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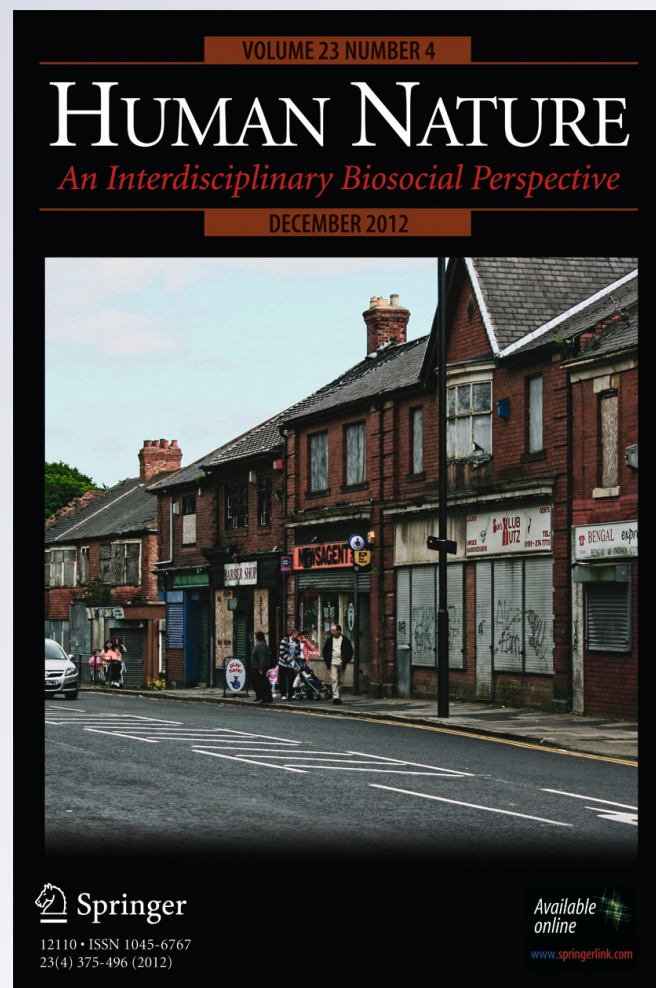
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Adaptive Social Learning Strategies in Temporally and Spatially Varying Environments

How Temporal vs. Spatial Variation, Number of Cultural Traits, and Costs of Learning Influence the Evolution of Conformist-Biased Transmission, Payoff-Biased Transmission, and Individual Learning

Wataru Nakahashi · Joe Yuichiro Wakano · Joseph Henrich

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Abstract Long before the origins of agriculture human ancestors had expanded across the globe into an immense variety of environments, from Australian deserts to Siberian tundra. Survival in these environments did not principally depend on genetic adaptations, but instead on evolved learning strategies that permitted the assembly of locally adaptive behavioral repertoires. To develop hypotheses about these learning strategies, we have modeled the evolution of learning strategies to assess what conditions and constraints favor which kinds of strategies. To build on prior work, we focus on clarifying how spatial variability, temporal variability, and the number of cultural traits influence the evolution of four types of strategies: (1) individual learning, (2) unbiased social learning, (3) payoff-biased social learning, and (4) conformist transmission. Using a combination of analytic and simulation methods, we show that spatial—but not temporal—variation strongly favors the

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emergence of conformist transmission. This effect intensifies when migration rates are relatively high and individual learning is costly. We also show that increasing the number of cultural traits above two favors the evolution of conformist transmission, which suggests that the assumption of only two traits in many models has been conservative. We close by discussing how (1) spatial variability represents only one way of introducing the low-level, nonadaptive phenotypic trait variation that so favors conformist transmission, the other obvious way being learning errors, and (2) our findings apply to the evolution of conformist transmission in social interactions. Throughout we emphasize how our models generate empirical predictions suitable for laboratory testing.

Keywords Learning strategies · Individual learning · Social learning · Conformist transmission · Payoff-biased transmission

The application of evolutionary principles to understanding the origin and operation of social learning in humans has generated a wide range of insights, as well as vibrant debates. Rooted in the seminal modeling work of Boyd and Richerson (1985), much theoretical work has explored the conditions and contexts favoring the evolution of social learning, often generating hypotheses about adaptive learning mechanisms using cues related to success, payoffs, trait content (direct bias), credibility, ethnic markers, adoption rates, and conformity (Kendal et al. 2009; McElreath et al. 2008; McElreath et al. 2003; McElreath and Strimling 2008; Rendell et al. 2007; Schlag 1998, 1999; Wakano and Aoki 2006; Wakano et al. 2004). Such theoretical work indicates that social learning mechanisms interact competitively and synergistically with each other, and with individual learning, at the population level. In addition to informing our understanding of how cultural abilities evolve in humans, and more recently in other species, such models provide disciplined theoretical foundations for generating specific evolutionary predictions about the contexts in which various learning strategies should be deployed, and the kind of cues likely to activate them.

While still in its gestational stage, the empirical testing of psychological and behavioral hypotheses generated by these evolutionary models has been surprisingly successful in both humans and other species, with evidence coming from economics, psychology, biology, and anthropology (e.g., Henrich and McElreath 2007; Laland 2004; McElreath et al. 2008). Recently, confirming earlier predictions, a blossoming of experimental studies in young children and infants is revealing solid evidence for imitative biases related to prestige, success, competence (reliability), dialect, and age (Chudek et al. 2012; Harris and Corriveau 2011; Stenberg 2009), most of which have previously been demonstrated in Western adults (Mesoudi 2009). Field evidence is also beginning to show converging lines of evidence for these adaptive biases in small-scale societies, and in economically important domains (Henrich and Broesch 2011). Some work has even connected these learning biases to the generation and maintenance of stable, adaptive cultural patterns in small-scale societies (Henrich and Henrich 2010). Finally, in nonhuman social learners, some of the best experimental tests of these models come from work with rats (Galef and Whiskin 2008) and fish (Laland et al. 2011).

Among the proposed social learning biases in this adaptive psychological suite is frequency-dependent biased transmission (Boyd and Richerson 1985: chap. 7). Because useful information is stored implicitly in the relative frequency of different cultural traits, learners might use the frequency of a trait in the population to more effectively select locally adaptive cultural traits, or at least avoid adopting maladaptive traits. Conformist transmission is a sub-category of frequency-dependent biased transmission in which individuals use the frequency of the most common trait, in a personal sample or the local population, as a cue in figuring out which trait to adopt, potentially integrating it with other information, such as personal experience, the relative success of those with different traits, and self-similarity (N. Henrich and Henrich 2007: chap. 2; Rendell et al. 2011). Conformist biases are adaptive to the degree that they can help learners integrate information gleaned from other members of their community, while allowing them to filter the errors that inevitably creep into the pathways of cultural transmission (Henrich and Boyd 2002). The basic logic underpinning conformist transmission is enshrined in the Condorcet Jury Theorem. Central to defining and identifying conformist transmission is recognizing that it requires a nonlinear increase in the likelihood of adopting a trait with increases in the frequency of that cultural trait. This distinguishes conformist biased strategies from unbiased transmission, in which learners acquire a particular trait in proportion to that trait's current frequency in the population (which, for example, occurs if learners copy a random person in the population).

Boyd and Richerson's (1985) initial efforts suggested that conformist transmission could outcompete unbiased transmission in a spatially variable environment. This model, however, was limited because it did not consider (a) a cost for conformist transmission, (b) any individual learning, (c) more than two traits or environments, or (d) temporally varying environments. To address some of these limitations, Henrich and Boyd (1998) constructed a simulation model containing a large mix of strategies involving combinations of individual learning, unbiased transmission, and conformist transmission in which learners had to adapt to a spatially and temporally varying environment. Later, Kameda and Nakanishi (2002) augmented Henrich and Boyd's code to consider conditions under which individual learning was costly and tested these predictions in a laboratory experiment. These simulations were limited in considering only two cultural traits and two different environments. Overall, this early work suggested that conformist transmission would outcompete unbiased transmission under a wide range of conditions, though not if the environment changed too often or individual learning was too inaccurate.

More recently, several authors have developed a combination of analytical and simulation work on temporally varying environments that both confirm and challenge earlier conclusions (Eriksson et al. 2007; Kandler and Laland 2009; Kendal et al. 2009; McElreath et al. 2008; Nakahashi 2007a; Wakano and Aoki 2007; Whitehead 2007). Some of this work suggests that in temporally varying environments both unbiased and payoff-biased transmission can dominate or even eliminate conformist transmission, reducing the range of conditions in which we expect conformist transmission to evolve. During roughly the same time period, work exploring the impact of spatially variable environments on the evolution of social learning considered only unbiased transmission (Aoki 2010; Aoki and Nakahashi 2008). Here we bring these two strands of modeling together.

While these prior efforts make important contributions to understanding the evolutionary-theoretic hypotheses that should drive empirical inquiry, we think the focus on modeling (a) only two (distinguishable) cultural traits, (b) temporally varying environments, and (c) error-free cultural transmission has actually obscured some of the conditions most favorable to the evolution of conformist transmission. Our goal here is twofold. First, we develop an n -trait ($n \geq 2$) model in a spatially varying environment to illustrate how these two elements influence the evolution of conformist-biased learning strategies vis-à-vis unbiased transmission, payoff-biased transmission, and individual learning. Although we do not explicitly model transmission error here, we argue below that spatial mixing creates a selective environment similar to that produced by transmission errors. Second, to most effectively illustrate the contrast between the effects of temporal and spatial variation on favored learning strategies, we draw on and in some cases further develop results from two parallel models that focus only on temporal variation.

We first present our baseline model of the evolution of social learning strategies for n different cultural traits in a spatially varying environment, and we introduce the two parallel models for temporally varying environments. Next we present the baseline results for the simplest cases. We then incrementally add complexity to this baseline case by (a) adding a fitness cost for using conformist transmission, (b) analyzing how the number of cultural traits impacts the outcomes, (c) including payoff-biased learning strategies, and (d) modifying the life cycle such that individual learners can only learn before migration to a new site. Throughout the paper, we develop the models and present the results in the main text, leaving the derivations themselves in the electronic supplemental materials [ESM]. We have done this in an effort to communicate effectively with empirically oriented evolutionary researchers who might test these hypotheses about learning strategies. We close by itemizing the empirical predictions, and by relating our findings to the effects of transmission error and the evolution of social behavior in contexts of cooperation, coordination, and complementarity.

Comparable Spatial and Temporal Models

Here we develop parallel models of the evolution of different social learning strategies in both spatially and temporally varying environments. The spatially varying model is developed in full in this paper by extending Aoki and Nakahashi (2008), and it is solved analytically. To compare the effects of spatial vs. temporal variability, we draw on findings from two similar models of temporal variability: one developed here that most closely parallels our spatial model in using pure strategies, and a second, previously published model (Nakahashi 2007a) that uses mixed strategies similar to those explored by Henrich and Boyd (1998). We use both models because neither can be fully solved analytically, so we draw on analytical results where possible and otherwise rely on simulations for comparisons. Nakahashi (2007b) has previously shown that these two models of temporal variability generate similar results under most conditions. Comparing results across these similar models allows us to illuminate the differential impacts of spatial vs. temporal variation on the evolution of social learning in general, and on conformist transmission specifically.

The Baseline Spatial Model

In our structured population, individuals may occupy any of n different sites in a spatially heterogeneous world. Each site has a different environment with a specific corresponding cultural trait (learnable phenotype) that is adaptive at that site. Thus, we distinguish n traits/phenotypes, each of which is locally adapted to one particular environment but maladaptive in the $n-1$ other environments. Traits that are maladaptive in all n environments are not incorporated into the dynamics.

