

The evolution of conformist social learning can cause population collapse in realistically variable environments[☆]

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Abstract

Why do societies collapse? We use an individual-based evolutionary model to show that, in environmental conditions dominated by low-frequency variation (“red noise”), extirpation may be an outcome of the evolution of cultural capacity. Previous analytical models predicted an equilibrium between individual learners and social learners, or a contingent strategy in which individuals learn socially or individually depending on the circumstances. However, in red noise environments, whose main signature is that variation is concentrated in relatively large, relatively rare excursions, individual learning may be selected from the population. If the social learning system comes to lack sufficient individual learning or cognitively costly adaptive biases, behavior ceases tracking environmental variation. Then, when the environment does change, fitness declines and the population may collapse or even be extirpated. The modeled scenario broadly fits some human population collapses and might also explain nonhuman extirpations. Varying model parameters showed that the fixation of social learning is less likely when individual learning is less costly, when the environment is less red or more variable, with larger population sizes, and when learning is not conformist or is from parents rather than from the general population. Once social learning is fixed, extirpation is likely except when social learning is biased towards successful models. Thus, the risk of population collapse may be reduced by promoting individual learning and innovation over cultural conformity, or by preferential selection of relatively fit individuals as models for social learning.

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1. Introduction

The collapse of societies has intrigued humans for millennia (Tainter, 1988). Rapid rates of change in the global environment have sparked a recent surge of interest into the relationship between societal collapse and environmental change (Diamond, 2005; Wright, 2004). Using archaeological, anthropological and historical sources, Diamond (2005) and Wright (2004) conclude that such collapses are almost invariably related to interactions

between the cultural behavior of humans and their ecological environment.

Ecology and culture may interact in many ways. Some suggest that environmental variation was key to the evolution of cultural capacity in humans (Richerson & Boyd, 2005) and possibly other species (Rendell & Whitehead, 2001). If the environment of an organism varies considerably, but not predictably, over time scales of the order of a generation to tens of generations, then direct genetic determination will not allow behavior to track the environment efficiently. Forms of phenotypic plasticity will be selected (Agrawal, 2001). With more cognitively capable organisms this often takes the form of individual learning, so that an individual explores its environment and adjusts its behavior adaptively. However, individual learning has costs which may include time, energy, predation risk, as well as the development and maintenance of a behavioral control system

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(the brain). Once a species is using individual learning to track environmental variation, then a less-costly strategy of social learning may invade (Boyd & Richerson, 1985). Social learners use information provided by the behavior of others to regulate their own behavior, through mechanisms such as imitation and emulation (Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Social learning can lead to the homogenization of behavior among groups of individuals. By some definitions (including that of Laland & Hoppitt, 2003) this is culture.

However, if social learning becomes the sole learning strategy, with individual learners extirpated, the behavior of the population will no longer be able to track environmental variation, as individuals will only be reacting to each other and not to the underlying environment. Several analytical models examining the evolution of culture have predicted a population equilibrium between individual learning and social learning, with the individual learners tracking the environment more closely but paying higher costs (e.g., Aoki, Wakano, & Feldman, 2005; Boyd & Richerson, 1985; Feldman, Aoki, & Kumm, 1996; Wakano, Aoki, & Feldman, 2004). Alternatively, and probably more realistically in the case of humans (e.g., Boyd & Richerson, 1995; Enquist, Eriksson, & Ghirlanda, 2007; Kameda & Nakanishi, 2002; Wakano & Aoki, 2006), a contingent strategy may evolve in which individuals adopt either social or individual learning depending on the circumstances.

How robust are these equilibria? Using an individual-based stochastic model, Whitehead (2007) found that with some patterns of environmental variation, the fixation of social learning at the expense of individual learning is a frequent outcome. Similarly, a population of individuals who adopt individual or social learning on a contingent basis may be vulnerable to invasion by pure social learners who do not pay the costs of contingency.

Here, we use a modification of the individual-based model (described in Whitehead, 2007) to show that a consequence of the decline or demise of individual learning as a pure strategy or as part of a contingent strategy is that the population becomes at high risk of collapse or extirpation. The “ $1/f$ noise” family of models is used to introduce environmental variation. The slope of the inverse of the frequency spectrum (ω) characterizes different types of $1/f$ noise. $1/f$ noise provides good descriptions of natural environmental fluctuation and has considerable empirical support (Halley, 1996). In Appendix A, we describe and justify the concept of $1/f$ noise as a descriptor of environmental variation. $1/f$, or red, noise is an important concept borrowed by evolutionary biologists from the physical environmental sciences. The important intuition is that noise in the real world is typically organized such that variation tends to be more or less concentrated in relatively rare, relatively large events. Red noise is important because evolutionary processes are myopic. Thus, the evolution of costly mechanisms of environmental tracking like individual learning will tend to be selected against, relative to “cheap”

conformist learning, in long runs of relatively invariant times only to be “ambushed” by rare large amplitude excursions. A principal purpose of our paper is to illustrate that for this reason $1/f$ noise is a potentially important phenomenon in human evolution.

In the “standard” version of our model, contingent horizontal/individual learners compete with pure horizontal learners in a red noise environment with $\omega=1$ [see Eq. (3) below], a modal pattern of variation in the population trajectories of real species (Inchausti & Halley, 2002). The model assumes that the strategies themselves are faithfully inherited (genetically or culturally) from parents, although we discuss how variants of this process would modify the results, in particular the times to extirpation. We focus the analysis on extirpations for economy of presentation. Less than complete losses of costly learning strategies may lead to population collapses less severe than extinction. By varying the parameters and form of the model, we explore the circumstances in which the viability of a population is at risk due to the ways its members control their behavior. Thus we identify factors that promote and alleviate collapse.

Our results indicate how different patterns of environmental variation, and modes of social learning, affect population variation through the evolution of learning strategies. They provide a novel perspective for interpreting some historical and anthropological records of population declines and may have political or sociological implications.

