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Testing the Cognitive and Cultural Niche Theories of Human Evolution

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The "cognitive niche" and "cultural niche" are two competing theories of human evolution. One point over which they disagree is the importance of gene-culture interactions. Here, I use three models to evaluate this disagreement: (*i*) an asocial baseline model, (*ii*) a model of the cognitive niche, which includes a form of social learning that prevents gene-culture co-evolution, and (*iii*) a model of the cultural niche, which allows gene-culture co-evolution. Intelligence can evolve in all three models, and social transmission increases the range of conditions under which it can do so. However, only the model of the cultural niche (*i*) produces periods of evolutionary stasis, (*ii*) produces a positive relationship between population size and the rate of cultural and genetic evolution, and (*iii*) results in behaviors that are difficult to discover dominating the population. I review the available evidence for such patterns in human evolution and conclude that the cultural niche provides a more comprehensive explanation for human evolution than does the cognitive niche.

Human cognitive ability is so remarkable that Western philosophy has traditionally held the view that it is the fundamental distinction between humanity and all other animals (e.g., Aristotle 340BC). However, work on animal cognition has shown that numerous human psychological traits have precedents in other, often distantly related, species (Laland and Galef Jr 2009). Nonetheless, humans remain a unique conjunction of numerous cognitive traits, and the evolutionary explanation for this remains unresolved. Researchers are increasingly turning to co-evolutionary processes to explain human cognition (Pinker 2010; Kaplan and Robson 2002; Heyes 2012; Enquist et al. 2008; Sterelny 2012; Uomini and Meyer 2013; Morgan et al. 2015). In these scenarios, selection for enhanced cognition became engaged in a positive feedback loop during human evolution. For example, it has been suggested that hominin sociality selected for increased intelligence, which facilitated more complex group living, and so on (Mithen 1999).

The "cognitive niche" (Pinker 2010; Barrett, Cosmides, and Tooby 2007; Cosmides and Tooby 2001) is a more holistic theory for the evolution of human intelligence and has received considerable attention over the past few decades. By this account, human intelligence results from selection for an "improvisational intelligence" (i.e., an intelligence capable of generating complex solutions to novel problems) because the costs required to sustain such an intelligence were outweighed by the benefits of the numerous solutions such an intelligence could generate. The cognitive niche is a co-evolutionary theory, arguing that the genetic change underlying increases in certain mental capacities generated selection for increases in others, and so on. For example, "it is surely no coincidence that the psychological abilities underlying technological know-how, open-ended communication, and cooperation among nonkin are all hyper-developed in the same species [humans]; each enhances the value of the other two" (Pinker 2010). So, in this account, the multiple facets of human intelligence were mutually reinforcing on an evolutionary timescale.

Although the cognitive niche includes social transmission and language in the co-evolutionary process, it has recently come under criticism for not taking full account of the importance of culture in human evolution (Heyes 2012; Boyd, Richerson, and Henrich 2011; Shea 2012; Whiten and Erdal 2012). Critics emphasize the population level process of cultural evolution (Boyd, Richerson, and Henrich 2011; Richerson and Boyd 2005; Mesoudi 2011), by which transmission and refinement across generations can produce complex behaviors without corresponding genetic change. Thus, it is argued that human success lies more in our ability to cumulatively build upon knowledge than to improvise novel solutions, and as such we are better described as inhabiting the "cultural", as opposed to "cognitive", niche (Boyd, Richerson, and Henrich 2011).

It might seem this disagreement results from differing levels of explanation; whilst the cognitive niche focuses on the genetic evolution of human cognition, the cultural niche focuses on the subsequent cultural evolution. However, this stratification is not possible because, according to the cultural niche, cultural and genetic evolution are engaged in a single co-evolutionary process, with the products of cultural evolution altering or generating selection on genes, such that neither can be understood in isolation (Boyd, Richerson, and Henrich 2011; Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). This conceptualization of evolution is called "gene-culture co-evolution" (Lumsden and Wilson 1981; Laland and Brown 2011), and regards culture as a second, evolving, form of inheritance, alongside and interacting with genetic inheritance (Boyd, Richerson, and Henrich 2011; Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). As a range of taxa, including chimpanzees, exhibit simple cultures (Laland and Galef Jr 2009), gene-culture interactions could have been a long-term feature of human evolution. However, advocates of the cognitive niche downplay the importance of gene-culture interactions, describing them as "superfluous" (Pinker 2010).

