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# 1 Cumulative cultural evolution within evolving 2 population structures

3

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5

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12 population size; population structure; social learning

13

14

15 **Abstract**

16 Our species possesses the peculiar ability to accumulate cultural innovations over multiple  
17 generations, a phenomenon termed cumulative cultural evolution (CCE). Recent years have  
18 seen a proliferation of empirical and theoretical work exploring the interplay between  
19 demography and CCE. This has generated intense discussion about whether demographic  
20 models can help explain historical patterns of cultural changes. Here, we synthesise empirical  
21 and theoretical studies from multiple fields to highlight how both population size and  
22 structure shape the pool of cultural information that individuals can build upon to innovate,  
23 present the potential pathways through which humans' unique social structure might  
24 promote CCE, and discuss whether humans' social networks might partly result from  
25 selection pressures linked to our extensive reliance on culturally accumulated knowledge.

26

## 27 **Problem-solving in populations over multiple generations**

28 A central feature of our species is our unprecedented capacity to develop sophisticated  
29 cultural practices that have allowed us to colonize and permanently occupy environments for  
30 which we are poorly suited genetically [1, 2]. This capacity can be viewed as a form of  
31 problem-solving by which humans have successfully solved complex ecological challenges.  
32 This form of problem solving, however, is peculiar in that it operates at the population level,  
33 rather than solely within individuals, and over multiple generations [2, 3]. Both traditional  
34 and more modern technologies have not been produced by a single individual but have  
35 emerged over centuries through incremental improvements resulting from the efforts of  
36 multiple generations of individuals. This process - known as **cumulative cultural evolution**  
37 (CCE) - is powered by our ability to selectively learn adaptive social information which results  
38 in the gradual accumulation of **innovations**, and can give rise to cultural traits (such as  
39 technologies) that are beyond individuals' inventive capacities [2-7].

40 Drawing predominantly on ideas from evolutionary theory, anthropologists, biologists  
41 and psychologists have developed a rigorous theoretical framework that applies the notion  
42 of descent with modification to material culture, and have investigated the role of population  
43 dynamics in the production, transmission and maintenance of cultural traits [8-10]. An  
44 influential finding of early theoretical models is that our social learning abilities interact with  
45 **demography** to affect CCE, and, more specifically, that the size of the population within  
46 which cultural information is shared strongly constrains CCE [11].

47 Recent years have seen a proliferation of empirical and theoretical work exploring the  
48 interplay of demography and CCE, and demographic factors are increasingly invoked to  
49 explain historical patterns of cultural changes [11-19]. While this research has advanced our  
50 understanding of the link between demography and CCE and opened up promising new

51 avenues, it has also revealed a need to better articulate empirical research and theoretical  
52 models. Here we present the theory, discuss misconceptions, outline future challenges, and  
53 highlight new directions in research on demography and CCE.

54

#### 55 **Strength in numbers**

56 Demography has long been considered a potential explanation for cultural changes  
57 documented in the archaeological record [20-22], but it is with the theoretical work of  
58 Shennan [23] and Henrich [11] that the idea gained prominence among evolutionary human  
59 scientists. The main idea behind demographic models of cultural evolution is that, given that  
60 CCE only operates when at least some information is transmitted socially between  
61 generations [24-26], the **effective population size** (which depends on both population size  
62 and interconnectedness) can buffer the risk of losing cultural information (see Box 1). In  
63 Henrich's seminal model [11], for instance, individuals belong to a population of constant  
64 size and possess a psychological propensity to learn from successful individuals. This  
65 propensity creates a selective force that promotes the transmission of beneficial cultural  
66 traits and outweighs the degrading effects of learning errors when populations are large  
67 enough (Figure 1). These results suggest that decreases in effective population size (due to  
68 phenomena such as plagues, war or volcanic eruptions) might result in losses in individuals'  
69 level of skills (often proxied in the archaeological literature as the number of tools, or toolkit  
70 complexity) by constraining CCE. Several regional losses of cultural traits documented in the  
71 archaeological record, such as prehistoric Tasmania, have consequently been attributed to  
72 decreases in population size and connectedness [11, 19]. Conversely, the emergence of more  
73 complex cultural traits have been hypothesized to result from increases in population sizes  
74 and/or densities [13, 14].

75

## 76 **Experimental tests of the relationship between population size and CCE**

77 One approach that has been used to evaluate the plausibility of demographic models of CCE  
78 involves lab experiments. Typically, participants who are part of groups of different sizes are  
79 tasked to improve a piece of technology. To date, 5 experiments from 4 different research  
80 groups provide support for a positive effect of group size on cultural complexity [27-31] (but  
81 see [32, 33]). One study, for instance, exposed naïve participants in groups of 2, 4, 8 and 16  
82 to demonstrations showing how to produce virtual arrowheads and fishing nets, and tracked  
83 the efficiency of those tools across time [27]. The larger the group, the less likely tools were  
84 to deteriorate, the more likely they were to improve, and the more likely a diversity of tool  
85 types were to be maintained. Using chains of participants and alternative tasks involving  
86 image-editing and knot-tying techniques, another study similarly showed that the  
87 deterioration of a technique is less likely (and its improvement more likely) in larger groups  
88 [29]. Additionally, these experiments show that individuals use cues such as success to  
89 choose from whom they learn, lending plausibility to the assumption of Henrich's model that  
90 individuals selectively learn from successful **demonstrators**.

