

Prestige as a Driving Force in Cultural Transmission

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Abstract

Copying role-models can be an efficient method for acquiring knowledge. A common bias when choosing a role-model to copy is success bias: copying whoever appears more successful. This bias depends on the performance of the role-model alone, with no other factors. We propose an additional bias that may be prevalent in cultural transmission: influence bias, in which role-model choice is affected by the number of individuals that have already copied each potential role-model. We combine success and influence bias together to a “prestige bias” and analyze its effects on cultural-evolutionary dynamics using mathematical analysis and stochastic simulations. We find analytic approximations to our stochastic model, facilitating further mathematical analysis and reducing the computational complexity of simulations. We validate these approximations using simulations, and demonstrate their robustness to model assumptions. We also find approximations to the fixation probability and the fixation time of an invading advantageous cultural trait, in both constant and changing environments, which resemble Kimura’s approximations for population-genetic models. These approximations show that success bias effectively plays the part of natural selection, whereas influence bias effectively reduces the population size. It also accelerates the evolutionary dynamics, as can be expected in a *rich-getting-richer* process. Our model may provide a good description of cultural transmission, especially in human societies where social media is popular. Further work is needed to test if this model could predict various phenomena in cultural evolution when extended with the effects of selection and innovation.

Introduction

28 **Cultural transmission.** In cultural transmission, individuals transmit cultural traits (i.e., behavior, beliefs, norms) to one another, typically via learning and demonstrating (Cavalli-Sforza and Feldman, 30 1981). Examples for cultural traits in humans are behavioral patterns, such as personalities and habits, transmitted via both verbally and by observations (O'Brien et al., 2010). Although cultural 32 transmission is most common in humans, it is also observed in other animals such as chimpanzees (Horner et al., 2010; Kendal et al., 2015), dolphins and whales (Whitehead, 2017). In elephants, 34 McComb et al. (2001) showed that once a matriarch is removed from the group, the group's survival instincts are inferior and that "the possession of enhanced discriminatory abilities by the oldest 36 individual [matriarch] in a group can influence the social knowledge of the group as a whole." By playing audio recordings of African elephants, they showed that groups with a matriarch recognize 38 and react better to hostile or friendly calls than groups without a matriarch. Battesti et al. (2012) showed that choice of oviposition site in fruit flies is culturally transmitted: inexperienced flies that 40 spent some time with experienced flies chose the same type of oviposition site even without directly observing this behavior. How the information is transmitted is still an open question, but it has been 42 suggested that flies may use olfactory cues like other animals, such as rodents and bees.

Direction of transmission. Similar to genetic transmission, culturally transmitted traits can be trans- 44 mitted from parents to offspring, and their effects of can be physiological rather than behavioral. For example, parents can "teach" their children to be strong or tall, within some biological limits, by 46 instructing them to maintain a specific diet and engage in physical activity. Contrary to genetic transmission, cultural transmission can be non-vertical, that is, traits may be transmitted via social learning 48 from non-parental individuals, and even unrelated individuals such as teachers, leaders, media, or any stranger that interacts with the learning individual. Thus, cultural transmission may combine 50 vertical transmission, where parents transmit to their offspring; oblique transmission, where adults transmit traits to unrelated offspring; and horizontal transmission, where peers from the same age 52 cohort transmit to one another. Vertical transmission is also possible in the opposite direction: parents may copy traits from their offspring (Cavalli-Sforza and Feldman, 1981; Creanza et al., 2017).

54 **Transmission biases.** In social learning, transmission biases cause a trait to have a disproportionate probability to be transmitted compared to its frequency in the population. Although more common in 56 cultural transmission, transmission biases do occur in genetic transmission. For example, *wtf* genes in yeast bias their transmission to the gamete by secreting a long life-expectancy poison together with a 58 short life-expectancy antidote, so that a gamete without the gene will perish because the poison will outlive the antidote (Eickbush et al., 2019). Importantly, even when a trait is disfavored by natural 60 selection, it may still spread in a population due to transmission biases that are strong enough to overcome selection (Boyd and Richerson, 1988, Ch. 8 pg. 279). Cohen et al. (2021) show that 62 cooperative behavior can evolve in an individual due to horizontal transmission bias even when there is no benefit to it, or when it benefits its competitors.

64 **Success bias.** Rendell et al. (2010) have conducted a tournament between learning strategies. Each
strategy defines when individuals observe and copy from others, and when they engage in individual
66 learning, in which an individual learns a cultural trait on his own. The best strategies had a high
frequency of social learning relative to individual learning, even when the transmission error was
68 almost 50%. From these results we understand that all the winning strategies were mostly based on
success biased social learning, meaning it contributed more to the general success of the population
70 than individual learning. However, all winning strategies included individual learning to some degree,
implying that success-biased learning alone isn't the best way to advance, even when success is
72 measured accurately.

Evaluating success. Boyd and Richerson (1988, Ch. 5) suggest that the evaluation of success can
74 be divided into three groups: *direct bias*, *indirect bias* and *frequency-dependent bias*. A direct bias
occurs when a variation of a trait is more attractive than others, and is evaluated by *directly* testing the
76 variation of the trait. For example, an individual observing a Ping-Pong match can attempt both of the
observed paddle grips to determine which grip is better. An indirect bias occurs when an individual
78 uses the value of one trait to determine the attractiveness of another, so it *indirectly* evaluates the
attractiveness of the role-model. For example, an observer may copy the paddle grip of the Ping-Pong
80 player who scored more points in the match, thus indirectly evaluating the grip by the points scored. A
frequency-dependent bias occurs when an individual has a probability to copy a variant of the trait that
82 higher or lower than trait's frequency among demonstrators. For example, when an individual is 80%
likely to copy the common paddle grip even when only 60% of the population is using it, it is said to be
84 frequency-biased, or in this case, conformist. Frequency bias could be negative, i.e., non-conformist
bias. Conformity and non-conformity are well-known biases in cultural transmission (Molleman et al.,
86 2013), and its effect on cultural evolution have been studied with both models (Denton et al., 2020a,b)
and experiments (Aljadeff et al., 2020).

88 **Prestige.** Prestige means having a good reputation or high esteem, therefore does not directly signify
success (although it may imply it), making it an indirect bias. Both Boyd and Richerson (1988, Ch.
90 8) and Fogarty et al. (2017) suggest that prestige biases are probably more common in humans than
success biases. Boyd and Richerson (1988, Ch. 8) add that maladaptive traits may spread widely
92 in a population if indirect biases are strong enough. They suggest that such biases could lead to a
runaway process caused by a cultural equivalent of sexual selection (Andersson, 1994). On the other
94 hand, Henrich and Broesch (2011) suggest that prestige biases, over generations, can lead to cultural
adaptations, and that although prestige can lead to maladaptive traits spreading in the population, it
96 can also accelerate the spread of adaptive traits. Prestige is often mentioned in the cultural-evolution
literature, but seldom modeled.

98 **Influence bias.** Today, social media provides an easy way to estimate the social and cultural influence
individuals have over others, and therefore may have an effect on decision making. Online social
100 networks such as *Facebook* or *Instagram* are known to affect the influence of individuals (Anagnos-
topoulos et al., 2008; Peng et al., 2018; Diga and Kelleher, 2009), and specific marketing practices
102 were invented to capitalize on this effect (Lee et al., 2012). Here, we model such influence as an

indirect bias in cultural transmission, in which the choice of a role-model depends on the choices
 104 made by other individuals that have already chosen a role-model. In addition to using influence bias as
 an easy way to approximate role-models worth, it can also be a used to approximate it better than the
 106 copier's own estimation. This bias can save the copier costs: time, effort etc, and it can also improve
 its choice of role-model.

108 This bias depends on the state of a role-model rather than on its trait, in contrast to frequency biases
 such as conformity (Hamilton, 1964), which depend on the frequency of a trait in the population or in
 110 a sample of role-models. We define a model of cultural transmission with prestige bias that combines
 both success and influence biases, provide analytic approximations for this model, and analyze its
 112 dynamics.

Models and Methods

114 We begin with a continuous trait model with indirect bias suggested by Boyd and Richerson (1988),
 develop an extension with influence bias, and then develop a model with a dichotomous trait. We
 116 implemented our stochastic models and approximations, performed statistical analyses, and produced
 figures using Python (Van Rossum et al., 2007) with NumPy (Van Der Walt et al., 2011) and Matplotlib
 118 (Hunter, 2007).

Source code is available at <https://github.com/yoavram-lab/PrestigeBias>.

120 Continuous trait

We follow the model of Boyd and Richerson (1988), assuming only oblique transmission of the trait
 122 and omitting the indirect trait in order to reduce model complexity. We consider a population of N
 individuals, described by a single trait with a continuous value. Each generation, N naive individuals,
 124 or copiers, choose an individual from the previous generation, or role-models, from which they will
 copy their trait. Similar to a Wright-Fisher model, we assume non-overlapping generations such that
 126 the entire population is replaced in each generation. The population at time t can be described by
 $\mathbf{A}(t) = (A_1(t), \dots, A_N(t))$ where $A_i(t)$ is trait value of individual i at time t . We assume the initial
 128 population is drawn from a standard normal distribution, $\mathbf{A}(0) \sim N(0, 1)$. Cultural transmission is
 modeled by a function F such that

$$130 \quad A_i(t+1) = F_i(\mathbf{A}(t)) . \quad (1)$$

Success bias. Boyd and Richerson (1988, Ch. 8, p. 247-249) describe a blended transmission algo-
 132 rithm by defining F as a weighted average of the traits of all role-models,

$$F_i(\mathbf{A}) = \sum_{j=1}^N G_{i,j} \cdot A_{i,j} , \quad (2)$$

134 where $G_{i,j}$ is the success bias of role-model j in the eyes of copier i ,

$$G_{i,j} = \frac{\beta(A_{i,j})}{\sum_{k=1}^N \beta(A_{i,k})}, \quad (3)$$

136 $A_{i,j}$ is the absolute trait value copier i estimates for role-model j with some error $e_i \sim N(0, \eta^2)$,

$$A_{i,j} = A_j + e_i, \quad (4)$$

138 and $\beta(\cdot)$ is the bias function that quantifies the success bias of a role-model,

$$\beta(A_{i,j}) = b \cdot \exp\left(-\frac{(A_{i,j} - \hat{A})^2}{2J}\right), \quad (5)$$

140 with \hat{A} as the arbitrary optimal trait value, and J and b as parameters that control the bias strength.
Therefore, $G_{i,j}$ is a relative success score that copier i assigns to role-model j , equivalent to relative
142 fitness in evolutionary-genetic transmission models.

