Cultural evolutionary dynamics with prestige bias

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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. Here, we propose an additional transmission bias that may be common in cultural transmission: "influence bias", in which the choice of a role-model depends on the number of individuals that have already copied from that role-model. We combine success and influence bias together to form a "prestige bias", and analyze its effects 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 reduces the computational complexity of simulations. We validate these approximations using simulations, and demonstrate their robustness to model assumptions. We also find approximations to the fixation probability and the fixation time of an invading cultural trait, in both constant and changing environments. These approximations are similar to Kimura's approximations for population-genetic models. These similarities show that 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 extends the literature that attempt to describe of cultural transmission, especially in human societies where social media is popular and thus influence bias may be expected. Further work is needed to test if this model could predict various phenomena in cultural evolution.

Introduction

Cultural transmission. In cultural transmission, individuals transmit cultural traits (i.e., behavior, beliefs, norms) to one another, typically via learning and demonstrating (Cavalli-Sforza and Feldman, 1981). Examples for cultural traits in humans are behavioral patterns, such as personalities and habits, transmitted via both verbally and by observations (O'Brien et al., 2010).

Although cultural transmission is most common in humans, it is also observed in other animals, e.g., chimpanzees (Horner et al., 2010; Kendal et al., 2015), dolphins and whales (Whitehead, 2017), elephants (McComb et al., 2001), and even flies (Battesti et al., 2012).

Cultural transmission may combine vertical transmission, where parents transmit to their offspring; oblique transmission, where adults (teachers, leaders, strangers) transmit traits to unrelated offspring; and horizontal transmission, where peers from the same age cohort transmit to one another. Vertical transmission is also possible in the opposite direction: parents may copy traits from their offspring (Cavalli-Sforza and Feldman, 1981; Creanza et al., 2017). It has been demonstrated that non-vertical cultural transmission can maintain maladaptive traits, which can be beneficial in changing environments (Ram et al., 2018a).

Vertical transmission is also possible in the opposite direction: parents may copy traits from their offspring (Cavalli-Sforza and Feldman, 1981; Creanza et al., 2017).

Cultural transmission biases may cause a trait to have a disproportionate probability to be transmitted compared to its frequency in the population. Importantly, even when a trait is disfavored by natural selection, it may still spread in a population due to transmission biases that are strong enough to overcome selection (Boyd and Richerson, 1988, Ch. 8 pg. 279). For example, Cohen et al. (2021) 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.

Indeed, in a tournament between learning strategies conducted by Rendell et al. (2010), most winner included a mixture of success-biased social learning and individual learning, implying that success-biased learning is a good strategy, but that by itself is not enough, even if success is measured accurately.

Boyd and Richerson (1988, Ch. 5) have suggested that the evaluation of success can be divided into three groups: *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 both of the observed paddle grips to determine which grip is better. 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. 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, when the common paddle grip is used by 60% of the demonstrators, then if the probability to copy this grip is 80%, then

transmission is under positive frequency bias, also called conformity; if the probability is 40%, then transmission is under negative frequency bias, or non-conformity (Molleman et al., 2013). The effects of conformity and non-conformity on cultural evolution have been studied with both models (Denton et al., 2022, 2020) and experiments (Aljadeff et al., 2020).

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

Influence bias. Today, social media provides an easy way to estimate the social and cultural influence individuals have over others, and therefore may have an effect on decision making. Online social networks such as *Facebook* and *Instagram* are known to affect the influence of individuals (Anagnostopoulos et al., 2008; Diga and Kelleher, 2009; Peng et al., 2018), and specific marketing practices were invented to capitalize on this effect (Lee et al., 2012). Here, we model such influence as an indirect bias in cultural transmission, in which the choice of a role-model depends on the choices made by other individuals that have already chosen a role-model. Influence can be easily estimated, so costs may be lower than estimating success. In some cases it could be a more accurate estimation as well.

Influence bias is a context-based, rather than a content-based bias–it does not depend on the phenotype but rather on the number of copiers that already copied each role-model. IT also differs from frequency biases such as conformity (Denton et al., 2022), 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.

Here, we define a model of cultural transmission with prestige bias that combines both success and influence biases, find 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 (Kimura, 1962; Kimura and Ohta, 1969), 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 (1988), 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 (Van Rossum et al., 2007) with NumPy (Van Der Walt et al., 2011) and Matplotlib (Hunter, 2007). Source code is available at https://github.com/yoavram-lab/PrestigeBias.

Continuous trait

We follow the model of Boyd and Richerson (1988), 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 (1988, 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,

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

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 (1988) 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

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

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132   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,
134   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,
136   $\sum_{j=1}^{N} K_{i,j} = i$, and there are $N - i$ copiers that have yet to choose a role-model. The stochastic process
of role-model choice,

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

is described by the recurrence equation

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

where $S_{i,j} = 1$ if the i-th copier chose role-model j and 0 otherwise, and the initial state is $K_{0,j} =$
142   0.

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

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

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

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

150   Here, the bias weight α_{ij} is a characteristic of the interaction of role-model j with copier i that
determines the relative significance of success and influence in the role-model's overall prestige in the
152   eyes of the copier.

We assume every individual evaluates the importance of success and influence differently. Addition-
154   ally, 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
156   than his actual skill. We therefore modeled α_{ij} to be the relation between every copiers intrinsic
significance of estimation, and every role-models personal emphasis.

