

Effective population size for culturally evolving traits

Dominik Deffner^{1*}, Anne Kandler¹ & Laurel Fogarty¹

¹Department of Human Behavior, Ecology and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

*Corresponding author: dominik.deffner@eva.mpg.de

ABSTRACT

Population size has long been considered an important driver of cultural diversity and complexity. Results from population genetics, however, demonstrate that in populations with complex demographic structure or mode of inheritance, it is not the census population size, N , but the effective size of a population, N_e , that determines important evolutionary parameters. Here, we examine the concept of effective population size for traits that evolve culturally, through processes of innovation and social learning. We use mathematical and computational modeling approaches to investigate how cultural N_e and levels of diversity depend on (1) the way traits are learned, (2) population connectedness, and (3) social network structure. We show that one-to-many and frequency-dependent transmission can temporally or permanently lower effective population size compared to census numbers. We caution that migration and cultural exchange can have counter-intuitive effects on N_e . Network density in random networks leaves N_e unchanged, scale-free networks tend to decrease and small-world networks tend to increase N_e compared to census numbers. For one-to-many transmission and different network structures, effective size and cultural diversity are closely associated. For connectedness, however, even small amounts of migration and cultural exchange result in high diversity independently of N_e . Our results highlight the importance of carefully defining effective population size for cultural systems and show that inferring N_e requires detailed knowledge about underlying cultural and demographic processes.

AUTHOR SUMMARY

Human populations show immense cultural diversity and researchers have regarded population size as an important driver of cultural variation and complexity. Our approach is based on cultural evolutionary theory which applies ideas about evolution to understand how cultural traits change over time. We employ insights from population genetics about the “effective” size of a population (i.e. the size that matters for important evolutionary outcomes) to understand how and when larger populations can be expected to be more culturally diverse. Specifically, we provide a formal derivation for cultural effective population size and use mathematical and computational models to study how effective size and cultural diversity depend on (1) the way culture is transmitted, (2) levels of migration and cultural exchange, as well as (3) social network structure. Our results highlight the importance of effective sizes for cultural evolution and provide heuristics for empirical researchers to decide when census numbers could be used as proxies for the theoretically relevant effective numbers and when they should not.

Keywords: Cultural evolution, effective population size, cultural complexity, networks, demography.

1

1. INTRODUCTION

2 Cultural evolutionary dynamics are governed by individual-level cognitive processes and
3 demographic properties of the population [Cavalli-Sforza and Feldman, 1981, Boyd and
4 Richerson, 1985]. Archaeologists and anthropologists have been particularly interested in
5 the ways population size might shape cultural processes [see Derex and Mesoudi, 2020,
6 Strassberg and Creanza, 2021, for recent reviews]. When researchers consider the impact of
7 population size on cultural evolution, they predominantly refer to the number of individuals
8 in a population. This census population size N is readily observable in real-world situations
9 and can be quantified by counting how many people are present at a certain place and time.

10 Results from population genetics, however, have long demonstrated that in most real-world
11 populations it is not this census size, but the effective size, N_e , that is the correct measure
12 to use when calculating important evolutionary parameters such as genetic diversity and
13 divergence times between populations [Ewens, 2012].

14 **1.1. What is effective population size and why do we need it?** The effective pop-
15 ulation size is a theoretical construct that links complex populations to simpler, idealised
16 models. This way, the effective size makes it possible to directly compare any number
17 of complex populations—each with their own complicating factors—in a way that would
18 otherwise be impossible. A commonly used simplified model in population genetics is the
19 Wright-Fisher model [Fisher, 1923, Wright, 1931, Ewens, 2012], and much of what we under-
20 stand about evolution comes from our understanding of evolution in such idealised models.
21 The effective population size is defined in relation to this model as the size of an ideal
22 Wright-Fisher population that experiences genetic drift at the same rate as a particular
23 study population (see section 2 for details).

24 To understand what we gain from the effective size, even if we are not particularly
25 interested in Wright-Fisher models, let us assume there are two populations, A and B, that
26 produce a particular cultural trait with many possible variants. We now want to know
27 whether population size affects the number of different traits in a population. Population
28 A has a large census population size of 1000 individuals, population B has a smaller census
29 size of just 500. Using a theoretical model of a cultural evolutionary process [e.g. Shennan,
30 2001, Henrich, 2004, Powell et al., 2009, Fogarty et al., 2017], we conclude that larger
31 populations should have larger or more complex cultural repertoires. Can we expect to find
32 this demographic relationship in data on census population sizes and cultural repertoire
33 sizes from both populations [e.g. Oswalt, 1976]? The answer is that—regardless of how
34 good the model is—the relationship is unlikely to be found unless these real populations
35 are identical in some evolutionarily important ways. If they do not have the same age
36 structure, demographic history, or, as we show below, cultural transmission mechanisms
37 and interaction patterns, the populations are not directly comparable, except through their
38 relation to a simpler model—through their effective population sizes.

39 Imagine we now discover that, 10 generations ago, population A had a population bot-
40 tleneck where its census size fell to only 10 individuals before recovering to its current value
41 of 1000. Genetic evolution will be affected by this bottleneck for a number of generations
42 (culture might recover from such events much faster than genetics [Fogarty and Kandler,
43 2020]). Both populations are otherwise identical and conform to the assumptions of the
44 Wright-Fisher model, which we detail below. Accordingly, the effective population size of
45 the small, stable population B is 500, the same as its census size. The effective size of
46 population A, however, is only around 92 (see appendix 1 for calculation). We can now
47 use results from population genetics to calculate how many cultural traits we expect to
48 see in each population, given certain transmission mechanisms and innovation rates. For
49 population B with $N_e = 500$, the expected number of traits is 223. For population A with
50 $N_e \approx 92$, we expect to see on average 41 traits in a given generation (see appendix 1 for full
51 details). Thus, although a relationship exists between effective population size and cultural
52 diversity, a straightforward relationship does not exist between census size and diversity.
53 Using census numbers or more informal definitions of effective size will produce incorrect
54 results. As real populations differ from one another and from the assumptions of an ideal

55 Wright-Fisher model in numerous evolutionarily important ways, the ability to unify and
56 compare them is invaluable. This is relevant for any question where we need to understand
57 the effects of drift and selection in cultural processes across populations.

58 For many animal and plant species, researchers have investigated the relationship between
59 observed census size N and calculated (genetic) effective size N_e . In one large-scale study,
60 ratios of N_e to N were found to vary between 0.19 in a species of pine tree to 3.69 in a
61 species of mosquito [Waples et al., 2013]. This demonstrates that, across species, a large
62 range of relationships between census and effective sizes are possible and N_e can also exceed
63 the census size N —a possibility we expand on below. Estimates of this ratio for humans
64 suggest that the genetic effective size is considerably lower than our census size with an N_e
65 of around 10,000 compared to a census size of around 7 billion at the time of publication
66 [Tenesa et al., 2007], possibly reflecting population bottlenecks in the past. All of this
67 strongly suggests that in order to understand how demography affects cultural evolution,
68 and which empirical comparisons are meaningful, we need to gain a better understanding
69 of the cultural equivalent of N_e .

70 **1.2. Cultural effective population size - history and outline.** The importance of ef-
71 fective population size has been partially acknowledged in the cultural evolution literature
72 and the concept is often invoked. Henrich et al. [2016], for example, write: “The theory
73 explicitly predicts that it is the size of the population that shares information—the effective
74 cultural population size—that matters, and if there is extensive contact between local or
75 linguistic groups, there is no reason to expect census population size to correspond to the
76 theoretically relevant population”. More recently, Derex and Mesoudi [2020] also claim that
77 effective population size “depends on both population size and interconnectedness”. How-
78 ever, the definition of N_e as “the population that shares information” is not always correct
79 and corresponds more closely to the ‘breeding population’ rather than the effective size. We
80 hope to show that it is not only the number of individuals sharing information, also called
81 “cultural equivalent N ” [Cavalli-Sforza and Feldman, 1981], but the exact details of how
82 information is passed on between individuals that should be expected to influence cultural
83 effective population size. Furthermore, it remains unclear whether and how different forms
84 of population interconnectedness as well as social network characteristics might influence
85 effective population size for culture, though intuition suggests that this influence may be
86 strong. In a first formal treatment for cultural evolution, Premo [2016] used simulation
87 models to investigate effective population size and its relationship with cultural complex-
88 ity. In the context of models by Shennan [2001] and Henrich [2004], the results show that
89 natural and cultural selection can weaken the relationship between census population size,
90 cultural diversity and mean skill level. This work did not formally derive an appropriate
91 measure for cultural effective size and examined the influence of selection within the scope
92 of two domain-specific models.

93 Here we aim to provide this formal derivation and systematically examine the concept
94 of effective population size for cultural evolution. We first introduce drift and effective
95 population size as employed in standard models of population genetics. After deriving
96 appropriate formulations of N_e , we use different modeling approaches to investigate how
97 cultural N_e depends on (1) the way traits are learned, namely one-to-many and frequency-
98 dependent (i.e conformist and anti-conformist) transmission, (2) population connectedness
99 through either migration or cultural exchange, and (3) social network structure. In each

100 case, we relate effective numbers to the emerging levels of cultural diversity. We conclude
101 by discussing implications for the role of demography in cultural evolution and provide
102 heuristics for empirical researchers to decide when census numbers might be used as proxies
103 for the theoretically relevant effective numbers.

104 2. DRIFT AND EFFECTIVE POPULATION SIZE IN POPULATION GENETICS.

105 We first provide a basic introduction to the Wright-Fisher population, genetic drift, and
106 the concept of effective population size as developed for genetic evolution.

107 **2.1. The Wright-Fisher population and genetic drift.** The classic Wright-Fisher pop-
108 ulation is a closed, randomly mating population of N individuals without selection and mu-
109 tation [Fisher, 1923, Wright, 1931, Fisher, 1931, Ewens, 2012]. For each discrete generation,
110 new individuals are formed by random sampling, with replacement, of gametes produced
111 by the previous generation. The number of offspring for a given member of the parental
112 generation is a binomially distributed random variable with both mean and variance of ap-
113 proximately 1 (for haploid populations; see appendix 2 for explanation). Genetic drift de-
114 scribes the random change in allele frequencies from generation to generation by the chance
115 success of some alleles relative to others [Wright, 1929, Masel, 2011, Whitlock and Phillips,
116 2014]. While per definition unpredictable in any particular instance, on average, drift causes
117 populations to change in broadly systematic ways: drift reduces the number of alleles in
118 a population, increases the differences among populations and results in higher variability
119 of allele frequencies over time. Crucially, the magnitude of allele frequency changes due
120 to genetic drift is inversely related to the size of the Wright-Fisher population—the larger
121 the number of individuals, the smaller the effects of genetic drift. These consequences are
122 illustrated in Fig. 1 which shows the frequency of one allele in populations of different sizes,
123 $N = 10$ (Fig. 1A), $N = 100$ (Fig. 1B), $N = 1000$ (Fig. 1C) or $N = 10000$ (Fig. 1D). Colored
124 lines show trajectories for 8 separate populations evolving over 100 generations. In small
125 populations, random sampling of alleles leads to strong fluctuations in allele frequencies
126 over time. After relatively few generations, populations diverge and the allele either goes to
127 fixation or extinct. Both outcomes are expected to happen half of the time as the allele was
128 at 50% initial frequency. The larger the population, the smaller are temporal fluctuations
129 in allele frequency and the longer it takes until populations diverge. Given enough time, in
130 the absence of other evolutionary forces, even very large populations will diverge as much
131 as smaller populations and the allele will go to fixation/extinction. Population size, thus,
132 affects the rate of drift but not its eventual outcome.

