

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22

From cultural traditions to cumulative culture: parameterizing the differences between
human and nonhuman culture

Marius Kempe¹, Stephen J. Lycett², Alex Mesoudi^{1*}

¹Department of Anthropology and Centre for the Coevolution of Biology and Culture,
Durham University, Dawson Building, South Road, Durham, DH1 3LE, UK

²Department of Anthropology, School of Anthropology and Conservation, Marlowe
Building, The University of Kent, Canterbury, Kent, CT2 7NR, UK

*Author for correspondence (a.a.mesoudi@durham.ac.uk).

Running head: Human and nonhuman culture

Word count: 7107

Figures: 7

23 ABSTRACT

24 Diverse species exhibit cultural traditions, i.e. population-specific profiles of socially
25 learned traits, from songbird dialects to primate tool-use behaviors. However, only
26 humans appear to possess cumulative culture, in which cultural traits increase in
27 complexity over successive generations. Theoretically, it is currently unclear what
28 factors give rise to these phenomena, and consequently why cultural traditions are
29 found in several species but cumulative culture in only one. Here, we address this by
30 constructing and analyzing cultural evolutionary models of both phenomena that
31 replicate empirically attestable levels of cultural variation and complexity in
32 chimpanzees and humans. In our model of cultural traditions (Model 1), we find that
33 realistic cultural variation between populations can be maintained even when
34 individuals in different populations invent the same traits and migration between
35 populations is frequent, and under a range of levels of social learning accuracy. This
36 lends support to claims that putative cultural traditions are indeed cultural (rather than
37 genetic) in origin, and suggests that cultural traditions should be widespread in species
38 capable of social learning. Our model of cumulative culture (Model 2) indicates that
39 both the accuracy of social learning and the number of cultural demonstrators interact
40 to determine the complexity of a trait that can be maintained in a population.

41 Combining these models (Model 3) creates two qualitatively distinct regimes in which
42 there are either a few, simple traits, or many, complex traits. We suggest that these
43 regimes correspond to nonhuman and human cultures, respectively. The rarity of
44 cumulative culture in nature may result from this interaction between social learning
45 accuracy and number of demonstrators.

46 **Keywords:** animal culture; cultural evolution; demography; innovation; social
47 learning

48 **1. Introduction**

49 Many animal species exhibit *social learning*, i.e. the acquisition of information from
50 conspecifics through learning (Galef and Laland, 2005); examples include the
51 transmission of food preferences in rats (Laland and Plotkin, 1990), shoaling routes
52 and nest site locations in fish (Helfman and Schultz, 1984), and foraging locations in
53 bees and ants (Leadbeater and Chittka, 2007). Some of these species show cultural
54 differences in the ‘trait-profiles’ of different populations, termed *cultural traditions*
55 (Fragaszy and Perry, 2003). Examples include differences in the song dialects of
56 different bird populations (Catchpole and Slater, 1995) and in the presence or absence
57 of various tool-use and gestural behaviors in different populations of chimpanzees
58 (Lycett et al., 2007; Whiten et al., 1999), orangutans (van Schaik et al., 2003) and
59 capuchins (Perry et al., 2003). Humans, however, as well as exhibiting social learning
60 and cultural traditions, appear to be the only species to unambiguously also have
61 *cumulative culture*, where cultural traits are preserved and modified over successive
62 generations resulting in a ‘ratcheting up’ of the complexity or efficiency of those traits
63 (Boyd and Richerson, 1996; Dean et al., 2013; Enquist et al., 2011; Tomasello, 1999).
64 A common criterion for cumulative culture is that cultural traits become too complex
65 for a single individual to invent in their lifetime. Whereas this does not appear to
66 apply to any non-human cultural traits, such as chimpanzee nut-cracking, birdsong
67 dialects or fish shoaling routes (although for possible reports in chimpanzees see
68 Boesch et al., 2009; Sanz et al., 2010), such traits are commonplace in human cultural
69 endeavors such as technology, science, and mathematics (Basalla, 1988; May, 1966;
70 Oswalt, 1976; Price, 1963; Wilder, 1968). It is highly unlikely that string theory,
71 smartphones and space travel, for example, lie within the inventive capacities of a
72 single individual. Even so-called ‘simple’ early human technologies, such as certain

73 types of stone tools, show evidence of having accumulated in complexity over
74 multiple generations (Lycett and von Cramon-Taubadel, 2013; Roche, 2005; Simão,
75 2002). This cumulative culture, it is argued, has been instrumental in allowing our
76 species to invade and inhabit virtually every terrestrial environment on the planet,
77 while our closest primate relatives remain highly restricted in range and number
78 (Boyd et al., 2011; Hill et al., 2009).

79

80 Our aim here is to construct simple models to identify the potential factors responsible
81 for both the emergence and maintenance of cultural traditions, and for the shift from
82 cultural traditions to cumulative culture that appears to be a hallmark of our species.
83 Models are particularly useful here given the difficulty of directly studying such
84 phenomena. Comparative studies have begun to address the underlying cognitive
85 abilities that allow humans and other great ape species to solve simple cumulative-like
86 tasks (Dean et al., 2012). However, comparative studies are limited because (i) only a
87 single extant species (*Homo sapiens*) has cumulative culture, thus providing limited
88 data points to test causal hypotheses, and (ii) the acquisition of cumulative cultural
89 traits in humans typically takes many years and is thus not amenable to experimental
90 investigation. Archaeological evidence can be used to indicate the emergence of
91 cumulative culture in the *Homo* lineage (d'Errico and Stringer, 2011; Roche, 2005).
92 However, the archaeological record provides only indirect evidence of the cognitive
93 or demographic changes that might be associated with these phenomena.

94

95 Previous models have examined either the evolutionary origin of social learning (Aoki
96 et al., 2005; Boyd and Richerson, 1985; Enquist et al., 2007; Rogers, 1988), or the
97 number of independent (non-cumulative) traits in a single population (Enquist et al.,

98 2010; Lehmann et al., 2011; Strimling et al., 2009), or the dynamics of cumulative
99 culture in a single population (Mesoudi, 2011; Pradhan et al., 2012) or at a
100 macroscopic level that does not permit the study of demographic factors such as
101 population size or migration (Enquist et al., 2011; Lewis and Laland, 2012). While all
102 of these models have generated useful inferences about cultural dynamics, none have
103 directly addressed the emergence and maintenance of between-group cultural
104 traditions, which requires the simulation of multiple populations, and none have
105 sought to explain the transition from non-cumulative traditions to cumulative culture.
106 Here we attempt to fill this gap by first modelling cultural traditions and explicitly
107 comparing our model output to empirical data on non-human primate traditions. We
108 then present a model of cumulative culture that builds on previous individual-based
109 models of non-cumulative culture. Finally, we combine these models, finding that the
110 emergence of cumulative culture most likely occurred through the interaction of the
111 accuracy of social learning and the number of demonstrators from whom individuals
112 copy.

113

114 **2. Model 1: Cultural traditions**

115 We take as our starting point a model constructed by Strimling et al. (2009), in which
116 independent (i.e. non-cumulative) cultural traits are acquired by individuals in a single
117 population. To this we add multiple populations and migration between those
118 populations, in order to permit the emergence of between-population cultural
119 traditions. In their model, Strimling et al. showed how the number of different traits
120 found in the population and the number of traits known by each individual increased
121 as a function of population size, individuals' social learning accuracy, and individuals'
122 innovativeness. We are therefore interested in whether, and if so how, cultural

123 traditions are also shaped by these factors, in addition to the novel factor of migration.
124 As in Strimling et al.'s original model, we make several simplifying assumptions,
125 such as that cultural traits have identical cultural fitness and have no effect on
126 biological fitness, and that individuals do not vary in their social learning accuracy or
127 innovativeness. While these assumptions are most likely unrealistic and deserve
128 scrutiny in future research, these tactical simplifications allow us to focus on the
129 aforementioned key factors that have been the subject of previous research
130 (population size, social learning accuracy and individual innovativeness) in this new
131 multi-group context.

132

133 Strimling et al's (2009) model contains three stages. First, one of the N individuals in
134 the population is picked at random, dies, and is replaced by a naive individual.