2. Methods

The model, shown diagrammatically in Fig. 1, considers a univariate environment with value $y(t)$ at time t , so after 12 time units, $y(12)$ might be 0.17. The realized behavior of individual i at time t is expressed by a univariate measure $x(i,t)$, so after 12 time units the behavior of individual i , $x(i,12)$ might be 0.24. Both x and y are unbounded and can, theoretically, range between minus and plus infinity. The fitness of individual i at time t is given by a Gaussian function of the difference between $x(i,t)$ and $y(t)$ (as in Boyd & Richerson, 1985), 0.07 for individual i at time 12 in the example:

$$w(i,t) = \frac{D \cdot e^{-\frac{[x(i,t)-y(t)]^2}{2q^2}}}{C_{u(i,t)}} \quad (1)$$

Thus the closer $x(i,t)$ is to $y(t)$, the better an individual’s behavior tracks the environment, and the more successful it is likely to be. q is the standard deviation of the fitness function, such that a small q gives large penalties for failing to track the environment closely. Without loss of generality, we set $q=0.8494$ so that if $x(i,t)$ is one unit from $y(t)$ there is a 50% drop in fitness. $x(i,t)$ is made up of a target value of the behavior at time t , $X(i,t,u(i,t))$, plus some normally distributed random error with mean zero and standard deviation σ , the behavioral accuracy.

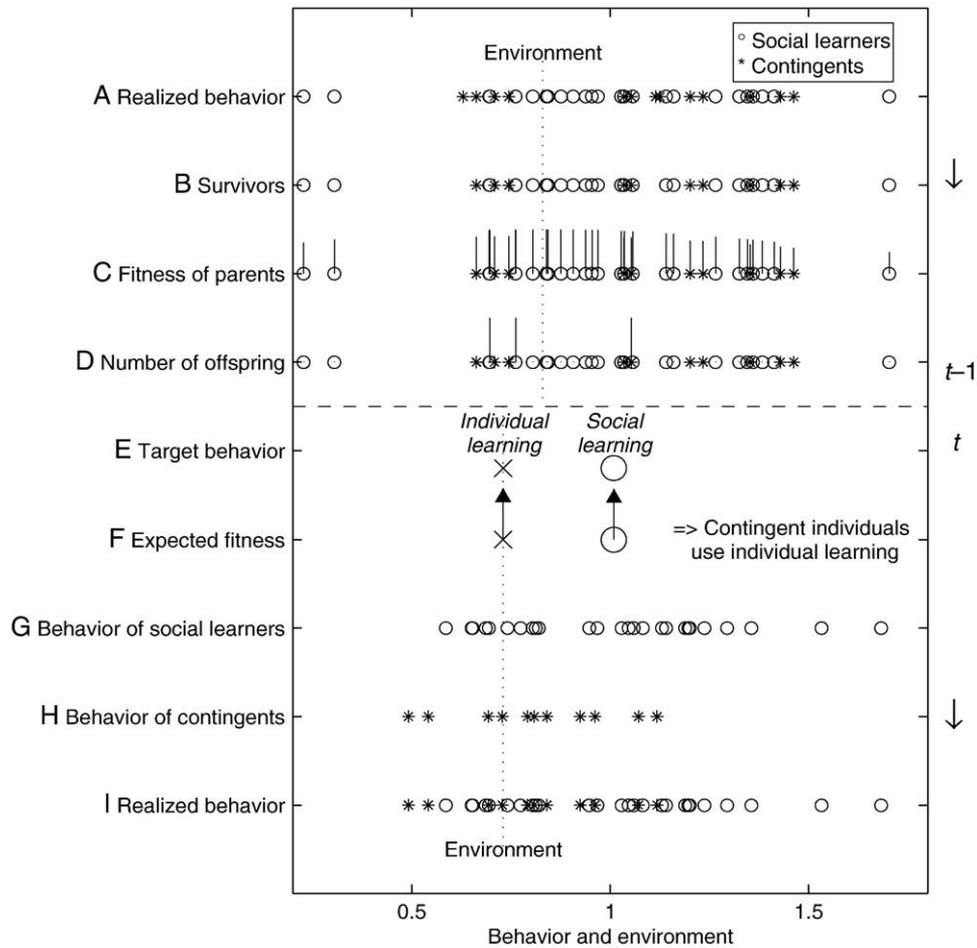


Fig. 1. Illustration of the major elements of one time cycle of the standard model, containing horizontal social learners and contingent individuals who can either learn socially or individually. The x -axis gives the distribution of behavioral phenotypes in the population, as well as the environmental variation. (A) The realized behavior in time unit $t-1$ is roughly normally distributed, with about equal numbers of pure social learners and contingents; (B) a small proportion of the individuals do not survive; (C) the fitness of the survivors declines with the distance of their behavior from the environmental optimum, and contingent individuals pay a small premium for their flexibility; (D) three offspring are born to replace those who did not survive, with their parents generally being individuals of high fitness; (E) with a new time unit (t) the environmental optimum has changed, and this environmental optimum is the target behavior of individual learners, while the mean behavior of the survivors in time unit $t-1$ is the target behavior of social learners; (F) the expected fitness of individual learners is slightly higher than that of social learners, so, in this time step, contingent individuals choose individual learning; (G) the realized behavior of the social learners is normally distributed around the target (mean behavior of survivors in previous time unit); (H) the behavior of the contingent individuals is normally distributed around the target for individual learners (the environmental optimum); (I) the behavior of the population is that of the social learners plus contingent individuals. Notice that the contingent learners (*) are reasonably well centered on the changed environment in time unit t , whereas the social learners (O) have not adjusted and have on average ended up rather far from the environmental optimum.

$u(i,t)$ is a categorical variable indicating the learning tactic used by organism i at time t , which can be either genetic determination ($u=G$), vertical social learning from parents ($u=V$), horizontal social learning from the general population ($u=H$), or individual learning ($u=I$). $C_{u(i,t)}$ reflects the cost of that learning tactic, with individual learning being more costly (as in previous models, e.g., Boyd & Richerson, 1985). Costs of vertical social learning are generally assumed to be less than those of horizontal social learning as fewer models are observed and there is less integration of information, while genetic determination is cheapest. Thus, $C_G < C_V < C_H < C_I$. Each individual possesses a learning strategy, which contains one or more potential tactics and is inherited genetically (haploid

population without mutation) or culturally (socially learned without error) from its parent.

D varies between learning strategies, reflecting the cost of contingency, so that if an individual has many options available, it pays a cost which is indicated by a low value of D .

In most runs of the model there were two possible learning strategies. The baseline was a contingent horizontal/individual learning strategy following the reasoning of Boyd and Richerson (1995), Henrich and Boyd (1998), Kameda and Nakanishi (2002) and Wakano and Aoki (2006) that such a contingent scenario may best represent the general human learning strategy. These individuals have both social and individual learning tactics available to them at each time unit

and adopt that tactic with maximum expected fitness (see Whitehead, 2007, for how expected fitness is calculated), but their actual fitness whichever tactic is chosen is discounted by $D=0.95$. In the standard version of the model, the alternative to the baseline horizontal/individual contingent strategy is pure horizontal learning (in which case, as no contingency is available, $D=1$).