91       Importantly, some of these experiments relied on designs that only loosely reflect  
92 Henrich's initial assumptions (Box 2). Most, for instance, provide individuals with the  
93 opportunity to simultaneously learn and combine information from multiple demonstrators  
94 (a several-among-many design) [28-31] while Henrich's model assumes that individuals  
95 always select a *single* source of information from a larger pool of demonstrators. Some  
96 experiments that have relied on the former design, however, allowed participants to allocate  
97 their learning time strategically, which means that individuals' learning strategies might still,  
98 in practice, be consistent with Henrich's assumptions [29]. Yet mechanisms that are not part

99 of Henrich's model, such as combining information from multiple demonstrators to generate  
100 new solutions, certainly did play a role in these experiments [29-31]. Due to this disconnect  
101 between experimental tests and theoretical models, it is not always clear whether  
102 experimental studies showing positive effects of demography offer genuine support for  
103 specific theoretical claims, nor whether purported failures to detect any effect of  
104 demography are valid challenges to theoretical models (see Box 2 for further discussion).

105

### 106 **Real-world tests of the relationship between population size and CCE**

107 A complementary and more direct approach to test the relationship between population size  
108 and CCE is to look for a correlation between toolkit size and population size using real-world  
109 ethnographic and archaeological data. Results with this approach have been mixed. Some  
110 studies support the hypothesis [13, 14, 34, 35], but others do not [36-39] (although [40]  
111 point out that some of these studies rely on the same datasets, and should not count as  
112 independent tests).

113         The difficulty with testing demographic models using real-world data is that human  
114 populations are typically embedded within extended networks of cultural exchange, making  
115 it difficult to gather meaningful estimates of population size. This constitutes a major  
116 obstacle for anthropologists and archaeologists because theoretical models explicitly link  
117 cultural complexity to the size of the population *that shares information* (i.e. the effective  
118 cultural population size) [11]. This implies that tests of demographic hypotheses should  
119 control for contact rates between inter-connected populations, which is typically challenging  
120 (but see [34]). Proponents of demographic hypotheses have therefore argued that studies  
121 which reported null results are invalid because they do not take contact rates into account  
122 and typically treat culturally connected groups as independent, culturally isolated

123 populations [40] (see Box 3 for other mismatches between models and empirical tests).

124         Other studies have tested demographic effects where they may not be predicted to  
125 occur. One study, for instance, found no evidence that larger populations support more  
126 complex folk tales, with complexity operationalised as number of tale types, number of  
127 narrative motifs within tales, and number of component details within tales [41]. Yet folk  
128 tales are very different to the technology that is the focus of most demographic models.  
129 Tools that are more efficient and have higher payoffs are typically associated with an  
130 increasing number of component elements [42], which means that they tend to be more  
131 complex. However, if complexity is not associated with higher payoffs, then theoretical  
132 models do not predict that population size should necessarily affect it. The function of  
133 folktales, for instance, is to convey meaning. If similar meaning can be conveyed by simpler  
134 folktales, we should not necessarily expect to observe the most complex folktales in larger  
135 populations. The same line of reasoning applies to the evolution of language, which  
136 functionally adapts to the needs of efficient communication [43]. Studies that have  
137 investigated the relationship between speaker population sizes and phoneme inventory sizes  
138 [44-46] or rates of language change [47-49] have yielded mixed results. However, because  
139 language also evolves to become more learnable [50], we should not necessarily expect  
140 larger populations to produce more new words nor have larger phoneme inventory size.  
141 Furthermore, folk tales and other forms of expressive culture may serve as markers of group  
142 membership and some models have suggested that smaller groups will have more  
143 exaggerated markers [51]. This suggests that a clearer picture about the relationship  
144 between demography and the evolution of expressive cultural traits might emerge by moving  
145 away from arbitrarily chosen measures of complexity and by taking into account that  
146 functional and symbolic cultural traits exhibit different evolutionary dynamics [52].

147 It is also worth stressing that, contrary to recent claims [53], no theoretical work ever  
148 predicted that population size should *solely* determine the number of tools (or any other  
149 measure of cultural complexity) found in human populations. Many factors are expected to  
150 affect toolkit complexity in natural populations, including mobility, subsistence practices and  
151 ecological factors. The risk hypothesis, for instance, holds that populations living in harsh  
152 environments create more numerous and specialised tools to mitigate the risk of resource  
153 failure due to stochastic variation [36-39, 54, 55]. Importantly, the risk hypothesis and the  
154 population size hypothesis differ in what they aim to explain [56]. The risk hypothesis  
155 explains what determines the size and complexity of toolkits (i.e. what creates the need for  
156 cultural complexity). The population size hypothesis is about the constraints imposed on CCE.  
157 Claims that the absence of correlation between population size and toolkit complexity  
158 disprove demographic models are based on misconceptions about those models (see Box 3).

159 Inconclusive studies about the relationship between population size and CCE have  
160 had the merit of stimulating new work and led to important refinements to early theoretical  
161 work. Models with different assumptions have shown that the effects of effective population  
162 size hold when more conservative or alternative assumptions are considered (e.g. restricting  
163 potential demonstrators to a limited number of acquaintances [57]; conformist transmission  
164 [58, 59] but see [60]; adding costs to acquiring knowledge [61]; and alternative pathways to  
165 innovation [62]). However, recent studies also suggest that the relationship between  
166 effective population size and CCE can be mediated by numerous factors ([58, 62-66]), and  
167 that there are numerous challenges in detecting demographic effects on CCE in real-world  
168 data (see Box 3).

169 Despite these challenges, there is little doubt that changing the effective size of a  
170 population will alter the cultural information available to subsequent generations of learners,

171 which will most likely constrain what can be achieved by individuals. In this context,  
172 promising new work has started to investigate more broadly how constraints on information  
173 flow within populations can further promote or hinder the gradual accumulation of cultural  
174 innovations.

175

#### 176 **Beyond numbers: CCE in social networks**

177 Human populations do not consist of a collection of isolated groups of varying sizes. Multiple  
178 groups are typically connected by migratory and trade activities, which results in wide,  
179 heterogenous social networks. The role of connectedness on CCE was already acknowledged  
180 in early theoretical models [11, 13]. A simulation model that explicitly implemented  
181 migratory activity among subdivided populations, for instance, showed that increasing the  
182 migration rate has a similar effect to increasing the size of an isolated population [13]. This is  
183 because increases in both population size and migratory activity increase the effective  
184 number of individuals available as demonstrators, and so reduce the risk of losing cultural  
185 information.