Boyd and Richerson (1988) note that the deterministic blended transmission algorithm they use has
144 alternatives. We thus develop a similar stochastic model with transmission from a single random
role-model. Instead of eq. (2), we define the transmission function F as a random variable with its
146 distribution given by

$$\Pr(F_i(\mathbf{A}) = A_j) = G_{i,j}, \quad (6)$$

148 such that $G_{i,j}$ gives the probability of copier i to choose to copy the trait of role-model j .

Influence bias. Here we introduce a new element to the model. We assume that in each generation,
150 copiers choose their role-models one by one. We denote $K_{i,j}$ as the number of copiers that chose
role-model j after copier i chose a role-model. Thus, i out of N copiers already chose a role-model,
152 $\sum_{j=1}^N K_{i,j} = i$, and there are $N - i$ copiers that have yet to choose a role-model. The stochastic process
of role-model choice,

$$\{\mathbf{K}_i = (K_{i,1}, \dots, K_{i,N})\}_{i=1}^N, \quad (7)$$

is described by the recurrence equation

$$K_{i,j} = K_{i-1,j} + S_{i,j}, \quad i, j = 1, 2, \dots, N, \quad (8)$$

where $S_{i,j} = 1$ if the i -th copier chose role-model j and 0 otherwise, and the initial state is $K_{0,j} =$
158 0.

Following eq. (6), the probability that the i -th copier chose role-model j is given by the prestige of
160 role-model j in the eyes of copier i ,

$$\Pr(S_{i,j} = 1 \mid S_{1,j}, S_{2,j}, \dots, S_{i-1,j}) = G_{i,j}. \quad (9)$$

162 The prestige $G_{i,j}$ of role-model j in the eyes of copier i is determined by the estimated biased trait
 value $\beta(A_{i,j})$ and the number of copiers that chose role-model j before copier i , $K_{i-1,j}$, replacing
 164 eq. (3) of Boyd and Richerson (1988) with

$$G_{i,j} = \frac{\alpha_{ij} \cdot \beta(A_{i,j}) + (1 - \alpha_{ij}) \cdot K_{i-1,j}}{W_i}. \quad (10)$$

166 Here, the bias weight α_{ij} is a characteristic of the interaction of role-model j with copier i , that
 determines the relative significance of success and influence within the role-model's overall prestige,
 168 in the eyes of the copier. The trait of role-model j estimated by copier i , $A_{i,j}$, remains as in eq. (4),
 and W_i is a normalizing factor that sums the numerator over all role-models ($1 \leq j \leq N$) to ensure
 170 $\sum_{j=1}^N G_{i,j} = 1$.

Dichotomous trait

172 To allow for mathematical analysis of the model, we introduce a simplified version where the trait
 only has two phenotypes: the optimal phenotype \hat{A} and the sub-optimal phenotype A . All role-models
 174 with the same phenotype will contribute to the probability of that phenotype to be transmitted, and
 thus influence is determined by the number of copiers that have already chosen a role-model with
 176 either phenotype. In addition, we assume homogeneous α for simplicity and for easier mathematical
 analysis. Therefore, the probability of the i -th copier to copy phenotype A is

$$G_{i,A} = \frac{(N - X)\alpha'\beta(A) + K_{i,A}}{i - 1 + (N - X)\alpha'\beta(A) + X\alpha'\beta(\hat{A})} = \frac{(N - X)\alpha'\beta(A) + K_{i,A}}{i - 1 + (N - X)\alpha'\beta(A) + \alpha'X} \quad (11)$$

where X is the number of role-models with trait \hat{A} and $K_{i,A}$ is the number of copiers that already chose
 180 A when copier i chooses a role-model and α' is the odd ratio of the bias weight $\alpha' = \frac{\alpha}{1-\alpha}$.

We prove this equation later, based on the proof of the Dirichlet-Multinomial approximation.

182 Initially, we assume the population has a single individual with phenotype \hat{A} and $N - 1$ individuals
 with phenotype A . The rest of the details follow the continuous trait model.

184 Results

Approximations

186 Our model is defined by two nested stochastic processes. Change over multiple generations is described
 by the phenotype distribution at each generation, $\{\mathbf{A}(t)\}_t$. The transition from one generation to the
 188 next is described by the number of copiers each role-model has after i copiers have chosen a role-
 model, $\{\mathbf{K}_i\}_{i=1}^N$. We emphasize that the models are nested: $\mathbf{A}(t + 1)$ can be computed from $\mathbf{A}(t)$
 190 by evaluating \mathbf{K}_N . However, the former requires iterating over eqs. (8) and (9). Thus, we sought to
 find an equivalent stochastic process that has the same joint distribution as \mathbf{K}_N . We found two such
 192 approximations, summarized here and explained in detail below. In both we assume either α_j is a

trait of role-model j only (contrary to α_{ij} that included the relation with copier i), or a completely
 194 homogeneous α .

1. The number of copiers of a specific role-model at each step, $K_{i,j}$, follows the *generalized*
 196 *binomial distribution* (Drezner and Farnum, 1993) and therefore,

(a) the expected number of copiers of role-model j equals its prestige in the eyes of the first
 198 copier, multiplied by the total number of copiers, that is, $E[K_{N,j}] = N \cdot G_{1,j}$ if trait
 estimation error is uniform for all copiers ($e = e_i$ for $i = 1, \dots, N$).

(b) the expected number of copiers of each role-model equals its relative biased trait value,
 similar to the role of relative fitness in population-genetic models, that is, $E[K_{N,j}] =$
 202 $\beta(A_j + e)/\bar{\beta}$ if the bias weight is uniform for all role-models ($\alpha = \alpha_j$ for $j = 1, \dots, N$),
 where $\bar{\beta} = 1/N \sum_{j=1}^N \beta(A_j + e)$ is the population mean estimated trait value.

2. The role-model choice process, $\{\mathbf{K}_i\}_{i=1}^N$, is equivalent to a *Pólya urn* model if trait estimation
 error is uniform for all copiers ($e = e_i$ for all $i = 1, \dots, N$), meaning there's no meaning for the
 206 order of copiers. Therefore, the number of copiers of all role-models, $\mathbf{K}_i = (K_{i,1}, \dots, K_{i,N})$,
 follows a Dirichlet-Multinomial distribution, $\mathbf{K}_i \sim DM(N, \mathbf{G}_1)$, where $\mathbf{G}_1 = (G_{1,1}, \dots, G_{1,N})$
 208 is the prestige vector of all role-models in the "eyes" of the first copier. Note that here $G_{i,j}$ is
 only a function of the trait values A_j and the bias weights α_j , as the estimation error is uniform,
 210 meaning all copiers are identical.

Generalized binomial distribution

212 The generalized binomial distribution (GBD) emerges from a series of dependent Bernoulli trials (in
 contrast to the standard binomial distribution in which trials are independent) and is parameterized by
 214 $GBD(n, p, \theta)$ where n is the number of trials, p is the probability of success of the first trial, and θ is
 the correlation between trials ($\theta = 0$ gives the standard binomial distribution).

216

Result 1 (GBD approximation). *The number of copiers of role-model j after i copiers have chosen a*
 218 *role-model follows the GBD, $K_{i,j} \sim GBD(i, \alpha_i \cdot \beta(A_j + e))$ if $e_i = e$ for all role-models $i = 1, \dots, N$.*

Proof. We denote $Q_j(k, i) = P(K_{i,j} = k \mid K_{i-1,j})$ as the probability that exactly k out of i copiers
 220 choose role-model j given $K_{i-1,j}$ our of $i-1$ copiers chose role-model j . Using conditional probability
 and eq. (8),

$$222 \quad Q_j(k, i) = P_j(S_{i,j} = 1 \mid k-1, i-1) \cdot Q_j(k-1, i-1) + P_j(S_{i,j} = 0 \mid k, i-1) \cdot Q_j(k, i-1), \quad (12)$$

where $S_{i,j} = 1$ when the i -th copier chooses role-model j . Equation (12) is equivalent to eq. (2.1) by
 224 Drezner and Farnum (1993), which completes the proof.

Corollary 1. $E[K_{N,j}] = N \cdot G_{1,j}$.

226 *Proof.* Drezner and Farnum (1993, eq. (2.3)) show that $E[k] = N \cdot Q_j(1, 1)$ (modified from their
notation). $Q_j(1, 1)$ is the initial probability to choose role-model j , before any role-model choices are
228 made. $Q_j(1, 1) = G_{1,j}$ by definition, which completes the proof.

Corollary 2. $E[K_{Nj}] = \alpha_j \cdot \beta(A_j + e) / \overline{\alpha \cdot \beta(A + e)}$, where the averaging in the denominator is over
230 the role-models index, j .

Proof. The initial prestige of role-model j based on eq. (10) is

$$232 \quad G_{1,j} = \frac{\alpha_j \cdot \beta(A_j + e)}{\sum_{m=1}^N \alpha_m \cdot \beta(A_m + e)} . \quad (13)$$

The denominator of eq. (13) can also be formulated as:

$$234 \quad \sum_{m=1}^N \alpha_m \beta(A_m + e) = N \cdot \overline{\alpha \cdot \beta(A + e)} , \quad (14)$$

where $\overline{\alpha \beta(A + e)}$ is the mean value of $\alpha_m \cdot \beta(A_m + e)$ for all m . Using eq. (14) and **Corollary 1** we
236 get,

$$E[K_{Nj}] = \alpha_j \cdot \beta(A_j + e) / \overline{\alpha \cdot \beta(A + e)} , \quad (15)$$

238 completing the proof.

The special case where the bias weight is uniform for all role-models ($\alpha = \alpha_j$ for $j = 1, \dots, N$) is
240 interesting, because we can evaluate the expected number of copiers using a linear equation

$$E[K_{Nj}] = N \cdot \frac{\alpha \cdot \beta(A_j + e)}{\sum_{m=1}^N \alpha \cdot \beta(A_m + e)} = \beta(A_j + e) / \overline{\beta(A + e)} , \quad (16)$$

242 where the only variable is $A_j + e$, because $\overline{\beta(A + e)}$ is the mean of the distribution we draw the trait
values from, modified by some constant parameters of β . We can then denote $L = 1 / \overline{\beta(A + e)}$ and
244 write

$$E[K_{Nj}] = L \cdot \beta(A_j + e) . \quad (17)$$

246 **Numerical validation.** To validate our results we ran 1,000 simulations of the full model, and
compared the results with corollary 2. We compare the distribution of number of copiers by plotting
248 the histograms of both our simulations results and the expected values based on corollary 2. We used
the average of the 1,000 simulations to eliminate drift errors, as can be seen in fig. 1.

250 Although basic, fig. 1 shows good fit of the GBD approximation. This validation is initial, and the
more extensive validations we do on the Dirichlet-Multinomial approximation, because it is what we
252 will use in our analysts.