135 Second, the naive individual picks one other individual at random and independently
136 learns every trait that individual knows with probability a per trait (where $0 < a < 1$).

137 Third, the individual invents a random number of new traits with expectation μ . (Note
138 that social learning and innovation are therefore modelled as separate processes; for
139 simplicity, Strimling et al. assumed that social learning cannot itself give rise to new
140 traits through inferential copying errors.) To this we add a fourth stage, in which the

141 individual migrates to another population with probability $\frac{m}{2}$ (where $0 \leq m \leq 2$).

142 There are p such populations in the metapopulation, and the individual is equally
143 likely to migrate to any of the $p - 1$ other populations. When the individual migrates, it
144 swaps population memberships with a randomly chosen member of its target
145 population, so that the size of each population remains constant. Because each
146 migration event involves two individuals and the target population is picked at

147 random, the expected number of individuals who migrate away from any given

148 population in one timestep is $\frac{m}{2} + \frac{m}{2} \frac{(p-1)}{p-1} = m$; this is why m is halved above.

149

150 In order to model multiple populations of such learners, we must also decide which
151 traits individuals invent. Strimling et al. (2009) do not specify this, assuming only that
152 individuals always invent traits that are currently unknown in the population.

153 Lehmann et al. (2011), using a similar model, assume that there are a very large
154 number of traits, tending towards infinity, and individuals invent a random trait
155 chosen from this set. This strikes us as unrealistic, particularly for foraging or gestural
156 behaviours that are constrained by the affordances of the objects and food types found
157 in a species' habitat, and motor constraints on the possible gestures or calls that can be
158 produced. Thus, we assume instead that there are infinitely many traits which are
159 invented in a fixed sequence that is the same in all populations. We use the simplest
160 possible sequence, in which traits are labeled by the natural numbers and invented in
161 the order 1, 2, 3, etc. Individuals always invent the first trait in the sequence that is not
162 currently known by any individual in their population. For example, if traits 1, 2, 4
163 and 5 are present in the population, then a naïve individual will first invent trait 3,
164 rather than trait 6. This represents an idealized situation in which individuals' physical
165 and cognitive predispositions and the nature of their physical and social environments
166 create a clear ranking in the "obviousness" of traits; for example, tool techniques for
167 foraging easily-visible food resources may be invented before techniques for foraging
168 hard-to-find foods, and foraging technologies in general may be invented before
169 social or symbolic behaviors that are less important for survival. While this situation

170 is clearly idealized, it is more realistic than assuming random draws from a large set
 171 of traits, and it is simple enough to analyze. Note that, as in Strimling et al. and
 172 Lehmann et al.'s models, these traits are not cumulative; later traits do not build on
 173 earlier traits, and an individual can socially learn any set of traits irrespective of the
 174 traits' position in the sequence. A trait may also be lost from the population and later
 175 re-invented without affecting any other traits.

176

177 Fig. 1 shows the time course and end result of one simulation of the model, at this
 178 point with no migration (i.e. $m = 0$). In this and all subsequent simulations we ran the
 179 model until the values of the various measurements (e.g. number of traits) had clearly
 180 reached a stable value and were performing random walks around that value. Fig. 1a
 181 shows that the number of different traits known in each population, called S by
 182 Strimling et al., hovers around the expected value they derived in their Equation 3,
 183 providing a replication of their model and confirming the validity of ours. Fig. 1b
 184 shows the trait-profiles present in each population at the end of the simulation.

185 Intuitively, one expects that if all populations invent the same traits in the same order,
 186 different populations will have identical trait profiles. However, the trait-profiles in
 187 Fig. 1b clearly show variation between populations. To quantify this variation we
 188 define s , the cultural similarity between two populations, in the same way as Enquist

189 et al. (2011): $s = \frac{|X \cap Y|}{|X \cup Y|}$..., where X is the set of traits known in the first population

190 and Y is the set known in the second. Thus, s is the proportion of all traits known in
 191 either population that are known in both populations. To compare more than two
 192 populations we define \bar{s} as the mean similarity between every possible combination of
 193 populations in a metapopulation.

194

195

[Figure 1 here]

196

197

Fig. 2 shows how the mean similarity between populations \bar{s} increases with

198

population size N (in a decelerating fashion) and accuracy of social learning a (in an

199

accelerating fashion). Fig. 2c shows how \bar{s} varies across the parameter space created

200

by N and a , demonstrating that no realistic parameter values generate complete inter-

201

population homogeneity. The reason that the assumption of a fixed sequence of traits

202

does not lead to complete inter-population homogeneity is trait loss due to imperfect

203

social learning. We show in the Appendix that in the absence of migration, the

204

probability that a trait will spread beyond its inventor is $\frac{a}{1+a}$. Since a must be less

205

than 1, this probability is always less than $\frac{1}{2}$. In other words, most newly invented

206

traits die out with their inventor, even with high fidelity cultural transmission. This

207

feature of the model accords reasonably with evidence on chimpanzee (*P. t.*

208

schweinfurhii) inventions documented at Mahale, Tanzania, where approximately

209

43% of innovations documented over a 30-year period did not spread (Nishida et al.,

210

2009). In the model, this frequent loss of traits is balanced by the re-invention of traits

211

that have been lost, and this dynamic creates the moderate (and realistic) dissimilarity

212

between population trait-profiles.

213

214

[Figure 2 here]

215

216

We now analyze the effects of migration. Fig. 3 shows how the mean number of

217

different traits known in a population \bar{S} and the mean similarity between populations

218 \bar{s} both increase with m . We show values from simulations with m ranging from 0 (no
219 migration) to 0.5 (half of all individuals migrate); the latter may be realistic in both
220 chimpanzees, where one sex typically disperses (Hiraiwa-Hasegawa, Hasegawa, &
221 Nishida, 1984), and humans, where there is frequent migration of both sexes (Hill et
222 al., 2011). As expected, migration makes populations more similar in their trait-
223 profiles, but even frequent migration does not completely homogenize them.
224 Migration also increases the total number of traits known, because migrants can bring
225 traits that have not been invented in the target population; this resembles the
226 beneficial effect of migration on accumulation found by Powell et al. (2009), but not
227 as pronounced. A possible empirical example of this is the introduction of ant-fishing
228 into the Kasekela chimpanzee (*P. t. schweinfurthii*) community by a female immigrant
229 from the Mitumba community at Gombe, Tanzania (O'Malley et al., 2012).

230

231

[Figure 3 here]

232

233 To compare the results shown in Fig. 3b with empirical data, we calculated the values
234 of \bar{s} from data reported on chimpanzees (*Pan troglodytes*) (Whiten et al., 1999) and
235 orangutans (*Pongo pygmaeus*) (van Schaik et al., 2003), ignoring all comparisons
236 involving traits thought to be absent for ecological reasons or insufficient observation.
237 The values of \bar{s} were approximately 0.46 and 0.32, respectively. Note that these
238 values probably underestimate the true values, because these studies only included
239 traits that the investigators suspected *a priori* might vary between populations. With
240 this in mind, Figs. 2c and 3 show that the model produces realistic between-
241 population variability.

242

243 **3. Model 2: Cumulative culture**

244 We now construct and analyse a model of cumulative culture in a single population,
245 before adding the assumption of multiple populations in the following section. For our
246 cumulative culture model, we take as our starting point Enquist et al.'s (2010) model
247 which expanded Strimling et al.'s (2009) to include multiple demonstrators. Hence
248 our model has two parameters: a , the accuracy of social learning (as before), and n ,
249 the number of cultural models (where in Model 1, as well as in previous models of
250 cumulative culture such as Mesoudi [2011], $n = 1$, but which in Model 2 can vary). As
251 in Model 1, both parameters are assumed to be constant across all individuals. The
252 population consists of N individuals, and as above, in each time step a randomly
253 chosen individual dies and is replaced by a naive individual. The individual then
254 randomly picks n other individuals from the population to be its cultural
255 demonstrators. The individual attempts to learn the trait from each of the n
256 demonstrators in turn. Whether this learning is successful depends on whether or not
257 the demonstrators carry the trait and on a . Finally, after attempting to learn socially
258 from all n demonstrators, the individual innovates with probability μ .

