

Influence bias in cultural evolutionary dynamics

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Abstract

If the traits of more successful individuals are more likely to be adopted, the resulting cultural transmission is described as being success-biased. Prestige may be used as a proxy for success. Here, we model influence bias as a combination of indirect success bias and prestige bias, the latter meaning that the choice of a role-model depends on the number of individuals that have already copied that role-model. The effect of prestige on cultural evolutionary dynamics is analyzed using mathematical analysis and stochastic simulations. Analytic approximations to the stochastic role-model choice process facilitate the mathematical analysis and reduce the computational complexity of simulations. Approximations are given 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 prestige bias effectively plays the role of genetic drift. Influence bias, which may be strong in communities where social media are prevalent, also accelerates the evolutionary dynamics, as can be expected in a rich-get-richer process.

Introduction

22 Cultural transmission of attitudes, preferences, beliefs, norms, and behaviors may combine vertical
transmission, in which parents transmit to their offspring; oblique transmission, in which adults
24 (teachers, leaders, and even strangers) transmit to unrelated offspring; and horizontal transmission, in
which individuals from the same age cohort transmit to one another [6]. It has been demonstrated that
26 non-vertical cultural transmission can maintain maladaptive traits, which can be beneficial in changing
environments [23, 56].

28 Transmission biases may cause a cultural trait to have a higher rate of transmission than its frequency in
the population. *Success bias* occurs when individuals prefer to copy from role models that demonstrate
30 success in some activity, such as fishing, growing yams, using medicinal plants [26], or hunting [55],
and it can increase the probability of learning a trait that is present in those successful individuals [54].
32 Indeed, in a tournament between learning strategies [9], most winning strategies included a mixture
of success-biased social learning and individual learning, implying that success-biased learning is a
34 good strategy, but that by itself it is not enough to best other strategies, even when success is measured
accurately.

36 Boyd and Richerson [7, Ch. 5] suggested that the assessment of success can be divided to three
categories: *direct bias*, *indirect bias* and *frequency-dependent bias*. Direct bias occurs when one
38 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 try the observed paddle grips to determine
40 which grip is better. Frequency-dependent bias occurs when the probability of copying a phenotype
is higher or lower than the frequency of the phenotype among demonstrators. For example, suppose
42 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
44 by 40% of copiers, then transmission is under negative frequency bias, or *anti-conformity* [17]. The
effects of conformity and anti-conformity on cultural evolution have been studied with both models
46 [37, 38, 53] and experiments [5]. Indirect bias occurs when a copier uses some observed phenotype to
evaluate the attractiveness of a potential role-model. For example, an observer may copy the paddle
48 grip of the ping-pong player who scored more points in the match, thus indirectly evaluating the grip
by the points scored. However, this may cause mismatches between the copied trait and the rest of
50 the cultural or genetic repertoire of the individual [52]. Furthermore, Boyd and Richerson [7, Ch. 8]
suggest that maladaptive traits may spread widely in a population if indirect bias is strong enough,
52 e.g., by a runaway process caused by a cultural equivalent of sexual selection [10]. Indeed, helping
behaviors can evolve due to horizontal transmission bias even without any benefit to the recipient, or
54 when the benefit is much larger than the cost [36].

Henrich and Broesch [26] studied such indirect success biases, which they call cross-domain success
56 bias or *prestige bias* (e.g., great fishermen may be chosen as role-models for growing yams). They
suggested that such biases, over generations, can lead to cultural adaptations, and that although prestige
58 can lead to maladaptive traits spreading in the population, it can also accelerate the spread of adaptive

traits [7, Ch. 8]. Prestige bias may be more common in humans than success bias [8], and prestige is
60 often mentioned in the cultural evolution literature, although there are few models of it; see Chellappoo
(2021) for a philosophical critique of the concept of prestige itself.

62 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).
64 Indeed, Chudek et al. [32] 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
66 year old children. Henrich and Gil-White [28] gave a similar definition of prestige as “freely conferred
deference”, in contrast to *dominance*, and provided examples from the anthropological literature.

68 Jimenez & Mesoudi [1] suggest that cultural evolution theory is a major factor in human ecological
success. They mention that a way to acquire adaptive social information is by preferentially copying
70 competent individuals within a valuable domain, and they call it success bias as we do in this paper.
They also mention that competence within a domain is often difficult or impossible to directly asses,
72 therefore people tend to use indirect cues of success, as suggested by Henrich and Gil-White [28].

Henrich and Gil-White [28] noted that “the most skilled/knowledgeable role-models will, on average,
74 end up with the biggest and most lavish clienteles, so the size and lavishness of a given model’s
clientele size (the *prestige*) provides a convenient and reliable proxy for that person’s information
76 quality”. Therefore, they predicted that skilled individuals have higher status, people preferentially
copy them more than others, and therefore prestigious individuals may be influential even beyond their
78 domain of expertise.

Here, we examine the effect of both success and prestige biases, and their relationship in contribution to
80 the cultural evolution of populations. We call the joint contribution of both biases *influence bias*. This
is an important distinction, as prestige is a context-dependent bias, rather than a content-dependent
82 bias: it does not depend on the phenotype itself but rather on the number of copiers that have already
copied each role-model, which may be easier and more accurate to estimate than success. Prestige
84 bias is also frequency independent (see Corollary 1 below), and thus it differs from conformity, which
depend on the frequency of a trait in the population or in a sample of role-models, rather than the
86 social dynamics of copying.

In contemporary human society, social media make it especially easy to estimate the social and cultural
88 influence individuals have over others, which can have an effect on decision making. Online social
networks such as *Facebook* and *Instagram* are known to affect the influence of individuals [40, 41, 42],
90 and specific marketing practices have been invented to capitalize on this effect [39].

In the following, we develop a stochastic model of cultural transmission with influence bias that com-
92 bines both cross-domain indirect success bias and prestige bias. We develop analytic approximations
for this model and analyze its dynamics. We also find approximations for the probability and time to
94 fixation of a ‘successful’ phenotype (i.e., that is subject to success bias). Comparing these approxi-
mations to Kimura’s approximations for the fixation of a favorable allele [21, 46], we demonstrate that
96 success and influence bias play the role of natural selection and genetic drift, respectively.

Models

98 We begin with a continuous trait model with indirect bias, previously suggested by Boyd and Richerson [7]. We extend this model to include influence bias. We then develop a dichotomous trait model.
100 Note that the indirect bias is due to an indirect evaluation, in which a certain phenotype is used to evaluate the success of potential role-models.
102 We implement our stochastic models and approximations, perform statistical analyses, and produce figures using Python [43] with NumPy [44] and Matplotlib [45]. Source code is available at
104 <https://github.com/yoavram-lab/PrestigeBias>.

Continuous trait

106 We follow the Boyd and Richerson model [7], assuming only oblique transmission of a single trait. Consider a population of N individuals, described by a single trait that takes continuous values.
108 Each generation, N naive individuals, or copiers, each chooses a single role-model from the entire previous generation. The copier then copies its trait value from the chosen role-model. Note that our
110 transmission models are slightly different from those modeled before, e.g. [7, 38, 58], in which the population is infinite and each copier samples n role-models and then copies its trait from one or more
112 of the sampled role-models.

Similar to a Wright-Fisher model, generations are non-overlapping, and the entire population is
114 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 , and the initial population is drawn from a standard
116 normal distribution, $\mathbf{A}(0) \sim N(0, 1)$. Cultural transmission is modeled by a function F such that

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

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

$$120 \quad F_i(\mathbf{A}) = \sum_{j=1}^N G_{i,j} \cdot A_{i,j} , \quad (2)$$

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

$$122 \quad G_{i,j} = \frac{\beta(A_{i,j})}{\sum_{k=1}^N \beta(A_{i,k})} , \quad (3)$$

$A_{i,j}$ is the absolute trait value that copier i estimates for role-model j with some error $e_i \sim$
124 $N(0, \eta^2)$,

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

126 and $\beta(\cdot)$ is the bias function that quantifies the success bias of a role-model [7, eq. 5.11],

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

128 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 .