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

160   **Dichotomous trait**

To allow for mathematical analysis of the model, we introduce a simplified version where the trait
162   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

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164 thus influence is determined by the number of copiers that have already chosen a role-model with either phenotype. In addition, we assume homogeneous α for simplicity and for easier mathematical
166 analysis. Therefore, the probability of the i-th copier to copy phenotype A is

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

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

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

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

Results

174 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
176 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 $\mathbf{A}(t)$
178 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
180 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
182 homogeneous α.

Generalized binomial approximation. The number of copiers of a specific role-model at each step,
184 $K_{i,j}$, follows the *generalized binomial distribution* (Drezner and Farnum, 1993) and therefore,

(i) the expected number of copiers of role-model j equals its prestige in the eyes of the first copier,
186 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 $i = 1, \ldots, N$); and (ii) the expected number of copiers of each role-
188 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
190 $j = 1, \ldots, N$), 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
192 *Pólya urn* model if trait estimation error is uniform for all copiers ($e = e_i$ for all $i = 1, \ldots, N$), meaning there's no meaning for the order of copiers.

194 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 $GBD(n, p, \theta)$ 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 (1993), 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. $E[K_{N,j}] = N \cdot G_{1,j}$.

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

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

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

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

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

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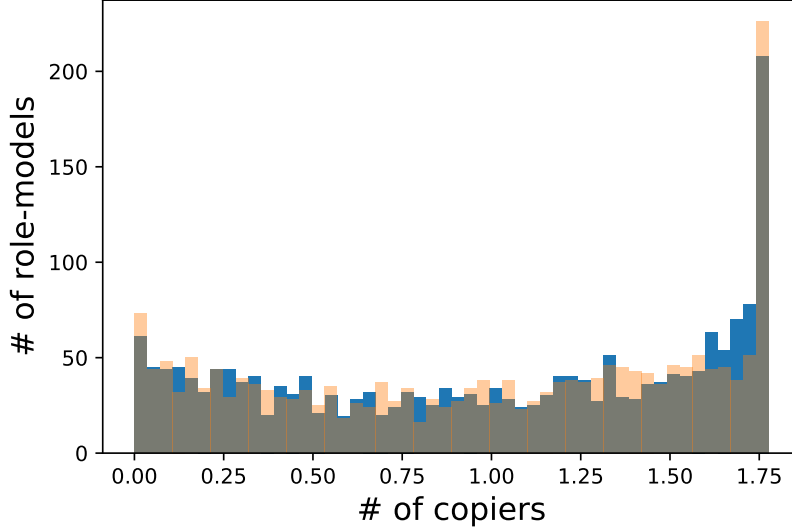230 the average of the $1,000$ simulations to eliminate drift errors, as can be seen in fig. 1.

Figure 1: 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, $\beta(A) = 0.956$.

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

Dirichlet-Multinomial distribution approximation

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

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

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
242 new balls that were added to the urn after i draws of the color j.

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

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

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

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 proof.

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

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

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 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 expected theoretical DM distribution as can be seen in fig. 2 (a). The difference in distributions was not perceived when plotting both distributions on the same figure, so we used the difference instead. The maximum difference is 0.5 role-models, which indicate a very good fit. In addition, we tested the likelihood of the observed data to be drawn from the DM distribution, against a shuffle of the parameters vector of the DM distribution itself, as seen in fig. 2 (b). We see that the negative log likelihood of the observed data is much higher than any other shuffled version of the parameters vector, supporting our approximation more.

Next, we examined the fixation probability and fixation time of a favored phenotype $\hat{A}$ when invading a population of phenotype A and compared results from the full model and the DM approximation. We find that the number of simulations needed to sufficiently approximate our model with the DM approximation is roughly $1,000$ (Figure 3). Next, we examined the robustness of the DM approximation to relaxing the approximation assumptions. First, we relaxed our assumption of no estimation error e. Estimation error in the original model was drawn from a normal distribution, and added to the trait value before evaluation of the bias ($A_{ij} = A_j + e_i$). When estimation error is applied, we sample J_i for each copier i from a normal distribution with varying scale (variance). Even when the standard deviation is 0.1, the fixation probability and time is similar (fig. 4). We also relaxed our 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
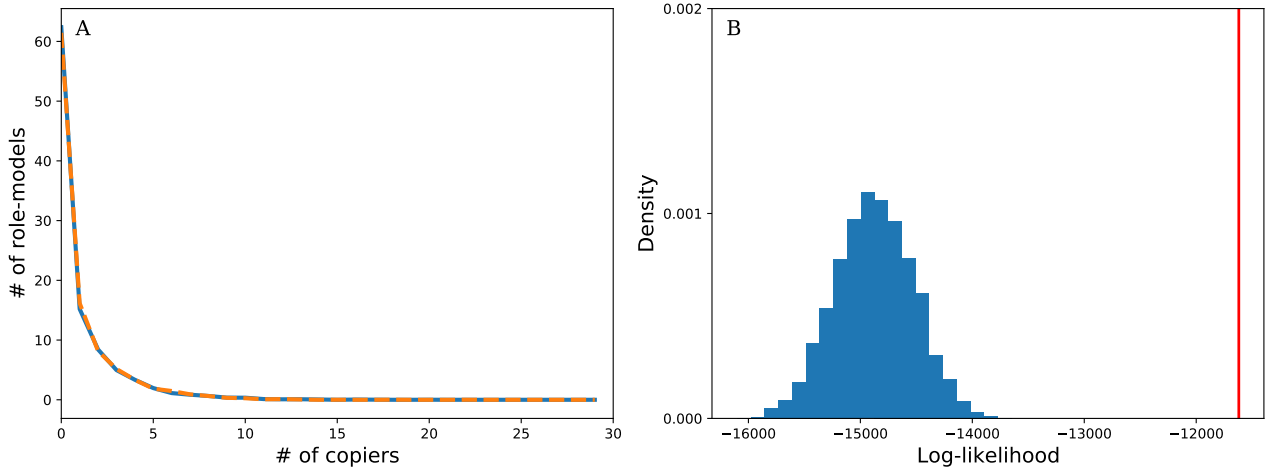
Figure 2: Numerical validation of the DM approximation. We performed computational "experiments" of the role-model choice process and compared them to the DM distribution. **(A)** The difference between the DM distribution (orange) and the empirical distribution of the experiments (blue) is very small. **(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.

