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1 **Modelling persistence over generations in biological and cultural evolution**
2 **based on differential paces of change**

3

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23 ABSTRACT

24 Paces of change are faster in cultural evolution than in biological evolution due to different
25 levels of stability in information storage. This study develops mathematical models to
26 investigate the consequences of differential mutation rates on the ability of groups of
27 information units to survive over many generations. We examined the ability of groups
28 composed of connected units to live on despite the occurrence of deleterious mutations that
29 occur at probabilities ranging from 10^{-1} to 10^{-6} . It appears that the degree of connection
30 between units should be high enough for groups to persist across generations, but this alone did
31 not ensure their survival; when groups of units were limited in size and subjected to high
32 mutation rates, they did not survive for very long. By contrast, a significant proportion of
33 groups were able to survive numerous generations if mutation rates were low and/or group size
34 was large. The results revealed that the mean number of surviving generations was minimized
35 for certain sizes of groups. When allowing information units to duplicate at each generation,
36 simulation showed that a great number of groups avoided extinction even when mutating at the
37 rate of cultural change if the initial group size was large and the duplication rate was high
38 enough to counteract the consequences of environmental perturbations. The modelling
39 described in this study sets out the conditions under which groups of units can survive along
40 generations. It should serve as a basis for further investigations about the links between
41 processes of biological and cultural changes.

42

43 *Keywords:* Transmission, Replication, Mutation, Survival, Extinction

44 **1. Introduction**

45 Cultural evolution and biological evolution are both cumulative processes of information,
46 but how far can they be compared? Cultural evolution would follow patterns of
47 transformational change, meaning that cultures as wholes are transformed through successive
48 stages in which the transmission of acquired knowledge induces a Lamarckian type of
49 inheritance. By contrast, biological evolution is variational, which means that populations
50 evolve through changes in the proportions of their different types of individuals under the
51 influence of Darwinian sorting processes (Lewontin, 1983; Gould, 1987). Some authors have
52 therefore claimed that the parallels found between both phenomena are no more than
53 misleading analogies, which would proscribe the development of an evolutionary theory of
54 culture (Gould, 1987; Maynard Smith, 1988). As Kronfeldner (2007) explains, however,
55 although cultural evolution is based on the inheritance of acquired characters, it also includes
56 processes of variation and sorting, so it is Darwinian in a sense and cannot be considered as a
57 classic example of Lamarckian evolution, which justifies the comparison of biological and
58 cultural evolution.

59 A first biological school of thought considers that cultural dynamics can be modeled using
60 mathematical tools similar to those developed in population genetics. This makes it possible to
61 investigate the rules of transmission and selection particular to cultural traits, basing the
62 analysis on people's conformism with regard to ideas, practices, beliefs and knowledge
63 (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Mesoudi, 2011). A more
64 radical approach, memetics, even claims that culture is supported by particulate mental
65 representations called memes, which are transmitted by passing from one mind to another and
66 are replicated with the same high fidelity as genes (Dawkins, 1976; Blackmore, 1999; Aunger,
67 2002).

68 Drawing on cognitive considerations, a second school of thought stresses that ideas do not
69 colonize brains by mere copying. Ideas are assimilated and produced by the mind through

70 inferential processes. This means that they are reconstructed and possibly transformed each
71 time they are transmitted, thus preventing faithful reproduction throughout successive
72 replications (Sperber, 1996; Boyer, 1999; Atran, 2001; Scott-Philipps et al., 2018).
73 Psychological and environmental factors constrain mental representations, thus sorting
74 variation by reducing the number of possible mental representations to a limited number of
75 cultural attractors. The implementation of these attractors under public representations – i.e.,
76 behaviors, words or artefacts – ensures information transmission. It has been shown, for
77 instance, that communication processes preferentially maintain socially shared representations
78 (Lyons and Kashima, 2001). As a consequence, replication and selection are linked to
79 attraction processes in cultural change, rather than representing separate mechanisms as it is for
80 genetic change (Sperber, 1996; Claidière et al., 2014).

81 After years of debate between the biological and cognitive schools of thought, both
82 perspectives have converged to a significant extent. They currently agree that there is no such
83 thing as cultural gene-like particles that replicate by mere imitation; they also agree that,
84 despite the fact that cultural attractors vary along a continuum, they can be considered as
85 discrete units in mathematical models (Henrich and Boyd, 2002; Henrich et al., 2008; Claidière
86 and Sperber, 2007; Claidière et al., 2014). Disagreements remain about the definition of
87 cultural variants. It should be noted, however, that a similar situation prevails in biology, where
88 genes can be alternately viewed as abstract information units, DNA structures, or functional
89 entities that involve regulatory mechanisms (Keller, 2000; Acerbi and Mesoudi, 2015).

90 A main discrepancy between biological and cultural evolution lies in the stability of
91 information storage. The pace of cultural change is significantly faster than the pace of
92 biological change (Perreault, 2012). The cognitive school emphasizes that unlike genes, which
93 replicate with high fidelity, cultural variants are regularly modified across transmission chains:
94 it is legitimate to ask whether any comparison with genes is relevant if cultural variants tend to
95 be transformed each time they are transmitted (Sperber, 1996). As noted by Williams (1992),

96 information units can propagate and be subjected to selection provided that selection affects
97 them at a greater rate than mutation and drift.