When the horizontal social learning tactic ($u=H$) is employed, the mean realized behavior of all surviving individuals in the previous time unit, $\{j\}$, is used as the target behavior, $X(i,t,H)=\text{Mean}[x(j,t-1)]$. This approximates situations such as averaging the behavior of a number of randomly chosen models or copying the modal behavior. It is conformist, in the sense of a frequency-dependent bias in transmission. Under individual learning ($u=I$) the target behavior is that which maximizes fitness, $X(i,t,I)=y(t)$.

The probability of survival of an individual between consecutive time units is $\mu (=0.975$, giving a generation time of 40 time units). Only survivors reproduce, and the number of offspring of individual i which survive to time unit $t+1$ is Poisson distributed with mean:

$$\frac{w(i,t) \cdot 2 \cdot (1 - \mu) \cdot N(0)}{\mu \cdot [\bar{w}(0) \cdot N(0) + \bar{w}(t) \cdot N(t)]} \quad (2)$$

where $N(t)$ is the population size after time t ; $N(0)$ the original, input, population size; and $\bar{w}(t)$ is the mean of $w(j,t)$, which is the mean fitness at time unit t . This gives an expected reproductive rate among individuals i at time t proportional to $w(i,t)$, density-dependence with a carrying capacity of $N(0) \cdot [2\bar{w}(t) - \bar{w}(0)]/\bar{w}(t)$, and so a population size generally increasing with the mean fitness of its members. The maximum population size at very high fitness [$\bar{w}(t) \gg \bar{w}(0)$] is $2 \cdot N(0)$. The maximal rate of increase of the population at very high fitness is $(1 - \mu) \cdot [2 \cdot N(0) - N(t)]/N(t)$, giving the potential for a quick recovery from low population sizes.

Environmental trajectories were produced using $1/f$ noise (Halley, 1996). Starting off with Gaussian “white noise”, in which each element is an independent normally distributed random variable with mean 0 and standard deviation 1, Y ($t=1, \dots, T$), for any slope of the inverse of the noise frequency spectrum, ω , a new trajectory can be calculated:

$$y = \frac{\delta \cdot S^{-1}[S(Y)^{-\omega}]}{\text{SD}(S^{-1}[S(Y)^{-\omega}])} \quad (3)$$

where S is the Fourier transform, and S^{-1} the inverse Fourier transform (see Appendix A). The spectrum for white noise is flat, so that $S(Y)^{-\omega}$ produces an inverse frequency spectrum with slope ω . For white noise $\omega=0$, while for red noise, in which lower frequencies have greater energy, $\omega>0$. δ sets the standard deviation of y , in other words the amount of noise. In the standard runs of the model, we chose $\omega=1$ as this is very close to the mean spectral exponent of the 544 series of natural population dynamics studied by Inchausti and Halley

(2002). In some respects, this is a relatively conservative assumption. Proxy records for the temperature spectrum for the last 100,000 years frequently have $\omega>1$ over many time scales (e.g., Ditlevsen, Svensmark, & Johnsen, 1996), which increases the effects that we model (see below).

Initially, the population included $N(0)/2$ individuals possessing each of the two learning strategies (contingent horizontal/individual and horizontal social learning), each assumed to have a different parent, with intrinsic and target behavior $X=\text{Normal}(0, \sigma)$, and realized behavior $x=\text{Normal}(X, \sigma)$ for this parental generation.

The model run proceeded until either the population was extirpated ($N(t)=0$) or $t=32,768$ (2^{15}) time units. The time series of population size and numbers of individuals with each strategy was examined for fixation (the first time when all remaining individuals possessed the same strategy) and population extirpation.

There were 100 runs with each set of parameters. The “standard” runs had the following parameters: $C_I/C_H=1.06$ (the ratio of costs for individual vs. horizontal social learning; because of standardization in Eq. (2), the absolute values of the costs are immaterial), $\sigma=0.25$, $\omega=1$, $\delta=4$, $N(0)=1500$. To examine the robustness of the results, a set of runs were carried out with each of these parameters raised and then with each lowered (Table 1).

Finally, instead of the contingent horizontal/individual and horizontal social learning strategies being the only available options, sets of runs were carried out with different sets of learning strategies or variations on the tactics which constituted the strategies:

- Horizontal social learning and individual learning strategies. This is the relatively simple situation without contingent strategies.
- Contingent vertical/individual and vertical social learning strategies. $C_I/C_V=1.12$.
- Multiple strategies. This is the set of strategies whose dynamics (until, but not beyond, fixation) are explored by Whitehead (2007). There are four basic tactics (all introduced above): individual learning, horizontal social learning and vertical social learning, plus genetic determination (with very low cost, $C_I/C_G=1.18$) in which the target behavior of an individual is fixed through its life and the same as the target behavior of its parent. The population is initially divided into 15 equal-sized sets of individuals with each of the following strategies: genetic determinists, vertical social learners, horizontal social learners, individual social learners and all contingent combinations of two to four of the basic tactics (such as individual/genetic, vertical/individual/genetic, etc.). Individuals with contingent strategies have their tactical set available to them at each time unit, adopting the tactic with maximum expected fitness as in the standard model. Fitness is discounted by a factor of $D=0.95$ for strategies with

Table 1
Summary of results of runs of individual-based model of the evolution of learning strategies

Type of run [parameters] (variant type)	Number of runs with			Mean time to fixation	Mean time from fixation to extirpation
	Fixation	Extirpation	Horizontal learning dominant		
Standard [$\sigma=0.25$ $C_I/C_H=1.06$ $N(0)=1500$ $\omega=1$, $\delta=4$]	35/100	34/100	100/100	12,313	2578
High learning costs [$C_I/C_H=1.14$]	84/100	84/100	100/100	8260	1883
Low learning costs [$C_I/C_H=1.02$]	13/100	12/100	99/100	15,482	2822
Inaccurate behavior [$\sigma=0.75$]	74/100	66/100	100/100	9760	2984
Accurate behavior [$\sigma=0.08$]	42/100	42/100	100/100	12,105	1881
More red environment [$\omega=2$]	100/100	82/100	100/100	4173	3974
Less red environment [$\omega=0$]	100/100	0/100	0/100	337	–
More variable environment [$\delta=8$]	0/100	0/100	99/100	–	–
Less variable environment [$\delta=1$]	100/100	46/100	100/100	4404	3553
Large population size [$N(0)=5000$]	5/100	5/100	100/100	12,406	3215
Small population size [$N(0)=500$]	87/100	86/100	100/100	9295	1469
Horizontal or individual strategies (a)	17/100	17/100	100/100	12,173	2009
Vertical or vertical/individual contingent strategies (b)	100/100	0/100	0/100	523	–
All 15 strategies (c)	27/100	22/100	100/100	15,339	2362
Biased learning (d)	99/100	0/100	100/100	4561	–
Random models for social learning with error (e1)	1/100	0/100	0/100	29,252	–
Random models for social learning without error (e2)	14/100	13/100	100/100	17,104	970

two tactics available, $D=0.95^2$ with three and $D=0.95^3$ if all four tactics are possible. This element of the model is justified if the addition of each tactic decreases some resource, such as available time, by some fixed proportion.