Individuals are of three genetically distinct types: unbiased social learners (UT: unbiased transmission is linearly frequency-dependent), conformist-biased social learners (CT: conformist transmission is nonlinearly frequency-dependent), and individual learners (IL). Later, we add payoff-biased social learners (PT: payoff-biased transmission copies according to payoff differences). UT acquire their cultural traits by copying a random member of the previous or parental generation in the site they occupy (oblique transmission: Cavalli-Sforza and Feldman 1981). CT acquire their traits by copying the most common trait in the previous generation at their sites, but they suffer a mortality cost d owing to abilities or activities associated with figuring out the most common trait. IL always acquire the trait that is adapted to the environment of the site they currently occupy, but they suffer a cost c owing to mistakes made before the mature behavior is realized. The parameter s is the selective cost of not acquiring the locally adaptive trait. We typically assume that $0 \leq d < c < s < 1$, meaning that individual learning is the most costly (c) strategy, followed by conformist transmission (d), and then unbiased social learning (which costs zero). The parameter s can be thought of as the fitness consequences of not figuring out what the locally adaptive thing to do is. Traits with high s have relatively larger fitness consequences.

To track the numbers of individuals with each of our three different strategies, we use capitalized letters (X_{ij} , U_{ij} , Z_{ij}) indexed by i and j to respectively mark the current site in which the individuals live, and the current phenotypic trait exhibited by those individuals. Let X_{ij} ($1 \leq i \leq n$, $1 \leq j \leq n$) be the number of UT at site i that are adapted to the environment of site j . Then, at site i there are $X_i = \sum_{j=1}^n X_{ij}$ UT in all, of which X_{ii} possess the locally adaptive trait and $X_i - X_{ii}$ possess one of the locally nonadaptive traits. Similarly, let U_{ij} be the number of CT at site i that are adapted to the environment of site j . Then, at site i there are $U_i = \sum_{j=1}^n U_{ij}$ CT, of which U_{ii} possess the locally adaptive trait and $U_i - U_{ii}$ possess one of the locally nonadaptive traits. Let Z_i ($1 \leq i \leq n$) be the number of IL at site i . IL always acquire the trait that is adapted to the environment of the site they occupy, but they suffer a cost from the efforts and accidents of trial-and-error learning. The total population size at site i is $N_i = X_i + U_i + Z_i$. These numbers are enumerated at the adult stage just prior to reproduction.

The Life Cycle

The life cycle begins with reproduction, where each individual gives birth asexually to $b(N_i)$ offspring according to the discrete logistic equation:

$$b(N_i) = 1 + r(1 - N_i/K) \quad (1)$$

Here, $r > 0$ and $K > 0$ are assumed to be the same for each site. Since the offspring are genetically identical to their parents, the numbers of UT, CT, and IL among the newborns at site i are $X_i b(N_i)$, $U_i b(N_i)$, and $Z_i b(N_i)$, respectively.

At the second step of the life cycle social learning occurs, either unbiased or conformist-biased, as UT and CT acquire their traits by copying the parental generation. All members of the parental generation die immediately afterward. As a result, the number of UT at site i that are adapted to the environment of site j becomes

$$X_i b(N_i) (X_{ij} + U_{ij} + Z_i \delta_{ij}) / N_i \tag{2}$$

where δ_{ij} is Kronecker's delta ($\delta_{ij} = 1$ when $i = j$ and 0 otherwise).

The number of CT at site i that are adapted to the environment of site j becomes

$$(1 - d) U_i b(N_i) \rho_{ij} \tag{3}$$

where

$$\rho_{ij} = \frac{[(X_{ij} + U_{ij} + Z_i \delta_{ij}) / N_i]^a}{\sum_{k=1}^n [(X_{ik} + U_{ik} + Z_i \delta_{ik}) / N_i]^a} \tag{4}$$

Here, a is the strength of conformist bias, and CT always imitate the most common trait when $a = \infty$. Developed in Nakahashi (2007a), this formulation of conformist transmission guarantees that the probability of acquiring the most common trait in a local population is greater than the frequency of that trait in the population (assuming $a > 1$).

The third and fourth events in the life cycle are migration followed by individual learning for IL. For migration, a fixed fraction of the individuals at each site emigrate, yielding a constant forward migration rate. Here we use an island model with reciprocal migration between all pairs of sites at rate $m / (n - 1)$ ($0 < m \leq 1/2$). After migration, IL acquire the cultural trait suitable to their new (post-migration) environment, but they suffer a fixed mortality cost, c . Note that this assumption gives IL an advantage over the social learning strategies, which do not update their trait after migration. Below, we show that this assumption is crucial for the survival of individual learning, and it works against the success of CT in the spatial model.

The final stage in the life cycle is viability selection, in which all individuals with the locally adaptive trait survive while only a fraction $1 - s$ of individuals with the maladaptive trait survive.

Recursions for the Baseline Spatial Model

The above assumptions entail the following recursions:

$$X'_{ii} = (1 - m) X_i b(N_i) \frac{X_{ii} + U_{ii} + Z_i}{N_i} + \frac{m}{n - 1} \sum_{k \neq i}^n X_k b(N_k) \frac{X_{ki} + U_{ki}}{N_k} \tag{5}$$

$$X'_{ij} = (1 - s) \left\{ (1 - m) X_i b(N_i) \frac{X_{ij} + U_{ij}}{N_i} + \frac{m}{n - 1} X_j b(N_j) \frac{X_{ij} + U_{ij} + Z_j}{N_j} + \frac{m}{n - 1} \sum_{k \neq i, j}^n X_k b(N_k) \frac{X_{kj} + U_{kj}}{N_k} \right\} \tag{6}$$

$$U'_{ii} = (1 - d) \left\{ (1 - m) U_i b(N_i) \rho_{ii} + \frac{m}{n - 1} \sum_{k \neq i}^n U_k b(N_k) \rho_{ki} \right\} \tag{7}$$

$$U'_{ij} = (1 - d)(1 - s) \left\{ (1 - m) U_i b(N_i) \rho_{ij} + \frac{m}{n - 1} \sum_{k \neq i}^n U_k b(N_k) \rho_{kj} \right\} \tag{8}$$

$$Z'_i = (1 - c) \left\{ (1 - m) Z_i b(N_i) + \frac{m}{n - 1} \sum_{k \neq i}^n U_k b(N_k) \right\} \tag{9}$$

where $1 \leq i \leq n$, $1 \leq j \leq n$, and $j \neq i$ in Eqs. 6 and 8.

The Baseline Temporal Models

Now we develop a parallel model for a temporally varying environment using the same pure strategies, and then we discuss a similar model involving mixed strategies (from Nakahashi 2007a). Both temporally varying models assume a single adaptive cultural trait or behavioral phenotype (fitness=1) corresponding to each environmental state, and other traits that are equally maladaptive (fitness=1-s; the cost of maladaptive behavior is s). The environment changes every ℓ generations ($\ell \geq 1$), so that one post-change generation experiences a different environmental state from the previous generation, and $\ell - 1$ subsequent generations experience the same state as that post-change generation. That is, larger values of ℓ imply more environmental stability. Here we use a fixed duration between environmental shifts in place of a randomly varying environment to maintain mathematical tractability. Prior work suggests that, for our purposes, this assumption does not produce essentially different results (Nakahashi 2007b).

For our pure strategy temporal model, as in the spatial model, we assume the existence of three genetically encoded and asexually reproducing learning strategies: individual learners (IL), unbiased social learners (UT), and conformist social learners (CT). Later we introduce payoff-biased social learners (PT). IL always achieve the adaptive trait via individual learning, but they suffer a fixed cost c . Social learners (UT, CT, and later PT) copy a trait from the previous generation. When the environment changes, social learners always copy a maladaptive (wrong) trait and only IL behave correctly. UT acquire their trait by copying a random member of the parental generation. Paralleling our spatial model, CT acquire the cultural trait j with probability P_j , as in Eq. 4, where a gives the strength of conformist transmission:

$$P_j = \frac{b_j^a}{b_0^a + b_1^a + b_2^a + \dots} \tag{10}$$

This means that the probability that CT imitate trait j is expressed by (10), where b_0, b_1, b_2, \dots are the frequencies of individuals in the previous generation with the traits 0, 1, 2, ..., respectively. CT suffer a mortality cost d .

All this means that the fitness of IL is $1 - c$ while the fitnesses of UT and CT are, respectively, 1 and $1 - d$ if they have acquired the currently adaptive trait, and $1 - s$ and

$(1 - d)(1 - s)$ if they have not acquired the adaptive trait. As above, we typically assume $0 \leq d < c < s < 1$.

To extract as much analytical insight as possible from these two models (before moving to simulations), we have allowed for some differences vis-à-vis our spatial model. Both of these temporally varying models assume that the number of possible environmental states is infinite, so that when the environment changes it never reverts to an earlier state (infinite environmental states model). This makes these models most comparable to our spatial model when n in the spatial model is large (infinite), though we show that n does not have to be particularly large before it approximates the infinite solution.

Recursions for the Baseline Temporal Model with Pure Strategies

We set the initial condition such that the environment is in state 0 in generation 0 and all members have trait 0. In the next generation (generation 1) the environment changes to state 1 and trait 1 becomes optimal. We suppose that trait i is optimal in state i . In a periodically changing environment, the environment changes every ℓ generations so the environment changes from state i to state $i + 1$ between generation $i\ell$ and generation $i\ell + 1$.

Suppose that the population is now in generation k and the environment is in state n . Let the frequency of UT, CT, and IL after natural selection be $x^{(k)}$, $u^{(k)}$, and $z^{(k)}$ ($x^{(k)} + u^{(k)} + z^{(k)} = 1$), respectively, and that of trait i be $b_i^{(k)}$ and $P_i^{(k)} =$

$(b_i^{(k)})^a / \sum_{j=0}^n (b_j^{(k)})^a$. Then,

$$x^{(k)} = \frac{b_n^{(k-1)} + (1 - s)(1 - b_n^{(k-1)})}{T_{k-1}} x^{(k-1)} \tag{11}$$

$$u^{(k)} = (1 - d) \frac{P_n^{(k-1)} + (1 - s)(1 - P_n^{(k-1)})}{T_{k-1}} u^{(k-1)} \tag{12}$$

$$z^{(k)} = \frac{1 - c}{T_{k-1}} z^{(k-1)} \tag{13}$$

$$b_n^{(k)} = \left\{ \begin{array}{l} \frac{(1-c)z^{(k-1)}}{T_{k-1}} \text{ (post-change generations)} \\ \frac{b_n^{(k-1)}x^{(k-1)} + (1-d)P_n^{(k-1)}u^{(k-1)} + (1-c)z^{(k-1)}}{T_{k-1}} \text{ (other generations)} \end{array} \right\} \tag{14}$$

$$b_m^{(k)} = (1 - s) \frac{b_m^{(k-1)}x^{(k-1)} + (1 - d)P_m^{(k-1)}u^{(k-1)}}{T_{k-1}} \quad (m < n) \tag{15}$$

where

$$T_k = \left\{ \begin{array}{l} (1-s)x^{(k)} + (1-d)(1-s)u^{(k)} + (1-c)z^{(k)} \text{ (post-change generations)} \\ \left\{ b_n^{(k)} + (1-s)(1-b_n^{(k)}) \right\} x^{(k)} + (1-d) \left\{ P_n^{(k)} + (1-s)(1-P_n^{(k)}) \right\} u^{(k)} + (1-c)z^{(k)} \text{ (other generations)} \end{array} \right\} \quad (16)$$

From this model we will sometimes extract analytical insights, and we supplement with simulations when necessary.