98 It is often suggested that high-fidelity social learning is required for cultural evolution to
99 occur (Enquist et al., 2010; Lewis and Laland, 2012; Andersson, 2013), and a great deal of
100 research has investigated the mechanisms that allow faithful copying and accumulation of
101 improvements (Tomasello, 1999; Eerkens, 2000; Tennie et al., 2009; Dean et al., 2014; Whiten
102 2017). The fidelity of cultural transmission is a problematic concept, however, and it is
103 difficult to measure (Charbonneau, 2020). Several authors have addressed fidelity by
104 investigating transmission chains in laboratory experiments and mathematical models. In such
105 studies, the information is passed from one individual to another along a chain, making it
106 possible to examine factors that may affect the final outcome of the transmission process
107 (Eerkens, 2000; Henrich and Boyd, 2002; Griffiths et al., 2008; Claidière and Sperber, 2007;
108 Muthukrishna et al., 2014; Claidière et al., 2014; Fay et al., 2019; Saldana et al., 2019). A main
109 result is that low transmission fidelity of cultural traits does not prevent the development of a
110 cumulative process at the population level, provided that psychological mechanisms ensure the
111 stabilization of traits through convergent corrections and transformations (Henrich and Boyd,
112 2002; Griffiths et al., 2008; Henrich, 2008; Claidière and André, 2012; Claidière et al., 2014;
113 Truskanov and Prat, 2018; Saldana et al., 2019).

114 Against this background, it should be recalled that the genes themselves are not invariant.
115 Outside of the copying errors that occur in the replication of DNA sequences, a minimal degree
116 of gene mutability is required to ensure evolvability (Keller, 2000). The rate of mutation per
117 base pair at each replication is approximately 10^{-8} in many organisms, while mutation rates per
118 gene are of the order of 10^{-5} – 10^{-6} (Kondrashov and Kondrashov, 2010). As for other contrasts
119 between biological and cultural evolution, differences in the stability of information units
120 appear to be more quantitative than qualitative (Claidière and André, 2012).

121 Most mutations affecting DNA sequences are neutral (Kimura, 1983), and the same may be
122 said for cultural variants, as illustrated by the various alterations of language units. However,
123 while harmful genetic mutations are far more common than beneficial ones in living beings
124 (Fisher, 1930), the opposite likely applies to cultural systems. Here, change is partly guided by
125 intentional agents, providing a bias that favors improvement (Boyd and Richerson, 1985;
126 Kronfeldner, 2007). However, this does not preclude the occurrence of detrimental behaviors
127 such as tobacco consumption or food taboos. Maladaptive beliefs and practices are actually
128 common in human societies (Edgerton, 2000; Richerson and Boyd, 2005; Boyd, 2018).
129 Moreover, failure to transmit a piece of critical knowledge, for instance, could endanger not
130 only the transmission of related skills but even group survival (Henrich, 2000) in the same way
131 that a lethal gene compromises the life of an organism.

132 It has been argued that population size reduction may lead to the disappearance of
133 techniques or practices in human cultures (Henrich, 2004; Powell et al., 2009; d'Errico et al.,
134 2009; Muthukrishna et al., 2014). This has been referred to as the 'treadmill model' which
135 posits that that imperfect transmission is responsible for a constant loss of information from
136 one generation to the next, and that larger populations better compensate for the loss of cultural
137 traits because there are more individuals capable of producing and transmitting innovations
138 (Kline and Boyd, 2010). This view has been challenged on both empirical and theoretical
139 grounds (Andersson and Read, 2016; Collard et al., 2016; Vaesen et al., 2016; Fay et al., 2019).
140 While the repertoire of cultural traits may be influenced by population size under specific
141 conditions, other factors such as enhanced communication systems and environmental risks
142 may also play a major role (Fogarty and Creanza, 2017; Fay et al., 2019). More generally, we
143 lack information on how rates of changes and the number of traits can influence the survival of
144 organisms and social organizations at the evolutionary level.

145 Most models of cultural evolution to date have been based on rates of mutation that were
146 sufficiently low in terms of selection pressures to ensure the continuity of the evolutionary

147 process (Andersson, 2013; Claidière et al., 2014). The present study investigates the full range
148 of mutation probabilities exhibited by biological and cultural changes, from low ($p = 10^{-6}$) to
149 high (10^{-1}) rates of deleterious changes at each generation. It should be noted that these rates
150 may result from copying errors, but in the case of cultural changes they also involve attraction
151 processes. Custom-designed mathematical models express the constraints that govern natural
152 phenomena. They examine the ability of groups of units to persist over generations despite the
153 occurrence of intrinsic or extrinsic adverse events. Intrinsic events are deleterious mutations
154 that can entail group extinction. Extrinsic events are environmental catastrophes (e.g. droughts,
155 wildfires, epidemics) which cause massive population die-offs. We assess how many
156 generations of groups composed of units with different mutation rates survive despite the
157 regular occurrence of such adverse events.

158

159 **2. Model**

160 *2.1. Survival of groups experiencing deleterious mutations*

161 We develop a model based on information units that associate to form groups, and we
162 examine the influence of mutation rates on group longevity. The information units can be
163 viewed as genetic or cultural variants. The groups can be viewed as cells, organisms, complex
164 artefacts or social organizations (Eldredge, 1985; Bouchard and Huneman, 2013). For instance,
165 organisms may be considered as groups constituted by the association of genetic structures,
166 and complex artefacts as sets of cultural variants.