259

260 The trait has an infinite number of complexity levels. Learning any given level is
261 dependent on having learned all previous levels. The levels represent cumulative
262 improvements that can be made to the basic, level 1 trait. Thus, they may roughly
263 correspond to Oswalt's (1976) "techno-units," or to successive modifications to a
264 technology or social practice; plausible definitions and examples of different levels
265 are given by Pradhan et al. (2012). In our model, individuals learn these levels as
266 follows: for each demonstrator, the individual learns the first level of the trait that it
267 does not already know with probability a , and moves on to the next level if successful,

268 which it again learns with probability a , and so on. Thus the probability of a naive
269 individual learning a given level l from a demonstrator who knows at least l levels of
270 the trait is a^l . After social learning, each individual has a probability μ of improving
271 its knowledge of the trait by one level through innovation.

272

273 We are interested in understanding how \bar{l} , the mean level of cultural complexity that a
274 population maintains, depends on the accuracy of social learning a , the number of
275 cultural models n , and the innovativeness μ . In each simulation of the model the
276 population begins completely unknowledgeable. Fig. 4 shows the time course and end
277 result of one simulation of the model. In Fig. 4a we see that the mean level of the trait
278 in the population initially rises and then stabilizes; Fig. 4b shows the resulting
279 distribution of levels amongst the individuals of the population.

280

281

[Figure 4 here]

282

283 Fig. 5 shows the effects of a and n on the mean level \bar{l} of the trait that is maintained in
284 the population. The mean level \bar{l} increases linearly with n (Fig. 5a), and non-linearly
285 with a (Fig. 5b). When varying the innovativeness μ in simulations, we found that
286 increasing μ from 0.1 to 1 increases \bar{l} by ≈ 3 regardless of the values of the other
287 parameters; thus, the effects of a and n are much stronger than the effect of μ . This
288 replicates previous modelling results that innovation is far less important for
289 cumulative culture than is social learning accuracy (Lewis and Laland, 2012) or
290 number of demonstrators (Enquist et al., 2010).

291

292 Fig. 5c shows how \bar{l} varies across the parameter space created by a and n . Enquist et
293 al. (2010) showed that only if $an > 1$ could the trait be stably maintained in the
294 population through social learning in their model. Since the trait in their model
295 corresponds to the basic level 1 trait of ours, this result clearly applies here too. Much
296 of the parameter space features realistic levels of accumulation; compare the values of
297 \bar{l} shown in Fig. 5c to the mean techno-unit values of 3-7 found by an empirical
298 analysis of the complexity of marine foraging technology in a number of Oceanic
299 human populations (Kline and Boyd, 2010). However, there are clearly many different
300 combinations of a and n that will maintain a given mean level \bar{l} in the population;
301 thus, observing a given level of accumulation in a population does not allow us to
302 completely identify the values of a and n for that population.

303

304

[Figure 5 here]

305

306 **4. Model 3: Combined model**

307

308

309

310

311

312

313

314

315

316

Here we combine our two models to ask under what conditions cultural traditions become cumulative. Imagine that each trait in Model 1 comes in the infinite number of levels described in Model 2, and that instead of choosing only one cultural demonstrator, naive individuals choose n cultural demonstrators, learn from them, and then both invent new traits and improve existing ones. The structure of the traits and trait levels in this model is shown in Fig. 6. As illustrated in the figure, the difference between traits and trait levels is that ‘traits’ measure the quantity of cultural traits and ‘trait level’ measures their complexity. The combined model then simulates the dynamics of independent cumulative traits within and between populations that interact by migration. To fully analyse this combined model, a choice must be made as

317 to how cumulative traits are improved; whether, for example, there is a fixed expected
318 number of improvements per individual, or whether more knowledgeable individuals
319 make on average more improvements. Unfortunately there is little empirical evidence
320 on this question.

321

322 [Figure 6 here]

323

324 Without deciding this one way or another, we can still make useful statements about
325 the combined model. Consider the expected number of different traits S in a
326 population. If $n = 1$, Strimling et al. (2009) derived an analytical approximation for S ,
327 which shows that, for realistic but high values of these parameters, say $N = 100$, $a =$
328 0.9 , and $\mu = 0.5$, then $S \approx 133$ traits. On the other hand, if $n > 1$ no analytical
329 approximation for S is known, but we can approximate S by following Strimling et al.
330 and noting that $S = \mu NT$, where T is the expected lifetime, in generations, of a newly
331 invented trait. We conducted simulations that showed that even for very small values
332 of the parameters which satisfy the criterion $an > 1$, say $N = 30$, $a = 0.65$, and $n = 2$,
333 then $T \approx 100$, and T increases very rapidly with increases in the parameters.

334 Assuming additionally a low value for innovativeness, e.g. $\mu = 0.1$, then $S \approx 300$ traits
335 (Fig. 7) and rises very quickly into the thousands and tens of thousands of traits with
336 increases in the parameters. Moreover, the condition $an > 1$ is also the condition for
337 cumulative culture to arise, as noted above.

338

339 [Figure 7 here]

340

341 **5. Discussion**

342 Our models give results that mimic the phenomena of between-population cultural
343 traditions and cumulative culture in reasonably realistic ways. In our model of cultural
344 traditions (Model 1) we find that realistic differences between populations are
345 maintained despite assuming that all individuals invent the same traits in the same
346 order, individuals learn from only a single demonstrator, and despite frequent
347 migration between populations. This occurs because traits die out with non-negligible
348 frequency, and most traits do not spread beyond their inventor. In our model of
349 cumulative culture (Model 2), we find that the accuracy of social learning and the
350 number of cultural demonstrators interact to determine the cumulative level of a trait
351 that a population can stably maintain, and that portions of the parameter space feature
352 realistic levels of accumulation.

353

354 Results from Model 1 show that it is surprisingly easy to generate realistic cultural
355 traditions, defined as moderately dissimilar trait profiles in different populations
356 linked by migration, in contrast to the lack of spread of any cultural traits (the absence
357 of culture), or the homogenisation of all populations to an identical trait profile (the
358 absence of traditions). Inter-population similarity increases with social learning
359 accuracy, population size and migration rate, but traditions reliably emerge at broad
360 ranges of values of these parameters rather than a specific range. Even assuming very
361 inaccurate social learning (e.g. $a = 0.1$), as is often claimed to characterize non-human
362 social learning, we still obtain values of inter-population similarity that match those
363 found empirically, at realistic population sizes and migration rates (Fig. 2). In general,
364 Model 1 is in line with analyses indicating that behavioural traditions in non-human
365 primates are cultural rather than genetic (Lycett et al., 2007; 2010), and in fact
366 suggests that stable cultural traditions may be more widespread in nature than

367 currently thought. Indeed, since the landmark paper by Whiten et al. (1999), more and
368 more cultural traditions have been identified in diverse species as researchers have
369 begun to look for such patterns (Laland and Galef, 2009). Furthermore, the time series
370 in Fig. 1a imply that phenomena such as chimpanzee cultures have inherent historical
371 dimensions (Lycett, 2010), which have begun to be investigated using archaeological
372 (Haslam et al., 2009) and phylogenetic (Lycett et al., 2010) methods. On the grounds
373 of phylogenetic homology, we might also therefore expect traditions in prehistoric
374 hominins to have displayed similar historical dynamics (Kuhn, 2004; Lycett, 2013).

375

376 Results from Model 2 imply that cumulative culture is more difficult to generate: note
377 the large parameter space in Fig. 5c where accumulation does not occur (i.e. $\bar{l} = 1$).
378 Cumulative culture requires some combination of high fidelity social learning and
379 multiple demonstrators, replicating the findings of previous macroscopic (Henrich,
380 2004; Lewis and Laland, 2012) and non-cumulative (Enquist et al., 2010) models. The
381 relative unimportance of individuals' innovativeness is supported by comparative
382 work showing that humans appear to possess unusually high-fidelity social learning,
383 and are roughly comparable in their individual learning abilities, compared to other
384 great apes (Dean et al., 2012; Herrmann et al., 2007). This reinforces arguments that
385 humans inhabit a 'cultural niche' (Boyd et al., 2011), characterized by faithful social
386 learning rather than particularly enhanced individual cognitive abilities.