To complement our use of the pure strategy model in temporally varying environments, we also draw on results from a mixed strategy model that is otherwise very similar to the above model (Nakahashi 2007a). In this model, individuals have two parameters. The first sets the degree of reliance on either individual or social learning. The second specifies the strength of conformist transmission, a . That is, the probability that an individual who relies on social learning imitates trait j with the frequency b_j in the previous generation is expressed as (10). Below we will also sometimes present analytical findings from this model to provide a point of comparison.

To compare spatial variability with temporal variability, we focus on comparing the impact of the parameter m , which gives the migration rate among sites in the spatial model (and thus the degree of mixing), with the parameter $R = 1/\ell$. Since ℓ is the number of periods between environmental shifts, ranging from 2 to infinity, R gives a measure of temporal variability between 0 and 0.5, which parallels that provided by m .

Comparison of Results for Baseline Models

Let's begin with the simplest cases. For the spatial model, we initially assume n , the number of cultural traits (and sites), is large and that the cost of using conformist transmission is zero ($d=0$). By assuming that n is large ($n \rightarrow \infty$) we can most directly compare our spatial and temporal models. We also assume a is large such that CT always copy the most common trait from the previous generation. As we go along, we show that in many cases when CT are stable, only $a=\infty$ is stable against invasion by strategies with other values of a . Appendix A (in the ESM) presents the formal details and derivations.

Under these conditions, for different parameter combinations the spatial model reveals only three unique and stable equilibria: (a) all IL, (b) all CT, or (c) extinction. IL are the unique stable equilibrium if

$$c < ms \quad (17)$$

and

$$\frac{c}{1-c} < r < \frac{2+c}{1-c} \quad (18)$$

The first condition means that the cost of individual learning must be low relative to the product of the migration rate and the cost of not acquiring the locally adaptive trait. The second condition specifies that the intrinsic rate of population growth must fall into an intermediate range that depends only on c .

There is a second set of conditions in which CT are a unique stable equilibrium if $c > ms$ (the reverse of the above condition) and

$$r > \frac{ms}{1 - ms} \quad (19)$$

This means that if c and r are sufficiently large (relative to the product of m and s), CT is the unique stable equilibrium. Moreover, as shown in Appendix A, when CT are a stable equilibrium, CT with larger values of a can continually invade, so a will go to its maximum value. Thus, our assuming $a = \infty$ likely does little harm.

If neither of these two different equilibrium conditions holds, it means this population will go extinct because its intrinsic rate of reproduction is too low for the conditions imposed by the combination of selection, migration, and the costs of individual learning.

In the temporal model with pure strategies, we show that IL are a unique and stable equilibrium when

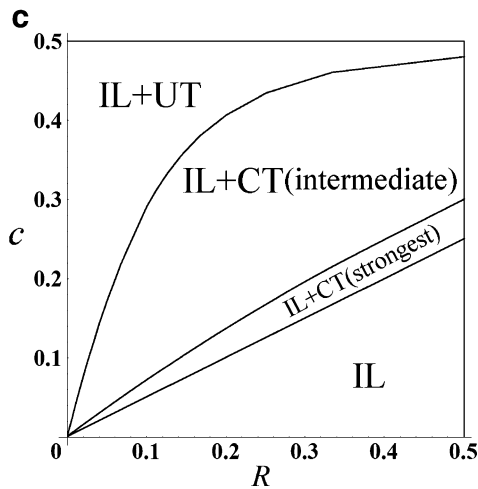
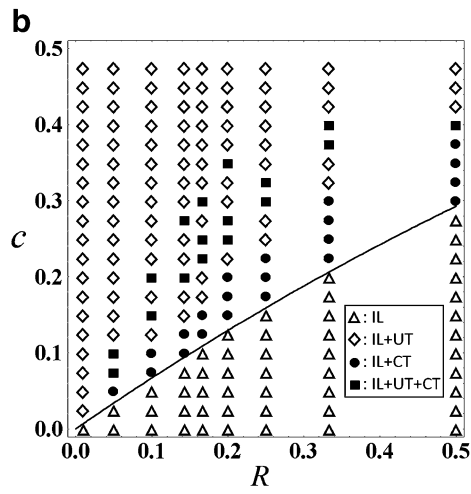
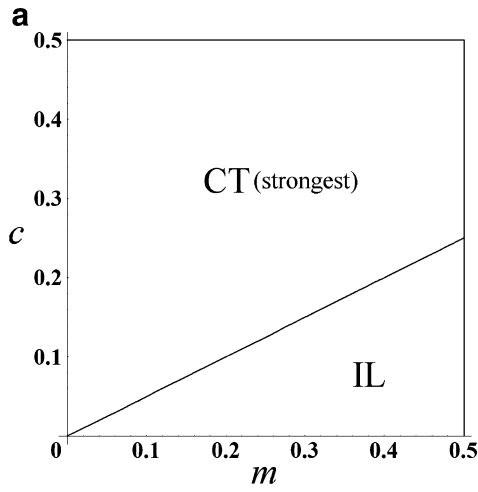
$$R = \frac{1}{\ell} > \frac{\ln(1 - c)}{\ln(1 - s)} \quad (20)$$

This indicates that IL are favored when environments are unstable (R is large), individual learning is cheap (c is small), and getting the locally adaptive traits is important (s is large). When this condition does not hold, numerical simulations indicate that the population consists of a fluctuating composition of IL, CT, and UT. Below, when we introduce payoff-biased social learners (PT), we solve this model analytically. Appendix B (in the ESM) supplies these derivations.

Figures 1a, b, and c provide a comparison of our spatial and temporal models in the (m, c) - or (R, c) -parameter space. We have set s rather high at 0.5, which biases the plots in favor of IL. Despite this, Fig. 1a shows that in a spatially varying environment, conformist bias is always at its maximum strength and is uniquely favored, except when individual learning is cheap and migration rates are high. Figure 1b shows the results of our simulations superimposed on our analytically derived line demarcating the stable region for IL. Figure 1c shows the analytical results drawn from Nakahashi (2007a) using a mixed-strategy approach. Viewing Fig. 1b and c highlights the similarity between the pure- and mixed-strategy approaches and reveals that in both approaches CT are generally only favored for intermediate values of c . If the environment is sufficiently stable and the costs of individual learning are high, a mixture of UT and IL emerge. The mixed-strategy model (Fig. 1c) indicates that conformist bias does not evolve to its maximum strength, except in the narrow band shown.

Making Conformist Transmission Costly

The above results assume that using conformist transmission is costless and, in particular, no more costly than using unbiased social learning. Now we assume that using conformist transmission imposes a mortality cost, $d > 0$, by assuming that $0 < d < c < s < 1$.



For the spatial model we now have five different unique stable equilibria for different parameter values. For IL, nothing changes. If (17) and (18) hold, IL are the unique stable equilibrium. This occurs when the costs of individual learning (c) are sufficiently small and r falls into an intermediate range.

In the second situation, CT are a unique stable equilibrium if these three conditions are satisfied:

$$d < 1 - \frac{1 - c}{1 - ms} \tag{21}$$

$$d < 1 - \frac{1 - m}{1 - ms} - \frac{m(1 - s)^2}{(1 - ms)^2} \tag{22}$$

$$r > \frac{1 - (1 - d)(1 - ms)}{(1 - d)(1 - ms)} \tag{23}$$

The first two conditions set thresholds for the costs of conformist transmission. The first condition (21) guarantees that CT outcompete IL, which means the maximum value of d depends on c and the product of m and s . The more costly individual learning is, the larger the range of conditions favoring CT. The product of m and s captures the penalty suffered by migrating CTs when they first arrive in a new site. The second threshold for d (22) depends only on m and s , and it gives the conditions for outcompeting UT. Here larger values of both m and s raise the threshold for d : when d is below this threshold, CT outcompete UT. Condition 23 merely guarantees that the population reproduces sufficiently rapidly to avoid extinction.

In the third regime, assuming (21) and (23) from above are satisfied (so, no IL and no extinction), a polymorphic stable equilibrium of UT and CT will exist when the cost of conformist transmission falls into this range:

$$1 - \frac{1 - m}{1 - ms} - \frac{m(1 - s)^2}{(1 - ms)^2} < d < 1 - \frac{1 - m}{1 - ms} \tag{24}$$

◀ **Fig. 1** Comparable plots in the (m, c) - and (R, c) -parameter space for spatially and temporally varying environments when $d=0$ and n is infinite ($s=0.5, K=100$, and $r=0.5$). **a** The stable equilibrium strategies in a spatially heterogeneous environment assuming ($0 < m < 1/2$ and $0 < c < s$). In the “IL” region, IL are a unique stable equilibrium, while in the “CT (strongest)” region, CT are a unique stable equilibrium in which CT have the strongest conformity bias (where $a=\infty$). **b** Numerical simulation of equilibrium pure strategies in a temporally changing environment ($0 < R < 1/2, 0 < c < s, a=10$). Δ indicates that IL are the stable equilibrium, \diamond indicates a polymorphic stable state for IL and UT, \bullet indicates a polymorphic equilibrium of IL and CT, and \blacksquare indicates a polymorphic equilibrium of IL, UT, and CT. Filled markers indicate the points where CT exist. The line in **(b)** represents the threshold for the purely IL equilibrium, captured by Eq. 20. The precise region where CT can exist is impossible to obtain analytically, and the numerical simulations suggest a complex relationship among the parameters. **c** The evolutionarily stable strategy (mixed strategy) in temporally changing environments is shown in the (R, c) -parameter space ($0 < R < 1/2, 0 < c < s$). The region “IL” indicates that IL are the unique stable equilibrium; the region “IL+CT(strongest)” indicates that mixed strategies with both individual learning and conformist transmission are an evolutionarily stable strategy, and that conformist transmission (when used) is at its maximum strength; the “IL+CT(intermediate)” region indicates stable mixed strategies involving individual learning and conformist transmission (but at which conformist transmission is not maximum strength); and the “IL+UT” region indicates a stable mixed strategy involving both individual learning and unbiased transmission

Fig. 2 comparable plots in the (m, c) - and (R, c) -parameter space for spatially and temporally varying environments when conformist transmission is costly ($d=0.05$) and n is infinite ($s=0.5$, $K=100$, and $r=0.5$). **a** The equilibrium in a spatially heterogeneous environment assuming ($0 < m < 1/2$ and $0 < c < s$). In the “IL” region all organisms are individual learners (IL equilibrium), whereas in the “CT” region all organisms are social learners with the strongest conformity bias (CT equilibrium); in the “UT+IL” region the polymorphic equilibrium consists of unbiased social learners and individual learners, whereas the “UT+CT” region is a polymorphic equilibrium of unbiased social learners and conformist social learners. **b** The outcomes of numerical simulations of pure strategies at equilibrium in a temporally changing environment ($0 < R < 1/2$, $0 < c < s$, $a=10$) are shown. Δ means that all organisms become individual learners; \diamond marks a polymorphic equilibrium of individual learners and social learners with unbiased transmission; \bullet marks a polymorphic equilibrium of individual learners and social learners with conformist transmission, and \blacksquare marks a polymorphic equilibrium of individual learners, unbiased social learners, and conformist social learners. Filled points indicate situations in which some conformist social learners exist. The line represents the analytical threshold for the pure individual learning equilibrium (Eq. 20)

In the fourth regime, a mixture of IL and UT are a unique stable equilibrium if

$$ms < c < \min[m, 1 - (1 - d)(1 - ms)] \tag{25}$$

as long as

$$r > \frac{c}{1 - c} \tag{26}$$

Note that if $d=0$, condition 25 is never satisfied, and this is generally a rather narrow region.