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 of the full model (fig. 5).

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 conditioned 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 (Kimura, 1962; Kimura and Ohta, 1969; Otto and Whitlock, 2006). We are mainly interested in the effect of the bias weight, α, which determines the relative effect of success and influence on prestige bias, given by eq. (10). For simplicity, we do not include role-model estimation error in this analysis, i.e $e_i = 0$ for every copier i. As shown above, transmission in our model is approximately DM distributed (corollary 3 and eq. (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,*

$$E[x' - x] \approx x(1-x)(1-\beta) , \quad V(x' - x) \approx x(1-x)\left(\frac{1}{\alpha N + (1-\alpha)}\right) . \tag{17}$$
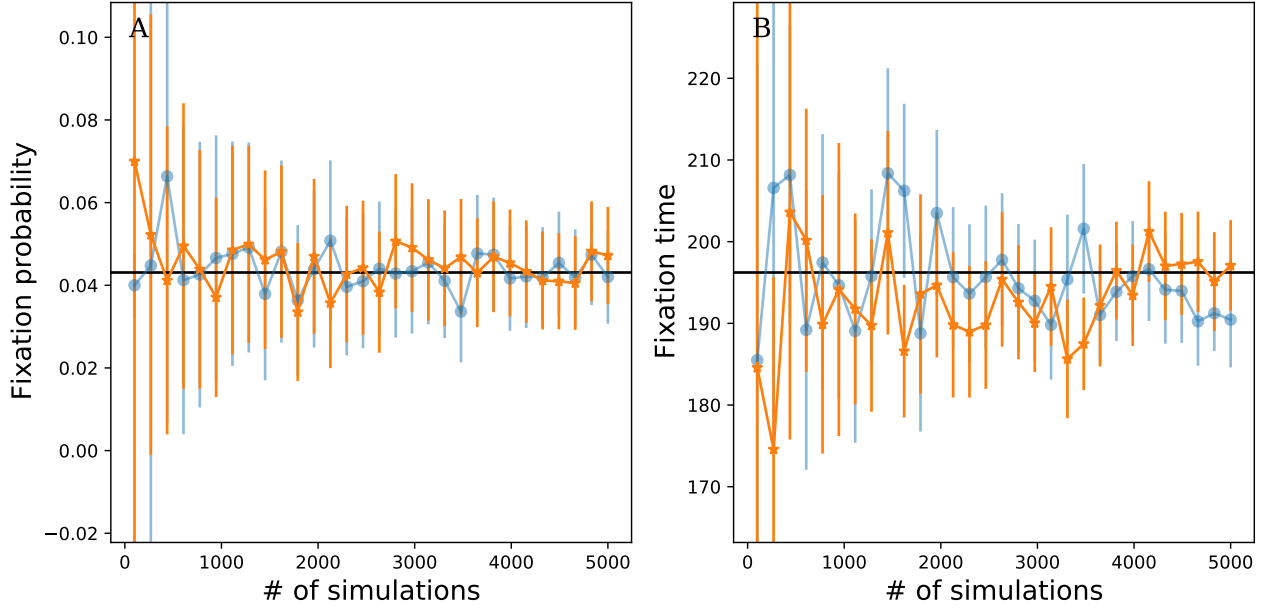
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Figure 3: DM Approximation precision as function of number of simulations. Our DM approximation (orange) agrees with stochastic simulation results (blue) when using 1,000 or more simulations. Both fluctuate around the analytic fixation probability 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, $\beta(A) = 0.956$.

302 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

304 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-

306 equation approximation of the classical Wright-Fisher model, the expectation and variance of the change in frequency are $E[x' - x] = x + x(1 - x)s + o(s)$ and $V[x' - x] = x(1 - x)/N_e$ (Kimura, 1962,

308 eq. 7). Therefore, we have the following result.