387

388 The dependence of cumulative culture on two different factors may help to explain its
389 rarity in nature. Our analysis of the combined Model 3 reinforced this further,
390 showing that social learning accuracy and number of demonstrators interact to
391 generate two qualitative regimes dictating both number of traits and trait complexity.

392 When $an < 1$, the number of traits known in the population is relatively low and there
393 is no cumulative culture. When $an > 1$, many traits are known in the population and
394 there can be cumulative culture. To our knowledge, this is the first time this link
395 between trait number and trait complexity has been drawn. It seems plausible that
396 these regimes correspond qualitatively to nonhuman and human cultures, respectively:
397 human culture is not only cumulative, as noted in the Introduction, but also has a huge
398 number of both cumulative and non-cumulative traits (see Mesoudi et al., 2004 for
399 estimations of the magnitude of human cultural variation).

400

401 We caution that the models we have presented contain many simplifying assumptions.
402 We assumed that our parameters (e.g. innovativeness, social learning accuracy)
403 operate identically across all individuals, whereas in reality these probably vary across
404 individuals. The extent to which this individual variation is important, or just averages
405 out at the population level, remains to be determined. More complex and realistic
406 social learning biases are possible, such as copying successful individuals (Mesoudi,
407 2008) or conforming to the group majority (Henrich and Boyd, 1998). However, we
408 note that adding such biases is not straightforward given the ambiguous and often
409 conflicting evidence across non-human species for biases such as conformity (van
410 Leeuwen and Haun, 2013). Moreover, we might expect in some cases that such biases
411 will magnify our findings: conformity, for example, emphasises between-population
412 variation (Henrich and Boyd, 1998), thus reinforcing our conclusion that cultural
413 traditions should be commonplace. Another interesting question is whether our
414 assumption in Model 2 that individuals copy n demonstrators once per generation is
415 reasonable. It is also possible that individuals may sample the same demonstrator(s)
416 multiple times over their lifetime. Whether multiple learning trials, as well as (or

417 instead of) access to multiple models, facilitates cumulative culture, and which of
418 these is a more realistic assumption, remains to be explored.

419

420 The emergence of cumulative culture in human evolution is sometimes framed in
421 terms of cognition vs. demography: was there some genetically-derived change in
422 hominin cognition such that social learning became more accurate (e.g. via imitation
423 or teaching) and which allowed cumulative culture to take off (Klein, 2009), or did
424 cumulative culture emerge when populations became large enough to support
425 increasing cultural complexity (Henrich, 2004; Powell et al., 2009)? Our models
426 suggest that the answer to this question is unlikely to be one or the other, and the
427 interaction between social learning accuracy and number of demonstrators is key. We
428 also note that our (and other modellers') parameters do not necessarily neatly map
429 onto 'cognition' and 'demography'. While it is possible that social learning accuracy
430 improved through some genetically-based adaptation for imitation or theory of mind,
431 it could equally have increased through purely cultural means. Examples of this in
432 recent history might include the invention of writing or the printing press, which
433 would have dramatically reduced errors in cultural transmission (see Mesoudi, 2011
434 for a cumulative culture model incorporating such cultural innovations). Some kind of
435 prehistoric equivalent may have similarly driven increases in early hominin social
436 learning accuracy, and hence cumulative culture. Similarly, an increase in the number
437 of demonstrators may have depended straightforwardly on the overall population size.
438 Alternatively, it may have required cognitive changes that allowed a shift from
439 vertical uniparental cultural transmission to 'many-to-one' cultural transmission
440 (Cavalli-Sforza and Feldman, 1981), independently of overall population size.

441 Modelling alone cannot ultimately address such questions, but can guide comparative
442 and archaeological study to begin to answer them.

443

444 In conclusion, we have presented a set of models that extend and combine previous
445 theoretical findings concerning the emergence of cultural traditions and cumulative
446 culture. Regarding the former, we find that empirically realistic patterns of cultural
447 traditions are surprisingly easy to generate with minimal assumptions, supporting
448 recent work suggesting that cultural traditions are widespread in nature. Regarding the
449 latter, we reinforce previous findings that cumulative culture can only emerge through
450 an interaction of social learning accuracy and number of demonstrators, and that these
451 conditions favour both a rapid increase in the number and cumulative complexity of
452 cultural traits. We suggest that this two-parameter threshold is why cumulative culture
453 is restricted to just our own species.

454

455 **Acknowledgements**

456 This research was supported by Leverhulme Trust Research Project Grant F/07
457 476/AR awarded to AM and SJL. We thank Jeremy Kendal, Rachel Kendal and Peter
458 Richerson for comments on an earlier draft.

459

460 **References**

- 461 Aoki, K., Wakano, J. Y., Feldman, M. W., 2005. The emergence of social learning in a
462 temporally changing environment: A theoretical model. *Current Anthropology*
463 46, 334-340.
- 464 Basalla, G., 1988. *The evolution of technology*. Cambridge University Press,
465 Cambridge.
- 466 Boesch, C., Head, J., Robbins, M. M., 2009. Complex tool sets for honey extraction
467 among chimpanzees in Loango National Park, Gabon. *Journal of Human*
468 *Evolution* 56, 560-569.
- 469 Boyd, R., Richerson, P. J., 1985. *Culture and the evolutionary process*. University of
470 Chicago Press, Chicago, IL.
- 471 Boyd, R., Richerson, P. J., 1996. Why culture is common, but cultural evolution is
472 rare. *Proceedings of The British Academy* 88, 77-93.
- 473 Boyd, R., Richerson, P. J., Henrich, J., 2011. The cultural niche: Why social learning
474 is essential for human adaptation. *Proceedings of the National Academy of*
475 *Sciences* 108, 10918-10925.
- 476 Catchpole, C. K., Slater, P. J. B., 1995. *Bird song: Biological themes and variations*.
477 Cambridge University Press, Cambridge.
- 478 Cavalli-Sforza, L. L., Feldman, M. W., 1981. *Cultural transmission and evolution*.
479 Princeton Univ. Press, Princeton.
- 480 d'Errico, F., Stringer, C. B., 2011. Evolution, revolution or saltation scenario for the
481 emergence of modern cultures? *Philosophical Transactions of the Royal*
482 *Society B: Biological Sciences* 366, 1060-1069.

- 483 Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., Laland, K. N., 2012.
484 Identification of the social and cognitive processes underlying human
485 cumulative culture. *Science* 335, 1114-1118.
- 486 Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., Kendal, R. L., 2013. Human
487 cumulative culture: A comparative perspective. *Biological Reviews*.
- 488 Enquist, M., Eriksson, K., Ghirlanda, S., 2007. Critical social learning: A solution to
489 Rogers' paradox of nonadaptive culture. *American Anthropologist* 109, 727-
490 734.
- 491 Enquist, M., Ghirlanda, S., Eriksson, K., 2011. Modelling the evolution and diversity
492 of cumulative culture. *Philosophical Transactions of the Royal Society B* 366,
493 412-423.
- 494 Enquist, M., Strimling, P., Eriksson, K., Laland, K., Sjostrand, J., 2010. One cultural
495 parent makes no culture. *Animal Behaviour* 79, 1353-1362.
- 496 Fragaszy, D. M., Perry, S., 2003. *The biology of traditions: Models and evidence*.
497 Cambridge University Press, Cambridge.
- 498 Galef, B. G., Laland, K. N., 2005. Social learning in animals: Empirical studies and
499 theoretical models. *BioScience* 55, 489-499.
- 500 Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de La Torre, I.,
501 DeStefano, A., Du, A., Hardy, B., Harris, J., Marchant, L., 2009. Primate
502 archaeology. *Nature* 460, 339-344.
- 503 Helfman, G. S., Schultz, E. T., 1984. Social transmission of behavioral traditions in a
504 coral-reef fish. *Animal Behaviour* 32, 379-384.
- 505 Henrich, J., 2004. Demography and cultural evolution: How adaptive cultural
506 processes can produce maladaptive losses - the Tasmanian case. *American*
507 *Antiquity* 69, 197-214.