- (d) Contingent horizontal/individual and horizontal social learning strategies (as in the standard runs), but with biased social learning. In this version of the model, horizontal learners bias their learning by the fitness of the other members of the population so that $X(i,t,H)=\text{Mean}[x(j,t-1)\cdot w(j,t-1)]/\text{Mean}[w(j,t-1)]$. More fit individuals have more influence on the behavior of horizontal social learners in the next generation. This is success-based bias (see [Henrich & Gil-White, 2001](#)).
- (e) Contingent horizontal/individual and horizontal social learning strategies (as in the standard runs), but with random models for social learning. While earlier research indicated that conformism, as represented in our standard model, is an expected result of cultural evolution ([Henrich & Boyd, 1998](#)), recent work has found that this is not necessarily the case ([Eriksson, Enquist, & Ghirlanda, 2007](#); [Kameda & Nakanishi, 2002](#); [Nakahashi, 2007](#); [Wakano & Aoki, 2007](#)). Thus we ran variants of the model in which each social learner, instead of adopting the mean (standard runs) or weighted mean (variant d above) of the behavior of the survivors of the previous time period, chooses a model randomly from the survivors of the previous generation. This formulation has been used in previous analytical models (e.g., [Henrich & Boyd, 1998](#)). In variant e1, the introduction of randomly chosen models for social learning is the only change

to the standard model. This gives horizontal social learners particularly varied behavior as they have two sources of variation: that of the models of their behavior, and the error term σ . In variant e2, the behavior of social learners is not varied by the error term σ , giving the behavior of the horizontal social learners a similar variance to that in the standard model, as well as to the variance of the behavior of the individual learners.

3. Results

The results of the model runs are summarized in [Table 1](#) and a typical trajectory for a run using the “standard” parameters in which the population was extirpated is illustrated in [Fig. 2](#). The proportion of horizontal social learners generally grows, but more quickly during times with little short-term environmental variation, as individual learning, and the contingent baseline strategy which includes it, is more favored with short-term environmental variation. In 35% of the standard runs the contingent individuals that can learn individually are lost. After this fixation of pure horizontal learning, occurring very approximately 12,000 time units from the start, the population completely loses most of its ability to track the environment, and, when the environment changes, mean fitness declines and the population drops ([Fig. 2](#)). When the population reaches very low levels, selection may return behavior towards the environmental optimum (as there are very few individuals in the population, and one who is incidentally blessed with suitable behavior, because of the error (σ) around the target behavior, can have many offspring and so change the mean behavior of the population). However,

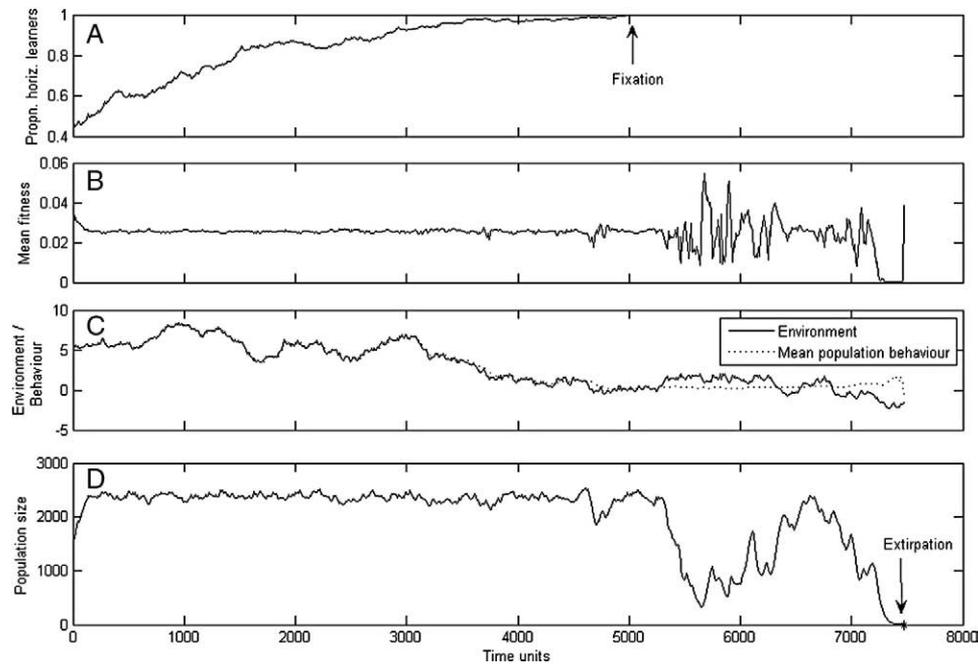


Fig. 2. Typical trajectory for a run of the model of the evolution of learning strategies in a population using the standard parameters. Panels: (A) The proportion of individuals with a pure horizontal social learning strategy in the population; (B) the mean population fitness; (C) the ability of the mean population behavior to track the environment; and (D) the population size. The spikes in mean fitness following fixation of social learning occur because when the environment is being poorly tracked, population size is low, and so when the environment coincidentally matches behavior, population size increases sharply because it is far from carrying capacity.

increasing separation between the culturally determined behavior of the conformist population and the environment drives the population to extirpation almost invariably (Table 1). With the standard parameters, extirpation occurred in 34 of the 35 runs in which horizontal learners became fixed, on average about 2600 time units, or 65 generations, following the fixation of social learning.