130 Boyd and Richerson [7] note that the deterministic blended transmission algorithm they use has alternatives. We can develop a similar stochastic model with transmission from a single random
132 role-model where instead of eq. (2), we define the transmission function F as a random variable with its distribution given by

$$134 \quad \Pr(F_i(\mathbf{A}) = A_j) = G_{i,j}; \quad (6)$$

here $G_{i,j}$ is the probability that copier i chooses to copy the trait of role-model j .

136 **Prestige bias.** Here we introduce a new element to the model by assuming that in each generation, copiers choose their role-models one by one. We formulate this assumption in the following. Denote
138 by $K_{i,j}$ the number of copiers that choose role-model j after copier i chose a role-model. Thus, i out of N copiers had already chosen a role-model, $\sum_{j=1}^N K_{i,j} = i$, and there are $N - i$ copiers that have yet
140 to choose a role-model. The stochastic process of role-model choice,

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

142 is described by the recurrence equation

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

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

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

$$148 \quad \Pr(S_{i,j} = 1 \mid S_{1,j}, S_{2,j}, \dots, S_{i-1,j}) = G_{i,j}. \quad (9)$$

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

$$152 \quad G_{i,j} = \frac{\alpha_{ij} \cdot \beta(A_{i,j}) + (1 - \alpha_{ij}) \cdot K_{i-1,j}}{W_i}, \quad (10)$$

where W_i is a normalizing factor that sums the numerator over all role-models ($1 \leq j \leq N$) to ensure
154 $\sum_{j=1}^N G_{i,j} = 1$.

Here, the bias weight $\alpha_{i,j}$ determines the relative weighting of success and prestige bias. It is a characteristic of the interaction of role-model j with copier i that determines the relative significance of direct success vs. prestige in the role-model's overall influence in the eyes of the copier. Different individuals may evaluate the importance of success and prestige differently. Additionally, we assume each role-model displays its prestige and success individually. For example, individuals with more followers but lacking skill may emphasize the number of their followers rather than their skill. Finally, the trait of role-model j estimated by copier i , $A_{i,j}$, remains as in eq. (4).

Dichotomous trait

We introduce a simplified version of the above model where the trait has only two phenotypes: an optimal phenotype \hat{A} and a sub-optimal phenotype A . All role-models with the same phenotype will contribute to the probability that that phenotype is 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, which entails exchangeability between role-models. Therefore, the probability that the i -th copier copies phenotype A is

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

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; assuming that $\beta(\hat{A}) = 1$; and defining $\alpha' = \frac{\alpha}{1-\alpha}$ as the odds ratio of the bias weight. Complementing this, the probability of the i -th copier to copy phenotype \hat{A} is $G_{i,\hat{A}} = 1 - G_{i,A}$.

Results

Our models are defined by two nested stochastic processes. Change over multiple generations is described by the dynamics of the phenotype distribution at each generation, $\{\mathbf{A}(t)\}_t$, see eq. (1). 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, $\{\mathbf{K}_i\}_{i=1}^N$, see eq. (7). We emphasize that the models are nested: $\mathbf{A}(t+1)$ can be computed from $\mathbf{A}(t)$ by evaluating \mathbf{K}_N , where $K_{N,j}$ is the number of copiers that chose role-model j after all copiers chose a role model. 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 approximations for the distribution of \mathbf{K}_N , summarized here and explained in detail below. In both we assume that the bias weight is either completely homogeneous, $\alpha_{i,j} = \alpha$, or that $\alpha_{i,j} = \alpha_j$ is a bias of role-model j only, meaning it does not vary between copiers. Note that these approximations apply for both the and the continuous trait (eq. (10)) and the dichotomous trait (eq. (11)) models.

Generalized binomial approximation. The number of copiers of a specific role-model at each step, $K_{i,j}$, follows the *generalized binomial distribution* [18] and therefore,

190 (i) the expected number of copiers of role-model j equals its influence 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
192 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
194 models, that is, $E[K_{N,j}] = \beta(A_j + e)/\bar{\beta}$ 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.

196 **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 $i = 1, \dots, N$).

198 Generalized binomial distribution

The generalized binomial distribution (GBD) emerges from a series of dependent Bernoulli trials
200 (in contrast to the standard binomial distribution in which trials are independent) and is denoted by
 $GBD(n, p, \theta)$ where n is the number of trials, p is the probability of success of the first trial, and θ is
202 the correlation between trials (the latter can be estimated from data, but its value is insignificant for
our approximation). Note that $\theta = 0$ gives the standard binomial distribution.

204

Result 1 (Generalized binomial approximation). *The number of copiers of role-model j after i copiers
206 have chosen a role-model follows the generalized binomial distribution, $K_{i,j} \sim GBD(i, \alpha_j \cdot \beta(A_j + e), \theta)$
if $e_i = e$ for all role-models $i = 1, \dots, N$, and θ is the correlation between successive role-model
208 choices.*

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

$$212 \quad Q_j(k, i) = P_j(S_{i,j} = 1 \mid k - 1, i - 1) \cdot Q_j(k - 1, i - 1) + P_j(S_{i,j} = 0 \mid k, i - 1) \cdot Q_j(k, i - 1), \quad (12)$$

where $S_{i,j} = 1$ when the i -th copier chooses role-model j . Equation (12) is equivalent to eq. (2.1) in
214 [18], which completes the proof.

This result gives the following corollary on the expected number of followers of a given role-model j
216 by the end of the role-model choice process, $K_{N,j}$.

218 **Corollary 1.** *The expected number of copiers of role-model j after all copiers have chosen a role-
model is $E[K_{N,j}] = N \cdot G_{1,j}$, where $G_{1,j}$ is the probability of the first copier to copy role-model j . In
220 addition, $E[K_{N,j}] = \alpha_j \cdot \beta(A_j + e) / \alpha \cdot \beta(A + e)$, where the averaging in the denominator is over the
role-models index, j .*

222 *Proof.* The expected value of the GBD is $E[K_{N,j}] = N \cdot Q_j(1, 1)$, see Drezner and Farnum [18,
eq. (2.3)]. Here, $Q_j(1, 1)$ is the initial probability to choose role-model j , before any role-model
224 choices are made, such that $Q_j(1, 1) = G_{1,j}$ by definition. The rest of the proof is in Appendix A.

From Corollary 1 we see that if there is no success bias, meaning $Q_j(1, 1) = q$ for j in $1, \dots, N$, then
 226 the expected number of copiers will be Binomial distributed. This proves that prestige bias is not
 frequency dependent.

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

$$230 \quad E[K_{N,j}] = N \cdot \frac{\alpha \cdot \beta(A_j + e)}{\sum_{m=1}^N \alpha \cdot \beta(A_m + e)} = \beta(A_j + e) \sqrt{\frac{1}{\beta(A + e)}}, \quad (13)$$

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

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

234 **Numerical validation.** To validate that GBD approximation for the number of copiers of a role-
 model is correct (eq. (13)), we ran 1,000 simulations of the full model, and compared the results with
 236 Corollary 1. We compare the distribution of number of copiers by plotting the histograms of both our
 simulations results and the expected values based on Corollary 1.

