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Cite this article: Morgan TJH, Suchow JW, Griffiths TL. 2022 The experimental evolution of human culture: flexibility, fidelity and environmental instability. *Proc. R. Soc. B* **289**: 20221614.

<https://doi.org/10.1098/rspb.2022.1614>

Received: 19 August 2022

Accepted: 7 October 2022

Subject Category:

Behaviour

Subject Areas:

behaviour, cognition, evolution

Keywords:

evolution, cultural evolution, cognition, experimental evolution, social learning, conformist transmission

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.6251631>.

The experimental evolution of human culture: flexibility, fidelity and environmental instability

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The past 2 Myr have seen both unprecedented environmental instability and the evolution of the human capacity for complex culture. This, along with the observation that cultural evolution occurs faster than genetic evolution, has led to the suggestion that culture is an adaptation to an unstable environment. We test this hypothesis by examining the ability of human social learning to respond to environmental changes. We do this by inserting human participants ($n = 4800$) into evolutionary simulations with a changing environment while varying the social information available to individuals across five conditions. We find that human social learning shows some signs of adaptation to environmental instability, including critical social learning, the adoption of up-and-coming traits and, unexpectedly, contrariness. However, these are insufficient to avoid significant fitness declines when the environment changes, and many individuals are highly conformist, which exacerbates the fitness effects of environmental change. We conclude that human social learning reflects a compromise between the competing needs for flexibility to accommodate environmental change and fidelity to accurately transmit valuable cultural information.

1. Introduction

For most species, adaptation occurs through a combination of short-term plasticity and long-term genetic change. Although many animals also learn from each other [1], the products of such social learning rarely accumulate over time or exceed the capacity of any one individual [2]. Our species, however, is an exception: we extensively adapt through culture [3,4], which routinely involves complex beliefs, technologies and practices that evolved across generations. Cultural adaptation is a population-level process that in many ways mirrors genetic evolution [5,6], with innovation and social learning being the cultural analogues of genetic mutation and transmission. However, there are many important differences. For one, whereas genetic mutations are random with respect to fitness, cultural innovations can be guided by reasoning [7]. Moreover, whereas genetic transmission occurs across generations, from parents to offspring at the moment of conception, cultural transmission can occur both across and within generations, between any individuals, and at any time. These differences allow cultural evolution to proceed far faster than genetic change [8]. Moreover, the lengthening of human life-history magnified this discrepancy by slowing genetic evolution while supporting complex cognition that facilitated cultural evolution [9,10].

Given the fast pace of cultural evolution, it has been argued that culture itself is an adaptation allowing us to keep pace with an increasingly unstable environment [11]. Indeed, the past 2 Myr, during which human brain size grew tremendously [12] and cumulative cultural capacities emerged [13], have been a time of unprecedented temporal environmental variation. For instance, a 41 kyr

temperature oscillation began 1.5 Ma, being replaced with a more severe 100 kyr cycle around 650 ka [14]. Temperature change has also been observed on faster timescales, including a series of sudden temperature increases of up to 7°C during the last glacial period (approx. 115–12 ka) that lasted just a few hundred years [15], and sudden warming followed by gradual cooling, likely caused by the collapse, and subsequent regrowth, of North Atlantic icecaps [16]. Similar fluctuations are also seen in the previous inter-glacial (approx. 125–115 ka) with temperature dropping up to 15°C, but recovering within as few as 70 years [17]. Such rapid change may continue further back in time, however, datasets with sufficient resolution to test this hypothesis are not currently available. Collectively, these results suggest that our species, including our capacity for cultural inheritance, evolved during a period of intense climatic instability.

The hypothesized mechanism by which climactic instability generates selection for culture is that instability creates environmental novelties which require behavioural innovations and culture is an effective means to acquire innovations. There is evidence from multiple taxa supporting the link between brain size and success in novel environments [18–20], and the mediating cause has been identified as innovation rate in the case of birds [21]. Moreover, fossil evidence suggests that brain size increases during times of environmental instability, for instance in elephants [22]. Thus, the link between environmental instability, innovation and brain size appears widespread. In addition to this, humans uniquely evolved the additional capacity for complex culture, which appears to have coevolved with brain size in primates [10].

While the hypothesis that culture is an adaptation to an unstable environment is compelling, it has nonetheless run against a body of cultural evolutionary theory that shows that rapid environmental change can favour asocial, as opposed to social, learning. This is because, as with any system of inheritance, culture risks transmitting out-of-date information, and this risk grows as environments become increasingly unstable. For instance, a model of the evolution of social learning in an otherwise asocial population found that the equilibrium frequency of social learners is inversely proportional to the frequency of environmental change [23]. Further work found that pure social learning can persist (albeit at low frequencies) provided that, for every generation in which the environment changes, there are at least two in which it does not; and that a mixed strategy including *some* social learning is always stable, but the amount of social learning decreases with the rate of environmental change [24]. As such, the most rapid temperature changes discussed above, which occur suddenly and revert within 70 years, may be so fast that selection favoured individual plasticity as opposed to the inheritance of cultural practices that developed over multiple generations.

One way this tension would be resolved is if historical environmental variability fell in a middle ground: fast enough for genetic evolution to be insufficient, but slow enough for multi-generational cultural processes to keep up. Though possible, this would seem to depend on a remarkably well-calibrated rate of environmental change to favour the extreme reliance on social learning characteristic of our species. Moreover, such a possibility is hard to test and is challenged by evidence of decadal and centennial environmental change mentioned above, as well as the fact that while many species experienced environmental instability, only humans evolved

complex culture. Thus, social learning *per se* is unlikely to have been favoured by environmental instability.