Fixation of social learning was generally more likely when costs of individual learning were larger, behavior tracked the environment less accurately, when the environment was redder or less variable and when the population was smaller (Table 1). Conversely, populations were more resilient to the fixation of social learning when costs of individual learning were lower, when the environment was more variable and when the population was larger. With white noise ($\omega=0$), the contingent strategy became fixed and horizontal social learning was eliminated. These trends make intuitive sense, as increasing individual learning costs and lowering the accuracy of behavior will decrease the relative benefits of individual learning and make fixation of social learning more likely. A less variable or redder environment will also devalue individual learning and make the fixation of horizontal learning more likely, as changes in the environment between adjacent time intervals diminish. Fixation will also be less probable in a larger population, partially because of slower drift. Also, a few individual learners make up a very small proportion of a large population and so there will be relatively little reliable

information for the social learners to copy, giving the few individual learners a relative advantage.

Once social learning became fixed, the probability of population extirpation was high, and roughly equal, for all parameter sets, except when the environmental variability was reduced. In this case the environmental optimum was less likely to drift away from the mean population behavior, and population fitness was less compromised.

Of the other strategy sets used, replacing contingent horizontal/individual learning by individual learning as the default learning strategy little changed the results (Table 1). When many strategies competed against one another, horizontal learning always became dominant, as in the standard runs, but it was less often fixed. In contrast, when horizontal learning was replaced by vertical (i.e., parental) learning, the contingent strategy became fixed and the populations were never extirpated, presumably because vertical learning, although cheaper, did not track environmental variation with $\omega=1$ particularly well without the assistance of substantial individual learning. Horizontal learning biased towards successful individuals seemed effective. Although it became fixed particularly quickly, populations were never extirpated (Table 1). Despite tracking the environment less well than the standard contingent strategy, the tracking was sufficiently good to prevent extirpation. (The mean absolute difference between the population's behavior, $\text{Mean}[x(j,t)]$, and the environmental optimum, $y(t)$, increased by about 16% after fixation with

biased horizontal learning, as compared to 514% in the standard runs with unbiased horizontal learning.)

Model variants e1 and e2 investigate the consequences of nonconformist social learning, with social learners choosing models randomly rather than adopting the population mean as in the standard model. When the nonconformists were given error (σ) around the target behavior (that of their randomly chosen models) then population collapse was avoided (Table 1; variant e1), as now social learning was more variable than individual learning and less competitive (Table 1). With the error term removed, so that individual and social learning had similar variances, extirpations occurred but at a lower rate than with the standard model. This difference appears to stem from the fact that, for individuals with contingent strategies, expected fitness is calculated, and a decision about which tactic to employ is made, before the error term (σ) is added. Thus if the error term is not added to the social learning tactic (variant e2), there is an advantage to contingent individuals who have a nonconformist social learning tactic available, in that their choice of tactic is more accurate. This maintains the contingent strategy in competition with pure social learning and reduces the risk of collapse.

4. Discussion

4.1. General limitations of the model

Our individual-based stochastic model is more complex and realistic than previous analytical models, and it is reassuring that the introduction of 15 alternative strategies little changed the general results (Table 1). However, it is still simplistic. We consider some general limitations of the model here and discuss more specific issues in the subsections that follow.

The model ignores migration of individuals and ideas to and from populations. Such movements will tend to mitigate population collapses. The model is most relevant for situations when a reasonably isolated population is facing environmental change.

The model assumes a univariate environment, but all environments are multidimensional. If one of these dimensions has an overwhelming influence on variability in individual fitness, then its characteristics will shape the evolution of learning strategies within the population (Whitehead, 2007) as well as the population's propensity for collapse. On the other hand, if several environmental variables have significant influence on fitness, and they have different patterns of variability, then contingent strategies may be particularly favored (Whitehead, 2007) so protecting the population against the collapse scenario modeled in this paper.

In the case of humans, and maybe for other species, the model is simplistic in its assumption of fixed, discrete learning strategies. However, if the model strategy is considered to be that which is preferred, or more likely to

be used, by an individual then the trajectories and predictions of the model should still approximately hold.

Another simplification of the model is in the mode of inheritance of behavioral control strategy. The model assumes it to be genetic inheritance without mutations, or vertical cultural inheritance with no errors, so that offspring always possess the same control strategy as their parent. Mutations or errors leading individuals to use different control strategies from their parents would have little effect on the process unless they were common enough so that individual learners were likely to be reintroduced into the population between the fixation of social learners and extirpation. (This works out at a rate greater than about 0.01 mutant/error individual learners per generation with the modeled parameters.)

The inheritance of a learning strategy might be more complex than the faithful transmission of the parental strategy; an individual's learning strategy could be formed in various ways by its social influences. This could potentially change the evolutionary dynamics in several ways. It might assist population survival if, for instance, relatively asocial individuals could become individual learners, despite possessing socially learning parents. Conversely, the pressure for cultural conformism could extinguish individual learning from the population much more quickly than selection on characters faithfully inherited from parents, the process operating in the model. Additionally, prestige systems (Henrich & Gil-White, 2001) can build up general conformity to cultural ideals that are costly and slow to change in the face of adverse events. In the case considered below, the Greenland Norse might have survived if they could have brought themselves to adopt some of the ways of the "savage", non-Christian Inuit. Both conformity and prestige systems might suppress the emergence of individual learners from a homogeneous population of social learners, thus making population collapse or extirpation more likely. We do not think that the mode of inheritance of the learning strategy will modify the general effect of red noise. In the case of any reasonably faithful inheritance system, the effect of long runs of years with low variation will favor less use of costly learning strategies which will in turn handicap adaptation when rare strong shocks are experienced.

The model uses a parental mode of inheritance of learning strategy for convenience. In the case of humans, we do not claim that different individuals or societies have discrete learning strategies faithfully inherited from their parents. Human societies and individual humans have characteristic ways of controlling their behavior. There are conformists, innovators, and so on. These differences are most likely the result of culture, to which the inheritance mode assumed by our model provides a first-order approximation. More generally, second-order cultures such as "cultures of innovation," "cultures of exploration," "cultures of obedience" or "cultures of conformity" will have profound effects on population resilience.

The model results indicate that a conformist form of social learning promotes collapse. Populations in which individuals choose learning models at random are less at risk of collapse than those in which there is a bias towards the most frequent forms of behavior (Table 1). As noted in the Results section, these differences are proximately due to rather technical aspects of the formulation of the model. However, they are based on the intuitive proposition that, at times of environmental stability within a red noise environment, conformist learning is more effective (closer to the environmental optimum) than unbiased social learning and therefore more likely to eliminate individual learning (even though over evolutionary scales environmental stability and conformism are predicted to be negatively related; Nakahashi, 2007; Wakano & Aoki, 2007).