133 **2.2. Effective population size.** The effective size of a population, N_e , is a fundamen-
134 tal concept in population genetics that allows researchers to quantify the effect of drift on
135 evolution [Wright, 1931, Kimura and Crow, 1963, Charlesworth, 2009]. N_e is defined as
136 the size of an idealized Wright-Fisher population that is identical in some key measure of
137 genetic drift to a particular study population. Jointly with the mutation rate, N_e deter-
138 mines the expected number of neutral or weakly selected genetic variants maintained in a
139 population and is thus important for correctly calculating the variability in a population.
140 In combination with the strength of selection, N_e also governs how effective selection can be
141 in spreading favourable mutations and eliminating deleterious ones thus shaping the course
142 of adaptive evolution [Charlesworth, 2009].

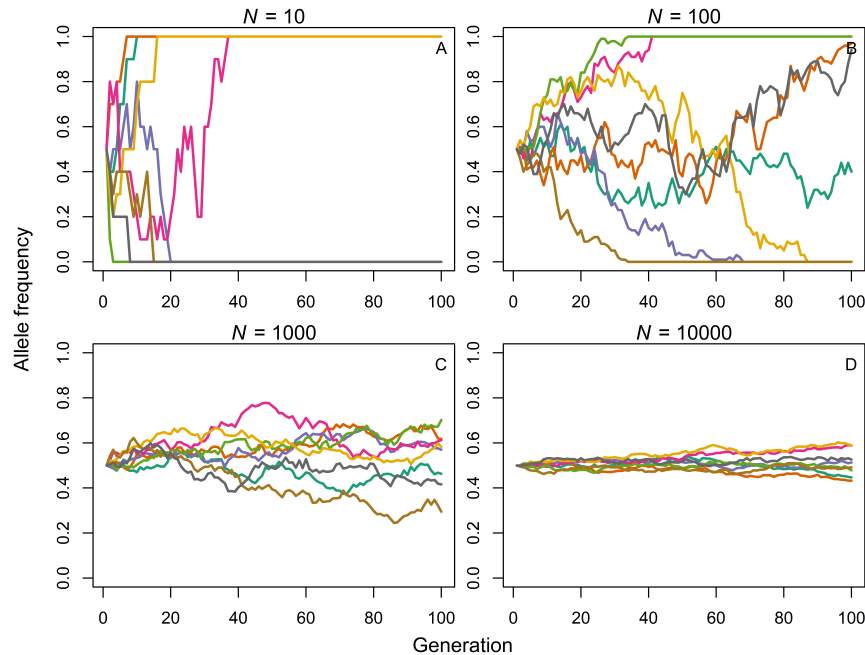


Figure 1. Drift. Frequency of a focal allele over 100 generations. Each line shows evolution in a separate population of size $N = 10$ (A), $N = 100$ (B), $N = 1000$ (C) or $N = 10000$ (D). All simulations start at the same initial allele frequency of 0.5.

143 Different aspects of the evolution of the Wright-Fisher population have been used to
 144 define N_e . These most often agree but diverge under some circumstances relevant to cul-
 145 tural systems. Therefore, we consider two commonly used measures, inbreeding effective
 146 population size, N_e^i , and variance effective population size, N_e^v . In appendix 3, we provide
 147 derivations for haploid populations for situations when (1) there is variation in offspring
 148 numbers and (2) population sizes might differ between parental and offspring generation.
 149 The identity-by-descent (or inbreeding) effective population size N_e^i utilizes the fact that,
 150 for finite populations, there is a certain probability for two randomly selected individuals
 151 to come from the same parent. It is calculated as:

$$(1) \quad N_e^i = \frac{N_{t-1}\bar{k} - 1}{\bar{k} - 1 + \frac{\sigma^2}{k}},$$

152 where N_{t-1} is the census size in the parental generation, \bar{k} is the mean number of offspring
 153 and σ^2 is the variance in offspring number among members of the parental generation.

154 The variance effective population size N_e^v , in contrast, focuses on the amount of random
 155 variation in allele frequencies from one generation to the next and can be calculated as:

$$(2) \quad N_e^v = \frac{(N_{t-1} - 1)\bar{k}}{\frac{\sigma^2}{k}}.$$

156 Note that the inbreeding effective number is intimately related to the size of the popula-
 157 tion in the parental generation, while the variance effective number is related to the size of
 158 the population in the offspring generation [Crow and Kimura, 1970]. To understand why,
 159 imagine two parents, one carrying allele A , one carrying allele B , randomly producing a

160 large number of offspring. While this scenario will result in a high probability that two
161 offspring share the same parent, the frequency of both alleles will still be close to 50% in
162 the offspring generation (i.e. low inbreeding effective size and high variance effective size).
163 If, on the other hand, a large number of parents produces only a handful of offspring, there
164 will only be a small probability that two offspring share the same parent, while allele fre-
165 quencies will differ greatly among generations (i.e. high inbreeding effective size and low
166 variance effective size).

167 The inbreeding effective number is appropriate when researchers are interested in the
168 change in homozygosity due to random drift. The variance effective number, in contrast,
169 is appropriate when researchers are interested in the amount of gene-frequency drift or the
170 increase in variance among subgroups [Kimura and Crow, 1963, Crow and Denniston, 1988].
171 Despite these differences, for constant population sizes (i.e. $\bar{k} = 1$), both effective numbers
172 agree and equations simplify to:

$$(3) \quad N_e = \frac{N - 1}{\sigma^2}.$$

173 In the following, we will only differentiate between the two formulations when necessary
174 and otherwise use the simplified version given by Eq. (3).

175 3. DETERMINANTS OF EFFECTIVE POPULATION SIZE IN CULTURAL EVOLUTION

176 Researchers have identified several factors influencing N_e in genetic evolution [see e.g.
177 Charlesworth, 2009]. In the case of cultural evolution, the relationship between census
178 population size and the effective size may be considerably more complex. For example, the
179 mode of transmission has been shown to be an important factor in determining effective
180 size in genetic systems. In the case of culture, there are many more possible modes of
181 transmission [Cavalli-Sforza and Feldman, 1981, Boyd and Richerson, 1985, Kendal et al.,
182 2018] each of which may have unique effects. Therefore, in order to correctly use the concept
183 of an effective size in cultural systems, a uniquely cultural theory must be developed.

184 Traits that evolve culturally do so through processes of innovation and cultural trans-
185 mission. So, we now consider cultural rather than biological reproduction and allow \bar{k} to
186 represent the average number of naive individuals to which a role model transmits their
187 cultural trait. Similarly, σ^2 represents the variance in this ‘cultural influence’. Eq. (3) im-
188 plies that, in general, increasing the variance among individuals in the number of cultural
189 offspring they leave reduces the effective population size, and decreasing that variance in-
190 creases N_e . Thus, it is clear that any process that systematically alters the way in which
191 cultural role models are chosen, through the mode of transmission, demography or social
192 network structure, will change the variance in cultural influence and the effective population
193 size for culturally evolving traits.

194 **3.1. Simulation set-up.** As the derivation of analytical results for effective population
195 sizes becomes unfeasible for most of the situations considered in this paper, we develop a
196 simulation framework based on the Wright-Fisher dynamic [Kimura and Crow, 1964]. We
197 consider a population of census size N where individuals are characterized by the variant of
198 a single cultural trait they have adopted. In each time step, a new generation of individuals
199 is formed and each naive individual adopts its cultural variant, if not specified differently,
200 through unbiased cultural transmission from the previous generation. In more detail, the

201 probability that a naive individual chooses variant i of M cultural variants present in the
202 previous generation is given by:

$$(4) \quad p_i = \frac{n_i}{\sum_{m=1}^M n_m} (1 - \mu),$$

203 where n_i is the frequency of variant i in the appropriate pool of role models. With
204 probability μ an innovation takes place and a new, not previously seen variant is introduced
205 into the cultural system. To calculate the effective population size in various scenarios, we
206 first let the system evolve through unbiased transmission until it reaches its equilibrium
207 state. We then run 300 generations assuming the transmission dynamics described below
208 and record the “cultural influence” of each individual in a specific generation by determining
209 its number of cultural offspring in the next generation. This provides us with estimates for
210 \bar{k} and σ^2 (conditioned on the assumed transmission dynamic) needed to calculate effective
211 population sizes according to Eqs. (1) and (2). Additionally, to relate effective population
212 sizes to resulting levels of cultural diversity, we record two diversity measures, the Simpson
213 diversity index (SDI) and the number of unique cultural variants. The SDI is calculated
214 as $D = 1 - \sum_{i=1}^S (n_i/N)^2$, where n_i is the frequency of individuals carrying variant i in
215 the population and S is the total number of unique cultural variants [Simpson, 1949]. This
216 index ranges from 0 to 1, where high scores indicate high cultural diversity and low scores
217 indicate low cultural diversity.

218 To account for transmission processes different from unbiased transmission, we adapted
219 Eq. (4). For *one-to-many transmission*, we assign, in each generation, R individuals at
220 random as role models and record the frequency n_i in Eq. (4) only from these R individuals.
221 For *frequency-dependent transmission*, we assume that the probability for adopting variant
222 i of M cultural variants present in the population is given by:

$$(5) \quad p_i = \frac{n_i^\theta}{\sum_{m=1}^M n_m^\theta} (1 - \mu),$$

223 where n_i is the frequency of variant i in the whole population and θ controls the direction
224 and strength of frequency-dependent bias [McElreath et al., 2008]. When $\theta = 1$, cultural
225 transmission is unbiased; as θ becomes larger than 1, individuals become increasingly likely
226 to adopt high-frequency variants. When $0 < \theta < 1$, individuals disproportionately adopt
227 low-frequency variants.

228 To account for *migration* or *cultural exchange*, we use two, initially independent, pop-
229 ulations evolving through unbiased transmission. In case of migration, per time step, an
230 average of mN randomly chosen individuals from one population permanently migrate to
231 the other population; they carry their cultural variants with them and consequently serve
232 as potential role models for the next generation. The variable m controls the migration
233 rate. To keep population sizes constant, the same number of individuals immigrates from
234 the other population. In the case of cultural exchange, per time step, an average of eN
235 randomly chosen individuals do not permanently migrate between populations, but are
236 available as additional role models and, thereby, increase the size of the parental generation
237 in both populations. The variable e controls the cultural exchange rate.

