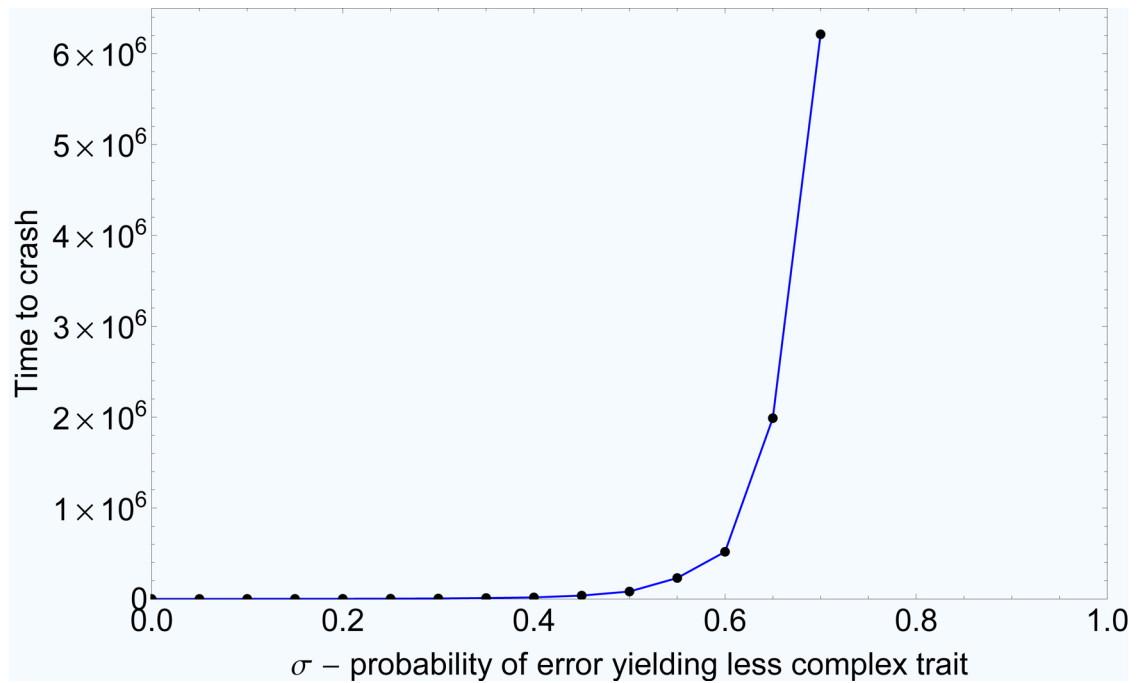


Figure 10. Using a very small population of  $M=10$ , we here see that  $\sigma$  must take on substantially higher values if stability is to be maintained. Model parameters:  $M=10$ ,  $q=0.95$ , and  $\epsilon=5$ .

lutionary role of cultural transmission fidelity that was introduced by Andersson (2011). Andersson (2011) argued that fidelity is likely to have played a role in the evolution of culture that is similar to the role that it has played in biological evolution—that it controls a limitation (a “Glass Ceiling”) on the level of complexity (see Section 2) that can be maintained by cultural transmission. The hypothesis that I developed and explored here is that this limitation would call for the emergence of mechanisms—which I refer to as pedagogical adaptations—for handling transmission errors, at least partly analogous to genetic mechanisms with a similar function.

The dynamics of the model (see Section 5) were explored using four main parameters: (i)  $q$ —the replication fidelity per unit of complexity, which was found by Andersson (2011) to control the level of the Glass Ceiling. The  $q$  parameter has been found to be the only factor that really has an impact on long-term trait complexity; (ii)  $N$ —the size of the population, which was found to mainly affect the incidence of crashes, not the complexity of traits; (iii)  $\varepsilon$ —which controls the strength of the selection pressure that drives complexity; see Equation 1. Selection pressures are obviously needed for adaptive cumulative evolution to take place. But, surprisingly perhaps, the level of sustainable trait complexity is not affected by selection strength; see Equation 4 and Andersson (2011) for a derivation and discussion. I here found (see Figure 3) that a strong selection pressure also de-stabilizes rather than stabilizes the dynamics; also this effect may be somewhat counter-intuitive; and, finally, (iv)  $\sigma$ —was introduced in Section 6.2 to control the rate at which errors would lead to a less complex but functional trait rather than a failed trait. Introducing such a mechanism strongly stabilized the dynamics and made even very small populations stable.