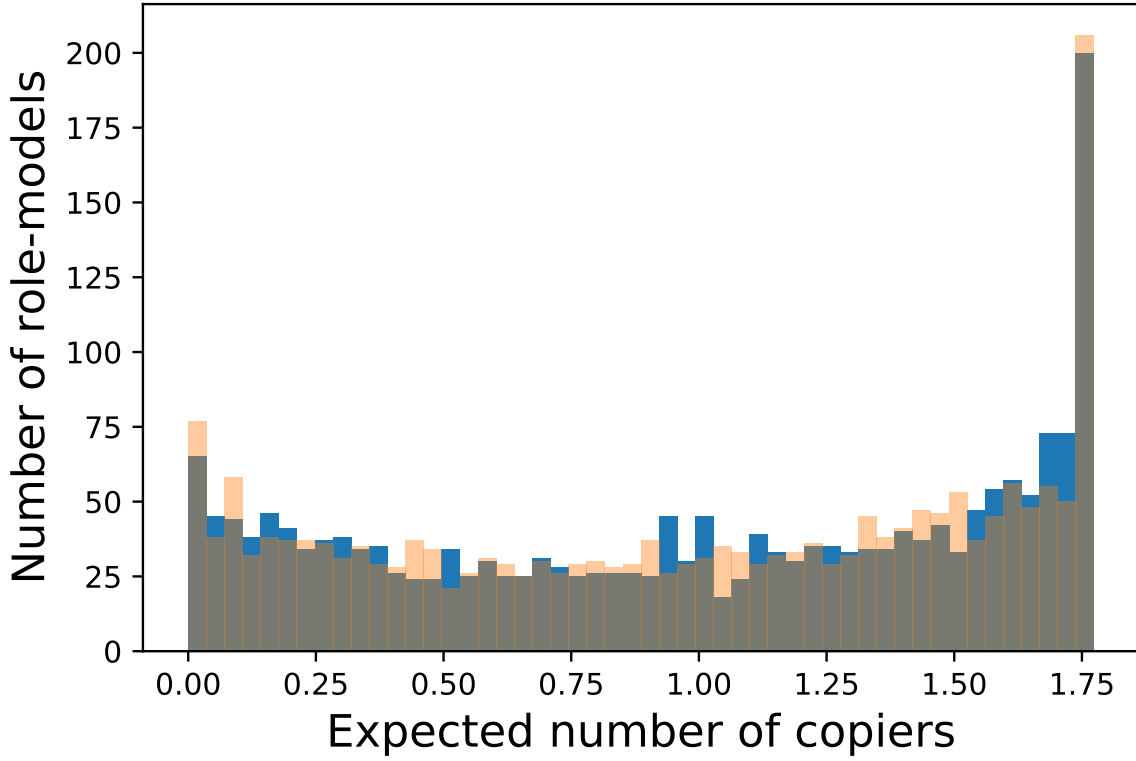


Figure 1: Numerical validation for the GBD approximation. The approximation (orange) fits simulation results (blue) well when using 1,000 simulations for both models. Here, population size, $N = 2,000$; bias weight, $\alpha = 0.1$; idea phenotype value, $\hat{A} = 1$; role-model traits $\mathbf{A} \sim N(0, 1)$; success bias value, $\beta(A) = 0.956$.

Dirichlet-Multinomial distribution

Pólya urn model. This stochastic process consists of N draws from an urn with an initial amount of colored balls of M colors. When a ball is drawn, it is then placed back in the urn together with an additional new ball of the same color. Let $\mathbf{U}_i = \{u_{i,1}, u_{i,2}, \dots, u_{i,M}\}$ where $u_{i,j}$ is the number of balls of the j -th color in the urn after i draws. Let $S_{i,j} = 1$ when drawing a j -colored ball on the i -th draw, and 0 otherwise. The probability that $S_{i,j} = 1$ given \mathbf{U}_{i-1} is

$$P(S_{i,j} = 1 \mid \mathbf{U}_{i-1}) = \frac{u_{i-1,j}}{\sum_{m=1}^M u_{i-1,m}} = \frac{o_j + w_{i-1,j}}{\sum_{m=1}^M o_m + w_{i-1,m}} = \frac{o_j + w_{i-1,j}}{i - 1 + \sum_{m=1}^M o_m}, \quad (18)$$

where o_j is the initial number of balls of the color j in the urn, and $w_{i,j}$ is the cumulative number of new balls that were added to the urn after i draws of the color j .

262

Result 2 (Pólya urn model). The role-model choice process, $\{\mathbf{K}_i\}_{i=1}^N$, is equivalent to a Pólya urn model if both trait estimation error and bias weight are uniform in the population, $e = e_j$ and $\alpha = \alpha_j$ for all $j = 1, \dots, N$.

266 *Proof.* Denote $\alpha' = \frac{\alpha}{1-\alpha}$ as the bias weight ratio, and $A'_j = A_j + e$. From eq. (10) and because $\sum_{j=1}^N K_{i,j} = i$, we have

$$268 \quad G_{i,j} = \frac{\alpha' \beta(A'_j) + K_{i-1,j}}{\sum_{m=1}^N \alpha' \beta(A'_m) + K_{i-1,m}} = \frac{\alpha' \beta(A'_j) + K_{i-1,j}}{i - 1 + \sum_{m=1}^N \alpha' \beta(A'_m)}. \quad (19)$$

Substituting $M = N$, $\alpha_j = \alpha' \beta(A'_j)$, and $w_{i,j} = K_{i,j}$ in eq. (18) gives eq. (19), thus completing the
270 proof.

Frigyik et al. (2010, section 2) prove that the proportion of different colored balls in a *Pólya urn*
272 *model* converges to the Dirichlet distribution as the number of draws approaches infinity, based on
the *Martingale Convergence Theorem* (Durrett, 1999). We therefore have an approximation for the
274 relative prestige each role-model has when evaluated by copiers. Thus, choosing the role-models for
all copiers is equivalent to drawing from a Multinomial distribution where the parameters are the
276 modified weights from a Dirichlet distribution and we have the following corollary.

278 **Corollary 3.** *The number of copiers of each role-model follows a Dirichlet-Multinomial distribution, $\mathbf{K}_i \sim DM(N, \mathbf{G}_1)$, under the conditions of Result 2.*

280 **Numerical validation.** To validate our analytical result (corollary 3) and test its sensitivity to the
assumptions ($e_i = e$ and $\alpha_i = \alpha$ for $i = 1, \dots, N$) we compare it to results of stochastic simulations of
282 the full model. First, we computed an observed distribution of the number of copiers from the average
empirical distribution of multiple simulations. We then compared this observed distribution with the
284 expected theoretical DM distribution as can be seen in fig. 2 (a). The difference in distributions was
not perceived when plotting both distributions on the same figure, so we used the difference instead.
286 The maximum difference is 0.5 role-models, which indicate a very good fit. In addition, we tested
the likelihood of the observed data to be drawn from the DM distribution, against a shuffle of the
288 parameters vector of the DM distribution itself, as seen in fig. 2 (b). We see that the negative log
likelihood of the observed data is much higher than any other shuffled version of the parameters vector,
290 supporting our approximation more.

Next, we examined the fixation probability and fixation time of an advantageous phenotype \hat{A} when
292 invading a population of phenotype A and compared results from the full model and the DM approx-
imation. We find that the number of simulations needed to sufficiently approximate our model with
294 the DM approximation is roughly 1,000 (Figure 3). Next, we examined the robustness of the DM
approximation to relaxing the approximation assumptions. First, we relaxed our assumption of no
296 estimation error e . Estimation error in the original model was drawn from a normal distribution, and
added to the trait value before evaluation of the bias ($A_{ij} = A_j + e_i$). When estimation error is applied,
298 we sample J_i for each copier i from a normal distribution with varying scale (variance). Even when
the standard deviation is 0.1, the fixation probability and time is similar (fig. 4). We also relaxed our
300 assumption of a uniform bias weight α (i.e., $\alpha_i = \alpha$). We allowed α to vary in the population, drawing

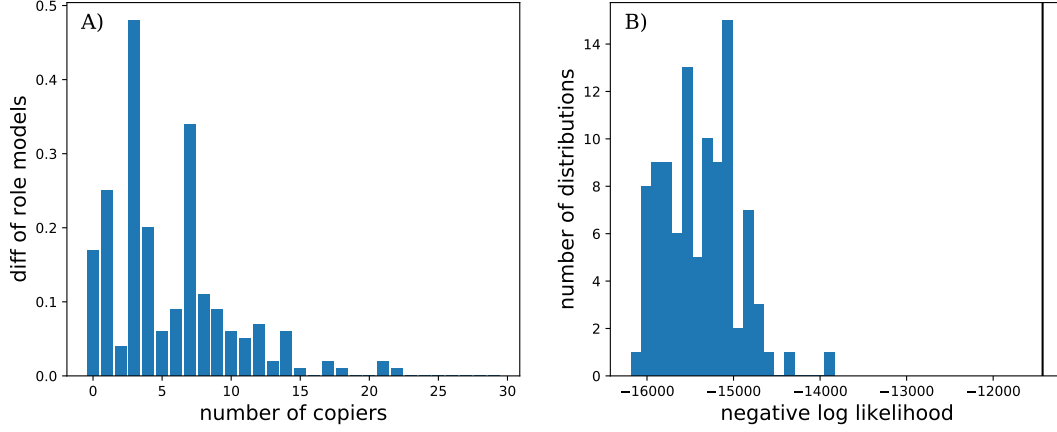


Figure 2: Goodness of fit of Dirichlet-Multinomial approximation to the model. The difference between the DM approximation distribution to observed model distribution (a) is very small, with the highest difference at 0.5 role-models. The optimal negative log likelihood (b) is given when using the DM approximation (black vertical line), and is much better when compared to a shuffled vector of the DM distribution (blue bars). Here, population size, $N = 100$; number of distributions averaged, $m = 100$; phenotype values, $\hat{A} = 1$, $A \sim N(0, 1)$; homogeneous success bias weight, $\alpha = 0.5$.

α_j for each role-model j from a normal distribution such that $\alpha_j \sim N(0.5, x)$ where $x \in [10^{-7}, 10^{-1}]$.

302 We found again that results of the DM approximation are similar to those from stochastic simulations of the full model (fig. 5).

304 Fixation probability and time

After finding that the DM distribution is a good approximation of the (within-generation) role-model choice process, we turn our attention to the (between-generation) evolutionary dynamics. We focus on the fixation probability and fixation time of an advantageous phenotype, using a diffusion-equation approximation approach, similar to analyses of population-genetic models (Kimura, 1962; Kimura and Ohta, 1969; Otto and Whitlock, 2006). We are mainly interested in the effect of the bias weight, α , which determines the relative effect of success and influence on prestige bias, given by eq. (10). For simplicity, we do not include role-model estimation error in this analysis, i.e $e_i = 0$ for every copier i . As shown above, transmission in our model is approximately DM distributed (corollary 3 and eq. (19)).