In the fifth regime, UT are a unique stable equilibrium if these three conditions are satisfied:

$$d > 1 - \frac{1 - m}{1 - ms} \tag{27}$$

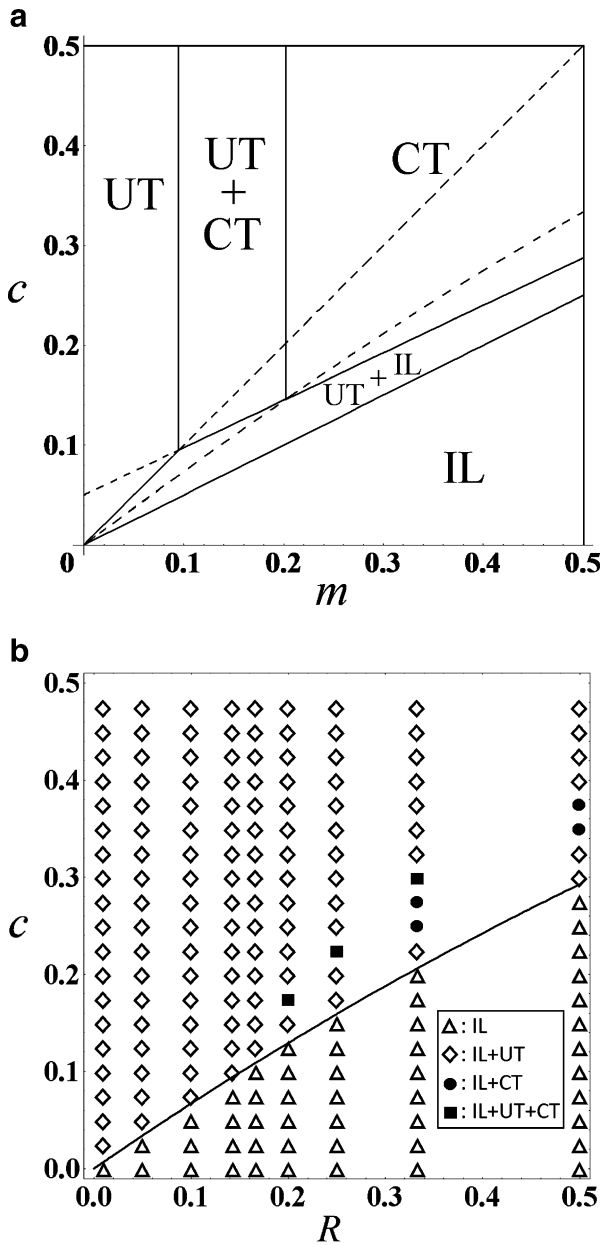
$$c > m \tag{28}$$

$$r > \frac{m}{1 - m} \tag{29}$$

Finally, if the intrinsic rate of growth of the population is too slow, the population will go extinct.

For the pure-strategy temporal model with $d>0$ we can analytically derive the region in which IL are the unique stable strategy, and it turns out to be the same as in (20). However, beyond this, we must rely on simulations of our pure strategy model. Below we also discuss the mixed-strategy temporal model.

Figure 2 compares our analytical results for the spatial model with our simulations of the temporal model for the case when $d=0.05$ (otherwise using the same parameters as in Fig. 1). For the spatial case, adding costs for conformist transmission means that (a) when mixing rates are sufficiently low, UT can be a unique stable equilibrium; (b) when mixing rates are intermediate, UT can coexist with CT; and (c) a narrow polymorphic region of equilibria involving UT and IL separates stable regions of UT, CT, or mixes of CT and UT, from those with pure stable IL. By contrast, in the temporal model, CT are only found in mixtures with IL or sometimes



with both IL and UT, and this region is limited to a rather narrow band. By comparing Fig. 2b with Fig. 1b we see that occurrences of CT seem even sparser and limited to an even narrower band of the (R, c) -parameter space.

For the mixed-strategy temporal model, the outcome depends on how the relationship of d with the strength of conformist transmission (a) is modeled. If we express d as a function of a , $d(a)$, and set $d(1)=0$ to match the pure strategy model (UT is costless), then we can show that if the derivative of d at $a=1$ is greater than

zero, $d'(1) > 0$, then the stable regions of IL and UT in Fig. 1c expand. Since social learners must investigate the frequencies of cultural traits when $a > 1$, and this is probably costly, assuming $d'(1) > 0$ is defensible. This analysis indicates that the findings from our two temporal models are at least qualitatively consistent.

Overall, making conformist transmission costly relative to unbiased transmission does not qualitatively alter the results from our simplest models (Fig. 1). In the spatial model, assuming even moderate amounts of mixing, CT always exist as long as individual learning is sufficiently costly. Within this parameter range, the more mixing there is, the more CT are favored. By contrast, in the models with temporally varying environments, CT are favored in an even narrower band of parameters than in the earlier temporal model.

How Does the Number of Cultural Traits Influence the Evolution of Conformist Transmission?

Thus far we have assumed that the number of cultural traits (n), as well as the number of sites in the spatial model, is large ($n \rightarrow \infty$). This has allowed us to simplify the mathematical expressions above and provide a more direct comparison with the infinite trait models of temporally varying environments. Now we consider how increasing n above two traits influences the evolution of conformist transmission. This is especially important since most prior models have assumed only two cultural traits. Exploring this also allows us to consider how broadly applicable our prior assumption of large n is.

The effect of trait number (n) in the spatial model is to increase the range of conditions favoring CT over polymorphic equilibria of CT and UT, and to increase the range of conditions favoring polymorphic equilibria of CT and UT *over* UT alone. Since the conditions favoring the fixation of IL are the same as those above, this leaves us with five additional equilibrium situations.

In the first of our five equilibrium situations, CT are a unique stable equilibrium if (21), (23), and

$$d < 1 - \frac{1 - m}{1 - ms} - \frac{m(1 - s)^2}{(1 - ms)^2} - \frac{(1 - s)sm^2}{(n - 1)(1 - ms)^2} \tag{30}$$

are satisfied. This inequality reveals the relationship between n and d . As n increases, the fourth term on the right-hand side of this inequality shrinks by a fraction $1/(n - 1)$. Thus, as n gets large, this term goes to zero (reducing the condition back to that shown in condition 22), which increases the maximum value of d under which CT are still favored over other strategies.

If d is larger than in condition 30 while (21) and (23) are still satisfied, then UT and CT will exist in a stable polymorphic equilibrium provided d is not too large. Inequality 31 sets the range for d at this equilibrium:

$$1 - \frac{1 - m}{1 - ms} - \frac{m(1 - s)^2}{(1 - ms)^2} - \frac{(1 - s)sm^2}{(n - 1)(1 - ms)^2} < d < 1 - \frac{1 - m(1 - \theta)}{1 - ms} \tag{31}$$

where

$$\theta = \left\{ m - s - \frac{(1-s)m}{n-1} + \sqrt{\left[m - s - \frac{(1-s)m}{n-1} \right]^2 + 4 \frac{(1-s)m^2}{n-1}} \right\} / 2m \quad (32)$$

If both c and d are sufficiently large, UT are the third unique stable equilibrium. CT are prevented from invading if d exceeds the upper threshold set in inequality (31). IL are prevented from invading, and extinction is avoided if c and r exceed these thresholds:

$$c > m(1 - \theta) \quad (33)$$

$$r > \frac{m(1 - \theta)}{1 - m(1 - \theta)} \quad (34)$$

A fourth equilibrium situation arises in which combinations of IL and UT create a unique stable equilibrium. Under these circumstances, c must fall between these thresholds:

$$ms < c < \min[m(1 - \theta), 1 - (1 - d)(1 - ms)] \quad (35)$$

This condition guarantees that CT cannot invade when individual learning is sufficiently costly that IL cannot completely take over. To avoid extinction, r must be sufficiently large to satisfy (26).

The final situation is that the entire population goes extinct. This occurs if r is too small and falls below the lowest of the threshold conditions for r (inequalities 34, 26, and 23). In these models, the intrinsic growth rate (r) only affects whether the entire population goes extinct and does not affect the evolution of conformity or the other strategies.

It is somewhat difficult to tell from these complicated expressions precisely how n influences the conditions favoring the evolution of different learning strategies. However, as we graphically show in Fig. 3a and prove in Appendix A, increasing n above two substantially increases the conditions favoring CT. Figure 3a shows the stable strategies for $n=2, 4, 8, 16,$ and ∞ . As n increases, the values of m favoring stable CT expand, while those favoring UT and combinations of UT and CT contract. The largest impact of n occurs in moving from two traits to four traits, with only a small change from eight to sixteen traits. Here, when CT are favored, the strongest form of conformist transmission is always favored ($a=\infty$). It is important to realize that here we have set $d=0.05$. Had we set $d=0$, all the bars would have had the darkest shading (all CT at maximum strength). Appendix A formally proves that increasing n decreases the size of the region for fixation in UT and increases the size of the region for fixation in CT.

Now we compare our spatial and temporal models. To obtain comparable results for the temporal case, we draw on the mixed strategy model. This provides us with the two extremes: when there are only two (recognizable) traits, and when the number of traits is infinite. Figure 3 compares the impact of different values of n in our spatial

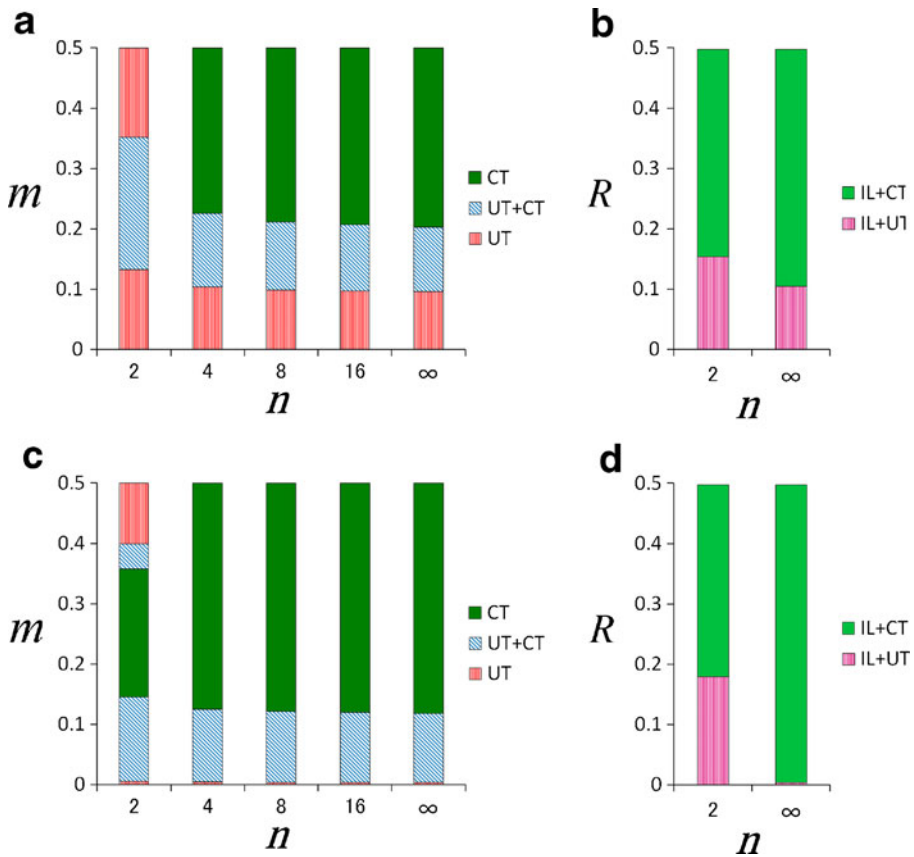


Fig. 3 These plots illustrate the relative impact of different numbers of cultural traits on the learning strategies favored in spatially and temporally varying environments. For (a) and (b), the parameters are the same as those used above: $s=0.5$ and $c=0.3$ (strong selection), whereas for (c) and (d) the parameters are $s=0.05$ and $c=0.03$ (weak selection), and for all figures, $K=100$ and $r=0.5$. The lower panels allow us to observe the effect of n on conformist transmission when s is an order of magnitude smaller than was used above. (a) and (c) show the effect of the number of traits (sites) in the spatial model by comparing $n=2, 4, 8, 16$, and ∞ , where $d=0.05$ and $d=0.005$, respectively. The regions are marked as in previous figures. For (a) and (c), CT have the strongest conformity bias. (b) and (d), drawing on models 2 and 3 of Nakahashi (2007a), show the effect of the number of traits in a temporally changing environment for $n=2$ and $n=\infty$. The “IL+CT” region marks the conditions where the favored mixed strategy deploys both individual learning and conformist transmission (with an intermediate strength)

and temporal models, incorporating both the parameters used in prior figures and the values of s , d , and c set an order of magnitude lower. Figure 3a and c show how increasing n increases the range of conditions dominated by conformist transmission at maximum strength. Figure 3b and d show the parameter ranges that favor mixed strategies with either IL and CT or IL and UT. It is never the case in the temporal model that CT are favored at its maximum strength, though increasing n from two to infinity substantially increases the size of the regions that include some CT, especially when s is small (compare Fig. 3b and d). This suggests, and results in Nakahashi (2007a) confirm, that increasing n in our temporal model expands the conditions favoring conformist biases in social learning.