I proceeded by (i) exploring the dynamics of the Glass Ceiling phenomenon, (ii) examining possible types of cultural traits based on their interaction with the Glass Ceiling; and, (iii) discussing pedagogical adaptations in the light of the requirements that I discovered. I will now briefly discuss and contextualize the results.

## SECTION 7.2: THE DYNAMICS OF THE GLASS CEILING

The Glass Ceiling derives its name from the fact that, in an important sense, *nothing* really happens at the Glass Ceiling. What it marks is a critical level of complexity beyond which losses from transmission errors are no longer compensated by selective advantages. The Glass Ceiling is thereby simply a statistical point of no return whose lack of immediate manifestations makes it potentially very hard to avoid. Trait lineages with a complexity exceeding this limit are doomed in the long run, but in the short run they may well prevail in the competition; see Figure 4. This means that there is nothing at the Glass Ceiling that stops selection from driving entire trait populations beyond the critical level, leading to the elimination of all long-term viable variants. This instability did not emerge in the model of Andersson (2011) for the reason that very large population

sizes were used (on the order of 10,000 trait variants rather than on the order of 10's to 100's of variants as used here); a large population size was here found to be a stabilizing factor (see Figure 9).

So, surprisingly perhaps, fidelity appears to do nothing in itself to ensure long-term stability under the assumption that complex traits tend to get favored by selection. If transmission fidelity increases, the level of the Glass Ceiling *goes up*—the Glass Ceiling moves but it does not change or go away. We must therefore seek the explanation for *stability* elsewhere.

## SECTION 7.3: TRAIT TYPES AND CHARACTERISTICS

Two categories of traits were identified in Section 6.2: (i) traits whose complexity “self-bound” under selection before the level of the Glass Ceiling; and, (ii) more open-ended traits where the pressure for increasing complexity remains strong across the present Glass Ceiling level.

Traits in category (i) may be all that animal culture and early hominin culture, lacking sophisticated cultural and physiological pedagogy, can stably maintain. An important type of such traits would be that where the function of the trait is specific and where, if you succeed, there is not much room for further improvement. I here also pointed to the possibility of adaptations for *avoiding* open-ended cumulativeness under the threat that cumulativeness itself leads to destabilization (see Section 6.2). Although a systematic review would be needed to say this with much confidence, it seems plausible that animal cultures could be describable as collections of traits that are neither generalized (in the sense of being re-used as basic components of other, more aggregated, traits) nor particularly open-ended; be it because of the resource that is targeted, because of cognitive limitations, or by virtue of adaptations that actually *limit* cumulativeness (Dean et al 2012; Tennie et al. 2009).

As for traits in category (ii), which I argue characterize *Homo* culture, my results suggest that if these are to be stably maintained, partial and imperfect learning must sufficiently often produce simpler but still functional variants rather than destroying the trait altogether. In this way, parts of the population would be persistently kept below the Glass Ceiling, which would prevent crashes from occurring. Trait transmission must, in other words, not only have a high fidelity, it must also provide robustness against the effects of imperfect learning. The emergence of physiological and cultural pedagogical adaptations is therefore likely to have been key to the emergence of type ii traits and hominin culture as we know it.