314 We start by finding the expectation and variance of the change in frequency from one generation to the next, which are the drift and diffusion terms of the diffusion equation.

316

Result 3 (Drift and diffusion terms in a constant environment). *Let x and x' be the frequency of type \hat{A} in a population with N individuals in the current and next generation, and β is the success coefficient of phenotype A , $\beta = \beta(A) < \beta(\hat{A}) = 1$. Then,*

320
$$E[x' - x] \approx x(1 - x)(1 - \beta), \quad V(x' - x) \approx x(1 - x) \left(\frac{1}{\alpha N + (1 - \alpha)} \right). \quad (20)$$

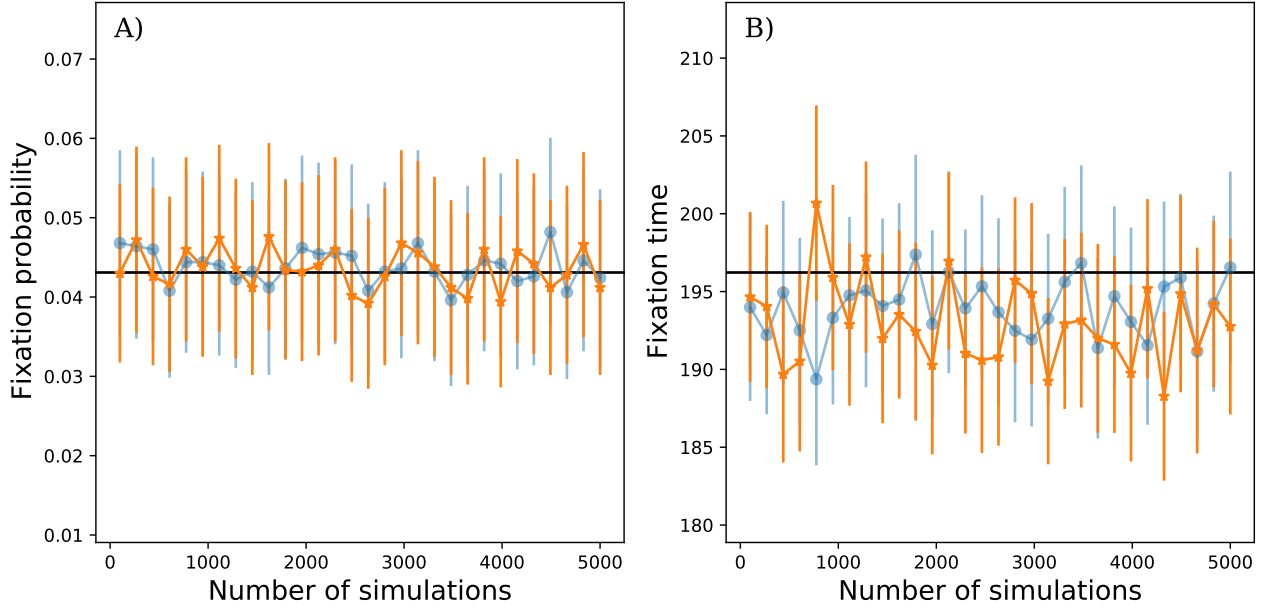


Figure 3: Minimum number of simulations required to get a good approximation. The approximation (orange) fits simulation results (blue) well when using 1,000 simulations for both models. The approximated value (black) is given by equation eq. (32). Markers for average value across simulations, error bars for 95% confidence interval. Here, population size, $N = 1000$; bias weight, $\alpha = 0.5$; phenotype values, $\hat{A} = 1$, $A = 0.7$; success bias value, $\beta(A) = 0.956$.

Proof. Let X be the number of individuals of type \hat{A} such that $x = X/N$. X' is the number of individuals with \hat{A} in the next generation. The expected number of individuals is (due to the DM approximation),

$$E[X'] = N \frac{\alpha_1}{\alpha_1 + \alpha_2}, \quad (21)$$

where $\alpha_1 = \alpha'X$ and $\alpha_2 = \alpha'(N - X)\beta$, from eq. (11). To use frequencies instead of counts,

$E[x'] = E[X'/N] = \frac{1}{N}E[X']$. Putting it together,

$$\begin{aligned} E[x'] &= \frac{1}{N} N \frac{\alpha'xN}{\alpha'xN + \alpha'N(1-x)\beta} = \frac{x}{x + (1-x)\beta} \\ &= \frac{x}{x + (1-x) - (1-x) + (1-x)\beta} = x \frac{1}{1 - (1-x)(1-\beta)} \\ &= x(1 + (1-x)(1-\beta) + o(\beta)) = x + x(1-x)(1-\beta) + o(\beta), \end{aligned} \quad (22)$$

following Durrett (2008, p. 253, ch 7.2) and because $1/(1-y) = 1 + y + y^2 + \dots$

By definition, x is constant, so $E[x] = x$. We therefore have

$$E[x' - x] = E[x'] - E[x] = x(1-x)(1-\beta) + o(1-\beta), \quad (23)$$

which gives us the drift term of the diffusion equation.

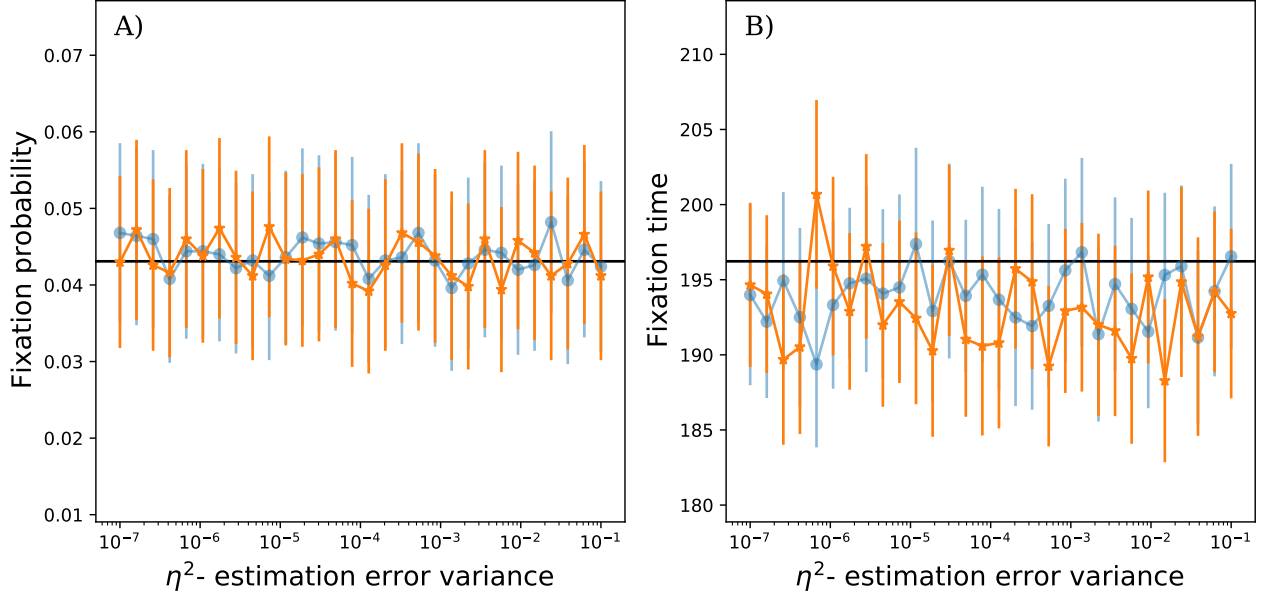


Figure 4: Robustness of DM approximations to inclusion of estimation error. Both the DM approximation (orange) and Kimura's equation (black line) fit the stochastic simulations (blue) well even with a high estimation error rate. Markers for average across simulations, error bars for 95% confidence intervals. 5,000 simulations per data point; population size, $N = 1000$; bias weight, $\alpha = 0.1$; phenotype values, $\hat{A} = 1, A = 0.7$; bias strength parameter $J \sim N(1, x^2)$ where $x \in [10^{-7}, 10^{-1}]$.

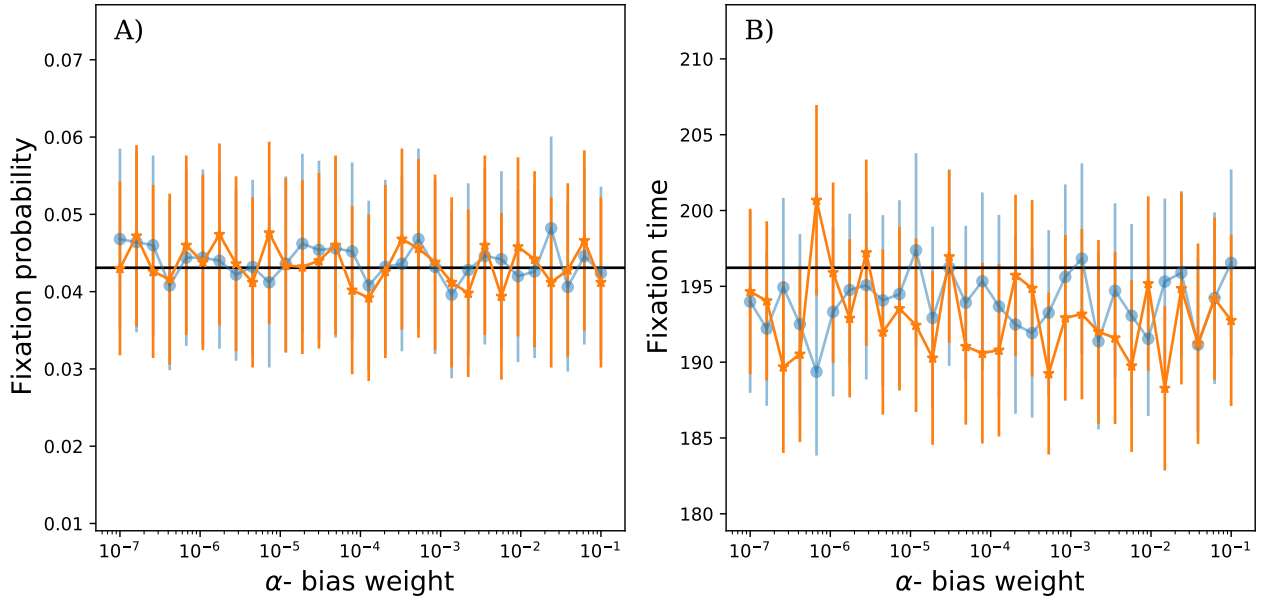


Figure 5: Robustness of DM approximations to variation in the bias weight α . Both the DM approximation (orange) and Kimura's equation (black line) fit the stochastic simulations (blue) well even with a high variation in success bias weight. Markers for average across 5,000 simulations, error bars are 95% confidence intervals. Here, population size, $N = 1000$; success bias weight normally distributed, $\alpha \sim N(0.5, x^2)$; phenotype values $\hat{A} = 1, A = 0.7$; success bias value, $\beta(A) = 0.956$.