186 More recent work, however, has started to investigate in greater detail how the  
187 structure of the population impacts the accumulation of cultural information. Unlike early  
188 models, recent studies decouple the maintenance of existing traits and the production of  
189 new traits, more explicitly modelling the pathways that give rise to innovation [62, 67-69].  
190 Recent models, for instance, assume that existing traits can not only be refined but also  
191 combined with other existing cultural traits. When **recombination** between existing traits is  
192 incorporated as a pathway towards innovation, increases in population size and  
193 connectedness can have different effects on CCE [68, 69]. This is because, while increases in  
194 population size systematically benefit CCE by reducing the risk of cultural loss, increases in

195 connectedness can *reduce* opportunities for innovation by homogenising cultural behaviours.  
196 This effect is illustrated by a recent lab experiment in which individuals could innovate by  
197 producing incremental changes within path-dependent technological trajectories  
198 (**refinement**) and by combining traits that have evolved along different trajectories  
199 (recombination) [67]. Results show that high levels of connectedness make individuals more  
200 likely to converge on similar solutions, which results in lower levels of cultural diversity and  
201 slower rates of innovation compared with less connected groups.

202         These results suggest that understanding the effect of demography on CCE requires  
203 us to consider not only how changes in connectedness affect the number of individuals  
204 available as demonstrators, but also how it shapes the cultural diversity to which individuals  
205 are exposed. When these two effects are considered simultaneously, models show that  
206 optimal rates of accumulation are reached for intermediate levels of connectedness [68, 69].  
207 This is because low levels of connectedness increase the risk of cultural loss by decreasing  
208 access to demonstrators, while high levels of connectedness reduce opportunities to  
209 innovate by homogenising cultural behaviours. At intermediate levels of connectedness,  
210 groups can accumulate cultural information while remaining culturally distinct, which keeps  
211 fueling innovation.

212         These results have implications for CCE both at the macroscale and the microscale. At  
213 the macroscale, human population have been historically fragmented due to geographic  
214 barriers, conflicts and other factors, resulting in long-standing culturally differentiated sub-  
215 populations. In this context, increased levels of between-group connectedness are unlikely to  
216 homogenise cultural behaviours. Nevertheless, recent models suggest that, because of new  
217 opportunities for recombination, contacts between culturally differentiated groups should  
218 result in rapid cultural changes whose magnitude far exceed what is predicted by models

219 that incorporate cultural loss alone [68]. This also suggests that population structures that  
220 allow for contacts between culturally differentiated groups might act as endogenous drivers  
221 of cultural change [67, 68], even though it should not be assumed that populations will  
222 develop and maintain more complex cultural repertoires without appropriate incentives to  
223 do so (Box 3).

224         Patterns of connectedness might also affect CCE at the microscale by influencing  
225 individuals' exploration of the design space. Network and organization scientists, for  
226 instance, have jointly shown that behaviours are more likely to become homogeneous in  
227 well-connected than in partially-connected groups when learners preferentially acquire  
228 information from the same demonstrator [70-72] (but see [73, 74]). Sociologists have  
229 similarly argued that behaviors tend to be more homogeneous within groups than between  
230 groups and that individuals with ties to otherwise unconnected groups have greater  
231 opportunities to develop new ideas because they are exposed to a broader diversity of  
232 information [75].

233         These studies illustrate how patterns of connectedness impact the quantity and  
234 diversity of information that individuals are exposed to and can draw on to make inferences,  
235 which in turn can impact populations' abilities to develop and maintain cultural traits. The  
236 benefits of sparsely interconnected networks on CCE in natural populations, however, remain  
237 to be properly evaluated. Complex cultural traits are typically hard to learn and several  
238 experiments have stressed the importance of multiple demonstrations and multiple learning  
239 attempts in the acquisition of complex skills [27, 76]. This suggests that occasional contacts  
240 between different individuals/groups might not allow complex skills to spread properly.  
241 Additionally, network scientists have stressed the importance of the number of sources of  
242 exposures for the adoption of unproven new solutions [77]. Experiments typically provide

243 participants with accurate information about alternative solutions, which allows them to  
244 confidently adopt the most rewarding ones. In noisy environments, however, interactions  
245 with multiple carriers might be critical for individuals to adopt alternative solutions [77] (see  
246 also [78] for an example of how the mean number of connections within a network affects  
247 the spread of cultural traits). Future research should test whether the optimal level of  
248 connectedness differs depending upon the characteristics of the cultural traits one is looking  
249 at. Dense networks, for instance, might be critical for the cultural evolution of hard to learn  
250 traits (for which transmission is the key bottleneck), while the cultural evolution of easy to  
251 learn traits whose efficiency can be readily assessed might be faster in sparsely connected  
252 networks.

253

#### 254 **Characterizing human social networks in the wild**

255 The effects of population interconnectedness on CCE suggests that cultural changes might be  
256 better understood by paying greater attention to the structure and evolution of human  
257 social networks. Mapping past, or even recent, social networks, however, is challenging.  
258 Archaeologists and geneticists are still struggling to infer past population sizes [15, 79, 80],  
259 let alone population structures [81]. In recent years, approaches relying on social network  
260 analyses have seen a rise among archaeologists, but many challenges have still to be solved  
261 before being able to distinguish spatio-temporal patterns in social interactions from noise in  
262 archaeological data [82-84].