We have analyzed the model only for collapses so severe that they lead to extirpation of the population. This choice of a measure of each system's vulnerability to collapse keeps the analysis relatively simple. Systems that are vulnerable to extirpation are also vulnerable to less extreme collapse (e.g., Fig. 2). Many human collapses considered in the literature describe cases in which the collapse amounts to a large drop in population, sometimes followed by a fairly prompt recovery. Our model also showed such behavior (Fig. 2). Selection during long periods of relatively low environmental variation will tend to favor inexpensive social learning strategies that are suboptimal in periods when variation rises. We conjecture that red noise will have similar effects on any system of costly adaptive phenotypic flexibility.

4.2. *The collapse of human societies*

Many have considered the causes of the collapse of human societies, and there have been a number of attempts at modeling the phenomenon mathematically. These range from systems models using catastrophe theory (Renfrew, 1979) to models of dynastic and territorial dynamics (Turchin, 2003). Four general processes have been invoked (e.g., Conrad & Demarest, 1984; Diamond, 2005; Turchin, 2003): external sociopolitical factors (such as conquest), internal sociopolitical factors (such as internal strife, civil war), external ecological factors (such as climate change) and internal ecological factors (such as the exhaustion or overexploitation of a key resource). However, to our knowledge, collapse has not been modeled from the perspective of the evolution of cultural capacity. Our model shows that evolutionary changes in the behavioral strategies that individuals use to interact with their environment can precipitate societal collapse. The mechanism that we consider, the loss of individual learning leading to excessive cultural conservatism in a red noise environment, although it is explicitly linked to the external environment, could play a role in a collapse driven by internal or external, sociopolitical or environmental, stressors or by some combination of them.

It is clear that under some conditions population collapse is a likely outcome of the evolution of cultural capacity. The posited equilibrium between social and individual learners (Aoki et al., 2005; Boyd & Richerson, 1985; Feldman et al., 1996; Wakano et al., 2004) or dominance of a contingent strategy with individual and social learning both available (Boyd & Richerson, 1995; Henrich & Boyd, 1998; Kameda & Nakanishi, 2002; Wakano & Aoki, 2006) may break down with “red” environmental variation. There can be periods with a fairly stable environment in which those individuals with individual learning in their set of tactics are at a fitness disadvantage and so are lost to the population (e.g., Fig. 2). Then, if the environment changes after the individual learners are gone, no one is tracking the changes, population behavior becomes suboptimal and extirpation may result.

How does this scenario relate to the trajectories of human societies? First, note that “collapse” as an outcome of our model, i.e., population extirpation, is a much more extreme event than the collapses considered by most writers on the subject. Collapse has been defined as a decline in “cultural values” (Spengler, 1962) or political complexity (Tainter, 1988) that may or may not be related to population changes. In Turchin's (2003) models of dynastic and territorial dynamics, collapse is viewed primarily as a loss of territory by a polity, and while declines in population size and population density are predicted, extirpation is not a conceived outcome. The recent, more ecologically oriented, writing in this area (Diamond, 2005; Wright, 2004) considers population decline to be a fundamental characteristic of collapse, but population extirpation is quite rare and restricted to physically and/or culturally isolated societies. As illustrated in Fig. 2 (at about 5500 time units), severe population decline without extirpation frequently occurred in our model runs following the fixation of social learning. The selective advantage of environmentally appropriate behavior following a collapse is so large that genetic mutations or cultural innovations that promote this will be strongly favored, perhaps resulting in large-scale cycles between individual and social learning as dominant population modes of the acquisition of behavior.

The disappearance of the Norse in Greenland as described by Diamond (2005) seems to follow the general scenario predicted by the model. An isolated population became culturally conservative. The climate changed making the Norse's behavioral norm for sustenance untenable, but they did not adopt effective alternative behavior used by the sympatric Inuit who persisted. The Norse perished leaving strong signs that they were no longer obtaining sufficient nourishment.

In other cases, such as the Maya, cultural conformism seems to have inhibited the ability to deal with ecological change, and severe declines in population resulted, but not extirpation (Webster, 2002). However, in these instances the trajectories also seem to agree with the general scenario of the model: that conformism plus unpredictable patterns of

low-frequency environmental change may reduce mean fitness and lead to population decline.

The model does not include a prominent element of both historical collapses in human societies, and our current predicament: the influence of humans and our cultures on environmental change. These can exacerbate the model scenario in two related modes. First, cultural behavior can, and often does, stabilize environmental variation through niche construction (Laland, Odling-Smee, & Feldman, 2000). Humans do this in many ways including the storage and transport of food and other resources. This artificial environmental stabilization, while it works, reduces the advantages of individual learning and makes it more likely that social learning, and cultural conformism, will become very common or fixed in the population. The command and control institutions necessary to make complex niche constructions work may restrict the capacity for innovation to a small elite who are overwhelmed by red noise events. Even the most sophisticated niche constructions are bound to be challenged by red environmental events, and when they fail, the environment may change very rapidly indeed because of human influence (Diamond, 2005), a situation potentially disastrous for a population of largely conformist social learners. Currently, successful methods of stabilizing the local environments of individual humans through heating, air-conditioning, transport and other systems which use fossil fuels are simultaneously destabilizing the global environment. Climatologists warn that anthropogenic climate change will inevitably lead to surprises (National Research Council, 2002).

Richerson and Boyd (2005) suggest that the capacity for complex social learning and culture arose in humans during the highly variable Pleistocene climate. Such an environment, with high variation over many time scales, may have particularly favored a contingent individual/social learning strategy. However, during the more recent Holocene, climate has been much less variable (Ditlevsen et al., 1996), potentially providing an environment favoring pure social learning strategies which could invade, become very common or fixed, and lead to societal collapse. The variance of the Holocene climate, while much smaller than that of the late Pleistocene, is dominated by abrupt low-frequency events (Mayewski et al., 2004); the spectrum remains red even if the intensity of variation was decreased across the spectrum. Some evidence suggests that the Holocene might have had this effect. Human encephalization (brain size relative to body size) declined slightly in the Holocene relative to the Late Pleistocene (Ruff, Trinkhaus, & Holliday, 1997), while the size of the cerebellum relative to the cerebral hemispheres increased (Weaver, 2006). Weaver (2006) suggests that the functional significance of this change has to do with better processing of rule-based cultural information. Guthrie's (2005) analysis of Upper Paleolithic art suggests that the people who lived under highly fluctuating climates were highly naturalistic. Supernatural themes were scarce in their art compared to that of Holocene

hunter-gatherers. Rappaport (1979: p. 100) argued that religion functions "to drape nature in supernatural veils... to provide her with some protection against human folly and excess." That is, supernatural beliefs may protect cultural adaptations from skeptical empirical examination. As Rappaport suggested, this may be highly adaptive to protect a complex fine-tuned cultural adaptation from excessive tinkering by inevitably error prone individual learning and collective innovation. But when the inevitable challenge comes, supernatural veils may defeat attempts to learn, innovate and borrow solutions to the new problem. Some combination of genetic and cultural changes might well have decreased individual learning relative to social learning in the Holocene, leading to a risk of collapse in the face of rare red noise events.