310 **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*

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

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

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

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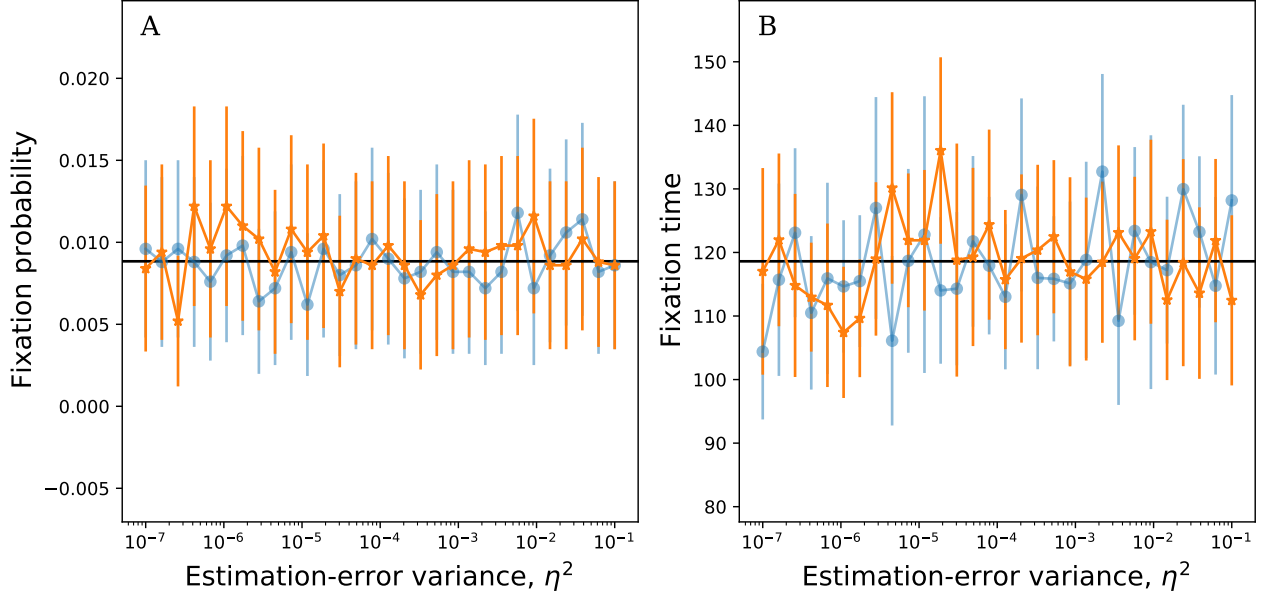
318 result:

11

Figure 4: 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 $\eta \in [10^{-7}, 10^{-1}]$.
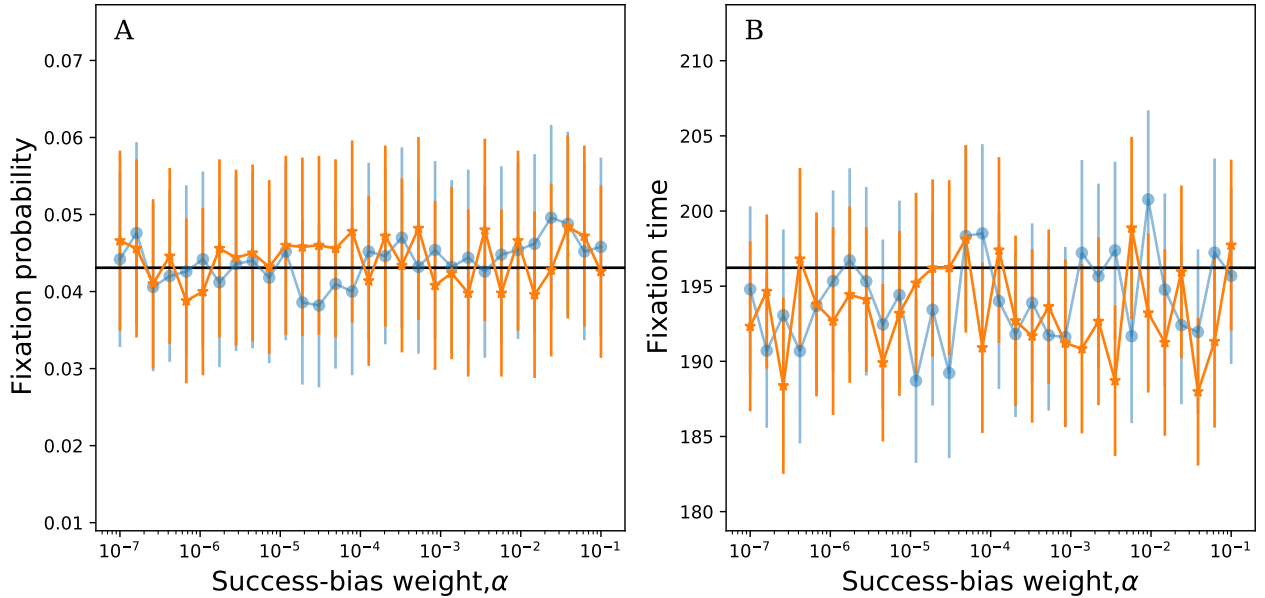

Figure 5: Robustness of DM approximations to variation in the bias weight α. Both the DM approximation (orange) and Kimura's equation (black line) fit the stochastic simulations (blue) well even with a high variation in success bias weight. Markers for average across 5,000 simulations, error bars are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

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

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

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

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

Result 6 (Fixation time).

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

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

$$u(x) = \frac{1 - e^{-2Sx}}{1 - e^{2S}} \tag{21}$$

and,

$$J_1 = \frac{2}{(1-\beta)(1 - e^{-2S})} \int_x^1 \frac{(e^{2S\xi} - 1)(e^{-2S\xi} - e^{-2S})}{\xi(1 - \xi)} d\xi, \tag{22}$$

$$J_2 = \frac{2}{(1-\beta)(1 - e^{-2S})} \int_0^p \frac{(e^{2S\xi} - 1)(1 - e^{-2S\xi})}{\xi(1 - \xi)} d\xi \tag{23}$$

$$T = \frac{1 - \pi}{1 - \beta} \int_0^x \frac{e^{2(1-\beta)\xi} - 1}{\xi(1 - \xi)} d\xi + \frac{\pi}{1 - \beta} \int_x^1 \frac{1 - e^{-2(1-\beta)(1-\xi)}}{\xi(1 - \xi)} d\xi \tag{24}$$

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

Numerical validation. We compare our approximations (eqs. (19) and (24)) 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, $s_e = 1 - \beta$, 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 our approximations (Figure 6).

