

# Cultural stability without copying

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## Abstract

What causes cultural stability? Culture can be studied as an evolving system, and the comparison between biological and cultural evolution has inspired a productive research agenda in which cultural stability is commonly attributed to the existence of mechanisms of high-fidelity cultural transmission. Other researchers have argued that no such copying processes are necessary to explain cultural stability, and that stability can also emerge as a by-product of convergent transformation (in which an item causes the production of another item whose form tends to deviate from that of the original item in a non random way). To investigate this issue, we present a series of stochastic simulation models of cultural evolution that make no prior assumptions about the type of processes by which cultural units propagate through a population. Results show that cultural stability can emerge and be maintained by convergent transformation alone, even in the absence of any form of copying or selection process. We also show that high-fidelity copying and convergent transformation are, contrary to some previous arguments, not opposing forces, and can in fact jointly contribute to cultural stability. Finally, we analyse how convergent transformation and high-fidelity copying can have different evolutionary signatures at the level of the population, and hence how their differing effects can be distinguished in the empirical record. Our models can be read as formalisations of Cultural Attraction Theory.

## 1 Introduction

2 Anthropologists have long documented the richness and diversity of human cultures (Bene-  
3 dict 1934, Murdock 1981, Brown 1991, Ember et al. 1998), and biologists have observed  
4 and described cultural traditions in several non-human species (e.g. Whiten et al. 1999,  
5 Rendell & Whitehead 2001, Laland & Galef 2009, Danchin et al. 2018, Aplin 2019). Re-  
6 searchers from many disciplines have emphasised the critical role that culture plays in  
7 the ecological success of humans (Richerson & Boyd 2005, Henrich 2016). However, in  
8 explaining culture, a critical question remains unresolved: what are the possible causes  
9 of cultural stability? This is important because without some degree of stability nothing  
10 would ever be recognised as cultural in the first place. Do humans, or other species, possess  
11 psychological mechanisms of inheritance able to copy cultural items—recipes, technology,  
12 belief systems, word meaning, and so on—with a degree of fidelity high enough to produce  
13 stable traditions? Are such mechanisms necessary to explain long-term cultural persis-  
14 tence or can cultural stability emerge as a byproduct of communication, mindreading,  
15 and other forms of ordinary social interaction?

16 Here we present a series of stochastic simulation models to investigate the different ways  
17 in which stability can emerge in an evolutionary system, such as culture. We focus in

18 particular on the role of convergent transformation: the possibility that one item causes  
19 the production of another item whose form tends to deviate from that of the original  
20 item in a non random way. Some formal models examine how convergent transformation  
21 and selection can interact with one another (Claidière & Sperber 2007, Claidière 2009,  
22 Claidière et al. 2018). Other models show how convergent transformation can support  
23 the evolution of social learning (Boyd & Richerson 1995, 1996) or have examined how  
24 convergent transformation influences the subsequent co-evolution of culture and cognition  
25 (Griffiths et al. 2008, Kirby et al. 2007, Thompson et al. 2016). Complementary to these  
26 research agendas we investigate the contribution that convergent transformation can make  
27 to the emergence of stable cultural traditions. We contrast convergent transformation  
28 with other hypothesised causes of cultural stability, in particular those inspired by the  
29 comparison with biological evolution, such as faithful transmission (copying), random  
30 error, and model selection.

31 We show that: (1) Cultural stability can emerge and be maintained by virtue of conver-  
32 gent transformation alone, in the absence of any form of high-fidelity copying or selection  
33 process. This effect is robust, not idiosyncratic, and occurs under a wide range of con-  
34 ditions; (2) As processes, copying and convergent transformation can be complementary  
35 (rather than opposite) in bringing about cultural stability, and convergent transforma-  
36 tion, even if weak, drives the stabilization; (3) While both selective high-fidelity copying  
37 and convergent transformation can produce stable cultural traditions (either separately  
38 or jointly), the underlying processes can be empirically distinguished through different  
39 evolutionary signatures at the level of the population. Collectively these findings suggest  
40 that cultural stability can emerge even in the absence of any biological adaptation for  
41 culture. They also provide an important tool for empirical research, because they identify  
42 a way to distinguish between the effects of different sources of stability in specific cases.  
43 These models are highly general, allowing us to investigate the causes of cultural stability  
44 with very few prior commitments about either (i) the granularity of cultural units, or (ii)  
45 the processes by which cultural units propagate through a population.

46 In the next section we describe the general framework that applies to all our models. We  
47 then describe each of our specific models in detail, and their results. Code for all models  
48 is available in an Open Science Framework repository at <https://osf.io/yncws/>

## 49 **General methods**

50 We consider a population of  $N$  items. (In Study 1 and Study 2,  $N = 100$ . In Study 3,  
51  $N = 10; 100; 1000$ .) At the beginning of each simulation, items are randomly placed in  
52 a continuous bidimensional (square) space with coordinates in the range  $(-1, 1)$ . This is  
53 effectively a variation space (inspired by Sperber 1996), with each axis representing an  
54 arbitrary dimension of a cultural item (e.g., size and width of an arrow-head). At each  
55 time step, the original population of items is replaced by a population of new items of  
56 equal size  $N$ . We study the evolution of the location of these items over time.

57 The location of each item at time  $t + 1$  is determined by applying a stochastic transforma-  
58 tion function that takes the location of an item at time  $t$  as input. The process proceeds  
59 through three stages:

- 60 1. *Sample population.* The population at time  $t$  is sampled in one of two different ways,  
61 either randomly or with bias. The sampled item's location is then used as input for

62 the transformation function.

63 2. *Apply transformation function.* A transformation function is applied which modifies  
64 the input location in either a convergent or a random way.

65 3. *Iterate & measure.* The transformations described above determine the output of  
66 the simulation at time  $t$ . This output is then used as the input for the same process  
67 at time  $t + 1$ . Measures of stability and similarity are taken at this stage.

## 68 Sample population

69 For each item at  $t + 1$ , the population at  $t$  is sampled in one of two ways, either random  
70 or biased.

71 • *Random sampling.* One item from the population at time  $t$  is sampled at random  
72 and used as input for the transformation function.

