

The evolution of social learning as phenotypic cue integration

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Abstract

Most analyses of the origins of cultural evolution focus on when and where social learning prevails over individual learning, overlooking the fact that there are other developmental inputs that influence phenotypic fit to the selective environment. This raises the question how the presence of other cue ‘channels’ affects the scope for social learning. Here, we present a model that considers the simultaneous evolution of (i) multiple forms of social learning (involving vertical or horizontal learning based on either prestige or conformity biases) within the broader context of other evolving inputs on phenotype determination, including (ii) heritable epigenetic factors, (iii) individual learning, (iv) environmental and cascading maternal effects, (v) conservative bet-hedging and (vi) genetic cues. In fluctuating environments that are autocorrelated (and hence predictable), we find that social learning from members of the same generation (horizontal social learning) explains the large majority of phenotypic variation, whereas other cues are much less important. Moreover, social learning based on prestige biases typically prevails in positively autocorrelated environments, whereas conformity biases prevail in negatively autocorrelated environments. Only when environments are unpredictable or horizontal social learning is characterised by an intrinsically low information content, other cues such as conservative bet-hedging or vertical prestige biases prevail.

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35 1 Introduction

36 Social learning, the ability to acquire information from other individuals, is a fundamen-
37 tal requirement to cultural evolution [1–4]. Indeed, a substantial amount of theoretical work has sought to
38 identify the ecological conditions in which selection favours social learning as opposed to indi-
39 vidual learning (see [3, 4] for reviews), finding that a mixture of both social and individual learning
40 is expected to evolve in fluctuating environments (e.g., [5–9]). However, the conventional focus on
41 the evolution of social versus individual learning overlooks that individuals can also obtain inform-
42 ation about their environments by other means. For example, in spatially varying environments
43 an individual’s genotype can become statistically associated to its environment through local ad-
44 aptation [10, 11], favouring the evolution of genetic cues for phenotypic development [12–15]. In
45 environments that fluctuate predictably over time, theory predicts that individuals are selectively
46 favoured to rely on transgenerational cues that stem from their parent’s phenotype or the parental
47 environment (e.g., [16–20]), transmitted through heritable DNA/histone modifications, parental
48 hormones or even parent-offspring teaching [21–24]. Next, rather than relying on direct or indirect
49 cues about the environment, individuals may also be selectively favoured to rely on mechanisms
50 that generate phenotypic variation instead (e.g., bet-hedging: [25, 26]). Consequently, the avail-
51 ability of cues other than social or individual learning raises the question how organisms should
52 integrate multiple cues when adapting to different environments and how, in turn, this affects the
53 evolutionary scope for social versus individual learning.

54 While there are a large number of theoretical studies which have analysed the evolutionary im-
55 plications of subsets of two or three developmental cues (e.g., [12, 27–30]), only a limited number
56 of these studies have sought to predict how organisms should integrate a larger number of available
57 cues [31–33]. These studies find that the rate of environmental change and the degree of environ-
58 mental predictability are key parameters in determining which cue is most important in phenotype
59 determination, while reliance on mixtures of multiple cues typically occurs in more restrictive set-
60 tings. However, these studies have only focused on integration of individual and parental cues (e.g.,
61 genetic cues, bet-hedging, parental effects and individual learning [phenotypic plasticity]). By con-

62 trast, the potential to acquire information via different socially learned cues is yet to be considered
63 in a context that tracks the joint evolution of multiple cues.

64 To understand how the integration of multiple cues affects the evolution of different social learn-
65 ing mechanisms, we develop a model that tracks the evolution of alternative behavioural phenotypes
66 in a spatiotemporally fluctuating environment. Organisms are selected to develop a behaviour that
67 closely matches the local environment by evolving sensitivity to a range of different cues, where
68 each of these cues potentially provides information about the local environment. Foremost, we con-
69 sider that individuals can evolve sensitivity to socially learned cues about the phenotypes of others,
70 who are either members of the parental generation (vertical social learning) or of the current gen-
71 eration (horizontal social learning). We then ask how vertical and horizontal social learning evolve
72 jointly with other cues that may affect behavioural development, be it genetic cues, individually
73 learned cues (here represented by within-generational phenotypic plasticity) and transgenerational
74 cues for phenotype determination as in previous models [31–33]. Moreover, because both hori-
75 zontal and vertical social learning can potentially involve different mechanisms to identify from
76 whom individuals should learn [3, 8], the current model allows sensitivity to evolve based on
77 prestige biases (individuals obtain cues from the most successful individual) and/or conformity
78 biases (individuals obtain cues from the most commonly observed phenotype) for vertical and ho-
79 rizontal social learning independently. Similar to many previous models (reviewed in [3, 4, 8]), our
80 model applies to those taxa for which such social cues already exist in some form (e.g., individuals
81 are able to rank others based on their perceived success). We then ask when sensitivity to these
82 cues evolves from scratch and what form such sensitivity then takes. (e.g., which combinations of
83 socially learnt cues are important relative to other cues?)

84 Existing theory on the evolution of social learning [3, 4, 8] often stresses the role of different
85 costs in driving the evolution of social and individual learning. For example, social learning is typ-
86 ically thought to result in outdated information relative to individual learning, whereas individual
87 learning is considered to take more effort, resulting in a producer-scrounger game over information
88 (e.g., [5, 8, 34–37]). The key focus of the current model is different, however, as we want to assess

89 what information different combinations of cues can provide and whether some cues can inherently
90 provide more information over and above others. Consequently, we make no a priori assumptions
91 about the relative costs and benefits of one type of cue versus the others, but rather have those
92 payoffs emerge from the ecological scenarios (via migration and timing of life-history events) that
93 impact the information content of the various cues.

94 **2 The model**

95 We performed individual-based simulations of a sexually reproducing population distributed over
96 $N_p = 40$ patches, each supporting a local population of $K = 100$ diploid, hermaphroditic individu-
97 als, largely based on a previous model on the evolution of transgenerational effects [17]. While
98 generations are non-overlapping in the sense that only individuals born during the current time step
99 reproduce, the model allows offspring to obtain information from individuals from the previous
100 generation through parental effects and vertical social learning. The simulations are written in C++
101 and the code is available at <https://doi.org/10.5281/zenodo.3924688>. Figure 1A gives an
102 overview of the different cue integration dynamics, while a more elaborate description is provided
103 in section S2 of the online supplement.