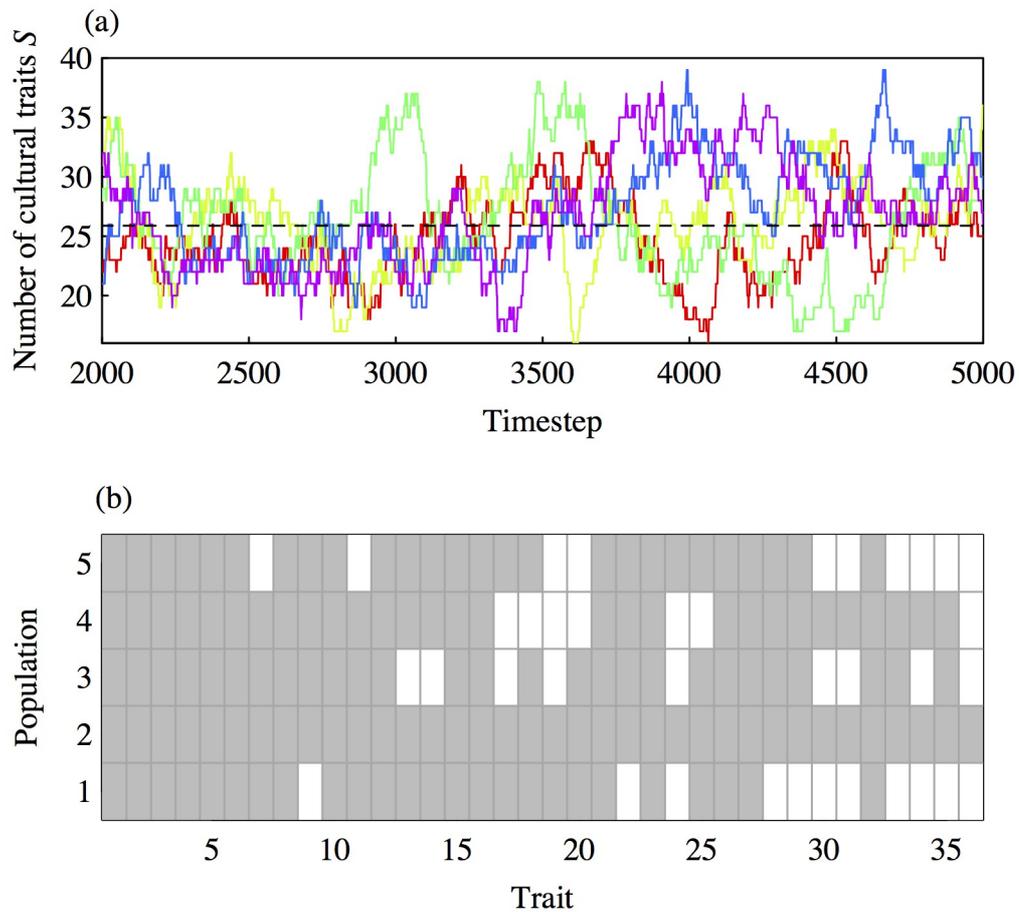
- 508 Henrich, J., Boyd, R., 1998. The evolution of conformist transmission and the
509 emergence of between-group differences. *Evolution and Human Behavior* 19,
510 215-241.
- 511 Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., Tomasello, M., 2007.
512 Humans have evolved specialized skills of social cognition: The cultural
513 intelligence hypothesis. *Science* 317, 1360-1366.
- 514 Hill, K. R., Barton, M., Hurtado, A. M., 2009. The emergence of human uniqueness.
515 *Evolutionary Anthropology* 18, 187-200.
- 516 Hill, K. R., Walker, R. S., Bozivecic, M., Eder, J., Headland, T., Hewlett, B., Hurtado,
517 A. M., Marlowe, F., Wiessner, P., Wood, B., 2011. Co-residence patterns in
518 hunter-gatherer societies show unique human social structure. *Science* 331,
519 1286-1289.
- 520 Hiraiwa-Hasegawa, M., Hasegawa, T., Nishida, T., 1984. Demographic study of a
521 large-sized unit-group of chimpanzees in the Mahale Mountains, Tanzania: A
522 preliminary report. *Primates* 25, 401-413.
- 523 Klein, R. G., 2009. *The human career: Human biological and cultural origins.*
524 University of Chicago Press, Chicago, IL.
- 525 Kline, M. A., Boyd, R., 2010. Population size predicts technological complexity in
526 Oceania. *Proceedings of the Royal Society B: Biological Sciences* 277, 2559-
527 2564.
- 528 Kuhn, S., 2004. *Evolutionary perspectives on technology and technological change.*
529 *World Archaeology* 36, 561-570.
- 530 Laland, K. N., Plotkin, H. C., 1990. Social learning and social transmission of
531 foraging information in Norway Rats (*Rattus norvegicus*). *Animal Learning*
532 *and Behavior* 18, 246-251.

- 533 Laland, K. N., Galef, B. G., 2009. The question of animal culture. Harvard University
534 Press.
- 535 Leadbeater, E., Chittka, L., 2007. Social learning in insects—from miniature brains to
536 consensus building. *Current Biology* 17, 703-713.
- 537 Lehmann, L., Aoki, K., Feldman, M. W., 2011. On the number of independent cultural
538 traits carried by individuals and populations. *Philosophical Transactions of the*
539 *Royal Society B* 366, 424-435.
- 540 Lewis, H. M., Laland, K. N., 2012. Transmission fidelity is the key to the build-up of
541 cumulative culture. *Philosophical Transactions of the Royal Society B* 367,
542 2171-2180.
- 543 Lycett, S. J., 2010. The importance of history in definitions of *culture*: Implications
544 from phylogenetic approaches to the study of social learning in chimpanzees.
545 *Learning & Behavior* 38, 252-264.
- 546 Lycett, S. J., 2013. Cultural transmission theory and fossil hominin behaviour: A
547 discussion of epistemological and methodological strengths. In: Ellen, R. F., et
548 al., Eds.), *Understanding cultural transmission in anthropology: A critical*
549 *synthesis*. Berghahn, New York.
- 550 Lycett, S. J., von Cramon-Taubadel, N., 2013. A 3D morphometric analysis of surface
551 geometry in Levallois cores: Patterns of stability and variability across regions
552 and their implications. *Journal of Archaeological Science* 40, 1508-1517.
- 553 Lycett, S. J., Collard, M., McGrew, W. C., 2007. Phylogenetic analyses of behavior
554 support existence of culture among wild chimpanzees. *Proceedings of the*
555 *National Academy of Sciences* 104, 17588.
- 556 Lycett, S. J., Collard, M., McGrew, W. C., 2010. Are behavioral differences among
557 wild chimpanzee communities genetic or cultural? An assessment using tool-

- 558 use data and phylogenetic methods. *American Journal of Physical*
559 *Anthropology* 142, 461-467.
- 560 May, K. O., 1966. Quantitative growth of the mathematical literature. *Science* 154,
561 1672.
- 562 Mesoudi, A., 2008. An experimental simulation of the 'copy-successful-individuals'
563 cultural learning strategy: Adaptive landscapes, producer-scrounger dynamics
564 and informational access costs. *Evolution and Human Behavior* 29, 350-363.
- 565 Mesoudi, A., 2011. Variable cultural acquisition costs constrain cumulative cultural
566 evolution. *PLOS One* 6, e18239.
- 567 Mesoudi, A., Whiten, A., Laland, K. N., 2004. Is human cultural evolution
568 Darwinian? Evidence reviewed from the perspective of the Origin of Species.
569 *Evolution* 58, 1-11.
- 570 Nishida, T., Matsusaka, T., McGrew, W. C., 2009. Emergence, propagation or
571 disappearance of novel behavioral patterns in the habituated chimpanzees of
572 Mahale: A review. *Primates* 50, 23-36.
- 573 O'Malley, R. C., Wallauer, W., Murray, C. M., Goodall, J., 2012. The appearance and
574 spread of ant fishing among the Kasekela chimpanzees of Gombe. *Current*
575 *Anthropology* 53, 650-663.
- 576 Oswalt, W. H., 1976. *An anthropological analysis of food-getting technology*. Wiley,
577 New York.
- 578 Perry, S., Panger, M., Rose, L. M., Baker, M., Gros-Luis, J., Jack, K., Mackinnon, K.
579 C., Manson, J., Fedigan, L., Pyle, K., 2003. Traditions in wild white-faced
580 capuchin monkeys. In: Fragaszy, D., Perry, S., (Eds.), *The biology of*
581 *traditions: Models and evidence*. Cambridge University Press, Cambridge, pp.
582 391-425.