The disagreement between the cognitive and cultural niche theories over the inclusion of culture in the co-evolutionary process, offers a means to evaluate the two. There already exists a large amount of theoretical evidence for the plausibility of gene-culture interactions (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Laland, Kumm, and Feldman 1995) alongside a smaller number of examples from human history (Chiao and Blizinsky 2010; Laland 2008; Hünemeier et al. 2012; Tishkoff et al. 2007). Perhaps the most famous of these is the spread of the allele for adult lactose tolerance in response to the cultural practice of dairy farming (Tishkoff et al. 2007). However, these examples are relatively recent, operating over the past few thousand years, whereas human intelligence evolved over millions of years. Thus, whilst evidence is growing for gene-culture interactions operating over such extensive timescales (Morgan et al. 2015; Uomini and Meyer 2013), the role of gene-culture co-evolution in the wholesale evolution of human intelligence is far from established. Here, I present three agent-based simulations investigating the evolution of intelligence alongside a ladder of increasingly complex, learnable behaviors; (*i*) an asocial baseline model without social transmission, (*ii*) a model of the cognitive niche, which includes social transmission, but not gene-culture interactions and (*iii*) a model of the cultural niche in which social transmission allows the inheritance of behavior and thus gene-culture co-evolution. The goal of this work is to evaluate the theories of the cognitive and cultural niche, and hence the importance of gene-culture interactions, by identifying differential predictions of the two and then comparing these predictions with available data on human evolution.

Models and Results

Model 1 - the asocial model

Consider a population of *n*, haploid, asexual organisms. Each organism's genome consists of a single (positive and continuous) locus, *I*, that corresponds to their intelligence. Although both the cognitive and cultural niche describe intelligence as a complex of co-evolving traits, as this is not a point of disagreement, for simplicity I reduce intelligence to a single locus. Each generation, organisms learn a behavior, *B*, from a series of increasingly complex behaviors (i.e., *B*=0, 1, 2, 3…), analogous to increasingly complex stone-tool technologies (e.g., Mode I, Mode II, Mode III…). The i^{th} individual's behavior is generated by rounding a value drawn from a normal distribution, with mean $I_i/2$ and variance $I_i/8$ (negative behaviors are set to 0). All simulations were repeated using other learning algorithms and obtained very similar results (see ESM). The fitness, *F*, of each individual is given by a baseline value, *f*, plus the value of their behavior, minus the cost of their intelligence, *c*, such that:

$$F_i = f + B_i - I_i c \quad (1)$$

(figure 1*a*). Negative fitnesses are set to 0. Individuals then reproduce according to the Wright/Fisher model, where repeated sampling with replacement from the parental generation, weighted by fitness, generates *n* offspring. The intelligence of offspring is drawn from a normal distribution with mean I_{parent} and variance *q*, where *q* affects the magnitude of the expected difference between parent and offspring. Negative values of *I* are set to 0. This process is repeated for each generation. Starting populations are composed of the offspring of a parent with *I*=2 to avoid any floor effects (figure 1*a*).

Results

Intelligence increases (and as a result, so does the complexity of behavior) provided that the expected payoff from the behaviors discovered is greater than the cost of the intelligence that discovered them. Given the learning algorithm used, this implies intelligence will evolve if *c*<0.5 (figure 1*b*-*c*), because the expected payoff for a given value of *I* is *I*/2. A modification of this model shows that a continuous ladder of behaviors is necessary for the evolution of intelligence. For example, if behaviors 1-4 are assumed to have no fitness benefit, a trough in fitness is created (figure 1*a*, dashed line) and intelligence will only evolve if *c*=0, or extremely large mutations are permitted (figure 1*d*).