104 **2.1 Environment**

105 Each patch is either in one of two local environmental states (low: θ_{low} , or high: θ_{high}), reflecting,
106 for example, the local temperature or the amount of available resources. Patches can change en-
107 vironmental state independently from other patches at each time step: with probability p a patch
108 retains its current environmental state during the next time step, whereas with probability $1 - p$ it
109 changes to the opposite environmental state (similar to two-state models in e.g., [4, 6], but different
110 from models in which the environment continuously varies around an average value [16, 33] or
111 where the environment always attains novel values [4, 6]). Following [17], we assume that both
112 environments change at identical rates, so the global equilibrium frequency f_{high} of patches in envir-

113 onmental state θ_{high} is given by $f_{\text{high}} = 1 - f_{\text{low}} = 1/2$, while the between-generation environmental
 114 autocorrelation of any patch is $\rho(\theta_t, \theta_{t+1}) = 2p - 1$, so that when $p = 0$ (rapid change), the autocorrel-
 115 ation is -1 , when $p = 1$ (no change), the autocorrelation is 1 and when $p = 0.5$ (random change), the
 116 autocorrelation is 0. In Figure S10, we consider values of global equilibrium frequency of patches
 117 in environmental state θ_{high} other than $f_{\text{high}} = 1/2$ (see also [18, 19] for the effect of asymmetries in
 118 patch frequencies), but findings are similar to results presented in the main text (e.g., see Figure 2).

119 2.2 Reproduction and juvenile phenotype determination

120 Before reproduction, adults experience survival selection based on their adult phenotype u_{ad} (see
 121 eq. [3] below), where the probability of adult survival $S(u_{\text{ad}}, \theta)$ differs between low and high en-
 122 vironments respectively (see Figure 1B and the online supplementary information). Subsequently,
 123 K newborn offspring are produced by surviving adults. Each newborn offspring is produced by
 124 randomly selecting a mother and a father from among the surviving adult breeders, potentially
 125 allowing for selfing in case the number of survivors is very small.

126 Upon birth, an individual offspring then determines its juvenile phenotype u_{juv} according to ge-
 127 netic, maternal environmental, maternal phenotypic and vertical social cues (see Figure 1A and eq.
 128 1 below). The juvenile phenotype is also affected by individual learning of the local environment
 129 (via juvenile environmental cues), where we assume that individual learning occurs before migra-
 130 tion unless indicated otherwise. Consequently, the juvenile phenotype u_{juv} that is developed after
 131 individual learning is a logistic function of a weighted sum \bar{x}_{juv} of different cues an individual has
 132 received. We have

$$133 \quad u_{\text{juv}} = \frac{1}{1 + \exp(-\bar{x}_{\text{juv}})} \quad (1)$$

$$134 \quad \bar{x}_{\text{juv}} = a_{\text{g}}x_{\text{gen}} + a_{\text{ind}}x_{\text{ind}} \\ 135 \quad \quad \quad + m_{\text{m}}x_{\text{mat,phen}} + m_{\text{e}}x_{\text{mat,envt}} \\ 136 \quad \quad \quad + v_{\text{p}}x_{\text{vert,prestige}} + v_{\text{c}}x_{\text{vert,conformity}}, \quad (2)$$

137

138 where the x_i s are the values of each of the different cues (see section S2.2 in the Online Supplement
139 where we set out the details of the different cues). We then allow the influence of each cue on
140 juvenile phenotype determination to evolve, by assuming that cues are weighed by a set of evolving
141 sensitivity loci, here reflected by variables a_g (genetic cue), a_{ind} (individual learning), m_m (maternal
142 phenotypic cue), m_e (maternal environmental cue), v_p (vertical social learning; prestige bias) and
143 v_c (vertical social learning; conformity bias) respectively. For the sake of tractability, we assume
144 that each sensitivity locus is diploid and unlinked to other loci. The value of each sensitivity locus
145 is restricted to $[-10, 10]$. In the absence of any other cues, a sensitivity value $v_p = 0$ (vertical
146 social learning sensitivity based on prestige) implies that juveniles attain an intermediate juvenile
147 phenotype of $u_{\text{juv}} = 1/2$. A negative value of v_p implies that when individuals receive a high versus
148 a low value of the $x_{\text{vert,prestige}}$ cue, they are more likely to develop a low phenotype ($u_{\text{juv}} < 1/2$)
149 versus a high phenotype ($u_{\text{juv}} > 1/2$). The opposite relationship applies when v_p is positive.

150 Regarding the timing and place of the different types of learning, we assume that individual
151 learning occurs in the natal environment prior to migration (see life cycle in Figure 1). However,
152 in Supplementary Figure S7G-L, we consider a scenario in which individual learning occurs after
153 migration to the remote environment. Similar to individual learning, vertical social learning is
154 assumed to occur prior to migration throughout the main text. However, in Supplementary Figure
155 S6G-L, individuals are assumed to perform vertical social learning after migration. By contrast,
156 horizontal social learning is assumed to occur after migration and hence only affects phenotypic
157 development later in life throughout the main text (see eqns. [3,4]). However, in Supplementary
158 Figure S7A-F, we relax these assumptions regarding the timing of horizontal social learning, by
159 assuming that individuals perform horizontal social learning in their natal environment.

160 After juvenile phenotype determination, individuals migrate with probability d to a randomly
161 chosen remote site, while they remain at the natal site with probability $1 - d$. Consequently, we
162 assume that horizontal social learning (see below) occurs after migration.

163 **2.3 Adult phenotype determination**

164 After juvenile phenotype determination, all adults from the previous generation die and individuals
165 learn from other individuals of their current generation (horizontal social learning). As noted be-
166 fore, horizontal social learning occurs only after migration (but see Supplementary Figures S7A -
167 F). Information acquired from horizontally learned social cues is then used by individuals to update
168 the various cue weightings \bar{x}_{juv} in eq. (2) and develop an adult phenotype. Consequently, the adult
169 phenotype u_{ad} that is developed after horizontal social learning is an updated logistic function of a
170 weighted sum \bar{x}_{ad} of the various cues an individual has received. We have

$$171 \quad u_{\text{ad}} = \frac{1}{1 + \exp(-\bar{x}_{\text{ad}})} \quad (3)$$

$$172 \quad \bar{x}_{\text{ad}} = \bar{x}_{\text{juv}} + h_{\text{p}}x_{\text{horiz,prestige}} + h_{\text{c}}x_{\text{horiz,conformity}}, \quad (4)$$

173

174 where h_{p} (horizontal social learning; prestige bias) and h_{c} (horizontal social learning; conformity
175 bias) again reflect unlinked and evolving diploid loci (again bounded between -10 and 10) that
176 reflect sensitivity to both horizontally learned social cues $x_{\text{horiz,prestige}}$ and $x_{\text{horiz,conformity}}$ respectively.
177 A full description of the socially learned cues is given in section 2 of the online supplement.