Changing environment . After finding a good approximation in constant environment, where the favorable trait is always $\hat{A}$, we proceeded to find an approximation for a changing environment. Following Ram et al. (2018b), we find the following expressions for the expectation and variance of the change in frequency between t generations. The proof is in Appendix C.

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 at time t. Then,*

$$E[X_t/N - x] \simeq x(1 - x)S_t/N_e , \quad and \quad V(X_t/N - x) \simeq tx(1 - x)/N_e , \tag{25}$$
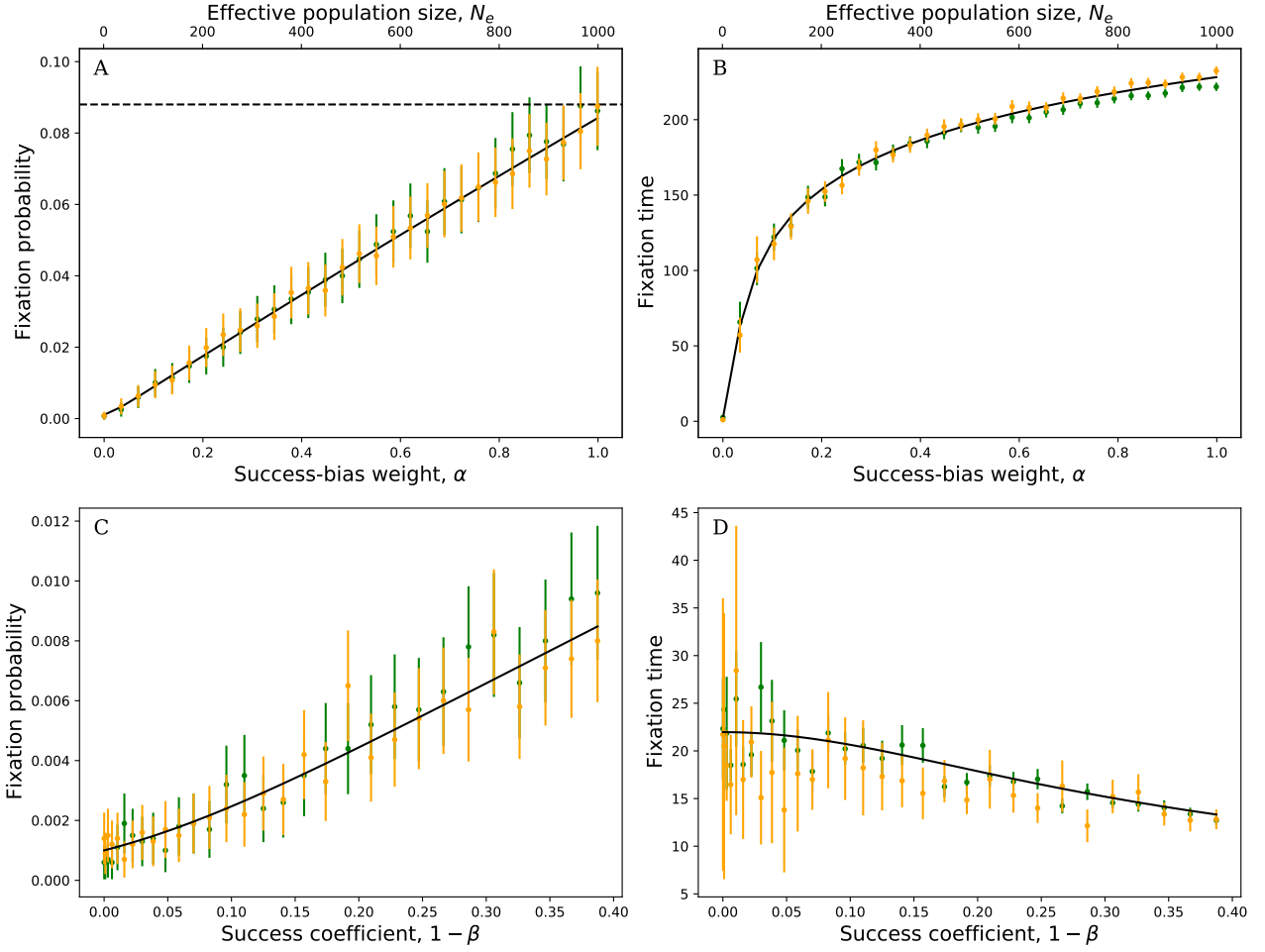
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Figure 6: Fixation probability and time in a constant environment. Fixation probability and time (in generations) as a function of the success-bias weight α (bottom x-axis), or effective population size N_e (top x-axis) in the top row, and as a function 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 $2s_e = 2(1 - \beta)$ (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).

348   *where $S_t = \sum\limits_{i=1}^{t} N(1 - \beta_t)$.*

Using the drift and diffusion terms and following Ram et al. (2018b), we can approximate the fixation

350   probability in a changing environment using

$$\tilde{\pi} = \frac{1 - e^{-2\frac{S_n}{n}N_e x}}{1 - e^{-2\frac{S_n}{n}N_e}} \tag{26}$$

352   where $\frac{S_n}{n} = \frac{k-l}{k+l}(1 - \beta)$ and $n = k + l$. That is, we use the average selection coefficient during a cycle of $k + l$ generations as the selection coefficient eq. (19).