238 To account for *social network structure*, we arrange the N individuals in the population
239 according to different network topologies (random networks, scale-free networks and small-
240 world networks); this restricts the pool of role models for each individual: the probability

241 of choosing cultural variant i , p_i as given in Eq. (4), is determined only from its direct
242 neighbours in the network. Our aim here is not to replicate realistic social networks but to
243 use prototypical network types to illustrate potential effects of network structure on effective
244 population sizes. Such extreme cases are often useful to identify causal effects and school
245 intuition [see Broom and Voelkl, 2012, Giaimo et al., 2018, for similar analyses for genetic
246 evolution]. All networks considered here are undirected and are generated as follows:

- 247 (1) Random networks: In random networks, any two individuals have the same prob-
248 ability of being connected. The Erdős-Rényi model generates such a graph by
249 starting with a set of N isolated nodes and creating every possible edge with the
250 same constant probability p [Erdős and Rényi, 1960]. For undirected graphs, there
251 are $\frac{N(N-1)}{2}$ possible ties and p gives the expected proportion of those potential ties
252 that are realized in the network (i.e. the network density).
- 253 (2) Scale-free networks: A network is said to be scale free if the fraction of nodes with
254 degree k follows a power law $k^{-\alpha}$, where $\alpha > 1$. The Barabási-Albert model is
255 an algorithm that uses a preferential attachment mechanism to generate such net-
256 works [Barabási and Albert, 1999, Albert and Barabási, 2002]. Here, it is assumed
257 that new nodes are added to the network two at a time. New nodes are connected
258 to existing node i (out of J total nodes) with a probability P_i that is proportional
259 to the number of links k_i that a node already has: $P_i = \frac{k_i^\pi}{\sum_{j=1}^J k_j^\pi}$. That is, well-
260 connected nodes are likely to get even more connected over time. The power of this
261 preferential attachment is controlled by a parameter π , where $\pi = 1$ produces linear
262 preferential attachment, $0 < \pi < 1$ produces “sub-linear” attachment, and $\pi > 1$
263 produces “super-linear” attachment.
- 264 (3) Small-world networks: Small-world networks are graphs with short average path
265 lengths between nodes and a high clustering coefficient. High clustering means that
266 nodes that you are connected to are also likely to be connected to each other (e.g.
267 most of your friends are also friends among themselves). The Watts-Strogatz model
268 creates a small-world network in two basic steps [Watts and Strogatz, 1998]: We
269 start with a lattice of N nodes with each node being connected to its K closest
270 neighbors on either side. Each edge in the network is then rewired with a certain
271 probability p_r while avoiding duplicates or self-loops. After the first step the graph
272 is a perfect ring lattice. So when $p_r = 0$, no edges are rewired and the model returns
273 a ring lattice. In contrast, when $p_r = 1$, all of the edges are rewired and the ring
274 lattice is transformed into a random graph.

275 All simulation results shown in the following are based on 1000 independent simulations
276 per parameter combination.

277 **3.2. Process of cultural transmission.** We already know from genetic studies that the
278 mode of inheritance can greatly alter effective population size [e.g. Charlesworth, 2009]. In
279 cultural systems, the ways in which cultural variants can be passed on between individuals,
280 from cultural ‘parents’ to cultural ‘offspring’, are even more numerous and complex [e.g.
281 Cavalli-Sforza and Feldman, 1981, Boyd and Richerson, 1985, Kendal et al., 2018]. In the fol-
282 lowing, we analyze how processes of cultural transmission can influence effective population
283 size. We consider two transmission processes, *one-to-many transmission* and *frequency-*
284 *dependent transmission*, whose internal dynamics differ in interesting ways. While the

285 number of transmitting individuals per generation is fixed under one-to-many transmission,
286 it emerges dynamically from the interplay between the transmission mechanism and the
287 frequency spectrum of the cultural variants under frequency-dependent transmission.

288 *3.2.1. One-to-Many Transmission.* We define one-to-many transmission as the situation
289 where only a small, pre-defined, number of individuals can transmit their cultural variant
290 to members of the next generation. This transmission process may drastically change the
291 variance in cultural influence and, thus, the effective population size depending on the
292 number of role models, R . Here, R individuals can pass on their variant and $N - R$
293 individuals cannot. In other words, each generation, we have a transmitting sub-population
294 of size R and a non-transmitting sub-population of size $N - R$. In this case, the variance
295 of cultural influence can be calculated as follows (see appendix 4 for the full details):

$$(6) \quad \sigma_{\text{OTM}}^2 = \frac{N - 1}{R}.$$

296 As R increases, i.e. as more role models have the chance to pass on their cultural trait,
297 the variance of cultural influence in the population decreases, and for $R = N$ we recover
298 the expression for the variance of cultural influence in the standard Wright-Fisher model.
299 Thus, the effective population size, N_e , for our one-to-many transmission model is simply
300 the size of the transmitting sub-population per generation:

$$(7) \quad N_e = \frac{N - 1}{\sigma_{\text{OTM}}^2} = \frac{N - 1}{\frac{N - 1}{R}} = R.$$

301 Figs. 2A and B show the variance in cultural influence, given in Eq. (6), and the effective
302 population sizes, given in Eq. (7), for different R values. The grey dots represent the
303 mean values of the effective population size generated by the simulation model described
304 in section 3.1 and, reassuringly, analytical and simulation results match very well. When
305 everyone is a potential role model (i.e. $R = N$), we recover the standard Wright-Fisher
306 model with a variance of cultural influence of approximately 1 and an effective population
307 size of $N_e = N$. Restricting the pool of role models results in an increased variance in
308 cultural influence and decreased effective population size. In the extreme case where the
309 whole population learns from only one individual per generation, the effective population
310 size is 1.

311 Figs. 2C and D describe the cultural composition of the population at equilibrium by
312 recording the level of diversity via the Simpson index and number of unique cultural vari-
313 ants in the population. Levels of cultural diversity are jointly determined by the effective
314 population size and innovation rate μ (remember that census size is always constant).

315 *3.2.2. Frequency-dependent transmission.* We now turn to frequency-dependent cultural
316 transmission where the number of transmitting individuals is not fixed but emerges from
317 the interplay between the transmission process and the frequencies of cultural variants.
318 This form of transmission is well-documented in both human [e.g. Deffner et al., 2020,
319 Van Leeuwen et al., 2018] and non-human animals [e.g. Aplin et al., 2017, Danchin et al.,
320 2018]. Positive frequency-dependent transmission, or conformity, occurs when the most
321 common variants in a population are disproportionately more likely to be adopted. In
322 contrast, negative frequency-dependent transmission, or anti-conformity, occurs when the
323 rarest variants are disproportionately more likely to be copied.

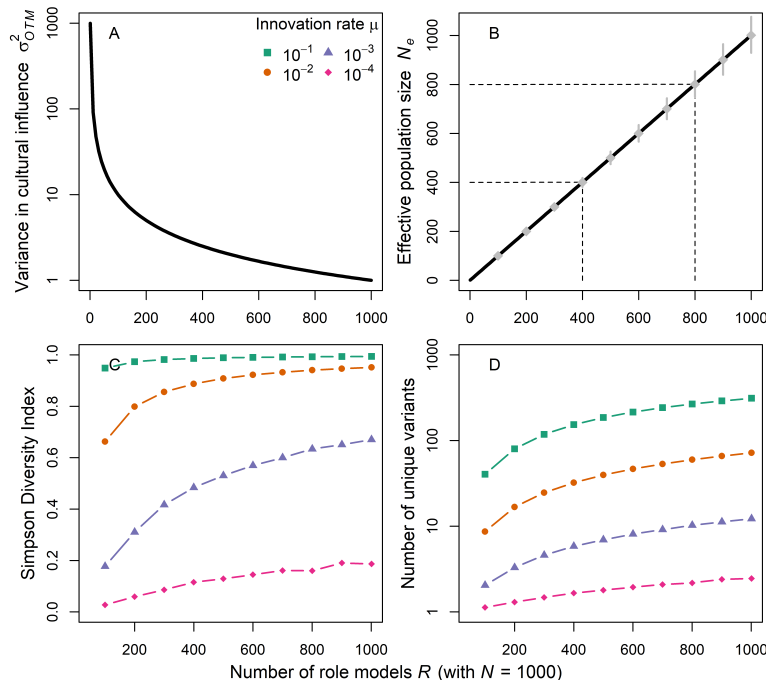


Figure 2. One-to-many transmission. Variance in cultural influence (σ_{OTM}^2 ; 2A), effective population size (N_e ; 2B), mean Simpson diversity (2C) and mean number of unique cultural variants (2D) for different numbers of cultural role models R (with census population size $N = 1000$). Analytical results were confirmed by stochastic simulations. Grey diamonds in plot 2B show means and 90% prediction intervals for 1000 independent simulations (with $\mu = 10^{-4}$).

324 This dynamic is modelled in our simulation framework through Eq. (5). After a burn-
 325 in phase under unbiased transmission, i.e. $\theta = 1$, we change the θ value and record how
 326 effective population sizes change over time (see Fig. 3). We start by analysing relatively
 327 strong frequency-dependent transmission which results in situations where almost the whole
 328 population adopts the same cultural variant (for conformity; $\theta = 1.5$, right column) or all
 329 cultural variants have similar frequencies (for anti-conformity; $\theta = 0.5$, left column). Fig. 3
 330 shows that the change in transmission process leads to an immediate, and partly substantial,
 331 decrease in effective population size, followed by a fast recovery. The severity of the peak
 332 as well as the new equilibrium after the change is influenced by the innovation rate.

333 Strong conformity substantially increases the probability that the most common variants
 334 are adopted and, therefore, reduces the number of transmitting individuals. This increases
 335 the variance in cultural influence and decreases the effective population size. As time
 336 progresses, one variant spreads through the population and almost reaches fixation. Because
 337 there is no variation in variant frequency for conformity to act on anymore, every individual
 338 (at least every individual that does not carry an innovation) is equally likely to pass on their
 339 variant to the next generation; this resembles the situation in the standard Wright-Fisher
 340 model. Consequently, at equilibrium $N_e \approx N$. We note that in the case of conformity,
 341 at equilibrium, higher innovation rates only result in a very slight decrease in effective
 342 population size (see Fig. 3 bottom row, right) as innovations are quickly driven to extinction.