A tweak to this hypothesis is that *strategic* use of social learning broadened the conditions under which social learning is favoured and allowed it to remain effective in the face of high-frequency environmental change. Theory clearly shows this is possible: the success of social learning in an unstable environment increases when individuals collect and evaluate *both* asocial and social information [25] or if social learners additionally collect asocial information when social information is inadequate (referred to as ‘critical social learning’ [26]). Theory also suggests that as different social learning rules compete to parasitize the information produced by asocial learners, selection will favour whatever social learning psychology relies on the lowest frequency of asocial learning to be effective, thereby maximizing the frequency of social learning in the population [27]. Consistent with this, an evolutionary tournament that pitted different learning strategies against each other was won by a strategy that engaged in a great deal of social learning, was a highly effective information parasite, and timed its social learning to avoid periods of environmental change [28]. Experimental data on this topic is limited, although humans have been observed to respond to environmental instability by selectively adopting ‘up-and-coming’ options, presumably on the assumption that these traits are being favoured by novel conditions [29].

While such transmission biases *can* render social learning adaptive against high-frequency environmental change, this is not necessarily the case and, in fact, other biases have been documented to decrease the fitness of social learning following environmental change. One example is *conformist transmission*, the tendency to disproportionately adopt majority beliefs [5,30]. Because conformist transmission blocks the spread of low-frequency traits, and because innovations necessarily start at low frequencies, conformist transmission prevents populations from tracking environmental change. Nonetheless, theory shows that conformist transmission is broadly favoured by selection [31,32], even to the extent that it causes catastrophic fitness decreases after environmental change [33]. There is also empirical evidence for conformist transmission in humans [34–39]. Therefore, while human social learning is clearly sensitive to a range of factors, it is not clear whether it accommodates environmental change any better than random social learning. As a result, how the evolution of culture proceeded against Pleistocene climactic instability remains uncertain.

Here, we present a series of experimental evolutionary simulations [40] that directly assess how humans use social learning to respond to environmental change. An experimental evolutionary simulation can be understood via its relation to theoretical agent-based simulations: computer programs in which simulated agents, with programmed AI, inhabit and evolve within a virtual world. Such simulations give insights into real-world processes, however, they necessitate many simplifying assumptions concerning the agents, their cognition, and the world they inhabit. Experimental evolutionary simulations differ in that agents do not need any AI because human participants make decisions on their behalf. As such, while the agents inhabit a simulated world, and have a simulated genome, their decisions, and the effect of those decisions on evolutionary dynamics, reflect real human psychology.

Across 180 simulations, we consider five different forms of social information. These range from seeing only the decision

Table 1. Summary of experimental conditions.

period	condition	number of simulations	social information	critical social learning
1 ($n = 1600$)	1	36	poor	no
2 ($n = 1600$)	2		moderate	
	3		rich	
3 ($n = 1600$)	4		moderate	yes
	5		rich	

of a single randomly chosen demonstrator (as per [23]), to seeing the decisions of multiple individuals from multiple generations with the option of additionally receiving asocial information. These richer forms of social information enable conformist transmission [5,30], the identification of up-and-coming traits [29] and critical social learning [26]. Across these conditions, we find that human social learning exhibits features that both help and hinder its evolution in an unstable environment: On the one hand, individuals use social consensus to strategically time contrariness and critical social learning, which improves the adaptive value of culture. Moreover, a minority of persistently contrary participants create a beneficial reservoir of cultural variation. On the other hand, most individuals are highly conformist, which creates cultural inertia that causes more severe decreases in fitness following environmental change. We conclude that human social learning is a compromise between the competing needs of flexibility and fidelity.

2. Methods

Data were collected online, using the experiment-automation platform Dallinger (<https://dallinger.readthedocs.io>). Data were collected in three periods between 25 September 2015 and 25 October 2015, with the first period focused on condition 1, the second conditions 2 and 3, and the third conditions 4 and 5.¹ In total, 4800 participants took part (1600 in each period) recruited from Amazon's Mechanical Turk in batches of 40 (participants who took part in one period could not take part in the others). Within each period, each participant took part in multiple evolutionary simulations (in series, randomly ordered), and within each simulation they took on the role of a single agent. In total, 180 simulations were conducted, each with a population size of 40 agents and lasting 40 generations, totalling 1600 agents per simulation.

All simulations involved an unstable simulated environment that changed between two states. An agent's fitness depended on the correct identification of the current state by their associated participant. Within each simulation, a simulated genome marked each agent as either an asocial or social learner and this affected the stimuli presented to the corresponding participant. All populations were initially composed entirely of asocial learners, but the social learning allele could arise via mutation and, if favoured, spread via selection. Across conditions, we varied the richness of the stimuli associated with the social learning allele (table 1).

Below we describe the methods, first focusing on the participant experience, involving (1) recruitment, (2) the task and (3) the experimental procedure. We then describe the larger simulation of which this was a part, including (4) the environment and (5) genetics, fitness and reproduction.

(a) Recruitment

Participants were recruited via Amazon's Mechanical Turk to take part in a computer-based binary choice task. Participants were

recruited in batches of 40 (enough to complete a single generation of a simulation), with another batch being recruited once all participants in the current batch had completed the experiment. Participants who failed attention checks (described below), dropped out during the experiment, or submitted incomplete or malformed data were automatically replaced. Recruitment was limited to US participants for whom at least 95% of their previous tasks on Mechanical Turk had been approved.

(b) The task

Within each simulation, participants completed a single trial of a task where they were asked to determine whether an array of 80 blue or yellow dots contained more blue or more yellow dots. After receiving relevant information, participants made their decision by clicking one of two buttons, labelled 'blue' and 'yellow', respectively, and moved on to the next simulation without receiving feedback.

Participants who were assigned the asocial allele saw the array of dots for 1 s (figure 1*a*). The dots were non-overlapping, with radii drawn from a uniform distribution ranging from 10 to 20 pixels. Fifty-two dots were of the majority colour (versus a minority of 28), this value was chosen based on pilot work that found participants answered correctly on greater than 95% of such trials, making asocial information highly reliable.