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

Dirichlet-Multinomial distribution approximation

242 **Pólya urn model.** This stochastic process consists of N draws from an urn with an initial number of
 colored balls of M colors. When a ball is drawn, it is then placed back in the urn together with an
 244 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,
 246 and 0 otherwise. The probability that $S_{i,j} = 1$ given \mathbf{U}_{i-1} is

$$P(S_{i,j} = 1 \mid \mathbf{U}_{i-1}) = \frac{u_{i-1,j}}{\sum_{m=1}^M u_{i-1,m}} = \frac{o_j + w_{i-1,j}}{\sum_{m=1}^M o_m + w_{i-1,m}} = \frac{o_j + w_{i-1,j}}{i - 1 + \sum_{m=1}^M o_m}, \quad (15)$$

248 where o_j is the initial number of balls of 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 color j .

250

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

254 *Proof.* Write $\alpha' = \frac{\alpha}{1-\alpha}$ 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

$$256 \quad G_{i,j} = \frac{\alpha' \beta(A'_j) + K_{i-1,j}}{\sum_{m=1}^N [\alpha' \beta(A'_m) + K_{i-1,m}]} = \frac{\alpha' \beta(A'_j) + K_{i-1,j}}{i - 1 + \sum_{m=1}^N \alpha' \beta(A'_m)}. \quad (16)$$

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
258 proof.

Frigyik et al. [19, section 2] prove that the proportion of different colored balls in a *Pólya urn model*
260 converges to the Dirichlet distribution as the number of draws (the population size, N , in our model) approaches infinity, based on the *Martingale Convergence Theorem* [20]. We therefore have an approximation for the relative influence each role-model has when evaluated by copiers. Thus, choosing
262 the role-models for all copiers is equivalent to drawing from a multinomial distribution where the parameters are the modified weights from a Dirichlet distribution and we have the following corollary.
264

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

268 **Numerical validation.** We next validated the DM approximation of our model and tested its sensitivity to the assumptions ($e_i = e$ and $\alpha_i = \alpha$ for $i = 1, \dots, N$) by comparing results of stochastic simulations
270 of our model (eq. (11)) with the DM approximation (Corollary 2). We used a relatively small population size, $N = 100$, thus validating that the approximation is in good agreement even for
272 small N , despite the assumption of large N in the proof by Frigyik et al. [19, section 2]. First, we computed an observed distribution of the number of copiers from the average empirical distribution
274 of multiple simulations. We then compared this observed distribution with the expected theoretical DM distribution (Figure S2A). The difference in distributions was not perceived when plotting both
276 distributions on the same figure, so we used the difference instead. The maximum difference is 0.5 role-models, which indicates 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 the DM distribution
278 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, strongly supporting our approximation.
280

Next, we examined the fixation probability and fixation time of a favored phenotype \hat{A} when invading
282 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
284 with 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
286 the DM approximation to relaxing the following assumptions. First, we relaxed our assumption of no estimation error e . Estimation error in the original model was drawn from a normal distribution,
288 and added to the trait value before evaluation of the bias ($A_{i,j} = A_j + e_i$). When estimation error

is applied, we sample e_i for each copier i from a normal distribution with expected value zero and variance η^2 . Even when the estimation error variance is 0.1, both the fixation probability and fixation time approximations are accurate (Figure S4). 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 α_j for each role-model j from a normal distribution such that $\alpha_j \sim N(0.5, q)$ where q is between 10^{-7} and 10^{-1} . We found again that results of the DM approximation are similar to those from stochastic simulations of the full model (Figure S5).

296 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 conditional fixation time (conditioned on the population reaching fixation) of a favored phenotype, using a diffusion-equation approximation approach, similar to analyses of population-genetic models [21, 46, 47]. We are mainly interested in the effect of the bias weight, α , which determines the relative effect of success and prestige on influence bias, given by eq. (10). For simplicity, we use the dichotomous model, and 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 2 and eq. (16)).

306 Drift and diffusion terms in a constant environment. 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. Let x and x' be the frequency of phenotype \hat{A} in a population with N individuals in the current and next generation, respectively. We set β to be the success bias of phenotype A relative to phenotype \hat{A} , such that $\beta = \beta(A)/\beta(\hat{A}) < 1$. Then (see Appendix B for derivation),

$$\begin{aligned} E[x' - x] &= x(1 - x)(1 - \beta) + o(1 - \beta) , \\ V(x' - x) &= x(1 - x) \left(\frac{1}{\alpha N + (1 - \alpha)} \right) + o \left(\frac{1}{\alpha N + (1 - \alpha)} \right) . \end{aligned} \quad (17)$$

This analysis gives an interesting 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 $E[x' - x] = sx(1 - x) + o(s)$ and $V[x' - x] = x(1 - x)/N_e$ [21, eq. 7], respectively. Therefore, we have the following result.

320 Result 3 (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

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

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

Using our effective selection coefficient, $s = 1 - \beta$, and effective population size, N_e , with the population-genetics fixation probability approximation given by Kimura [21, eq. 8], we obtain the following result.

Result 4 (Fixation probability). *The fixation probability of an invading phenotype favored by success bias is approximately*

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

where x is the initial frequency of the invading phenotype.

Similarly, we can use $1 - \beta$ and N_e in the population-genetics fixation time approximation given by [46, eq. 17].

Result 5 (Fixation time). *The expected fixation time (conditioned on fixation) from an initial frequency x is approximately*

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

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

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

Note that these integrals cannot be solved in closed form, and are estimated numerically.

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 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 approximated by our approximations (Figure 1).

Changing environment . After finding a good approximation in a constant environment, where the favorable trait is always \hat{A} , we proceeded to find an approximation for a periodically changing environment. Following [23], we denote k as the number of generations in which the invading phenotype is favored by success bias, and l as the number of generations in which the resident phenotype is