178 **3 Results**

179 **3.1 Result 1: sensitivity to a single cue dominates, but multiple cues are in-** 180 **involved in adaptation**

181 Figure 2 depicts four example scenarios -- in which the intrinsic reliability of different cues is
182 varied -- that demonstrate how sensitivities to cues jointly evolve in environments that change at
183 different rates of change $1 - p$. To highlight the relative importance of each cue, Figure 2 shows the
184 proportion of variance in the adult phenotype (measured at the logistic scale) that is explained by
185 sensitivity to each cue, while the evolved values of the sensitivities a_i , m_i , h_i and v_i (see eqns. [2,

186 4]) are depicted in Figure S2.

187 Throughout Figure 2, we find that sensitivity to a single cue explains the large majority of
188 phenotypic variation in adult phenotypes, at least when environments are sufficiently predictable
189 (by being either sufficiently positively or negatively autocorrelated). Moreover, dominant cues are
190 always individually or socially learned, as opposed to genetic cues or maternal effects. In pos-
191 itively autocorrelated environments (left-hand side of each panel in Figure 2), either individual
192 learning (green lines) or social learning driven by prestige biases (horizontal [yellow] or vertical
193 [pink]) prevails. Evolved sensitivities to all other cues explain substantially less phenotypic vari-
194 ance. The prevalence of individual and social learning in predictable environments is unsurprising,
195 as either acquiring direct cues about the environment (individual learning) or obtaining cues about
196 the sampled phenotype with the highest survival in the current environment (prestige-based social
197 learning) provides most information about current conditions.

198 Only when environments become unpredictable (around the middle of each panel in Figure 2),
199 do individuals start to rely on multiple cues, yet actual sensitivities to the different cues are close to
200 zero (see Figure S2). When environments become largely unpredictable, individuals do not make
201 use of much information at all, but rather develop a conservative bet-hedging strategy with $u_{ad} = 0.5$.

202 When environments are negatively autocorrelated (right-hand sides of Figure 2B-D), again
203 either individual or social learning prevails. Interestingly, however, if horizontal social learning
204 prevails, it is typically based on conformity biases rather than the prestige biases that are observed
205 in positively autocorrelated environments. Moreover, we find that sometimes multiple cues pre-
206 dominate (e.g., right-hand side of Figure 2C), such as a combination of horizontal social learning
207 based on conformity (grey lines) and vertical social learning (pink lines) based on prestige.

208 Figures 2B-D show that once the information content of socially learned cues is high enough,
209 they explain the majority of phenotypic variance, while individual learning is far less important.
210 This raises the question what phenotypic information is learned from others in the absence of
211 individual learning, as previous theory suggests that combinations of individual learning and social
212 learning are expected to evolve (e.g., [3, 4, 8]). Figure S3 shows that even when individual learning

213 cannot evolve, social learning still prevails over all other cues. Indeed, social learning still prevails
214 when it only coevolves with genetic cues on phenotype determination (Figure S3A) or maternal
215 cues (Figure S3B). Only when there are no other cues than horizontally learned social cues is
216 there no scope for adaptation (Figure S3C). This is unsurprising, as either individual learning or
217 genes/maternal cues are necessary to result in an adaptive response where phenotypes become
218 associated to their respective environments.

219 **3.2 Result 2: timing of environmental change matters**

220 So far, we have considered a scenario where the environment changes between juvenility and adult-
221 hood. In Figure S5 we consider a scenario where the environment changes at birth instead, implying
222 that non-migrant juveniles and adults encounter the same environmental conditions. For example,
223 this may reflect fluctuating environments where early-life conditions are highly predictive of the
224 later-life environment [38–40]. We now find that either vertical or horizontal social learning based
225 on prestige biases dominates all other cues for all rates of change (Figure S5B-D), even in a ran-
226 domly fluctuating environment. As change only happens at birth, the predicted survival of indi-
227 viduals in the current juvenile environment will be highly predictive of adult selective conditions
228 for any rate of change.

229 Figure 3 generalises the findings above while varying key parameters that affect fidelity of the
230 different cues. Specifically, we vary the fidelity of maternal environmental cues versus individual
231 learning (x -axis) and the fidelity of vertical versus horizontal social learning (y -axis) for both pos-
232 itively (panels A and C) and negatively autocorrelated environments (panels B and D; see Figure
233 S6 for similar results when varying the migration rate). Similar to Figure S5, Figure 3 shows that
234 horizontal social learning prevails over a large range of the parameter space when the environment
235 changes at birth, as the survival of juveniles is fully informative about the later-life environment
236 (Figure S5C, D). Only when horizontal social learning becomes highly error prone (towards bot-
237 tom of each panel), is horizontal social learning replaced by vertical social learning. In either case
238 however, social learning is mostly based on prestige biases. Also, we find that there is little differ-

239 ence between positively and negatively autocorrelated environments once the environment changes
240 at birth, as in this case, the rate of change does not affect the relationship between environments
241 experienced between juvenility and adulthood (Figure S5C, D, see also Figure S5).

242 By contrast, when the timing of environmental change occurs between juvenility and adulthood,
243 horizontal social learning prevails in a more limited range of parameters (compare Figure 3A, B vs
244 C, D). Interestingly, we find that the fidelity of individual learning affects the evolutionary scope
245 of different social learning mechanisms, as prestige based horizontal social learning predominates
246 when individually learned cues have a low fidelity ($q_{\text{ind}} \approx 0.5$, left hand side of each panel in
247 Figure 3A, B). By contrast, conformity based horizontal social learning predominates once the
248 fidelity of individual learning increases. Moreover, also here we find that conformity is more likely
249 to prevail in negatively autocorrelated environments than in positively autocorrelated ones (see also
250 Figure 2B-D). Finally, in a limited range of parameters where the fidelity of individual learning and
251 horizontal and vertical social learning is low ($\sigma_h = \sigma_v = 0.5$, $q_{\text{ind}} = 0.5$), we find that environmental
252 maternal effects prevail as it is the only cue that has a considerable fidelity (as $q_{\text{mat}} = 1$).

253 Overall, Figure 3 shows that horizontal social learning (based on either prestige or conformity)
254 often predominates when it comes to the development of the adult phenotype. This raises the
255 question what cues are important in the development of juvenile phenotypes, as those serve as
256 models for horizontal social learning. Figure S4 shows that individual learning and vertical prestige
257 biases (and rarely also maternal effects) are the most important cues in the development of juvenile
258 phenotypes.