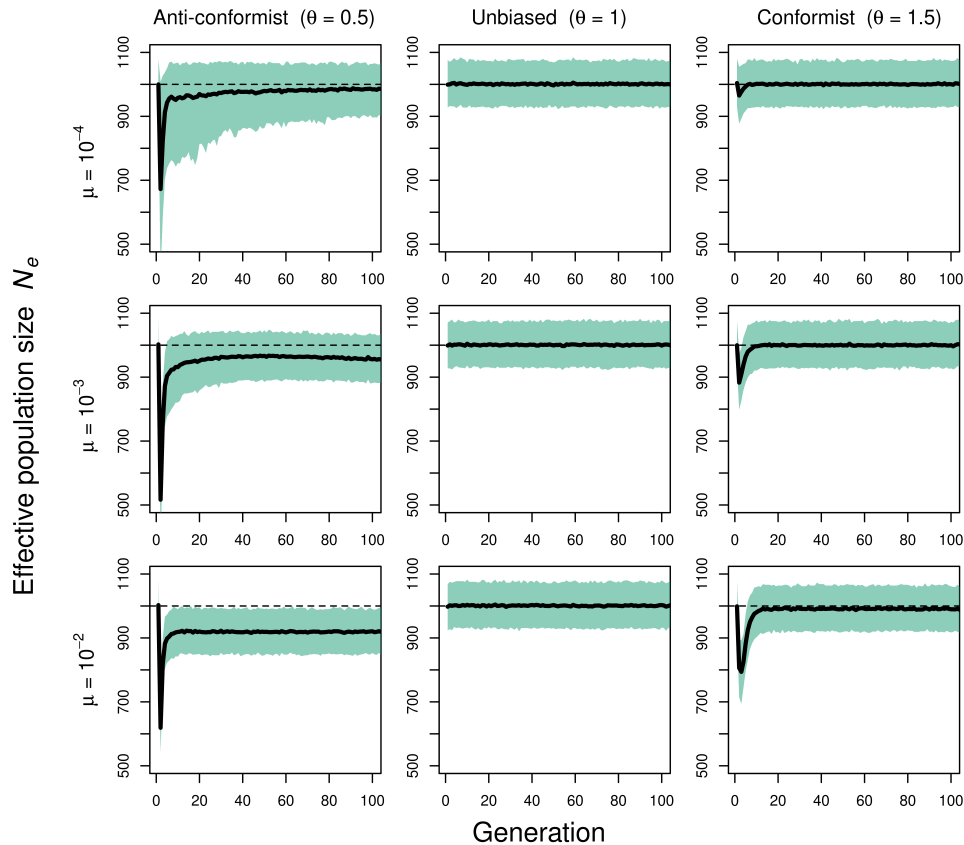


Figure 3. Frequency-dependent transmission. Effective population size (including 90% PIs) for anti-conformist ($\theta = 0.5$; left), unbiased ($\theta = 1$; center) and conformist transmission ($\theta = 1.5$; right) and different innovation rates μ . Plots show trajectories for 100 generations after switch in transmission mode (1000 independent simulations; $N = 1000$).

343 Strong anti-conformity substantially increases the probability that the rarest variants
344 are copied, again reducing the number of transmitting individuals. As time progresses,
345 variants become equally distributed and, consequently, individuals do not differ greatly
346 in the likelihood of passing their variants to the next generation. But in contrast to the
347 conformist situation, the effective population size at equilibrium is greatly influenced by
348 the innovation rates; per definition, innovations are rare and, thereby, the target of anti-
349 conformity. The higher the innovation rate, the more likely a variant is present in the
350 population at low frequency and, therefore, the higher the differences between individuals
351 in their cultural influence.

352 Importantly, we note that the dynamics displayed in Fig. 3 only occur under rela-
353 tively strong frequency-dependent transmission. In appendix 5, Fig. S1, we show that
354 weaker forms of frequency-dependent transmission leave effective population sizes largely
355 unchanged as now the change in transmission mode does not generate sufficiently large
356 differences in individuals' likelihood to pass on their cultural variant.

357 Summarizing, cultural transmission processes different from unbiased transmission do
358 not necessarily lead to a divergence between census and effective population size. This only

359 happens if transmission processes, such as one-to-many and strong frequency-dependent
360 transmission, produce substantial heterogeneity in the probability with which individuals
361 pass on their cultural variant to the next generation, i.e. their cultural influence.

362 **3.3. Population connectedness.** In the previous sections, we analyzed the impact of dif-
363 ferent processes of cultural transmission on the effective size of a cultural population. We
364 now turn to the question of how population properties themselves might influence N_e . Em-
365 pirical tests of demographic hypotheses often consider connectedness among groups, which
366 has been assumed to change the effective size of the populations under consideration [Hen-
367 rich et al., 2016, Derex and Mesoudi, 2020]. We start by analyzing the effects of population
368 connectedness in the form of migration and cultural exchange.

369 Fig. 4 shows effective population sizes and diversity indices for various degrees of mi-
370 gration on the left and cultural exchange on the right. Irrespective of its rate, migration
371 as we defined it influenced neither inbreeding nor variance effective population size. While
372 introducing new variants into the population, migration in our model does not systemati-
373 cally change the probability individuals get to pass on their cultural traits. As population
374 sizes are constant and individuals still learn from random members of the parental gener-
375 ation, whether they are recent immigrants or not, this scenario corresponds to the stan-
376 dard Wright-Fisher population. Although effective numbers remain unchanged, even small
377 amounts of migration increase both measures of cultural diversity compared to isolated pop-
378 ulations. Further raising migration rates leaves diversity largely unchanged indicating that
379 being connected through migration at all has the largest impact on diversity irrespective of
380 the specific rate. Note that if migration increases the census size in a focal population, the
381 effective size tracks this increase (see Fig. S2 in appendix 5 for a scenario where constant
382 immigration raises the effective size and cultural diversity in a focal population).

383 Cultural exchange, on the other hand, increases the inbreeding effective population size
384 but not the variance effective size. Why is this? In case of cultural exchange, there are
385 $N(1 + e)$ individuals in the parental generation that pass on their cultural variants to only
386 N individuals in the offspring generation. For the inbreeding effective size, this reduces the
387 probability that two randomly picked individuals copy the same role model in the parental
388 generation as there is now a greater pool of individuals to learn from. In contrast, for
389 the variance effective size, only the number of learners matters such that changing the
390 number of role models has no effect. In practice, this means that in cases where cultural
391 exchange, or similar processes, are important features of a population’s cultural life, the
392 relationship between census population size and effective population size will depend on
393 the measure chosen. Looking at diversity, small rates of cultural exchange lead to the
394 strongest increase in Simpson diversity and the number of unique variants independently of
395 the effective population size.

396 Summarizing, the effects of connectedness on effective population sizes are subtle, prob-
397 ably difficult to detect, and depend on the exact form of connectedness and effective size
398 formulation.

399 **3.4. Social network structure.** So far, we have considered panmictic (or “well-mixed”)
400 populations. Real populations, however, are often highly structured in terms of kinship,
401 peer relationships or social class, all influencing who individuals are most likely to interact
402 with and learn from [Knox et al., 2006, Borgatti et al., 2018, Derex and Mesoudi, 2020].

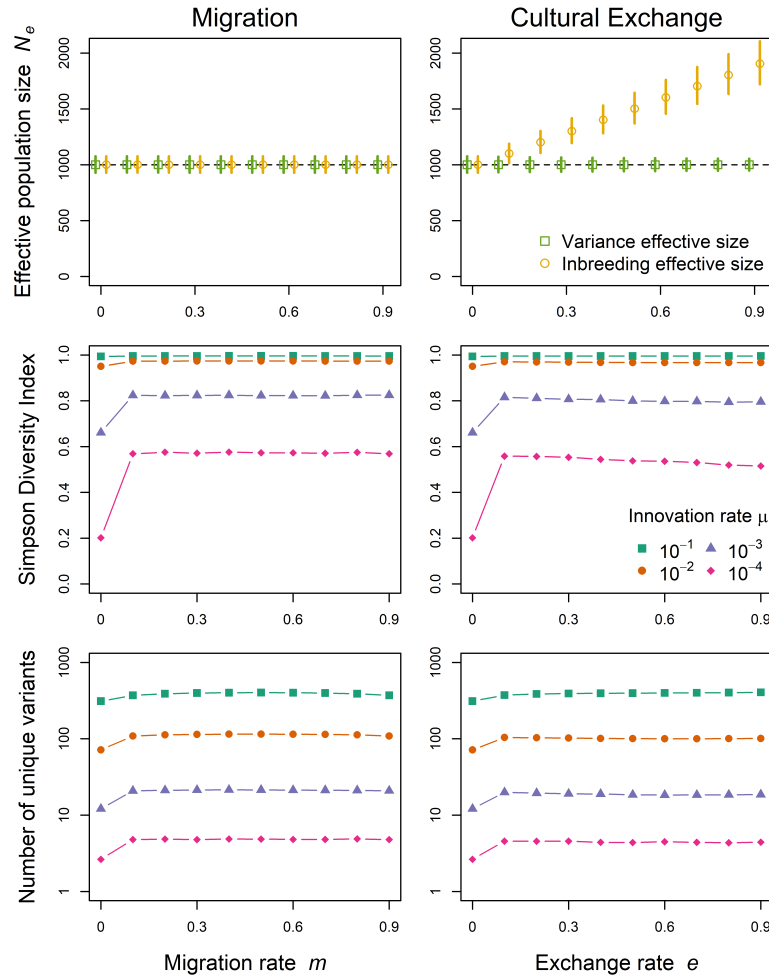


Figure 4. Population connectedness. Variance (green squares) and inbreeding (yellow circles) effective population sizes (including 90% PIs; top), Simpson diversity (center) and mean numbers of unique variants (bottom) for different migration rates m on the left and cultural exchange rates e on the right. We need to differentiate between effective size formulations because population sizes might differ between parental and offspring generations. Results come from 1000 independent stochastic simulations with census population size $N = 1000$.

403 To reflect individual heterogeneity in potential role models and mimic different ways of
 404 information flow, we arrange the N individuals of the population in networks with different
 405 properties (see Fig. 5, top row, and section 3.1 for a more detailed description).

406 Fig. 5, second row, shows how the way interactions between individuals are structured
 407 affects the effective population size. In random networks, irrespective of network density
 408 (i.e. the ratio between observed and possible edges), the effective size always equals the
 409 census size of the population. As every individual has the same probability p of being
 410 connected to any other individual, the number of links are binomially distributed and there
 411 is no systematic difference in individuals' probability to pass on their cultural variants.
 412 Density also does not affect levels of cultural diversity such that strongly interconnected
 413 populations are not more diverse if connections are random.