Participants who were assigned the social allele received *social information*, accurate information about the decision made by one or more other participants. Across simulations, the social information took five forms, as follows. (1) 'Poor': the decision of a single participant randomly selected from the previous generation of the same simulation (figure 1*b*). (2) 'Moderate': the decisions of all 40 participants from the previous generation of the same simulation (figure 1*b*). (3) 'Rich': the decisions of all 120 participants from the previous three generations of the same simulation, broken down by generation. (4) 'Critical-moderate': moderate social information with the option to additionally receive asocial information (i.e. the dot presentation). (5) 'Critical-rich': rich social information with the option to additionally receive asocial information. As such, in the first three conditions, social learners could not see the dots directly.

(c) Procedure

Upon agreeing to take part, participants were given instructions and completed five practice trials in which they received asocial information (i.e. they saw the dots). These trials were extremely easy (64 versus 16 dots) and served to familiarize participants with the task. Participants then took part in multiple simulations in a random order, completing a single trial in each simulation. However, randomly placed among the simulation trials were 12 trials that served to check that participants were paying attention. These trials involved only asocial information and were also very easy (60 versus 20 dots). If a participant responded correctly in fewer than 10 of these 12 trials, they were deemed to be inattentive, their data was discarded, and another participant was

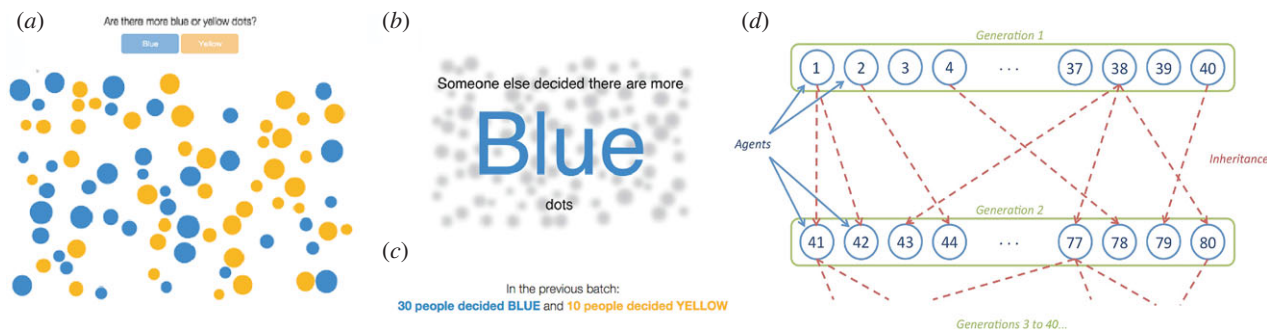


Figure 1. Experimental design. (a) The task interface seen by asocial learners: participants were presented with a display showing 80 blue or yellow dots and were asked to decide which colour was the most numerous. (b,c) The task interface seen by social learners in the (b) poor and (c) moderate conditions: participants did not see the dots themselves but were instead told what a previous participant, or the previous generation of participants, had decided. Rich information was the same, but covered the three most recent generations (e.g. ‘Three batches ago, X people decided BLUE and Y people decided YELLOW. Two batches ago ...’ and so on). Note that, within the social information, generations are referred to as ‘batches’. This word was chosen as it was considered more comprehensible to participants who did not know they were in an evolutionary simulation. (d) A diagram of the simulation structure: Human participants take part as agents, which are arranged into 40 non-overlapping generations of 40 individuals. As the simulation proceeds, genetic and cultural inheritance occurs between generations. (Online version in colour.)

automatically recruited to replace them. Upon completing all trials, participants were thanked, debriefed and paid.

Experimental sessions lasted around 10 min and participants were paid \$1 for taking part, with a bonus of up to \$1 depending on their performance. Participants earned 1 point for each simulation trial they answered correctly but paid 0.15 points to view the dots when taking part as a social learner in the critical social learning conditions. Their bonus b (in US dollars) was calculated as

$$b = \max\left(2\left(\frac{p}{t} - 0.5\right), 0\right),$$

where p is the number of points earned and t is the number of trials. Thus, performance at chance or below did not earn a bonus, while engaging in critical social learning came at a small cost.

(d) The environment

Each simulation took place within a simulated environment which was in one of two states, ‘blue’ or ‘yellow’. The environmental state accurately determined the colour of the majority of dots. The initial state of the environment was randomized for each simulation, and it changed every 10 generations, switching to the other state. Such changes rendered social information (which comes from participants in prior generations) out of date.

In the ‘poor’ condition, participants were not informed that the environment could change (as per [23]), but in all other conditions they were (although they were not told when or how often this occurred). In the ‘poor’ condition, the environment changed after the 10th, 20th, 30th and 40th generations. In the other conditions, environmental change was randomly staggered such that environments were not in sync across simulations, although they still changed every 10 generations within each simulation. This was to prevent participants applying their experience from one simulation to another.

(e) Genetics, fitness and reproduction

Within each simulation, each agent was assigned a haploid genome containing a single locus with two possible alleles; ‘asocial’ and ‘social’. Participants whose agent had the asocial allele (henceforth ‘asocial learners’) received asocial information, while participants whose agent had the social allele (henceforth ‘social learners’) received social information.

In all simulations, the first generation of agents were all asocial learners (the first three generations in the case of simulations with ‘rich’ social information); however, after that the social allele was allowed to invade via mutation, with a mutation rate of 0.1.

After making a decision, agents were assigned a fitness score f as follows: Agents started with a baseline fitness of 0.3, the payoff from being correct was 1, while the cost of collecting asocial information was 0.3. Thus, asocial information provides a costly, but reliable, cue, while social information is cheap, but potentially out of date. Note that social learners in the ‘critical social learning’ conditions (4 and 5) who chose to additionally view asocial information also paid this cost. These values were then squared, thereby increasing the strength of selection, and allowing the production of robust evolutionary dynamics over 40 generations. The resulting values are

$$f = \begin{cases} 1, & \text{asocial or critical, and right} \\ 0, & \text{asocial or critical, and wrong} \\ 1.69, & \text{social and right} \\ 0.09, & \text{social and wrong} \end{cases}$$

Once all 40 participants within a generation had completed all trials, a new group of 40 participants was recruited. Within each simulation, each new participant was assigned to a new agent that inherited the allele of an agent from the previous generation of the same simulation (subject to mutation), with the parent agent selected with probability proportional to their fitness (see schematic in figure 1d). Note that while this led to differential reproduction, fitness did not affect the probability that a participant was chosen to be copied by social learners. As such, selection acted directly on genes, but not cultural traits.