Note that $d=0$ in Fig. 3b and d, whereas $d=0.05$ and $d=0.005$ (respectively) in Fig. 3a and c, so this figure is biased against the evolution of CT in spatially varying environments. Consequently, we focus on the effects of increasing n in the different models, not on the size of the regions with CT. Above, we discussed the challenges of assuming $d>0$ in the mixed strategy model; note that if we assume $d=0$ in the spatial model, the importance of n cannot be observed since CT completely dominate for $n \geq 2$.

In Fig. 1a ($n=2$), the dominance of UT at both low and high migration rates, with a mixture of UT and CT in the middle range, highlights an interesting feature of these evolutionary processes. When m is low (few migrants), UT get the adaptive trait almost as often as CT. Since CT pay a mortality cost for their conformist abilities, UT can dominate at low m . As m increases, CT nonmigrants get the adaptive trait relatively more frequently than UT nonmigrants, resulting in a polymorphic equilibrium. When m is high, many CT and UT are migrants to new sites. At new sites, CT never have the locally adaptive trait and thus suffer both mortality costs s and d . Compared with CT, UT migrants are more likely to possess the locally adaptive trait for their new site (which is nonadaptive back in their home site). This effect is strongest when $n=2$ because UT migrants who have adopted the locally nonadaptive trait in their home population always end up moving into a site in which their trait is now adaptive. CT migrants never end up in such a site. However, as n increases, the chances of UT ending up in a site where their behavior is locally adaptive plummets as $\frac{1}{n-1}$.

Relations with Prior Models Using a Heuristic Approach

Both the spatial and temporal models indicate that increasing n above 2 substantially expands the conditions favoring the evolution of conformist transmission, though increasing n above about 8 yields only small and diminishing effects (at least in the spatial model). This means that considering more than two traits is important for understanding the conditions favoring the evolution of conformist transmission. It also means that our above assumption of n being large provides a good approximation for a wide range of conditions.

To intuitively understand how larger values of $n (>2)$ empower conformist transmission, let's go back to the original formulation used by Boyd and Richerson (1985):

$$B(p) = p + Dp(1 - p)(2p - 1) \tag{36}$$

Here, $B(p)$ is the probability of a conformist learner acquiring a particular trait, whose frequency in the population is captured by p . D gives the strength of conformist transmission, which we will assume is 1 (its maximum) for this example. This was derived assuming two cultural traits exist ($n=2$) and that individuals select three models each, at random, from that population, giving weight D to the most common variant in their small sample.

Now we compare two situations: the first with two traits ($n=2$) and the second with many traits ($n>2$). In both situations we assume that there is only one locally adaptive trait and assign it a frequency of p . Our conformist learner (CT) selects three models at random from the population, and the probabilities for the trio possessing 0, 1, 2, or 3 of the locally adaptive traits are the same in both our $n=2$ situation and our $n>2$ situation: $(1 - p)^3$, $3p(1 - p)^2$, $3(1 - p)p^2$, p^3 . In the two-trait situation, CT

always imitate the locally adaptive trait when the number of models with the adaptive trait is 2 or 3 but never imitates when only 0 or 1 of models has the adaptive trait. When $n=2$, the probability of imitating the adaptive trait is $B = 3(1 - p)p^2 + p^3 = p + p(1 - p)(2p - 1)$, so $B > p$ when $p > 1/2$. By contrast, in the situation with $n > 2$, CT always imitate the adaptive trait when two or three models display this trait, sometimes imitate it when one model displays it, and never imitate it when none of the three has it. That is, in this situation, even when the number of models with the adaptive trait is 1, the other two targets sometimes have *different* nonadaptive traits so that conformists still imitate the adaptive trait with a probability of $1/3$. The probability that CT imitate the adaptive trait depends on the frequencies of the other nonadaptive traits. This probability, B , is largest when the frequencies of nonadaptive traits are the same (i.e., $(1 - p)/(n - 1)$) and smallest when the frequency of one nonadaptive trait is by far the largest, almost $1 - p$. When the frequencies of the nonadaptive traits are the same, the probability of imitating the locally adaptive trait is

$$\begin{aligned}
 B &= p(1 - p)^2 \left[1 - (n - 1) \left(\frac{1}{n-1} \right)^2 \right] + 3(1 - p)p^2 + p^3 \\
 &= p \left[1 + \frac{(1-p)(np-1)}{n-1} \right]
 \end{aligned}
 \tag{37}$$

Thus, $B > p$ when $p > 1/n$. When the frequency of one of the many nonadaptive traits is almost $1 - p$, the probability of acquiring the adaptive trait is the same as in the two-trait situation. In general:

$$p + p(1 - p)(2p - 1) < B \leq p \left[1 + \frac{(1 - p)(np - 1)}{n - 1} \right]
 \tag{38}$$

For UT, the probability of acquiring the adaptive trait is the same (p) in both the $n=2$ and the $n > 2$ situations because the frequency of the adaptive trait is the same in both cases. So, CT can be favored over UT even when $1/n < p < 1/2$.

Figure 4 summarizes this heuristic analysis and indicates that increasing the number of cultural traits increases the strength of the selective forces favoring the evolution of conformist transmission, regardless of the particular expression used to

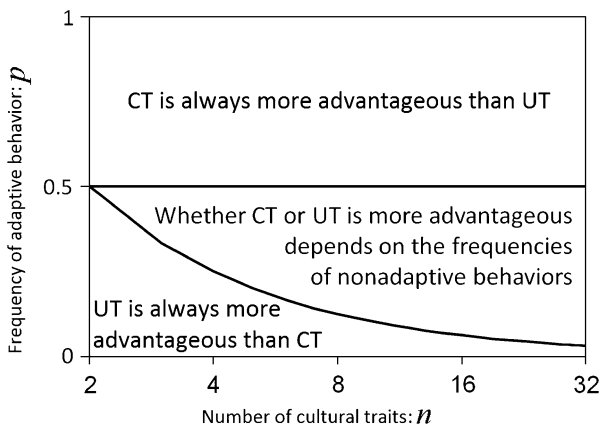


Fig. 4 Illustration of our heuristic analysis of the effects of increasing the number of cultural traits on the relative advantage of CT vs. UT

capture the idea behind conformist transmission. Importantly, note that there are no explicit fitness costs or environmental variation in this heuristic approach.

So far, we have made the simplifying assumption that n is both the number of sites and the number of cultural traits. Appendix A explores how our results change if we separate the number of sites from the number of traits. By assuming that the number of sites is large (infinite) and the number of traits is n , we show that the qualitative results do not change. The threshold values for the invasion of CT into a population of UT and for the stability of a pure CT equilibrium increase by a factor of $\frac{n}{n-1}$. As n increases, the ratio approaches 1, so the thresholds for m approach the results presented above. This indicates that as long as the number of sites is large, our conclusions are not substantially affected by matching the number of sites with the number of cultural traits.

The basic insights from this section will be important below in our discussion of how, even in the absence of spatial variability, learning and transmission errors can create a steady inflow of suboptimal cultural traits (increasing n) that mimics the inflow created by spatial variability and mixing. This means that these insights are likely important in considering situations involving both static and temporally varying environments, and especially in situations of cumulative cultural evolution in which transmission errors are likely to increase as trait complexity and diversity increases.

How Does the Inclusion of Payoff-Bias Social Learning Change the Previous Results?

While much work has examined the evolution of conformist learning strategies in competition with individual learning and unbiased or vertical transmission strategies, less work has examined whether conformist transmission can evolve in the presence of strategies that use the payoff differences among cultural traits in figuring out what to adopt (Kendal et al. 2009). Now, we add payoff-biased cultural learning (PT) to our set of pure strategies and examine what happens in both spatially and temporally varying environments.

To the above baseline model we add the strategy PT, which copies the cultural trait with the highest payoff in the local population (the site) at mortality cost g . We typically assume that $0 \leq d < g < c < s < 1$. This assumption seems plausible, given that PT have a more complicated task than CT, which involves assessing payoffs or at least relative payoff differences for the cultural traits present. There may be particular situations in which $d > g$; this will expand the range of conditions favoring PT.

Using the same notation as above for the baseline spatial model, we can write the recursions for the frequency of PT. V_{ii} and V_{ij} represent the number of PT at site i who possess the locally adaptive cultural trait and the number of PT who possess the trait that is adaptive at site j , respectively:

$$V'_{ii} = (1 - g)(1 - m)V_i b(N_i) \tag{39}$$

$$V'_{ij} = \frac{(1 - g)(1 - s)mV_j b(N_j)}{n - 1} \tag{40}$$

The other recursions presented above are modified slightly to include the values for V . A full derivation can be found in Appendix A.

Given the potency of payoff-biased cultural learning in other contexts (Kendal et al. 2009; McElreath et al. 2008), our results are surprisingly stark. If the cost to PT is larger than that to CT (i.e., $g > d$), PT *never* evolve. That is, our findings presented above hold, unchanged (Figs. 1a and 2a hold even if PT enters the fray). If both CT and PT suffer the same mortality costs ($d = g$), they are neutrally stable—both always learn the adaptive trait for their home site and suffer a cost when they migrate.

The temporal model gives quite different results. Here we focus on our pure strategy model and rely on a combination of analytical and numerical simulation results. We begin by presenting key findings from the available analytical results and then combine them with simulations to generate a comparison with our spatial model. The derivation can be found in Appendix B.

Analytically, we show that IL are the stable equilibrium when

$$R = \frac{1}{\ell} > \frac{\ln(1 - c)}{\ln(1 - s)} \tag{41}$$

and PT can invade IL when

$$R = \frac{1}{\ell} < \frac{\ln(1 - c) - \ln(1 - g)}{\ln(1 - s)} \tag{42}$$

Assuming mutation maintains IL in the population at some low frequency, PT remain stable at high frequency in the population when

$$R = \frac{1}{\ell} > \frac{\ln(1 - g)}{\ln(1 - s)} \tag{43}$$

We could not analytically delineate the region where CT can exist, but numerical simulation suggests complex relationships with the parameters. Our simulations all indicate that CT are not very important in a temporally varying environment, especially when PT are in the mix. Logically, if PT suffer no additional learning cost, PT are favored over UT/CT. But if PT suffer a cost (g), UT/CT can invade a PT+IL because when the frequencies of PT and IL are sufficiently large, UT can easily imitate the locally adaptive trait, so the frequency of PT cannot exceed some value. Of course, the details should depend on g and d .