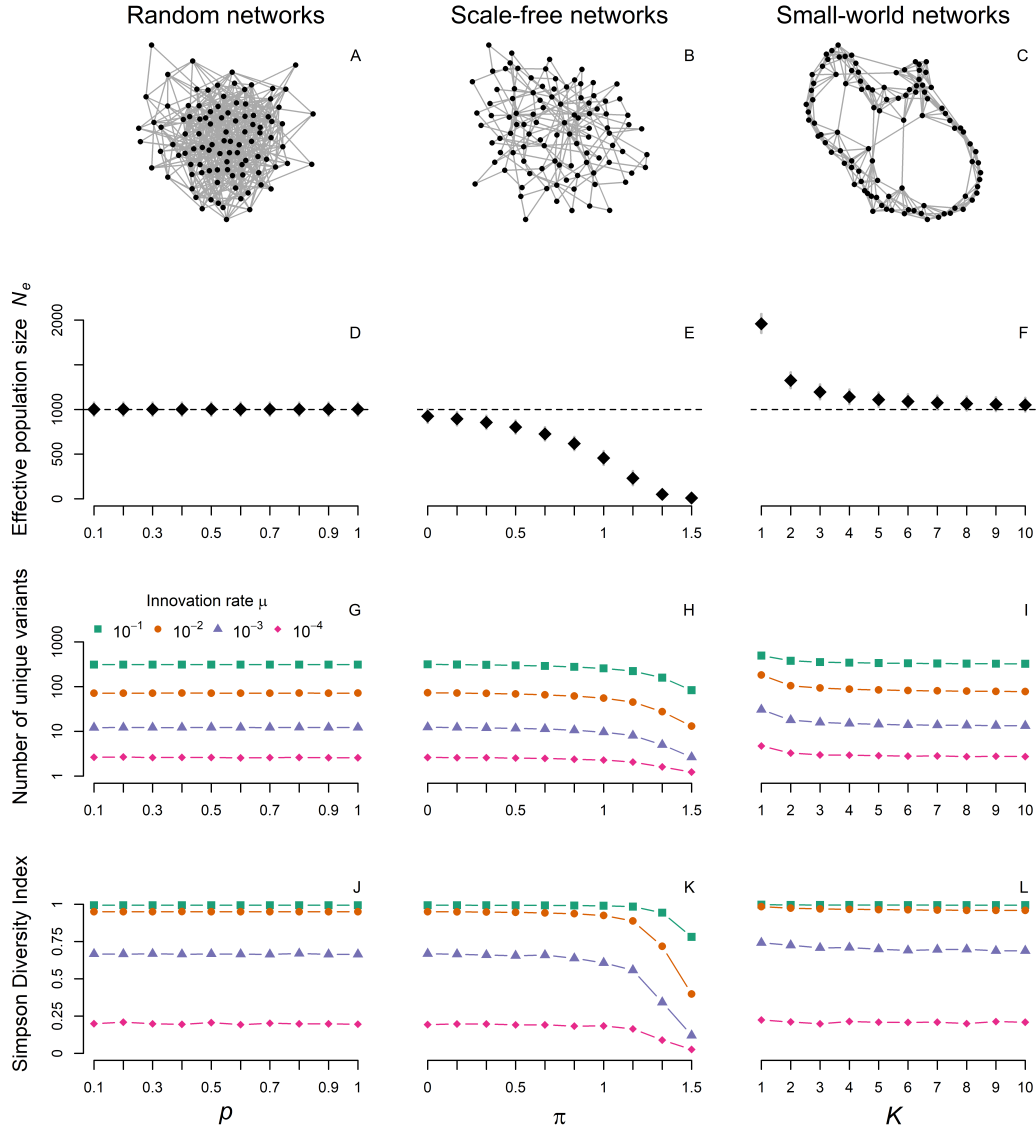


Figure 5. Social network structure. Exemplary networks (A-C), effective population sizes (with 90% PIs; D-F), mean numbers of unique cultural variants (G-I) and Simpson diversity indices (J-L) for random (Erdős-Rényi), scale-free (Barabási-Albert) and small-world (Watts-Strogatz) networks. Parameter p gives the probability any two nodes are connected in random networks, π is the power of preferential attachment creating scale-free networks and K represents the number of initial neighbors on each side in small-world networks (with $p_r = 0.01$). Note that because of structural differences between network types, the ranges of parameter values on the x-axes are not directly comparable. All graphs are created using the *igraph R* package [Csardi et al., 2006]. Results come from 1000 independent simulations with census population size $N = 1000$. On the top, only 100 nodes are drawn for ease of illustration with $p = 0.1$, $\pi = 1$ and $K = 4$.

414 The situation is very different for scale-free networks. Per definition, their power-law
415 degree distribution implies drastically different levels of cultural influence depending on
416 network position. Individuals central to the network will spread their cultural variant to
417 a great number of individuals while more peripheral individuals will pass on their variant
418 to just a few. This increased variance in cultural influence results in substantially lower
419 effective numbers and also lower levels of cultural diversity. In the extreme case, strong
420 preferential attachment results in a star-shaped network and all individuals will learn from
421 few very central models.

422 Finally, effective numbers tend to be greater than census numbers for small-world net-
423 works. This demonstrates that N_e can also exceed N in cultural systems. As a consequence
424 of strongly local cultural transmission, the variance in cultural influence is reduced com-
425 pared to random or fully-connected networks. That way, rare cultural variants that would
426 otherwise be quickly lost due to drift, can be shared in local clusters maintaining higher
427 levels of cultural diversity. As either the number of initial neighbors, K , or the rewiring
428 probability, p_r (not shown here), goes up, we approach a fully connected network where
429 everyone can learn from anyone else and N_e approaches census size N .

430

4. DISCUSSION

431 We have systematically examined effective population size, a concept derived from the-
432 oretical population genetics, for culturally evolving traits. The effective size allows us to
433 compare populations, where it would otherwise be difficult to do so. We showed that both
434 modes of cultural transmission and relevant elements of population structure can change
435 the effective size compared to the census size, sometimes considerably. One-to-many and
436 frequency-dependent transmission can substantially lower effective population size with the
437 strongest effects of frequency dependence occurring when the system is out-of-equilibrium.
438 Investigating different forms of connectedness between populations, we found that migra-
439 tion as we define it does not increase N_e and cultural exchange among groups increases
440 inbreeding effective number but not variance effective number. This implies that consid-
441 erable precision and caution is needed in defining cultural effective sizes. Finally, while
442 random networks with varying densities leave N_e unchanged, scale-free networks tend to
443 decrease and small-world networks tend to increase N_e compared to the census number.

444 Population size has been invoked to explain several patterns of cultural change, most
445 notably the emergence and loss of cultural complexity observed in the ethnographic and
446 archaeological record. Several theoretical models have been developed to better understand
447 the interplay between learning and demography in generating cultural complexity [Shennan,
448 2001, Henrich, 2004, Powell et al., 2009, Fogarty et al., 2017]. Although quite diverse in
449 terms of underlying mechanisms, these models generally agree in predicting more complex
450 cultural repertoires in larger populations. Both real-world ethnographic and archaeological
451 data as well as controlled lab experiments have been used to test the relationship between
452 population size and cultural complexity. Results with both approaches have been mixed
453 with some studies supporting the hypothesis [e.g. Powell et al., 2009, Kline and Boyd, 2010,
454 Derex et al., 2013, Muthukrishna et al., 2014, Kempe and Mesoudi, 2014] but others not
455 [e.g. Collard et al., 2005, Caldwell and Millen, 2010, Fay et al., 2019].

456 These inconsistent findings do not necessarily refute the theoretical models but might
457 instead reflect a poor correspondence between theory and empirical tests. Here, we have

458 demonstrated that obtaining correct and comparable values for the population size in com-
459 plex cultural scenarios is not straightforward. In order for the results from theoretical
460 models to apply correctly to empirical cases, we need to ensure that model parameters are
461 correctly translated into measures from complex real-world scenarios.

462 Our results show that, when there are a few highly influential individuals who—through
463 transmission modes—strongly influence the cultural makeup of the population, the census
464 size and the effective size can diverge. Similarly, where populations are organised into
465 social networks in which individuals are heterogeneous with respect to their degree, the
466 ratio between census and effective size can either increase or decrease depending on network
467 structure. These results also highlight that even relatively small populations might be able
468 to maintain comparatively high levels of cultural diversity if connections are structured in
469 a certain way. Through predominantly local transmission in small-world networks, cultural
470 variants can persist in parts of the network over long periods of time resisting the effects of
471 drift. In this case, larger local clusters or more links between clusters somewhat counter-
472 intuitively reduce the effective population size even though individuals now share ties with
473 more potential cultural models.

474 In cultural evolutionary studies, effective size has mostly been invoked as a rhetorical
475 device to explain why the demographic hypothesis fails to predict observed levels of com-
476 plexity in certain cases [however, see Premo, 2016, for a first formal approach]. Our results
477 suggest that this reasoning is too simplistic. For instance, the effects of interconnectedness
478 depend not only on the exact process of exchange but also on the way effective size is de-
479 fined. Neither migration nor cultural exchange, as we have modelled them, have consistent
480 effects on the effective population size. These results do not imply that connectedness be-
481 tween populations is not an important factor for cultural dynamics, rather that its effect
482 is likely not through increasing the effective size of a population. The finding that small
483 amounts of cultural exchange result in the most diverse populations confirms previous the-
484 oretical results suggesting that partial connectivity among populations maximizes cultural
485 accumulation [Baldini, 2015, Derex et al., 2018].

486 Overall, these results highlight that census numbers cannot generally be relied on when
487 evaluating hypotheses about the effects of demography on culture. It is the effective size that
488 matters and inferring effective population sizes requires detailed knowledge about underlying
489 cultural and demographic processes. To our knowledge, there are no existing methods
490 applicable to estimating effective size in complex cultural systems [for genetic data, see Foll
491 et al., 2015, for an approximate Bayesian computation method to infer genome-wide average
492 effective population size]. The basic theory of N_e in cultural systems is complicated and
493 in need of considerable development before estimation could become feasible through, for
494 instance, generative inference [Kandler and Powell, 2018]. Estimation methods will need to
495 take account of several relevant mechanistic deviations from ideal models simultaneously,
496 where, for example, transmission modes and social networks both play important roles.

497 Our results can also be used as more informal heuristics to decide when census numbers
498 could be used as proxies for the theoretically relevant effective numbers. In societies where
499 cultural influence is highly skewed in favor of a small elite, for instance, there is no reason
500 to expect that the overall size of that population should be related to cultural complexity.
501 In relatively egalitarian societies, in contrast, where all individuals are equally likely to
502 transmit their ideas and behaviors, census size could be a reasonable approximation of

503 effective size. With respect to transmission biases (or social learning strategies), our results
504 suggest that census numbers might be used as proxies for N_e as long as biases are relatively
505 weak and do not drastically change the relative success of certain cultural variants. Further,
506 if due to recent transformative events, cultural systems are out of equilibrium, researchers
507 should not expect census numbers to conform to the theoretically relevant quantity. Finally,
508 if social network structure prevents ideas from flowing freely through the community, census
509 numbers might still be appropriate to test demographic hypotheses as long as connections
510 are relatively random. Most real-world social ties, however, are unlikely to be random and,
511 in that case, census population size might as well under- or overestimate the effective size
512 of cultural populations depending on exact network configurations.