3. Analyses

We conducted four analyses looking at population-level patterns across generations, and two further analyses examining how individuals responded to social information. Unless stated otherwise, all data were subject to Bayesian analysis using Markov chain Monte Carlo (MCMC) methods via the R package rjags [41] to generate posterior samples and, thus, parameter estimates. All models involved three parallel chains for each parameter, the Gelman–Rubin statistic was used to check for convergence (upper C.I. < 1.01), and all estimated values are based on an effective sample size of at least 3000.

(a) Population-level analyses

To describe the population dynamics, we modelled four outcomes across generations and experimental conditions:

(1) whether an agent had the asocial or social allele ($n = 216\,000$); (2) whether a social learner answered correctly, given they did not choose to see the dots if in the critical-moderate or critical-rich conditions ($n = 120\,377$); (3) whether a social learner was contrary, given they did not choose to see the dots if in the critical-moderate or critical-rich conditions ($n = 112\,410$, contrariness is defined below); and (4) whether participants on social trials (where critical social learning was possible) additionally chose to view asocial information ($n = 49\,079$). Collectively, these outcomes characterize the frequency, success and behaviour of the social learners over time. In addition to accounting for generation and experimental condition, we also included hierarchically modelled effects for each repeat-simulation or participant, as appropriate (see full model descriptions below).

Contrariness was defined as follows. With poor social information, contrariness is making the opposite decision to the lone demonstrator. With moderate social information, it is making the opposite decision to the majority of the 40 demonstrators (cases where the demonstrators were split evenly were excluded from the analysis). Due to the generational structure of rich social information, there is no single way to define contrariness in this case, but we adopted the definition as going against what the majority of the 120 demonstrators do (cases where the demonstrators were split evenly were excluded from the analysis).

In all cases, time was measured not in terms of the number of generations for which the simulation had been running (ranging from 1 to 40), but instead as the number of generations since the environment changed (ranging from 0 to 9), henceforth referred to as the 'effective generation'. In addition, estimates were fit separately for each effective generation, meaning we did not assume any particular pattern in the dynamics over time. Data from the first 10 generations were excluded to allow simulations to reach equilibrium, after which the remaining data shows the response of the population to multiple bouts of environmental change. Pooling the data into effective generations allows more accurate inferences to be drawn about the evolutionary dynamics following each instance of change.

The analysis of gene frequency is as follows:

$$S \sim \mathcal{B}(p),$$

and

$$\text{logit}(p) = \beta_{G,C} + \varepsilon_N,$$

where S is whether each agent had the social allele (1 = they did, 0 = they did not), G is their effective generation (an integer from 0 to 9), C is their experimental condition (an integer label, from 1 to 5) and N is the numeric ID of the repeat-simulation (an integer from 1 to 180). In addition, \mathcal{B} is the Bernoulli distribution, while β and ε are parameters to be estimated. The priors were as follows:

$$\beta_{0:9,1:5} \sim \mathcal{N}(0, 10),$$

$$\varepsilon_{1:180} \sim \mathcal{N}(0, \sigma),$$

and

$$\sigma \sim \mathcal{E}(4),$$

where σ is the standard deviation of the repeat-simulation level effects and \mathcal{E} is the exponential distribution.

The other three analyses of population dynamics had the same structure, but with the following differences: In the analysis of decision accuracy the outcome variable is whether a participant made the right decision on a given

trial (1 = they did, 0 = they didn't). In the analysis of contrariness, the outcome variable is whether a participant was contrary on a given trial (1 = they were, 0 = they weren't), and instead of effects of each repeat-simulation, the model included hierarchically modelled effects for each participant as follows:

$$\text{logit}(p) = \beta_{G,C} + \varepsilon_Q,$$

$$\varepsilon_{1:3578} \sim \mathcal{N}(0, \sigma),$$

and

$$\sigma \sim \mathcal{E}(1),$$

where Q is the numeric ID of the participant. In the analysis of critical social learning, the outcome variable is whether a participant with the social allele additionally chose to view asocial information (1 = they did, 0 = they didn't), and effects for each repeat-simulation were again replaced with hierarchical effects for each participant (with 1200 total participants).

(b) Individual-level analyses

To further understand how individuals used social information we conducted two analyses testing for conformist transmission. In the first, we examined the response to moderate social information, in the absence of critical social learning (i.e. data from condition 2). The analysis modelled whether a social learner chose blue, given the proportion of demonstrators who chose blue. We used an established function to test for conformist transmission [35,42] and included hierarchical participant effects to account for individual variation in sensitivity to social information. The model structure is as follows:

$$B \sim \mathcal{B}(p),$$

$$\text{logit}(p) = \beta_1 + (\beta_2 + \varepsilon_Q)S,$$

and

$$S = \frac{R^{\beta_3}}{R^{\beta_3} + (1 - R)^{\beta_3}} - 0.5,$$

where B is whether the participant chose blue (1 = they did, 0 = they didn't), Q is the numeric ID of the participant (an integer from 1 to 1600) and R is the proportion of demonstrators choosing blue. The parameter β_1 is the baseline propensity to choose blue, β_2 is the sensitivity to social influence and β_3 determines whether social learning is conformist. Values of β_3 over 1 guarantee conformist transmission, although, given the logit function, lower values can also indicate conformist transmission if β_2 is high enough. The priors are as follows:

$$\beta_{1,2} \sim \mathcal{N}(0, 5),$$

$$\beta_3 \sim \mathcal{G}(2, 1),$$

$$\varepsilon_{1:1600} \sim \mathcal{N}(0, \sigma),$$

and

$$\sigma \sim \mathcal{E}(0.1),$$

where \mathcal{G} is the Gamma distribution.