263         Comparative and ethnographic studies, however, are already providing valuable  
264 information about human population structure. Comparisons between human hunter-  
265 gatherer societies and non-human primate societies, for instance, have shed light on what  
266 has been called the deep social structure of human societies [85]. Contrary to most non-

267 human primate societies, which are composed of independent, single-group structures,  
268 human societies are federations of multifamily groups [85, 86]. This unique multigroup  
269 structure results in extensive networks of unrelated individuals that might be conducive to  
270 CCE [87]. Data on interactions between same-sex adults from two hunter-gatherer  
271 populations, for instance, reveal that individuals typically interact with more than 300 same-  
272 sex adults in a lifetime (although including opposite-sex adults and children results in  
273 estimates as high as 1000). In comparison, male chimpanzees are estimated to interact with  
274 only about 20 other males in a lifetime [87] (see also [88] for a discussion on the large-scale  
275 social networks of hunter-gatherer groups).

276         Other studies among hunter-gatherer populations have started to more finely  
277 characterize hunter-gatherer networks. One study, for instance, used trackers to map in-  
278 camp networks in two hunter-gatherer populations and showed that individuals invest early  
279 in their childhood in a few close friends who bridge densely connected families [89]. These  
280 strong friendships increase the global efficiency of hunter-gatherer in-camp networks, which  
281 might facilitate the flow of social information (Figure 2). More recently, characterization of  
282 hunter-gatherer networks has been extended to between-camp interactions and has been  
283 used to simulate the accumulation of cultural innovations over real networks [90]. Results  
284 confirm that hunter-gatherers' social structures are made of multiple levels of clustering, and  
285 simulations suggest that this sparsely interconnected hierarchical network structure might  
286 accelerate CCE by allowing the coexistence of multiple cultural lineages and promoting the  
287 emergence of innovations (but see Box 4).

288         The few studies that have investigated networks in hunter-gatherers, however, have  
289 been limited to interview data and proximity measures [87, 89, 90]. Actual measurements of  
290 cultural transmission remain scarce, and the extent to which proximity networks accurately

291 reflect transmission networks is currently unknown. Investigation of the co-occurrence of  
292 plant uses in dyads in one hunter-gatherer population, for instance, showed that not all  
293 knowledge is equally shared [91]. More specifically, results show that medicinal plants were  
294 mostly shared between spouses and kin, while plants that serve other functions were shared  
295 much more widely. This suggests that knowledge-sharing networks are content-specific and  
296 supports the idea that hunter-gatherer multi-level social structure enables culturally  
297 differentiated units to remain stable despite occasional co-residence [90]. This work also  
298 suggests that both **structural barriers** (i.e. lack of contact between individuals) and  
299 **behavioral barriers** (i.e. unwillingness to share cultural knowledge) have to be taken into  
300 account to properly evaluate the effects of population structure on CCE. Indeed, structural  
301 and behavioral barriers combine to result in an **effective population structure** that  
302 ultimately determines opportunities for cultural transmission. Contact between different  
303 ethnolinguistic groups, for instance, can potentially bring different cultural traits together  
304 due to significant between-group cultural distance. However, language barriers, endogamy,  
305 rivalry and other behavioural barriers such as in-group conformity might limit opportunities  
306 for cultural exchange between those groups [92, 93].

307         These results suggest that our understanding of the relationship between  
308 demography and CCE would benefit from a better understanding of how and why individuals  
309 form social ties both within- and between-groups and the extent to which different types of  
310 ties (such as kin-based, affine-based and friendship-based) are conducive to cultural  
311 transmission. This will permit more realistic implementation of cultural transmission into  
312 theoretical models. Indeed, while the combination of vertical cultural transmission (i.e.  
313 learning from parents) and success-biased learning is empirically supported and provides a  
314 useful first approximation of the dynamics of social learning in groups [40], multiple factors

315 are likely to affect opportunities for social learning. Anthropological studies, for instance,  
316 have shown that social ties are more likely to form between people who share similar traits  
317 (i.e. homophily [94, 95]). Furthermore, understanding how individuals form social ties is an  
318 important avenue for future research because the way individuals form ties ultimately feeds  
319 back into the evolution of social networks (homophily, for instance, is known to introduce  
320 local structure into networks [95, 96]).

321

### 322 **How did human social networks get their shape?**

323 Even if questions remain regarding the effects of specific network properties on CCE, it  
324 seems clear that humans live within unusually large and uniquely structured social networks.  
325 This raises questions about how and why humans have come to form large networks of  
326 unrelated or weakly related individuals.

327         Recently, it has been argued that, because individuals from culturally differentiated  
328 groups might have greatly benefited from increased between-group interactions, selection  
329 might have acted at the individual level to affect individuals' propensity to interact with out-  
330 group members [17]. This might have involved changes in conscious behavioural choices (e.g.  
331 adjustments to out-group contacts due to perceived immediate benefits) and/or unconscious  
332 influence on behaviour (e.g. decreased fear of foreigners or tendency to disperse) [17].  
333 Congruently, a recent simulation model that investigated whether network structure itself  
334 can evolve as a result of ecological pressures related to skill acquisition confirmed that  
335 selection can impact individuals' propensity to form random ties (such as non kin ties) [97].  
336 Yet, it is not clear whether the acquisition of social information creates sufficiently strong  
337 incentives for individuals to overcome rivalry and other behavioural barriers that tend to  
338 reduce opportunities for cultural transmission between unrelated individuals. Moreover,

339 increasing contacts is only one part of the problem, as many cultural traits are unlikely to be  
340 properly acquired without a demonstrator's willingness to share information [98-100].