513 In summary, in order to use the concept of effective population size as an explanatory tool
514 in cultural systems, we must first understand how uniquely cultural processes impact its
515 calculation and use this understanding to develop sophisticated estimation methods capable
516 of capturing the complexity of real world cultural dynamics.

Data Availability. This manuscript does not contain any empirical data. Simulation and plotting code necessary to reproduce all results and figures in the manuscript can be found on GitHub: <https://github.com/DominikDeffner/CulturalEffectivePopulationSize>.

Acknowledgement. We thank members of the Department for Human Behavior, Ecology and Culture at the Max Planck Institute for Evolutionary Anthropology in Leipzig for constructive discussions and criticisms which helped improving this paper.

Competing Interests. The authors declare no competing interests. This work has been funded by the Max Planck Society.

REFERENCES

- Luigi Luca Cavalli-Sforza and Marcus W Feldman. *Cultural transmission and evolution: a quantitative approach*. Princeton University Press, 1981.
- Robert Boyd and Peter J Richerson. *Culture and the evolutionary process*. University of Chicago press, 1985.
- Maxime Derex and Alex Mesoudi. Cumulative cultural evolution within evolving population structures. *Trends in Cognitive Sciences*, 2020.
- Sarah Saxton Strassberg and Nicole Creanza. Cultural evolution and prehistoric demography. *Philosophical Transactions of the Royal Society B*, 376(1816):20190713, 2021.
- Warren J Ewens. *Mathematical population genetics 1: theoretical introduction*, volume 27. Springer Science & Business Media, 2012.
- Ronald A Fisher. On the dominance ratio. *Proceedings of the Royal Society of Edinburgh*, 42:321–341, 1923.
- Sewall Wright. Evolution in mendelian populations. *Genetics*, 16(2):97–159, 1931.
- Stephen Shennan. Demography and cultural innovation: a model and its implications for the emergence of modern human culture. *Cambridge Archaeological Journal*, 11(1):5–16, 2001.
- Joseph Henrich. Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses. the tasmanian case. *American Antiquity*, 69(2):197–214, 2004.

- Adam Powell, Stephen Shennan, and Mark G Thomas. Late pleistocene demography and the appearance of modern human behavior. *Science*, 324(5932):1298–1301, 2009.
- Laurel Fogarty, Joe Yuichiro Wakano, Marcus W Feldman, and Kenichi Aoki. The driving forces of cultural complexity. *Human Nature*, 28(1):39–52, 2017.
- Wendell H Oswalt. *An anthropological analysis of food-getting technology*. John Wiley & Sons, New York, 1976.
- Laurel Fogarty and Anne Kandler. The fundamentals of cultural adaptation: implications for human adaptation. *Scientific Reports*, 10(1):1–11, 2020.
- Robin S Waples, Gordon Luikart, James R Faulkner, and David A Tallmon. Simple life-history traits explain key effective population size ratios across diverse taxa. *Proceedings of the Royal Society B: Biological Sciences*, 280(1768):20131339, 2013.
- Albert Tenesa, Pau Navarro, Ben J Hayes, David L Duffy, Geraldine M Clarke, Mike E Goddard, and Peter M Visscher. Recent human effective population size estimated from linkage disequilibrium. *Genome Research*, 17(4):520–526, 2007.
- Joseph Henrich, Robert Boyd, Maxime Derex, Michelle A Kline, Alex Mesoudi, Michael Muthukrishna, Adam T Powell, Stephen J Shennan, and Mark G Thomas. Understanding cumulative cultural evolution. *Proceedings of the National Academy of Sciences*, 113(44):E6724–E6725, 2016.
- Lukas S Premo. Effective population size and the effects of demography on cultural diversity and technological complexity. *American Antiquity*, 81(4):605–622, 2016.
- Ronald A Fisher. The distribution of gene ratios for rare mutations. *Proceedings of the Royal Society of Edinburgh*, 50:204–219, 1931.
- Sewall Wright. The evolution of dominance. *The American Naturalist*, 63(689):556–561, 1929.
- Joanna Masel. Genetic drift. *Current Biology*, 21(20):R837–R838, 2011.
- Michael C Whitlock and Patrick C Phillips. Drift: Introduction. *eLS*, 2014.
- Motoo Kimura and James F Crow. The measurement of effective population number. *Evolution*, pages 279–288, 1963.
- Brian Charlesworth. Effective population size and patterns of molecular evolution and variation. *Nature Reviews Genetics*, 10(3):195–205, 2009.
- James F Crow and Motoo Kimura. *An introduction to population genetics theory*. Harper & Row, New York, 1970.
- James F Crow and Carter Denniston. Inbreeding and variance effective population numbers. *Evolution*, 42(3):482–495, 1988.
- Rachel L Kendal, Neeltje J Boogert, Luke Rendell, Kevin N Laland, Mike Webster, and Patricia L Jones. Social learning strategies: Bridge-building between fields. *Trends in Cognitive Sciences*, 22(7):651–665, 2018.
- Motoo Kimura and James F Crow. The number of alleles that can be maintained in a finite population. *Genetics*, 49(4):725, 1964.
- Edward H Simpson. Measurement of diversity. *Nature*, 163(4148):688–688, 1949.
- Richard McElreath, Adrian V Bell, Charles Efferson, Mark Lubell, Peter J Richerson, and Timothy Waring. Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1509):3515–3528, 2008.

- Mark Broom and Bernhard Voelkl. Two measures of effective population size for graphs. *Evolution*, 66(5):1613–1623, 2012.
- Stefano Giaimo, Jordi Arranz, and Arne Traulsen. Invasion and effective size of graph-structured populations. *PLoS Computational Biology*, 14(11):e1006559, 2018.
- Paul Erdős and Alfréd Rényi. On the evolution of random graphs. *Publ. Math. Inst. Hung. Acad. Sci.*, 5(1):17–60, 1960.
- Albert-László Barabási and Réka Albert. Emergence of scaling in random networks. *Science*, 286(5439):509–512, 1999.
- Réka Albert and Albert-László Barabási. Statistical mechanics of complex networks. *Reviews of Modern Physics*, 74(1):47, 2002.
- Duncan J Watts and Steven H Strogatz. Collective dynamics of ‘small-world’ networks. *Nature*, 393(6684):440–442, 1998.
- Dominik Deffner, Vivien Kleinow, and Richard McElreath. Dynamic social learning in temporally and spatially variable environments. *Royal Society Open Science*, 7(12):200734, 2020.
- Edwin JC Van Leeuwen, Emma Cohen, Emma Collier-Baker, Christian J Rapold, Marie Schäfer, Sebastian Schütte, and Daniel BM Haun. The development of human social learning across seven societies. *Nature Communications*, 9(1):1–7, 2018.
- Lucy M Aplin, Ben C Sheldon, and Richard McElreath. Conformity does not perpetuate suboptimal traditions in a wild population of songbirds. *Proceedings of the National Academy of Sciences*, 114(30):7830–7837, 2017.
- Etienne Danchin, Sabine Nöbel, Arnaud Pocheville, Anne-Cecile Dagaëff, Léa Demay, Mathilde Alphand, Sarah Ranty-Roby, Lara Van Renssen, Magdalena Monier, Eva Gazagne, et al. Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science*, 362(6418):1025–1030, 2018.
- Hannah Knox, Mike Savage, and Penny Harvey. Social networks and the study of relations: networks as method, metaphor and form. *Economy and Society*, 35(1):113–140, 2006.
- Stephen P Borgatti, Martin G Everett, and Jeffrey C Johnson. *Analyzing social networks*. Sage, 2018.
- Gabor Csardi, Tamas Nepusz, et al. The igraph software package for complex network research. *InterJournal, complex systems*, 1695(5):1–9, 2006.
- Michelle A Kline and Robert Boyd. Population size predicts technological complexity in oceania. *Proceedings of the Royal Society B: Biological Sciences*, 277(1693):2559–2564, 2010.
- Maxime Derex, Marie-Pauline Beugin, Bernard Godelle, and Michel Raymond. Experimental evidence for the influence of group size on cultural complexity. *Nature*, 503(7476):389–391, 2013.
- Michael Muthukrishna, Ben W Shulman, Vlad Vasilescu, and Joseph Henrich. Sociality influences cultural complexity. *Proceedings of the Royal Society B: Biological Sciences*, 281(1774):20132511, 2014.
- Marius Kempe and Alex Mesoudi. An experimental demonstration of the effect of group size on cultural accumulation. *Evolution and Human Behavior*, 35(4):285–290, 2014.
- Mark Collard, Michael Kemery, and Samantha Banks. Causes of toolkit variation among hunter-gatherers: a test of four competing hypotheses. *Canadian Journal of Archaeology/Journal Canadien d’Archéologie*, pages 1–19, 2005.

- Mark Collard, Briggs Buchanan, and Michael J O'Brien. Population size as an explanation for patterns in the paleolithic archaeological record: more caution is needed. *Current Anthropology*, 54(S8):S388–S396, 2013.
- Christine A Caldwell and Ailsa E Millen. Human cumulative culture in the laboratory: effects of (micro) population size. *Learning & Behavior*, 38(3):310–318, 2010.
- Nicolas Fay, Naomi De Kleine, Bradley Walker, and Christine A Caldwell. Increasing population size can inhibit cumulative cultural evolution. *Proceedings of the National Academy of Sciences*, 116(14):6726–6731, 2019.
- Ryan Baldini. Revisiting the effect of population size on cumulative cultural evolution. *Journal of Cognition and Culture*, 15(3-4):320–336, 2015.
- Maxime Derex, Charles Perreault, and Robert Boyd. Divide and conquer: intermediate levels of population fragmentation maximize cultural accumulation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1743):20170062, 2018.
- Matthieu Foll, Hyunjin Shim, and Jeffrey D Jensen. Wfabc: a wright–fisher abc-based approach for inferring effective population sizes and selection coefficients from time-sampled data. *Molecular Ecology Resources*, 15(1):87–98, 2015.
- Anne Kandler and Adam Powell. Generative inference for cultural evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1743):20170056, 2018.

Supplementary material for

“Effective population size for culturally evolving traits”

Dominik Deffner^{1*}, Anne Kandler¹ & Laurel Fogarty¹

¹Department of Human Behavior, Ecology and Culture,
Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

*Corresponding author: dominik_deffner@eva.mpg.de

Overview

Appendix (1) shows how to calculate effective population size and expected number of cultural traits for the simple example used in section 1.1. in the introduction.

Appendix (2) explains why both mean and variance in offspring number are approximately 1 for in the haploid Wright-Fisher population.

Appendix (3) shows the derivation of both inbreeding and variance effective population sizes as appropriate for cultural evolution.