We also examined the response to rich social information (i.e. data from condition 3). The analysis was similar to that above; however, because rich social information presented the decisions of three generations of prior participants, we modelled each generation as having a separate additive influence. The model structure is as follows:

$$B \sim \mathcal{B}(p),$$

$$\text{logit}(p) = \beta_1 + (\beta_2 \varepsilon_Q)(S_1 + \beta_4 S_2 + \beta_5 S_3),$$

and

$$S_g = \frac{R_g^{\beta_3}}{R_g^{\beta_3} + (1 - R_g)^{\beta_3}} - 0.5,$$

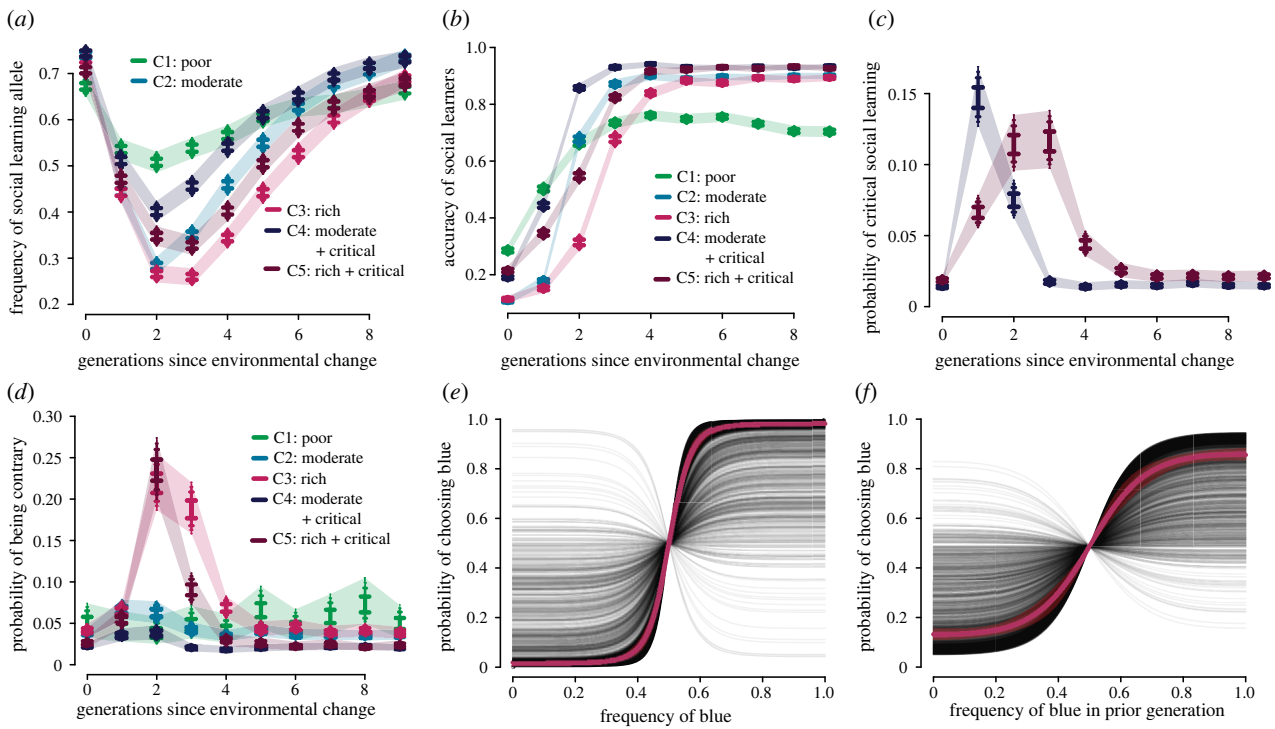


Figure 2. The evolution of social learning in a changing environment. (a–d) Intervals show the 50%, 80%, 90% and 95% credible intervals. Shaded regions link the 95% credible intervals to aid reading. (a) The social learning allele became less frequent following environmental change. This drop was exacerbated by the richness of social information, but attenuated by the option of gathering asocial information. (b) The accuracy of social learners falls immediately after environmental change, but recovers thereafter. Again, this drop was exacerbated by the richness of social information, but attenuated by the option of gathering asocial information. (c) Where critical social learning was permitted, social learners were more likely to gather asocial information shortly after environmental change in response to lowered consensus. (d) Contrariness was overall quite low, but with rich social information it peaked two generations after environmental change as participants adopted up-and-coming traits. A much smaller peak is present with moderate social information. (e,f) The red line and shaded area (barely wider than the line) shows the expected behaviour of the average participant with the 95% credible interval. The grey lines show the median estimate for each individual participant. With both moderate (e) and rich (f) social information the typical response is highly conformist, although there is great inter-individual variation. (f) specifically shows the response to the most recent generation of participants. The response to earlier generations was weaker, particularly the second most recent generation. (Online version in colour.)

where R_g is the proportion of demonstrators who chose blue g generations ago. Note that: the intensity of conformist transmission (β_3) is shared across all three generations; the individual level effects are multiplicative instead of additive (this change was made to improve MCMC sampling efficiency); and β_2 determines the influence of the most recent generation, while β_4 and β_5 determine the *relative* influence of the second and third most recent generations, respectively. Unless the same as above, the priors are as follows:

$$\beta_{4,5} \sim \mathcal{N}(1, 1),$$

$$\varepsilon_{1:1480} \sim \mathcal{N}(0, \sigma),$$

and

$$\sigma \sim \mathcal{E}(1).$$

4. Results

Parameter estimates are presented as posterior medians and the 95% central posterior interval. For full estimates of the frequency of the social learning allele, the accuracy of social learners, the rate of contrariness and the rate of conditional social learning for each condition and each generation after environmental change, see the electronic supplementary material. Due to the sheer number of possible contrasts between conditions and/or generations (minimally 1075, maximally 14535), such contrasts are not provided, but they can be readily computed from the model output.