259 **4 Discussion**

260 Here we provide the first model of how individual and social learning are predicted to coevolve
261 with a multitude of other cues on phenotype determination. Our analysis finds that individual
262 learning or social learning (either horizontal or vertical) typically prevails over all other cues, be
263 it genetic cues, maternal environmental cues, maternal phenotypic cues (i.e., cascading maternal

264 effects) or bet-hedging (i.e., no sensitivity to any cue). Only when cues provide little information
265 about the future do we find that individuals resort to conservative bet-hedging (middle of Figure 2,
266 Supplementary Figure S7C, F). Alternatively, when all other cues prove to be unreliable do we find
267 that environmental maternal effects are selectively favoured (see Figure 3 and Figure S8A).

268 The prevalence of individual and social learning is to be expected, as individual learning allows
269 individuals to directly detect the state of the local environment. Social learning provides more indir-
270 ect information about local conditions, as it relies on direct or indirect measures of the performance
271 of others in the local environment: when social learning is based on prestige biases, individuals use
272 cues from the sampled individual with the best performance in the local environment. Figure S8
273 shows that even when these cues are based on a sample of just $n = 2$ individuals, we still find that
274 socially learned cues (mostly based on conformity biases) prevail in a large range of the parameter
275 space. Being able to rank the performance of others' phenotypes provides highly accurate in-
276 formation about the local environment, particularly when the sampled phenotypes themselves have
277 accumulated information about the local environment resulting from individual learning or – when
278 individual learning is absent – from selection-based cues that inform about the local environment
279 (genes or cascading maternal effects: see Figure S3).

280 **4.1 Social learning in positively versus negatively autocorrelated environ-** 281 **ments**

282 When environments are negatively autocorrelated (with environmental change occurring between
283 juvenility and adulthood), Figures 2B,C and 3A,B show that conformity biases are considerably
284 more likely to prevail than prestige biases. To understand why horizontal conformity biases prevail
285 over prestige biases, Figure 4 considers the informative value of all learned cues by depicting
286 their correlations with the adult selective environment. Surprisingly, in negatively autocorrelated
287 environments, cues based on horizontal conformism correlate positively (and relatively strongly)
288 with the adult selective environment, whereas horizontal prestige cues are only weakly negatively
289 correlated. Less surprising is that vertically learned and individually learned cues are all negatively

290 correlated with the environment (with individual learned cues exhibiting negative correlations of the
291 strongest magnitude), as the environment experienced by adults of generation $t - 1$ and by juveniles
292 in generation t is most likely opposite to the selective environment that will be experienced later by
293 adults in generation t .

294 Why do correlations of these different types of social learning with the selective environment
295 diverge in negatively autocorrelated environments (Figure 4)? Note that juveniles will initially use
296 individual/vertical learning to develop a phenotype opposite to their current juvenile environment.
297 This is because long-term selection (in a negatively autocorrelated environment) has shaped reac-
298 tion norms to anticipate that selective conditions experienced in adulthood are likely to differ from
299 the environment experienced as a juvenile (indeed, reaction norms based on individual/vertical so-
300 cial learning are negative on the right-hand sides of Figure S2B-D, so that juveniles born in a low
301 environment are likely to develop a phenotype matching a high environment). Once phenotypes
302 based on individual/vertical learning have developed, juveniles perform horizontal social learning.
303 However, as most juveniles now have phenotypes mismatched to their current juvenile environment
304 (but matched to later conditions), individuals are most likely to take prestige-based cues from ju-
305 venile models with more intermediate phenotypes (as models with more extreme phenotypes have
306 very low predicted survival values in their juvenile environment and are thus disregarded). In turn,
307 phenotypes of intermediate value are equally likely to occur in any environment, thus resulting in a
308 correlation between horizontal prestige and the adult selective environment of a small magnitude.
309 By contrast, when socially learned cues are based on horizontal conformity biases, a cue is taken
310 that simply reflects the majority of phenotypes without considering any measure of current survival.
311 Consequently, if a majority of sampled juveniles has a low phenotype, this is a good indicator that
312 the adult selective environment will likely be in a low state too. Consequently, conformity-based
313 horizontal social cues become strongly (and positively) correlated with the selective environment.

314 Figure 3A,B also shows that the fidelity of individually learned cues affects the prevalence
315 of different horizontally learned social cues. When individually learned cues have a low fidelity
316 ($q_{\text{ind}} \approx 0.5$), we find that horizontal prestige based cues predominate, while horizontal conformity

317 based cues prevail otherwise. Why are prestige biased and conformity based social cues differen-
318 tially affected by the fidelity of individual learning? For low fidelities of individual learning, the
319 distribution of phenotypes in each local deme (before horizontal social learning occurs) is relatively
320 broad, as even modest environmental fluctuations at rates $1 - p = 0.2$ (Figure 3A) distort strong as-
321 sociations between phenotypes and their local environment created by local adaptation [12, 17].
322 Consequently, horizontal social learning based on the most frequent phenotype provides little in-
323 formation, as each local deme has a mixture of low and high-adapted phenotypes. By contrast,
324 prestige-based measures of predicted phenotypic performance in the current environment provide
325 a more direct measure of the current environment and therefore prevail. However, once individual
326 learning has a higher fidelity, it allows individuals to modulate their phenotype and match it with
327 the local environment. Consequently, individual learning creates a strong association between the
328 number of individuals with a low versus a high phenotype and their local environment, thus increas-
329 ing the value of conformity-based horizontal social learning, as this is based on strong differences
330 in the numbers of low versus high phenotypes between both environments.

331 **4.2 Why is vertical social learning based on conformity so rare?**

332 Another finding of the current study is that vertical social learning based on conformity rarely
333 predominates, similar to genetic and maternal environmental cues. Vertical conformity biases rarely
334 dominate because they rely on cues about the distribution of parental adult phenotypes, which are,
335 to a large part, a result of cues received in their own juvenile environment at time $t - 1$, resulting
336 in outdated information about adult selection at time t . Indeed, Figure 4 shows that the magnitude
337 of the correlation of vertical conformity based cues is small relative to other cues. By contrast,
338 cues based on vertical prestige biases reflect the performance of parental phenotypes in the current
339 (juvenile) environment and are therefore superior to vertical conformism. Moreover, while the
340 relative importance of horizontal prestige versus horizontal conformity is affected by the fidelity
341 of individual learning (see previous paragraph), there is no such interaction between individual
342 learning and the prevalence of vertical prestige vs vertical conformity cues (see bottom of each

343 panel in Figure 3). Again, because individually learned cues provide more recent information about
344 the environment than vertically learned cues, any increase in the fidelity of individual learning tends
345 to replace vertical social learning, rather than affect the evolutionary scope of vertical conformity
346 versus prestige. As found previously [41], the above demonstrates that the order of individual
347 learning versus social learning is likely to strongly affect the evolutionary scope of different forms
348 of social learning.