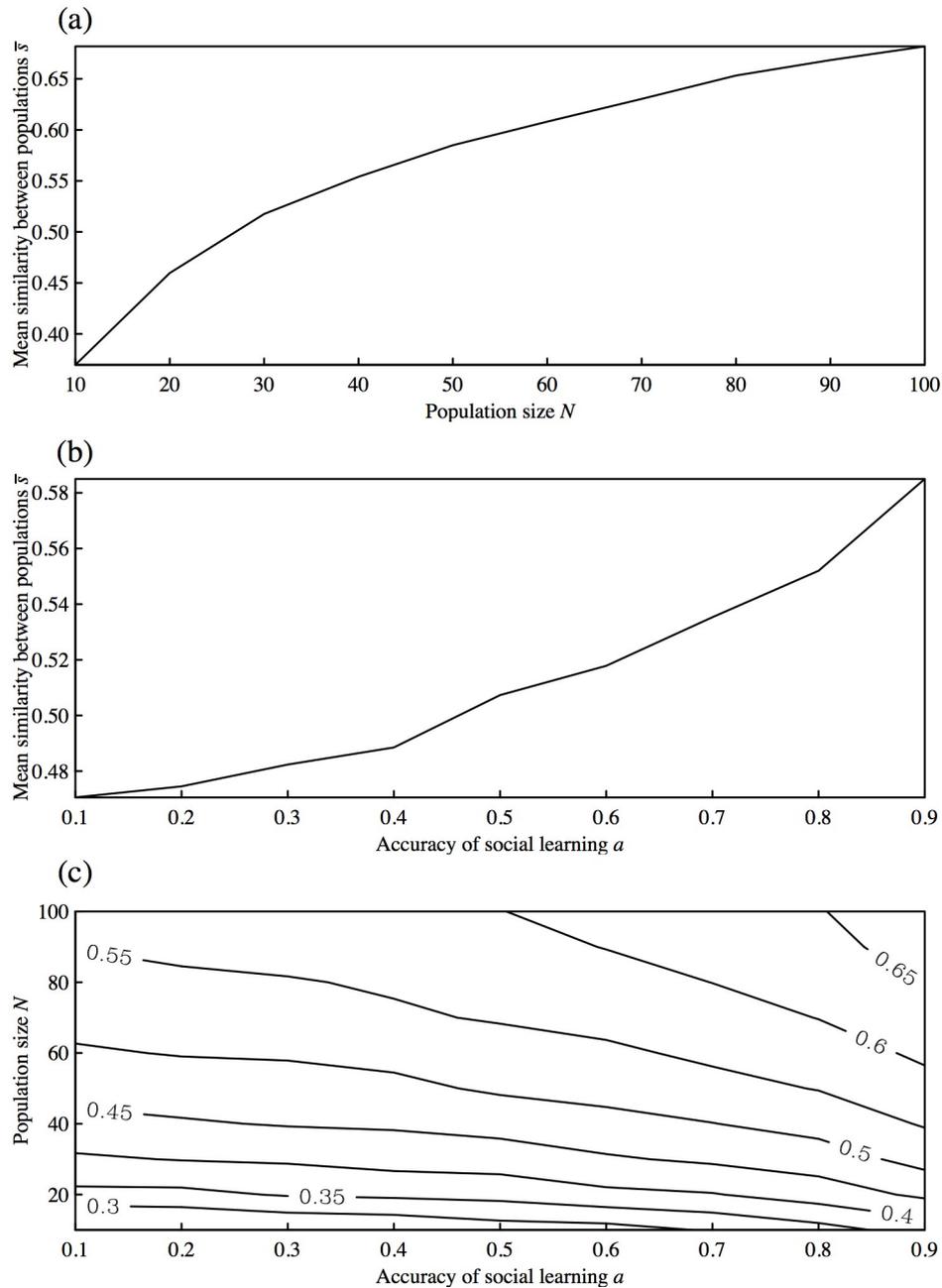
- 583 Powell, A., Shennan, S., Thomas, M. G., 2009. Late Pleistocene demography and the
584 appearance of modern human behavior. *Science* 324, 1298-1301.
- 585 Pradhan, G. R., Tennie, C., van Schaik, C. P., 2012. Social organization and the
586 evolution of cumulative technology in apes and hominins. *Journal of Human*
587 *Evolution* 63, 180-190.
- 588 Price, D. J. S., 1963. *Little science, big science*. Columbia Univ. Press, New York.
- 589 Roche, H., 2005. From simple flaking to shaping: Stone knapping evolution among
590 early hominids. In: Roux, V., Bril, B., (Eds.), *Stone knapping: The necessary*
591 *conditions for a uniquely hominid behaviour*. McDonald Institute
592 *Monographs*, Cambridge, pp. 35-48.
- 593 Rogers, A. R., 1988. Does biology constrain culture? *American Anthropologist* 90,
594 819-831.
- 595 Sanz, C. M., Schoning, C., Morgan, D. B., 2010. Chimpanzees prey on army ants with
596 specialized tool set. *American Journal of Primatology* 72, 17-24.
- 597 Simão, J., 2002. Tools evolve: The artificial selection and evolution of paleolithic
598 stone tools. *Behavioral and Brain Sciences* 25, 419.
- 599 Strimling, P., Sjostrand, J., Enquist, M., Eriksson, K., 2009. Accumulation of
600 independent cultural traits. *Theoretical Population Biology* 76, 77-83.
- 601 Tomasello, M., 1999. *The cultural origins of human cognition*. Harvard University
602 *Press*, Cambridge, MA.
- 603 van Leeuwen, E. J. C., Haun, D., 2013. Conformity in nonhuman primates: Fad or
604 fact? *Evolution and Human Behavior* 34, 1-7.
- 605 van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I.,
606 Suzuki, A., Utami, S. S., Merrill, M., 2003. Orangutan cultures and the
607 evolution of material culture. *Science* 299, 102-105.

- 608 Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y.,
609 Tutin, C. E. G., Wrangham, R. W., Boesch, C., 1999. Cultures in chimpanzees.
610 Nature 399, 682-685.
- 611 Wilder, R. L., 1968. Evolution of mathematical concepts. Open University Press,
612 Milton Keynes.
- 613
- 614