Model 2 – the cognitive niche

Organisms possess a second genetic locus, *S*, which represents their capacity for social transmission (positive and continuous like *I*). The function of social transmission in this model is to reduce the cost of information acquisition, and it does not facilitate the transmission of information across generations as this would allow gene-culture co-evolution

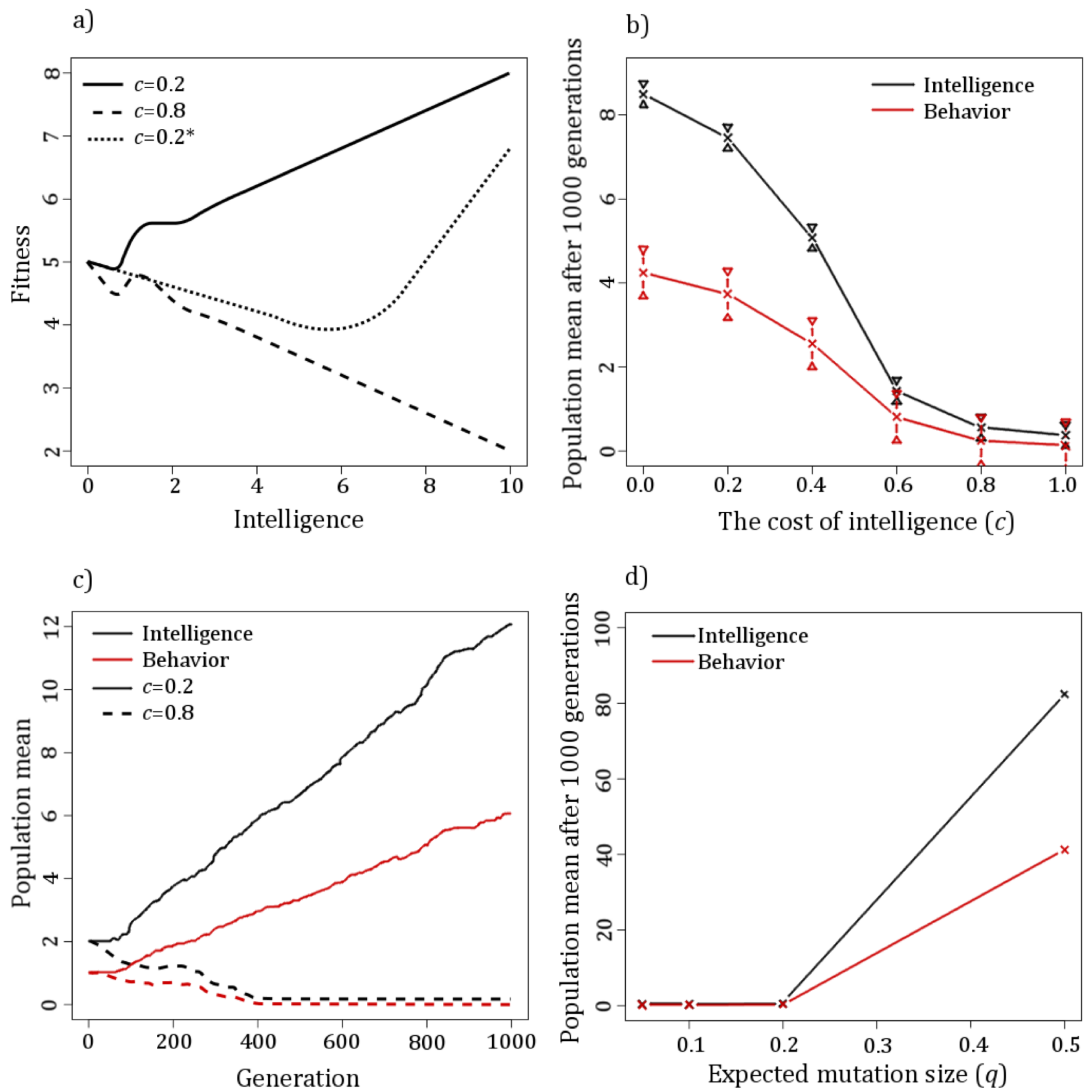

Figure 1. The results of the asocial model. Intervals show average values from 10 repeats (+/- one standard deviation). Unless otherwise stated parameter values are: n=1000, q=0.05, f=5 and c=0.2. (*a*) If c<0.5, expected fitness increases with intelligence, otherwise this relationship is reversed. If the first four behaviors confer no benefit, even cheap intelligence initially causes a drop in fitness, but the positive relationship is restored once beneficial behaviors are reached. The kink for low values of intelligence is present because so few behaviors are likely to be discovered that the fitness function is somewhat step-like. (*b*) Intelligence evolves provided c<0.5 and its evolution is more rapid for lower values of c. (*c*) The evolutionary dynamic is continuous and roughly linear, and the average behavior is around half the average intelligence. (*d*) Assuming that behaviors 1 to 4 confer no fitness benefit, intelligence can only evolve if the expected size of mutations is high enough.

(see discussion). As such, whilst social transmission comes at a cost, c_s, it also brings a benefit, b_s, that reduces the cost of intelligence. Fitness is now calculated as:

$$F_i = f + B_i - I_i c - S_i c_s + min(I_i, S_i) b_s \qquad (2)$$