(a) Gene frequency

The frequency of the social learning allele dropped markedly after environmental change in all conditions (figure 2a). The drop was smallest with poor social information (dropping by 0.16, [0.14, 0.18] over two generations following environmental change), but bigger with moderate or rich social information (dropping by 0.46, [0.44, 0.47] and 0.46, [0.45, 0.48], respectively). Moreover, rich social information slowed the recovery of the social learning allele following change; with moderate social information there was a marked recovery from two to three generations after change (increasing by 0.07, [0.05, 0.09]), but not so in with rich social information (–0.01, [–0.03, 0.01]). With rich social information, the social learning allele began to spread between the third and fourth generations after change (0.08, [0.06, 0.1]).

The magnitude of the drop was lower when critical social learning was permitted, both with critical-moderate (0.34, [0.32, 0.36]) and critical-rich (0.36, [0.34, 0.38]) social information. However, critical social learning did not prevent the delay in the recovery of the social learning allele with rich social information (change between 2 and 3 generations after change with critical-rich information: –0.02, [–0.04, 0]).

Once the environment had been stable for an extended period (i.e. 10 generations after change), the social allele was less prevalent with poor social information (0.67, [0.65, 0.69]) than in any other condition (moderate: 0.74,

[0.72, 0.76], rich: 0.73, [0.71, 0.75], critical-moderate: 0.74, [0.72, 0.76], critical-rich: 0.74, [0.72, 0.76]).

(b) Social accuracy

In all conditions, the accuracy of social learners was at a minimum immediately after environmental change (figure 2b). After such change, social learners fared best with poor information (accuracy of 0.29, [0.27, 0.3]), and worst with moderate or rich social information (0.11, [0.1, 0.12] and 0.11, [0.1, 0.13], respectively). Critical social learning improved performance after environmental change, but not to the level seen with poor information (critical-moderate: 0.19, [0.18, 0.21], critical-rich: 0.21, [0.2, 0.23]).

Subsequently, performance increased in all conditions. With poor social information it increased rapidly at first, but soon after slowed (increasing by 0.22, [0.19, 0.24] between 0 and 1 generations after change, but by only 0.07, [0.05, 0.1] two generations later). With moderate and rich social information, the increase was very small in the first generation (0.07, [0.05, 0.09] and 0.04, [0.02, 0.06], respectively), but accelerated thereafter (0.5, [0.47, 0.53] and 0.16, [0.13, 0.19], respectively, in the next generation), although note that the rise in accuracy was slower with rich social information than with moderate social information.

Critical social learning increased both minimum accuracy (critical-moderate: 0.19, [0.18, 0.21], critical-rich: 0.21, [0.2, 0.23]) and the rate at which accuracy increased (increasing by 0.25, [0.23, 0.28] and 0.13, [0.11, 0.16] by the first generation after change with critical-moderate and critical-rich information, respectively), greatly reducing the initial delay. However, as with rich information, accuracy with critical-rich information was slower to recover than with critical-moderate social information.

Long after environmental change, the accuracy of social learners was much lower with poor information than in any other condition, and critical social learning increased accuracy further (poor: 0.7, [0.68, 0.72], moderate: 0.9, [0.89, 0.91], rich: 0.89, [0.88, 0.91], critical-moderate: 0.93, [0.92, 0.94], critical-rich: 0.93, [0.92, 0.94]). While social accuracy was stable five generations after change in most conditions, it slowly declined with poor information (0.75, [0.73, 0.77] five generations after change, versus 0.7, [0.68, 0.72] nine generations after change).

(c) Critical social learning

The use of critical social learning (paying to receive asocial information in addition to social information) was generally low, but spiked shortly after environmental change (figure 2c). In the generations first experiencing a novel environment, critical social learning was quite rare (critical-moderate: 0.01, [0.01, 0.02], critical-rich: 0.02, [0.02, 0.02]), but it increased rapidly thereafter. With critical-moderate information critical social learning peaked one generation after environmental change (0.15, [0.13, 0.17]), returning to baseline levels two generations later. With critical-rich information, critical social learning grew more slowly, peaking in the second and third generations after environmental change (0.11, [0.09, 0.13] and 0.11, [0.1, 0.14], respectively), returning to baseline levels three generations later. Thus, the pattern was similar with both kinds of information, but the spike was slower (and longer-lasting) with critical-rich information than with critical-moderate information.

There was considerable individual variation in critical social learning (participant standard deviation: 3.26, [3.07, 3.47]). While 40% of participants never engaged in critical social learning, 10% of participants did so on the majority of trials, and the remaining 50% did so on a minority of trials. This skewed distribution causes an apparent mismatch between model estimates and raw-data averages: the model estimates the rate of critical social learning one generation after change and with critical-moderate information to be approximately 0.15, while the proportion of trials on which critical social learning occurred is approximately 0.25. This is because the model estimates are based on the behaviour of the typical participant (typical meaning 'average on the logit scale'), while the raw-data average pools data from all participants and does not use the logit scale. As such, the raw-data average is more greatly affected by the minority of participants who engage heavily in critical social learning than is the model estimate. Nonetheless, the general pattern of a spike in critical social learning following environmental change is present in both the raw-data and model predictions.

(d) Contrariness

Contrariness (doing the opposite of what the social information suggests, assuming critical social learning is not used, see definition above) was somewhat unusual, but far from rare (figure 2d). With poor information, contrariness was steady over time, with model estimates for the rate of contrariness ranging from a low of 0.04, [0.03, 0.06] (one generation after change) to 0.07, [0.05, 0.1] (eight generations after change). With moderate or rich information, model estimates suggest baseline contrariness is similar (0.04, [0.03, 0.04] and 0.04, [0.03, 0.05], respectively, nine generations after change), although it was lower with critical-moderate and critical-rich information (0.02, [0.02, 0.02] and 0.02, [0.02, 0.03], respectively, nine generations after change).

