Prestige bias in cultural evolutionary dynamics

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Abstract

A common bias in cultural transmission is to copy whoever appears more successful. This success bias only depends on the performance of the role-model. Because success may be difficult to estimate, it has been suggested that individuals may indirectly estimate success by using prestige as a proxy for success. Here, we model prestige bias as a combination of indirect success bias and influence bias, the latter meaning that the choice of a role-model depends on the number of individuals that have already copied from that role-model. We analyze the effect of prestige on cultural evolutionary dynamics using mathematical analysis and stochastic simulations. We find analytic approximations to the stochastic role-model choice process, which facilitate further mathematical analysis and reduce the computational complexity of simulations. We also find approximations to the fixation probability and the fixation time of an invading cultural trait in different environments. We show that indirect success bias effectively plays the role of natural selection, whereas influence bias effectively plays the role of genetic drift. Influence bias also accelerates the evolutionary dynamics, as can be expected in a *rich-getting-richer* process. Our model describes and analyses cultural transmission, especially in human societies where social media is popular.

Introduction

In cultural transmission, individuals transmit cultural traits (i.e., behaviors, beliefs, norms) to one another, typically by learning and demonstrating [8]. Examples for cultural traits in humans are norms, preferences, tools, ideas, and language, potentially transmitted verbally and/or by observations [11]. Although cultural transmission is common in humans, it is also observed in other animals, e.g. chimpanzees [26, 28], dolphins and whales [48], elephants [34], and even flies [4] and fish [44].

Cultural transmission may combine vertical transmission, in which parents transmit to their offspring; oblique transmission, in which adults (teachers, leaders, and even strangers) transmit to unrelated offspring; and horizontal transmission, in which peers from the same age cohort transmit to one another [8, 11]. It has been demonstrated that non-vertical cultural transmission can maintain maladaptive traits, which can be beneficial in changing environments [41].

Transmission biases may cause a cultural trait to have a disproportionate probability to be transmitted compared to its frequency in the population. *Success bias* occurs when individuals prefer to copy from role models that demonstrate success in some activity, such as fishing, growing yams, using medicinal plants [24], or hunting [35], and it can increase the probability of learning a successful trait [5]. Indeed, in a tournament between learning strategies conducted by Rendell et al. [42], most winner strategies included a mixture of success-biased social learning and individual learning, implying that success-biased learning is a good strategy, but that by itself it is not enough to best other strategies, even when success is measured accurately.

Boyd and Richerson [7, Ch. 5] have suggested that the evaluation of success can be divided to three categories: *direct bias*, *indirect bias* and *frequency-dependent bias*. A direct bias occurs when one phenotype is more attractive than other phenotypes, and is evaluated by *directly* testing the trait. For example, an individual observing a ping-pong match can attempt the observed paddle grips to determine which grip is better. A frequency-dependent bias occurs when the probability to copy a phenotype is higher or lower than the frequency of the phenotype among demonstrators. For example, suppose the common paddle grip is used by 60% of the demonstrators; if the this grip is adopted by 80% of copiers, then transmission is under positive frequency bias, also called *conformity*; if it is adopted by 40% of copiers, then transmission is under negative frequency bias, or *non-conformity* [36]. The effects of conformity and non-conformity on cultural evolution have been studied with both models [12, 13, 14] and experiments [1]. An indirect bias occurs when an individual uses one phenotype to determine the attractiveness of another phenotype. For example, an observer may copy the paddle grip of the ping-pong player who scored more points in the match, thus indirectly evaluating the grip by the points scored. This, however, may cause mismatches between the copied trait and the rest of the cultural or genetic repertoire of the individual [32]. Furthermore, Boyd and Richerson [7, Ch. 8] have suggested that maladaptive traits may spread widely in a population if indirect biases are strong enough, e.g., by a runaway process caused by a cultural equivalent of sexual selection [3]. Indeed, Cohen et al. [10] have shown that helping behaviors can evolve due to horizontal transmission bias even without any benefit to the recipient, or when the benefit is much larger than the cost.

Henrich and Broesch [24] have studied such indirect success biases, which they call cross-domain success bias or *prestige bias* (e.g., great fishermen may be chosen as role-models for growing yams). They have suggested that such biases, over generations, can lead to cultural adaptations, and that although prestige can lead to maladaptive traits spreading in the population, it can also accelerate the spread of adaptive traits. Boyd and Richerson [7, Ch. 8] and Fogarty et al. [22] have suggested that prestige biases are probably more common in humans than success biases, and prestige is often mentioned in the cultural evolution literature, however there are few models of prestige bias.

A broader definition of prestige is the "widespread respect and admiration felt for someone or something on the basis of a perception of their achievements or quality" (New Oxford American Dictionary). Indeed, Chudek et al. [9] have defined prestige bias as "a tendency to learn from individuals to whom others have preferentially attended, learned or deferred", and demonstrated its occurrence in in 3-4 year old children. Henrich and Gil-White [25] gave a similar definition of prestige as "freely conferred deference", in contrast to *dominance*, and provided examples from the anthropological literature.

To distinguish this form of indirect bias from other definitions of prestige, we call it *influence bias*. This is an important distinction, as influence is a context-based bias, rather than a content-based bias: it does not depend on the phenotype itself but rather on the number of copiers that already copied each role-model, which may be easier and more accurate to estimate compared to success. Influence bias also differs from frequency biases such as conformity, which depend on the frequency of a trait in the population or in a sample of role-models, rather than the social dynamics of copying.

In contemporary human society, social media makes it especially easy to estimate the social and cultural influence individuals have over others, and therefore can have an effect on decision making. Online social networks such as *Facebook* and *Instagram* are known to affect the influence of individuals [2, 15, 40], and specific marketing practices were invented to capitalize on this effect [33].

In the following, we develop a stochastic model of cultural transmission with prestige bias. In our model, prestige combines both cross-domain indirect success bias and influence bias. We develop analytic approximations for this model and analyze its dynamics. We find approximations for the probability and time for fixation of a 'successful' phenotype (i.e., that is favored by success bias). Comparing these approximations to Kimura's approximations for the fixation of a favorable allele [29, 30], we demonstrate that success and influence bias play the role of natural selection and genetic drift, respectively.

Models

We begin with a continuous trait model with indirect bias suggested by Boyd and Richerson [7], develop an extension with influence bias, and then develop a model with a dichotomous trait. We implemented our stochastic models and approximations, performed statistical analyses, and produced figures using Python [46] with NumPy [45] and Matplotlib [27]. Source code is available at https://github.com/yoavram-lab/PrestigeBias.

Continuous trait

We follow the model of Boyd and Richerson [7], assuming only oblique transmission of the trait 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, 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 the entire population is replaced in each generation. The population at time t can be described by $\mathbf{A}(t) = \big(A_1(t), \ldots, A_N(t)\big)$ where $A_i(t)$ is trait value of individual i at time t. We assume the initial 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

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

Success bias. Boyd and Richerson [7, Ch. 8, p. 247-249] describe a blended transmission algorithm by defining F as a weighted average of the traits of all role-models,

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

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

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

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

$$A_{i,j} = A_j + e_i, \tag{4}$$

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

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

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 fitness in evolutionary-genetic transmission models.

Boyd and Richerson [7] note that the deterministic blended transmission algorithm they use has 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 distribution given by

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

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,
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,
$\sum_{j=1}^{N} K_{i,j} = i$, and there are $N - i$ copiers that have yet to choose a role-model. The stochastic process
of role-model choice,

$$\left\{ \mathbf{K}_i = (K_{i,1}, \ldots, K_{i,N}) \right\}_{i=1}^{N} , \tag{7}$$

is described by the recurrence equation

$$K_{i,j} = K_{i-1,j} + S_{i,j}, \quad i, j = 1, 2, \ldots, N , \tag{8}$$

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

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

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

The prestige $G_{i,j}$ of role-model j in the eyes of copier i is determined by success–the estimated biased
trait value $\beta(A_{i,j})$–and influence–the number of copiers that chose role-model j before copier i, $K_{i-1,j}$,
replacing eq. (3) of Boyd and Richerson [7] with

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

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 direct success vs. influence in the role-model's overall prestige
in the eyes of the copier.