Appendix (4) derives the appropriate formula for calculating the pooled variance for transmitting and non-transmitting sub-populations that is used to calculate effective population size for one-to-many transmission.

Appendix (5) contains additional results.

1. CALCULATIONS FOR EXAMPLE USED IN SECTION 1.1. IN THE INTRODUCTION

Remember that we assumed there are two populations, A and B, with current census population sizes of 1000 and 500 individuals, respectively. Population A had a population bottleneck ten generations ago when its census size fell to just 10 individuals before immediately returning to its current size of 1000. If population size is fluctuating over time and we have information from a total of T non-overlapping generations, the effective size N_e is given by the harmonic mean (i.e. the reciprocal of the arithmetic mean of the reciprocals) of the population sizes at each point in time t :

$$(1.1) \quad N_e = \frac{1}{\frac{1}{T} \sum_{t=1}^T \frac{1}{N_t}}$$

In our example, for population A, $N_1 = 10$ and $N_{[2:10]} = 1000$, for population B, $N_{[1:10]} = 500$. Plugging these values into Eq. (1.1) gives the effective population sizes of $N_e = 91.7$ for population A and $N_e = 500$ for population B.

Based on these effective sizes and assuming a certain innovation rate (here $\mu = 0.1$) and unbiased cultural transmission, we can use results from population genetics [see Ewens, 2012, p. 115] to approximate the mean number of cultural traits we expect to see each generation, $E(K)$, as follows:

$$(1.2) \quad E(K) \approx \theta + \int_{N_e^{-1}}^1 \theta x^{-1} (1-x)^{\theta-1} dx,$$

where $\theta = 2N_e\mu$ is the standard population mutation parameter. For population B with $N_e = 500$, the expected number of traits is, thus, $E(K) \approx 223$. For population A with $N_e = 91.7$, we expect to see on average $E(K) \approx 41$ traits in a given generation.

2. PROPERTIES OF THE HAPLOID WRIGHT-FISHER POPULATION

Both mean and variance in offspring number are roughly 1 for a haploid Wright-Fisher population. Why is this the case? For the Wright-Fisher population with a population size of N , N parents are chosen at random with replacement from the full population. From the point of view of any focal individual, the probability of being chosen as a parent to any one of the N offspring is $p = 1/N$, the probability of not being chosen, correspondingly, is $q = 1 - 1/N$. We conduct N trials and so the number of offspring produced by any member of the population is a binomially distributed random variable. The mean of this is simply $\bar{k} = Np = N/N = 1$. The variance is $\sigma^2 = Npq$. This is $\sigma^2 = N \left(\frac{1}{N}\right) \left(1 - \frac{1}{N}\right)$. Simplifying, we get $\sigma^2 = 1 - \frac{1}{N}$. It is common here to neglect terms on the order of $\frac{1}{N}$; they are very small because N is usually very large, giving us $\sigma^2 \approx 1$.

3. DERIVATION OF INBREEDING AND VARIANCE N_e

Different aspects of the evolution of the Wright-Fisher population have been used to define N_e . We seek expressions for both inbreeding and variance effective numbers for situations where (1) there is variation in offspring numbers and (2) population sizes might differ between parental and offspring generation. Here, we follow the general presentation of Kimura and Crow [1963], but make adjustments for haploid populations where necessary. Haploids are characterized by only one set of variants, whereas diploids are characterized by two sets. In cultural transmission, learners adopt a single variant of a cultural trait from one or several role models, there is no inheritance of two corresponding alleles from sexually reproducing parents.

Consider a population of N_{t-1} individuals each contributing a variable number, k_i , of offspring to the next generation. In general, the mean number of offspring is

$$(3.1) \quad \bar{k} = \frac{\sum_{i=1}^{N_{t-1}} k_i}{N_{t-1}},$$

and the variance in offspring number is

$$(3.2) \quad \sigma^2 = \frac{\sum_{i=1}^{N_{t-1}} k_i^2}{N_{t-1}} - \bar{k}^2.$$

3.1. Inbreeding effective population size. The identity-by-descent (or inbreeding) effective population size N_e^i utilizes the fact that in finite populations there is a certain probability that two randomly selected individuals in generation t are descendant from the same parent. As this single-generation probability of identity by descent, P_t , in the ideal

Wright-Fisher population is simply $1/N_{t-1}$, we can use an estimate of this probability in the real population to calculate the effective population size as $N_e^i = 1/P_t$. For our example, the number of ways in which two offspring from a given parent i can be selected is $k_i(k_i - 1)/2$. Summing over all members of the parental generation, the total number of ways in which two offspring from the same parent can be selected is $\sum_{i=1}^{N_{t-1}} k_i(k_i - 1)/2$, whereas the total number of offspring pairs is $N_{t-1}\bar{k}(N_{t-1}\bar{k} - 1)/2$. Dividing the former by the latter, P_t can thus be calculated as

$$(3.3) \quad P_t = \frac{\sum_{i=1}^{N_{t-1}} k_i(k_i - 1)}{N_{t-1}\bar{k}(N_{t-1}\bar{k} - 1)} = \frac{\sum_{i=1}^{N_{t-1}} k_i^2 - \sum_{i=1}^{N_{t-1}} k_i}{N_{t-1}\bar{k}(N_{t-1}\bar{k} - 1)}.$$

From the definition of the mean (\bar{k} ; see equation 3.1),

$$(3.4) \quad \sum_{i=1}^{N_{t-1}} k_i = N_{t-1}\bar{k}.$$

and from the definition of the variance (σ^2 ; see equation 3.2),

$$(3.5) \quad \sum_{i=1}^{N_{t-1}} k_i^2 = N_{t-1}\sigma^2 + N_{t-1}\bar{k}^2.$$

Substituting these into equation 3.3 results in

$$(3.6) \quad P_t = \frac{N_{t-1}\sigma^2 + N_{t-1}\bar{k}^2 - N_{t-1}\bar{k}}{N_{t-1}\bar{k}(N_{t-1}\bar{k} - 1)}.$$

Rearranging, we can calculate the inbreeding effective number for haploid populations as

$$(3.7) \quad N_e^i = \frac{1}{P_t} = \frac{N_{t-1}\bar{k} - 1}{\bar{k} - 1 + \frac{\sigma^2}{\bar{k}}}.$$

3.2. Variance effective population size. The variance effective population size N_e^v , in contrast, focuses on the amount of random variation in allele frequencies from one generation to the next. Assume that p is the frequency of an allele in an ideal Wright-Fisher population of size N . The sampling variance of the gene frequency drift from parent to offspring generation is $V_{\delta p} = p(1 - p)/N$ and, therefore, $N_e^v = p(1 - p)/V_{\delta p}$. Similarly to above, we seek an expression for $V_{\delta p}$ to infer the corresponding effective number. Again, assume there is a population of N_{t-1} individuals each contributing a number of k_i offspring to the next generation. Let p denote the frequency of allele A in the population and let n_1 be the number of individuals carrying allele A ($n_1 = N_{t-1}p$). The number of A alleles contributed to the next generation is $\sum_{i=1}^{n_1} k_i$. Thus, the increment in A alleles from generation $t - 1$ to generation t is given by:

$$(3.8) \quad N_{t-1}\bar{k}\delta p = \sum_{i=1}^{n_1} k_i - N_{t-1}\bar{k}p.$$

Expressing p as $\sum_1^{n_1} \frac{\bar{k}}{N_{t-1}\bar{k}}$ and substituting into equation (3.8) gives,

$$(3.9) \quad N_{t-1}\bar{k}\delta p = \sum_{i=1}^{n_1} (k_i - \bar{k}).$$

Using expectation notation, we now write an expression for the variance in the change in p , $V_{\delta p} = \mathbf{E}[\delta p]^2$.

$$(3.10) \quad \begin{aligned} (N_{t-1}\bar{k})^2 V_{\delta p} &= \mathbf{E}\left[\sum_{i=1}^{n_1} (k_i - \bar{k})\right]^2 \\ &= n_1\sigma^2 + n_1(n_1 - 1)C_{kk'}, \end{aligned}$$

where $C_{kk'} = -\frac{\sigma^2}{N_{t-1}-1}$ is the covariance in offspring number for randomly selected pairs from the parental generation. Substituting this and simplifying results in

$$(3.11) \quad = \frac{\sigma^2}{N_{t-1} - 1} n_1 (N_{t-1} - n_1).$$

If we then replace n_1 by $N_{t-1}p$, we get

$$(3.12) \quad (N_{t-1}\bar{k})^2 V_{\delta p} = \frac{\sigma^2}{N_{t-1} - 1} N_{t-1}p (N_{t-1} - N_{t-1}p),$$

and

$$(3.13) \quad \bar{k}^2 V_{\delta p} = \frac{\sigma^2}{N_{t-1} - 1} (1 - p).$$

Replacing $V_{\delta p}$ with $\frac{p(1-p)}{N_e^v}$ gives

$$(3.14) \quad \bar{k}^2 \frac{p(1-p)}{N_e^v} = \frac{\sigma^2}{N_{t-1} - 1} (1 - p).$$

Solving for N_e^v results in

$$(3.15) \quad N_e^v = \frac{(N_{t-1} - 1)\bar{k}^2}{\sigma^2} = \frac{(N_{t-1} - 1)\bar{k}}{\frac{\sigma^2}{\bar{k}}}.$$

4. EXPRESSING THE VARIANCE OF THE FULL POPULATION IN TERMS OF SUB-POPULATION VARIANCES AND MEANS

The combined variance, σ_c^2 , is given by

$$(4.1) \quad \sigma_c^2 = \frac{1}{N} \sum_{i=1}^N (k_i - \bar{k}_c)^2,$$

where, again, N is the total population size, k_i is the number of cultural offspring of the i^{th} individual in the parental generation, and \bar{k}_c is the combined mean offspring number for the whole population (including both the group of cultural transmitters and the group of non-transmitters). To write a general expression for the variance in the full population, we split the population into two arbitrary groups of size n_1 and n_2 where $n_1 + n_2 = N$. We label the mean offspring number within those subpopulations as \bar{k}_1 and \bar{k}_2 respectively, and the variances in offspring number, similarly, as σ_1^2 and σ_2^2 .