354   **Numerical validation.** Comparing our approximation, eq. (26) to numerical simulations, we find that the approximation fits simulations results well for variable bias weights, α, which corresponds to the

356   effective population size (Figure 7A).

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However, the approximation is more sensitive to the value of the success bias coefficient β (Figure 7B). 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 the β values (0.65 and below), the fixation probability exceeds even the constant environment approximation (which is the upper limit). However, this is to be expected, because the diffusion-equation approximations assume weak selection (i.e., low selection coefficient s).

When k is the number of generations where the invading phenotype is favored, and l when the original trait is, we found that for large k-to-l ratio (while keeping constant total cycle length, $n = k + l = 100$), the changing environment approximation, eq. (26) converges to the constant environment approximation, eq. (19), see Figure 7C and Figure 7D.

Result 8. *The effective population size doesn't affect the goodness of fit of the approximation. The success coefficient however, must be even lower than before for the approximation to fit.*

The proof is seen in Figure 7A,B. 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 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 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 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 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 disfavored ones is very high, it is very similar to a constant environment model.
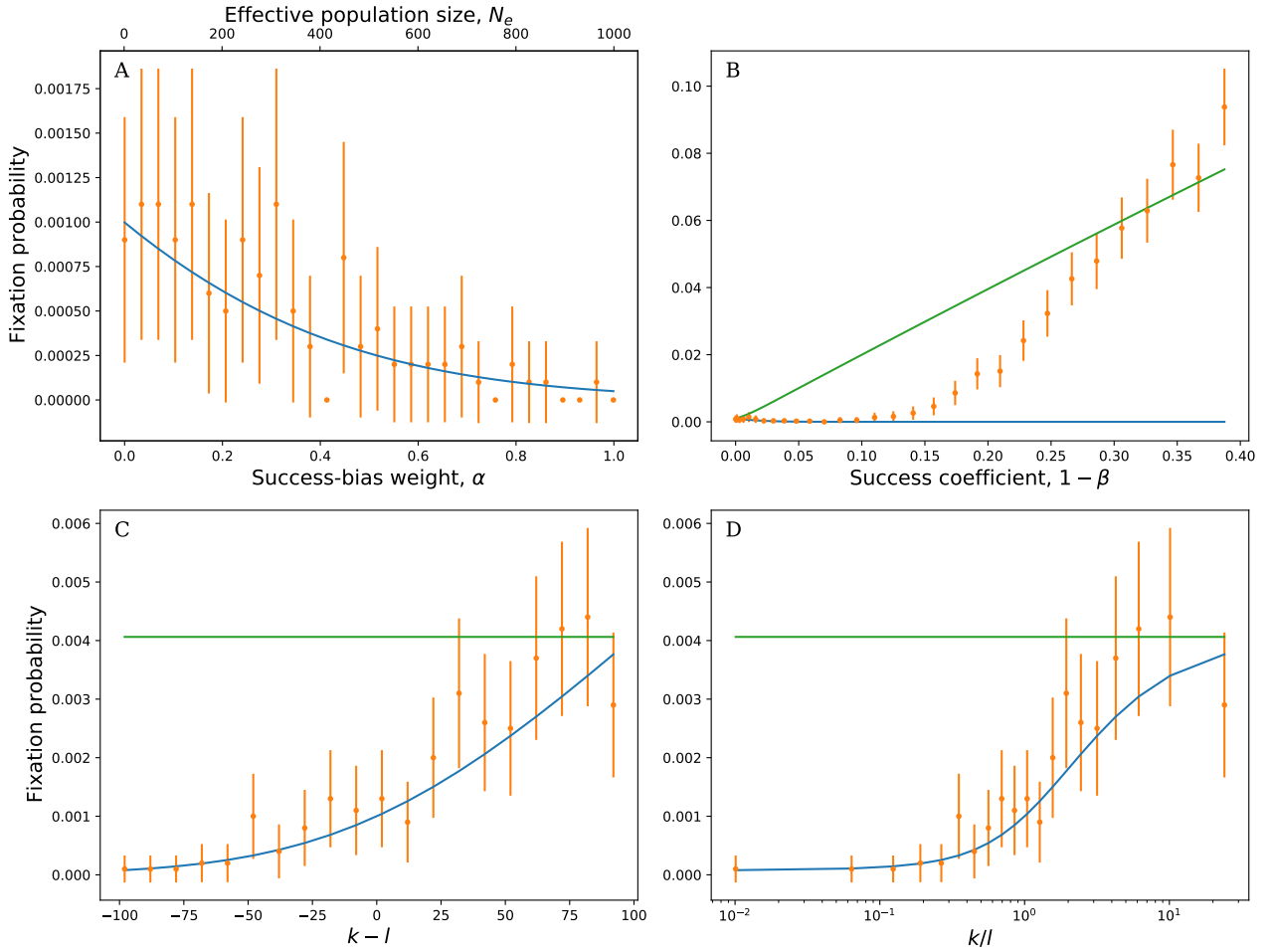
Figure 7: Fixation probability in a changing environment. **(A)** Fixation probability decreases with the the success-bias weight (bottom x-axis) and effective population size (top x-axis). The approximation (blue; eq. (26)) agrees with simulation results (orange). **(B)** Fixation probability increases 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. (26)). 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