Figure 5 combines our analytical and simulation results for this temporal pure-strategy model. It can be compared with Fig. 2a, since our spatial model's results do not change with the addition of PT (assuming $g > d > 0$). On Fig. 5, the lower curve represents the analytically derived threshold of the IL equilibrium (41). The upper curve demarcates the threshold at which PT can exist at equilibrium 42, and the vertical line represents the threshold of an *almost* purely PT equilibrium 43.

For the temporal model, this combination of numerical and analytical findings suggests five different regions. Two regions involve equilibria of pure strategies of either PT or IL. A third region permits combinations of UT and PT while a fourth region has combinations of IL and UT. The final region always includes IL, mixed with either UT or CT, or both. Comparison of Figs. 2b and 5 reveals the dramatic impact of introducing PT into the mix of pure strategies, as PT dominate when both c

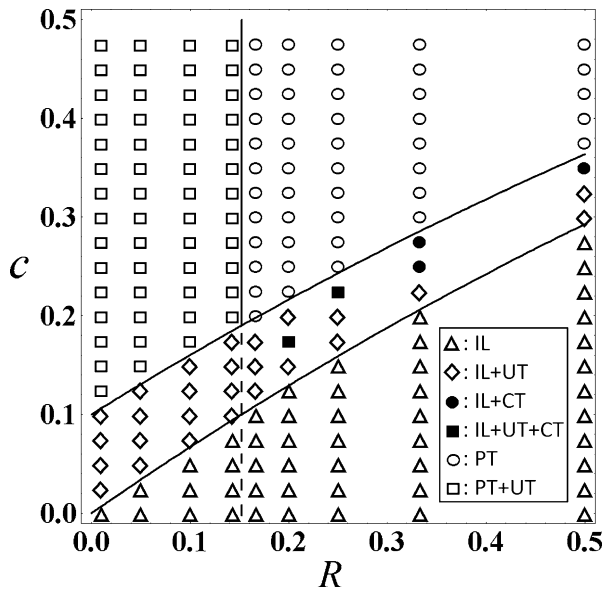


Fig. 5 Equilibrium regions for our pure-strategy temporal model in (R, c) -parameter space ($s=0.5, a=10, g=0.1, n=\infty$ and $d=0.05$). Numerically, we obtain the equilibrium frequencies of UT, CT, PT, and IL from several initial frequencies. Δ means that IL evolve to fixation. \circ indicates that PT evolve to fixation. \square indicates a polymorphic equilibrium of UT and PT. \diamond indicates a polymorphic equilibrium of IL and UT. \bullet indicates a polymorphic equilibrium of IL and CT. \blacksquare indicates a polymorphic equilibrium of IL, UT, and CT. Filled markers indicate where CT exist at equilibrium. The lower curve represents the analytically derived threshold of the IL equilibrium. The upper curve demarcates the threshold at which PT exist at equilibrium. The vertical line represents the threshold for a purely PT equilibrium

and R are high and occur in a polymorphic equilibrium with UT when c is high and R is low (stable environments).

To illustrate the dynamics of our models with PT, Fig. 6 presents two simulation runs, one for our spatial model (Fig. 6a) and the second for our temporal model (Fig. 6b). Both models used these common parameters: $s=0.5, c=0.3, g=0.1, d=0, a=10, K=100$, and $r=0.5$. Note that $a=10$ is sufficiently strong to closely approximate $a=\infty$. For the spatial model we set the initial number of UT, CT, PT, and IL to be $X_{ij} = U_{ij} = V_{ij} = \frac{K}{4n}$ for all i, j , and $Z_i = K/4$. That is, the initial frequencies of UT, CT, PT, and IL are 0.25. We also set $n=4$ so as not to give CT too much of an advantage in the spatial model, and $m=0.2$. For the temporal model we set the initial frequencies of UT, CT, PT, and IL at 0.25, and $\ell=5$ ($R=0.2$) to parallel the setting of m in our spatial model.

Both Figs. 5 and 6 reveal a fairly stark contrast in how CT and PT respond to selection in spatially vs. temporally varying environments. If anything, adding PT to a mix of strategies accentuates the difference in the selective regimes created by these environments.

When IL Cannot Learn after Migration or Environmental Shifts

Thus far our models have permitted an asymmetry among the four pure learning strategies by assuming that IL can immediately acquire the locally adaptive trait after

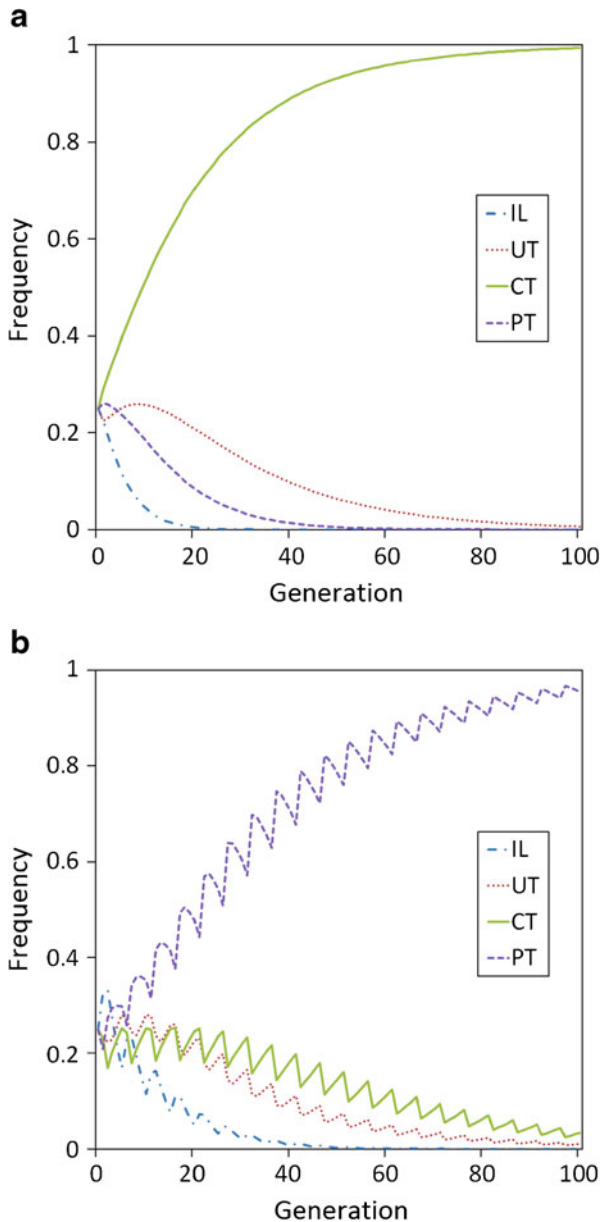


Fig. 6 Illustrative evolutionary dynamics for our four different pure strategies in **(a)** spatially and **(b)** temporally varying environments for parameters $s=0.5$, $c=0.3$, $g=0.1$, $d=0$, and $a=10$. We set the initial frequencies of UT, CT, PT, and IL at 0.25. In **(a)**, $m=0.2$, $K=100$, and $r=0.5$, and in **(b)**, $\ell=5$ ($R=0.2$)

migration, or after an environmental shift, but UT, CT, and PT cannot learn new traits later in their life cycle. Here we present results from analyses in which we level the playing field so that IL cannot re-learn its adult trait after migration, or after an environmental shift. Like the social learners, IL are stuck with whatever they learned while growing up. Our results indicate that this assumption about IL has suppressed

the success of CT in our spatially varying model while having no effect in our temporally varying model.

For the spatial model, Appendix A shows how we altered our baseline recursions to accommodate this change in the life cycle of IL. We present only the results here. When CT suffer no cost (i.e., $d=0$), fixation of CT and extinction are the only possible stable equilibria (UT, PT, and IL never evolve). If d is greater than zero but still smaller than g and c , IL and PT never evolve. That is, if $0 < d < g < c < s < 1$, there are only four stable outcomes: (1) all CT, (2) all UT, (3) mixtures of CT and UT, and (4) extinction. CT are the unique stable equilibrium if inequalities 31 and 23 hold, which guarantees that d is sufficiently small to prevent UT from invading, and r is sufficiently large to prevent extinction. These are two of the three conditions previously necessary for CT to remain stable in the model, when IL could learn after migration. The third condition is no longer necessary, since it was the required condition to hold IL at bay—the advantage IL obtained by being able to learn after migration. The second equilibrium situation parallels the above case and occurs when d falls into an intermediate range set by inequality 32, assuming that r is sufficiently large that (23) is not violated. In the third situation, UT emerge as the sole stable equilibrium if d exceeds the upper threshold marked by (32) and r is sufficiently large that (34) holds. Finally, if r fails to exceed either (23) or (34), extinction is the only long-term result.

The results are quite different in our pure-strategy temporal model, detailed in Appendix B. This constraint on IL means that they cannot adapt immediately to obtain the locally adaptive trait when the environment changes. If IL cannot adapt, then neither can any of the social learning strategies (UT, PT, and CT). Any constraint placed on IL in this temporal model that delays acquisition of the locally adaptive trait is subsequently imposed downstream on UT, PT, and CT, since they ultimately rely on IL to figure out the locally adaptive trait. This means that there is no qualitative difference in the findings for this version of the temporal model compared with the case when IL can acquire the currently adaptive trait immediately after the environmental shift.

Overall, leveling the playing field to constrain IL expands the range of conditions favoring CT (and social learning more generally) in the spatial model, but it does not change the conditions in the temporal model. Future work should examine what happens when all of our strategies can learn after migration but before selection.

Discussion

In broadening, applying, and contextualizing our modeling results we focus on three areas. First we discuss how the spatial variation we analyzed above, which powerfully favors the evolution of conformist transmission, represents but one source of low-level, nonadaptive, phenotypic trait variation. By nonadaptive trait variation we mean the presence of additional cultural variants (phenotypes) that are distinct to the learner, but not distinguishable from many other variants in terms of payoffs in the current environment. It is this nonadaptive variation, not spatial variation per se, that favors conformist transmission. Other factors, such as learning errors or transmission noise, will also produce a similarly persistent, low-volume inflow of nonadaptive

variation. This means that even in the absence of spatial variability, conformist transmission can provide an adaptive advantage. Second, with empirical tests in mind, we develop a set of predictions from our formal results that are suitable to experimental testing. Third, although our models are focused on cultural traits applied in nonsocial contexts (e.g., which berries are edible), we consider the evolution in conformist transmission for acquiring traits or strategies for interacting in social situations. We argue, contrary to recent claims, that conformist transmission can still be adaptive in situations involving cooperation and punishment, and even in situations involving complementarities.

Learning Error as Source of Nonadaptive Variation

The kind of nonadaptive phenotypic trait variation (cultural traits) created in our spatial model by a combination of environmental differences among sites and migration is merely one manifestation of a more general adaptive challenge with which successful social learning strategies must contend. Conformist transmission is frequently favored in these spatially varying environments because of its ability to successfully ignore, or avoid acquiring, the nonadaptive cultural traits brought in via migration from other sites. There are, however, a variety of processes that can generate a similar adaptive challenge to that created by spatial environmental variation, including errors or noise produced during learning and transmission (which we did not explicitly model).