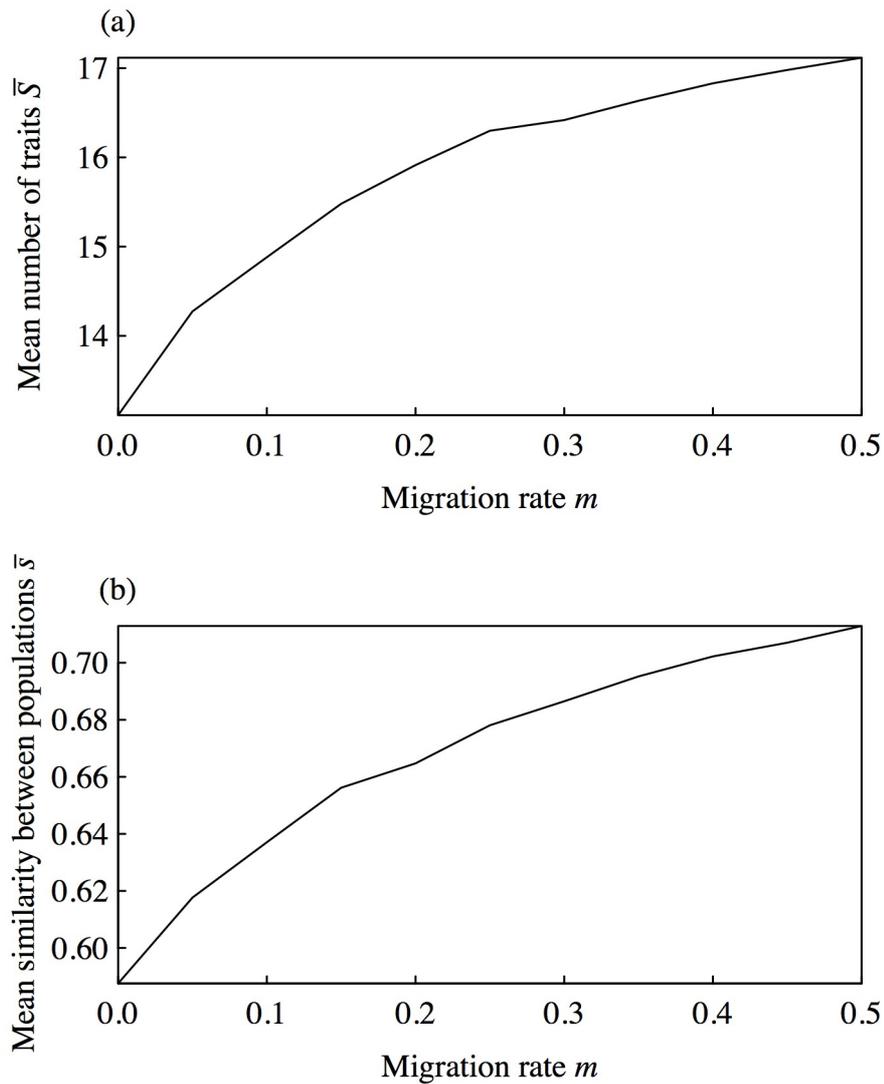
615 **Figures**

617 Figure 1. One simulation of the cultural differences model. (a) Time series of the
 618 number of traits S known in each population. The initial part of the simulation is not
 619 shown. The dashed line shows the exact expected value derived by Strimling et al
 620 (2009, Equation 3). (b) Trait-profiles of each population at the end of the simulation,
 621 with grey cells marking the presence of a given trait in a given population and white
 622 cells marking its absence. The average similarity \bar{s} between the populations is 0.71.
 623 Parameter values: $N = 100$, $a = 0.9$, $\mu = 0.1$, $m = 0$, $p = 5$.

624

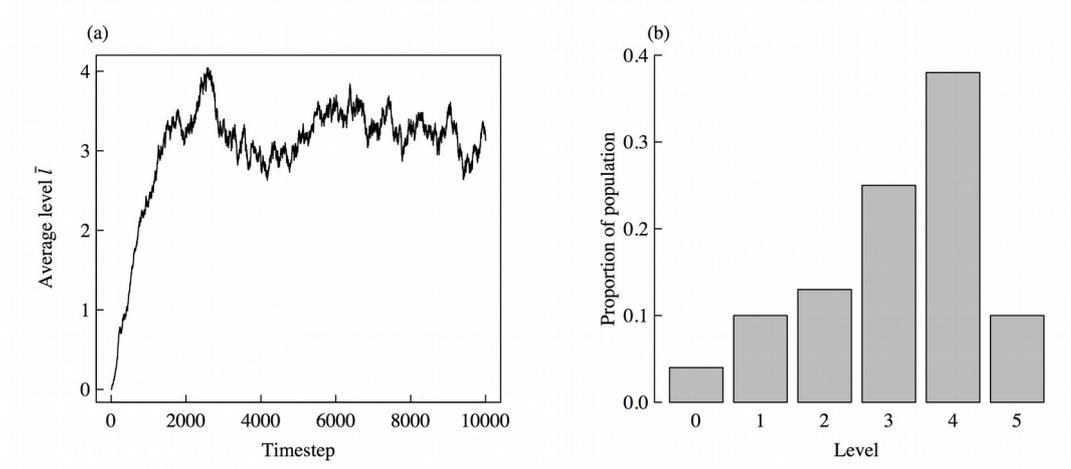


626 Figure 2. The effect of (a) the population size N , (b) the accuracy of social learning a ,
 627 and (c) both, on the mean similarity between populations \bar{s} . Panel (c) shows the value
 628 of \bar{s} on a contour plot in an analogous way to a geographical map showing the height
 629 of a mountain at various points in space. All panels show the value found after 2000
 630 timesteps, averaged over 1500 simulations with parameter values $\mu = 0.1$, $p = 5$, and
 631 $m = 0$; in (a) $a = 0.9$ and in (b) $N = 50$.

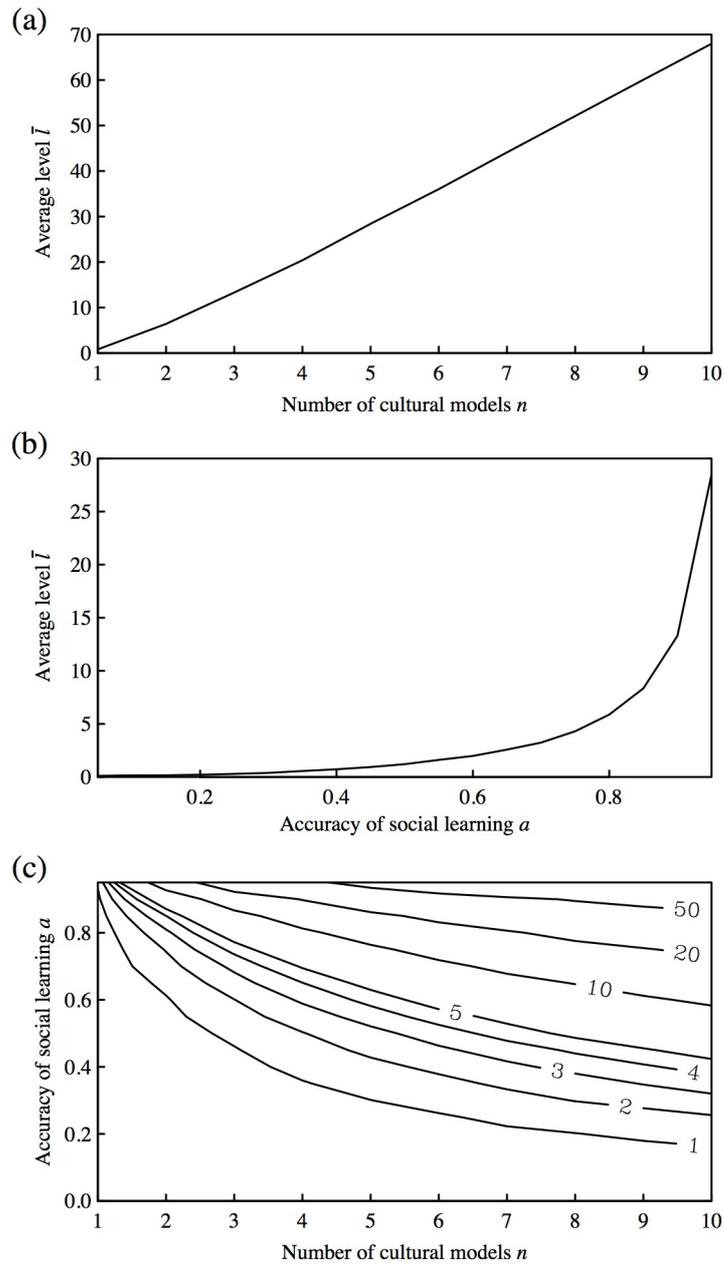


634 Figure 3. The effect of the migration rate m on (a) the mean number of different traits
 635 across all populations \bar{S} and (b) the mean similarity between populations \bar{s} . Both
 636 panels show the value found after 2000 timesteps, averaged over 2000 simulations
 637 with parameter values $N = 50$, $a = 0.9$, $\mu = 0.1$, and $p = 5$.