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

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between the estimated and the ideal trait values,

$$\alpha^* = argmin \sum_{j=1}^{N} \frac{\alpha A_j + (1-\alpha)K_j}{\sum_{l=1}^{N} \alpha A_l + (1-\alpha)K_l} \cdot (\hat{A} - A_j)^2 \,, \qquad (27)$$

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

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 8). Moreover, their estimation error is much lower compared to a constant success-bias weight, which gives roughly the same high estimation error to all copiers (compare Figure 8B and C): in this example, the adaptive weight estimation error converges to 0.046, whereas a constant weight gives values > 0.74.
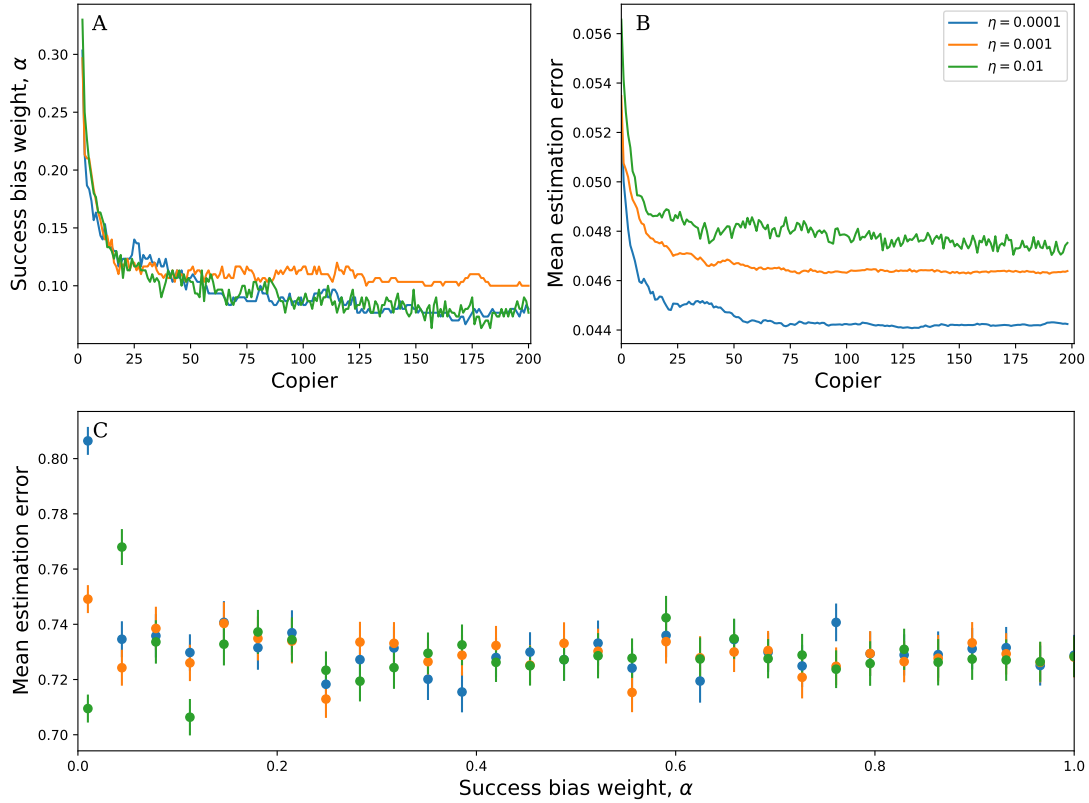

Figure 8: Advantage of an adaptive success-bias weight. Both success-bias weight α (**A**) and estimation error (**B**) decrease during the role-model choosing process, demonstrating that influence becomes more favored as more copiers have made their choice. However, when α is homogeneous (**C**), the 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.

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 in other traits (Henrich and Broesch, 2011).

Inspired by a model by Boyd and Richerson (1988), we developed a cultural-evolution model with prestige bias that includes both success and influence biases, where the latter is a bias towards role-models with many copiers. This is accomplished by a role-model choice process: each copier, in its turn, chooses a role-model, and that choice is affected both by the estimated success of each potential role-model and the number of copiers that already chose each role-mode (eq. 10).

This resulted in 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, rather than 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 6).

We also analyzed a cyclic changing environment in which the identity of the success-biased trait switches after a fixed amount of generations (Figure 7). 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 8). 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 (2009), 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 (2009) 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 (Erhart and Overdorff, 1999). 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 (2001) 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 (2001) 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 (2002), 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-

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

Empirical evidence of prestige bias Chudek et al. (2012) report the first direct tests in children that
472 suggest the existence of prestige bias, defined as the tendency to learn from individuals to whom
others have preferentially attended, learned, or deferred. Their definition of prestige is similar to our
474 influence bias. They showed that the odds of 3-4 years-old children learning from an adult role-model
to whom bystanders had previously preferentially attended for 10 seconds were more than twice those
476 of their learning from a role-models whom bystanders ignored. They also note that prestige effects are
domain sensitive: they found that prestigious role-models were attended more when demonstrating
478 artifact use, whereas role-models presenting food preferences had less attendants, suggesting that the
domain itself (artifact use vs. food preference) can affect the attendance, and hence the prestige of the
480 role-model. This lead Chudek et al. (2012) to suggest that when the trait is costly to learn individually,
prestige will have a stronger bias. It would be interesting to include costs in our model to try and
482 observe these effects and dynamics in a large population.