Now, it is possible to express the variance of the complete population (σ_c^2) in terms of the means and variances of the two subpopulations.

$$(4.2) \quad \begin{aligned} N\sigma_c^2 &= \sum_{i=1}^N (k_i - \bar{k}_c)^2 \\ &= \sum_{i=1}^{n_1} (k_i - \bar{k}_c)^2 + \sum_{i=n_1+1}^N (k_i - \bar{k}_c)^2. \end{aligned}$$

With some rearranging, we get

$$(4.3) \quad \begin{aligned} N\sigma_c^2 &= \sum_{i=1}^{n_1} ((k_i - \bar{k}_1) - (\bar{k}_c - \bar{k}_1))^2 + \sum_{i=n_1+1}^N ((k_i - \bar{k}_2) - (\bar{k}_c - \bar{k}_2))^2 \\ &= \sum_{i=1}^{n_1} (k_i - \bar{k}_1)^2 + n_1 (\bar{k}_c - \bar{k}_1)^2 + \sum_{i=n_1+1}^N (k_i - \bar{k}_2)^2 + n_2 (\bar{k}_c - \bar{k}_2)^2, \end{aligned}$$

using the fact that in general $\sum_{j=1}^M k_j - \bar{k}_M = 0$. So, we have

$$(4.4) \quad N\sigma_c^2 = n_1\sigma_1^2 + n_2\sigma_2^2 + D_N,$$

where

$$(4.5) \quad D_N = n_1 (\bar{k}_1 - \bar{k}_c)^2 + n_2 (\bar{k}_2 - \bar{k}_c)^2.$$

To allow some simplifications we can rewrite D_N as

$$(4.6) \quad D_N = \frac{n_1 n_2}{N} (\bar{k}_1 - \bar{k}_2)^2.$$

Details of this simplification can be found in O'Neill [2014]. The decomposed expression for σ_c^2 , then is

$$(4.7) \quad \sigma_c^2 = \frac{n_1\sigma_1^2 + n_2\sigma_2^2 + \frac{n_1 n_2}{N} (\bar{k}_1 - \bar{k}_2)^2}{N}.$$

Now, to apply this to our population and to the calculation of effective population size, we make the following assumptions. Population 1 is the transmitting population. Therefore, $n_1 = R, n_2 = (N - R)$. \bar{k}_1 is the mean number of cultural offspring per individual in the

transmitting sub-population. Given that there are N learners and R role models, we get that $\bar{k}_1 = \frac{N}{R}$, and the mean for the other sub-population is 0, since they cannot pass on their trait ($\bar{k}_2 = 0$). The variance for the non-transmitters (σ_2^2) is the same, 0. The variance for the transmitting population is obtained in the same way as the variance for the full Wright-Fisher population and is $\frac{N}{R} \left(1 - \frac{1}{R}\right)$.

Inserting these values into equation 4.7 results in

$$(4.8) \quad \sigma_c^2 = \frac{R \frac{N}{R} \left(1 - \frac{1}{R}\right) + (N - R)(0) + \frac{R(N-R)}{N} \left(\frac{N}{R} - 0\right)^2}{N},$$

which simplifies to

$$(4.9) \quad \sigma_c^2 = \frac{N - 1}{R},$$

the solution for σ_{OTM}^2 shown in the main text (equation 6).

5. ADDITIONAL RESULTS

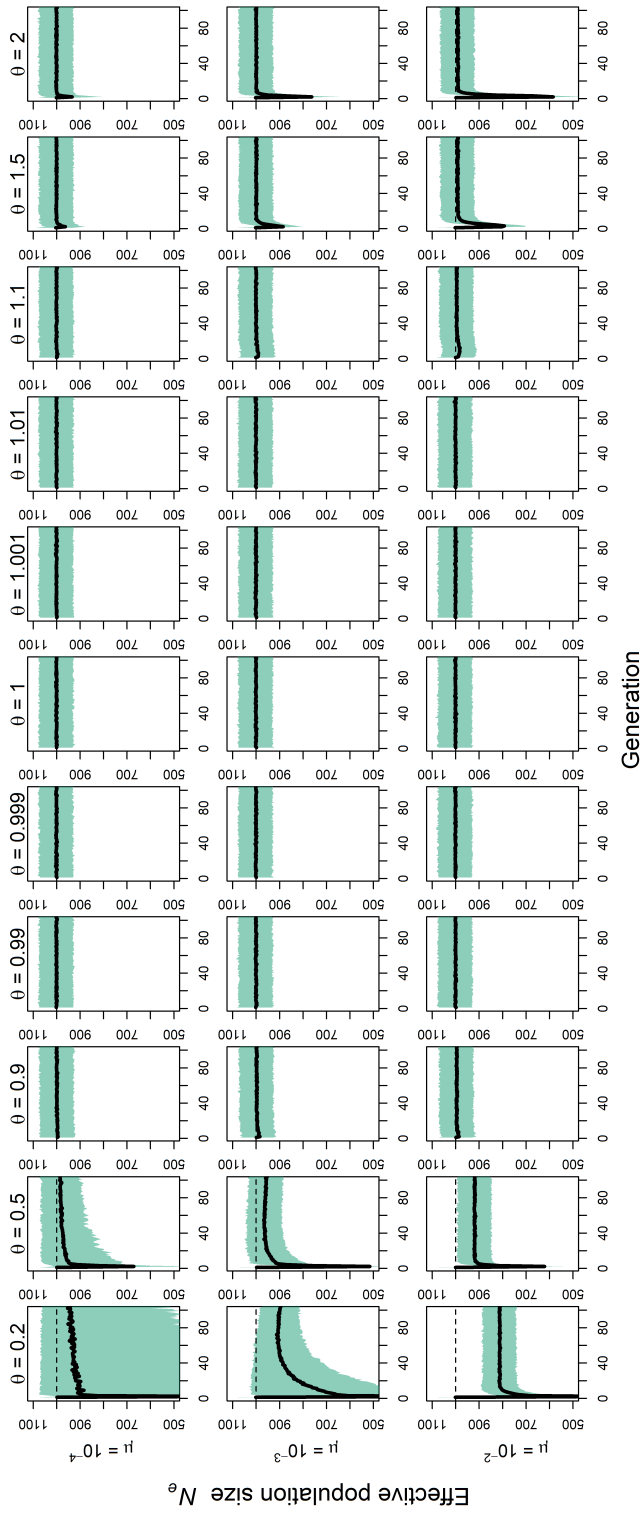


Figure S1. Frequency-dependent transmission for wider ranges of conformity exponent θ . Effective population size (including 90% PIs) for different levels of anti-conformist ($\theta < 1$), unbiased ($\theta = 1$) and conformist transmission ($\theta > 1$) and different innovation rates μ . Plots show trajectories for 100 generations after switch in transmission mode (1000 independent simulations; $N = 1000$).

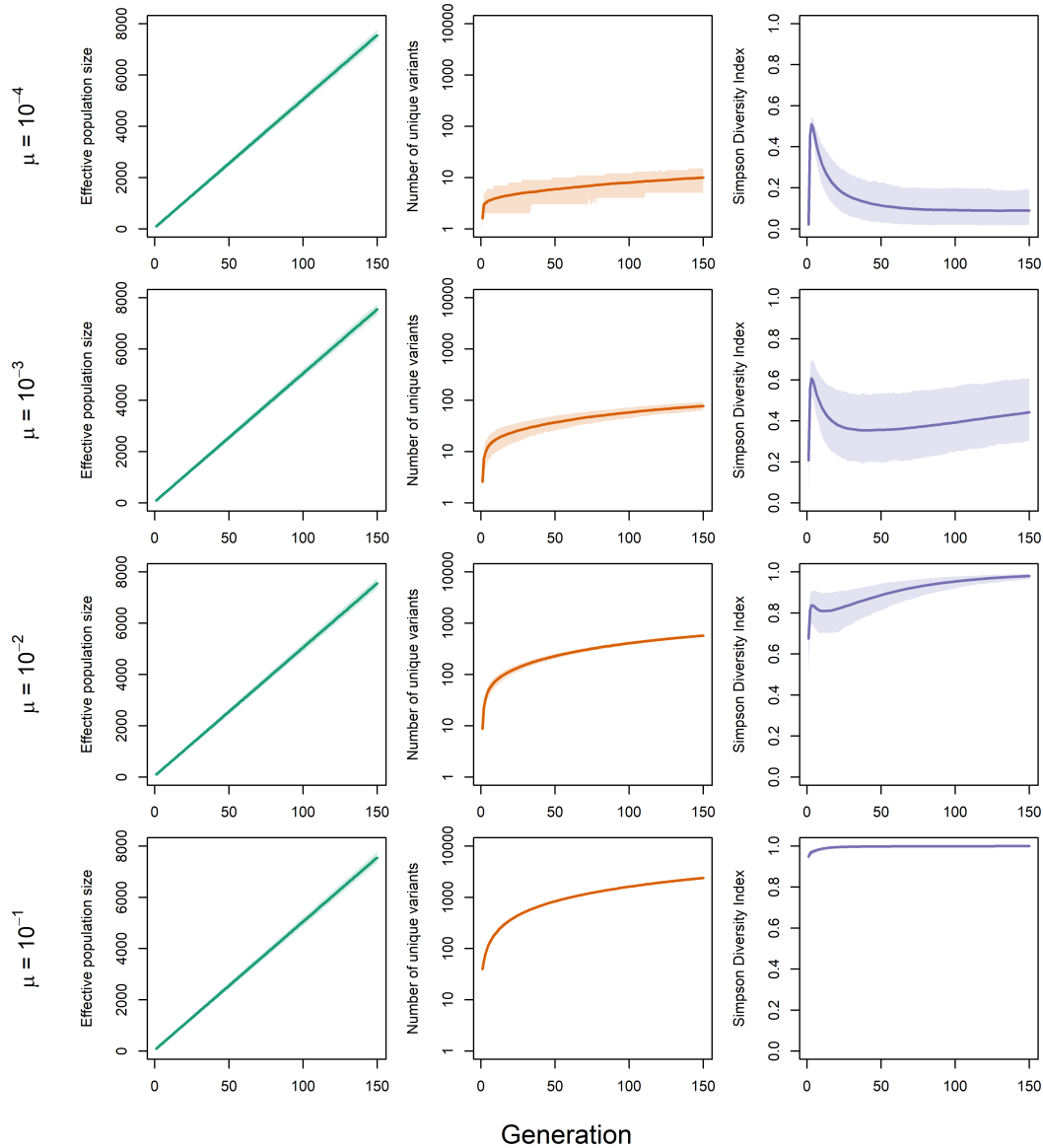


Figure S2. Alternative migration mechanism that gradually increases the census size N in a focal population. We start by letting a large source population with $N = 10000$ and a small focal population with $N = 100$ evolve separately until they reach equilibrium; each generation, we then let a fixed number of individuals migrate from the source population to the focal population and record effective numbers and diversity indices in the focal population. Effective population size (left), number of unique cultural variants (center) and Simpson Diversity (right) for different innovation rates μ . Plots show trajectories for 150 generations after immigration starts (1000 independent simulations with 50 immigrants per generation).

REFERENCES

- Warren J Ewens. *Mathematical population genetics 1: theoretical introduction*, volume 27. Springer Science & Business Media, 2012.
- Motoo Kimura and James F Crow. The measurement of effective population number. *Evolution*, pages 279–288, 1963.
- B. O'Neill. Some Useful Moment Results in Sampling Problems. *American Statistician*, 68 (4):282–296, 2014. ISSN 15372731. 10.1080/00031305.2014.966589.