With rich and critical-rich information there was a large spike in contrariness peaking two generations after environmental change (reaching 0.22, [0.19, 0.25] and 0.23, [0.2, 0.27], respectively). With critical-rich information the spike was short-lived, and contrariness returned to baseline levels two generations later. With rich information, the spike was longer-lasting, and baseline levels were not regained until three generations later. Similar, but much smaller contrariness spikes are seen with moderate and critical-moderate information, with contrariness peaking one generation after change (0.07, [0.05, 0.08] and 0.04, [0.03, 0.04]). While these spikes are small, the statistical evidence for them is strong (i.e. 95% central posterior intervals for the difference in contrariness between 0 and 1 generations after change exclude 0).

There was considerable individual variation in contrariness (participant standard deviation: 2.00, [1.92, 2.07]). Around 40% of participants were never contrary; however, a minority of around 5% were contrary more often than not, while the remaining 45% of participants were contrary on a minority of trials. Again, this skewed distribution causes a mismatch between model estimates (which correspond to an average participant on the logit scale) and raw-data averages (which average across participants, not on the logit scale) wherein the model's estimates are lower (e.g. the raw average rate of contrariness with poor information is 0.14, above the model estimate of approx. 0.05). Thus, actual rates of contrariness are higher than the model

output might suggest, but the model nonetheless captures generational dynamics accurately.

(e) Conformist transmission

With moderate social information, participants showed no prior preference for choosing blue or yellow (β_1 : 0.01, [-0.03, 0.05]), but a great deal of social influence (β_2 : 7.9 [7.5, 8.4]). Moreover, the response to consensus was highly conformist (β_3 : 3.6, [3.0, 4.3]; figure 2e). There was a great deal of individual variation (participant standard deviation: 5.1 [4.7, 5.5]) with most participants being highly conformist, but a minority showing little social influence or being contrary.

With rich social information, the pattern was similar: Participants showed a minor preference for choosing yellow as opposed to blue (β_1 : -0.05, [-0.09, -0.01]), but a great deal of social influence (β_2 : 3.7 [3.3, 4.0]). Moreover, the response to consensus was highly conformist (β_3 : 2.3, [1.7, 3.2]; figure 2f). Relative to social information from the most recent prior generation, social information from two generations ago had a much smaller influence (β_4 : 0.20 [0.09, 0.33]), while information from three generations ago fell between the two (β_5 : 0.83 [0.76, 0.90]). As with moderate social information, there was a great deal of individual variation (participant standard deviation: 0.66 [0.63, 0.70]), with most participants being highly conformist, but a minority showing little social influence or even being highly contrary.

5. Discussion

We have presented results from a series of experimental evolutionary simulations in which a social learning allele invaded an asocial population in a changing environment. Across five different forms of social information, we find that environmental change causes the social learning allele to drop in frequency and decreases the accuracy of social learners, but also leads to spikes of critical social learning and contrariness.

Perhaps counterintuitively, the drop in the social learning allele is smallest with poor social information. In part this reflects the inferior performance of social learning with poor information during periods of environmental stability: this low performance means that the social learning allele does not spread as far as in the other conditions and the increased prevalence of *asocial* learning makes the population more adaptable to change. The result that moderate and rich social information exacerbate the negative effects of environmental change fits with other work that found conformist transmission can allow social learning to spread to such a degree that populations go extinct following environmental change [33].

Another cross-condition result is that rich social information, containing the decisions of individuals from the prior three generations, creates a lag in the evolutionary dynamics. The drop in the frequency of the social allele, the drop in the accuracy of the social learners and the spike in critical social learning all last longer with rich information than with moderate information (which was drawn from only the single most recent prior generation). This result can be imagined as multi-generational social information creating cultural inertia that prevents rapid cultural adaptation following environmental change. Indeed, the analysis of conformist transmission with rich information found that participants weighted information from three generations

ago almost as heavily as information from the most recent prior generation. The possibility of cultural inertia has implications for the evolution of the post-reproductive phase of human life history [9], and the role of post-reproductive individuals in conserving and transmitting information [43]. While it may well be true that post-reproductive individuals can recall and share valuable information with other individuals, unless this information is readily updated it may in fact increase the risk posed by environmental change.

A final general result is that critical social learning [26] is broadly beneficial: despite the cost it brings, it nonetheless reduces the drop in the social learning allele and improves decision-making accuracy. Thus, our results support theory arguing for critical social learning as an adaptive decision-making mechanism, although the adaptive value of critical social learning may decrease if asocial information collection is prohibitively costly.

Concerning the extent to which human social learning is adapted to a changing environment, we find signs of this, but also clear indications of adaptations for high-fidelity transmission that exacerbate the problems caused by environmental change. The largest indication of such high-fidelity transmission is conformism. As noted above, conformist transmission can be so problematic following environmental change that populations can collapse [33]. Similar problems have been noted elsewhere [44]. One possible solution to this comes from theory suggesting that an adaptive conformist tendency is likely to be weak, such that rare-but-adaptive traits are not prevented from spreading [45,46]. However, this is not what we find: despite being aware of the possibility of environmental change, the conformist pattern in participants' decision-making was strong and led to severe declines in the frequency of the social learning allele.

Alongside these signs of high-fidelity transmission, however, were clear indications of attempts to account for environmental change. For instance, when participants were permitted to engage in critical social learning, they were much more likely to do so immediately following environmental change than during periods of stability. This is adaptive assuming that asocial learning is costly, and so should be used only when necessary, for instance, when culture is misleading due to environmental change. In this experiment, the only cue of environmental change was the consensus among demonstrators, and so participants must have noted the decrease in consensus, taken this as an indication of environmental change and responded by gathering their own information.