Both mistakes in individual learning and a variety of errors in cultural transmission can create the same kind of low-level trait variation as do environmental variation and migration. Even in a completely static environment, errors and mistakes by both individual and social learners can inject a steady flow of nonadaptive cultural traits (increasing n and effectively m) into the local population. Individual learners may sometimes “goof-up” and “invent” something that is both new and nonadaptive. Social learners are likely to create a great variety of novel and less-adaptive cultural traits, especially when acquiring more-complex cultural traits, by (a) misperceiving what their models are doing, (b) making errors during the inferential steps of imitation, or (c) misremembering elements of cultural traits at some later time (Henrich and Boyd 2002). Successful social learners need to figure out how to avoid this constant injection of nonadaptive variation. Conformist transmission provides one way to “squeeze out” this nonadaptive variation at (potentially) a low cost (see analogy with robust estimators in Boyd and Richerson 1985: Chapter 7).

Of course, there are other ways to address this challenge. Payoff-biased strategies can avoid this nonadaptive variation, but these strategies are likely more costly in general, and potentially *quite a bit* more costly. And, if a learner’s payoff information is itself noisy, then conformist transmission can still be a superior strategy (Henrich and Boyd 2002; McElreath et al. 2008)—especially if the learner accurately perceives that he or she is likely to be less well informed about payoffs than many others in the local population. Other important strategies that can address this problem include blending mechanisms, which present a theoretical cousin of conformist biases, and the use of ethnic markers (Boyd and Richerson 1985: Chapter 4, 1987; McElreath et al. 2003).

It is also not the case that one need choose between payoff and conformist biases. Consider a social learning strategy that samples M models from the local

population and estimates which N of these M models have the highest payoffs, or are the most successful. Our integrated learner then applies conformist learning to these N . When payoff differences are nonexistent, or too noisy to be successfully differentiated, this algorithm reduces to pure conformist transmission. When payoff differences between traits can be recognized, but traits can be misperceived (the model is doing A, but learners misread it as B), this heuristic improves the accuracy of payoff-biased learning. This, and other more complex heuristics, can obtain the noise-reducing benefits of conformist transmission while still achieving the rapid adaptability and flexibility of payoff-biased learning (Henrich and Boyd 2002).

We think this may be particularly important for understanding cumulative cultural evolution. As tools, for example, evolve culturally to become more complicated, errors in cultural transmission will increasingly introduce nonadaptive variation at the same time as payoff differences get harder to detect, or at least to trace to particular differences in the tools, or their manufacture. After selectively sampling those with higher payoffs, copying the most common step or technique in the manufacture of a complicated tool can still allow learners to avoid copying nonadaptive variation.

Predictions

One of the primary goals of evolutionary modeling is to generate clear, precise, empirical predictions about the operation of psychological mechanisms, and specifically in this case about the cognitive mechanisms that underpin our cultural learning abilities. Here we outline four testable predictions, derived from our modeling efforts above:

1. Increasing the migration rates (m) among different environments (local populations) should increase individuals' reliance on conformist transmission, provided the costs of individual learning are not too low (Fig. 2a). By contrast, increasing the rate of environmental fluctuations should not have similarly sharp effects (see Fig. 2b, focusing on increasing R).

2. Increasing n , the number of cultural traits, in the presence of low-level trait variation should increase individuals' reliance on conformist transmission. This is best illustrated in Figs. 3a and 4. The degree of increase in reliance on conformist transmission should be more pronounced in moving from two traits to four traits, with increases declining thereafter. See Fig. 4 for a heuristic relationship. Increasing both m and n raises the rate of influx of local nonadaptive traits variation. Similar predictions should hold if learning errors or transmission noise is increased, even in stable environments.

3. Increasing the costs of individual learning (c) in an environment with persistently low levels of trait variation should increase individuals' reliance on conformist transmission, provided that the levels of trait variation are not too low (Fig. 2a).

4. Increasing the costs of nonadaptive behavior (s) should decrease individuals' reliance on conformist transmission and increase reliance on individual learning provided other costs (c , d , g) are constant.

These predictions can drive new field and experimental research on learning strategies, while informing existing work showing substantial heterogeneity in individual strategies (Efferson et al. 2008a, b; McElreath et al. 2008).

Social Interaction, Reputation, Punishment, and Cooperation

Like much prior work, our models analyze the evolution of different social learning strategies by assuming that the traits being learned are nonsocial, or at least that their payoffs do not depend on the frequency of other cultural traits in the local population. Skills or techniques related to food choice or tool manufacture might be most appropriate. Here we consider how using various learning strategies for acquiring social behavior might influence the evolution of conformist transmission, or at least the range of domains or types of problems to which it might be applied. We think our models are particularly useful in this regard, since, as we argue below, the cultural evolution of social behavior may often create a kind of spatial variability much like what we have modeled.

To explore this we consider three kinds of social interactions in groups, those involving (1) coordination, (2) cooperation, and (3) complementarity (Eriksson et al. 2007). In coordination games, conformist transmission is clearly an adaptive strategy as learners need to figure out what most people are doing among those with whom they are most likely to interact in the future. If everyone expects dowries to be paid along with daughters, then our learner adopts the practices associated with dowry. If bride prices or bride services are paid to the wife's family, then our learner adopts this strategy. The effectiveness of conformist transmission in these situations seems uncontroversial, though some have argued that payoff biases have the same result. This is true, but payoff-biased transmission requires learners to acquire and process payoff information, which is likely more costly relative to frequency information. The precise difference depends heavily on the costs of various sorts of information and their relative accuracy.

For many different coordination problems, cultural evolution can generate a wide variety of solutions. The important thing in a coordination problem is to do what the majority does. This applies to such problems as driving on the left or the right, relying on a lunar or a solar calendar, or closing the factory on a particular day of the week. If different groups wind up at different solutions, a kind of spatial variation can emerge that parallels what we have modeled above. The important thing for migrants is to acquire the most common behavior in whatever population they end up in, whereas nonmigrants just need to make sure they don't mistakenly copy a new arrival (from a group with a different coordinated solution).

The second and more controversial kind of social interaction involves problems of cooperation, and in particular situations of larger-scale or n -person cooperation. In this kind of social interaction the group does best if everyone cooperates, but defecting individuals can free-ride on the cooperation of others and receive higher payoffs than those who cooperate. Eriksson et al. (2007) have argued that learners ought not use conformist transmission in such a situation, and especially in acquiring the punishing strategies that are so often thought to stabilize human cooperation (Henrich 2004).

We, however, think this view fails to recognize two different lines of theoretical work. First, there is a large body of modeling showing how a variety of mechanisms related to punishment, signaling, reputation, and reciprocity can effectively turn cooperative dilemmas into coordination situations (N. Henrich and Henrich 2007). That is, formal cultural evolutionary models show how a multiplicity of stable social

norms are created by a variety of mechanisms that generate self-reinforcing incentives (Boyd et al. 2010; Gintis et al. 2001; Henrich and Boyd 2001; Panchanathan and Boyd 2004). The theoretical expectation from these models is that different social groups will culturally evolve different norms, since myriad behaviors are stable once they become common. From the perspective of conformist transmission, the emergence of self-reinforcing social norms that vary among social groups creates a situation that parallels our spatial model. Different groups (sites) have different self-enforcing social norms, so migrants need to figure out what locally won't get one a bad reputation or punished, and nonmigrants need to avoid learning from those who have made an error or are new arrivals to the group.

Second, some approaches to larger-scale cooperation have shown how including punishing strategies—while not leading to stable states as above—does slow the within-group decline of cooperation (when common) sufficiently that between-group competition can favor higher levels of cooperation overall in a large structured population (Boyd et al. 2003, 2011). Building on this work using simulations, Guzman et al. (2007) have explored the genetic evolution of payoff-biased and conformist transmission in a world in which the only problems individuals confront are those involving cooperation and punishment. This simulation suggests that natural selection will still, contrary to some suggestions (Hagen and Hammerstein 2006), favor the evolution of substantial conformist transmission. This simulation has a complex interaction of cultural and genetic evolution in which conformist transmission keeps culturally transmitted punishing and cooperating strategies common in some groups, and those groups proliferate. When conformist-biased learners migrate to noncooperative, nonpunishing groups, they rapidly stop paying the costs of cooperation and punishment, thus reducing the selection against them. Conformist transmission, cooperation, and punishment appear to be a potent culture-gene coevolutionary package. Using a setup similar to Guzman et al., Henrich and Boyd (2001) have analytically shown that once conformist transmission evolves to even a relatively weak degree, it can give rise to the same kind of stable social norms described above. Either way one looks at it, the kind of spatial variability that favors conformist transmission is again created.

The third type of social interaction involves complementary actions. In games of complementarity, individuals receive the highest payoffs when they bring skills, endowments, or know-how *different* from those of people with whom they are interacting. Copying the currently most common trait here is not the road to higher payoffs for sure. However, an empirical look at human societies reveals that they are organized in such a way so as to mitigate this concern. In the smallest-scale human societies, there is little division of labor or know-how, except by age and sex (Fried 1967). For example, although men vary in their skills, there are no obvious complementarities, and only small amounts of occupational specialization exist (Johnson 1995). There can be ritual specialists, but it is not clear why the existence of these relatively rare roles would inhibit the evolution of conformist transmission. As for sex and age, much prior theorizing on cultural learning mechanisms has suggested that learners use cues of both sex and age to hone their attention and learning efforts (Henrich and Gil-White 2001), and that conformist transmission should interface with such cues (Henrich and McElreath 2007). Men, for example, may be inclined to copy what most men do, whereas women should be inclined to copy what most women do.

Men and women, then, supply complementary skills to the household. Thus, cultural evolution solves this problem of complementarity by partitioning individuals into subgroups within which conformist transmission can operate effectively, and by making the complementary interaction occur between subgroups. At the group level, everyone merely needs to *coordinate* on the same cultural beliefs about the division of labor: for example, “males hunt and females gather” (which, again, can be effectively acquired by conformist transmission).

In more complex human societies, occupational specializations of the kind associated with complementary interactions emerge principally in relations *among* social groups, with whole groups, castes, classes, or guilds specializing in one or another skill (Barth 1965; Gadgil and Malhotra 1983). Farmers grow up among farmers, herders among herders, merchants among merchants, and nobles among nobles. Exploring this, cultural evolutionary models of complementary interactions in structured populations have shown how payoff-biased transmission will spontaneously give rise to specializations by local or ethnic groups in specific skills (Henrich and Boyd 2008). This means that payoff-biases—in the absence of conformist transmission—in situations of complementarity will spontaneously give rise to precisely the kind of spatial variation that favors the evolution of conformist transmission.

Conclusion

We have constructed, analyzed, and compared a series of formal models aimed at further elucidating the evolutionary foundations of different learning strategies. Our primary contribution is to clarify how spatial vs. temporal environmental variation differentially influences the evolution of three different social learning strategies and individual learning, as well as to examine how using more than two cultural traits affects the emergence of conformist transmission. Our models also examine the effects of different fitness costs for different strategies. Broadly speaking, we find that when individual learning is sufficiently costly, conformist transmission is favored in spatially varying environments while payoff-biased transmission is favored in temporally varying environments. With regard to the number of cultural traits, our results also show that by focusing on models with two cultural traits, much prior work has explored the circumstances least favorable to conformist transmission. A small increase in the number of cultural traits substantially expands the range of conditions favoring conformist transmission in both spatially and temporally varying environments. To facilitate empirical testing, we distilled our formal results into a series of predictions suited to experimentation.