That b_s is multiplied by the minimum of I and S means that there is no benefit to social transmission in the absence of intelligence. Starting populations are composed of the offspring of a parent with I=2 and S=2.

Results

Intelligence evolves provided that $c+c_s-b_s<0.5$. Accordingly, contingent on c_s and b_s, intelligence can evolve even if $c>0.5$ (figure 2). However, if the benefits of social transmission do not outweigh its own costs (i.e., $c_s>b_s$), then social transmission cannot evolve and the outcome is the same as in the first model; intelligence evolves if $c<0.5$. Finally, if social transmission is beneficial (i.e., $b_s>c_s$), but intelligence sufficiently cheap that social transmission is not necessary for the evolution of intelligence (i.e., $c<0.5$), then both intelligence and social transmission will evolve, but with social transmission lagging behind (figure 2*a*, and dotted lines in *b*).

Model 3 – the cultural niche

Social transmission now permits the inheritance of behaviors, thus allowing gene-culture co-evolution (as before, S comes with cost c_s, however, b_s is removed from the model). I assume behaviors are passed only from parents to their offspring and that this only occurs if the offspring is sufficiently intelligent ($round(I_{offspring}) \geq B_{parent}$), and both the offspring and parent are sufficiently proficient at social transmission ($round(S_{offspring}) \geq B_{parent}$ and $round(S_{parent}) \geq B_{parent}$). The latter applies to both parent and offspring in order to capture the dialogic nature of teaching and language. If these conditions are not met, no behavior is inherited. All offspring will still learn a behavior asocially (as in model 1) and will adopt this behavior if it is better than that which they