Similar patterns are seen in rates of contrariness, which spiked after change, dramatically so with rich or critical-rich information. Again, such contrariness is adaptive in cases where culture is misleading, and, if timed right, is doubly adaptive because it avoids the costs of asocial information collection. As with critical social learning, participants must have used consensus to guide their contrariness. With moderate, or critical-moderate, information, a small minority of participants responded to decreased consensus by gambling on the idea that the environment had recently changed and siding with the minority. With rich, and critical-rich, information participants could additionally observe the change in consensus over time. As the minority trait began to spread following change, a larger group of participants picked up on this and adopted the up-and-coming trait. Such behaviour has been noted elsewhere [29] and facilitated cultural

adaptation in our experiments. Nonetheless, such measures only partially offset the negative effects of environmental change, an observation that highlights the precariousness of humanity in the Anthropocene: we inhabit a culturally constructed world that developed across the remarkable climactic stability of the Holocene, and its fate is unclear should instability (anthropogenic or otherwise) return.

Contrariness more generally buffered culture against the effects of environmental change. For instance, even with poor social information where contrariness cannot be strategically timed, participants showed unexpectedly high rates of contrariness (14% of trials, theory typically assumes individuals are never contrary). This contrariness effectively created a reservoir of cultural exaptations that benefited the population following environmental change. Despite these benefits, the evolutionary basis for this behaviour is unclear, because the contrarians themselves paid a cost to do so (by going against social information that is typically accurate). Given the group-beneficial aspect of this behaviour, it is possible that it is an example of human prosociality [3,47–49], although it is not clear why the burden of such altruism is distributed so unevenly. Alternatively, such behaviour may in fact be individually beneficial by helping the contrarian stand out and attract a following [50]. Contrariness, or a more general disregard for social information, has repeatedly been observed in experimental studies of human social learning, and has typically been attributed to participants not trusting the experiment or not being sufficiently motivated to maximize their accuracy [34,39,49,51]. However, by highlighting the potential value of contrariness, this work suggests that it should be considered as a possible group-level adaptation. Moreover, even if it was not a target of selection, our work suggests it nonetheless has beneficial effects at the population level, and impacts cultural and genetic evolution.

One unexpected result was the scale of individual variation in social information use, contrariness and critical social learning. Many studies of social learning have documented individual variation in sensitivity to social information [34,52]. However, along with other similar results [39], this work suggests the scale of the variation is such that it spans qualitatively different behaviours. Most individuals follow the social information, but a minority are broadly indifferent to the decisions of others, while an even smaller group are deliberately contrary. Similarly, most participants occasionally use critical social learning, while a sizable minority never do so, and an even smaller minority do so most of the time. Consideration of the origin of variation on this scale raises further questions about the sensitivity of human social learning to contextual variables, individual states, cultural norms and developmental factors [53–56], which in turn questions the nature of what has evolved to facilitate human culture [57].

While this work suggests considerable limitations in the ability of human groups to culturally adapt to unstable environments, as with all experiments, our experimental setting was impoverished relative to the real-world. In particular, we excluded forms of social learning that may have further helped the population adapt, including for instance payoff-biased transmission, which has been shown to contribute to complex cultural adaptations both in theory and experimental settings [5,58–61]. Thus, the expansion of this work to include payoff-biased transmission would be a valuable step. However, in many cases, information about

payoffs may be opaque, noisy or unavailable until long after a decision is made, meaning payoff-biased transmission may not always be effective and, in some cases, may not be possible. Another alternative not included in this experiment is prestige-biased transmission [62], which accounts for the difficulty of perceiving payoffs by having individuals copy those who are generally successful, and/or deferred to by third parties, under the assumption that these are proxies for payoffs. Such behaviour has been documented experimentally [63–65] although ethnographic evidence is more mixed [66–68]. Nonetheless, allowing the possibility of prestige-biased transmission would be a valuable extension of this work.

One final factor missing in this work is the possibility of cumulative cultural evolution. In our experiment, populations adapted by switching between different options, with no possibility of refining the option to further increase payoffs. Such cumulative cultural evolution is clearly an important factor in the adaptive value of culture [25,69] and so its omission here is potentially important. Tasks open to cumulative improvement have been employed in largescale online experiments [61] although not yet in a changing environment.

The problem of adapting to a changing environment highlights two opposing functions of culture. One is to use collective decision-making to flexibly switch between options as the local environment demands. The other is to pass on valuable information from prior generations during periods of stability between bouts of environmental change. Such information may also be beyond the scope of any one individual, with high-fidelity transmission thus being critical to cumulative cultural change [70–72]. These two purposes are, seemingly, competing; the greater the fidelity of transmission, due to processes like conformist transmission, the harder it is for populations to keep up with environmental changes. Nonetheless, this work suggests human psychology represents a compromise between the two: transmission is typically conformist and high-fidelity, but there is also a considerable deal of contrariness, critical social learning and the adoption of up-and-coming traits all of which support social learning in a changing environment. The challenges in balancing these two needs, and in maintaining the adaptive value of culture in a changing environment, may explain why extensive cultural adaptation is unique to our species. Further work will provide a more comprehensive understanding of how human psychology meets the competing needs of fidelity and flexibility.

Ethics. Recruitment and testing were approved by the Committee for Protection of Human Subjects at University of California, Berkeley (protocol ID 2015-12-8227).

Data accessibility. Data and analysis code is available at <https://osf.io/kru5/>.

Supplementary results are provided in the electronic supplementary material [73].

Authors' contributions. T.J.H.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, software, validation, visualization, writing—original draft, writing—review and editing; J.W.S.: investigation, methodology, software, writing—review and editing; T.L.G.: conceptualization, funding acquisition, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work was funded by NSF grants 1456709 and 1408652.

Acknowledgements. We thank J. Hamrick, M. Pacer, S. Meylan, C. Ewing and A. Mitchell for their assistance in designing the experimental software, and R. Boyd, F. Reali and C. Cross for advice on the manuscript.

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