We believe our findings have broader implications for the evolution of social learning strategies beyond spatially and temporally varying environments for two reasons. First, spatial variability is merely one way to generate a low-level but persistent influx of nonadaptive trait variation that favors conformist transmission, with learning errors being another obvious process that could generate this selective force. This means that conformist transmission could be similarly favored even in static or temporally varying environments with transmission noise or learning errors. Second, although the learning challenge in our model is nonsocial, we argue that social interactions involving coordination, cooperation, and complementarity can and

do generate a kind of variation among groups that parallels our model's spatial variation. This suggests that conformist transmission to acquire phenotypes for social interactions could also be favored for similar reasons.

Better understanding conformist transmission at both proximate and ultimate levels is important for a number of reasons. To begin, it may provide a readily available explanation for some of the apparent “clumpiness” observed in cultural variation (Henrich and Boyd 1998), addressing the question of why local groups, for example, might vary on numerous cultural dimensions (Bell et al. 2009). It may also help explain the group-level heritability found in the branching signals revealed in the application of phylogenetic methods to cultural datasets (Collard et al. 2006; Lipo et al. 2006), something which is difficult to explain if vertical cultural transmission is assumed. Third, because conformist transmission enhances the stability of local norms, it may help explain the impressive persistence of maladaptive behaviors, and potentially societal collapses (Whitehead and Richerson 2009), in societies throughout the ethnographic and historical record (Durham 1991; Edgerton 1992). And finally, by reducing the variation within groups and assorting like phenotypes together, conformist transmission may increase the importance of the between-group components of cultural evolution relative to the within-group components. This suggests that cultural evolutionary processes might have quite a different character with regard to the evolution of social behavior when compared with vertically transmitted genetic evolution (Bell et al. 2009; Boyd and Richerson 1985; Currie and Mace 2009; Henrich and Boyd 2001).

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References

- Aoki, K. (2010). Evolution of the social-learner-explorer strategy in an environmentally heterogeneous two-island model. *Evolution*, *64*(9), 2575–2586. doi:10.1111/j.1558-5646.2010.01017.x.
- Aoki, K., & Nakahashi, W. (2008). Evolution of learning in subdivided populations that occupy environmentally heterogeneous sites. *Theoretical Population Biology*, *74*(4), 356–368. doi:10.1016/j.tpb.2008.09.006.
- Barth, F. (1965). *Political leadership among Swat Pathans*. Toronto: Oxford University Press.
- Bell, A. V., Richerson, P. J., & McElreath, R. (2009). Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proceedings of the National Academy of Sciences (USA)*, *106*(42), 17671–17674. doi:10.1073/pnas.0903232106.
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- Boyd, R., & Richerson, P. J. (1987). The evolution of ethnic markers. *Cultural Anthropology*, *2*(1), 27–38.
- Boyd, R., Gintis, H., Bowles, S., & Richerson, P. J. (2003). The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences (USA)*, *100*(6), 3531–3535.
- Boyd, R., Gintis, H., & Bowles, S. (2010). Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science*, *328*(5978), 617–620.
- Boyd, R., Richerson, P. J., & Henrich, J. (2011). Rapid cultural adaptation can facilitate the evolution of large-scale cooperation. *Behavioral Ecology and Sociobiology*, *65*(3), 431–444.

- Cavalli-Sforza, L. L., & Feldman, M. W. (1981). *Cultural transmission and evolution: A quantitative approach*. Princeton: Princeton Univ. Press.
- Chudek, M., Heller, S., Birch, S., & Henrich, J. (2012). Prestige-biased cultural learning: bystander's differential attention to potential models influences children's learning. *Evolution and Human Behavior*, 33(1), 46–56.
- Collard, M., Shennan, S. J., & Tehrani, J. J. (2006). Branching, blending, and the evolution of cultural similarities and differences among human populations. *Evolution and Human Behavior*, 27(3), 169–184.
- Currie, T. E., & Mace, R. (2009). Political complexity predicts the spread of ethnolinguistic groups. *Proceedings of the National Academy of Sciences (USA)*, 106(18), 7339–7344. doi:10.1073/pnas.0804698106.
- Durham, W. (1991). *Coevolution: Genes, culture, and human diversity*. Stanford: Stanford University Press.
- Edgerton, R. B. (1992). *Sick societies: Challenging the myth of primitive harmony*. New York: Free Press.
- Efferson, C., Lalive, R., & Fehr, E. (2008). The coevolution of cultural groups and ingroup favoritism. *Science*, 321(5897), 1844–1849.
- Efferson, C., Lalive, R., Richerson, P. J., McElreath, R., & Lubell, M. (2008). Conformists and mavericks: the empirics of frequency-dependent cultural transmission. *Evolution and Human Behavior*, 29(1), 56–64. doi:10.1016/j.evolhumbehav.2007.08.003.
- Eriksson, K., Enquist, S., & Ghirlanda, S. (2007). Critical point in current theory of conformist social learning. *Journal of Evolutionary Psychology*, 5, 67–87.
- Fried, M. (1967). *The evolution of political society: An essay in political anthropology*. New York: Random House.
- Gadgil, M., & Malhotra, K. C. (1983). Adaptive significance of the Indian caste system: an ecological perspective. *Annals of Human Biology*, 10(5), 465–478.
- Galef, B. G., & Whiskin, E. E. (2008). Use of social information by sodium- and protein-deficient rats: test of a prediction (Boyd & Richerson 1988). *Animal Behaviour*, 75, 627–630.
- Gintis, H., Smith, E. A., & Bowles, S. (2001). Costly signaling and cooperation. *Journal of Theoretical Biology*, 213(1), 103–119.
- Guzman, R. A., Rodriguez-Sickert, C., & Rowthorn, R. (2007). When in Rome, do as the Romans do: the coevolution of altruistic punishment, conformist learning, and cooperation. *Evolution and Human Behavior*, 28(2), 112–117.
- Hagen, E. H., & Hammerstein, P. (2006). Game theory and human evolution: a critique of some recent interpretations of experimental games. *Theoretical Population Biology*, 69(3), 339–348.
- Harris, P. L., & Corriveau, K. H. (2011). Young children's selective trust in informants. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 1179–1187.
- Henrich, J. (2004). Cultural group selection, coevolutionary processes and large-scale cooperation. *Journal of Economic Behavior & Organization*, 53, 3–35.
- Henrich, J., & Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior*, 19, 215–242.
- Henrich, J., & Boyd, R. (2001). Why people punish defectors: weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical Biology*, 208, 79–89.
- Henrich, J., & Boyd, R. (2002). On modeling cultural evolution: why replicators are not necessary for cultural evolution. *Journal of Cognition and Culture*, 2(2), 87–112.
- Henrich, J., & Boyd, R. (2008). Division of labor, economic specialization, and the evolution of social stratification. *Current Anthropology*, 49(4), 715–724.
- Henrich, J., & Broesch, J. (2011). On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases. *Philosophical Transactions of the Royal Society*, 366, 1139–1148.
- Henrich, J., & Gil-White, F. (2001). The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, 22(3), 165–196.
- Henrich, J., & Henrich, N. (2010). The evolution of cultural adaptations: Fijian taboos during pregnancy and lactation protect against marine toxins. *Proceedings of the Royal Society B: Biological Sciences*, published online at <http://rspb.royalsocietypublishing.org/content/early/2010/07/26/rspb.2010.1191.short?rss=1>.
- Henrich, J., & McElreath, R. (2007). Dual inheritance theory: The evolution of human cultural capacities and cultural evolution. In R. Dunbar & L. Barrett (Eds.), *Oxford handbook of evolutionary psychology* (pp. 555–570). Oxford: Oxford University Press.
- Henrich, N., & Henrich, J. (2007). *Why humans cooperate: A cultural and evolutionary explanation*. Oxford: Oxford University Press.

- Johnson, A. (1995). A Guttman scale analysis of Matsigenka men's manufacturing skills. *Cultural Anthropology Methods*, 7, 1–3.
- Kameda, T., & Nakanishi, D. (2002). Cost-benefit analysis of social/cultural learning in a nonstationary uncertain environment: an evolutionary simulation and an experiment with human subjects. *Evolution and Human Behavior*, 23, 373–393.
- Kandler, A., & Laland, K. N. (2009). An investigation of the relationship between innovation and cultural diversity. *Theoretical Population Biology*, 76(1), 59–67. doi:10.1016/j.tpb.2009.04.004.
- Kendal, J., Giraldeau, L. A., & Laland, K. (2009). The evolution of social learning rules: payoff-biased and frequency-dependent biased transmission. *Journal of Theoretical Biology*, 260(2), 210–219.
- Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, 32(1), 4–14.
- Laland, K. N., Atton, N., & Webster, M. M. (2011). From fish to fashion: experimental and theoretical insights into the evolution of culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 958–968.
- Lipo, C. P., O'Brien, M. J., Collard, M., & Shennan, S. (Eds.). (2006). *Mapping our ancestors*. Piscataway: AldineTransaction.
- McElreath, R., & Strimling, P. (2008). When natural selection favors imitation of parents. *Current Anthropology*, 49(2), 307–316. doi:10.1086/524364.
- McElreath, R., Boyd, R., & Richerson, P. J. (2003). Shared norms and the evolution of ethnic markers. *Current Anthropology*, 44(1), 122–129.
- McElreath, R., Bell, A. V., Efferson, C., Lubell, M., Richerson, P. J., & Waring, T. (2008). Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1509), 3515–3528. doi:10.1098/rstb.2008.0131.
- Mesoudi, A. (2009). How cultural evolutionary theory can inform social psychology and vice versa. *Psychological Review*, 116(4), 929–952.
- Nakahashi, W. (2007a). The evolution of conformist transmission in social learning when the environment changes periodically. *Theoretical Population Biology*, 72(1), 52–66. doi:10.1016/j.tpb.2007.03.003.
- Nakahashi, W. (2007b). *The evolution of conformist transmission in social learning when the environment fluctuates*. PhD thesis, University of Tokyo.
- Panchanathan, K., & Boyd, R. (2004). Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature*, 432, 499–502.
- Rendell, L., Hoppitt, W., & Kendall, J. (2007). Is all learning innovation? *The Behavioral and Brain Sciences*, 30(4), 421–422.
- Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, 15(2), 68–76.
- Schlag, K. H. (1998). Why imitate, and if so, how? A boundedly rational approach to multi-armed bandits. *Journal of Economic Theory*, 78, 130–156.
- Schlag, K. H. (1999). Which one should I imitate? *Journal of Mathematical Economics*, 31(4), 493–527.
- Stenberg, G. (2009). Selectivity in infant social referencing. *Infancy*, 14(4), 457–473.
- Wakano, J. Y., & Aoki, K. (2006). A mixed strategy model for the emergence and intensification of social learning in a periodically changing natural environment. *Theoretical Population Biology*, 70(4), 486–497. doi:10.1016/j.tpb.2006.04.003.
- Wakano, J. Y., & Aoki, K. (2007). Do social learning and conformist bias coevolve? Henrich and Boyd revisited. *Theoretical Population Biology*, 72(4), 504–512. doi:10.1016/j.tpb.2007.04.003.
- Wakano, J. Y., Aoki, K., & Feldman, M. W. (2004). Evolution of social learning: a mathematical analysis. *Theoretical Population Biology*, 66(3), 249–258. doi:10.1016/j.tpb.2004.06.005.
- Whitehead, H. (2007). Learning, climate and the evolution of cultural capacity. *Journal of Theoretical Biology*, 245(2), 341–350. doi:10.1016/j.jtbi.2006.10.001.
- Whitehead, H., & Richerson, P. J. (2009). The evolution of conformist social learning can cause population collapse in realistically variable environments. *Evolution and Human Behavior*, 30(4), 261–273. doi:10.1016/j.evolhumbehav.2009.02.003.

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