332 Using the variance of the DM distribution,

$$V(X') = N \frac{\alpha_1}{\alpha_1 + \alpha_2} \left(1 - \frac{\alpha_1}{\alpha_1 + \alpha_2}\right) \left(\frac{N + \alpha_1 + \alpha_2}{1 + \alpha_1 + \alpha_2}\right). \quad (24)$$

334 Again, we want to use frequencies so we have $V(X'/N) = \frac{1}{N^2} V(x')$. Putting it together with our model notations,

$$336 \quad V(x') = \frac{1}{N^2} N \frac{x}{x + (1-x)\beta} \left(1 - \frac{x}{x + (1-x)\beta}\right) \left(\frac{N + \alpha'xN + \alpha'N(1-x)\beta}{1 + \alpha'xN + \alpha'N(1-x)\beta}\right). \quad (25)$$

Following Durrett (2008, ch 7.2), we assume $\beta \approx 1$, such that

$$338 \quad \frac{x}{x + (1-x)\beta} \approx x \quad (26)$$

and for the entire variance expression we get

$$340 \quad V(x') \approx \frac{1}{N} x(1-x) \left(\frac{N + \alpha'xN + \alpha'N - \alpha'xN}{1 + \alpha'xN + \alpha'N - \alpha'xN}\right) = x(1-x) \left(\frac{1 + \alpha'}{1 + \alpha'N}\right). \quad (27)$$

Now because x is a constant, $V(x) = 0$, and therefore

$$342 \quad V(x' - x) = V(x') - V(x) \approx x(1-x) \left(\frac{1 + \alpha'}{1 + \alpha'N}\right). \quad (28)$$

α' is the odds ratio of the bias weight,

$$344 \quad \alpha' = \frac{\alpha}{1 - \alpha}. \quad (29)$$

Combining eq. (28) and eq. (29) we get:

$$346 \quad V(x' - x) \approx x(1-x) \left(\frac{1 + \frac{\alpha}{1-\alpha}}{1 + \frac{\alpha}{1-\alpha}N}\right) = x(1-x) \left(\frac{1}{\alpha N + (1-\alpha)}\right). \quad (30)$$

This gives the diffusion term of the diffusion equation, which completes the proof.

348 This analysis gives a surprising result relating the parameters α and β to parameters of the classical Wright-Fisher model from population genetics: the selection coefficient s , a measure of the effect of
 350 natural selection on the change in frequency of genotypes, and the effective population size, N_e , a measure of the effect of random genetic drift on the change in frequency of genotypes. In a diffusion-
 352 equation approximation of the classical Wright-Fisher model, the expectation and variance of the change in frequency are $E[x' - x] = x + x(1-x)s + o(s)$ and $V[x' - x] = x(1-x)/N_e$ (Kimura, 1962,
 354 eq. 7). Therefore, we have the following result.

356 **Result 4** (Effective selection coefficient and population size). *The effective selection coefficient s and effective population size N_e can be written in terms of the success coefficient β (eq. (5)), the bias*

358 weight α (eq. (10)), and the population size N as

$$s = 1 - \beta(A), \quad N_e = \alpha N + (1 - \alpha). \quad (31)$$

360 Using our effective selection coefficient, $1 - \beta$, and effective population size, N_e , with the population-
genetics fixation probability approximation given by Kimura (1962, eq. 8), we get the following result.
362

Result 5 (Fixation probability). *The fixation probability is approximately*

$$364 \quad \pi = \frac{1 - e^{-2(1-\beta)N_e x}}{1 - e^{-2(1-\beta)N_e}} \quad (32)$$

where x is the initial frequency of the advantageous phenotype \hat{A} .

366 Similarly, we can use $1 - \beta$ and N_e in the population-genetics fixation time approximation given by
Kimura and Ohta (1969, eq. 17).

368

Result 6 (Fixation time approximation).

$$T = J_1 + \frac{1 - u(x)}{u(x)} \cdot J_2, \quad (33)$$

370 where, given $S = Ne(1 - \beta)$ and $x = \frac{1}{N_e}$,

$$u(x) = \frac{1 - e^{-2Sx}}{1 - e^{-2S}} \quad (34)$$

372 and,

$$J_1 = \frac{2}{(1 - \beta)(1 - e^{-2S})} \int_x^1 \frac{(e^{2S\xi} - 1)(e^{-2S\xi} - e^{-2S})}{\xi(1 - \xi)} d\xi, \quad (35)$$

374

$$J_2 = \frac{2}{(1 - \beta)(1 - e^{-2S})} \int_0^p \frac{(e^{2S\xi} - 1)(1 - e^{-2S\xi})}{\xi(1 - \xi)} d\xi \quad (36)$$

$$376 \quad T = \frac{1 - \pi}{1 - \beta} \int_0^x \frac{e^{2(1-\beta)\xi} - 1}{\xi(1 - \xi)} d\xi + \frac{\pi}{1 - \beta} \int_x^1 \frac{1 - e^{-2(1-\beta)(1-\xi)}}{\xi(1 - \xi)} d\xi \quad (37)$$

Note that these integrals cannot be solved in closed form, so we can only estimate them numeri-
378 cally.

Numerical validation. To validate our analysis we performed multiple simulations comparing our
380 binary model with the classic Wright-Fisher model, using different α and β each time, and using the
corresponding values of $s = 1 - \beta$ and $N_e = \alpha N + (1 - \alpha)$ for the Wright-Fisher simulations.

382 We find see that the two models have similar dynamics, and both are well approximated the the
approximations in eqs. (32) and (37).

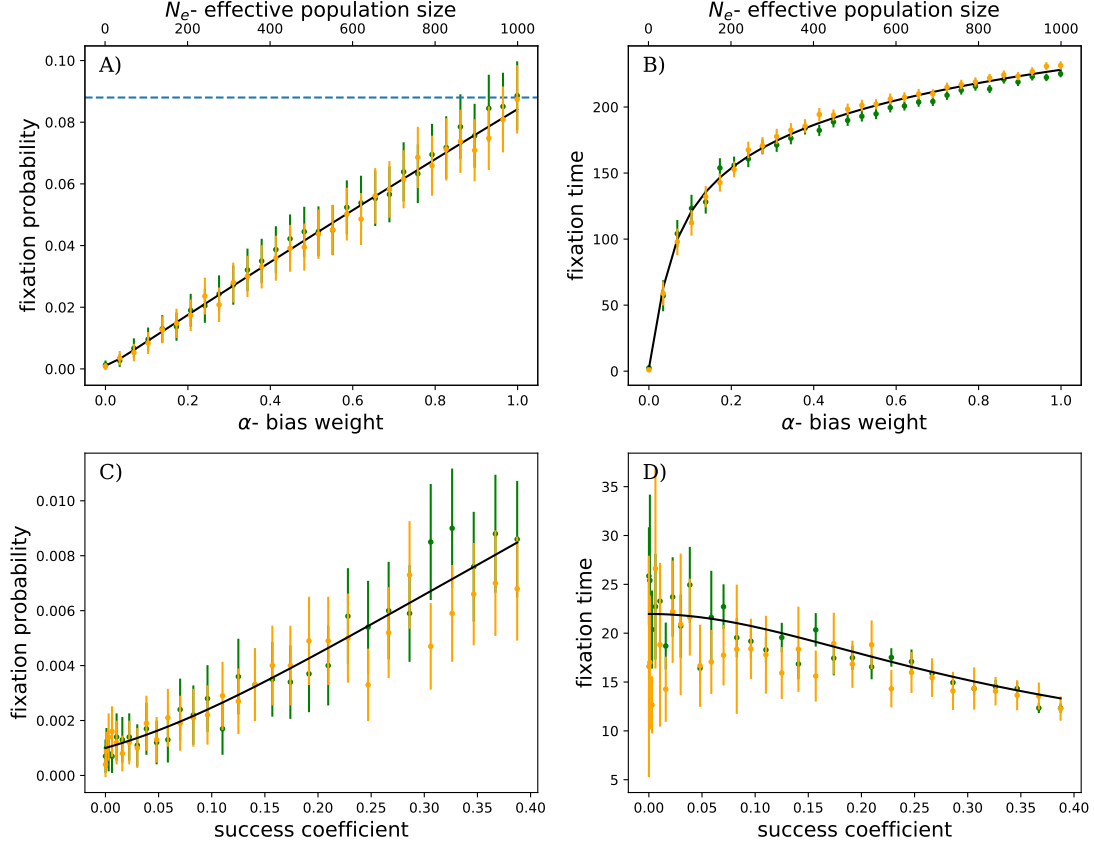


Figure 6: Fixation probability and time approximation for varying bias weight and success coefficient. Fixation probability (A) and time (B) for varying bias weight on the bottom x-axis. The corresponds effective population size is on the top x-axis. The approximation (black) fits DM simulations results (green) and Wright-Fisher simulation results (orange) when using eq. (32). Fixation probability (A) is limited at approximately $2s$ (blue), as in the classic WF model. Markers are averages of 10,000 simulations, error bars show 95% confidence intervals for (A,B) and 75% for (C,D). Here, Population size, $N = 1,000$; phenotype values, $\hat{A} = 1$, $A = 0.7$ (A,B), $A = a \cdot \hat{A}$, $a \in [0.01, 0.99]$ (C,D); success coefficient, $1 - \beta = s = 0.044$ (A,B); bias weight, $\alpha = 0.01$ (C,D).

384 After finding a good approximation for our model in a constant environment, when the favorable
 trait is always \hat{A} , we continued to find an approximation for our model in a changing environment.
 386 Following Ram et al. (2018), we find the following expressions for the expectation and variance of the
 change in frequency between t generations.

388

Result 7 (Drift and diffusion terms in a changing environment). *Let x be the initial frequency of the
 390 invading phenotype and X_t is the number of individuals with the phenotype at time t . Then,*

$$E[X_t/N - x] \simeq x(1 - x)S_t/N, \quad V(X_t/N - x) = V(X_t/N) \simeq x(1 - x)t/N_e, \quad (38)$$

392 where $S_t = \sum_{i=1}^t N(1 - \beta_i)$.