341 Another possible way by which selection might have promoted the emergence of  
342 networks that are conducive to CCE is by acting on variation that exists at the group level [17,  
343 101]. Indeed, anthropologists have long stressed the role of cultural institutions in promoting  
344 both information sharing and interactions between non-kin [87, 101-103]. Among the Ache  
345 and Hadza, for instance, ritual relationships, mediated by activities such as club fight rituals,  
346 have been shown to promote inter-band interaction. Quantitative analyses have revealed  
347 that ritual relationship is a more important predictor than kinship for different types of  
348 interactions, including opportunities for cultural transmission (such as observing tool making  
349 skills) [87]. Furthermore, anthropologists have stressed that certain groups have cultural  
350 beliefs that connect envy and harm, which make successful individuals more likely to hide  
351 information from other group members, thus inhibiting CCE compared to other groups [101].  
352 This suggests that groups that possess cultural institutions that promote information sharing  
353 and/or mobility might have attained higher cultural complexity and outcompeted groups  
354 with cultures less conducive to CCE [17, 101]. It is also worth noting that the maintenance of  
355 large networks of unrelated or weakly related individuals might have been further supported  
356 by the emergence of cultural innovations such as kin naming systems and stylistic markers of  
357 group identity that typically promote cooperative interactions between unrelated individuals  
358 [103]. Kin naming systems, for instance, allow familial relationships to extend to affine,  
359 distant kin and even non-kin [103] and might permit individuals to maintain privileged  
360 relationships with large numbers of individuals without requiring much cognitive effort nor  
361 physical cohabitation [104].

362 The question of whether humans' social structure might in part result from selection

363 pressures linked to our extensive reliance on culturally accumulated knowledge will have to  
364 be carefully evaluated. Indeed, chimpanzees also live among nonrelatives [105] and humans'  
365 propensity to form ties with non-kin might be due to reasons unrelated to CCE and that just  
366 happened to be conducive to the accumulation of cultural innovations. Archeologists, for  
367 instance, noted that an incest avoidance rule would give rise to the same kind of sparsely  
368 connected networks that might benefit CCE [56]. Alternative determinants of outgroup  
369 contacts include resource distribution [56], reciprocal cooperative exchange [106] and  
370 coalition formation [107], among others. Specific predictions should be formulated and  
371 properly tested to disentangle the respective effects of these various mechanisms on  
372 network structure. The hypothesis that CCE directly shapes network structure by acting on  
373 conscious behavioural choices, for instance, would predict that individuals should flexibly  
374 reinforce or weaken their investment in non-kin ties depending on the usefulness of the  
375 information they provide.

376

### 377 **Concluding remarks and future directions**

378 The proliferation of work exploring the interplay of demography and CCE has recently led to  
379 many misconceptions due to loose interpretations of early theoretical models (Box 2 and 3).  
380 Empirical tests that operationalize models in ways that are consistent with theoretical  
381 assumptions provide support for the hypothesis that effective population size constrains CCE.  
382 However, testing these models using real-world data remains difficult because multiple  
383 factors combine with demography to determine CCE and human populations are typically  
384 embedded within extended networks of cultural exchange. While these extended networks  
385 of contacts make it difficult to gather meaningful estimates of population size, recent  
386 research suggests that they might also affect CCE in ways that are not yet fully appreciated.

387 Understanding how population structure affects CCE will require us to understand precisely  
388 how structural and behavioral barriers constrain information flow in natural populations (Box  
389 4).

390           The effects of connectedness on the accumulation of cultural information raise many  
391 questions about the relationship between humans' unique social structure and CCE (see  
392 Outstanding Questions). Through the study of the nature and the emergence of non-kin ties,  
393 both within groups and between groups, as well as knowledge-sharing networks in natural  
394 populations, it will be possible to illuminate how humans have managed to accumulate  
395 cultural information in such an unprecedented way and determine whether our unique social  
396 structure results in part from selection pressures linked to our extensive reliance on  
397 culturally accumulated knowledge.

398

399 **Box 1: Demographic models of cultural change**

400 **Cultural drift.** Some of the earliest cultural evolution models adapted early 20<sup>th</sup> century  
401 models of genetic drift to the cultural case [8, 22, 23, 108]. Drift, whether genetic or cultural,  
402 is essentially sampling error. Drift models typically assume ‘unbiased transmission’ or  
403 ‘random copying’: each of  $N$  individuals within a finite and fixed-sized population possesses  
404 one of a set of discrete cultural traits. Each generation or timestep, individuals select another  
405 individual at random and acquire their cultural trait. This process results in the inevitable loss  
406 of trait variation. The speed with which traits are lost is dependent on  $N$ : smaller populations  
407 lose variation quicker. This is a highly simplistic model, but provides a useful base for  
408 exploring the effects of processes such as innovation and complex population structures such  
409 as island chains or bottlenecks on CCE, and has been used to explain archaeological  
410 assemblage diversity [22, 108].

411

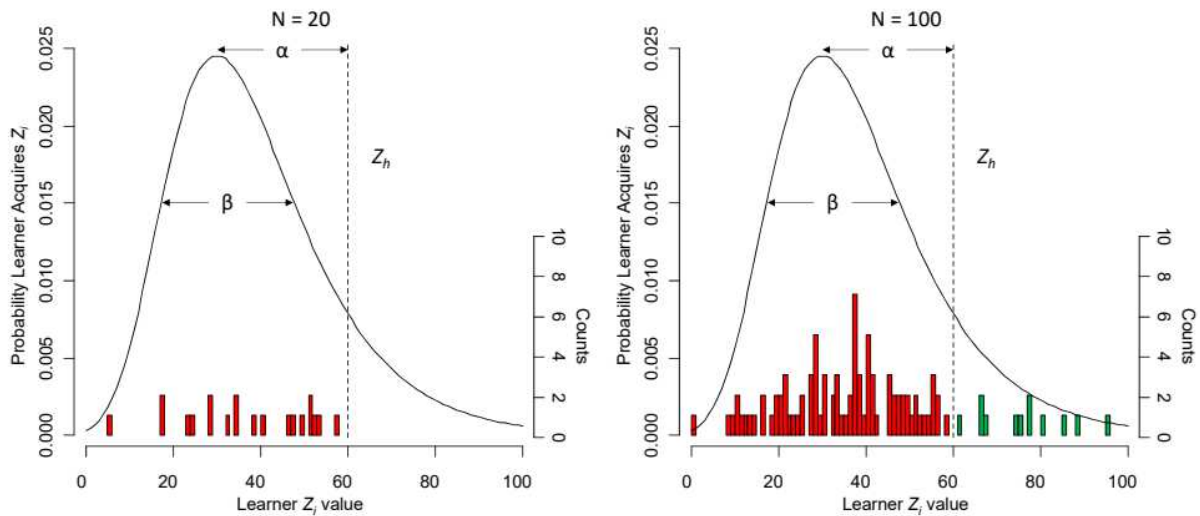
412 **The ‘Tasmanian’ model.** Perhaps the most influential demographic model of cultural  
413 evolution was formulated by Henrich [11]. This model was inspired by the empirical case of  
414 prehistoric Tasmania, which apparently lost complex technological traits (e.g. bone tools,  
415 warm clothing) around 10-12kya when Tasmania was cut off from the Australian mainland,  
416 thus decreasing the effective population size [20]. The model incorporates more  
417 psychologically plausible processes than simple drift models. Each of  $N$  individuals possesses  
418 a value of culturally transmitted ‘skill’ (e.g. basket-making), represented by a continuous  
419 variable  $z$ . Each timestep, each individual attempts to learn the skill value  $z_h$  of the highest-  
420 skilled member of the previous timestep,  $h$  (i.e. success biased transmission). Learning is  
421 imperfect, and affected by two kinds of processes. Learning error, determined by  $\alpha$ , always  
422 results in worse skill than  $z_h$ . Another parameter,  $\beta$ , determines the extent of inferences,