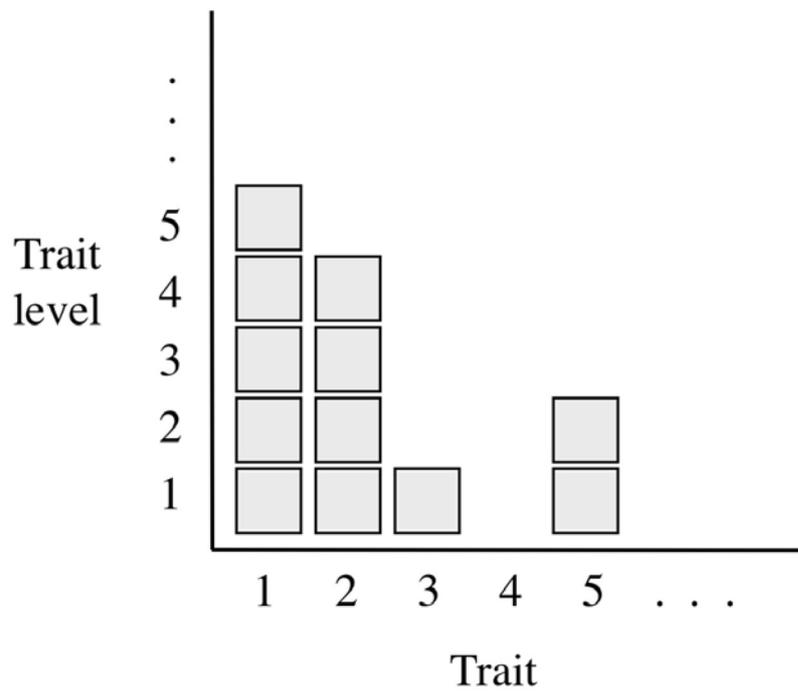
638



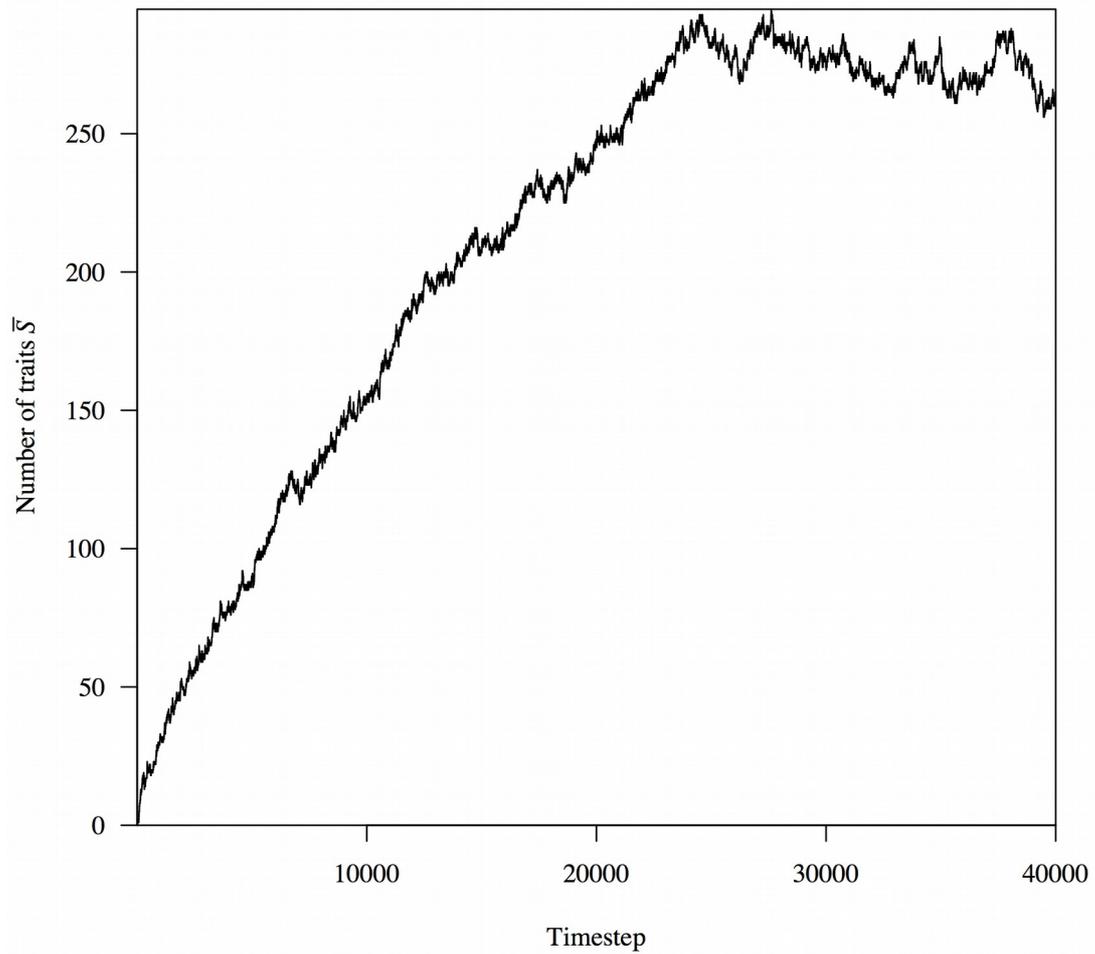
640 Figure 4. One simulation of the cumulative culture model. (a) Time series of the mean
 641 level \bar{l} known in the population. (b) The distribution of levels in the population at
 642 the end of the simulation. Parameter values: $N = 100$, $a = 0.7$, $n = 3$, $\mu = 0.1$.
 643



645 Figure 5. The effect of (a) the number of cultural models n , (b) the accuracy of social
 646 learning a , and (c) both, on the mean trait level \bar{l} maintained in the population. All
 647 panels show the value found after 10000 timesteps, averaged over 20 simulations,
 648 with $N = 100$ and $\mu = 0.1$; in (a) $a = 0.9$ and in (b) $n = 3$.



650 Figure 6. A schematic illustration of the structure of the traits and trait levels for one
 651 hypothetical individual in the combined Model 3. In this example, the individual
 652 knows trait number 1 to level 5, trait number 2 to level 4, trait number 3 only at the
 653 first level, does not know trait number 4, and knows trait number 5 to level 2.



655 Figure 7. The number of traits known in the population in one simulation of the
656 combined model. Parameter values: $N = 30$, $n = 2$, $a = 0.7$, $\mu = 0.1$, $m = 0$, $p = 1$.

657 **Appendix**

658 Imagine, in Strimling et al's model (i.e. with $m = 0$), that a focal individual has just
 659 invented a new trait. In the next timestep, one of three things can happen: the trait can
 660 be lost because the individual dies, the trait can continue to be known only by the
 661 inventor, or another individual can learn the trait. Let us denote the probabilities of
 662 these three events by p_{lost} , p_{kept} and p_{copied} . The trait will be lost if the inventor is
 663 randomly picked to die; thus,

$$664 \quad p_{lost} = \frac{1}{N}$$

665 The trait will be learned by another individual if the inventor does not die, and the
 666 individual randomly picks the inventor to learn from, and is successful at learning;
 667 thus,

$$668 \quad p_{copied} = \left(1 - \frac{1}{N}\right) \left(\frac{1}{N-1}\right) a = \frac{a}{N}$$

669 Finally,

$$670 \quad p_{kept} = 1 - p_{lost} - p_{copied} = 1 - \frac{1}{N} - \frac{a}{N} = \frac{N - a - 1}{N}$$

671 What is the probability $P(t)$ that the trait is learnt by another individual for the first
 672 time exactly t timesteps after it was invented? For this to happen, the trait must
 673 continue to be known only by the inventor for $t - 1$ timesteps, and must then be learnt
 674 by another individual on the t^{th} . Thus,

$$675 \quad P(t) = p_{kept}^{t-1} p_{copied} = \left(\frac{N - a - 1}{N}\right)^{t-1} \frac{a}{N}$$

676 Finally, what is the probability that the trait will ever spread beyond its inventor? This
 677 happens if $P(t)$ ever happens, i.e. with probability

$$678 \quad \sum_{t=1}^{\infty} P(t) = \sum_{t=1}^{\infty} \left(\frac{N - a - 1}{N}\right)^{t-1} \frac{a}{N}$$

679 Using the standard identity for infinite geometric series, this can be shown to be equal

680 to

681 $\frac{a}{1+a}$