167 The fate of groups is determined by mutations that are liable to affect information units.
168 Two events may occur at regular intervals: (1) a deleterious mutation, meaning that the group
169 is not viable and disappears, or (2) a mutation compatible with other units or no mutation,
170 meaning that the group survives. If the occurrence probability of deleterious mutation is p , the
171 probability that deleterious mutation not occurring is $1 - p$.

172 This model assumes that all information units simultaneously undergo transformative events.
 173 We may thus consider that a group either survives or disappears at regular intervals that we
 174 will call generations. Each group is composed of a fixed number of units (N). The probability
 175 that a group will survive is $(1 - p)^N$, while the probability that it will disappear is $1 - (1 - p)^N$.
 176 The probability of the survival of a group after a number of generations k is therefore
 177 calculated as $P_S(k) = (1 - p)^{Nk}$.

178 Without any further mechanisms, P_S values would rapidly reach 0 in any groups. However,
 179 groups represent integrated wholes that manage to survive perturbations through compensatory
 180 mechanisms that enable them to tolerate the occurrence of deleterious units. To account for this
 181 phenomenon, we introduced a connectivity coefficient α that reflects the intensity of linkage
 182 between units. Since the integration level of a group increases with the number of relationships
 183 between units, it also depends on the value of α and the number of units composing the group.
 184 In other words, the ability of a group to assimilate deleterious units is represented by a function
 185 $F(N, \alpha)$. The probability that a group of n units will undergo assimilated deleterious mutations
 186 is expressed as $p^n F(N, \alpha)$.

187 As the mutations of different units are independent, the number of units becoming
 188 deleterious follows a binomial distribution of N and p parameters. At each generation, the
 189 occurrence "the group survives" corresponds to {no deleterious mutations occur} or {an
 190 assimilated deleterious mutation occurs} or {2 assimilated deleterious mutations occur} or { N
 191 assimilated deleterious mutations occur}. As these events cannot occur simultaneously, the
 192 probability of group survival at each generation is the sum of the probabilities of these events:

193

$$194 \quad P_S(1) = (1 - p)^N + \left[\sum_{j=1}^N C_n^j p^j (1 - p)^{n-j} \right] F(N, \alpha)$$

195

196 When a group is alive at the $k - 1^{\text{st}}$ generation, we consider all integrated units with
 197 deleterious mutations to be compatible with their group when they attain the k^{th} generation. We
 198 therefore assume that separate generation events are independent. The probability of survival
 199 of a group at k generations is thus:

200

$$202 \quad P_S(k) = [(1 - p)^N + [1 - (1 - p)^N] F(N, \alpha)]^k$$

201 (1)

203 In the absence of a process ensuring the integration of deleterious units, $F(N, \alpha) = 0$, and
 204 $P_S(k)$ would reach 0 when k increases. In the contrary case of groups assimilating all the
 205 deleterious mutations, then $F(N, \alpha) = 1$ and $P_S(k) = 1$ for every k value. More generally,
 206 $F(N, \alpha)$ is a growing function of both N and α , and varies from 0 to 1. We assume that:

207

$$209 \quad F(N, \alpha) = \frac{\alpha N}{1 + \alpha N}$$

208 (2)

210

211 From equations (1) and (2), the probability of survival is computed as:

212

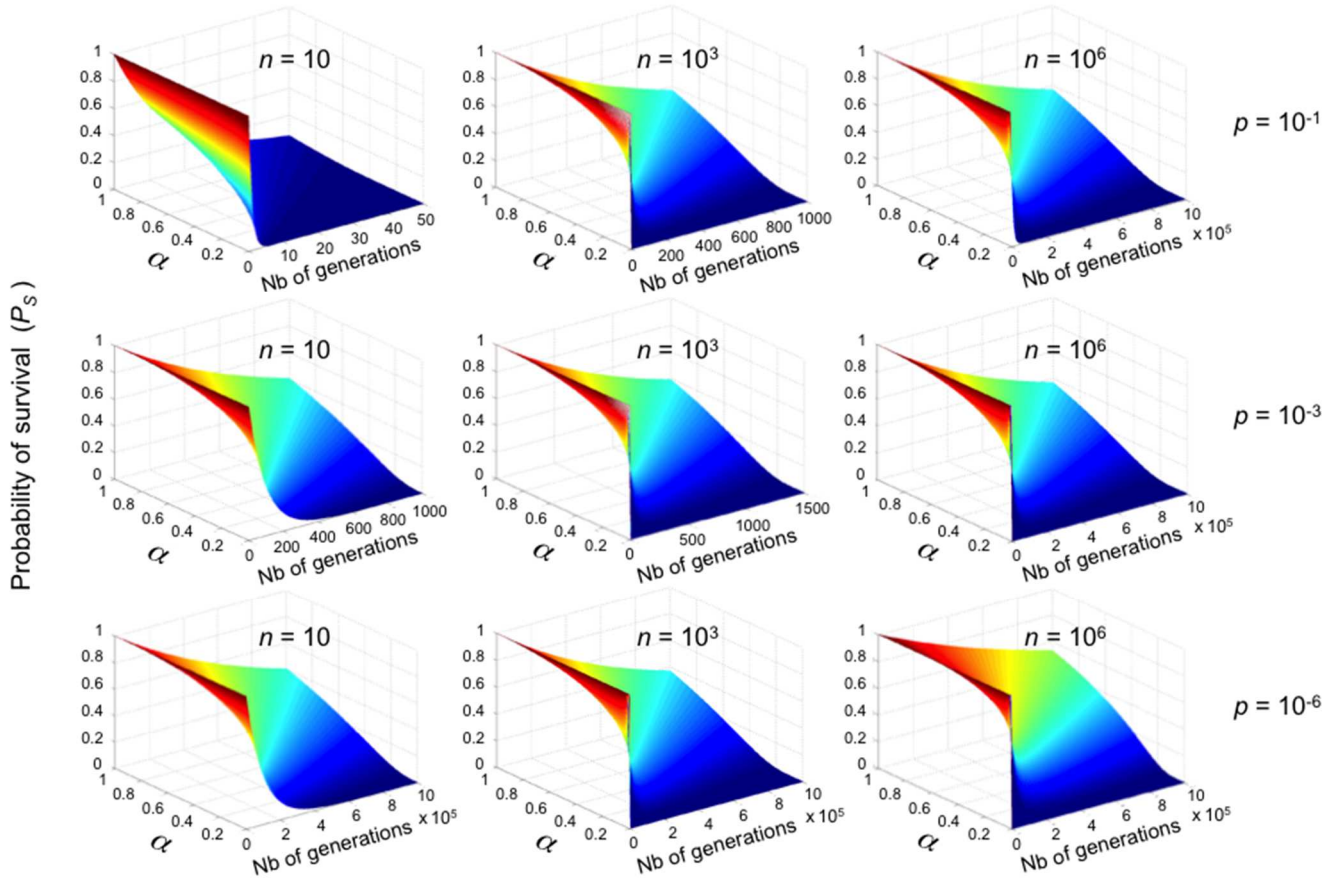
$$213 \quad P_S(k) = \left[(1 - p)^N + [1 - (1 - p)^N] \frac{\alpha N}{1 + \alpha N} \right]^k$$