423 experiments, luck and other factors that on average make skill levels worse, but sometimes  
424 better, than  $z_h$ . Combining these, Henrich assumed that the skill of a naive individual is drawn  
425 from a Gumbel distribution (Figure 1).  $N$  interacts with the latter  $\beta$  term: the more individuals  
426 there are, the more likely one of those individuals is to exceed  $z_h$ , representing an increase in  
427 cumulative cultural knowledge/skill. If  $N$  is too small, then all learners will acquire values  
428 around the mode of the distribution, which is less than  $z_h$ , resulting in a decrease in cultural  
429 complexity. Subsequent empirical work has shown that this Gumbel distribution is a  
430 reasonable approximation of social learning dynamics [109] (but see [110] for a critique of  
431 this model).

432

433 **Population structure and trait recombination.** Subsequent models have extended the  
434 Tasmanian model to investigate in greater detail how the structure of the population impacts  
435 both the maintenance and the production of cultural traits. Stochastic simulations of the  
436 Tasmanian model with multiple sub-populations show that increasing the migration rate has  
437 a similar effect to increasing the size of an isolated population on CCE, because both increase  
438 variation within sub-populations and so reduce the risk of losing cultural information [13].  
439 Recent studies have more explicitly modelled the pathways that give rise to innovation and  
440 revealed that the effect of migration can even be more pronounced when cultural traits can  
441 combine to form innovations that are “greater than the sum of their parts” [68]. However,  
442 too frequent contact might not be beneficial to CCE because it prevents populations from  
443 remaining culturally distinct, and reduces opportunities to innovate [68, 69].

444



445 **Figure 1: Gumbel distribution from Henrich's Tasmanian model**

446 The distributions depict the probability of a learner  $i$  acquiring different values of skill,  $z(z_i)$ ,  
 447 for two different population sizes  $N$ . The vertical dotted line shows the  $z$  value of the highest-  
 448 skilled demonstrator being copied ( $z_h$ ). Learning error, determined by  $\alpha$ , reduces the  
 449 likelihood of  $z_h$  being reached. Inferences, experiments and luck, determined by  $\beta$ , increase  
 450 the chances of the learner improving on  $z_h$  (the area under the curve to the right of the  
 451 dotted line). Vertical bars show  $N$  random draws from each distribution, representing  $N$   
 452 learners'  $z_i$  values. Red bars represent inferior  $z_i$  relative to  $z_h$ , green bars represent superior  
 453  $z_i$  relative to  $z_h$ . On the left, a small population ( $N=20$ ) results in a population-level decline in  
 454 skill, as no learner matches or exceeds  $z_h$ . On the right, a large population ( $N=100$ ) features  
 455 some learners who exceed  $z_h$ , resulting in an improvement in the next generation.

456

457 **Box 2: Linking models and data in the lab**

458 Experimental approaches are useful for investigating the relationship between demography  
459 and CCE because essential elements of theoretical models can be implemented under tightly  
460 controlled conditions, and tested against actual human behaviour (rather than modellers'  
461 assumptions about human behaviour) [111, 112].

462 As noted in the main text, the majority of experimental studies have found support  
463 for the general predictions of demographic models [27-31]. This is all the more surprising  
464 given that these studies are remarkably diverse in experimental tasks, group sizes and inter-  
465 individual interactions. Yet, it is worth highlighting that most experimental designs  
466 significantly deviate from the models they claim to test. In the main text we discuss one  
467 example, where experiments offer social learners the opportunity to combine information  
468 from multiple cultural demonstrators [29-31], rather than learn from a single successful  
469 demonstrator as in the most-cited demographic models (see Box 1). The role of  
470 recombination across existing cultural traits has been stressed by scholars from multiple  
471 fields [113-115], and increased opportunities for recombination certainly is one pathway by  
472 which effective population size might affect CCE [101]. Yet, most experiments are presented  
473 as tests of models that do not feature recombination between existing traits and in which  
474 effective population size mostly affects CCE by buffering the risk of losing cultural  
475 information (see Box 1). Still other experiments have relied on tasks in which cultural loss is  
476 unlikely to occur [31]. Thus, even though these experiments support the population size  
477 hypothesis, it is not always clear whether they provide appropriate tests of the theoretical  
478 models which they cite.