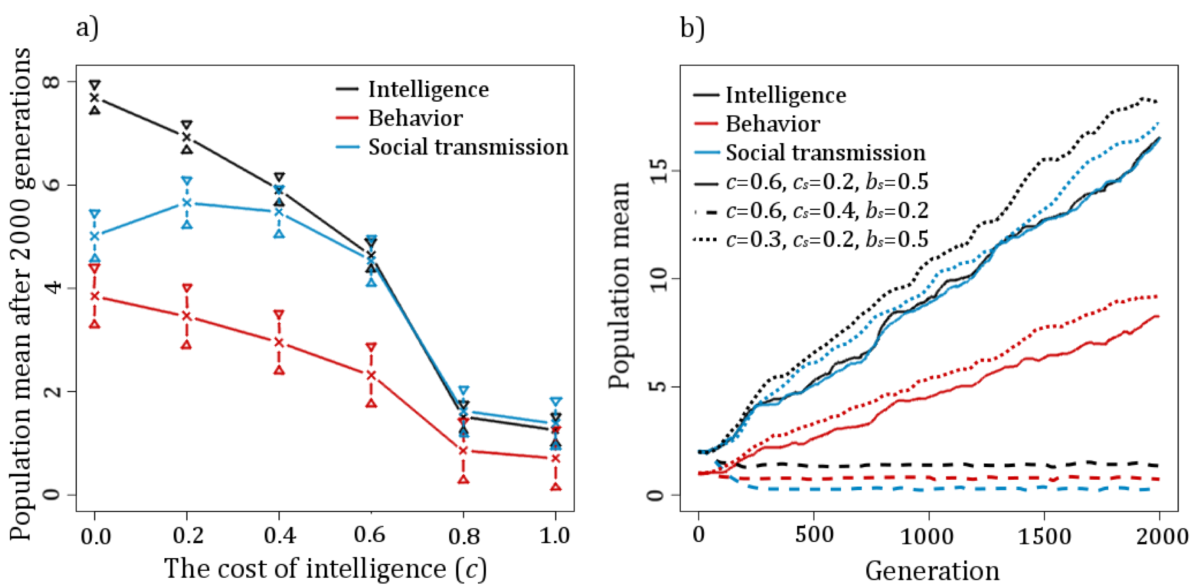

Figure 2. The results of the cognitive niche model. Unless otherwise stated, parameter values are: n=1000, q=0.05, f=5, c=0.6, c_s=0.2, and b_s=0.5. Intelligence evolves if $c+c_s<1$, however, if $c<0.5$ then social transmission is not necessary and it lags behind intelligence. (*a*) Averages from 10 repeats (+/- one standard deviation) after 2000 generations. (*b*) The evolutionary dynamic of each repeat is continuous and roughly linear.

have inherited. In this model the potential benefit of social transmission is in the inheritance of superior behaviors and fitness is calculated as:

$$F_i = f + B_i - I_i c - S_i c_s \qquad (3)$$

Starting populations are composed of the offspring of a parent with I=2, S=2 and B=0.

Results

Intelligence, social transmission and culture can all evolve provided that $c+c_s<1$ (figure 3*a*). However, if $c<0.5$ then social transmission is not necessary and an asocial population of innovators will evolve (figure 3*c*). The inclusion of cultural inheritance allows populations to sustain more complex behaviors for a given level of intelligence (compare figures 3*a* and 2*a*). However, the evolution of intelligence is considerably slower (compare figures 2*b* and 3*b*), with extended periods of stasis (figure 3*b*). Stases occur when the intelligence and capacity for social transmission of the agents readily sustains the current widespread behavior, but is unlikely to lead to the discovery and spread of the next behavior. In such cases there is actually selection against increases to either locus, as these result in larger costs but remain extremely unlikely to lead to the discovery of more complex behavior (see ESM). The stases persist until an individual capable of socially transmitting the next behavior successfully innovates, at which point selection changes to favor intelligence and social transmission sufficient to sustain this new behavior.

Stasis length can be decreased through a variety of changes (see ESM): (*i*) increasing the variance of the distribution from which asocially learnt behaviors are drawn, which makes the next behavior easier to discover. (*ii*) Lowering the costs of intelligence or social transmission, which weakens selection against increases in these traits and allows a greater number of intelligent mutants to persist (figure 3*a*). (*iii*) Increasing expected size of mutations, which increases the probability of highly intelligent offspring. (*iv*) Increasing the population size, which increases the probability of both a highly intelligent mutant, but also the number of attempts at innovation per generation (figure 3*d*).