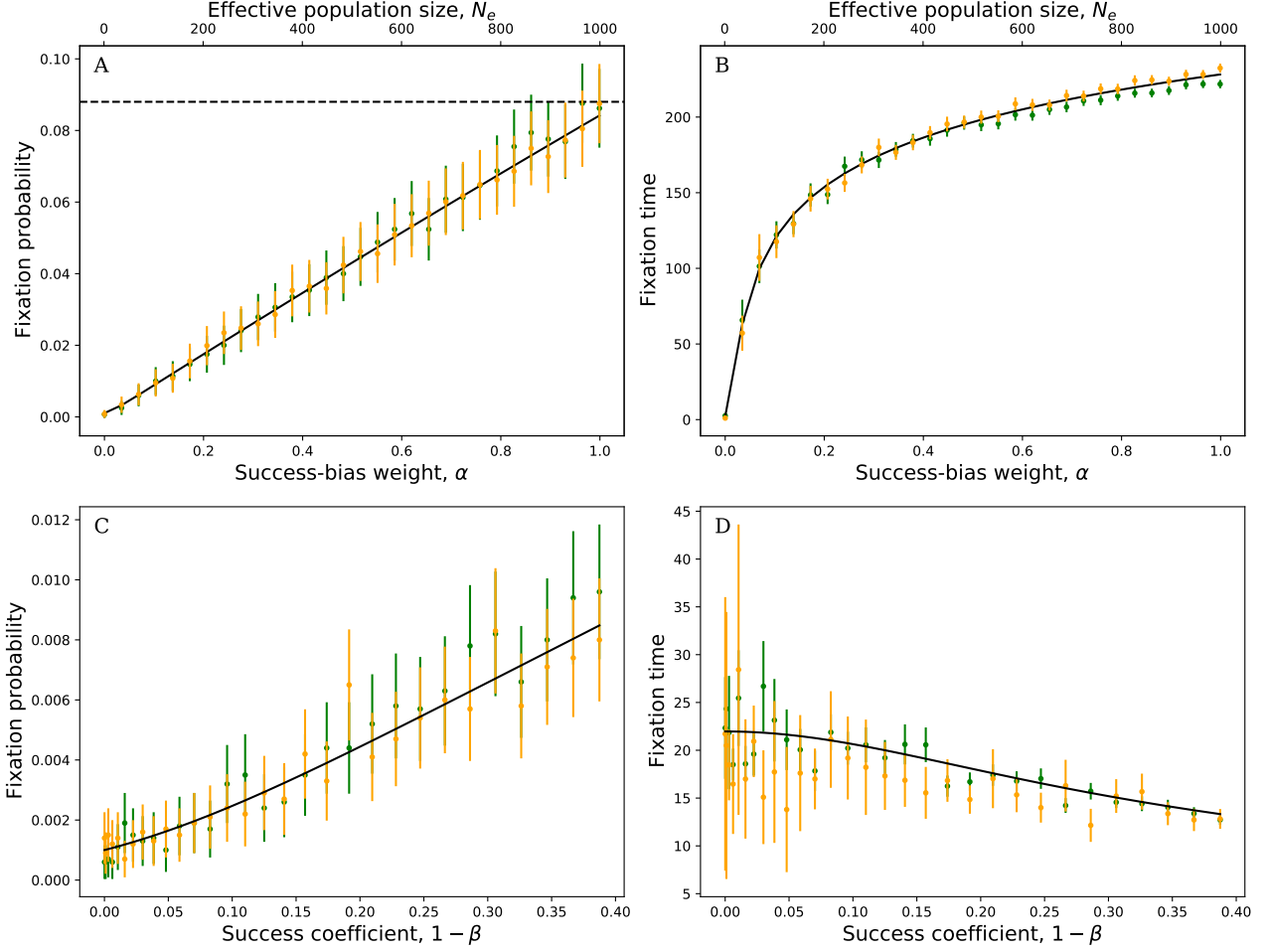


Figure 1: Fixation probability and time in a constant environment. Fixation probability and time (in generations) as a function of the success-bias weight α (bottom x-axis), or effective population size N_e (top x-axis) in the top row, and as a function of the success coefficient, $1 - \beta$, on the bottom row. The approximation (black; eq. (19)) agrees with both DM simulations (green) and Wright-Fisher simulation (orange). Fixation probability (A) is bounded by $2(1 - \beta)$ (dashed line). 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, $A = 0.7$ (panels A and B), A/\hat{A} varies between 0.01 and 0.99 (panels C and D), and $\hat{A} = 1$, which affects β via eq. (17); success coefficient, $1 - \beta = s = 0.044$ (panels A and B); success-bias weight, $\alpha = 0.01$ (panels C and D).

354 favored by success bias. Thus, during the first k generations of the environmental cycle, $\beta = \frac{\beta(A)}{\beta(\hat{A})} < 1$, where \hat{A} is the invading phenotype. During the following l generations of the environmental cycle, the phenotype favored by success bias is switched, such that $\frac{\beta(A)}{\beta(\hat{A})} > 1$. We then proceed to find
 356 expressions for the expectation and variance of the change in the frequency of phenotype \hat{A} after $n = k + l$ generations. The proof is in Appendix C.

358 **Drift and diffusion terms in a changing environment.** Let x be the initial frequency of the invading phenotype and X_t the number of individuals with that phenotype after n generations. Then,

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

362 where $S_n = \sum_{t=1}^n N(1 - \beta_t)$ and β_t is $\beta(A)$ at generation t .

Note that here, we have the average selection coefficient during a cycle of n generations as the selection
364 coefficient in eq. (19). Using the drift and diffusion terms and following [23], we can approximate the
fixation probability in a changing environment.

366

Result 6 (Fixation probability in a changing environment). *The fixation probability of an invading
368 phenotype under periodical environmental changes is approximately*

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

370 where x is the initial frequency of the invading phenotype.

Numerical validation. To validate the the approximation for the fixation probability in a changing
372 environment (eq. (23)), we compare it to results of simulations that use the DM approximation
(Corollary 2). We find that the approximation fits the simulation results well for variable bias weights,
374 α , which corresponds to the effective population size (Figure 2A).

However, the approximation is more sensitive to the value of the success bias coefficient β (Figure 2B).
376 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
378 phenotype goes 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-
380 equation approximation assumes weak selection, or in our case, weak success bias.

We found that for a large k/l ratio (with a constant cycle length, $n = k + l = 100$), the changing
382 environment approximation (eq. (23)) converges to the constant environment approximation (eq. (19)),
see Figure 2C and Figure 2D.

384 The approximation follows the trend of the simulation results for all α values. On increasing the success
coefficient α to more than 0.15, the simulation results were located above the changing environment
386 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 a large
388 number of cycles, and when the success coefficient α is too high, there might be very few cycles.
Either the ideal trait is copied by enough copiers so that the prestige is sufficient to negate the success
390 bias when the cycle changes (and the trait favored by the bias becomes the disfavored), or the opposite
happens, and the ideal trait goes extinct before there are enough copiers that copied it. We then tried to
392 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 disfavored
394 ones is very high, it is very similar to a constant environment model.