While the population sizes considered during the model runs (500, 1500 and 5000 breeding individuals) are within the ranges of some of the archetypal collapsed societies (the Greenland Norse for example), they are much smaller than others (such as the Maya) and minuscule in comparison with today's interconnected global human community. Hardware limitations mean that individual-based models of this phenomenon cannot be run with populations of more than some thousand individuals. Can we reasonably extrapolate the results of such model runs upwards to scales of millions (the Maya) or billions (the current human population)? The results of the model runs indicate that increased population size reduces the likelihood of fixation of social learning and thus extirpation (Table 1). Additionally, with very large population size, mutant or innovative (in the case of culturally determined learning strategies) individuals who might realign behavior in more environmentally appropriate ways are more likely to arise, although their impact on population behavior will be correspondingly smaller. Thus, extrapolation to much larger population sizes is moot, although the case of the Maya collapse (Webster, 2002) seems to fit many aspects of the model. We speculate that large populations will mitigate the chances of extirpation and the severity of collapses short of extirpation. Large populations, all else equal, will tend to have at least a few innovators who can introduce new adaptations. Henrich (2004) modeled the equilibrium toolkit complexity of a society as a function of population size. His model essentially depends upon uncommon reinvention of complex artifacts whose complexity is degraded in everyday transmission events. The same reinvention process should furnish adaptive novelties in a changing environment.

The time scales of the collapses in the model, about 2600 time units or 65 generations from fixation (Table 1), are reassuringly long in historical terms. However, as noted above, if the inheritance of learning strategy is through conformist culture or if culture affects environmental change, the speed of the process may greatly increase. In such cases, collapse could occur much more quickly than suggested by the results in Table 1. Turchin's (2003) review of the rise and collapse of agrarian states suggests that typical

time scales are a century to a millennium. This suggests that cultural rather than genetic evolution plays the dominant role in these events.

The cultures of modern human societies are cumulative in the sense that they tend to progressively improve (or ratchet) in some characteristic (such as the rate of resource extraction). There are several linked mechanisms by which this occurs, including natural variation and selection on cultural variants, guided variation by which individuals may choose more useful cultural variants, and innovations occurring within cultural norms (see [Boyd & Richerson, 1985](#); [Richerson & Boyd, 2005](#)). The principal result of cumulative cultural improvement is that social learning makes individuals more efficient at extracting fitness from the environment than their predecessors. In this respect, societies with cumulative cultures will be less supportive of individual learning and more prone to the effects that we have modeled. However, the possibility of improving individual fitness, even at times of environmental stability, will encourage innovative behavior, and, in turn, this potential will be adaptive for the population when the environment changes. In particular, if individual learning occurring within cultural norms is sensitive to environmental change so that socially learned information becomes generally more environmentally appropriate, then, as long as this within-culture innovation persists, it will help prevent societal collapse. Modern human culture contains many cumulative elements, and cumulative change is rapid. From the perspective of preventing collapse, some of these are positive and others are negative. An example of the former is environmentally oriented agricultural research, and of the latter the cumulative increase in size of houses and vehicles. Overall, the cumulative nature of modern human culture does not obviate the general conclusions of our modeling, but it does increase the complexity of the issue. Furthermore, a complex adaptation, perhaps including institutions or values, developed during a period of relatively stable environment may be made useless by the long-term variations characteristic of red noise, leaving the population vulnerable until a new complex adaptation could arise.

Our results might apply to collective as well as to individual behavior. The ability of a political system to innovate new policies in the face of threats may be much like individual learning (and will be dependent upon it). Individuals may be learning individually well enough, but if the policy-making elite favors traditional policies and does not take good advice from individual learners in the population in the face of environmental change, collapse will ensue.

Contemporary human society is even further from the assumptions of our model than its historical and prehistoric forebears. However, the threat of rapid environmental change is real, and the nature of our cultural evolution will be essential in determining how human populations and the global environment are affected. Rapid social and techno-

logical change in the contemporary world may be having the effect of increasing the need for individual learning. This needs to be environmentally relevant individual learning and to change societal behavior.

4.3. *Avoiding collapse*

The results of running the model with different parameter values and strategies ([Table 1](#)) suggest ways to avoid collapses, particularly by promoting individual learning. Increasing short-term environmental variability empowers individual learners, making fixation of social learning less likely and giving a population more behavioral flexibility. Another stabilizing factor is the replacement of horizontal social learning by vertical learning, which works because vertical learning is less efficient in a variable environment and so less likely to displace a strategy that includes individual learning. This result is somewhat counterintuitive, since we tend to think of vertical transmission as being conservative and hence to lead to slow adaptation in the face of a large environmental excursion.

Environmental engineering to increase short-term variation is unlikely to be socially acceptable. Trying to increase parental influence on behavior is even harder, as horizontal social learning is usually more effective in the short-term and likely to invade ([Whitehead, 2007](#)).

Probably the simplest strategic options for a society concerned about collapse are to encourage biased social learning, nonconformist social learning, individual learning and innovation. At least some members of the population need to be encouraged to watch the environment closely and consider how its changes can be adapted to, or, generally, individuals should look widely for behavioral models, ideally observing and weighing the effects of behavior on individual fitness. Modern educations presumably increase the tools that the educated have for individual learning. The copying of successful models guards against the possibility that, within the population, there is no effective awareness of the true environment. However, it is important to note that copying successful models is only effective in preventing collapse when success is a consequence of behavior that is environmentally appropriate, and not when high fitness is a result of the monopolization of resources, sexual selection or of pure chance. Merely reducing the costs of individual learning and innovation may not be enough; in very stable environments the individual learners will still be lost. Instead, individual learning and biasing social learning towards those with environmentally appropriate behavior should be promoted, given fitness equality and cultural conformism limited.