349 In some cases, prestige-based cues – which presuppose information of the predicted survival
350 of observed phenotypes – will not be available, so that individuals have to resort to other means
351 of cue integration. In this case, conformity-based cues may be more general, as they do not rely
352 on direct environmental information, but on a type of ‘crowdsourcing’ in which the most prevalent
353 phenotype of the crowd informs one about the coming environment. Figure S9 shows that when
354 social learning is only based on conformism (while prestige-based cues are excluded), horizontal
355 social learning indeed replaces prestige-based social learning. However, the same does not hold for
356 vertical prestige-based cues, as those are replaced by environmental maternal effects and individual
357 learning. Consequently, we find again that vertical social learning based on conformity does not
358 prevail.

359 While a direct measure of survival as required by prestige-based cues may typically not be
360 feasible, more indirect measures of prestige are still possible, for example when survival depends on
361 some aspect of phenotypic quality (apart from the phenotype itself; e.g., health or energy reserves)
362 and this quality can be observed, a ranking would be possible. However, the ability to rank others
363 dependent on quality could also imply that a focal individual may have information about its own
364 quality as well, which is something that is not included in the current model. It is likely that
365 personal information about a focal individual’s state may affect the likelihood that it engages in
366 individual or social learning. For example, when genes or maternal effects already provide a good
367 solution for a particular individual, there will not be much reason to copy others. By contrast,
368 when genes or maternal effects provide suboptimal solutions, there will be strong reasons to copy
369 others. Consequently, if cue integration depends on an individual’s state, we would expect strong

370 between-individual differences in cue integration, so that multiple cues are used by the population
371 as a whole. Indeed, such state-dependent [42] social information use may be an important for
372 explaining the existence of consistent individual differences in social learning strategies between
373 individuals [43, 44] and should be a subject of future modelling attempts.

374 **4.3 Socially learned cues based on detection versus selection**

375 In a seminal paper by Shea et al. [27] (see also [33]), the information content of different cues has
376 been classified as either selection-based or detection-based, with the aim of explaining differences
377 in inheritance fidelity. Selection-based cues arise when phenotypic variants become correlated
378 to a local environment through differential selection. An example are genetic cues, where local
379 adaptation results in the association of different genetic variants to different selective conditions
380 [12, 13, 15] or maternal phenotypic effects, where selection on the maternal phenotype before
381 reproduction results in associations between the maternal phenotype and the local environment
382 [16, 18, 19, 33]. By contrast, detection-based cues arise when information is directly detected
383 from the environment and subsequently used to modulate phenotypes (which can subsequently
384 be transmitted to offspring). The obvious example of such a detection-based effect is individual
385 learning, but also maternal environmental effects resemble a scenario where a phenotype is only
386 transmitted to offspring once it has been detected [27]. In case of social learning, prestige-based
387 cues are clearly detection-based, as they involve a measure of phenotypic performance in its current
388 environment. By contrast, conformity-based cues can be both selection and detection-based, as
389 conformity is a function of the distribution of the different phenotypes in the local deme: this
390 distribution is both a result of differential survival selection and of individuals modulating their
391 phenotypes via detection-based mechanisms (i.e., individual learning). Consequently, conformity-
392 based social learning can result in either short-term inheritance of variants (when those variants are
393 newly generated each generation through detection-based mechanisms), or it can result in long-term
394 inheritance (when a variant is copied because it is the most frequent due to differential selection).

395 **4.4 Future work**

396 The current study has only scratched the surface when it comes to integrating social learning and
397 cultural evolution with other forms of cue integration. To study the interplay of different cue in-
398 tegration mechanisms, our model considered a scenario of local adaptation to a spatiotemporally
399 environment that fluctuates between two types, as has been the subject of numerous previous mod-
400 els of cue integration (e.g., [17, 20, 32]). However, studies in the context of social learning have
401 considered different environmental configurations, such as a scenario in which the environment
402 changes into a previously unknown state (i.e., similar to 'infinite states' models of social learning
403 [4, 6]). It would be interesting to assess the consequences of more continuous forms of envir-
404 onmental variation for the evolution of cue integration. Based on somewhat similar models that
405 considered the effect of large environmental changes to adaptation, we expect that combinations of
406 multiple cues would prevail in such circumstances ([45], Figure 2 in [16]). In particular, we would
407 predict that not only individual learning prevails (to acquire information about the most recent state
408 of the environment; e.g., [4, 6]), but also mechanisms to ensure recently acquired phenotypes are
409 inherited across generations (e.g., (vertical) social learning and cascading maternal effects), as any
410 genetic inputs to the trait are likely to slowly evolve to an ever changing environment and hence be
411 largely outdated. Future studies are needed to consider the evolution of cue integration mechanisms
412 in such environmental configurations.

413 Also, the timing at which individuals obtain information from different types of cues could sub-
414 stantially affect the outcome (e.g., [36]). For the sake of tractability, our study focused on a scen-
415 ario in which individuals perform vertical social learning and individual learning before migration,
416 while horizontal social learning was performed following migration (see Figure 1). In Supplement-
417 ary Figures S6 and S7 we have, however, relaxed these assumptions, for different probabilities of
418 migration. Unsurprisingly, if migration is relatively low, the timing at which learning occurs has
419 little impact and outcomes are very similar to those in Figure 3. When dispersal probabilities are
420 higher, we find that the latest cues received (i.e., those received subsequent to migration) prevail
421 over all others. For example, in Supplementary Figure S6G-L, both vertical and horizontal social

422 learning occur subsequent to migration, whereas individual learning occurs prior to migration. As
423 a consequence, we find that individual learning is nearly absent when migration rates are high (Fig-
424 ure S6I, L). By contrast, when individual learning occurs subsequent to migration, it prevails for a
425 much wider range of the parameter space, particularly when migration rates are high (Figure S7I,
426 L). Finally, when neither cue is received subsequent to migration, we find that conservative bet-
427 hedging prevails when migration rates are high (Figure S7C, F). Hence, as noted in the main results
428 in which we varied the timing of environmental change, the timing of the different learning events
429 also matters for the predominance of different cues over others. We advocate for more studies that
430 systematically vary the timing at which (combinations of) different cues are obtained during the
431 life cycle.