479 Maybe more problematic are experiments where results showing no relationship  
480 between demography and CCE are used to question the validity of theoretical models

481 despite featuring different assumptions to those models. A recent experiment, for instance,  
482 had chains of participants make and throw paper airplanes, with each participant able to  
483 learn from 1, 2 or 4 previous participants [33]. Apparently contrary to the demographic  
484 hypothesis, flight distance only increased in the 1-demonstrator condition, not the 2- and 4-  
485 demonstrator conditions. Yet this experimental design prevented participants from learning  
486 from the demonstrator of their choice. Instead participants were forced to attend to  
487 multiple, randomly ordered demonstrators for 1.5 minutes each. Yet, Henrich's model  
488 explicitly holds that it is the combination of the amount of beneficial cultural information  
489 (which increases in larger groups) and the selective choices of cultural learners that  
490 promotes CCE. Fay et al.'s results are consistent with the former in showing that larger  
491 groups produce greater variation in distance flight and give participants access to more  
492 efficient planes. But the constraints imposed on social learning strategies inhibited CCE in  
493 large groups by making learning more difficult in those groups.

494         Discrepancies between experiments and models are not *inherently* a problem: the  
495 assumptions of models can always be challenged and mechanisms other than those  
496 considered in theoretical models are worth investigating. Yet, the experimental literature  
497 would benefit from being more explicit about the theoretical basis underpinning the specifics  
498 of experimental designs and how they relate to theoretical models.

499

500 **Box 3: Linking models and data in the wild**

501 Several studies have investigated whether there exists a correlation between toolkit size or  
502 composition and population size in natural populations [13, 14, 34-39], but there remain  
503 serious challenges in testing demographic effects on CCE in real world data.

504 One difficulty concerns limitations in what can be measured [58]. Henrich's model  
505 (see Box 1) describes the level of skill of an individual within a population, a variable that in  
506 an archaeological context can be interpreted as the number of tools or tool components  
507 attributable to an individual. Yet, archaeological studies typically only have access to  
508 population-level rather than individual-level data. This makes purported tests that use  
509 population-level assemblage measures largely irrelevant to Henrich's predictions [58]. Even  
510 though a recent model incorporating the appropriate population-level variable *does* predict a  
511 positive relationship between population size and toolkit size [58], these discrepancies  
512 illustrate the need to use appropriate measures when attempting to test a model and/or to  
513 adapt models so they can properly be tested using empirical data.

514 A second difficulty is that demography has multiple aspects that can be difficult to  
515 fully take into account in ethnographic and archaeological studies. In the main text we  
516 discuss one example of this, where empirical data regarding census population sizes are used  
517 to test (and purportedly fail to support) the Tasmanian model without taking contact rates  
518 into account. Furthermore, recent models suggest that historical variations in population size  
519 and connectedness are as important as immediate demographic contexts in determining  
520 cultural complexity in a population [58, 64, 68]. Some models, for instance, show that the  
521 number of traits in a population should depend not only on the current population size but  
522 also on the history of population growth and decline [58, 64]. This can blur the relationship  
523 between population size and CCE because growing populations can have fewer cultural traits

524 than smaller, declining populations. Similarly, two populations of the same size might be  
525 associated with toolkits of different sizes due to different demographic trajectories. Models  
526 also suggest that changes in interconnectedness can result in different outcomes including  
527 transient increases in cultural complexity [68]. The effects of population histories represent a  
528 challenge for archaeologists whose data represent a record of aggregated events spanning  
529 long periods of time during which both population size and interconnectedness might have  
530 varied. Further models are needed to determine what testable signatures these dynamics  
531 might have left in the past for archaeologists and historians to detect.

532         Finally, demographic factors determine an upper boundary to the level of cultural  
533 complexity that can be reached by a population, but do not entirely determine the actual  
534 level reached by a population. Assuming that increased cultural complexity is beneficial,  
535 increases in population size should result in increases in cultural complexity but only because  
536 this relaxes constraints on CCE. A full understanding of CCE in natural populations requires  
537 both drivers of CCE and constraints to be taken into account. To that end, more research is  
538 needed to identify the factors that combine with demography to determine CCE in natural  
539 populations, such as environmental harshness [54] and instability [116] or accumulated  
540 cultural traits themselves [61, 117, 118].

541

542 **Box 4: Is human multilevel social structure beneficial to CCE?**

543 Recent theoretical and experimental studies have challenged the assumption that anything  
544 that maximizes the flow of cultural information should positively impact innovation rates  
545 (Figure 2A-B). These results have led scholars to wonder whether CCE in human populations  
546 has benefited from our unique multilevel social structure via the partial constraints it  
547 imposes on information flow [67]. A recent simulation study provided support for this by  
548 showing that real hunter-gatherers' social networks allow the coexistence of multiple  
549 cultural lineages, thus promoting the emergence of innovations [90].

550         However, while characterizing actual networks is useful for understanding how  
551 cultural information is expected to spread, many (still largely unknown) parameters need to  
552 be taken into account before establishing whether, and if so why, human multilevel social  
553 structure promotes CCE. Previous work has shown, for instance, that the effect of network  
554 structure on CCE is mediated by factors such as individuals' probabilities of innovating  
555 (because even strong constraints on information flow prevent cultural diversification if  
556 innovation rates are low [69]) and the extent to which innovation depends on cultural  
557 diversity (because constraints on information flow both slow down and limit CCE when  
558 innovation does not depend on recombination [69]). In the aforementioned simulation study  
559 [90], both individuals' opportunity to innovate, and possibilities for recombination, were  
560 determined by the properties of an artificial cultural fitness that was designed to permit  
561 innovation through incremental improvement and recombination [67], but whose relevance  
562 to rates of CCE in natural populations is uncertain.