73 • *Biased sampling.* Two items from the population at time  $t$  are sampled at random,  
74 and whichever is closest to the origin  $(0, 0)$  (the centre of the space) is used as input  
75 for the transformation function. This effectively represents a selection process in  
76 which variants closer to the origin are fittest. The overall space can be understood,  
77 in this case, as a continuous, smooth fitness landscape with a single peak at the  
78 origin.

## 79 Apply transformation function

80 New items undergo one of two transformation functions: random or convergent. For  
81 each new item, both its distance from, and angle relative to, its input are determined by  
82 probability distributions, as described below (see also Figure 1).

83 • *Random transformation.* The position of the item at  $t + 1$  is equal to the position  
84 of its input modified by a distance  $\delta_r$  and an angle  $\beta_r$ :

85 –  $\delta_r$  is drawn from a lognormal distribution in the range  $(0, k)$ , where  $k$  is a  
86 parameter of the simulation.  $k$  can be thought of, intuitively, as the magnitude  
87 of ‘copying error’ of a mechanism of transmission.

88 –  $\beta_r$  is drawn from a uniform distribution in the range  $(-\pi, \pi)$  with 0 oriented  
89 towards the origin. Because this distribution is uniform, the angle between an  
90 item at time  $t + 1$  and its input at time  $t$  is random.

91 • *Convergent transformation.* The position of the item at time  $t + 1$  is equal to the  
92 position of its input at time  $t$  modified by a distance  $\delta_b$  and an angle  $\beta_b$ :

93 –  $\delta_b$  is drawn from a uniform distribution in the range  $(0, 2d)$ , with  $d$  being the  
94 distance of the input to the origin. This means that the distance between an  
95 item and its input is a function of the distance between the input and the  
96 origin. The closer an input is to the origin, the smaller the distance between  
97 it and the item at  $t + 1$  will be.

98 –  $\beta_b$  is drawn from a normal distribution in the range  $(-\pi, \pi)$  with  $\sigma = 1$  and  
99  $\mu = 0$ , and with 0 oriented towards the origin. Because this distribution is  
100 normal, the direction between an item at time  $t + 1$  and its input at time  $t$  is

101 not random. Instead, items are most likely to be located closer to the origin  
102 rather than away from it.

103 In case the final position of an item results out of the boundaries of the variation space,  
104 the transformation function is repeated until the item falls within it (different ways to  
105 handle these occurrences do not change our results, also because they are relatively rare).

106 These various functions reflect empirical aspects of the different processes by which sta-  
107 bility might be achieved. For random transformations,  $\delta_r$  is defined as a lognormal dis-  
108 tribution to reflect the idea that while most copying errors are small, exact replication  
109 is a marginal case; and  $\beta_r$  is defined as a uniform distribution to reflect the idea that  
110 copying errors are undirected. These two ideas are both common in the cultural evolu-  
111 tion literature. For convergent transformation,  $\delta_b$  is defined in terms of  $d$  to reflect the  
112 idea that similarity between items and their inputs is not a fixed quantity, as it usually is  
113 with copying-errors, but traits tend to transform more or less over time in virtue of their  
114 properties (Sperber 2000, Mesoudi & Whiten 2004, Claidière, Scott-Phillips & Sperber  
115 2014), in our case represented by their position in the variation space.

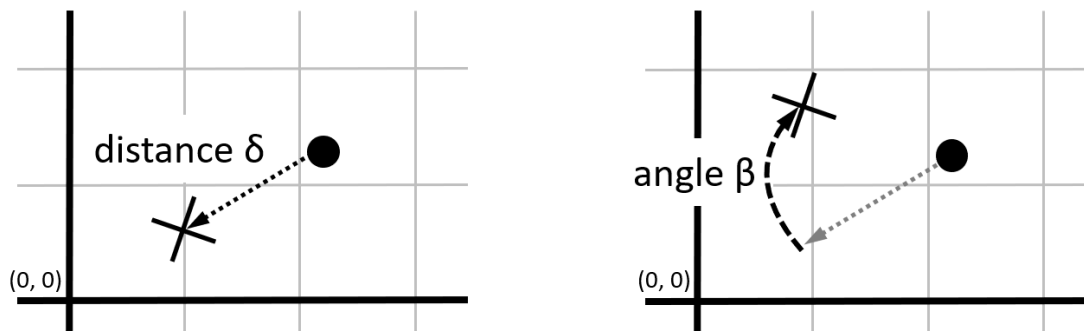


Figure 1: **Transformation function.** The input is depicted with a filled circle and the output with a cross. The transformation function determines a distance and an angle (see main text). The distance,  $\delta$ , is measured absolutely (left panel), whereas the angle,  $\beta$ , is measured relative to a straight line between input and origin (right panel).

## 116 Iterate & measure

117 Items of time step  $t$  are removed, and the items from time step  $t + 1$  serve as the inputs  
118 for the next time step. Once the location of each item at  $t + 1$  is set, we measure two  
119 aspects of the evolution of the system: stability and similarity.

120 • *Stability.* We take two types of measures relevant to stability: change in mean trait  
121 value and spread of the population .

122 – The mean trait value of the population (first moment) is, in evolutionary bi-  
123 ology, the most common measure used to represent whether a population is  
124 evolving or not (Hartl & Clark 1997). We take two types of measures of sta-  
125 bility based on mean trait value. First, we measure the change in mean trait  
126 value over time by calculating the barycentre of the population and then cal-  
127 culating the Euclidean distance between the barycentres at two different time

128 steps. These two time steps are either 1 time step apart, to measure short-term  
129 stability, or 100 time steps apart to measure longer-term stability. Second, we  
130 measure longer-term stability by measuring whether the population remains  
131 in the same location or instead drifts. To do this, we measure the distance  
132 between the barycentre as it is measured at time step 100 and the barycentre  
133 every 1000 time steps (1000, 2000, etc). We choose time step 100 as a reference  
134 because by this time the populations have generally converged upon a stable  
135 state (see Study 1).

136 – The spread of the population is a measure of the clustering of the items at  
137 a given time step. This is defined as the average distance of all items from  
138 the barycentre of the population. This measures the statistical distribution of  
139 variant in a population (second moment). This is relevant to cultural stability  
140 because it determines how scattered are items in the variation space.

141 Both types of measure (spread and change in mean trait value) are important as  
142 they can vary independently. For example, in cases of, say, disruptive selection, or  
143 stabilizing selection, the mean trait value could remain the same while the spread  
144 would change. In other words, stability is best understood in light of both spread  
145 and change in mean trait value.

146 • *Similarity.* The degree of similarity between an item and its input is measured as  
147 the Euclidean distance between them. Similarity at the level of the population is  
148 then the mean of these distances for all items in the population. This measure  
149 is used in Study 3 only, where we investigate whether different possible causes of  
150 stability have different evolutionary signatures at the level of the population.

151 This approach is highly general in two key ways. First, although for simplicity we referred  
152 to items and their inputs, the items could be seen as (i) individuals with cultural traits  
153 (with parent individuals as inputs), (ii) populations of cultural traits (with one trait being  
154 the ‘cultural model’ for another), or (iii) token expressions of cultural items (with tokens  
155 at one time step influencing the production of tokens at a later time step). Second,  
156 because both the sampling and transformation functions are defined strictly in terms of  
157 their effects, the model is agnostic about how these functions are realised materially, i.e.,  
158 about what sorts of processes are involved. Two examples are: (i) biased sampling can  
159 be thought of as a selection process acting on cultural trait with differential fitness, or  
160 as representing how individuals differentially acquire information from others based on  
161 factors such as prestige or success (i.e., model-based social learning strategies Hoppitt &  
162 Laland 2013, Kendal et al. 2018) (ii) convergent transformation can be thought of as a  
163 prior or cognitive bias in the reconstruction of cultural traits (Miton et al. 2015, Morin  
164 2016, Claidière et al. 2018) or as an ecological bias (Schillinger et al. 2014).

## 165 **Study 1: Stability without copying or selection?**

166 We first investigate the different conditions under which cultural stability obtains, or not.

### 167 **Methods**

168 We compare five conditions ( $N = 100$  in all cases):

- 169 a) *Baseline*. Here the position of all items at each time step is determined wholly  
170 at random i.e. there is no sampling or transformation, and hence no relationship  
171 between the population at time  $t$  and time  $t - 1$ .
- 172 b) *Replication*. Random sampling with no transformation (i.e.  $k = 0$ ).
- 173 c) *Unbiased*. Random sampling with random transformation, under three distinct  
174 values of  $k$  ( $k = 0.01; 0.1; 0.5$ ).
- 175 d) *Biased Sampling*. Biased sampling with random transformations, under three dis-  
176 tinct values of  $k$  ( $k = 0.01; 0.1; 0.5$ ).
- 177 e) *Convergent Transformation*. Random sampling with convergent transformation.

178 In this way we are able directly compare the effects of different sampling and transforma-  
179 tion functions on the behaviour and, in particular, the stabilisation, of the evolving system.  
180 We omit the final possibility—biased sampling with convergent transformation—only be-  
181 cause this will simply magnify the results observed in ‘Biased Sampling’ and ‘Convergent  
182 Transformation’.

### 183 **Results**

184 Figure 2 summarises the behaviour of the model under the different conditions that we  
185 study. All results presented are an average of 10 runs of simulations. Videos of represen-  
186 tative runs of simulations (b) to (e) are provided in the Supplementary Information<sup>1</sup>.

187 ‘Baseline’ (row (a)) behaves in a genuinely random way, as expected. There is no evolution  
188 towards stability. Items remain uniformly spread in the space, the mean trait value  
189 oscillates at random around the origin, and there is no effect of the scale of time steps  
190 at which the mean trait value is measured. This is because there are no causal relations  
191 between the items at any two time steps.

192 We do observe an emergence of stability in ‘Replication’ (row (b)). Spread decreases to  
193 0, as does mean trait value. This is due to the random sampling of inputs which, by  
194 chance, eventually leads some items at time  $t$  not to serve as an input for the next time  
195 step. Since an item at  $t + 1$  is always located at the same position as its input at time  $t$   
196 (because no new variation is introduced), the population eventually drifts to one of the  
197 locations occupied by an individual item at the beginning of the simulation. In short,  
198 stability is achieved here through the gradual elimination of variation in the population.

199 In ‘Unbiased’ (row (c)) we allowed new variation to be introduced randomly, and we find  
200 that this also leads to the emergence of stability over time. Spread decreases towards

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<sup>1</sup>Supplementary Information will be available with the final version of the draft.

201 0, as does change in mean trait value (both across 1 and 100 time steps)—but never  
202 quite reaches it. This is because novel variation is introduced at every time step. The  
203 asymptote is determined by the value of  $k$ : the lower the value of  $k$ , the more stability in  
204 the system.

205 In ‘Biased Sampling’ (row (d)), we observe a faster evolution towards stability than in  
206 ‘Unbiased’, for all three values of  $k$ . The most stable populations remain those with low  
207 values of  $k$ , as the selection can only winnow the novel variation once it has already been  
208 introduced by random transformations in the previous generation<sup>2</sup>.

209 Finally, in ‘Convergent Transformation’ (row (e)), we observe a quick evolution towards  
210 stability, with both spread and change in mean trait value decreasing asymptotically  
211 towards 0. As in ‘Biased Sampling’, the population is very stable in the long term (it  
212 remains located around the origin). Convergent transformation is sufficient, on its own,  
213 to cause long term stability.

214 Collectively, these results highlight two particularly relevant aspects of cultural stability.

215 First, a population under random transformation achieves stability only when coupled  
216 with a biased sampling process. This is clear when ‘Unbiased’ and ‘Biased Sampling’ are  
217 compared (see Figure 3). In ‘Unbiased’, in which sampling is random, there is short-  
218 but not longer-term stability, even when  $k$  is extremely low. Indeed, mean trait value  
219 drifts through time: although there is very little change in mean trait value between two  
220 successive time steps, over the long term the population drifts away randomly. High-  
221 fidelity transmission produces long term stability only when coupled with selection. In  
222 contrast, in ‘Biased Sampling’, the population clusters around the origin and stabilizes  
223 there.

224 Second, neither high-fidelity transmission nor selection are necessary for stability, either  
225 short- or longer-term. This is clearly shown in ‘Convergent Transformation’, in which  
226 both short- and longer-term stability occur despite the ubiquity of transformations and  
227 the absence of any biased sampling. ‘Convergent transformation’ produces dynamics more  
228 akin to ‘Biased Sampling’ than to ‘Unbiased’: in both cases the population converges  
229 towards the origin and stabilizes there, both in the short and long term.

## 230 **Study 2: Mixing random and convergent transformation**

231 In Study 1, convergent transformation produced on its own both short and long-term sta-  
232 bility. In reality, we might expect only some items in a population to undergo convergent  
233 transformation. Indeed, the relative importance of copying and small, convergent trans-  
234 formation is often debated (Claidière & Sperber 2007, Claidière, Smith, Kirby & Fagot  
235 2014, Acerbi & Mesoudi 2015, Claidière et al. 2018). To clarify these issues we develop a  
236 model mixing both types, and examine their interactions.

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<sup>2</sup>The “attractor” model in (Místa 2018) in fact reduces to our Biased Sampling condition, as there is no convergent transformation in the model.

## 237 **Methods**

238 To mix convergent and random transformations we constructed a model with random sam-  
239 pling and a function that determines which type of transformation—random or convergent—  
240 will occur. Specifically, the probability that the transformation will be convergent is equal  
241 to  $1 - d^\alpha$ , where  $d$  is the Euclidean distance between the input and the origin (scaled to a  
242 unit of  $\sqrt{2}$ , the maximum possible distance), and  $\alpha$  is a parameter of the model ranging  
243 between 0 and  $\infty$ . Otherwise, the transformation is random. Thus, the closer an input is  
244 to the origin, the more likely that transformation is convergent. The parameter  $\alpha$  controls  
245 the strength of this effect; or, more informally, the ‘reach’ of convergent transformation  
246 (see Figure 4). A high  $\alpha$  increases the overall probability that an item is transformed  
247 directionally instead of randomly. As  $\alpha$  decreases, so does the overall probability that an  
248 item is transformed in a convergent rather than random way.  $\alpha = 0$  reduces to model (c)  
249 in Study 1, and  $\alpha = \infty$  reduces to model (e). As in study 1,  $N = 100$ .

## 250 **Results**

251 For all the results described below  $\alpha = 0.1$  (Other values of  $\alpha$  ( $0 < \alpha < \infty$ ) produce  
252 qualitatively similar results.)  $k$  is set to either to 0.1 or 0.5 (parameter  $k$  regulates  
253 what can be thought as the magnitude of copying error). When  $k$  is lower ( $k = 0.1$ ) the  
254 population is more stable over both short- and longer-term, as expected (Figure 5). We see  
255 a clear increase in stability from the ‘Unbiased’ model with an equal value for  $k$  (compare  
256 to Figure 2(c)). Moreover, convergent transformation ensures that the population does  
257 not drift from the origin, even over the long term, but instead remains stable around it.  
258 In this way, convergent transformation has a similar effect as biased sampling.

259 Furthermore, this effect occurs even when most transformations are random. Indeed, the  
260 proportion of items that undergo convergent transformation is higher when  $k$  is lower than  
261 when it is higher (Figure 6). This occurs because once an input is brought within the  
262 vicinity of the origin by convergent transformation, future items are more likely to remain  
263 within that vicinity when  $k$  is low than when it is high. This means that in situations  
264 where there is both convergent transformation and high-fidelity transmission, these two  
265 factors can reinforce one another to secure stability.

266 Collectively these results open up questions of high relevance to the empirical study of  
267 culture. Stability can be achieved in more than one way, so how might we differentiate  
268 between these different possible causes? Is there a way to identify, in empirical records,  
269 whether one or the other of the different processes we have modelled is in fact at play in  
270 a given case? Study 3 investigates these questions.

## 271 **Study 3: Evolutionary signatures of different causes of stability**

272 Study 1 showed that the patterns of stabilisation observed in ‘Biased Sampling’ and  
273 ‘Convergent Transformation’ are similar, such that on the basis of observed stability  
274 alone we cannot infer which processes are responsible. Here we investigate whether these  
275 different possible causes of stability have different evolutionary signatures at the level of  
276 the population. We do this in two ways. First, we examine how a population already  
277 clustered around a particular point evolves over time. We are particularly interested in



278 whether there is a qualitative difference in population behaviour, and whether the two  
279 different types of transformation, random and convergent, affect differently the observed  
280 similarity from one generation to the next. Second, we investigate whether such effects  
281 are affected by population size.

## 282 **Methods**

283 In this study, we investigate how populations with a limited spread evolve over time.  
284 (A simulation starting with a large spread, as in the previous studies, is included in the  
285 Supplementary Information, showing equivalent results). To cluster the population, we  
286 started the simulation by first locating the items in one of the four corners randomly,  
287 with a 0.8 distance from the origin for both  $x$  and  $y$  coordinates, and then randomly  
288 distributing the items within 0.05 distance from that point. We ran simulations ‘Biased  
289 Sampling’ (with  $k = 0.1; 0.5$ ) and ‘Convergent Transformation’ with this new starting  
290 condition.

291 To examine how the populations evolve towards the origin, we track similarity between  
292 items and their inputs (see General Methods). As in previous models,  $N = 100$ . To  
293 investigate the impact of population size, we repeat the above process but now for three  
294 different population sizes ( $N = 10; 100; 1000$ ). We then measure how many time steps it  
295 takes for the populations to reach a stable state, which we operationalise as a change in  
296 mean trait value at each time step  $\leq 0.01$ .

## 297 **Results**

298 *Qualitative description.* Videos (available as Supplementary Information) show that bi-  
299 ased sampling and convergent transformation have qualitatively different evolutionary  
300 behaviours over time. In the case of ‘Biased Sampling’, the clustered population move  
301 together, in small steps, until it reaches the origin. We observe gradual evolution similar  
302 to a hill-climbing behaviour. In contrast, in the case of ‘Convergent Transformation’,  
303 the population rapidly re-converges on the origin. This can be described as the pop-  
304 ulation ‘jumping’ to the origin, with little effect of cultural inertia. This effect mirrors  
305 patterns observed in a number of real-world cases, such as rapid changes followed by quick  
306 stabilization in technological systems (e.g. Schiffer 2005).

307 *Fidelity.* In ‘Biased Sampling’ the mean distance between items and inputs is relatively  
308 low (depending on  $k$ ) and remains so throughout the simulation (see Figure 7). This is  
309 due to constant rate of random transformations. This represents well the assumption that  
310 transmission processes possess a specific degree of fidelity, both as it is characterized in  
311 the theoretical literature (e.g. Mesoudi 2011), and how it is implemented in other formal  
312 models [e.g.](Henrich & Boyd 2002, Enquist et al. 2010). In contrast, in ‘Convergent  
313 Transformation’ we observe at first high distance between items and their inputs (i.e. a  
314 low degree of similarity) and then a rapid decrease of distance (see Figure 7). This is  
315 due to the fact that the expected degree of similarity is not fixed, but instead depends on  
316 the specific location of the input. The further from the origin an item’s input is, the less  
317 similar we can expect the item to be from the input. This reflects the idea that the degree  
318 of fidelity by which a cultural trait is transmitted can depend on the specific variants of  
319 cultural items (e.g. Sperber 2000). In this latter case, the similarity of the items and the

320 overall degree of fidelity is not guaranteed by an intrinsic property of some underlying  
321 transmission process, but instead are emergent phenomena at the level of the population.

322 *Population size.* By varying population size we observe that the two different simula-  
323 tions show very different sensitivity to population size (Figure 8) There is no evidence  
324 of sensitivity to population size in ‘Convergent Transformation’, but there is in ‘Biased  
325 Sampling’, with larger populations taking less time to reach the same degree of stability  
326 as smaller ones. In fact, this is true both for populations that are at first randomly scat-  
327 tered, and for those that are at first already clustered (see Supplementary Information).  
328 This dependency on population size occurs because biased sampling is, fundamentally, a  
329 sorting process dependent on sample size: it is more likely to sample one item closer to  
330 the origin in a large population than in a small population.

331 In conclusion, two evolutionary signatures can distinguish between different causes of  
332 cultural stability: (1) qualitative and quantitative differences in the behaviour of the  
333 population as it converges on a stable form; (2) differences in sensitivity to population  
334 size.

## 335 Discussion

336 A key question for any scientific study of culture is, what are the causes of cultural  
337 stability? Many distinct research traditions, across evolution, psychology, and anthropol-  
338 ogy, have either argued or assumed that cultural stability, whether over shorter or longer  
339 timespans, necessarily requires psychological mechanisms (e.g. imitation) capable of copy-  
340 ing cultural items with some high degree of fidelity (Tomasello 2008, Tennie et al. 2009,  
341 Mesoudi 2011, Henrich 2016, Laland 2017). Accepting this assumption, some researchers  
342 have further argued that there has been biological natural selection for mechanisms of  
343 high-fidelity copying in humans, because such mechanisms are necessary to facilitate the  
344 emergence and persistence of culture, thus helping to explain how humans have adapted  
345 to an extraordinarily broad range of ecological conditions (Boyd & Richerson 1996, 2005,  
346 Tomasello 1999, Henrich 2016, Laland 2017).

347 We show that these conclusions cannot be reached so quickly. Stability can emerge in  
348 an evolutionary system without any mechanism of high-fidelity transmission (in Study  
349 1). This stability can hold for both short and long periods of time, if the mechanisms  
350 of transmission exhibit some some degree of convergent transformation. These points  
351 have previously been argued for mostly in a verbal way (Sperber 2000, Claidière & Sper-  
352 ber 2010, Charbonneau 2019; but see, for formal treatments Claidière & Sperber 2007,  
353 Claidière 2009, Claidière et al. 2018). Here we have subjected them to further formal  
354 probing and made them comparable with concurrent models, and found the arguments  
355 robust. High-fidelity copying is only one of several factors that can ensure intergener-  
356 ational stability in an evolutionary system (see also Henrich 2004, Griffiths et al. 2008,  
357 Acerbi et al. 2012, Dean et al. 2014).

358 Another important issue is the combined effect of high-fidelity copying and convergent  
359 transformation when they act together in an evolutionary system. Previous models have  
360 shown that, when copying is biased, and the biases act in the same direction of convergent  
361 transformation, the effects will reinforce each other (Henrich & Boyd 2002, Claidière et al.  
362 2018). When instead the effects of copying biases and convergent transformation are in  
363 opposition, the end-state depends on the relative force of the two (Claidière & Sperber

364 2007, Claidière et al. 2018). We analysed, in Study 2, the case of high-fidelity copying  
365 with unbiased sampling and convergent transformation, showing that the more faithful  
366 the copying the stronger the effect of convergent transformation. This result may appear  
367 surprising, because intuitively faithful copying will ‘lock’ items in a configuration different  
368 from where they would end if convergent transformation operates alone. However, given  
369 that copying is unbiased, it reinforces the only directional mechanism present, convergent  
370 transformation, making items close to the origin more stable than what they would be  
371 with a less faithful copying. This suggests that convergent transformation, even when  
372 of low magnitude, can counteract—or might in some cases even dominate—the effects of  
373 other factors with shifting directionality such as, for instance, model-based social learning  
374 strategies (Hoppitt & Laland 2013, Kendal et al. 2018).

375 Our results also identify evolutionary signatures of different possible sources of stability  
376 in an evolutionary system. The first signature concerns different levels of similarity while  
377 a population is undergoing change. A specific and clear example comes from the exper-  
378 imental literature on language evolution, which consistently shows the pattern observed  
379 for ‘Convergent transformation’ in our Study 3. Levels of intergenerational similarity are  
380 at first low, when the languages are unstructured and relatively inefficient, and later high,  
381 once the languages have evolved structure and greater levels of communicative efficiency.  
382 (Compare, for instance, our Figure 7 with Figures 2a and 4a from Kirby et al. 2008). Sim-  
383 ilar points apply to several other experimental datasets too, across a range of different  
384 cultural domains (e.g. Mesoudi et al. 2006, Lewandowsky et al. 2009, Miton et al. 2015,  
385 Ravignani et al. 2017, Claidière et al. 2018)

386 Our second evolutionary signature is differential sensitivity to population size. Many  
387 recent studies investigate the relationship between population size and the cumulative  
388 complexity of cultural items, in particular technology (Henrich 2004, Powell et al. 2009,  
389 2010, Querbes et al. 2014). The hypothesis here is that larger populations increase rates  
390 of technological progress, because larger population ensure lower risks that cultural traits  
391 become rare and are lost. Our study adds to this empirical literature an important  
392 additional finding about the relative rates of convergence upon new cultural items. More  
393 generally, where the stabilization of a cultural item in a population is influenced by the  
394 size of that population, this may be interpreted as (partial) evidence that biased selection  
395 plays a role; and conversely where there is no such relationship, convergent transformation  
396 is likely to be more important (Acerbi et al. 2017).

397 Our simulations can also be read as formal models of cultural attraction. Cultural Attrac-  
398 tion Theory (Sperber 1996, Claidière & Sperber 2007, Claidière, Smith, Kirby & Fagot  
399 2014, Morin 2016, Heintz 2017, Scott-Phillips et al. 2018) argues that convergent trans-  
400 formation is common in human social life, and that cultural stability is best seen as a  
401 condition where convergent transformations gravitate closely around an attractor. This  
402 claim is often presented and discussed in contrast with other evolutionary approaches to  
403 culture (Acerbi & Mesoudi 2015, Morin 2016, Sterelny 2017, Scott-Phillips et al. 2018).  
404 However resolution of these debates has been somewhat hindered by the relative absence  
405 of formal models of cultural attraction (but see Henrich & Boyd 2002, Claidière & Sperber  
406 2007, Claidière 2009). We have here removed that barrier, advancing debate onto key em-  
407 pirical questions about the exact psychological mechanisms that facilitate the emergence,  
408 spread, and stability of culture.

409 By virtue of their generality, our models can be extended in many ways to study cultural  
410 dynamics of many different types. Here we highlight three possibilities. (1) In our models,

411 the convergent transformation function is oriented towards one single point in the space  
412 (the origin), but the model can be easily adjusted to include multiple points of convergence  
413 (e.g. Claidière & Sperber 2007). (2) The functions for convergent transformation and  
414 biased sampling are presently both oriented towards the origin, but this can be easily  
415 altered by re-defining one or the other to be oriented to some other point in the space.  
416 (3) At present, the convergent transformation function is defined in such a way that the  
417 closer an item is to the origin, the more convergent are its effects. This can be modified  
418 by changing the convergent transformation function, or by changing the way in which  
419 convergent and random transformation interact (see Study 2).

420 More broadly, our findings suggest that cultural stability requires no cognitive adaptations  
421 (Sperber 2000, Sperber & Hirschfeld 2004, Morin 2016, Charbonneau 2019, Heyes 2018).  
422 Cultural traditions can instead emerge and remain stable (over various time spans) also  
423 as a consequence of processes whose proper function is not high-fidelity transmission, such  
424 as communication, mindreading and other forms of social interaction, as long as those  
425 processes lead to convergent transformation.

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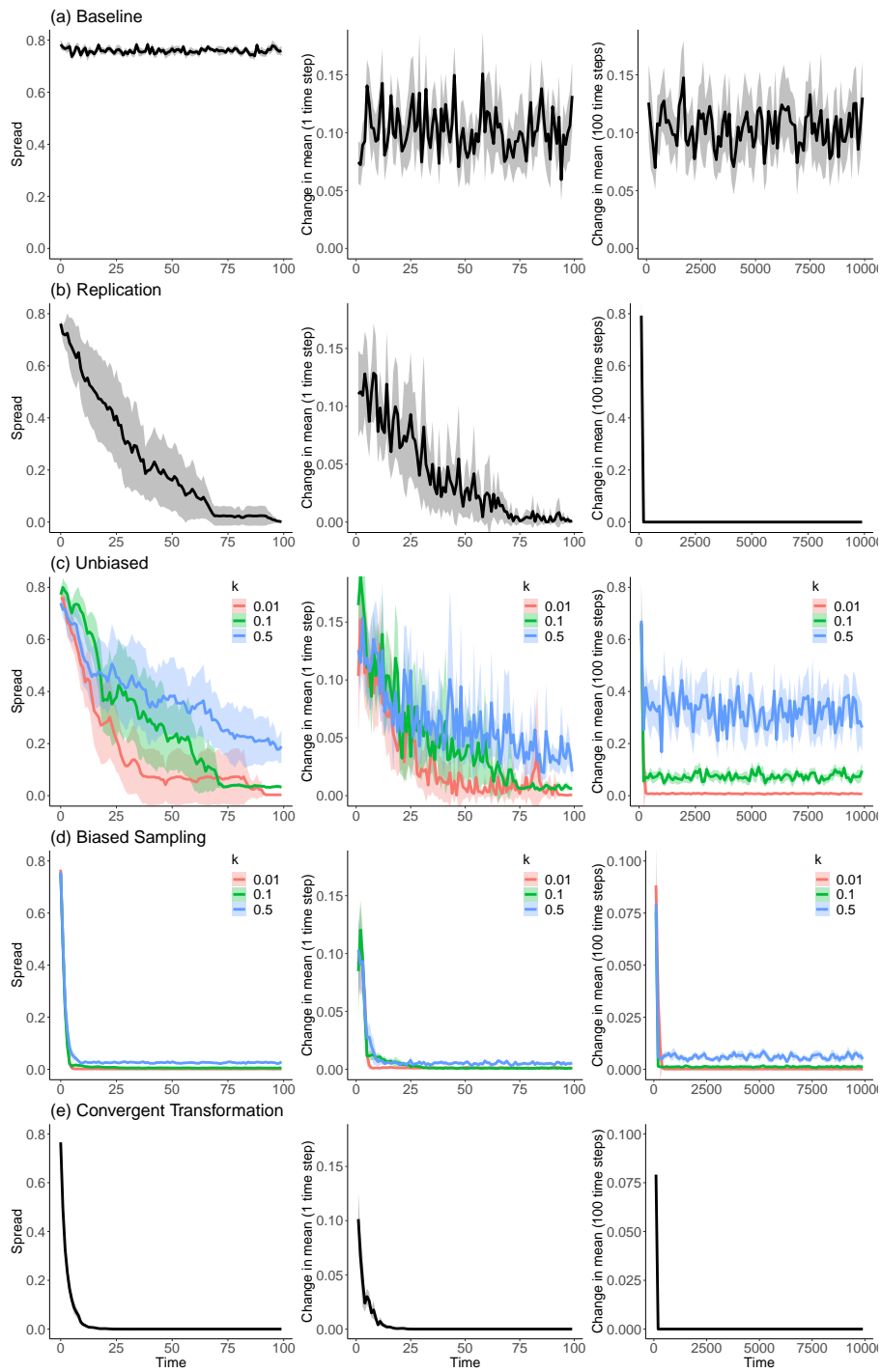


Figure 2: **Under what conditions does stability occur?** These 15 graphs report the behaviour of the model under the various conditions considered in Study 1. Each row represents a different simulation, or set of simulations, and each column measures a different aspect of stability. Simulations from top to bottom: (a) Baseline; (b) Replication; (c) Unbiased; (d) Biased Sampling; (e) Convergent Transformation. Measures of stability, from left to right: (i) Spread; (ii) Mean trait value across 1 time step (simulation ran for 100 time steps); (iii) Mean trait value across 100 times steps (simulation ran for 10,000 time steps). All results are averaged over 10 runs of simulations. The shaded area shows standard deviations. In all conditions  $N = 100$ .



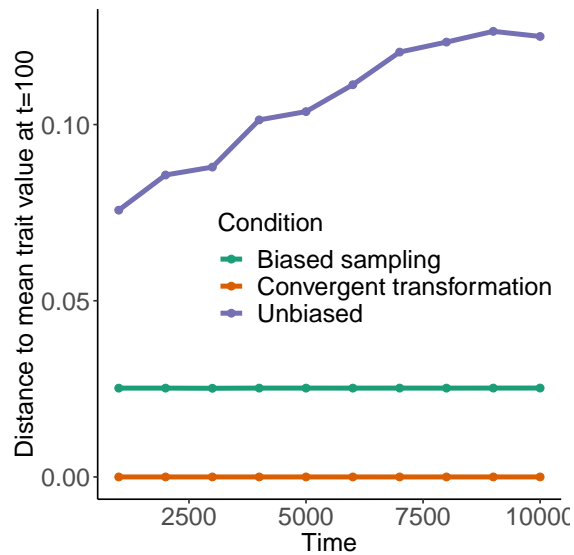


Figure 3: **Long term stability: comparisons.** Here we compare the distance between the mean trait value of the population at time step 100 with the mean trait value of the population at subsequent timesteps (1000, 2000, etc., up to 10000), across simulations ‘Unbiased’, ‘Biased Sampling’, and ‘Convergent Transformation’. This distance increases monotonically in ‘Unbiased’ simulation, but it does not change in either ‘Biased Sampling’ or ‘Convergent Transformation’. In other words, there is evolutionary drift in ‘Unbiased’, whereas ‘Biased Sampling’ and ‘Convergent Transformation’ produce long-term stability. The difference in distance between ‘Biased Sampling’ and ‘Convergent Transformation’ is due to the fact that ‘Biased Sampling’ was slightly slower to converge. Figure displays average of 10 runs. In all cases  $N = 100$  and  $k = 0.01$  (except in ‘Convergent Transformation’ where there is no  $k$ ).

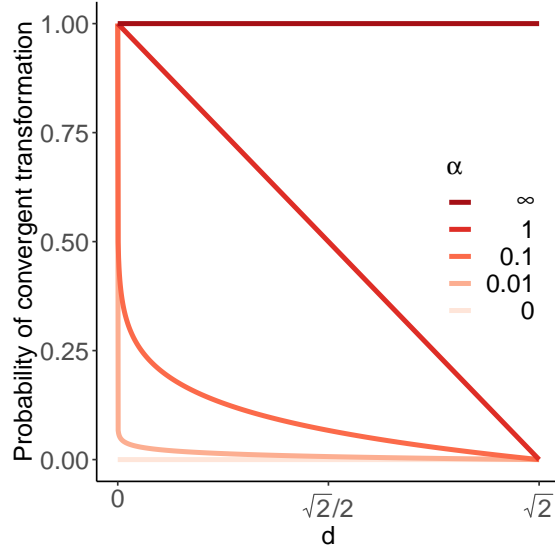


Figure 4: **Varying  $\alpha$  in the mixed model.** Probability landscape that a given item undergoes convergent transformation instead of random transformation, under different values of  $\alpha$ . With  $\alpha = \infty$ , all transformations are convergent, and with  $\alpha = 0$  all transformations are random. With  $0 < \alpha < \infty$  the further items are from the origin, the less likely they are (with decreasing probability) to undergo convergent transformation. Note that, for all  $\alpha > 0$ , there is always a non-null probability to undergo convergent transformation.

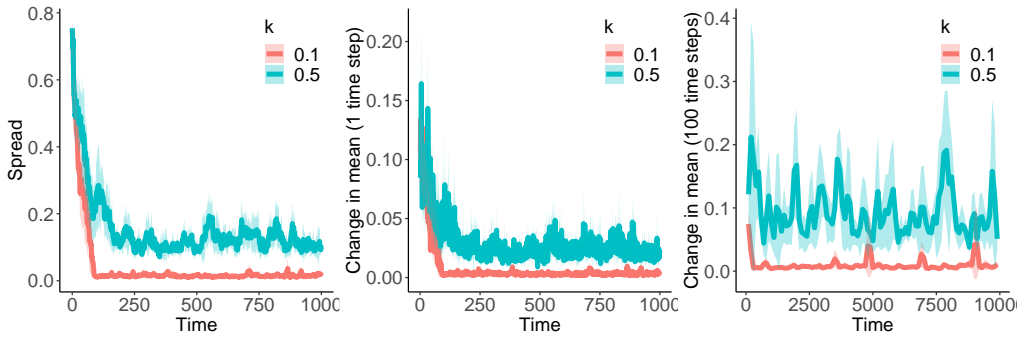


Figure 5: **Mixed model of random copying and convergent transformation.** Mixed model, with  $\alpha = 0.1$  and different copying fidelity ( $k = 0.1; 0.5$ ). Left: Spread; Centre: Mean trait value across 1 time step (simulation ran for 100 time steps); Right: trait value across 100 times steps (simulation ran for 10,000 time steps). All results are averaged over 10 runs of simulations, all with  $N = 100$ . The shaded area shows standard deviations.

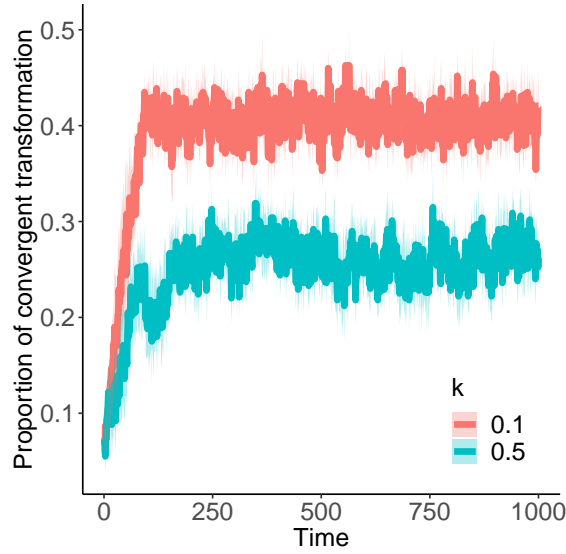


Figure 6: **Proportion of convergent transformation in mixed model.** Mixed model, with  $\alpha = 0.1$  and different copying fidelity ( $k = 0.1; 0.5$ ). Proportion of items that, at each time step, are subject to convergent transformation. The lower the value of  $k$ , the more it leads to convergent transformation, showing that a smaller value of  $k$  increases the mean probability of convergent transformation. Results are averaged over 10 runs of simulations, all with  $N = 100$ . The shaded area shows standard deviations.

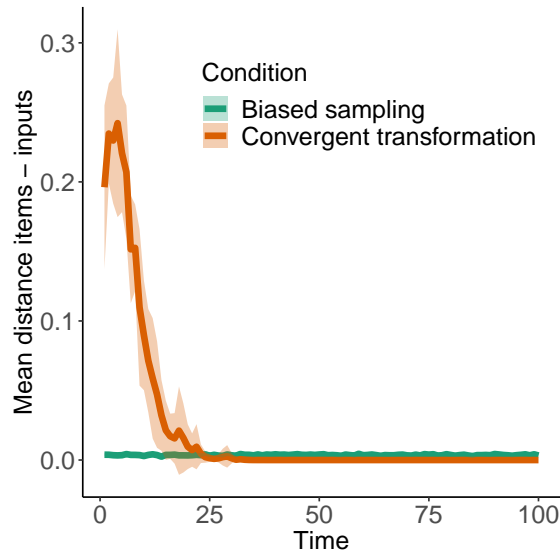


Figure 7: **Population-level similarity.** ‘Biased sampling’ with  $k = 0.1$ . ‘Convergent transformation’ as in Study 1. The population is clustered in one of the corners of the space (see text), and then evolves towards the origin. Similarity between items and their inputs remains low throughout the ‘Biased sampling’ simulation, whereas it varies in ‘Convergent transformation’, depending on the mean distance of the population to the origin. Results are averaged on 10 runs of the model. The shaded area shows standard deviations. In both conditions  $N = 100$ .

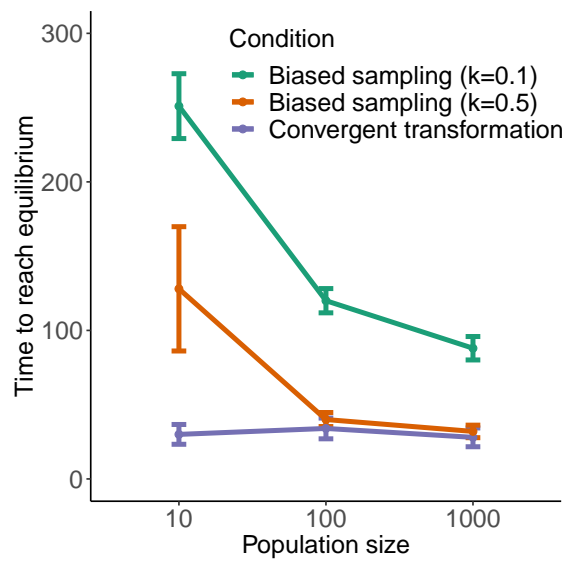


Figure 8: **Effects of population size.** Starting with a clustered population in one of the corners of the space (see text), we measure the number of time steps it takes for the change in mean trait value of the population to be  $\leq 0.01$  (we call this ‘equilibrium’ for short). This is measured for ‘Biased sampling’ at two different levels of  $k$  ( $k = 0.1; 0.5$ ) and for ‘Convergent transformation’. Results are averaged on 10 runs of the model. Bars show standard deviations.