According to Henrich and Broesch (2011), evolutionary theorists propose that natural selection has
484 favored the emergence of psychological biases for learning from those individuals most likely to
possess adaptive information. Thus, they studied Fijian villages to examine if and how such biases
486 emerge in a small-scale society. They found that Fijian villagers are more likely to learn from role-
models perceived as more successful/knowledgeable, both within and across domains. Their research
488 thus suggests that copying from those perceived as successful, rather than actually are successful, is a
common phenomena. They show that the social networks representing copier–role-model relationships
490 are centralized, suggesting that it is consistent with the prediction that people substantially share
notions about who is a good cultural model, but that individuals' role-model selections are influenced
492 by multiple factors.

We can also find prestige bias in more modern domains such as western medicine. Norredam and
494 Album (2007) examined literature from 1950 to 2005 on the effects of prestige on medicinal practices.
They found that active, specialized, biomedical, and high-technological types of medicine on organs
496 in the upper part of the bodies of young and middle-aged people were accorded high levels of prestige,
whereas medicine and practices with opposite characteristics had low levels of prestige. For example,
498 they found that surgery counts as the most prestigious specialty, while psychiatry is the less prestigious.
In addition, doctors tend to rank practices that require more time to master as more prestigious, while
500 other procedures that are considered easier to master are less prestigious. This means that there may be
very important practices that are neglected due to prestige bias. They concluded that such differences
502 in prestige may bear consequences for actual priority setting in healthcare systems.

Prestige bias can help to cheaply estimate and acquire knowledge, which may facilitate survival and
504 reproduction. However, it is not always the case, and there could be negative repercussions to this
bias, such as invasion of maladaptive traits. Takahashi and Ihara (2019) mention that social learning
506 not only takes the form of random copying of other individuals, but also involves learners' choice of
what to learn and from whom to learn. They suggest a best-of-k model where an individual samples *k*

role-models and chooses the one he deems most "successful". They mentioned that a previous mathematical analysis has shown that it may sometimes result in maladaptive cultural evolution when the payoffs associated with cultural variants vary stochastically. In such a case, learners may be selectively disfavored and in the long run replaced by unbiased learners, who simply copy someone chosen at random. They developed new mathematical models that are simpler and mathematically tractable. They found that best-of-k learning, unlike unbiased learning, can facilitate the invasion of an on average inferior variant that sometimes gives a very high payoff. Our model, which includes influence bias, is consistent with this claim. When a maladaptive trait is "piggybacking" a role-model with high influence, this trait could spread in the population. In addition, they show that best-of-k learning can be stable against invasion by unbiased learning if social learning is sometimes combined with individual learning. Our model only includes social learning, and not individual learning, but it could be interesting to combine it with individual learning and see how it affects the dynamics.

Prestige bias can also accelerate reversal of harmful traditions such as child marriage and domestic violence. Efferson et al. (2020) suggest a *spillover* mechanism, in which an intervention affects a large enough group in a target population, so that others not included in the intervention also change their behavior. They found that there are individuals who act as *agents*, who are often looked upon, and therefore they are ideal targets for interventions. This is similar to influential role-models in our model, where a prestigious individual will be copied more often, and will therefore spread his trait faster and wider in the population. They also suggest a way to use this phenomena to change existing traditions in a population. It is very clear however, that just as it can be used to end harmful traditions, the same agents could start harmful traditions.

Dunbar (2009) hypothesized that larger, more complex brains can store and manage more information and in turn, this information can support the costs of a larger brain. Following up on this, Muthukrishna and Henrich (2016) offered that prestige can directly affect human physical evolution. They present a 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, 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 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 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 ability to "cheaply" acquire adaptive knowledge via transmission biases such as prestige.

Further work. One path forward is an analysis of the dynamics of the adaptive success-bias weight model, in which every copier chooses its α. It would be interesting to see the if the mean estimation error and the adaptive weight, α^*, are converging to specific values, and how they are affected by the model parameters. It 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 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 by Van Vugt and Smith (2019) that are attributed to Confucius and Machiavelli. Confucius viewed leaders as role-models who exercise influence through possessing superior knowledge, skills, and (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 and violence. Van Vugt and Smith (2019) suggest that these two 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 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 to leadership style. The emerging cultural-evolutionary dynamics and their dependence on the costs and benefits are intriguing.

Conclusions. Here, we presented support for the existence of prestige biases in cultural transmission, including the commonly studied success bias. We introduced an influence bias, which has so far received less attention. We believe the combination of these biases may be a strong driving force in cultural evolution. We show that the relative effect of the two biases changes the effective population size such that the increasing the weight individuals give to influence bias, decreases the effective population size. We also find a clear advantage to individuals that can choose the relative weight of the two biases.

Acknowledgements

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Appendices

Appendix A   General binomial distribution approximation

Proving $\mathrm{E}[K_{Nj}] = \alpha_j \cdot \beta(A_j + e)\big/\overline{\alpha \cdot \beta(A + e)}$**, 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,

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

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,

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

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),

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

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,

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

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

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

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

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 (2008, 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 $S_t = \sum\limits_{i=1}^{t} N(1-\beta_t)$.

Proof. Let $s_t = N(1-\beta_t)$, and $S_n = \sum\limits_{i=1}^{n} s_i$, where β_t is $\beta(A)$ at generation t. We prove by induction both terms in eq. (25). From eq. (B3) we know that

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

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,

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

Using eq. (C1) we see that

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

Using eq. (B10) we get

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

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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.