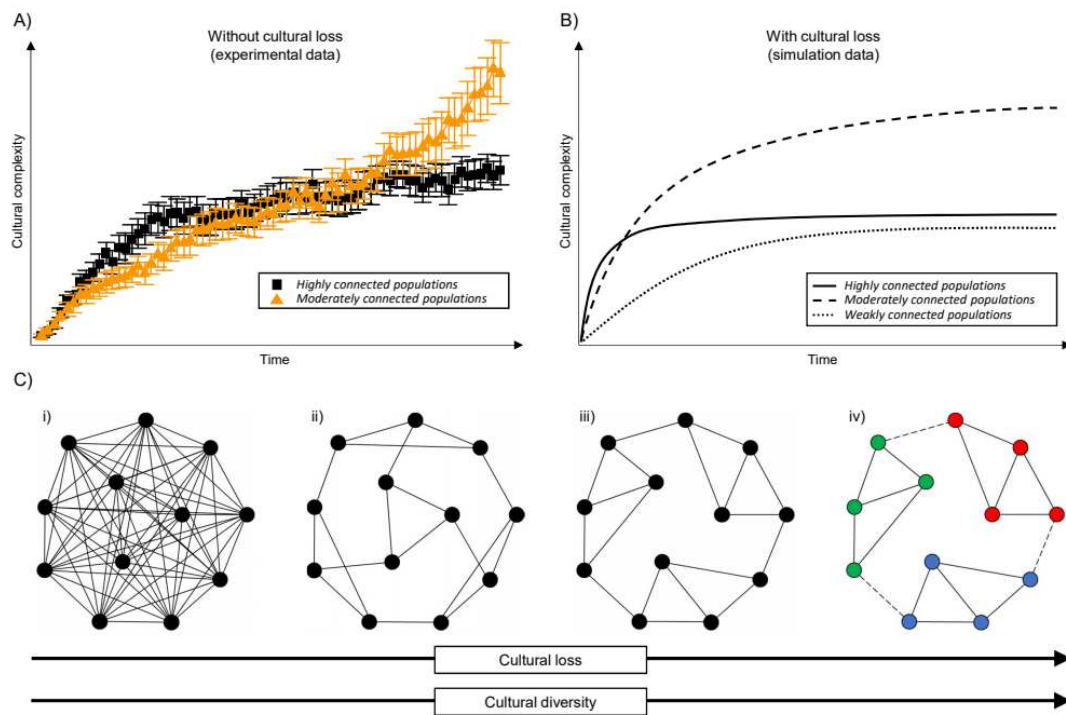
563         Maybe more importantly, the effect of network structure on cultural *loss* was not  
564 considered in those simulations [90]. When cultural loss is not taken into account,  
565 constraints on information flow necessarily benefit CCE by promoting cultural diversification.

566 In more realistic situations, constraints on information flow expose populations to higher  
567 rates of cultural loss, which can prevent cultural diversification [119]. Moreover, even if they  
568 have diverse cultural repertoires, sparsely connected populations can be unlikely to reach  
569 high levels of cultural complexity because of their inability to maintain complex cultural traits  
570 [69]. Thus, given our current limited knowledge about rates of loss and innovation, and  
571 opportunities for recombination, in real-world populations, it is not clear whether the  
572 network structure documented in [90] positively affects CCE or whether cultural complexity  
573 in hunter-gatherer populations would benefit from more connectedness by being less  
574 susceptible to cultural loss. Answering this question will require an evaluation of how sparse  
575 networks made of strong ties (e.g. kin and friendship ties) balance cultural loss and cultural  
576 diversity (Figure 2C).

577

578

579



580

581 **Figure 2: Trading cultural loss and diversity in structured populations.** (A) Experimental

582 results show that moderately connected populations are slower at accumulating innovations

583 but eventually reach higher levels of cultural complexity than highly connected populations

584 when innovation depends on cultural diversity. Adapted from [67]. (B) Simulation models

585 show that optimal rates of accumulation are reached for intermediate levels of

586 connectedness when populations are exposed to cultural loss. Relative rates of accumulation

587 between variously connected populations depend on parameters such as rates of innovation

588 and cultural loss, and the extent to which innovation depends on cultural diversity (not

589 shown). Adapted from [69]. (C) Patterns of connectedness affect both cultural loss and

590 diversity. (i) In fully connected networks made of permanent links (solid lines), the average

591 number of steps required to connect any two individuals (i.e. path length) is minimal and the

592 efficiency with which information spreads is maximal. This reduces the risks of cultural but

593 decreases cultural diversity. (ii) Removing ties increases the average path length between  
594 individuals and results in less efficient networks (e.g. from i to ii). (iii) Networks composed of  
595 individuals tied to the same number of neighbors can also vary in efficiency due to  
596 differences in average clustering coefficients (a measure that reflects the “cliquishness” of a  
597 network [120]). Increasing the average clustering coefficient results in less efficient networks  
598 (e.g. from ii to iii). (iv) Intermittent links between different parts of a network (dotted lines)  
599 further constrain information flow and result in substructures that are more likely to  
600 culturally diverge by isolation (illustrated by different colors) but also more likely to suffer  
601 from cultural loss.

602

603 **Glossary**

604 Behavioural barriers: blocks on information flow due to behavioural tendencies such as an  
605 unwillingness to teach hard-to-learn skills, despite contact

606

607 Cultural drift: cultural change due to random sampling error, which is heavily dependent on  
608 population size and structure (see Box 1)

609

610 Cumulative cultural evolution (CCE): the repeated modification and social learning of  
611 behavioural traits from individual to individual and over successive generations, such that the  
612 cultural traits improve in some desired measure of efficiency (typically a proxy for fitness)

613

614 Demography: the size and structure of a population of individuals within which CCE occurs

615

616 Demonstrator: an individual who serves as a source of social information

617

618 Effective population structure: the structure, resulting from the combined effects of  
619 structural and behavioral barriers, that constraints the flow of cultural information

620

621 Innovation: the generation of novel cultural variation, either via refinement or recombination

622 Recombination: the bringing together of existing cultural traits to form a new functional trait

623

624 Refinement: improving an existing cultural trait, typically through a small, gradual change

625 Structural barriers: blocks on information flow due to the structure of the population, e.g.

626 individuals simply not coming into contact with one another

627 Tasmanian model: an influential early model of how population size constrains CCE (see Box

628 1)

629

630

631

632

633

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641

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