432 In relation to the timing of cues, our model also assumes that selection only acts during adult-
433 hood, prior to reproduction (following previous models: [12, 16, 17]). By contrast, how individuals
434 integrate suits of different cues when selection acts on juveniles vs adults has yet to be assessed.
435 We would expect that selection on juveniles (e.g., prior to horizontal learning) would have a similar
436 effect to setting the timing of environmental change to birth (see Figure S5 and Figure 3C, D).
437 Once selection acts during early life, only those juvenile phenotypes that match the local envir-
438 onment will survive. Consequently, the juvenile phenotype becomes more informative about the
439 later-life environment, thus favouring higher levels of horizontal social learning as in Figure 3C,
440 D. Overall, future studies are needed to systematically analyse how adaptive cue integration varies
441 across different stages of the life cycle.

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448 **5 Figure captions**

449 **Figure 1** Panel A: The life cycle of the model and the different types of cues: abiotic enviro-
450 nmental cues (white arrows), heritable cues (red arrows), vertical social cues (purple arrows)
451 and horizontal social cues (yellow arrows). Panel B: survival probabilities in high and low en-
452 vironments for different adult phenotypes u_{ad} , where $S_{low} = 1 - 0.8u_{ad}^2$ and $S_{high} = 1 - 0.8(1 - u_{ad})^2$
453 (following eqns [1,2] in [17]). Throughout the main text, we assume that vertical social learning
454 and individual learning occur prior to migration, while horizontal social learning follows migra-
455 tion. However, we relax these assumptions in the Online Supplement: in Figure S6G-L vertical
456 social learning occurs after migration, in Figure S7A-H horizontal social learning occurs before
457 rather than after migration and in Figure S7G-L individual learning occurs after rather than before
458 migration (see section “future models” in discussion).

459 **Figure 2** The proportion of variance in adult phenotype (measured at the logistic scale) explained
460 by sensitivity to each cue when varying the probability of environmental change. Each dot reflects
461 the average proportion over $n = 5$ replicate simulations, while envelopes reflect sample standard
462 deviations. Panel A: in case there is substantial noise in horizontal and vertical social learning,
463 individual learning becomes the most important cue on phenotype determination. Panel B: with
464 no noise in horizontally and vertically learned cues, we find that horizontal social learning based
465 on prestige (h_p) prevails in positively autocorrelated environments, while individual learning (a_{ind})
466 prevails in negatively correlated environments. Interestingly, for strongly negatively autocorrel-

467 ated environments, we find that a combination of individual learning and horizontal social learning
 468 based on conformity (h_c) prevails. Panel C: when individually learned environmental cues are un-
 469 reliable ($q_{\text{ind}} = 0.5$), we find that this has little effect on horizontal social learning based on prestige
 470 (h_p ; compare with panel B), yet individuals now more strongly rely on vertically learned cues
 471 based on prestige rather than individually learned cues. Panel D: when both individually learned
 472 and horizontally learned cues are unreliable, vertically learned cues based on prestige prevail in
 473 autocorrelated environments. Parameters: Panel A: $\sigma_h = 1.0$ (high noise in horizontal social learn-
 474 ing), $\sigma_v = 1.0$ (high noise in vertical social learning), $q_{\text{ind}} = 1.0$ (high fidelity of individual learning).
 475 Panel B: $\sigma_h = \sigma_v = 0$, $q_{\text{ind}} = 1.0$. Panel C: $\sigma_h = \sigma_v = 0$, $q_{\text{ind}} = 0.5$. Panel D: $\sigma_h = 1.0$, $\sigma_v = 0$, $q_{\text{juv}} = 0.5$.
 476 Other parameters: $q_{\text{mat}} = 0.5$, $d = 0.1$, $n_c = n_h = n = 5$. Variance proportions were calculated through
 477 ordinary least squares multiple regression of \bar{x}_{ad} on the right-hand side terms in eq. [3] and then
 478 calculating $\eta^2 = \text{SS}_{\text{between}}/\text{SS}_{\text{total}}$ for each independent variable (i.e., the partial R^2 also known as the
 479 ‘classical’ η^2).

480 **Figure 3** The cue that explains the largest proportion of adult phenotypic variance when varying
 481 the fidelity of individually learned versus maternal cues (x -axis, with values varying from $q_{\text{ind}} =$
 482 $0.5, q_{\text{mat}} = 1.0$ [left-hand side] to $q_{\text{ind}} = 1.0, q_{\text{mat}} = 0.5$ [right-hand side]) and the fidelity of vertical
 483 versus horizontal socially learned cues (y -axis, with values varying from $\sigma_{\text{vert}} = 0, \sigma_{\text{horiz}} = 1$ [bottom]
 484 to $\sigma_{\text{vert}} = 1, \sigma_{\text{horiz}} = 0$ [top]). Panels A, B: environmental change occurs between juvenility and
 485 adulthood. Panels C, D: environmental change occurs at birth. Parameters: $d = 0.1$, $n_c = n_h = 5$.
 486 Migration rates d are varied in Figure S6, while the sample of potential socially learned model
 487 individuals $n = n_c = n_h$ is varied in Figure S8.

488 **Figure 4** Informational value of the different learned cues. Depicted are the correlations between
 489 the adult selective environment $\theta(t)$ and individually and socially learned cues at the preceding ju-
 490 venile stage. When environments are positively autocorrelated (left-hand side where $1 - p < 0.5$)
 491 we find that vertical conformity-based cues are (on average) the worst predictor of the selective
 492 environment, whereas horizontal prestige-based cues are the best predictor of the selective environ-

493 ment. By contrast, in negatively autocorrelated environments, horizontal conformism-based cues
494 are positively correlated with the selective environment, while all other cues are typically negat-
495 ively correlated. Individually learned cues and conformity-based horizontal social cues have the
496 largest magnitude in negatively autocorrelated environments. Each dot depicts the average correl-
497 ation over 5 replicate simulations, while envelopes reflect sample standard deviations. Parameters
498 as in Figure 2B.