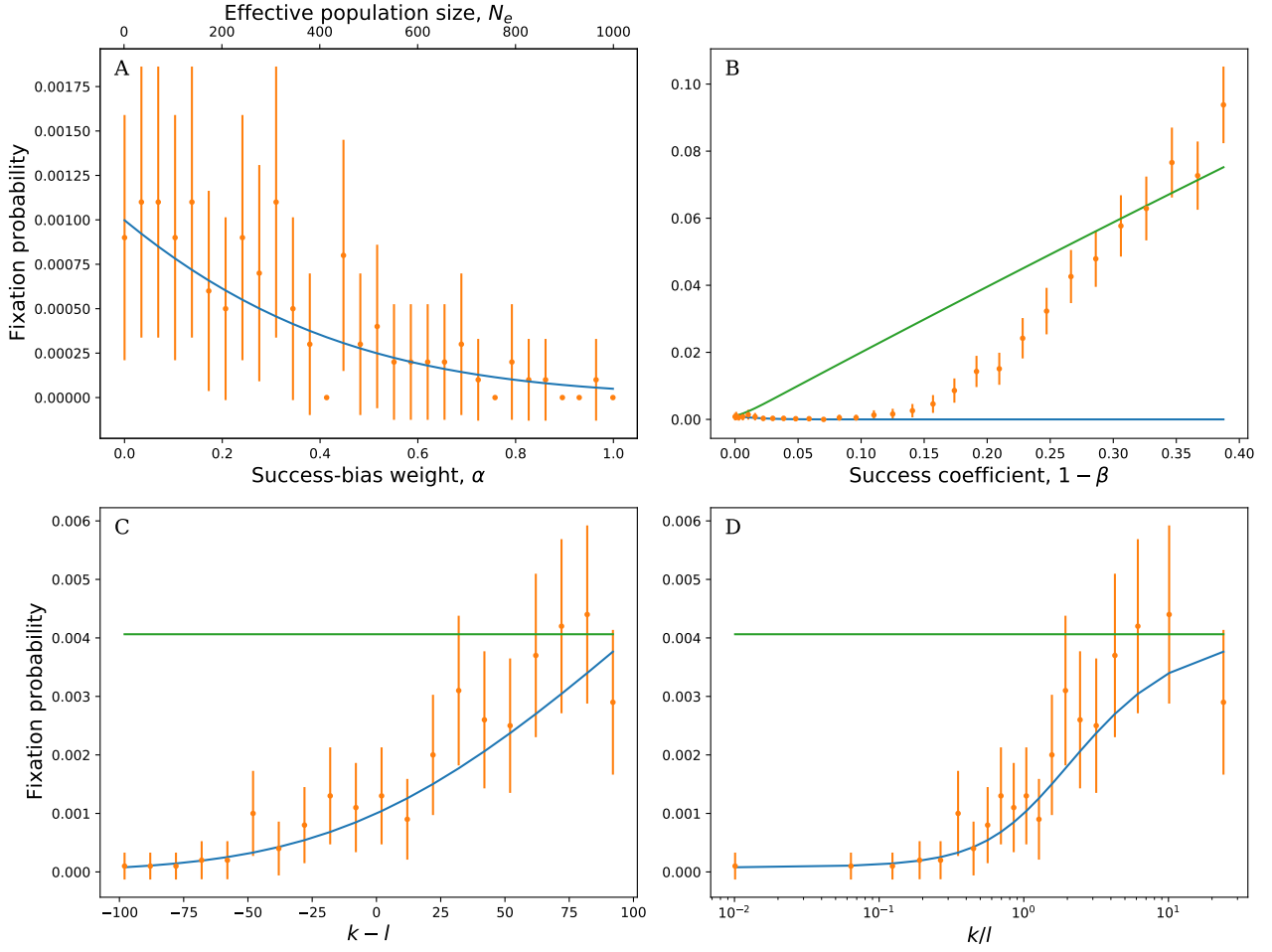


Figure 2: Fixation probability in a changing environment. (A) Fixation probability decreases with the success-bias weight (bottom x-axis) and effective population size (top x-axis). The approximation (blue; eq. (23)) agrees with simulation results (orange). (B) Fixation probability increases with the 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% (panels A, C, and D) and 95% (panel B) confidence intervals. Here, population size, $N = 1,000$; phenotype values, $\hat{A} = 1$ with $A = 0.9$ (panels A and B) and $A = 0.8$ (panels C and D); In panel A, the success coefficient is $1 - \beta = s = 0.005$; In panels B, C, and D, the success-bias weight is $\alpha = 0.1$.

Optimal success-bias weight

396 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

398 between the chosen trait value and the optimal trait value \hat{A} ,

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

400 where A_j is the trait of role-model j and K_j the number of copiers that already chose role-model j .
Simply put, each copier estimates what success-bias weight α^* will result in copying a trait that is
402 most similar to the ideal trait value \hat{A} . Indeed, if the trait value is correlated with fitness, the optimal
success-bias weight would increase the fitness of individuals. However, here we ignore the effects of
404 natural selection, focusing instead on selectively neutral traits.

We find that when copiers choose their success-bias weight according to eq. (24), it decreases with
406 the number of copiers that have already chosen a role-model (Figure 3). Moreover, their estimation
error is much lower compared to a constant success-bias weight, which gives roughly the same high
408 estimation error to all copiers (compare Figure 3B and C): in this example, the optimal success-bias
weight gives an estimation error (difference between the chosen and optimal trait) converges to 0.046,
410 whereas a constant success-bias weight gives values > 0.74 .

Discussion

412 Some cultural traits or cultural role-models may be copied more often than others due to transmission
biases. One such bias is success bias, in which copiers are more likely to copy a successful role-model.
414 Although many models assume that success can be accurately estimated, it has been suggested that
because it is hard to estimate success, a more common bias is *prestige bias*—a bias towards role-models
416 perceived to be successful. This perceived success can be determined by performance with respect to
another trait (indirect) [7, 26], or by the influence an individual has on others [28, 32].

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

Hence, our model has two “nested” stochastic processes: the role-model choice process within each
424 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
426 using the *generalized binomial distribution* (GBD, Result 1) and the *Dirichlet-Multinomial dis-*
tribution (DM, Corollary 2). The latter is especially useful, as it approximates the entire role-model
428 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.

430 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 approxi-

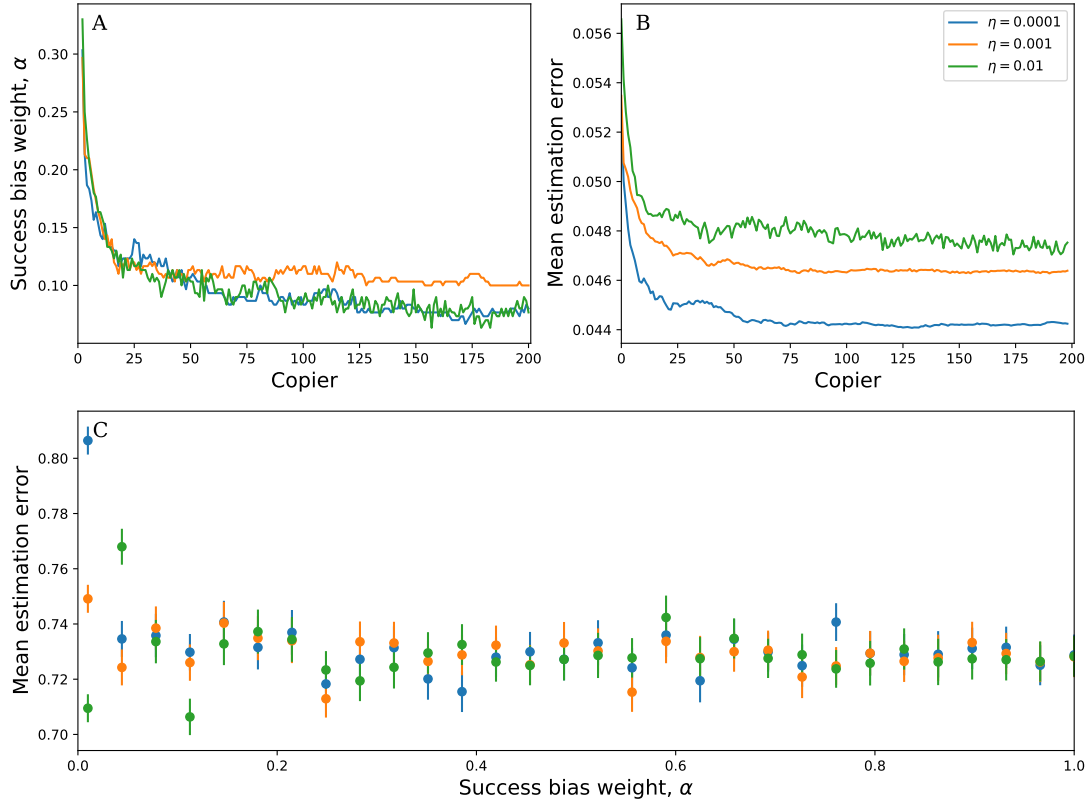


Figure 3: Advantage of an optimal success-bias weight. Both success-bias weight α (A) and estimation error (B) decrease during the role-model choosing process (within a single generation), demonstrating that prestige becomes more favored by copiers as more copiers have made their choice. However, when 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 optimal 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.

432 mations are similar to Kimura's evolutionary-genetic approximations, in that (i) the difference between
the resident and invading cultural trait values, $1 - \beta(A)$, is equivalent to the selection coefficient in
434 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 1).

436 We also analyzed a cyclic changing environment in which the identity of the success-biased trait
switches after a fixed amount of generations (Figure 2). We find that, similarly to the constant
438 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
440 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 generations in which
442 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.

444 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
446 process proceeds (that is, more copiers make their choices), both the success-bias weight (chosen by
copiers) and the estimation error decrease. The latter is significantly lower than in a population using
448 a constant, fixed success-bias weight, regardless of the value of the constant weight (Figure 3). This
suggests that the later a copier makes its choice, the more it should rely on choices of previous copiers,
450 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
452 can be.

Our decision to research and analyze a multi-bias model is preceded by several others. Ze Hong [59],
454 for example, presented a model that combines both frequency-dependent bias (including conformist
bias) and payoff bias. He has shown that an integrated learning strategy may be superior to relying on
456 either bias alone. Moreover, both are likely to contribute to the spread of variants with high payoff,
and the magnitude of conformist bias affects the evolutionary dynamics.

458 Chudek et al. [32] report the first direct tests in children that suggest the existence of prestige bias,
defined as the tendency to learn from individuals to whom others have preferentially attended, learned,
460 or deferred. Their definition of prestige is similar to ours. They showed that the odds of 3-4 years-old
children learning from an adult role-model to whom bystanders had previously preferentially attended
462 for 10 seconds were more than twice those of learning from a role model whom bystanders ignored.
They also note that prestige effects are domain sensitive: they found that prestigious role-models were
464 attended more when demonstrating artifact use, whereas role-models presenting food preferences had
less attendants, suggesting that the domain itself (artifact use vs. food preference) can affect the
466 attendance, and hence the prestige of the role-model. This led to the suggestion that when the trait is
costly to learn individually, prestige will have a stronger bias [32]. It would be interesting to include
468 costs in our model to try and observe these effects and dynamics in a large population.

According to Henrich and Broesch [26], natural selection has favored the emergence of psycholog-
470 ical biases for learning from those individuals most likely to possess adaptive information. They
authors studied Fijian villages to examine if and how such biases emerge in a small-scale society.
472 They found that Fijian villagers are more likely to learn from role-models perceived as more success-
ful/knowledgeable, both within and across domains. Their research thus suggests that copying from
474 those perceived as successful, rather than who are actually successful, is a common phenomenon. They
show that the social networks representing copier–role-model relationships are centralized, which is
476 consistent with the prediction that people substantially share notions about who is a good cultural
model, but that individuals’ role-model selections are influenced by multiple factors.

478 Prestige bias can help to cheaply estimate and acquire knowledge, which may facilitate survival and
reproduction. However, it is not always the case, and there could be negative repercussions to this
480 bias, such as invasion of maladaptive traits. Takahashi and Ihara [29] mention that social learning
not only takes the form of random copying of other individuals, but also involves learners’ choice
482 of what to learn and from whom to learn. They suggest a best-of-k model where an individual

samples k role-models and chooses the one he deems most "successful". They mention that a previous
484 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
486 selectively disfavored and in the long run replaced by unbiased learners, who simply copy someone
chosen at random. They developed new mathematical models that are simpler and mathematically
488 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 (see Fogarty et al. [57] and
490 references there). Our model, which includes influence bias, is consistent with this claim. When a
maladaptive trait is "piggybacking" on a role-model with high influence, the former could spread in
492 the population. In addition, best-of- k learning can be stable against invasion by unbiased learning if
social learning is sometimes combined with individual learning [29]. Our model includes only social
494 learning, and not individual learning, but it could be interesting to combine it with individual learning
and see how it affects the dynamics.

496 Prestige bias can also accelerate reversal of harmful traditions such as child marriage and domestic
violence. Efferson et al. [27] suggest a *spillover* mechanism, in which an intervention affects a large
498 enough group in a target population, so that others not included in the intervention also change their
behavior. They find that there are individuals who act as *agents*, who are often observed, and therefore
500 they are ideal targets for interventions. This is similar to influential role-models in our model, where a
prestigious individual will be copied more often, and will therefore spread their trait faster and wider
502 in the population. They also suggest a way to use this phenomenon 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
504 agents could start harmful traditions.

Dunbar [31] hypothesized that larger, more complex brains can store and manage more information
506 and in turn, this information can support the costs of a larger brain. Following this, Muthukrishnan
and Henrich [30] suggested that prestige can directly affect human physical evolution. They present a
508 concept called *cultural brains*—brains that evolved primarily for the acquisition of adaptive knowledge.
They then develop a model that predicts a strong relationship between brain size and group size,
510 because group size also provides access to more adaptive knowledge. They also presented the
cumulative cultural brain hypothesis, which proposes that human brains have evolved with an ability
512 and tendency for selective, 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
514 and biases include direct and indirect cues of the popularity of cultural traits (e.g. success and prestige
biases). They suggest that one of the reasons for the extreme increase in brain size in humans is the
516 ability to "cheaply" acquire adaptive knowledge via transmission biases such as prestige.

One path forward is an analysis of the dynamics of the optimal success-bias weight model, in which
518 every copier chooses its α . It would be interesting to see the if the mean estimation error and the
varying weight, α^* , converge to specific values, and how they are affected by the model parameters. It
520 may also be possible to relax the assumptions required for our approximations, such as homogeneous

estimation error and success-bias weight. Lastly, it would be interesting to analyze the continuous
522 model and determine how much it differs from the dichotomous model.

Another way to expand our model is to account for the two types of prestige or leadership suggested
524 by Van Vugt and Smith [25] that are attributed to Confucius and Machiavelli. Confucius viewed
leaders as role-models who exercise influence through possessing superior knowledge, skills, and
526 (outstanding) personal qualities. This fits the success bias in our model. In contrast, Machiavelli
viewed leaders as rulers who exercise influence by imposing costs through (the threat of) punishment
528 and violence. Van Vugt and Smith suggest that these opposing views are both partially supported by
the available evidence but each one on its own offers an incomplete view of the complex and dynamic
530 concept of leadership. Several adjustments could be made so that our model reflects these leadership
styles, such as assuming there is a correlation between phenotype and leadership style. The resulting
532 cultural-evolutionary dynamics and their dependence on the costs and benefits are intriguing.

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

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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 average in the denominator is over the role-models index, j .

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

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

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

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

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

$$E[K_{N,j}] = \alpha_j \cdot \beta(A_j + e) \left/ \overline{\alpha \cdot \beta(A + e)} \right. , \quad (A3)$$

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 be the success coefficient of phenotype A , $\beta = \beta(A) < \beta(\hat{A}) = 1$. Then,

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

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),

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

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,

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

following Durrett [22, p. 253, ch 7.2] and because $1/(1-y) = 1 + y + y^2 + \dots$

We therefore have

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

which gives us the drift term of the diffusion equation.

Using the variance of the DM distribution,

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

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,

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

Following Durrett [22, ch 7.2], we assume $\beta \approx 1$, such that

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

and for the entire variance expression we get

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

The current frequency x is a given, such that $V(x) = 0$, and therefore

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

α' is the odds ratio of the bias weight,

$$\alpha' = \frac{\alpha}{1 - \alpha}. \quad (\text{B9})$$

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

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

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

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

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

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

$$\begin{aligned} E \left[\frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) \right] &= E \left[\frac{X_t}{N} - \left(\frac{X_t}{N} \right)^2 \right] = E \left[\frac{X_t}{N} \right] - E \left[\left(\frac{X_t}{N} \right)^2 \right] \\ &= E \left[\frac{X_t}{N} \right] - V \left(\frac{X_t}{N} \right) - \left(E \left[\frac{X_t}{N} \right] \right)^2. \end{aligned} \quad (\text{C2})$$

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

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

From eq. (C1) we know that

$$\begin{aligned} E \left[\frac{X_{t+1}}{N} - \frac{X_t}{N} \right] &= \frac{1}{N} s_{t+1} E \left[\frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) \right] \simeq \frac{1}{N} s_{t+1} \left(E \left[\frac{X_t}{N} \right] \left(1 - E \left[\frac{X_t}{N} \right] \right) - \frac{1}{N_e} tx(1 - x) \right) \\ &\simeq \frac{1}{N} s_{t+1} \cdot E \left[\frac{X_t}{N} \right] \left(1 - E \left[\frac{X_t}{N} \right] \right) - \frac{1}{N_e N} s_{t+1} tx(1 - x). \end{aligned} \quad (\text{C4})$$

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

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

We now look at the induction assumption to see that

$$E \left[\frac{X_t}{N} - x \right] = E \left[\frac{X_t}{N} \right] - E[x] = E \left[\frac{X_t}{N} \right] - x , \quad (\text{C6})$$

so using the assumption we get

$$\begin{aligned} E \left[\frac{X_t}{N} \right] &\simeq \frac{1}{N} S_t x (1-x) + x , \\ 1 - E \left[\frac{X_t}{N} \right] &\simeq 1 - \frac{1}{N} S_t x (1-x) + x . \end{aligned} \quad (\text{C7})$$

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

$$\begin{aligned} E \left[\frac{X_{t+1}}{N} - \frac{X_t}{N} \right] &\simeq \frac{1}{N} s_{t+1} \left(\frac{1}{N} S_t x (1-x) + x \right) \left(1 - \frac{1}{N} S_t x (1-x) + x \right) \\ &\simeq \frac{1}{N} s_{t+1} \cdot x (1-x) , \end{aligned} \quad (\text{C8})$$

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

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

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

$$\begin{aligned} E \left[\frac{X_{t+1}}{N} - x \right] &\simeq \frac{1}{N} s_{t+1} \cdot x (1-x) + \frac{1}{N} S_t \cdot x (1-x) \\ &\simeq \frac{1}{N} x (1-x) (S_t + s_{t+1}) \simeq \frac{1}{N} S_{t+1} x (1-x) , \end{aligned} \quad (\text{C10})$$

which proves the drift term.

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

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

Using eq. (C1) we see that

$$\begin{aligned} E \left[\frac{X_{t+1}}{N} \middle| X_t \right] - E \left[\frac{X_t}{N} \middle| X_t \right] &= \frac{1}{N} s_{t+1} \frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) \\ E \left[\frac{X_{t+1}}{N} \middle| X_t \right] &= \frac{X_t}{N} + \frac{1}{N} s_{t+1} \frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) . \end{aligned} \quad (\text{C12})$$

Using eq. (B10) we get

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

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

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

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

$$V \left(E \left[\frac{X_{t+1}}{N} \middle| X_t \right] \right) = V \left(\frac{X_t}{N} + \frac{1}{N} s_{t+1} \frac{X_t}{N} \left(1 - \frac{X_t}{N} \right) \right) \quad (\text{C15})$$

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 find that

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

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

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

Using the induction assumption and eq. (C14),

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

which proves the diffusion term.

Supplementary Figures

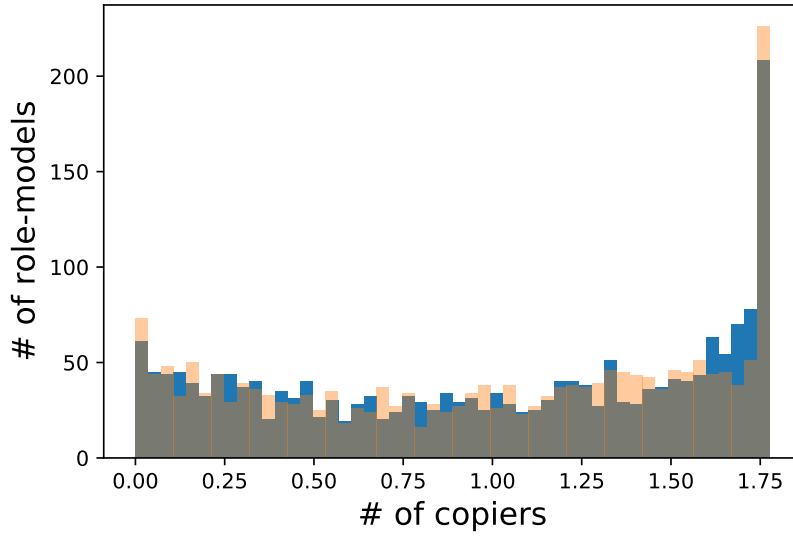


Figure S1: Numerical validation of the GB approximation. The approximation (orange) fits simulation results (blue) well when using 1,000 simulations. Here, population size, $N = 2,000$; bias weight, $\alpha = 0.1$; ideal phenotype value, $\hat{A} = 1$; role-model traits $\mathbf{A} \sim N(0, 1)$; success bias value, $\beta(A) = 0.956$.

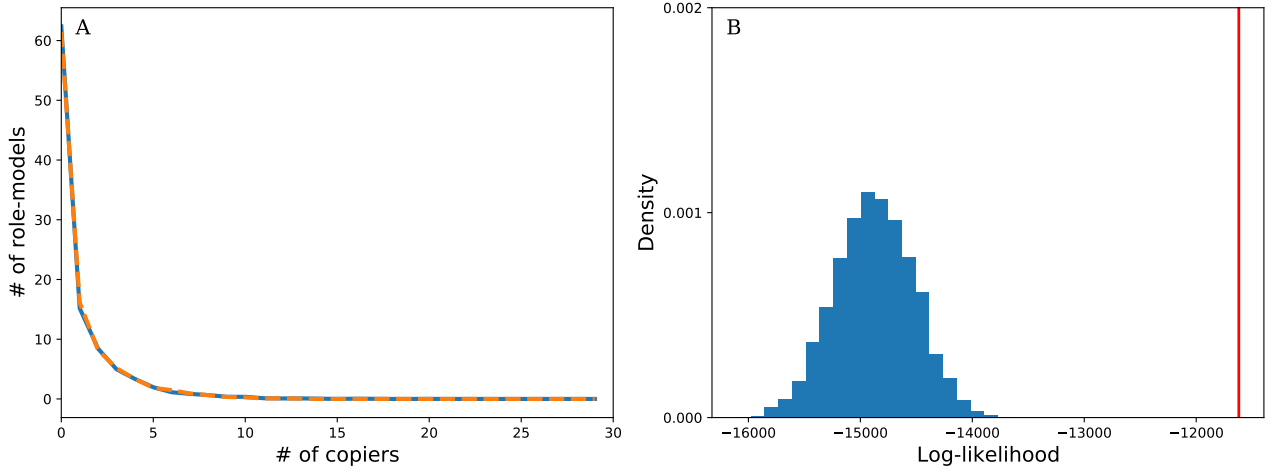


Figure S2: Numerical validation of the DM approximation. We performed computational simulations of the role-model choice process (Equation (10)) and compared the distribution of the number of copiers to simulations when using the DM distribution approximation (Corollary 2). **(A)** The difference between the DM distribution (orange) and the empirical distribution of the simulations (blue) is very small. **(B)** The log-likelihood of the DM distribution for results of the simulations (red vertical line) is much higher than the log-likelihood of permutations of simulations (blue histogram). Here, population size, $N = 100$; number of simulations, $m = 100$; 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.

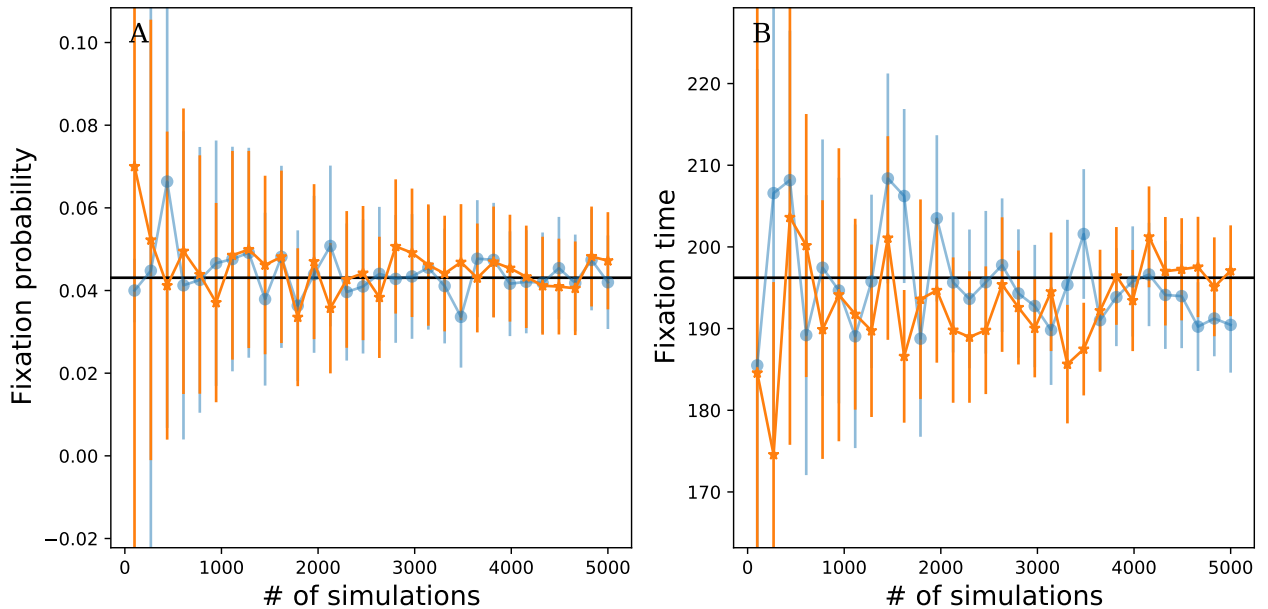


Figure S3: DM Approximation precision as function of number of simulations. Our DM approximation (orange) agrees with stochastic simulation results (blue) when using 1,000 or more simulations. Both fluctuate around the analytic fixation probability approximation (black; eq. (19)). Markers are averages 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, $\beta(A) = 0.956$.

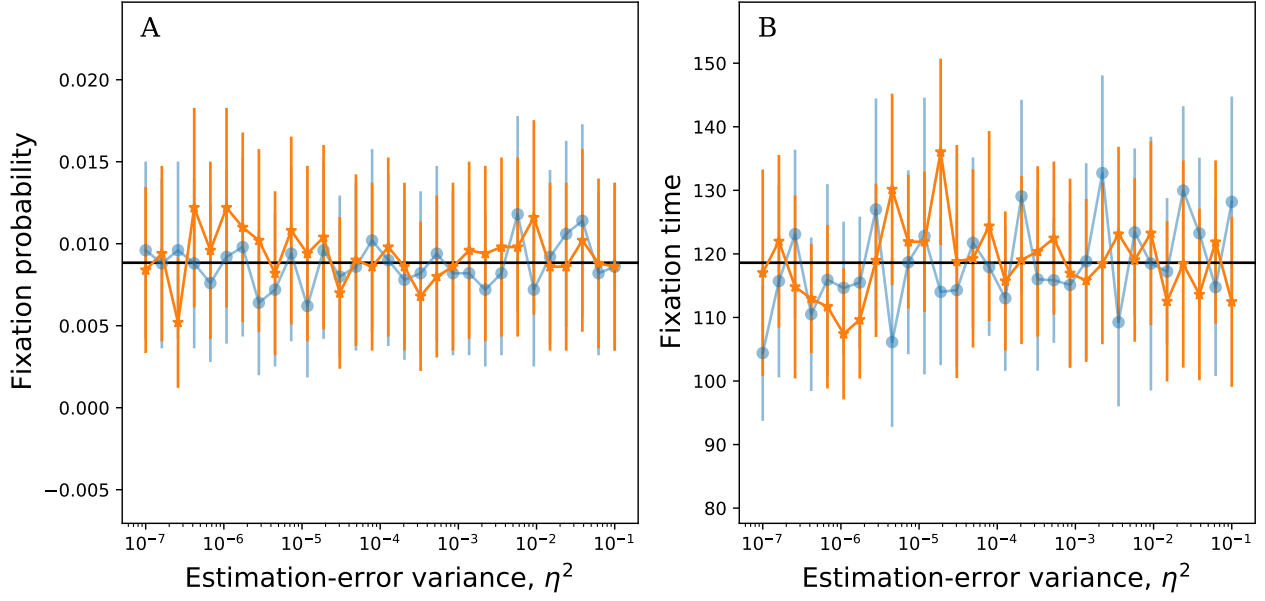


Figure S4: Robustness of DM approximations to success estimation error. Both the DM approximation (orange) and our approximation (black) agree with the stochastic simulations (blue), even with a high estimation error. Markers are averages across simulations, error bars are 95% confidence intervals. 5,000 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 is on the x-axis.

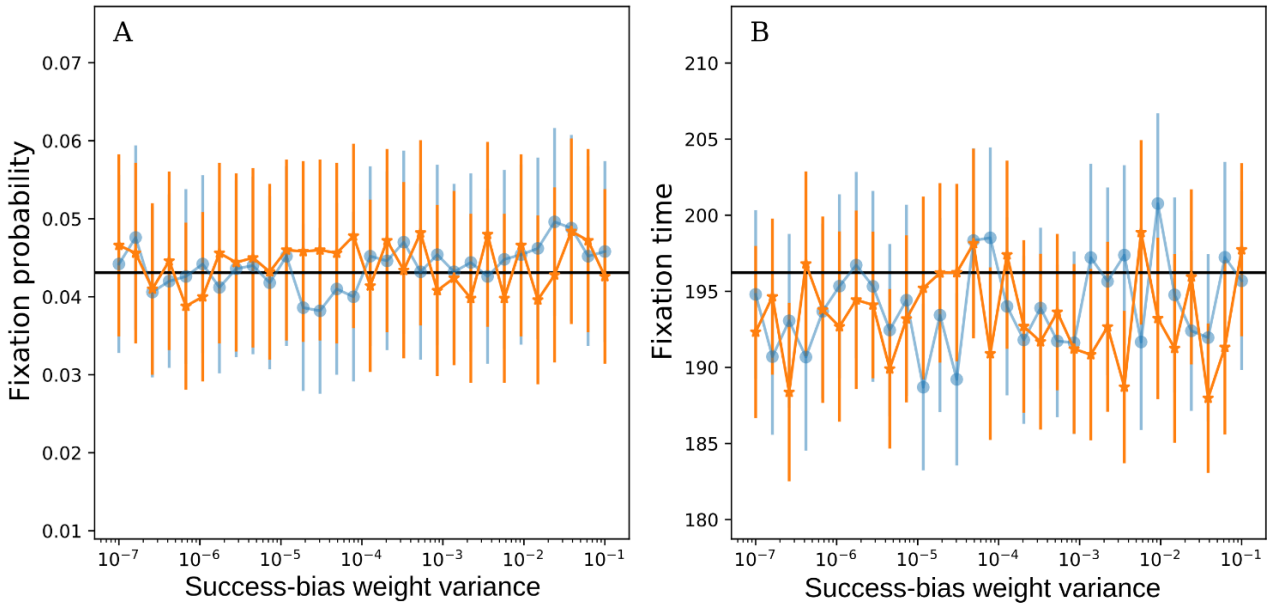


Figure S5: Robustness of DM approximations to variation in the bias weight α . Fixation probability does not seem to be affected by variation in success bias weight between role-models. Thus, both the DM approximation (orange) and Kimura's equation (black line) have a good fit to results of stochastic simulations (blue). Markers for average across 5,000 simulations, error bars are 95% confidence intervals. Here, population size, $N = 1000$; success bias weight is normally distributed, $\alpha_j \sim N(0.5, \epsilon^2)$ where $10^{-7} \leq \epsilon^2 \leq 10^{-1}$; phenotype values, $\hat{A} = 1, A = 0.7$; success bias value, $\beta(A) = 0.956$.