We assume every individual may evaluate the importance of success and influence differently. Additionally, we assume every role-model displays his influence and success individually. For example, a
person with more followers but lack of actual skill may emphasize the number of his followers rather
than his actual skill. We therefore defined $\alpha_{i,j}$ to be the relation between every copier's intrinsic
significance of estimation, and every role-model's personal emphasis.

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 $\sum_{j=1}^{N} G_{i,j} = 1$.

Dichotomous trait

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
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

either phenotype. In addition, for simplicity and for easier mathematical analysis, we assume α is homogeneous, such that we have exchangeability between role-models. Therefore, the probability of the i-th copier to copy phenotype A is

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

where X is the number of role-models with trait $\hat{A}$, $K_{i,A}$ is the number of copiers that already chose A when copier i chooses a role-model, $\beta(\hat{A}) = 1$, and $\alpha' = \frac{\alpha}{1-\alpha}$ is the odd ratio of the bias weight. Complementing this, the probability of the i-th copier to copy phenotype $\hat{A}$ is $G_{i,\hat{A}} = 1 - G_{i,A}$. The rest of the details follow the continuous trait model.

Results

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 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 $\mathbf{A}(t)$ 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 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 homogeneous α.

Generalized binomial approximation. The number of copiers of a specific role-model at each step, $K_{i,j}$, follows the *generalized binomial distribution* [16] and therefore,

(i) the expected number of copiers of role-model j equals its prestige in the eyes of the first 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 $i = 1, \dots, N$); and (ii) 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, $E[K_{N,j}] = \beta(A_j + e)/\overline{\beta}$ if the bias weight is uniform for all role-models ($\alpha = \alpha_j$ for $j = 1, \dots, N$), where $\overline{\beta} = 1/N \sum_{j=1}^{N} \beta(A_j + e)$ is the population mean estimated trait value.

Dirichlet-Multinomial approximation. 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 order of copiers.

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, meaning all copiers are identical.

Generalized binomial distribution

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

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$GBD(n, p, \theta)$ 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).

Result 1 (Generalized binomial approximation). *The number of copiers of role-model j after i copiers have chosen a 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 $i = 1, \ldots, N$.*

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 choose role-model j given $K_{i-1,j}$ our of $i - 1$ copiers chose role-model j. Using conditional probability and eq. (8),

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

where $S_{i,j} = 1$ when the i-th copier chooses role-model j. Equation (12) is equivalent to eq. (2.1) by Drezner and Farnum [16], which completes the proof.

This result gives the following two corollaries on the expected number of followers of a given role-model by the end of the role-model choice process. The proof of Corollary 2 is in Appendix A.

Corollary 1. *The expected number of copiers of role-model j after all copiers have chosen a role-model is $\mathrm{E}[K_{N,j}] = N \cdot G_{1,j}$, where $G_{1,j}$ is the probability of the first copier to copy role-model j.*

Proof. Drezner and Farnum [16, eq. (2.3)] show that $\mathrm{E}[k] = N \cdot Q_j(1, 1)$ (modified from their notation). $Q_j(1, 1)$ is the initial probability to choose role-model j, before any role-model choices are made. $Q_j(1, 1) = G_{1,j}$ by definition, which completes the proof.

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

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

$$\mathrm{E}[K_{Nj}] = N \cdot \frac{\alpha \cdot \beta(A_j + e)}{\sum\limits_{m=1}^{N} \alpha \cdot \beta(A_m + e)} = \beta(A_j + e) \bigg/ \overline{\beta(A + e)} , \quad (13)$$

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

$$\mathrm{E}[K_{Nj}] = L \cdot \beta(A_j + e) . \quad (14)$$

222 **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
224 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 Figure S1.

226 Although basic, Figure S1 shows good fit of the GB approximation. This validation is initial, and the more extensive validations we do on the Dirichlet-Multinomial approximation, because it is what we
228 will use in our analysts.

Dirichlet-Multinomial distribution approximation

230 **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
232 additional new ball of the same color. Let $\mathbf{U_i} = \{u_{i,1}, u_{i,2}, ..., u_{i,M}\}$ 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,
234 and 0 otherwise. The probability that $S_{i,j} = 1$ given $\mathbf{U_{i-1}}$ is

$$P(S_{i,j} = 1 \mid \mathbf{U_{i-1}}) = \frac{u_{i-1,j}}{\sum\limits_{m=1}^{M} u_{i-1,m}} = \frac{o_j + w_{i-1,j}}{\sum\limits_{m=1}^{M} o_m + w_{i-1,m}} = \frac{o_j + w_{i-1,j}}{i - 1 + \sum\limits_{m=1}^{M} o_m} \ , \tag{15}$$

236 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.

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

242 *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

$$G_{i,j} = \frac{\alpha'\beta(A'_j) + K_{i-1,j}}{\sum\limits_{m=1}^{N} \alpha'\beta(A'_m) + K_{i-1,m}} = \frac{\alpha'\beta(A'_j) + K_{i-1,j}}{i - 1 + \sum\limits_{m=1}^{N} \alpha'\beta(A'_m)} \ . \tag{16}$$

Substituting $M = N$, $o_j = \alpha'\beta(A'_j)$, and $w_{i,j} = K_{i,j}$ in eq. (15) gives eq. (16), thus completing the
246 proof.

Frigyik et al. [23, section 2] prove that the proportion of different colored balls in a *Pólya urn model*
248 converges to the Dirichlet distribution as the number of draws approaches infinity, based on the *Martingale Convergence Theorem* [18]. We therefore have an approximation for the relative prestige each
250 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 modified weights from a

252 Dirichlet distribution and we have the following corollary.

254 **Corollary 3.** *The number of copiers of each role-model follows a Dirichlet-Multinomial distribution,* $\mathbf{K_i} \sim \mathrm{DM}(N, \mathbf{G_1})$*, under the conditions of Result 2.*

256 **Numerical validation.** To validate our analytical result (Corollary 3) and test its sensitivity to the assumptions ($e_i = e$ and $\alpha_i = \alpha$ for $i = 1, \ldots, N$) we compare it to results of stochastic simulations of

258 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

260 expected theoretical DM distribution (Figure S2A). The difference in distributions was not perceived when plotting both distributions on the same figure, so we used the difference instead. The maximum

262 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 parameters vector of

264 the DM distribution itself (Figure S2B). We see that the negative log likelihood of the observed data is much higher than any other shuffled version of the parameters vector, supporting our approximation

266 more.

Next, we examined the fixation probability and fixation time of a favored phenotype $\hat{A}$ when invading

268 a population of phenotype A and compared results from the full model and the DM approximation. Thus, we assume the population has a single individual with phenotype $\hat{A}$ and $N - 1$ individuals with

270 phenotype A. We find that the number of simulations needed to sufficiently approximate our model with the DM approximation is roughly $1,000$ (Figure S3). We examined the robustness of the DM

272 approximation to relaxing the approximation assumptions. First, we relaxed our assumption of no estimation error e. Estimation error in the original model was drawn from a normal distribution, and

274 added to the trait value before evaluation of the bias ($A_{ij} = A_j + e_i$). When estimation error is applied, we sample J_i for each copier i from a normal distribution with varying scale (variance). Even when the

276 standard deviation is 0.1, the fixation probability and time is similar (Figure 1). We also relaxed our assumption of a uniform bias weight α (i.e., $\alpha_i = \alpha$). We allowed α to vary in the population, drawing

278 α_j for each role-model j from a normal distribution such that $\alpha_j \sim N(0.5, q)$ where $q \in [10^{-7}, 10^{-1}]$. We found again that results of the DM approximation are similar to those from stochastic simulations

280 of the full model (Figure 2).