## SECTION 7.4: THE ROLE OF PEDAGOGY IN STABILITY AND CUMULATIVITY

One may think of error correction and robustness as inherent to culturally carried knowledge and see no need for special explanations. I think this is far from the case. Error correction and robustness demands cognitive and procedural capabilities for identifying what is more and less critical to the function of a trait, what order that the learn-

ing of the sub-components of aggregated traits should take place in, and so on (e.g., Greenfield et al 2005; Thornton and Raihani 2008; Tostevin 2012; Wimsatt in press<sup>4</sup>). In other words, it demands pedagogy.

We found that the emergence and long-term stability of complex traits in hominin cultures is likely to have been conditioned on *two* services provided by complex pedagogical adaptations (in the sense of, e.g., Csibra and Gergely 2009; Tehrani and Riede 2008)—high fidelity and trait robustness under transmission. The presence of highly evolved teaching and learning mechanisms has been argued to have deep evolutionary roots (Csibra and Gergely 2011) and to at least at some level be universal and unique to the *Homo* genus (Csibra and Gergely 2009). Our results point to the evolution of pedagogy—both culturally and physiologically—as a crucial factor in human evolution, worthy of much further investigation.

### ACKNOWLEDGEMENTS

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### ENDNOTES

- 1 It is known today that simple cultural traditions are very widespread in the animal kingdom (see e.g., Laland and Janik 2006; Whiten et al. 2011 and the potential distinction between “tradition” and “culture”) and for all we know, simple animal culture may date all the way back to the Mesozoic (?), based on the existence of socially transmitted traditions in birds and the avian character of the brain of ca. 150 Ma [see Alonso et al. 2004] or even further back).
- 2 The paradox is this: without stabilizing enzymes, the replication fidelity of RNA allows about 100 base pairs to be retained by selection over time. But to code for an enzyme that boosts fidelity beyond that level, substantially more than 100 base pairs are needed.
- 3 For a broader argument about the need to challenge neo-Darwinian thinking in cultural evolution, see Andersson et al. (in press).
- 4 The discovery of DNA as the basis of biological heredity in the 1950s (Watson and Crick 1953 a, b) came two decades after the establishment of population genetics as the core of the Modern Synthesis in the 1930s.
- 5 Such as apprenticeship, imitation, emulation, communicative teaching and learning, etc.
- 6 A car engine would be *very* sensitive while car driving would be less so.
- 7 For example, computer games would be in the zone of proximal development of computers—the possibility emerges as the computer is being used for other purposes and it would not make sense without computers. This concept can then be much more highly resolved to describe an important aspect of how we go about solving problems also in the small.
- 8 Other schemes, that are more explicitly prestige- rather than success-biased, such as having multiple teachers or having a teacher caste that teaches all apprentices, essentially had an effect equivalent to using higher values of  $q$ ; which is in basic agreement with the results of Enquist et al. (2010). So, using a single cultural parent suffices for these purposes and makes for a much simpler and more transparent model.
- 9 Assuming equal probability of increasing and decreasing complexity is an arbitrary assumption so a short analysis of the effects on the dynamics is in order. Without mutations that decrease the complexity, the model will be very unstable for reasons that will become clearer later in the analysis of the model. However, the model is not sensitive to the exact proportion between mutations that increase and decrease complexity. What is important is that both types occur.
- 10 The size of this pool fluctuates even more than what is obvious in the

figure since the points are averaged over 100 steps.

- 11 Note that in Figure 3A, the selection pressure is sufficiently weak that the population survives the 20,000 cycles that are shown. It is, however, only a matter of time before it does collapse. A lower selection pressure only lowers the incidence of crashes since it causes the reservoir of potential role models to shrink more slowly. But there is no critical selection pressure below which crashes do not occur.
- 12 Recent evidence points to hafting being practiced at least sporadically even by ~500 ka; see Wilkins et al. (2012)
- 13 As Read (2006) points out, there are also examples of extant hunter-gatherer groups that are very small—predominantly in arctic biotopes with low carrying capacities—and that rely critically on the ability to maintain many and highly complex cultural traits.

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