Proof. Let $s_t = N(1 - \beta_t)$, and $S_n = \sum_{i=1}^n s_i$, where β_t is $\beta(A)$ at generation t . We prove by induction
394 both terms in eq. (38). From eq. (23) we know that

$$E \left[\frac{X_{t+1}}{N} - \frac{X_t}{N} \middle| X_t \right] = \frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) (1 - \beta_{t+1}) = \frac{1}{N} \frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) s_{t+1} . \quad (39)$$

396 Also note that using the definition of $V(y) = E[y^2] - (E[y])^2$

$$\begin{aligned} E \left[\frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) \right] &= E \left[\frac{X_t}{N} - \left(\frac{X_t}{N} \right)^2 \right] = E \left[\frac{X_t}{N} \right] - E \left[\left(\frac{X_t}{N} \right)^2 \right] \\ &= E \left[\frac{X_t}{N} \right] - V \left(\frac{X_t}{N} \right) - \left(E \left[\frac{X_t}{N} \right] \right)^2 . \end{aligned} \quad (40)$$

398 We can now use the induction assumption of $V(\frac{X_t}{N})$ to get

$$E \left[\frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) \right] \simeq E \left[\frac{X_t}{N} \right] \left(1 - E \left[\frac{X_t}{N} \right] \right) - \frac{1}{N_e} tx(1-x) . \quad (41)$$

400 From eq. (39) we know that

$$\begin{aligned} E \left[\frac{X_{t+1}}{N} - \frac{X_t}{N} \right] &= \frac{1}{N} s_{t+1} E \left[\frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) \right] \simeq \frac{1}{N} s_{t+1} \left(E \left[\frac{X_t}{N} \right] \left(1 - E \left[\frac{X_t}{N} \right] \right) - \frac{1}{N_e} tx(1-x) \right) \\ &\simeq \frac{1}{N} s_{t+1} \cdot E \left[\frac{X_t}{N} \right] \left(1 - E \left[\frac{X_t}{N} \right] \right) - \frac{1}{N_e N} s_{t+1} tx(1-x) . \end{aligned} \quad (42)$$

402 Now we omit $O(\frac{1}{N_e \cdot N})$ and get

$$E \left[\frac{X_{t+1}}{N} - \frac{X_t}{N} \right] \simeq \frac{1}{N} s_{t+1} \cdot E \left[\frac{X_t}{N} \right] \left(1 - E \left[\frac{X_t}{N} \right] \right) . \quad (43)$$

404 We now look at the induction assumption to see that

$$E \left[\frac{X_t}{N} - x \right] = E \left[\frac{X_t}{N} \right] - E[x] = E \left[\frac{X_t}{N} \right] - x , \quad (44)$$

406 so using the assumption we get

$$\begin{aligned} E \left[\frac{X_t}{N} \right] &\simeq \frac{1}{N} S_t x(1-x) + x \\ 1 - E \left[\frac{X_t}{N} \right] &\simeq 1 - \frac{1}{N} S_t x(1-x) + x . \end{aligned} \quad (45)$$

408 We use both expressions in eq. (43) and get

$$\begin{aligned} E \left[\frac{X_{t+1}}{N} - \frac{X_t}{N} \right] &\simeq \frac{1}{N} s_{t+1} \left(\frac{1}{N} S_t x (1-x) + x \right) \left(1 - \frac{1}{N} S_t x (1-x) + x \right) \\ &\simeq \frac{1}{N} s_{t+1} \cdot x (1-x) , \end{aligned} \quad (46)$$

410 after again omitting $O(\frac{1}{N^2})$ terms. To conclude the proof, we note that

$$E \left[\frac{X_{t+1}}{N} - x \right] = E \left[\frac{X_{t+1}}{N} - \frac{X_t}{N} \right] + E \left[\frac{X_t}{N} - x \right] , \quad (47)$$

412 so again using the induction assumption, together with eq. (46) we get

$$\begin{aligned} E \left[\frac{X_{t+1}}{N} - x \right] &\simeq \frac{1}{N} s_{t+1} \cdot x (1-x) + \frac{1}{N} S_t \cdot x (1-x) \\ &\simeq \frac{1}{N} x (1-x) (S_t + s_{t+1}) \simeq \frac{1}{N} S_{t+1} x (1-x) , \end{aligned} \quad (48)$$

414 which proves the drift term.

For the diffusion term, we use a property of variance,

$$416 \quad V \left(\frac{X_{t+1}}{N} \right) = E \left[V \left(\frac{X_{t+1}}{N} \middle| X_t \right) \right] + V \left(E \left[\frac{X_{t+1}}{N} \middle| X_t \right] \right) . \quad (49)$$

Using eq. (39) we see that

$$\begin{aligned} 418 \quad E \left[\frac{X_{t+1}}{N} \middle| X_t \right] - E \left[\frac{X_t}{N} \middle| X_t \right] &= \frac{1}{N} s_{t+1} \frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) \\ E \left[\frac{X_{t+1}}{N} \middle| X_t \right] &= \frac{X_t}{N} + \frac{1}{N} s_{t+1} \frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) . \end{aligned} \quad (50)$$

Using eq. (30) we get

$$420 \quad V \left(\frac{X_{t+1}}{N} \middle| X_t \right) = \frac{1}{N_e} \frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) , \quad (51)$$

and using the equation $y'(1-y') \simeq y(1-y)$ on the first part of eq. (49) we get

$$422 \quad E \left[V \left(\frac{X_{t+1}}{N} \middle| X_t \right) \right] = \frac{1}{N_e} E \left[\frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) \right] \simeq \frac{1}{N_e} x(1-x) . \quad (52)$$

Moving on to simplify the second part of eq. (49) using eq. (50),

$$424 \quad V \left(E \left[\frac{X_{t+1}}{N} \middle| X_t \right] \right) = V \left(\frac{X_t}{N} + \frac{1}{N} s_{t+1} \frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) \right) \quad (53)$$

Now, because $\frac{X_t}{N}$ is a frequency, i.e $0 \leq X_t/N \leq 1$, we know that $V\left(\frac{X_t}{N}\left(1 - \frac{X_t}{N}\right)\right) \leq \frac{1}{4}$. We therefore
 426 find that

$$V\left(\frac{1}{N}s_{t+1}\frac{X_t}{N}\left(1 - \frac{X_t}{N}\right)\right) \leq \frac{1}{4N^2}s_{t+1}^2; \quad (54)$$

428 and so it can be ignored. Combining our equations we get

$$V\left(E\left[\frac{X_{t+1}}{N}\middle|X_t\right]\right) = V\left(\frac{X_t}{N}\right) + O\left(\frac{1}{N^2}\right) \simeq V\left(\frac{X_t}{N}\right). \quad (55)$$

430 Using the induction assumption and eq. (52),

$$V\left(\frac{X_{t+1}}{N}\right) \simeq \frac{1}{N_e}x(1-x) + \frac{1}{N_e}tx(1-x) \simeq \frac{1}{N_e}x(1-x)(t+1) \quad (56)$$

432 which proves the diffusion term.

Using the drift and diffusion terms and following Ram et al. (2018), we can approximate the fixation
 434 probability in a changing environment using

$$\tilde{\pi} = \frac{1 - e^{-2\frac{S_n}{n}N_ex}}{1 - e^{-2\frac{S_n}{n}N_e}} \quad (57)$$

436 where $\frac{S_n}{n} = \frac{k-l}{k+l}(1-\beta)$ and $n = k+l$. That is, we use the average selection coefficient during a cycle of $k+l$ generations as the selection coefficient eq. (32).

438 **Numerical validation.** Comparing our approximation (eq. (57)) to numerical simulations, we find that the approximation fits simulations results well for variable bias weights, α , which corresponds to
 440 the effective population size (Figure 7A).

However, the approximation is more sensitive to the value of the success bias coefficient β (Figure 7B).
 442 We suspect that when β is too small, there will not be many cycles in the simulations, because either the population reaches a high frequency of the fitter phenotype after just a few cycles, or the fitter
 444 phenotype becomes extinct very quickly. For the β values (0.65 and below), the fixation probability exceeds even the constant environment approximation (which is the upper limit). However, this is to
 446 be expected, because the diffusion-equation approximations assume weak selection (i.e., low selection coefficient s).

448 When k is the number of generations where the invading phenotype is advantageous, and l when the original trait is, we found that for large k -to- l ratio (while keeping constant total cycle length,
 450 $n = k+l = 100$), the changing environment approximation (eq. (57)) converges to the constant environment approximation (eq. (32)), see Figure 7 (C,D).

452 Adaptive success-bias weight

We ran simulations of the role-model choice process during a single generation in which every copier
 454 evaluates its own optimal α value. This is the α value that minimizes the mean square error of

the difference between the estimated and the ideal trait values. This α is found by minimizing the
 456 following:

$$SMSE = \sum_{j=1}^N \frac{\alpha A_j + (1 - \alpha)K_j}{\sum_{l=1}^N \alpha A_l + (1 - \alpha)K_l} \cdot (\hat{A} - A_j)^2 \quad (58)$$

458 where A_j is the trait of role-model j and K_j the number of copiers that already chose him.

We see in fig. 8 a comparison between a model where every copier chooses its ideal success bias
 460 weight α_{ij} , and when α is a constant homogeneous value. We find that when copiers adapt their
 success-bias weight, their success-bias weight decreases with the number of copiers that have already
 462 chose a role-model (fig. 8). Moreover, their estimation error is much lower compared to a constant
 success-bias weight, which gives roughly the same high estimation error to all copiers (compare fig. 8b
 464 and c): the estimation error converges to 0.046 whereas a constant weight gives values > 0.74 in this
 example.

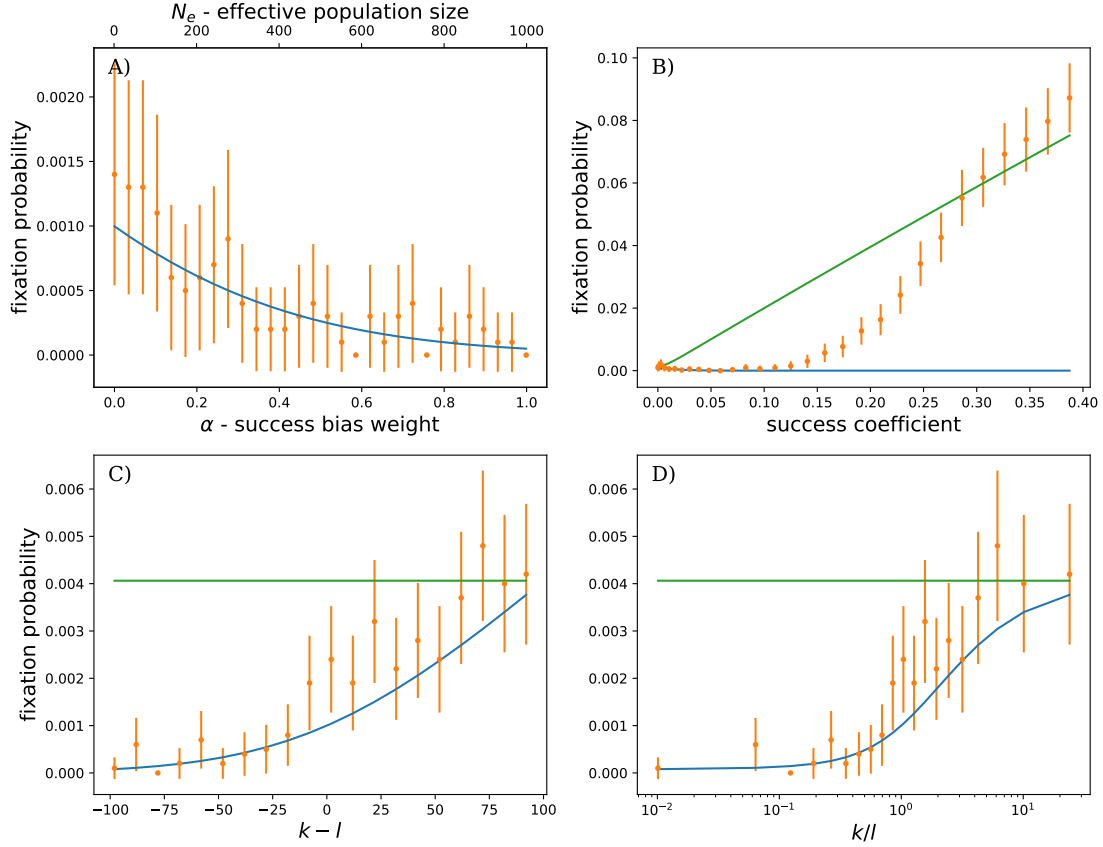


Figure 7: Sensitivity of fixation probability approximation in a changing environment to varying success coefficient and bias weight and robustness to varying ratios of cycles. (A) When the bias weight, or effective population size varies, the approximation (blue; eq. (57)) fits simulation results (orange). (B) When success bias is large ($1 - \beta > 0.1$), simulation results (orange) are underestimated by the approximation (blue; eq. (57)). With even larger success bias ($1 - \beta > 0.35$), even the constant environment approximation (green; eq. (32)) underestimate simulation results, likely because the diffusion equation approximation assumes weak selection. We can also see the robustness of the approximation to changes in cycle ratios (C,D): The approximation (blue) fits the simulations (orange) well for different sizes of the changing environment cycle, where k is the number of generations where the bias is advantageous, and l are the generations it is disadvantageous. When $k < l$ the approximation is good. When $k > l$, the approximation and the simulations are both very close to the constant environment approximation (green). Markers show average of 10,000 simulations, error bars show are 75% (A,C,D) and 95% (B) confidence intervals. Here, population size, $N = 1,000$; phenotype values, $\hat{A} = 1$, $A = 0.9$ (A,B), $A = 0.8$ (C,D); In (A) success bias/selection coefficient is: $1 - \beta = s = 0.005$; In (B,C,D) success bias weight is: $\alpha = 0.1$.

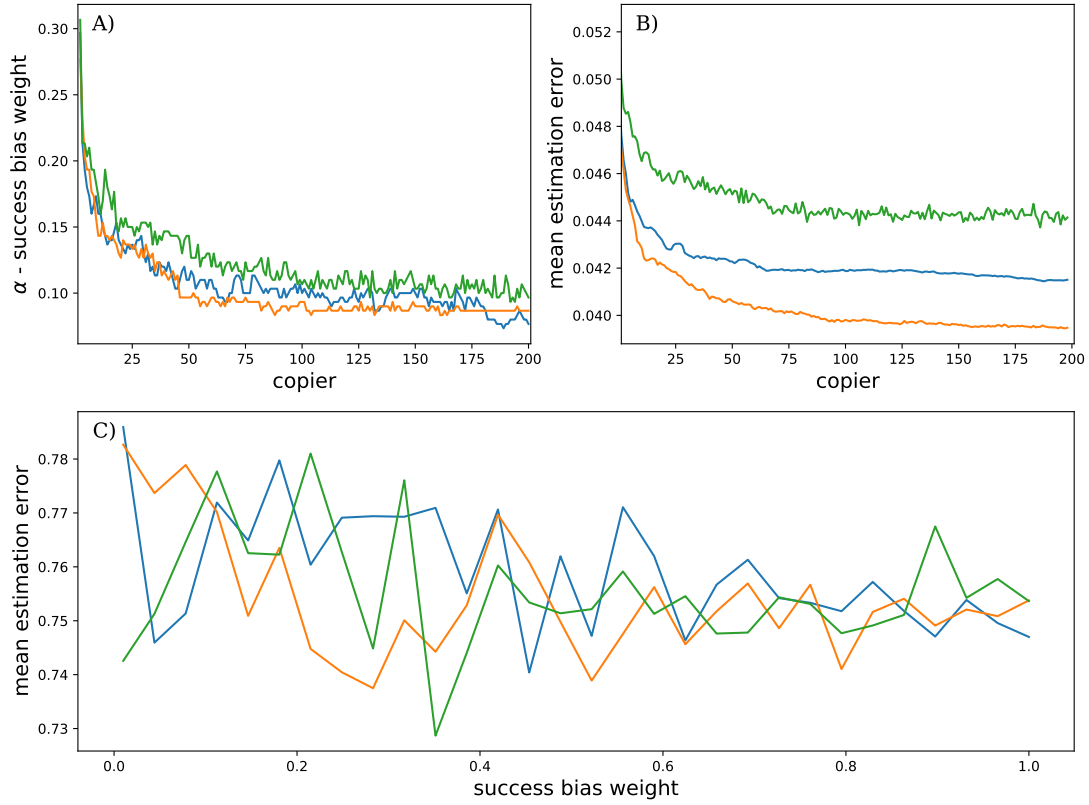


Figure 8: Advantage of an adaptive success-bias weight. Both success-bias weight α (a) and estimation error (b) decrease during the role-model choosing process, demonstrating that influence is becomes more advantageous as more copiers have made their choice. However, when α is homogeneous, the mean estimation error doesn't decrease, regardless of α or η . The mean estimation error in the homogeneous α model is larger by a factor of 10 than the adaptive α model. Here, population size $N = 200$; estimation error is normally distributed $e \sim N(0, \eta^2)$; standard deviation $\eta = 0.0001$ (blue), 0.001 (orange), 0.01 (green), plots are average of 300 simulations.

466 Discussion

Summary. During cultural transmission, cultural traits such as attitudes, values, beliefs, and behavioral patterns are transmitted between individuals, for example via copying and social learning. Some cultural traits or cultural role-models may be more likely to be copied due to transmission biases. A common one is success bias, in which copiers are more likely to copy a successful role-model. Many models assume that success can be accurately estimated. However, it has been suggested (Fogarty et al., 2017) that because estimating success is hard, a more common bias is *prestige bias*—a bias towards role-models perceived to be successful, portrayed by other traits or means.

Inspired by a model by Boyd and Richerson (1988), we developed a cultural-evolution model with prestige bias, which included both success and influence biases, where the latter is a bias towards role-models with many copiers. As shown in fig. 8, given the option to choose the ratio of success and influence, copiers will minimize their estimation error, hence will copy the traits that are closer to the ideal phenotype. We see that throughout the choosing process, the estimation error decreases, and the success bias rate also decreases. This suggests that the later a copier gets to choose, the less he should rely on his own estimation, and more on previous choices. This behavior fits the intuitive thought - the more information you have, using others as an information source, the more informative your choice can be, therefore minimizing the distance from your choice of trait to the ideal one.

In addition, we see that the process of choosing itself is necessary, and when using a constant ratio (α), the mean estimation error in the population is greater by a factor of 10, even when using the α the population converged to when being able to choose it (fig. 8). After we showing that choosing one's success bias weight is beneficial to the copier, we continued to create our models- continuous and dichotomous, that incorporated both success and influence. However, running simulations for a nested iterative model is costly, and analyzing such model mathematically is very hard. We therefor found approximations for the role-model choice process: the generalized binomial distribution (result 1) and the Dirichlet-Multinomial distribution (corollary 3). To use approximate our model with the GBD distribution, we must assume homogeneous estimation error, e , and homogeneous success bias weight, α . Both assumptions are necessary to this approximation, because it requires all copiers to be identical (order of copiers must not be a factor). For the DM approximation we can relax the assumption for α , and allow a varying α_j for each role-model j . This means that a copier is still not able to choose a success bias weight for itself, and instead it is a characteristic of the role-model only. Using the DM approximation, because it is easier to analyze, we found equivalents for Kimura's equations, for our dichotomous model. Following result 4 we found an approximation for the fixation probability of the ideal trait, and an approximation for the time of fixation. These approximations hold only when the equivalent for the selection coefficient, in our model $1 - \beta(A)$, is low (0.4 or lower). We also discovered that changing the success bias weight doesn't hurt the goodness of the approximations, and only affects the effective population size N_e . Once we found the equations for a constant environment, we moved on to a cyclic changing environment. Based on result 7, we found the approximations for the fixation probability and time to fixation. We discovered that as in the constant environment, the

504 effective population size doesn't affect the goodness of fit of the approximation. The success coefficient
however, must be even lower than before for the approximation to fit. When the success coefficient is
506 higher than 0.15, the simulation results were located above the changing environment approximation,
and below the constant environment approximation. We believe the reason is the structure of the cycle.
508 Our proof and approximation in the changing environment are for a large amount of cycles, and when
the success coefficient is too high, there might be very few cycles. Either the ideal trait is copied by
510 enough copiers so that the influence is sufficient to negate the success bias when the cycle changes
(and the beneficial trait becomes the maladaptive), or the opposite happens, and the ideal trait gets
512 extinct before there were enough copiers that copied it. We then tried to change the ratio between the
number of cycles where \hat{A} is beneficial and maladaptive. We showed that the approximation fits well
514 regardless of the ratio, but when the ratio of adaptive generations to maladaptive ones is very high, it
is very similar to a constant environment model.

516 **Prestige in the literature.** According to King and Cowlishaw (2009), there are two main approaches
to group decision-making in nature: leadership and consensus. Leaders may lead the group when
518 traveling, decide on a nesting site, or choose foraging patches. They found that leadership is mostly
observed when there are a lot of connections in the social network of the group, and when there are
520 individuals that present leadership behavior. Leaders would usually be high-ranking members of the
group: elders, individuals with many kin relations, or individuals possessing other dominant traits.
522 When no individual possesses such traits, or when there are not enough connections and relations in the
social network, decisions are more likely to be made by consensus. Leaders may carry selection costs,
524 e.g. due to higher predation risk, poisoning when exploring new foraging patches. In some cases,
the leader may be the hungriest or the weakest individual, while the others would prefer to follow the
526 leader and minimizing their risks and costs. However, leadership may also carry selection benefits.
For example, given the route to the foraging site was successful, the leader and his closest followers
528 would gain most or the best of the food, whereas in consensus decision making, the food would be
shared more equally. Or, sexual selection may also provide a selection benefit advantage to leaders,
530 who might gain more sexual partners due to their leadership of the group. King and Cowlishaw (2009)
describe benefits for the closest associates of a dominant baboon, such as protection from predators.
532 In some species, like the females of *Eulemur fulvus rufus* (Red lemur), leaders may arise due to
nutritional needs, and not due to possessing superior traits (Erhart and Overdorff, 1999).

534 In humans, leadership also has its costs and benefits. Leaders can make decisions that would most
benefit them and their closest followers, while still maintaining group cohesion. However, wrong
536 decision making that harms the group could result in harm.

In modern society humans strive for the prestigious positions, as they may reap rewards greater than
538 the risk and costs to achieve them, or due to individual personality and pressure/education from the
family.

540 Van Vugt and Smith (2019) suggest a different view of leadership. They note that most discussions
assume there is one type of leadership, as seen above, and so they differ in their definitions. Van Vugt
542 and Smith (2019) suggest a way to solve said contradiction by defining two types of leaderships:

prestige-based and dominance-based. They present classical views of leaderships by Confucius and
544 Machiavelli. Confucius views leaders as role-models who exercise influence through possessing
superior knowledge, skills, and (outstanding) personal qualities. This description is very similar to
546 success bias in our model. By contrast, Machiavelli views leaders as rulers who exercise influence by
imposing costs through (the threat of) punishment and violence. They say that these two opposing
548 views are both partially supported by the available evidence but each one on its own offers an
incomplete view into the complex and dynamic processes of leadership. Our model does not reflect
550 these leadership styles, but several adjustments could be made in order to match it, such as assuming
there is a correlation between phenotype to leadership style. The emerging cultural-evolutionary
552 dynamics and their dependence on the costs and benefits are intriguing.

Henrich and Gil-White (2001) support said claim that there are two types of leadership, and also
554 define the two as prestige based and dominance based leadership types. By their definition, the latter
is defined by acquiring social status by using aggression, intimidation and violence. It is also more
556 common than prestige in non humans. Their definition of prestige is somewhat synonymous with
ours. According to their manuscript, prestige is composed both of estimation in the eyes of people
558 (our success trait) and commanding position in people's minds, i.e number of copiers people think
they have, which they define as *influence* (similar to our definition for influence). In their paper, they
560 show that prestige evolved from natural selection, as an efficient process to extract reproductive benefit
from the flow of socially transmitted information. Simply put, prestige is a natural step where social
562 learning exists, due to saving costs of individual learning. It could be interesting in the future to expand
our model using this idea: observing the copier trait of *evaluation*, rather than only observing the
564 evolution of the trait copied. Henrich and Gil-White (2001) suggest that the most skilled role-models
will, on average, end up with most copiers. Their research, definitions and results, is consistent with
566 ours.

Furthermore, according to Boyd and Henrich (2002), the process of cultural evolution doesn't require
568 replication of representations. They base their assumption on three claims - mental representations are
non-discrete, cultural transmission is highly inaccurate, and mental representations are not replicated,
570 but rather are 'reconstructed' through an inferential process that is strongly affected by cognitive
'attractors.' In their paper they describe three different models to support their points. We see a high
572 similarity between their model and ours. Like them, we treat the cultural trait as non-discrete (in
the main model, before simplifying it to dichotomous in order to analyze it). We also assume error
574 in estimation, which the copiers aren't really replicating their role-models, but rather reconstructing
them to create a different trait, which is their representation of the role-model's trait. In addition, the
576 inferential process that they describe as strongly affected by cognitive attractors match our influence
bias, resulting in a very similar base assumptions in our models.

578 So far we presented the theory behind prestige, and it's appearance in nature. The following will show
the appearances of prestige biases in humans, and in recent times.

580 Chudek et al. (2012), for example, tested the existence of prestige in young children. Chudek et al.
(2012) report the first direct tests in children that suggest the existence of *prestige bias*, a tendency

582 to learn from individuals to whom others have preferentially attended, learned or deferred. Their
definition of prestige is similar to our *influence bias*, and brings concrete proof of its existence and
584 effects. Their study showed that the odds of 3-4 years-old children learning from an adult model to
whom bystanders had previously preferentially attended for 10 seconds were over twice those of their
586 learning from a model whom bystanders ignored. In addition to this first study, they also discovered
prestige effects are domain-sensitive. They saw that prestigious models were listened to by most when
588 demonstrating artifact-use, but not as much as when presenting food preferences. It lead Chudek et al.
(2012) to believe that when the trait is costly to learn individually, prestige will have a higher effect. It
590 would be interesting to include costs in our model to try and observe these effects and their dynamics
in the simulations of a larger population than this study.

592 Henrich and Broesch (2011) researched Fijian villages, looking for evidence of social learning biases
and their origins. They mention that:

594 evolutionary theorists propose that natural selection has favored the emergence of psy-
chological biases for learning from those individuals most likely to possess adaptive
596 information.

Their goal is to bridge from the laboratory to the field by examining if and how these biases emerge
598 in a small-scale society. During their research they found that:

Fijian villagers (ages 10 and up) are biased to learn from others perceived as more
600 successful/knowledgeable, both within and across domains (prestige effects).

Their research shows promising evidence for our prestige model, suggesting that copying from others
602 who are *perceived* as successful, rather than actually are successful. In their paper, they show that the
social networks representing copier-role-model relationships are centralized, suggesting:

604 This degree of centralization is consistent with the prediction that people substantially
share notions about who is a good cultural model (network centrality), but that individuals'
606 model selections are influenced by multiple factors.

We see here support for both our trait and our influence bias in their data.

608 Aside from children's learning biases and small villages in a relatively primitive population, we can
see prestige in more advanced domains as well, like western medicine. Norredam and Album (2007)
610 present a specific and important effect of prestige - its significance for medical specialties and diseases.
They examined literature from 1950 to 2005 regarding the effects of prestige on medicinal practices.
612 They discovered that active, specialized, biomedical, and high-technological types of medicine on
organs in the upper part of the bodies of young and middle-aged people were accorded high levels of
614 prestige, while medicine with opposite characteristics had low levels of prestige. They have concluded
that such differences in prestige bear consequences for actual priority setting in healthcare systems.
616 They discovered that surgery counts as the most prestigious specialty, while psychiatry is the less
prestigious. In addition, doctors tend to rank practices that require more time to master as more
618 prestigious, while other procedures that are considered *easier* are less prestigious. Simply put, they

found that the advance in technology and research was in accordance with the prestige rankings. This means that there may be very important practices that are neglected due to the prestige bias.

As we seen so far, prestige can explain many behaviors and evolution of cultural traits. It is a tool to cheaply estimate and acquire knowledge, which helps an individual to survive and breed. However, it is not always the case, and there could be negative repercussions to this bias, such as invasion of maladaptive traits.

Takahashi and Ihara (2019) mention that social learning not only takes the form of random copying of other individuals, but also involves learners' choice of what to learn and from whom to learn. They suggest a best-of-K model where an individual samples k role-models and choose the one he deems most "successful". They mentioned that a previous mathematical analysis has shown that it may sometimes result in maladaptive cultural evolution when the payoffs associated with cultural variants vary stochastically. In such a case, learners may be selectively disfavored and in the long run replaced by unbiased learners, who simply copy someone chosen at random. They develop new mathematical models that are simpler and mathematically tractable. They found that best-of-k learning, unlike unbiased learning, can facilitate the invasion of an on average inferior variant that sometimes gives a very high payoff. Our model, which includes influence bias, is consistent with that claim. When a maladaptive trait is "piggybacking" a role-model with high influence, said trait could spread in the population, as mentioned. In addition, they show that best-of-k learning can be stable against invasion by unbiased learning if social learning is sometimes combined with individual learning. Our model is based on copying based learning only, but it could be interesting to combine it with individual learning and see how it affects the dynamics of the population.

We discussed prestige in depth, and provided several proofs for its existence in nature, humans, and even medicine. We saw it could aid invasion of maladaptive traits, or neglect of important medicinal specialities. But, it can also accelerate reversal of harmful traditions. Harmful traditions can be child marriage, open defecation, and domestic violence, to name a few. Efferson et al. (2020) suggest a mechanism called *spillover*. By their definition, a spillover is when an intervention affect a large enough group in a target population, so that others not included in the intervention starts changing their behavior as well. In their research, they found that there are individuals who act as *agents*, who are often looked upon, and therefore they are ideal targets for interventions. This is the same concept as our role-models, where a more prestigious individual will be copied more, therefore spreading his trait wider in the population. Their research support therefore in our assumption that there are social biases, conformist influence specifically. They also suggest a way to use this phenomena to change existing traditions in a population. It is very clear however, that just as it can be used to end harmful traditions, the same agents could be used for any negative way that comes to mind.

Up until now, we showed that cultural transmission is a process that manifests in many species, with emphasis on humans. We also displayed similarities between this process and genetic transmission, while presenting differences between them, specifically selective biases such as influence and prestige. We also presented examples of good and bad usages of such biases. All of these are mainly presented as a parallel process to the natural selection process in regards to physical anatomy, or at least have

658 an indirect effect on it. Muthukrishna and Henrich (2016) offer a take on prestige as a factor of
human physical evolution directly. They present a concept called *cultural brains* | brains that evolved
660 primarily for the acquisition of adaptive knowledge. They build on the hypothesis of Dunbar (2009)
that shows that larger, more complex brains can store and manage more information and in turn, this
662 information can support the costs of a larger brain. Muthukrishna and Henrich (2016) built a model
that predicts a strong relationship between brain size and group size, because group size also provides
664 access to more adaptive knowledge. They later present their *cumulative cultural brain* hypothesis, an
approach which proposes that human brains have evolved with an ability and proclivity for selective,
666 high fidelity social learning. As part of this process, there are a variety of strategies and biases that
have evolved to hone in on the most adaptive knowledge. These strategies and biases include direct
668 and indirect cues of the popularity of cultural traits (e.g. success and prestige biases). In short, they
suggest that some of the reasons for the extreme increase in brain size in humans, are the ability to
670 "cheaply" acquire adaptive knowledge, i.e transmission biases, such as prestige.

Further work. In this paper we described several models and processes, analyzed them, and discov-
672 ered some interesting approximations and results. But even though, there's much more to research in
the direction we took, which can help us better model, understand, and maybe even predict, human
674 behavior, specifically in this era where social media is very accessible and informative. Specifically,
a deeper analysis of the first model, where every copier chooses its α , is preferred. It would be
676 interesting to see if the mean error value and the α are converging to specific values, and what
they depend on. Following that, it is possible to relax some assumptions we took in our main model
678 in order to find approximations for it - like homogeneous estimation error and success bias weight.
Lastly, it would be interesting to analyze the continuous model, instead of its dichotomous version.
680 As we've discussed it is probably a much more accurate model of cultural evolution.

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