Fixation probability and time

282 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

284 the fixation probability and conditional fixation time (conditioned on the population reaching fixation) of a favored phenotype, using a diffusion-equation approximation approach, similar to analyses of

286 population-genetic models [29, 30, 39]. 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

288 simplicity, we do not include role-model estimation error in this analysis, i.e $e_i = 0$ for every copier

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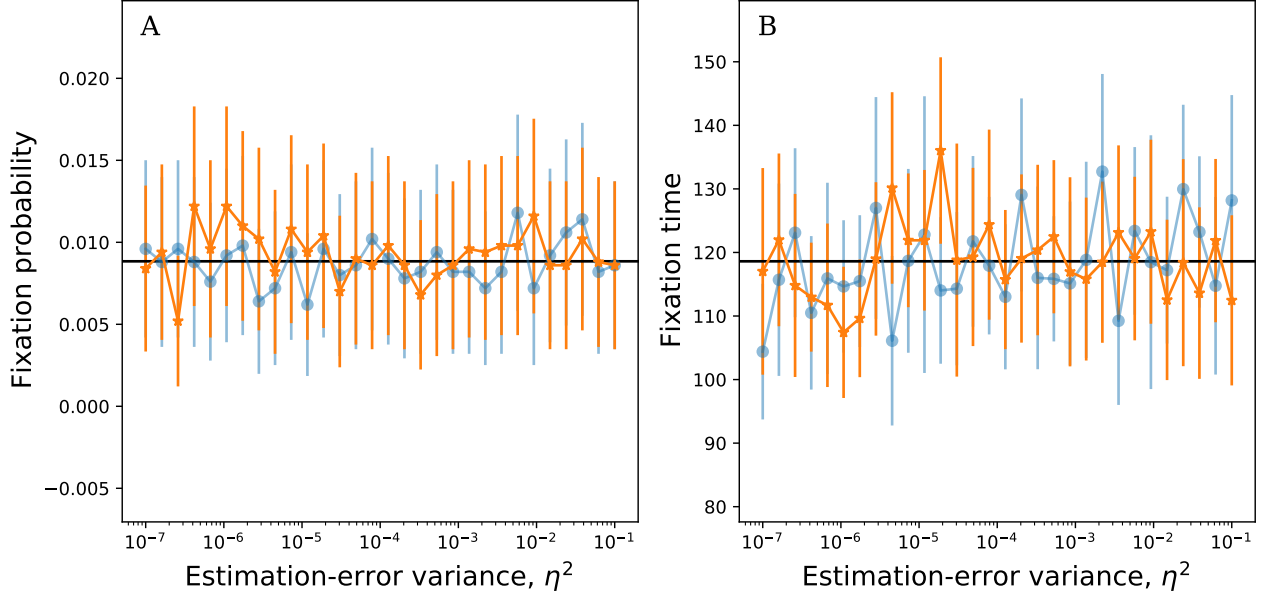
Figure 1: Robustness of DM approximations to success estimation error. Both the DM approximation (orange) and our approximation (black) agree with the stochastic simulations (blue), even with a high estimation error. Markers are averages across simulations, error bars are 95% confidence intervals. 5,000 simulations per data point; population size, $N = 1000$; success-bias weight, $\alpha = 0.1$; phenotype values, $\hat{A} = 1, A = 0.7$; bias strength parameter $J \sim N(1, \eta^2)$ where η^2 in on the x-axis.
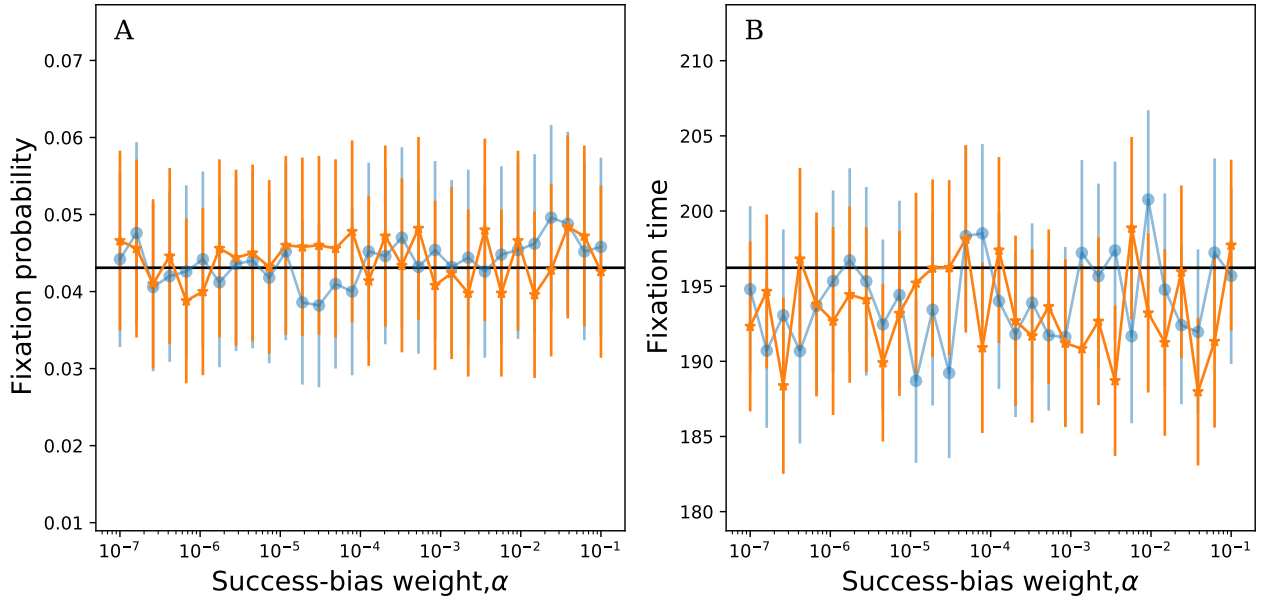
Figure 2: Robustness of DM approximations to variation in the bias weight α. Both the DM approximation (orange) and Kimura's equation (black line) fit the stochastic simulations (blue) well even with a high variation in success bias weight. Markers for average across 5,000 simulations, error bars are 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, $\beta(A) = 0.956$.

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i. As shown above, transmission in our model is approximately DM distributed (Corollary 3 and eq. (16)).

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. The proof is in Appendix B.

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,*

$$E[x' - x] \approx x(1 - x)(1 - \beta) , \quad V(x' - x) \approx x(1 - x)\left(\frac{1}{\alpha N + (1 - \alpha)}\right) . \tag{17}$$

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 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-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 $V[x' - x] = x(1 - x)/N_e$ [29, eq. 7]. Therefore, we have the following result.

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

$$s = 1 - \beta(A), \quad N_e = \alpha N + (1 - \alpha) . \tag{18}$$

Note that when $N \gg 1$, $N_e \approx \alpha N$, resulting in a very convenient expression.

Using our effective selection coefficient, $1 - \beta$, and effective population size, N_e, with the population-genetics fixation probability approximation given by Kimura [29, eq. 8], we get the following result:

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

$$\pi(x) = \frac{1 - e^{-2(1-\beta)N_e x}}{1 - e^{-2(1-\beta)N_e}} \tag{19}$$

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

318 Similarly, we can use $1 - \beta$ and N_e in the population-genetics fixation time approximation given by Kimura and Ohta [30, eq. 17].