214 (3)

215

216 Graphs drawn from this function are presented in Fig. 1. They show changes in P_S as a
 217 function of α and k for three values of p (10^{-1} , 10^{-3} , 10^{-6}) and N (10, 10^3 , 10^6). In most
 218 conditions, α must reach a minimum value of 0.5 for groups to persist over a significant
 219 number of generations. However, for mutation rates of 10^{-1} , small groups (10 units) disappear
 220 after a few dozen generations, whatever the value of α . When a rather high probability of

221 deleterious mutation (10^{-1} , 10^{-3}) is combined with limited group size (10 , 10^3), groups do not
 222 survive beyond thousands of generations. By contrast, 20–40% of groups are able to persist for
 223 at least one million generations when mutation rates are low (10^{-6}) and /or group size is large
 224 (10^6) (Fig. 1).



225
 226 **Fig. 1.** Probability of group survival (P_s) as a function of the connectivity coefficient (α) and
 227 the number of generations (k), for different group sizes (N) and probabilities of deleterious
 228 mutations (p). Color changes range from high P_s values (red) to low P_s values (blue).
 229

230 Based on previous equations, we calculated the mean number of surviving generations $\langle k \rangle$
 231 to express the influence of the parameters α , p and N :

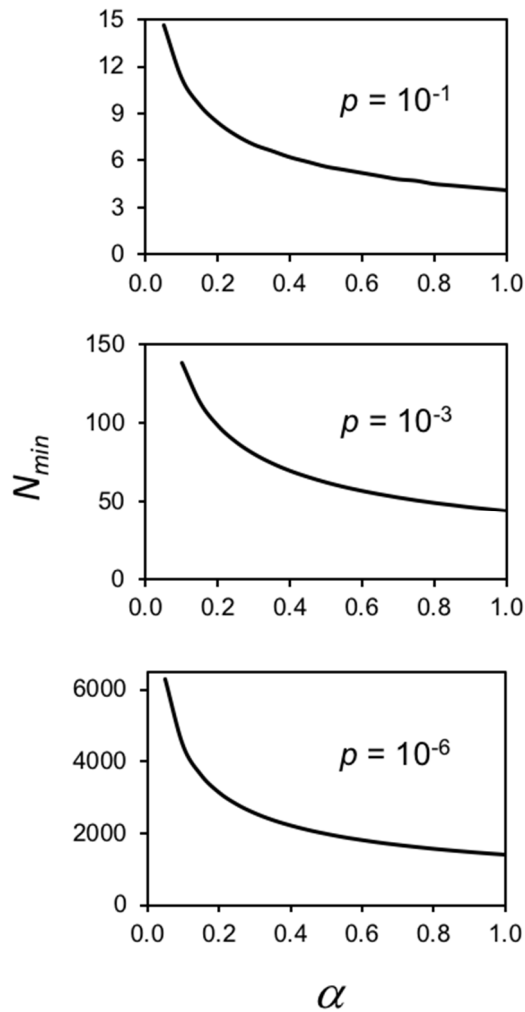
232

234
$$\langle k \rangle = \frac{1 + \alpha N}{1 - (1 - p)^N}$$

233

(4)

235 This equation indicates that $\langle k \rangle$ linearly increases with α , and monotonically decreases
 236 with p , but shows that some N values minimize $\langle k \rangle$. These values, symbolized as N_{min} , are the
 237 N values that nullify the derivative of $\langle k \rangle$ as a function of N . Figure 2 shows that N_{min} rapidly
 238 decreases when α increases. As α is a multiplication factor, its influence is weaker than that of
 239 p , which follows a power function. The magnitude range of N_{min} corresponds to the magnitude
 240 range of $1/p$, independently of the value of α . Moreover, N_{min} increases significantly when p
 241 decreases, meaning that the lower the probability of deleterious mutation, the higher the mean
 242 number of surviving generations will be (Fig. 2).
 243



244
 245 **Fig. 2.** Group sizes (N_{min}) which minimize the mean number of surviving generations as a
 246 function of the connectivity coefficient (α) for three probabilities of deleterious mutations (p).
 247

248 2.2. Survival of groups experiencing extreme environmental events

249 In the preceding section we considered how entities exhibiting different integration levels
250 cope with different rates of deleterious mutations. We will now examine the resilience of such
251 entities when facing extreme environmental events that produce massive population die-offs.

252 Environmental events are a binary variable. They occur randomly and independently for
253 each group with a probability p_{env} at each new generation. We explored three p_{env} values,
254 namely 10^{-2} , 10^{-3} and 10^{-4} , corresponding to one event in 100, 1 000 or 10 000 generations,
255 respectively. Assuming that an environmental event destroys 99% of groups in a population,
256 we used Monte Carlo simulations to investigate the fate of populations initially composed of
257 $N_0 = 1\ 000$ groups. At each generation, a group has a probability of survival $P_S(k)$. Equation
258 (3) was used to calculate how many groups are still alive at k generations with three values for
259 p (10^{-1} , 10^{-3} , 10^{-6}), N (10, 10^3 , 10^6) and α (0.2, 0.5, 0.8), thus obtaining the expected numbers
260 of surviving groups. Computations were performed using Matlab software (version 9.1, The
261 MathWorks Inc, Natick, MA).

262 Results are presented in Figure 3. It appears that, compared to other parameters, the
263 connectivity coefficient α has little effect on the number of generations produced by groups.
264 Also, groups cannot survive for more than hundreds or thousands of generations for any p and
265 N values when extreme events are frequent ($p_{env} = 10^{-2}$ or 10^{-3}). When extreme events are rare
266 ($p_{env} = 10^{-4}$), the mean number of generations ranges between 10 000 and 40 000 for $N = 10^6$
267 and/or $p = 10^{-6}$. It remains under one thousand in all other cases.

268

269 2.3. Survival of growing groups

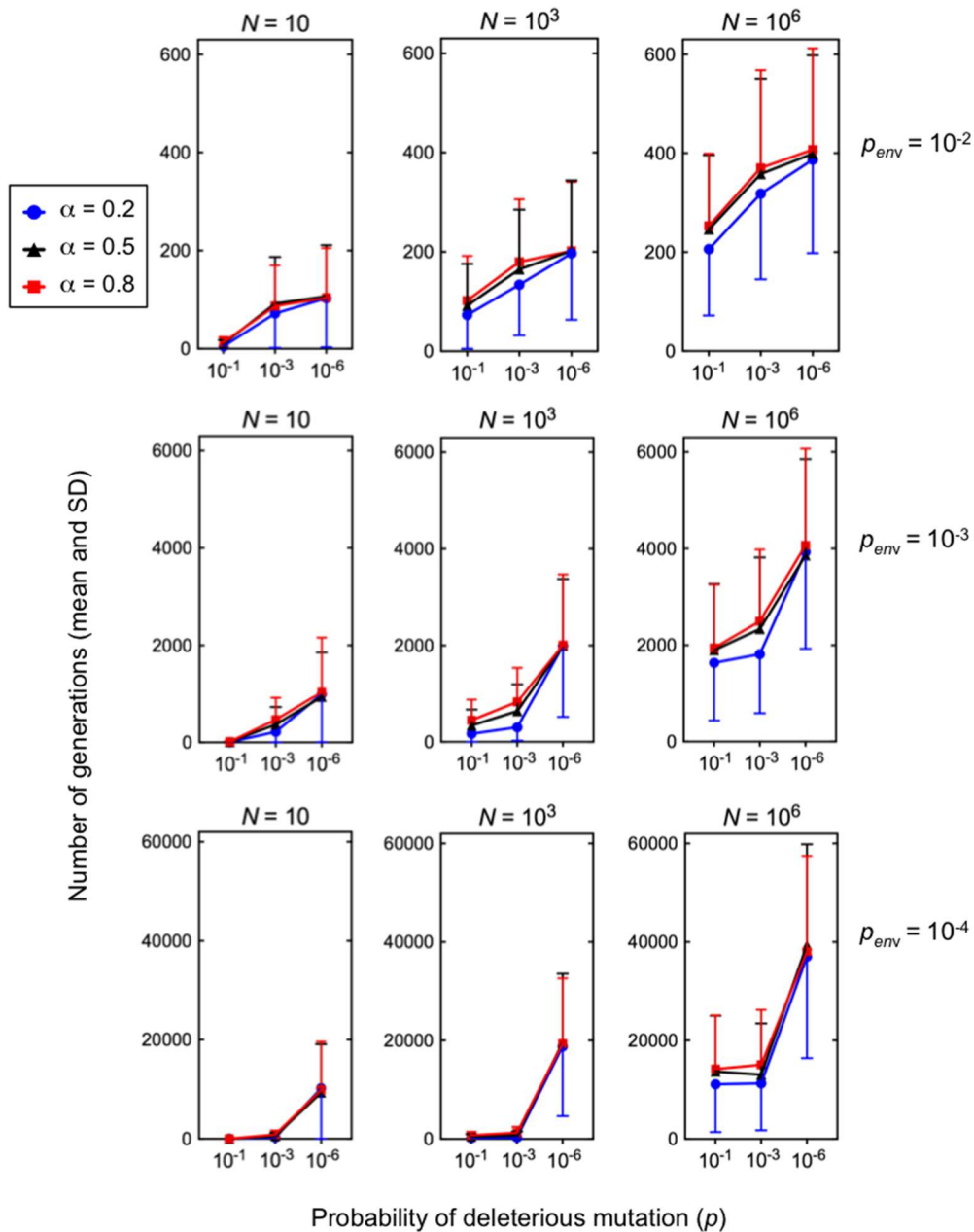
270 In the previous model the size of each group was kept stable to account for the fact that
271 groups of limited size could not persist for a large number of generations. However, evolving
272 groups can grow, possibly extending their longevity. Here, we assume that the number of units

273 per group increases with the number of generations. If the increase from one generation to the
 274 next is constant, the growth rate β is obtained by:

275

$$276 \frac{N(k+1)}{N(k)} = \beta$$

277



278

279 **Fig. 3.** Fate of groups of invariant size undergoing extreme environmental events assessed with
 280 Monte Carlo simulations for samples of 1 000 groups. Mean number of generations reached by
 281 groups as a function of connectivity coefficient (α), group size (N), probability of extreme
 282 environmental events (p_{env}) and probability of deleterious mutations (p).
 283

284 When β is higher than 1, more units appear than disappear, N is modified at each generation
 285 and the group grows. If the initial number of units $N_0 = N(0)$, then:

286

$$287 \quad N(k) = \beta^k N_0$$

288

289 and from equation (3) we obtain:

290

$$291 \quad P_S(k) = P_S(k-1) \times \left[\frac{(1-p)^{\beta^{k-1}N_0} + \alpha\beta^{k-1}N_0}{1 + \alpha\beta^{k-1}N_0} \right]$$

$$292 \quad (5)$$

293 where i is the generation index, and $k-1$ accounts for the fact that the transformation of a group at a
 294 given generation influences its survival at the next generation.

295

296 If a group grows from the duplication of units at each generation, the mean growth rate β
 297 can be calculated as a function of the duplication probability p_d of a unit. If there are no
 298 deleterious mutations when passing from generation k to $k+1$, we can consider that

299

$$300 \quad N(k+1) = N(k) + D(k)$$

301 where $D(k)$ is the number of units that have been duplicated; as the duplication of different units are
 302 independent, $D(k)$ follows a binomial law of parameters $N(k)$ and p_d .

303

304 As

305

$$306 \quad \beta = \frac{N(k+1)}{N(k)} = \frac{N(k)+D(k)}{N(k)},$$

307

308 then

309

310 $N(k) \beta = N(k) + D(k).$

311

312 By considering the conditional expectation, knowing $N(k)$ we can write:

313

315 $\beta = 1 + p_d$

314 (6)

316

317 Equations (5) and (6) can be used to calculate the probability of survival of a group as a
318 function of the duplication probability p_d . As in the previous section, Monte Carlo simulations
319 were used to investigate the fate of populations composed of 1 000 groups and experiencing
320 environmental events liable to destroy 99% of them at each generation. We explored three
321 values of the duplication probability p_d : 10^{-2} , 10^{-3} and 10^{-4} . The value of the connectivity
322 coefficient α was set at 0.5, and the expected number of surviving groups at k generations was
323 calculated for three values of p (10^{-1} , 10^{-3} , 10^{-6}), N_0 (10, 10^3 , 10^6) and p_{env} (10^{-2} , 10^{-3} , 10^{-4}). For
324 each generation we implemented the occurrence of environmental events then the duplication.
325 Computations were performed with *R 3.4.0* (R Core Team, 2017). The number of units of a
326 group that survived for a high number k of generations could be very large when few
327 environmental events occurred. In these situations, it became impossible to calculate $D(k)$ due
328 to the limitations of computer calculation. We considered that a group could not become
329 extinct if the computation of $D(k)$ was no longer possible.

330 The percentages of surviving groups are displayed in Table 1. They reveal that populations
331 of groups generally disappear rapidly when the probability of duplication is low or medium (p_d
332 = 10^{-4} or 10^{-3}) and/or the probability of environmental events is high or medium (p_{env} = 10^{-2}
333 or 10^{-3}), regardless of initial group size and the probability of deleterious mutations. In contrast,
334 most groups in a population survive if p_d is high (10^{-2}) and associated with large initial group

335 size ($N = 10^3$ or 10^6); this is also true for medium p_d values (10^{-3}) when associated with low
336 frequency events ($p_{env} = 10^{-4}$), and for medium and high p_d values (10^{-3} , 10^{-2}) when associated
337 with a low probability of deleterious mutations ($p = 10^{-6}$). The examination of the mean
338 number of generations attained by the groups that died out confirms such observations (Table
339 1); they could by and large only live on beyond 10 000 generations if environmental events
340 were infrequent ($p_{env} = 10^{-4}$), associated with a large initial group size ($N = 10^6$) or low
341 probability of deleterious mutations ($p = 10^{-6}$). Finally, it may be noted that high p_d values (10^{-2})
342 associated to low frequencies of environmental events ($p_{env} = 10^{-3}$ or 10^{-4}) allowed a
343 significant proportion of small initial size groups ($N = 10$) to survive and grow, even for
344 moderate rates of mutations ($p = 10^{-3}$) (Table 1).

Table 1

Fate of growing groups undergoing extreme environmental events assessed with Monte Carlo simulations for sample of 1 000 groups (connectivity coefficient $\alpha = 0.5$): percentage of surviving groups (and mean number of surviving generations \pm SD for extinct groups in brackets) as a function of initial group size (N), probabilities of duplication (p_d), extreme environmental events (p_{env}) and deleterious mutations (p).

N	p_d	$p_{env} = 10^{-2}$			$p_{env} = 10^{-3}$			$p_{env} = 10^{-4}$		
		$p = 10^{-1}$	$p = 10^{-3}$	$p = 10^{-6}$	$p = 10^{-1}$	$p = 10^{-3}$	$p = 10^{-6}$	$p = 10^{-1}$	$p = 10^{-3}$	$p = 10^{-6}$
10	10^{-4}	0% (9 \pm 8)	0% (87 \pm 84)	0% (99 \pm 96)	0% (10 \pm 9)	0% (368 \pm 363)	0% (982 \pm 961)	0% (10 \pm 9)	0% (579 \pm 568)	0% (10540 \pm 11902)
	10^{-3}	0% (10 \pm 8)	0% (86 \pm 86)	0% (97 \pm 95)	0% (10 \pm 8)	0% (384 \pm 381)	0% (1091 \pm 1414)	0% (10 \pm 9)	0% (545 \pm 536)	64% (29270 \pm 22783)
	10^{-2}	0% (10 \pm 9)	0% (91 \pm 112)	0% (110 \pm 125)	0% (11 \pm 11)	18% (876 \pm 1307)	68% (2804 \pm 2008)	0% (10 \pm 9)	36% (1057 \pm 1067)	99% (2469 \pm 359)
10^3	10^{-4}	0% (93 \pm 88)	0% (162 \pm 120)	0% (198 \pm 140)	0% (341 \pm 345)	0% (619 \pm 554)	0% (2018 \pm 1475)	0% (498 \pm 506)	0% (781 \pm 789)	0% (23020 \pm 19639)
	10^{-3}	0% (89 \pm 80)	0% (159 \pm 127)	0% (196 \pm 142)	0% (428 \pm 584)	0% (691 \pm 694)	0% (2342 \pm 1937)	7% (2910 \pm 8224)	9% (4297 \pm 10962)	89% (33970 \pm 15613)
	10^{-2}	0% (108 \pm 114)	0% (188 \pm 163)	0% (239 \pm 202)	48% (2970 \pm 1130)	55% (1896 \pm 1562)	89% (3105 \pm 1500)	81% (1635 \pm 760)	80% (1641 \pm 772)	99.9% (2025 \pm 223)
10^6	10^{-4}	0% (230 \pm 139)	0% (361 \pm 184)	0% (406 \pm 201)	0% (1853 \pm 1307)	0% (2367 \pm 1508)	0% (4033 \pm 2047)	0% (17240 \pm 14598)	0% (16800 \pm 15024)	0% (40710 \pm 24979)
	10^{-3}	0% (237 \pm 150)	0% (361 \pm 190)	0% (392 \pm 199)	0% (2289 \pm 1794)	0% (2739 \pm 2057)	0% (4310 \pm 2558)	86% (21600 \pm 11883)	87% (21960 \pm 10518)	98% (26100 \pm 12777)
	10^{-2}	0% (310 \pm 223)	0% (388 \pm 237)	0% (445 \pm 274)	95% (2099 \pm 1051)	94% (2124 \pm 1068)	99% (2253 \pm 1226)	100%	100%	100%

344 **3. Discussion**

345 A primary feature of life is its ability to persist across generations despite the occurrence of
346 adverse events. Each living being is the last link in an uninterrupted evolutionary chain, and
347 the same can be said for cultures and cultural evolution. By implementing the survival of
348 groups composed of abstract units in a mathematical model, we were able to calculate for how
349 many generations such groups can survive according to the mutation rates of units.

350 In this study, groups were attributed a varying coefficient of connectivity that enabled
351 them to survive despite the occurrence of deleterious mutations. We consistently found that
352 the coefficient had to reach a substantial value for groups to survive. This confirms the
353 necessary occurrence of integrative processes in the building of both phenotypic structures
354 (Raff, 1996; West-Eberhard, 2003) and cultural structures (Lévi-Strauss, 1958). However,
355 integration alone was not sufficient for group survival: groups that were composed of units of
356 limited number that were subjected to high mutation rates did not persist for more than
357 thousands of generations. By contrast, a significant proportion of groups were able to survive
358 through more than one million generations if mutation rates were low (10^{-6}) and/or group size
359 was large (10^6). This is a main conclusion provided by the model. It could be expected that
360 low mutation rates would lead to long chains of reproduction, as this fits the conditions of
361 biological evolution, but the second outcome was less expected: frequent changes in cultural
362 variants did not prevent groups of units from surviving over time, provided that they were
363 composed of large numbers of units. These results run counter to a main assumption in the
364 field of cultural evolution theory that the transmission of human cultures requires a high
365 stability of cultural traits (Claidière et al., 2018; Truskanov and Prat, 2018; Saldana et al.,
366 2019).

367 In our model, the mean number of surviving generations increased with the coefficient of
368 connectivity and decreased with mutation rates. We also found that this mean number was

369 minimized for certain sizes of groups. This means that groups of units have a higher chance of
370 survival when the initial number of units per group is greater than a size that minimizes the
371 mean number of surviving generations. This mean number could correspond to a critical
372 threshold generated by a strong Allee effect (Courchamp et al., 2008). The Allee effect is
373 caused by the integrative action of the connectivity coefficient, which confers higher
374 resilience to populations. Interestingly, lower probabilities of deleterious mutations were
375 associated with higher mean numbers of surviving generations. From an evolutionary
376 perspective, this means that groups undergoing cultural changes can initially be composed of
377 as few as ten units; it should be noted however that in the previous results of the model,
378 groups of this size did not persist for long. By contrast, groups undergoing biological changes
379 have to choose between two opposing strategies: either start out with at least two thousand
380 units to avoid going below the critical threshold, and then grow; or start with small group size
381 and avoid growing because survival rates decrease when group size remains below critical
382 threshold. In the second case, this means that if large size confers an advantage, groups should
383 be able to overcome this handicap.

384 In a second step, we implemented in the model the occurrence of extreme environmental
385 events that could destroy 99% of groups in a generation. Such catastrophes leading to massive
386 population die-offs have occurred periodically in evolutionary history, both in animals and
387 humans (Ameca y Juárez et al., 2012; Gurven and Davison, 2019). Our results show that the
388 connectivity coefficient had little influence on the probability of group survival compared to
389 the effect of other parameters such as group size, mutation rate and probability of extreme
390 events. This was due to the fact that the additional effect of this coefficient was weaker in
391 groups composed of higher numbers of units. We found that groups did not survive for more
392 than hundreds or thousands of generations for any p and N values when extreme events were
393 frequent, whereas they could survive for tens of thousands of generations when $N = 10^6$

394 and/or $p = 10^{-6}$ if the probability of extreme events remained low (10^{-4}). This effect of group
395 size and mutation rate was consistent with previous results for groups in the absence of
396 environmental catastrophes: groups survived numerous generations if mutation rates were low
397 and/or group size was large.

398 In a third step, we allowed information units to duplicate at each generation, which
399 provided groups with growth. This growth reflects the demographical increase allowed by
400 reproduction in living beings. In cultural evolution, growth can also occur through the
401 development of exchange networks that increase the effective size of pools of variants
402 (Muthukrishna et al., 2014; Creanza et al., 2017; Fogarty and Creanza, 2017). As an outcome,
403 all groups rapidly became extinct when the probability of extreme events was medium to high,
404 and rates of duplication medium to low. In particular, all the groups that were initially
405 composed of ten units and were submitted to mutation rates typical of cultural change (10^{-1})
406 disappeared after an average of ten generations. By contrast, groups survived longer when
407 medium and high rates of duplication were combined with a large initial group size, a low
408 probability of extreme events, or a low rate of deleterious mutations. When all these
409 conditions were met, very few groups disappeared in stochastic simulations. While this could
410 have been expected for deleterious mutation rates typical of genetic units, it is noteworthy that
411 between half and all the groups composed of units mutating at the rate of cultural change also
412 avoided extinction, provided that group size was sufficient and duplication rate was frequent
413 enough to counteract the consequences of environmental catastrophes.

414

415 **4. Conclusion**

416 Most previous studies of cultural evolution have focused on the transmission and spread of
417 advantageous traits. In particular, they have used the treadmill model to investigate the causes
418 responsible for the size of repertoires of cultural variants. This has shown that group size can

419 affect the number of variants through the proportion of individuals capable of transmitting
420 them (Henrich, 2004; Kline and Boyd, 2010; Andersson and Read, 2016), but also that
421 communication systems and environmental conditions can play an important role (Creanza et
422 al., 2017; Fogarty and Creanza, 2017; Fay et al., 2019), and that high transmission fidelity can
423 enhance the longevity of cultural variants (Enquist et al., 2010; Lewis and Laland, 2012;
424 Andersson, 2013). Our approach provides additional information by modelling the effects of
425 deleterious mutations and environmental catastrophes on the persistence of groups over
426 generations. Our overall results reveal that large groups of units with high mutation rates can
427 survive over many generations, regardless of the mode of transmission. This means that the
428 conditions for high transmission fidelity and stability can be relaxed for larger groups.
429 However, the question arises as to how large groups could be formed in the first place if small
430 groups were to die out when mutation rates are high. We found that a significant proportion of
431 small initial size groups survived over generations when rates of mutations were moderate,
432 provided their units could duplicate with a probability of 10^{-2} at each generation. This latter
433 value was the highest value considered in our study, but it actually remains relatively low. We
434 can expect that if small groups were allowed to grow at significantly higher rates for a period
435 of time, this would be sufficient to enable them to grow to larger sizes and survive over many
436 generations.

437 This modelling is a first explorative attempt to link processes of biological and cultural
438 changes through differential paces of changes. It sets out the conditions under which
439 organisms and organizations can persist along generations, and brings evidence that pool size
440 plays a significant role in cultural evolution. The high level of abstraction of our models does
441 however have certain limitations. Our results are valid for two-level structures with varying
442 rates of mutation. For a better reflection of real-life context, a further study should investigate
443 three-level structures in which information units associate to constitute individuals who in

444 turn associate to give rise to populations or pools of cultural variants. This re-introduction of
445 the individual level in modelling will make it possible to distinguish between the effects of
446 the numbers of units per group and those of demographic dynamics. Future research should
447 investigate the role of competition and selective processes on the evolution of populations
448 composed of individuals with varying levels of integration, and with varying mutation rates in
449 information units.

450

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