4.4. *Testing the model*

The principal conclusion of the model is that high levels of social learning and cultural conformism may imperil populations. This suggests potential tests. One approach starts with the development of an archaeological, historical

or other measure of behavioral conformism (to societal norms as opposed to the environmental optimum). For instance, in the archaeological record one might measure the variability of artifacts that have significance for interacting with the environment, such as agricultural or hunting tools. This could be measured for different populations, or the same population at different times, and compared with the rate of population decline.

A more sophisticated, and probably revealing, approach would also consider measures of environmental variation, and potentially other factors. So, for instance, how do measures of conformism and environmental change interact to affect population size trajectories and the health of its members? We would expect that early in the trajectory of an evolving society that it should be relatively resistant to shocks and that shocks should lead to adaptive changes in culture. Collapses will occur in response to shocks that are not necessarily especially severe, but, because of conformism, do not trigger adaptive responses. Such analyses could be carried out temporally within populations or using interpopulation comparisons.

4.5. Generalizing beyond humans

So far the results of the model have been discussed with reference to humans and human culture, but there is no technical reason why they should not apply to other cultural species. In about 1000 AD, long-finned pilot whales (*Globicephala melas*) disappeared from the North Pacific Ocean (Kasuya, 1975). This species is widespread, numerous and resilient to both anthropogenic and natural threats in the North Atlantic and Southern Oceans (Bernard & Reilly, 1999). It also possesses characteristics indicating a strong cultural influence on behavior (Rendell & Whitehead, 2001). Was this also a collapse driven by cultural conformism?

More generally still, any form of costly phenotypic flexibility will tend to diminish during periods of low environmental variation, leading to vulnerabilities when large amplitude variation occurs. Red noise, in effect, sets environmental traps in which low levels of short-term variation frequently select for less phenotypic flexibility than is necessary to readily survive low-frequency but high-amplitude changes. Perhaps the turnover of species as well as cultures is due to processes similar to those that we have modeled here. Is it possible for any adaptations to arise to the low frequency part of red noise? Maynard Smith (1978) argued that the costs of sex are so extreme that short-term selection would nearly always favor asexuality. The fact that sexual species are so common he attributed to species selection preserving sexual species during large amplitude environmental events when the asexual species tended to go extinct because they lacked the recombination necessary to generate genotypes adapted to the new environment. Perhaps human societies, most having passed through several large population downturns,

are accumulating adaptations to coping with low-frequency environmental variation.

In conclusion, while the models analyzed here are simplified and specialized, we believe that they point to a rather general problem organisms have in adapting to red noise environments.

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Appendix A. 1/f (Red) Noise

What is red or 1/f noise and why is it important? The color of noise is an analogy referring to patterns in the variance of a noisy electromagnetic signal. Here we are thinking of the signal being an environmental factor important to a human community, such as annual rainfall or the population density of an important biotic resource or pest. The patterns of variation in an ecological time series can be mapped from the time domain to the frequency domain using a mathematical algorithm called a Fourier transform, which transforms a time series into a series of sine and cosine terms, representing different frequencies. The amount of variance that is accounted for by a particular sine–cosine pair is a measure of the amount of variation at that frequency (Platt & Denman, 1975). If the time series has highly periodic components, these will be represented by a large amount of variance at one frequency. For instance, temperature varies strongly on the diurnal and annual time scales, and most environmental temperature time series will show strong, narrow spectral peaks at frequencies of 1 day^{-1} and $1/365 \text{ day}^{-1}$. However, much of the variation in temperature is typically not associated with the annual and diurnal cycles. For example, the presence of low- and high-pressure systems in the atmosphere has a time scale of a few days, but with a lot of variability. This part of the time series will be represented by a broad peak in the frequency centered at perhaps $1/5 \text{ day}^{-1}$.

Technically, the term *white noise* refers to a time series that has equal variation at all frequencies. Thus, solar radiation, which is approximately white in the visible wavelengths, is decomposed by a prism into a color spectrum that is roughly equally bright from red through blue. Many environmental time series have red spectra, in which a disproportionate amount of the variance is at long wave lengths (Vasseur & Yodzis, 2004). Many environmental time series have red spectra with a fairly uniform shape in which variance falls monotonically as a function of

frequency across all frequencies according to a power law. Thus red noise is often called $1/f$ noise (Halley, 1996).

Closely related to red noise is the statistical concept of “stationarity”. A statistical process is said to be stationary when the parameters of the distribution describing the data do not change as a function of time. The noise spectrum of many environmental processes is red out to rather long time scales (perhaps including the whole history of the earth), with the consequence that data from short records will be nonstationary. For example, Zachos, Pagani, Sloan, Thomas, and Billups (2001) show how the mean temperature of the earth has declined over the last 65 million years in a series of irregular drops (punctuated by some rises). At the same time the variance about the trend line has increased, especially with the advent of the Plio-Pleistocene ice ages. For example, the core of Martrat et al. (2007) suggests that over the last four glacials, the millennial and submillennial scale variation during the glacials has become less red. In a red nonstationary world, the future tends to have rare surprises. On short time scales, say a few generations, environments tend to be relatively similar, but every few generations something unusual happens. On time scales of tens of generations, there are even bigger surprises, and so on.

The environmental noise spectrum is presumably very important to evolutionary patterns. When environments vary little or on long enough time scales, selection acting on genes can track environmental fluctuations quite well (Whitehead, 2007). If variation is higher at higher frequencies, mechanisms of phenotypic flexibility like learning and social learning evolve to cope with such noise (Sterelny, 2003). Human culture can plausibly be tuned by selection on genes or by cultural evolutionary processes to cope with noise on a variety of scales (Boyd & Richerson, 1985). For example, investments in individual learning and the use of horizontal cultural transmission can be ramped up if high-frequency variation increases, whereas less use of these tools will be needed if variation is less and at lower frequencies. However, in a red, nonstationary environment, rare changes in the pattern of environmental variation will tend to find mechanisms of phenotypic flexibility poorly tuned to a new pattern of variation. To illustrate the potential importance of red noise in human evolution, we use a model of red noise to create selection pressures on social learning systems with different architectures. Depending upon the assumptions in the models, red noise can lead to more or less severe short run mistuning of the cultural system, handicapping adaptation to rare large environmental excursions represented by the red part of the environmental variance spectrum.

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