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Result 6 (Fixation time). *The fixation time (conditioned on fixation) from an initial frequency x is*
322 *approximately*

$$T(x) = J_1(x) + \frac{1 - \pi(x)}{\pi(x)} \cdot J_2(x), \tag{20}$$

324 *where $N_e = \alpha N + (1 - \alpha)$, $S = N_e(1 - \beta)$, and*

$$
\begin{aligned}
J_1(x) &= \frac{2}{(1 - \beta)(1 - e^{-2S})} \int_x^1 \frac{(e^{2S\xi} - 1)(e^{-2S\xi} - e^{-2S})}{\xi(1 - \xi)} d\xi\,, \\
J_2(x) &= \frac{2}{(1 - \beta)(1 - e^{-2S})} \int_0^x \frac{(e^{2S\xi} - 1)(1 - e^{-2S\xi})}{\xi(1 - \xi)} d\xi\,.
\end{aligned}
\tag{21}
$$

326 Note that these integrals cannot be solved in closed form, so we can only estimate them numerically.

328 **Numerical validation.** We compare our approximations (eqs. (19) and (20)) with results of simulations of our dichotomous model using various α and β values, as well as simulations of the
330 Wright-Fisher model, using the effective selection coefficient, $1 - \beta$, and effective population size, $N_e = \alpha N + (1 - \alpha)$. We find see that the two models have similar dynamics, and both are well
332 approximated our approximations (Figure 3).

Changing environment . After finding a good approximation in constant environment, where the
334 favorable trait is always $\hat{A}$, we proceeded to find an approximation for a changing environment. Following Ram et al. [41], we denote k as the number of generations in which the invading phenotype is
336 favored by success bias, and l as the number of generations in which the resident phenotype is favored by success bias. We then proceed to find expressions for the expectation and variance of the change
338 in frequency between $n = k + l$ generations. The proof is in Appendix C.

340 **Result 7** (Drift and diffusion terms in a changing environment). *Let x be the initial frequency of the invading phenotype and X_t is the number of individuals with the phenotype after n generation. Then,*

342
$$E[X_n/N - x] \simeq x(1 - x)S_n/N_e\,, \quad and \quad V(X_n/N - x) \simeq nx(1 - x)/N_e\,, \tag{22}$$

where $S_n = \sum\limits_{t=1}^{n} N(1 - \beta_t)$.
344 Note that here, we have the average selection coefficient during a cycle of n generations as the selection coefficient eq. (19). Using the drift and diffusion terms and following Ram et al. [41], we
346 can approximate the fixation probability in a changing environment using

$$\tilde{\pi}(x) = \frac{1 - e^{-2\frac{S_n}{n}N_e x}}{1 - e^{-2\frac{S_n}{n}N_e}}\,. \tag{23}$$

Figure 3: Fixation probability and time in a constant environment. Fixation probability and time (in generations) as a function of the success-bias weight α (bottom x-axis), or effective population size N_e (top x-axis) in the top row, and as a function of the success coefficient, $1 - \beta$, on the bottom row. The approximation (black; eq. (19)) agrees with both DM simulations (green) and Wright-Fisher simulation (orange). Fixation probability (A) is bounded by $2(1 - \beta)$ (blue). Markers are averages of $10,000$ simulations, error bars show 95% confidence intervals for panels A and B and 75% for panels C and D. Here, Population size, $N = 1,000$; phenotype values, $\hat{A} = 1$, $A = 0.7$ (A and B), $A = a \cdot \hat{A}$ with $0.01 \leq a \leq 0.99$ (panels C and D); success coefficient, $1 - \beta = s = 0.044$ (A and B); success-bias weight, $\alpha = 0.01$ (panels C and D).

Numerical validation. Comparing our approximation (eq. (23)) to simulations, we find that the approximation fits simulation results well for variable bias weights, α, which corresponds to the effective population size (Figure 4A).

However, the approximation is more sensitive to the value of the success bias coefficient β (Figure 4B). 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 phenotype becomes extinct very quickly. For such β values (below 0.65), the fixation probability exceeds even the constant environment approximation (which is the upper limit). We note that the diffusion-equation approximation assumes weak selection, or in our case, weak success bias.

13

We found that for a large k/l ratio (with a constant cycle length, $n = k + l = 100$), the changing

358 environment approximation (eq. (23)) converges to the constant environment approximation (eq. (19)), see Figure 4C and Figure 4D.

360 The approximation follows the trend of the simulation results for all α values. When increasing the success coefficient to more than 0.15, the simulation results were located above the changing

362 environment approximation, and below the constant environment approximation. We believe the reason is the structure of the cycle. Our proof and approximation in the changing environment are for

364 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 enough copiers so that the influence is sufficient to negate the success

366 bias when the cycle changes (and the trait favored by the bias becomes the disfavored), or the opposite happens, and the ideal trait gets extinct before there were enough copiers that copied it. We then tried

368 to change the ratio between the number of cycles where $\hat{A}$ is favored and disfavored. We showed that the approximation fits well regardless of the ratio, but when the ratio of favored generations to

370 disfavored ones is very high, it is very similar to a constant environment model.

Figure 4: Fixation probability in a changing environment. (A) Fixation probability decreases with the the success-bias weight (bottom x-axis) and effective population size (top x-axis). The approximation (blue; eq. (23)) agrees with simulation results (orange). **(B)** Fixation probability increases with the success coefficient, β. When success bias is large ($1 - \beta > 0.1$), simulation results (orange) are underestimated by the changing environment approximation (blue; eq. (23)). With even larger success bias ($1 - \beta > 0.35$), even the constant environment approximation (green; eq. (19)) slightly underestimates simulation results, likely because the diffusion equation approximation assumes weak "selection". **(C,D)** The approximation (blue) is robust to changes in environmental cycle length, as it agrees with simulations (orange) for different sizes of the changing environment cycle, where k and l are the number of generations each trait value is under success bias. When $k > l$, the approximation and the simulations are both very close to the constant environment approximation (green), because the more generations the rare phenotype is favored, the more similar it is to the constant environment model, where it is always favored by the success bias. Markers show average of $10,000$ simulations, error bars show 75% (A, C, and D) and 95% (B) confidence intervals. Here, population size, $N = 1,000$; phenotype values, $\hat{A} = 1$, $A = 0.9$ (A and B), $A = 0.8$ (C and D); In (A), the success coefficient is: $1 - \beta = s = 0.005$; In (B, C, and D) the success-bias weight is $\alpha = 0.1$.

Adaptive success-bias weight

372   We ran simulations of the role-model choice process during a single generation in which every copier evaluates its own optimal success-bias weight, α^*, which minimizes the expected squared error

15

374   between the estimated and the ideal trait values,

$$\alpha^* = argmin \sum_{j=1}^{N} \frac{\alpha A_j + (1 - \alpha)K_j}{\sum_{l=1}^{N} \alpha A_l + (1 - \alpha)K_l} (\hat{A} - A_j)^2 \, , \tag{24}$$

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

378   We find that when copiers adapt their success-bias weight, it decreases with the number of copiers that have already chosen a role-model (Figure 5). Moreover, their estimation error is much lower

380   compared to a constant success-bias weight, which gives roughly the same high estimation error to all copiers (compare Figure 5B and C): in this example, the adaptive weight estimation error converges

382   to 0.046, whereas a constant weight gives values > 0.74.

Figure 5: 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 becomes more favored as more copiers have made their choice. However, when α is homogeneous (**C**), 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 $e \sim N(0, \eta^2)$ with standard deviation $\eta = 0.0001$ (blue), 0.001 (orange), 0.01 (green), plots are average of 300 simulations.

16

Discussion

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 copied more often due to transmission biases. A common bias 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 that because it is hard to estimate success, a more common bias is *prestige bias*—a bias towards role-models perceived to be successful. This perceived success can be determined by performance in another trait, i.e., by indirect success [7, 24], or by the influence an individual has on others [9, 25].

We developed a cultural-evolution model with prestige bias that includes both indirect success and influence biases, where the latter is a bias towards role-models with many copiers. We model the these biases using a stochastic role-model choice process: each copier, in its turn, randomly chooses a role-model, and this choice is affected both by the estimated success of each potential role-model and the number of copiers that already chose each role-model (eq. 10).

Hence, we have a model with two "nested" stochastic processes: the role-model choice process within each generation, and the cultural-evolutionary process between generations. To simplify the mathematical and computational analysis, we developed analytic approximations for the role-model choice process using the the *generalized binomial distribution* (GBD, Result 1) and the *Dirichlet-Multinomial distribution* (DM, Corollary 3). The latter is especially useful, as it approximates the entire role-model choice process and only requires us to assume that the relative effect of success and influence is a characteristic of the role-model and not the copier.

Analyzing the model with the DM distribution, we found approximations for the fixation probability and fixation time of a cultural trait under biased transmission in a constant environment. Our approximations are similar to Kimura's evolutionary-genetic approximations, such that (i) the difference between the resident and invading cultural trait values, $1 - \beta(A)$, is equivalent to the selection coefficient in favor of a beneficial allele, s, and (ii) increasing the relative weight of influence versus success bias, α, decreases the effective population size, N_e (Figure 3).

We also analyzed a cyclic changing environment in which the identity of the success-biased trait switches after a fixed amount of generations (Figure 4). We find that, similarly to the constant environment approximation, a change in the success-bias weight α has no negative effects on the goodness-of-fit of the approximation to simulation results. We also showed that this approximation is more sensitive to changes in the success coefficient β than the constant environment approximation, and a lower value is required to have a good fit. The ratio between the number of generation in which the rare phenotype is under positive transmission bias and the number of generations in which it is under negative bias does not affect the goodness-of-fit of the approximation.

We also examined a scenario in which copiers can adapt their success-weight bias, α, to minimize their copying error, i.e., copy trait values closer to the optimal value. We found that as the role-model

choice process proceeds (that is, more copiers make their choices), both the success-bias weight (adapted by copiers) and the estimation error decrease. The latter is significantly lower compared to a population using a constant, fixed success-bias weight, regardless of the value of the constant weight (Figure 5). This suggests that the later a copier makes its choice, the more it should rely on choices of previous copiers, and the less it should rely on its own estimation. The rationale, then, is that the more information a copier has, e.g., by using others as information sources, the more informative and effective his choice can be.

Prestige in the literature. According to King and Cowlishaw [31], there are two main approaches to group decision making in nature: leadership and consensus. Leaders would usually be high-ranking members of the group: elders, individuals with many kin relations, or individuals possessing other dominant traits. King and Cowlishaw [31] describe benefits for the closest associates of a dominant baboon, such as protection from predators. 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 [21]. 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 decision making that harms the group could result in negative effects for the leader. In modern society, many humans strive for prestigious positions, as they may reap rewards greater than the risk and costs to achieve them, or due to individual personality and pressure or education from the family.

Henrich and Gil-White [25] suggested that there are two types of leadership: prestige-based and dominance-based leadership. In the latter, social status is acquired through aggression, intimidation and violence. It is also more common than prestige in non-human animals. Their definition of prestige seems to overlap with ours. They suggest prestige is composed of estimation in the eyes of other people (similar to our success bias) and commanding position in people's minds, i.e, the number of followers other people think one has, which they define as *influence*, similar to our influence bias. Henrich and Gil-White [25] show that prestige can evolve via natural selection as an efficient process to extract reproductive benefit from the flow of socially transmitted information. They back up their claims by creating testable predictions and using evidence from the literature and experiments of social sciences. Simply put, prestige can naturally evolve when social learning already exists to save costs of individual learning.

Furthermore, according to Boyd and Henrich [6], the process of cultural evolution doesn't require accurate replication of cultural traits, addressed as "representation" in their paper. They base their assumption on three claims: mental representations are non-discrete, cultural transmission is highly inaccurate, and mental representations are not replicated, but rather are 'reconstructed' through an inferential process that is strongly affected by cognitive 'attractors.' They describe three different models to support their points. We see a high similarity between their model and ours. Like them, we treat the cultural trait as non-discrete (in the main model, before simplifying it to facilitate analysis). We also assume error in estimation, such that copiers do not precisely replicate their role-models, but rather reconstruct them to create a potentially different trait, which is their representation of the role-

458 model's trait. In addition, the inferential process that they describe as strongly affected by cognitive attractors may include our definition of influence bias.

460 **Conclusions.** Here, we studied a model of cultural evolution under two transmission biases: the commonly studied success bias, together with influence bias, which has so far received less attention.
462 We found approximations for this complex dynamics. We then showed that success bias affects the evolutionary dynamics much like natural selection does, whereas influence bias has a similar effect to
464 random genetic drift. We also find a clear advantage to individuals that can choose the relative weight of the two biases.

Acknowledgements

References

[1] Aljadeff, N., Giraldeau, L.-A., and Lotem, A. (2020). Competitive advantage of rare behaviours induces adaptive diversity rather than social conformity in skill learning. *Proceedings of the Royal Society B*, 287(1933):20201259.

[2] Anagnostopoulos, A., Kumar, R., and Mahdian, M. (2008). Influence and correlation in social networks. In *Proceedings of the 14th ACM SIGKDD international conference on Knowledge discovery and data mining*, pages 7–15.

[3] Andersson, M. B. (1994). *Sexual selection*. Princeton University Press.

[4] Battesti, M., Moreno, C., Joly, D., and Mery, F. (2012). Spread of social information and dynamics of social transmission within drosophila groups. *Current Biology*, 22(4):309 – 313.

[5] Borofsky, T. M. and Feldman, M. W. (2022). Success-biased social learning in a one-consumer, two-resource model. *Theor. Popul. Biol.*, 146:29–35.

[6] Boyd, R. and Henrich, J. (2002). On modeling cognition and culture: Why cultural evolution does not require replication of representations. *Journal of Cognition and Culture*, 2(2):87 – 112.

[7] Boyd, R. and Richerson, P. J. (1988). *Culture and the evolutionary process*. University of Chicago press.

[8] Cavalli-Sforza, L. L. and Feldman, M. W. (1981). *Cultural transmission and evolution: A quantitative approach*. Number 16. Princeton University Press.

[9] Chudek, M., Heller, S., Birch, S., and 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.

[10] Cohen, D., Lewin-Epstein, O., Feldman, M. W., and Ram, Y. (2021). Non-vertical cultural transmission, assortment and the evolution of cooperation. *Proceedings of the Royal Society B*, 288(1951):20203162.

[11] Creanza, N., Kolodny, O., and Feldman, M. W. (2017). Cultural evolutionary theory: How culture evolves and why it matters. *Proceedings of the National Academy of Sciences USA*, 114(30):7782–7789.

[12] Denton, K. K., Liberman, U., and Feldman, M. W. (2021). On randomly changing conformity bias in cultural transmission. *Proceedings of the National Academy of Sciences USA*, 118(34).

[13] Denton, K. K., Ram, Y., and Feldman, M. W. (2022). Conformity and content-biased cultural transmission in the evolution of altruism. *Theoretical population biology*, 143:52–61.

[14] Denton, K. K., Ram, Y., Liberman, U., and Feldman, M. W. (2020). Cultural evolution of conformity and anticonformity. *Proceedings of the National Academy of Sciences USA*, 117(24):13603–13614.

[15] Diga, M. and Kelleher, T. (2009). Social media use, perceptions of decision-making power, and public relations roles. *Public Relations Review*, 35(4):440–442.

[16] Drezner, Z. and Farnum, N. (1993). A generalized binomial distribution. *Communications in Statistics - Theory and Methods*, 22(11):3051–3063.

[17] Dunbar, R. (2009). The social brain hypothesis and its implications for social evolution. *Annals of Human Biology*, 36(5):562–572.

[18] Durrett, R. (1999). *Essentials of stochastic processes*, volume 1. Springer.

[19] Durrett, R. (2008). *Probability models for DNA sequence evolution*, volume 2. Springer.

[20] Efferson, C., Vogt, S., and Fehr, E. (2020). The promise and the peril of using social influence to reverse harmful traditions. *Nature human behaviour*, 4(1):55–68.

[21] Erhart, E. M. and Overdorff, D. J. (1999). Female coordination of group travel in wild propithecus and eulemur. *International Journal of Primatology*, 20(6):927–940.

[22] Fogarty, L., Wakano, J. Y., Feldman, M. W., and Aoki, K. (2017). The driving forces of cultural complexity. *Human Nature*, 28(1):39–52.

[23] Frigyik, B. A., Kapila, A., and Gupta, M. R. (2010). Introduction to the dirichlet distribution and related processes. *Department of Electrical Engineering, University of Washignton, UWEETR-2010-0006*, (0006):1–27.

[24] Henrich, J. and Broesch, J. (2011). On the nature of cultural transmission networks: evidence from fijian villages for adaptive learning biases. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567):1139–1148.

[25] Henrich, J. and Gil-White, F. J. (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.

[26] Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., and de Waal, F. B. (2010). Prestige affects cultural learning in chimpanzees. *PloS one*, 5(5):e10625.

[27] Hunter, J. D. (2007). Matplotlib: A 2d graphics environment. *Computing in science & engineering*, 9(03):90–95.

[28] Kendal, R., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., and Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. *Evolution and Human Behavior*, 36(1):65–72.

[29] Kimura, M. (1962). On the probability of fixation of mutant genes in a population. *Genetics*, 47(6):713.

[30] Kimura, M. and Ohta, T. (1969). The average number of generations until fixation of a mutant gene in a finite population. *Genetics*, 61(3):763.

[31] King, A. J. and Cowlishaw, G. (2009). Leaders, followers, and group decision-making. *Communicative & Integrative Biology*, 2(2):147–150.

[32] Kolodny, O., Feldman, M. W., Lotem, A., and Ram, Y. (2022). Differential application of cultural practices at the family and individual levels may alter heritability estimates. *Behav. Brain Sci.*, 45:e167.

[33] Lee, W., Xiong, L., and Hu, C. (2012). The effect of facebook users' arousal and valence on intention to go to the festival: Applying an extension of the technology acceptance model. *International Journal of Hospitality Management*, 31(3):819–827.

[34] McComb, K., Moss, C., Durant, S. M., Baker, L., and Sayialel, S. (2001). Matriarchs as repositories of social knowledge in african elephants. *Science*, 292(5516):491–494.

[35] Mesoudi, A. and O'Brien, M. J. (2008). The cultural transmission of great basin projectile-point technology II: An agent-based computer simulation. *Am. Antiq.*, 73(4):627–644.

[36] Molleman, L., Pen, I., and Weissing, F. J. (2013). Effects of conformism on the cultural evolution of social behaviour. *PloS one*, 8(7):e68153.

[37] Muthukrishna, M. and Henrich, J. (2016). Innovation in the collective brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1690):20150192.

[38] Norredam, M. and Album, D. (2007). Prestige and its significance for medical specialties and diseases. *Scandinavian journal of public health*, 35(6):655–661.

[39] Otto, S. P. and Whitlock, M. C. (2006). Fixation probabilities and times. *Encyclopedia of Life Sciences*.

[40] Peng, S., Zhou, Y., Cao, L., Yu, S., Niu, J., and Jia, W. (2018). Influence analysis in social networks: A survey. *Journal of Network and Computer Applications*, 106:17–32.

[41] Ram, Y., Liberman, U., and Feldman, M. W. (2018). Evolution of vertical and oblique transmission under fluctuating selection. *Proceedings of the National Academy of Sciences USA*, 115(6):E1174–E1183.

[42] Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., Fogarty, L., Ghirlanda, S., Lillicrap, T., and Laland, K. N. (2010). Why copy others? insights from the social learning strategies tournament. *Science*, 328(5975):208–213.

[43] Takahashi, T. and Ihara, Y. (2019). Cultural and evolutionary dynamics with best-of-k learning when payoffs are uncertain. *Theoretical Population Biology*, 128:27–38.

[44] Truskanov, N., Emery, Y., and Bshary, R. (2020). Juvenile cleaner fish can socially learn the consequences of cheating. *Nat. Commun.*, 11(1):1–9.

[45] Van Der Walt, S., Colbert, S. C., and Varoquaux, G. (2011). The numpy array: a structure for efficient numerical computation. *Computing in science & engineering*, 13(2):22–30.

[46] Van Rossum, G. et al. (2007). Python programming language. In *USENIX annual technical conference*, volume 41, pages 1–36.

[47] Van Vugt, M. and Smith, J. E. (2019). A dual model of leadership and hierarchy: Evolutionary synthesis. *Trends in Cognitive Sciences*, 23(11):952–967.

[48] Whitehead, H. (2017). Gene–culture coevolution in whales and dolphins. *Proceedings of the National Academy of Sciences USA*, 114(30):7814–7821.

Appendices

Appendix A   General binomial distribution approximation

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

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

$$G_{1,j} = \frac{\alpha_j \cdot \beta(A_j + e)}{\sum\limits_{m=1}^{N} \alpha_m \cdot \beta(A_m + e)} \ . \tag{A1}$$

The denominator of eq. (A1) can also be formulated as:

$$\sum_{m=1}^{N} \alpha_m \beta(A_m + e) = N \cdot \overline{\alpha \cdot \beta(A + e)} \ , \tag{A2}$$

where $\overline{\alpha\beta(A + e)}$ is the mean value of $\alpha_m \cdot \beta(A_m + e)$ for all m. Using eq. (A2) and **Corollary 1** we get,

$$E[K_{Nj}] = \alpha_j \cdot \beta(A_j + e)\Big/\overline{\alpha \cdot \beta(A + e)} \ , \tag{A3}$$

Appendix B   Drift and diffusion in a constant environment

Proving 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,

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

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),

$$E[X'] = N\frac{\alpha_1}{\alpha_1 + \alpha_2} \ , \tag{B1}$$

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,

$$
\begin{aligned}
E[x'] &= \frac{1}{N}N\frac{\alpha'xN}{\alpha'xN + \alpha'N(1 - x)\beta} = \frac{x}{x + (1 - x)\beta} \\
&= \frac{x}{x + (1 - x) - (1 - x) + (1 - x)\beta} = x\frac{1}{1 - (1 - x)(1 - \beta)} \\
&= x\big(1 + (1 - x)(1 - \beta) + o(\beta)\big) = x + x(1 - x)(1 - \beta) + o(\beta) ,
\end{aligned}
\tag{B2}
$$

following Durrett [19, 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

$$
E[x' - x] = E[x'] - E[x] = x(1 - x)(1 - \beta) + o(1 - \beta) ,
\tag{B3}
$$

which gives us the drift term of the diffusion equation.

Using the variance of the DM distribution,

$$
V(X') = N\frac{\alpha_1}{\alpha_1 + \alpha_2}\left(1 - \frac{\alpha_1}{\alpha_1 + \alpha_2}\right)\left(\frac{N + \alpha_1 + \alpha_2}{1 + \alpha_1 + \alpha_2}\right) .
\tag{B4}
$$

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,

$$
V(x') = \frac{1}{N^2}N\frac{x}{x + (1 - x)\beta}\left(1 - \frac{x}{x + (1 - x)\beta}\right)\left(\frac{N + \alpha'xN + \alpha'N(1 - x)\beta}{1 + \alpha'xN + \alpha'N(1 - x)\beta}\right) .
\tag{B5}
$$

Following Durrett [19, ch 7.2], we assume $\beta \approx 1$, such that

$$
\frac{x}{x + (1 - x)\beta} \approx x
\tag{B6}
$$

and for the entire variance expression we get

$$
V(x') \approx \frac{1}{N}x(1 - x)\left(\frac{N + \alpha'xN + \alpha'N - \alpha'xN}{1 + \alpha'xN + \alpha'N - \alpha'xN}\right) = x(1 - x)\left(\frac{1 + \alpha'}{1 + \alpha'N}\right) .
\tag{B7}
$$

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

$$
V(x' - x) = V(x') - V(x) \approx x(1 - x)\left(\frac{1 + \alpha'}{1 + \alpha'N}\right) .
\tag{B8}
$$

α' is the odds ratio of the bias weight,

$$
\alpha' = \frac{\alpha}{1 - \alpha} .
\tag{B9}
$$

Combining eq. (B8) and eq. (B9) we get:

$$V(x' - x) \approx x(1 - x)\left(\frac{1 + \frac{\alpha}{1-\alpha}}{1 + \frac{\alpha}{1-\alpha}N}\right) = x(1 - x)\left(\frac{1}{\alpha N + (1 - \alpha)}\right) . \tag{B10}$$

This gives the diffusion term of the diffusion equation.

Appendix C Drift and diffusion in a changing environment

Proving drift and diffusion terms in a changing environment. Let x be the initial frequency of the invading phenotype and X_t is the number of individuals with the phenotype at time t. Then,

$$E[X_t/N - x] \simeq x(1 - x)S_t/N_e , \quad \text{and} \quad V(X_t/N - x) \simeq tx(1 - x)/N_e ,$$

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

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 both terms in eq. (22). From eq. (B3) we know that

$$E\left[\frac{X_{t+1}}{N} - \frac{X_t}{N}\bigg|X_t\right] = \frac{X_t}{N}\left(1 - \frac{X_t}{N}\right)(1 - \beta_{t+1}) = \frac{1}{N}\frac{X_t}{N}\left(1 - \frac{X_t}{N}\right)s_{t+1} . \tag{C1}$$

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

$$E\left[\frac{X_t}{N}\left(1 - \frac{X_t}{N}\right)\right] = E\left[\frac{X_t}{N} - \left(\frac{X_t}{N}\right)^2\right] = E\left[\frac{X_t}{N}\right] - E\left[\left(\frac{X_t}{N}\right)^2\right]$$

$$= E\left[\frac{X_t}{N}\right] - V\left(\frac{X_t}{N}\right) - \left(E\left[\frac{X_t}{N}\right]\right)^2 . \tag{C2}$$

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

$$E\left[\frac{X_t}{N}\left(1 - \frac{X_t}{N}\right)\right] \simeq E\left[\frac{X_t}{N}\right]\left(1 - E\left[\frac{X_t}{N}\right]\right) - \frac{1}{N_e}tx(1 - x) . \tag{C3}$$

From eq. (C1) we know that

$$E\left[\frac{X_{t+1}}{N} - \frac{X_t}{N}\right] = \frac{1}{N}s_{t+1}E\left[\frac{X_t}{N}\left(1 - \frac{X_t}{N}\right)\right] \simeq \frac{1}{N}s_{t+1}\left(E\left[\frac{X_t}{N}\right]\left(1 - E\left[\frac{X_t}{N}\right]\right) - \frac{1}{N_e}tx(1 - x)\right)$$

$$\simeq \frac{1}{N}s_{t+1} \cdot E\left[\frac{X_t}{N}\right]\left(1 - E\left[\frac{X_t}{N}\right]\right) - \frac{1}{N_eN}s_{t+1}tx(1 - x) . \tag{C4}$$

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

$$E\left[\frac{X_{t+1}}{N} - \frac{X_t}{N}\right] \simeq \frac{1}{N}s_{t+1} \cdot E\left[\frac{X_t}{N}\right]\left(1 - E\left[\frac{X_t}{N}\right]\right) . \tag{C5}$$

We now look at the induction assumption to see that

$$E\left[\frac{X_t}{N} - x\right] = E\left[\frac{X_t}{N}\right] - E[x] = E\left[\frac{X_t}{N}\right] - x, \tag{C6}$$

so using the assumption we get

$$E\left[\frac{X_t}{N}\right] \simeq \frac{1}{N}S_t x(1-x) + x,$$

$$1 - E\left[\frac{X_t}{N}\right] \simeq 1 - \frac{1}{N}S_t x(1-x) + x. \tag{C7}$$

We use both expressions in eq. (C5) and get

$$E\left[\frac{X_{t+1}}{N} - \frac{X_t}{N}\right] \simeq \frac{1}{N}s_{t+1}\left(\frac{1}{N}S_t x(1-x) + x\right)\left(1 - \frac{1}{N}S_t x(1-x) + x\right)$$

$$\simeq \frac{1}{N}s_{t+1} \cdot x(1-x), \tag{C8}$$

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

$$E\left[\frac{X_{t+1}}{N} - x\right] = E\left[\frac{X_{t+1}}{N} - \frac{X_t}{N}\right] + E\left[\frac{X_t}{N} - x\right], \tag{C9}$$

so again using the induction assumption, together with eq. (C8) we get

$$E\left[\frac{X_{t+1}}{N} - x\right] \simeq \frac{1}{N}s_{t+1} \cdot x(1-x) + \frac{1}{N}S_t \cdot x(1-x)$$

$$\simeq \frac{1}{N}x(1-x)(S_t + s_{t+1}) \simeq \frac{1}{N}S_{t+1}x(1-x), \tag{C10}$$

which proves the drift term.

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

$$V\left(\frac{X_{t+1}}{N}\right) = E\left[V\left(\frac{X_{t+1}}{N}\bigg|X_t\right)\right] + V\left(E\left[\frac{X_{t+1}}{N}\bigg|X_t\right]\right). \tag{C11}$$

Using eq. (C1) we see that

$$E\left[\frac{X_{t+1}}{N}\bigg|X_t\right] - E\left[\frac{X_t}{N}\bigg|X_t\right] = \frac{1}{N}s_{t+1}\frac{X_t}{N}\left(1 - \frac{X_t}{N}\right)$$

$$E\left[\frac{X_{t+1}}{N}\bigg|X_t\right] = \frac{X_t}{N} + \frac{1}{N}s_{t+1}\frac{X_t}{N}\left(1 - \frac{X_t}{N}\right). \tag{C12}$$

Using eq. (B10) we get

$$V\left(\frac{X_{t+1}}{N}\bigg|X_t\right) = \frac{1}{N_e}\frac{X_t}{N}\left(1 - \frac{X_t}{N}\right), \tag{C13}$$

and using the equation $y'(1 - y') \simeq y(1 - y)$ on the first part of eq. (C11) we get

$$E\left[V\left(\frac{X_{t+1}}{N}\Big|X_t\right)\right] = \frac{1}{N_e}E\left[\frac{X_t}{N}\left(1 - \frac{X_t}{N}\right)\right] \simeq \frac{1}{N_e}x(1 - x) \, . \tag{C14}$$

Moving on to simplify the second part of eq. (C11) using eq. (C12),

$$V\left(E\left[\frac{X_{t+1}}{N}\Big|X_t\right]\right) = V\left(\frac{X_t}{N} + \frac{1}{N}s_{t+1}\frac{X_t}{N}\left(1 - \frac{X_t}{N}\, . \right)\right) \tag{C15}$$

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

$$V\left(\frac{1}{N}s_{t+1}\frac{X_t}{N}\left(1 - \frac{X_t}{N}\right)\right) \le \frac{1}{4N^2}s_{t+1}^2; \, , \tag{C16}$$

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

$$V\left(E\left[\frac{X_{t+1}}{N}\Big|X_t\right]\right) = V\left(\frac{X_t}{N}\right) + O\left(\frac{1}{N^2}\right) \simeq V\left(\frac{X_t}{N}\right) \, . \tag{C17}$$

Using the induction assumption and eq. (C14),

$$V\left(\frac{X_{t+1}}{N}\right) \simeq \frac{1}{N_e}x(1 - x) + \frac{1}{N_e}tx(1 - x) \simeq \frac{1}{N_e}x(1 - x)(t + 1) \tag{C18}$$

which proves the diffusion term.
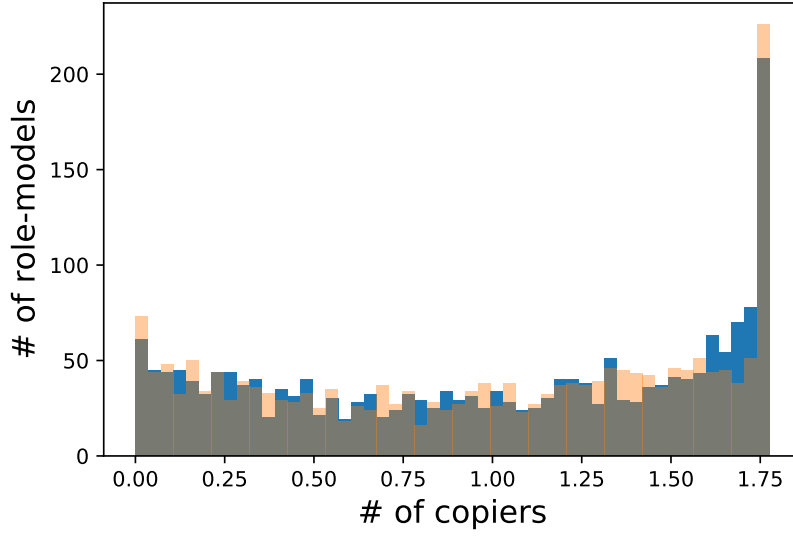
Supplementary Figures

Figure S1: Numerical validation of the GB 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, $\beta(A) = 0.956$.
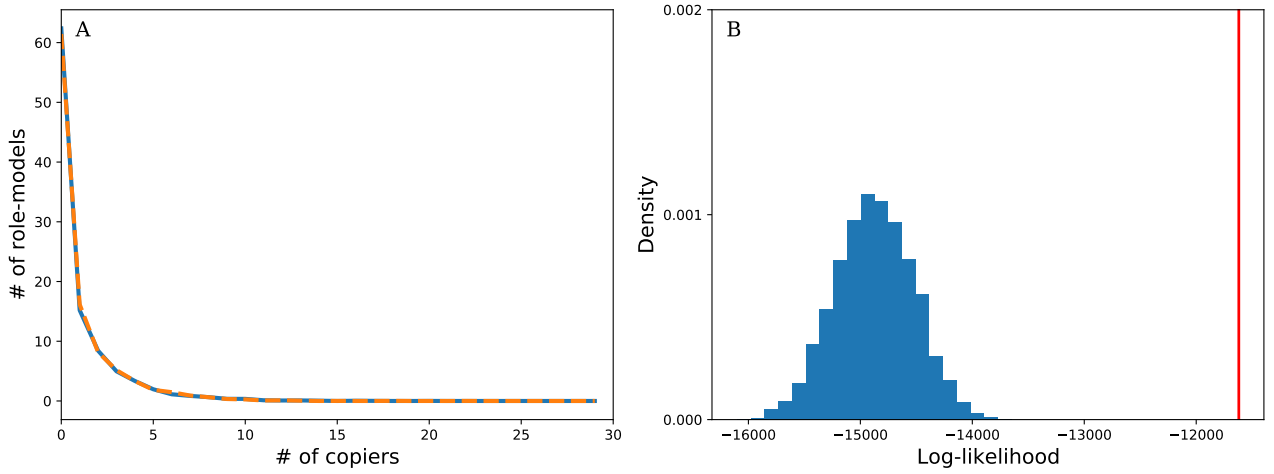
Figure S2: Numerical validation of the DM approximation. We performed computational "experiments" of the role-model choice process and compared them to the DM distribution. **(A)** The difference between the DM distribution (orange) and the empirical distribution of the experiments (blue) is very small. **(B)** The log-likelihood of the DM distribution for results of the experiments (red vertical line) is much higher compared to the log-likelihood of permutations of experiments (blue histogram). Here, population size, $N = 100$; number of experiments, $m = 100$; phenotype values, $\hat{A} = 1$, $A \sim N(0, 1)$; success-bias weight, $\alpha = 0.5$. No estimation error or bias is applied, and traits are estimated and copied perfectly.
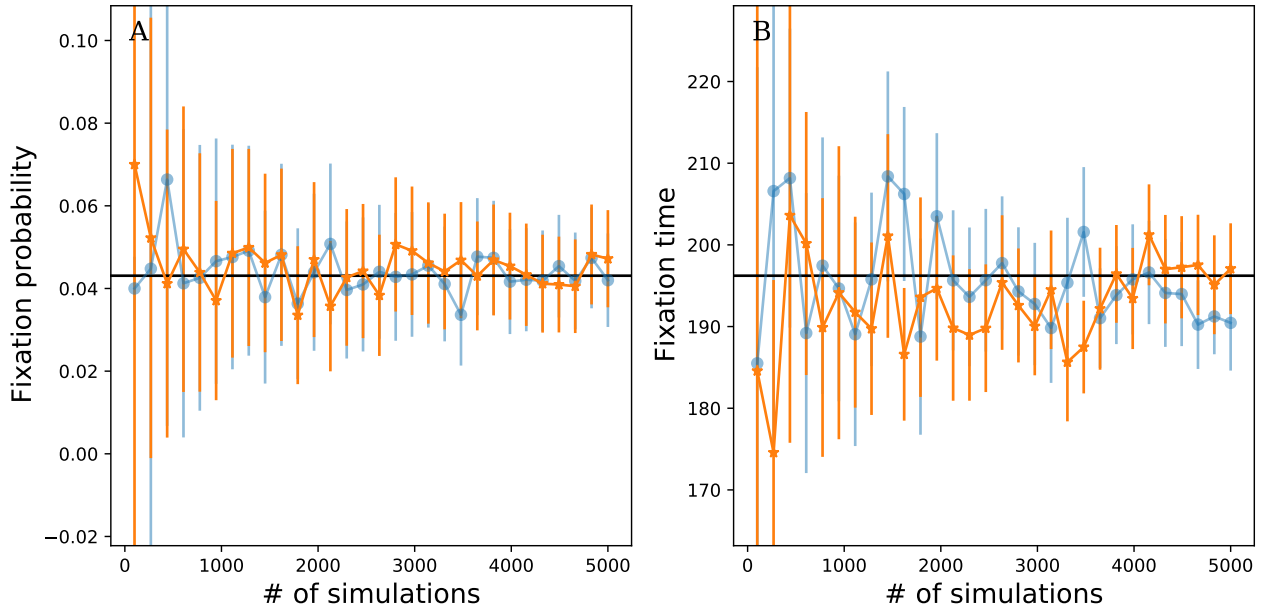

Figure S3: DM Approximation precision as function of number of simulations. Our DM approximation (orange) agrees with stochastic simulation results (blue) when using 1,000 or more simulations. Both fluctuate around the analytic fixation probability approximation (black; eq. (19)). Markers are averages across simulations, error bars are 95% confidence intervals. Here, population size, $N = 1000$; success-bias weight, $\alpha = 0.5$; phenotype values, $\hat{A} = 1$, $A = 0.7$; success-bias value, $\beta(A) = 0.956$.