Discussion

I have presented three models investigating the evolution of intelligence; an asocial baseline condition, and models of the cognitive niche and the cultural niche. All three models identify conditions under which intelligence will evolve. Furthermore, both models that include social transmission find that coevolutionary dynamics between intelligence and social transmission are possible and allow intelligence to evolve in the face of costs that would otherwise be insurmountable. However, the cognitive and cultural niche models produce different evolutionary dynamics. I now discuss these differences in light of the archaeological record of human evolution and contemporary human populations.

Evolutionary stasis

Whilst the cognitive niche model produces continuous evolutionary change, the cultural niche model produces extended periods of evolutionary stasis in both cultural and genetic evolution. Although the extent to which hominin stone tool evolution exhibits "stasis" is debated, it is clear that it was not continuous. For example, Oldowan tools, which appear from ~2.5mya (Semaw 2000), are produced for ~700,000 years (Schick and Toth 2006; Stout et al. 2010) with little by way of innovation until the appearance of Acheulean tool-making (Beyene et al. 2013). Oldowan inter-site variation rules out a stasis in the absolute sense (Roche et al. 1999), and

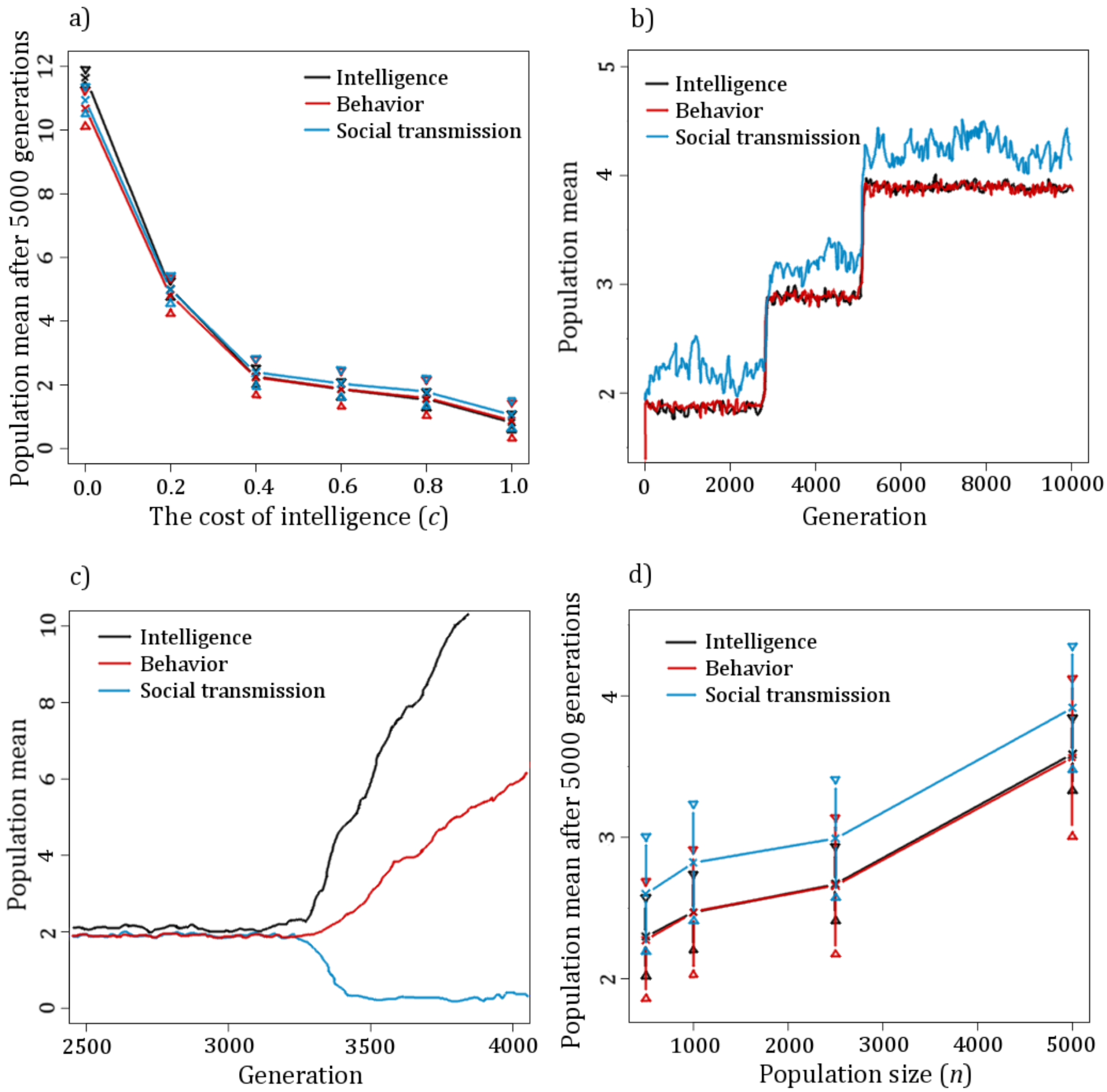

Figure 3. The results of the cultural niche model. Intervals show average values from 10 repeats (+/- one standard deviation), smooth lines show the results of a single repeat. Unless otherwise stated, parameter values are: n=1000, q=0.05, f=5, c=0.6 and c_s=0.2. (*a*) Intelligence will evolve provided that $c+c_s<1$, as this threshold is approached evolution becomes very slow. (*b*) The evolutionary dynamic is discontinuous, with extended stases punctuated by short periods of rapid change. (*c*) If c<0.5 then cultural transmission is not necessary for the evolution of intelligence and it can become left behind. In the case shown, c=0.2 and c_s=0.4. (*d*) Increasing the population size decreases the duration of each stasis, accelerating evolution.

there is some evidence that bifacial and discoidal knapping becomes more prevalent towards the end of the Oldowan (Barsky 2003). However, Oldowan variation may well be in response to ecological factors, such as raw material quality (Stout et al. 2010), and early

Oldowan sites show a remarkable level of skill, consistent with a stasis in complexity, if not detail (Semaw 2000). Accordingly, although the extent of stasis is debated, there are periods of rapid versus limited change, which I argue is consistent with the cultural niche model.

The dynamics of hominin brain evolution is less clear. Whilst some work supports gradual change (e.g., Lee and Wolpoff 2003), a recent analysis argues that many of the methods used presuppose a linear relationship and finds evidence of 5 periods of rapid change in overall hominin brain size (Shultz, Nelson, and Dunbar 2012). Suggestively, two of these steps coincide with the earliest known Acheulean tools (Beyene et al. 2013), consistent with gene-culture interactions, however, the other three show no clear overlap with cultural change. It is likely that other factors (social, demographic or ecological, see Bailey and Geary 2009; Potts 1998; Powell, Shennan, and Thomas 2009) would have modulated selection acting on intelligence and their combined effects may mask the step-like selection exerted by a single cultural trait. Consistent with this, in the ESM, I show that a model including the gene-culture interactions of four overlapping cultural traits results in the continuous evolution of intelligence alongside the more discrete evolution of each of the cultural traits. Thus, gene-culture interactions can produce both discrete and continuous genetic change, whilst without these interactions genetic change can only be continuous.

A possible criticism of the model is that the assumed continuous nature of intelligence could be preventing stases from appearing in the model of the cognitive niche. However, even if intelligence is assumed to increase through discrete steps, the model of the cognitive niche can only produce stases with extremely precise configuration of the mutation rate, and even then, such stases are limited to genetic, not cultural, evolution (see ESM). This suggests that periods of stasis in cultural or genetic change offer robust support for gene-culture interactions, and, hence, the cultural niche.

Population size

Whilst both theories suggest population size matters, only the cultural niche model produces the proposed positive relationship between population size and the rate of cultural and genetic evolution. This relationship is strongly supported by available data, which shows that the appearance of modern behaviors is associated with a threshold population density (Powell, Shennan, and Thomas 2009), that the appearance of microlithic technology in South Asia ~30kya coincides with an increase in population size (Petraglia et al. 2009) and that decreases in population size result in a decrease in cultural complexity (Henrich 2004). Theoretical work suggests that population size and cultural complexity can co-evolve, with innovations allowing increases in population size which in turn increase the rate of cultural evolution (Enquist et al. 2008; Ghirlanda and Enquist 2007). Accordingly, the cultural niche is strongly supported in this regard.

That the model of the cultural niche finds that population size also affects the rate of genetic evolution offers a testable prediction; the genetic effects of gene-culture co-evolution in human history should have become more pronounced as human populations grew. Whilst there is, as yet, no study investigating this question directly, there is evidence that a large number of human genes with functions related to cultural practices (e.g., diet, cooking, farming and migration) have been under strong selection over the past 100,000 years (Laland, Odling-Smee, and Myles 2010). Further work could assess whether such selection became increasingly prominent as populations grew.

Behavioral distribution

In the cognitive niche model, the behavioral distribution of the population matches the distribution of behaviors produced by asocial learning (given the learning algorithm used, the average behavior is around half the average intelligence). However, the inclusion of cultural inheritance, as per the cultural niche, breaks down this relationship, and instead the population becomes dominated by the best possible behavior that can be widely socially transmitted. Whilst there is little data regarding the distribution of behaviors amongst ancestral hominin populations, it is clear in modern human populations that behaviors are not distributed according to the ease with which they can be invented. For example, the Central Inuit technologies described by Boyd *et al.* (2011) clearly cannot be re-discovered by each generation and instead are sustained by social transmission. Accordingly, the observation that modern populations exhibit complex behaviors at greater levels than could be achieved by individual learning alone supports the cultural niche.

A criticism of the models

Before concluding, I will address in detail an aspect of the cognitive niche model that advocates of the cognitive niche may feel poorly represents the theory.

In the cognitive niche model, social transmission is reduced to a factor that lessens the cost of intelligence. This may seem unfair given that (*i*) the cognitive niche literature includes discussion of the transmission of behaviors (e.g., "This jackpot was a reward for extraordinary feats of folk reasoning in taxonomy, physiology, physics, and geometry, *some passed down from earlier generations*, some improvised on the spot." Pinker 2010, emphasis mine), and (*ii*) the model of the *cultural* niche *does* include the transmission of behaviors. However, as already discussed, the cognitive niche literature explicitly rules out the gene-culture interactions, and such interactions are a direct result of the transmission of behaviors. Accordingly, a different modeling approach is needed. The approach I adopted was suggested by the cognitive niche literature itself: "Language… lowers the cost of acquiring a complex skill" (Pinker 2010), "[Language] can also lower the original acquisition cost [of information]" (Pinker 2003), "[social transmission] dramatically lowers the cost of acquiring large… bodies of local, contingent information, making… intelligence cost-effective" (Barrett, Cosmides, and Tooby 2007). Simply put, you cannot include the social transmission of fitness relevant behaviors whilst precluding gene-culture interactions. Accordingly, as long as accounts of the cognitive niche exclude such interactions, the model presented here is an accurate rendition of the theory.

Conclusion

The "cultural niche", unlike the "cognitive niche", emphasizes the role of culturally transmitted information as a driving force in human evolution. Here I show that the inclusion of cultural inheritance changes the evolutionary process in three ways. Firstly, it creates long lasting stases in genetic and cultural evolution, which mirror the discontinuities observed in the archaeological record of stone tools (Schick and Toth 2006; de la Torre 2011; Hovers 2012; Stout et al. 2010). Secondly, it allows the rate of evolution to be affected by population size, which is in agreement with work suggesting an important role of demography in cultural evolution (Powell, Shennan, and Thomas 2009; Henrich 2004). Finally, it allows the best possible behaviors to dominate the population, which is agreement with observations of modern populations (Boyd, Richerson, and Henrich 2011). Thus, the cultural niche theory better fits available data and this work supports gene-culture interactions as integral to an understanding of human evolution.

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