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Figure 1

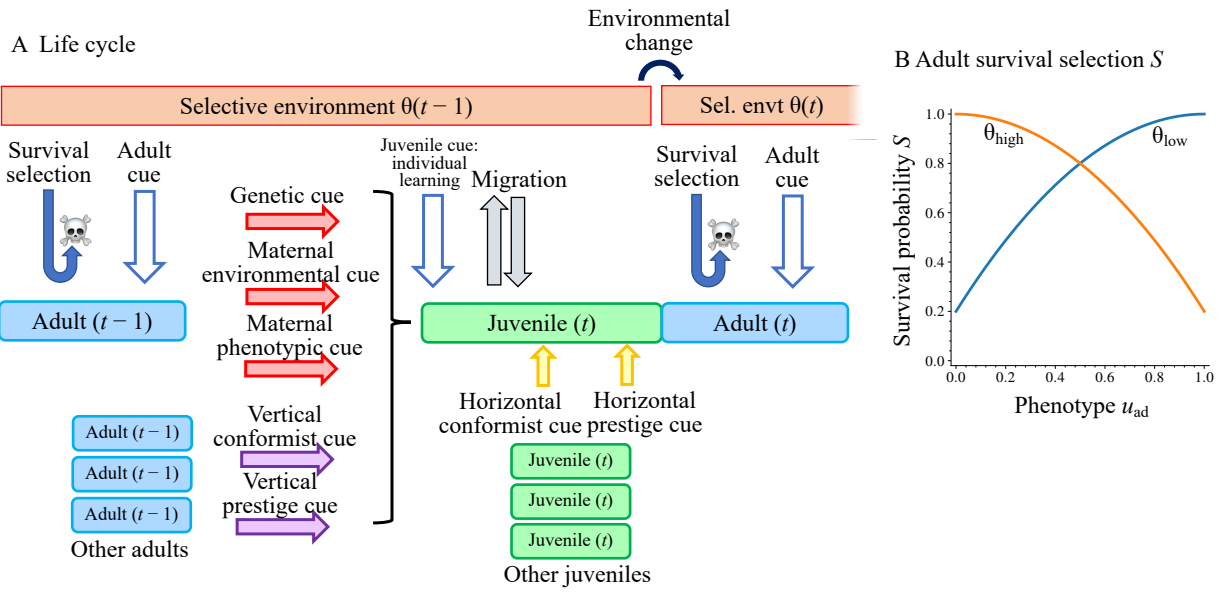


Figure 1:

622 **6 Figures**

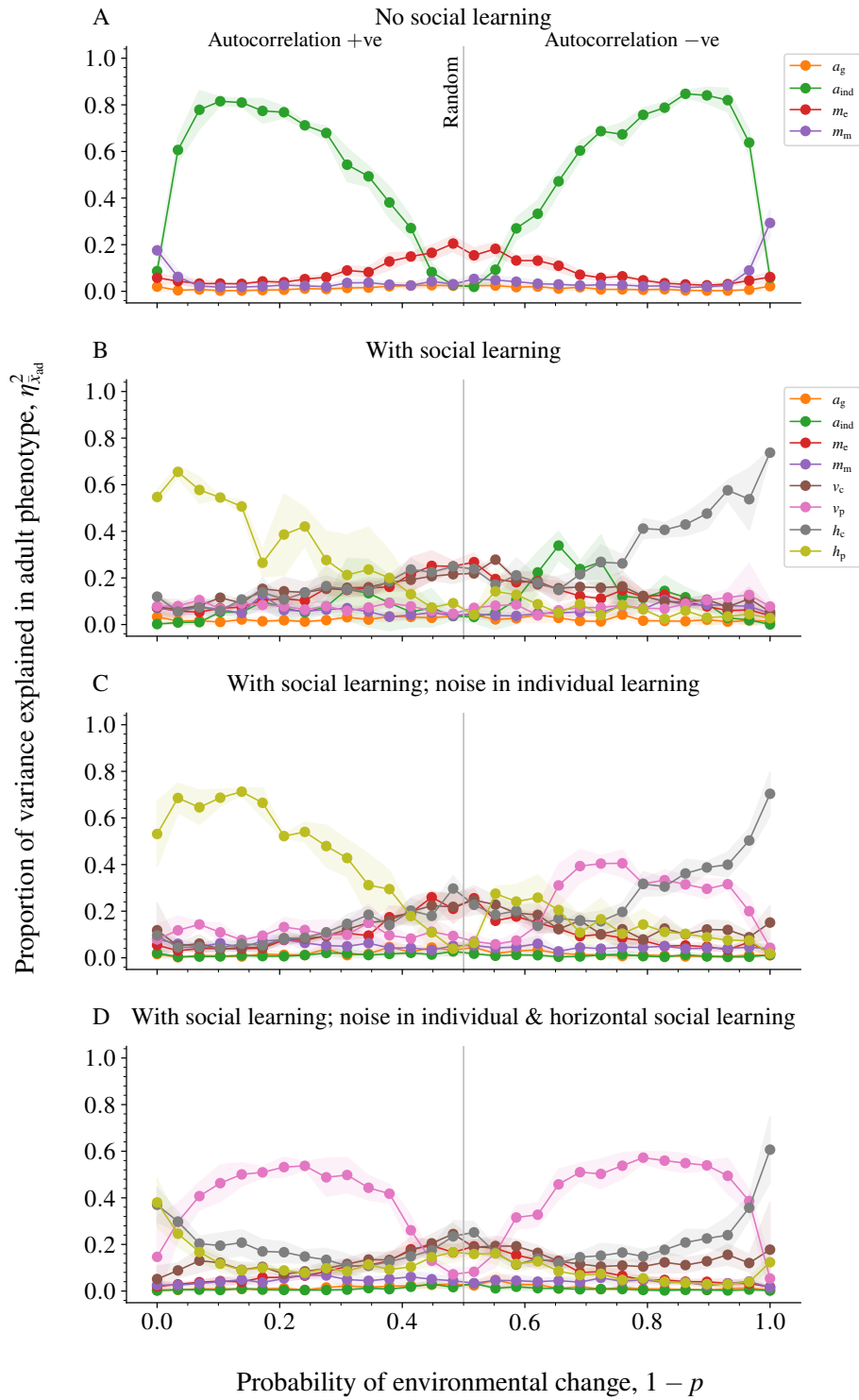


Figure 2:

Figure 3

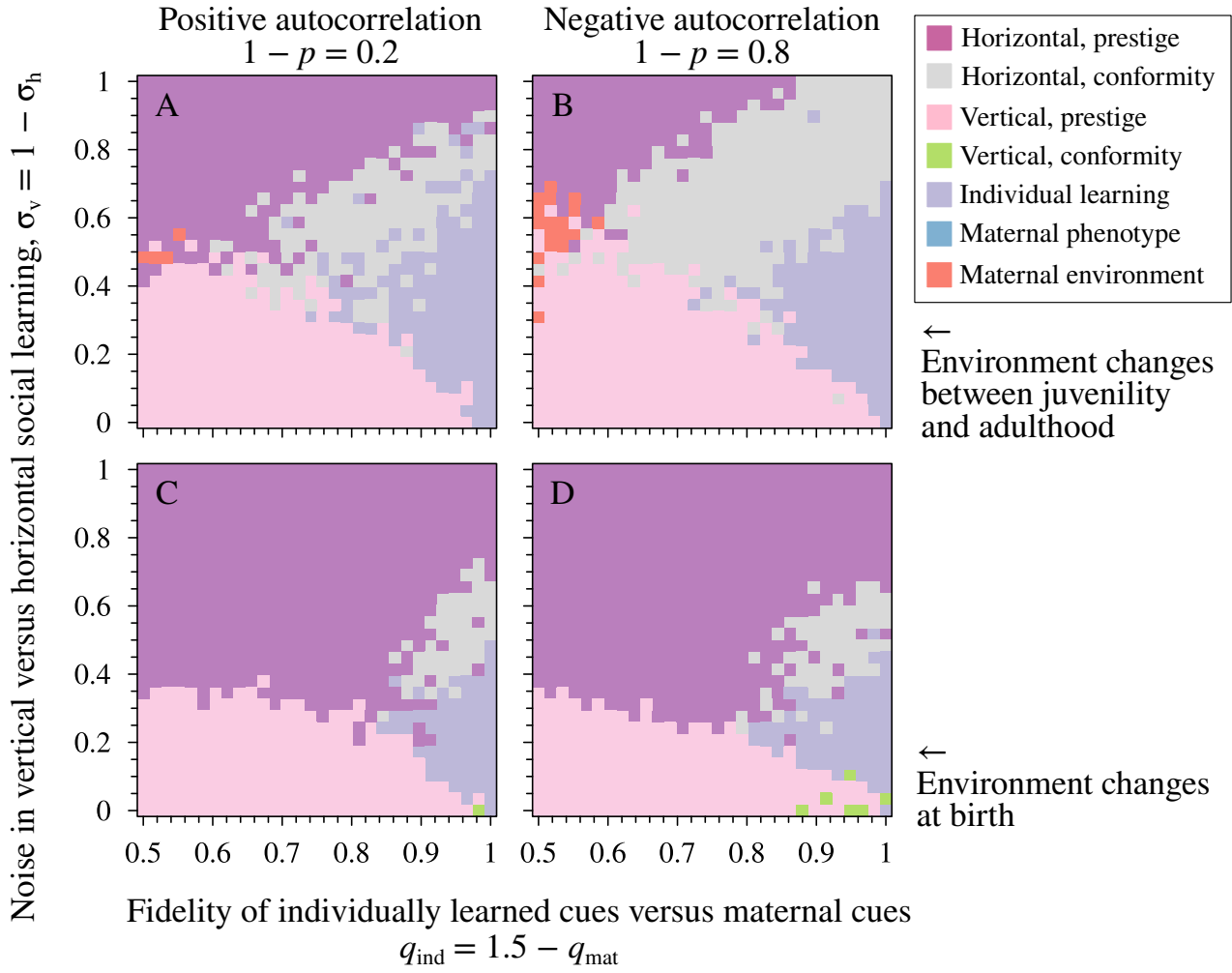


Figure 3:

Figure 4

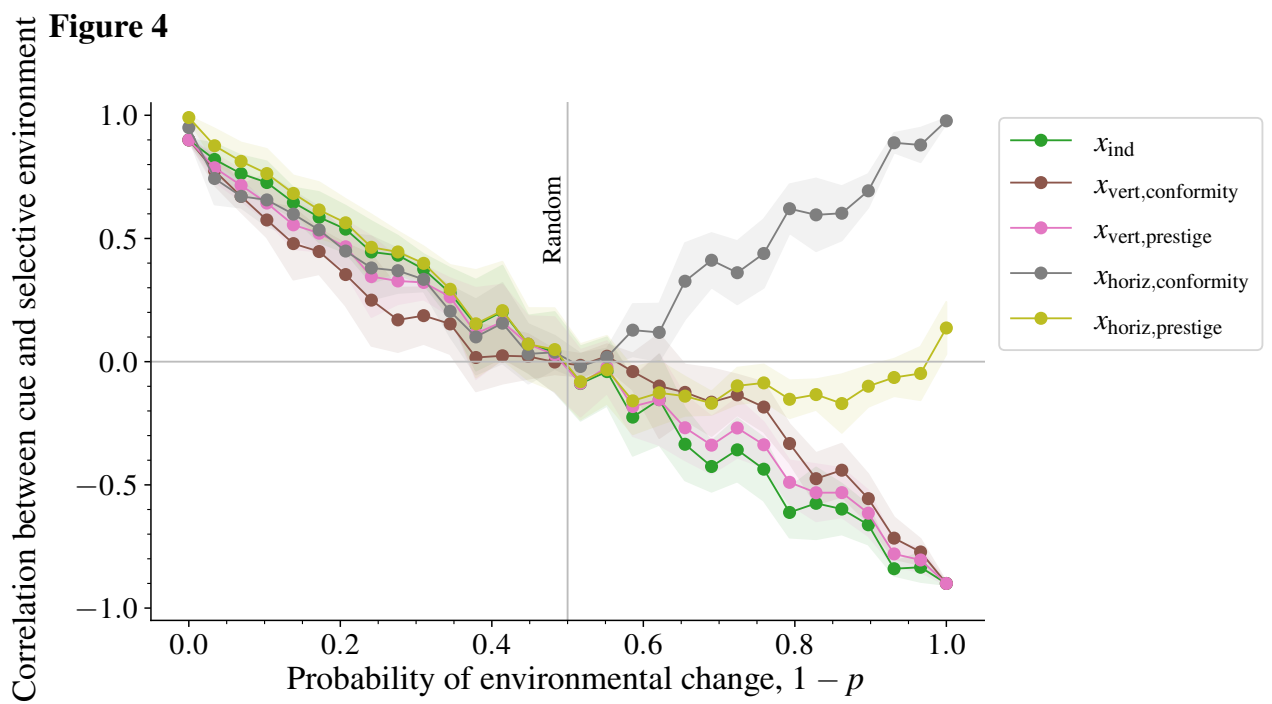


Figure 4: