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Cultural Evolution: A Review Of Theory, Findings and Controversies

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24 **Abstract**

25 The last two decades have seen an explosion in research analysing cultural change as a
26 Darwinian evolutionary process. Here I provide an overview of the theory of cultural
27 evolution, including its intellectual history, major theoretical tenets and methods, key
28 findings, and prominent criticisms and controversies. 'Culture' is defined as socially
29 transmitted information. Cultural evolution is the theory that this socially transmitted
30 information evolves in the manner laid out by Darwin in *The Origin of Species*, i.e. it
31 comprises a system of variation, differential fitness and inheritance. Cultural evolution is
32 not, however, neo-Darwinian, in that many of the details of genetic evolution may not
33 apply, such as particulate inheritance and random mutation. Following a brief history of
34 this idea, I review theoretical and empirical studies of cultural microevolution, which
35 entails both selection-like processes wherein some cultural variants are more likely to be
36 acquired and transmitted than others, plus transformative processes that alter cultural
37 information during transmission. I also review how phylogenetic methods have been used
38 to reconstruct cultural macroevolution, including the evolution of languages, technology
39 and social organisation. Finally, I discuss recent controversies and debates, including the
40 extent to which culture is proximate or ultimate, the relative role of selective and
41 transformative processes in cultural evolution, the basis of cumulative cultural evolution,
42 the evolution of large-scale human cooperation, and whether social learning is learned or
43 innate. I conclude by highlighting the value of using evolutionary methods to study culture
44 for both the social and biological sciences.

45

46 **Keywords:** cultural evolution; cultural transmission; cumulative culture; demography;
47 human evolution; social learning.

48 **Introduction**

49 *Cultural evolution* is the theory that cultural change in humans and other species can be
50 described as a Darwinian evolutionary process, and consequently that many of the
51 concepts, tools and methods used by biologists to study biological evolution can be
52 equally profitably applied to study cultural change (Mesoudi 2011a; Richerson and Boyd
53 2005; Richerson and Christiansen 2013). ‘Culture’ here entails any socially (rather than
54 genetically) transmitted information, such as beliefs, knowledge, skills or practices. Just
55 as biologists seek to explain the diversity and complexity of life and living organisms,
56 cultural evolution researchers seek to explain the diversity and complexity of culture and
57 cultural phenomena.

58

59 Evolutionary biologists to whom I speak are sometimes surprised by the depth and
60 diversity of modern cultural evolution research. Just three decades ago cultural evolution
61 research was the almost-secret passion of a handful of scholars, and limited in method to
62 rather technical mathematical models (Boyd and Richerson 1985; Cavalli-Sforza and
63 Feldman 1981). The last two decades, however, have seen an explosion in cultural
64 evolution research. The use of mathematical models continues to occupy the core of the
65 field (Aoki and Feldman 2014; Enquist et al. 2011; Kempe et al. 2014; Lehmann et al.
66 2011; H. M. Lewis and Laland 2012; McElreath and Henrich 2006), but has been
67 supplemented with laboratory experiments testing the assumptions and predictions of
68 those models (Derex et al. 2013; Kempe et al. 2012; Kirby et al. 2008; McElreath et al.
69 2008; Mesoudi and Whiten 2008; T. J. H. Morgan et al. 2011); field studies doing the same
70 in real-life settings (Aunger 2000; Henrich and Henrich 2010; Hewlett et al. 2011; Reyes-
71 Garcia et al. 2009); phylogenetic studies that reconstruct the evolutionary relationships

72 between languages (Bouckaert et al. 2012; Dunn et al. 2011; Pagel 2009), artefacts (Lipo
73 et al. 2006; Lycett 2009; O'Brien et al. 2014; Tehrani and Collard 2002) and texts
74 (Barbrook et al. 1998; Ross et al. 2013; Tehrani 2013); the study of historical dynamics
75 using ecological models (Turchin 2008; Turchin et al. 2013); and the comparative study of
76 non-human culture using many of the same methods as applied to humans (Dean et al.
77 2014; Laland and Galef 2009; Lycett et al. 2007; Whiten 2005).

78

79 The aim of this article is to review the theoretical foundations of this burgeoning work,
80 provide some examples of how evolutionary concepts and methods have illuminated
81 cultural phenomena, and explore recent controversies and outstanding research
82 questions in the field.

83

84 **A brief history of cultural evolution**

85 Long before Darwin published *The Origin of Species* in 1859, historical linguists were
86 constructing trees of historical descent for languages, based on the principle that more
87 similar contemporary languages most likely shared a more recent common ancestor (van
88 Wyhe 2005). In other words, that languages - which are socially transmitted, given that
89 there are no genes for specific languages such as English or Hindi - gradually evolve over
90 time and thus show the same descent with modification that Darwin was later to apply to
91 species. It is unclear whether these linguistic trees directly influenced Darwin (although
92 intriguingly, one of the major proponents of historical linguistics in England was Hensleigh
93 Wedgwood, Darwin's cousin and future brother-in-law: van Wyhe 2005). It *is* clear,
94 however, that Darwin very quickly saw clear parallels between how species and
95 languages change over time:

96

97 “The formation of different languages and of distinct species, and the
98 proofs that both have been developed through a gradual process, are
99 curiously parallel...We find in distinct languages striking homologies
100 due to community of descent. The frequent presence of rudiments,
101 both in languages and in species, is still more remarkable. Dominant
102 languages and dialects spread widely, and lead to the gradual
103 extinction of other tongues. A language, like a species, when once
104 extinct, never reappears. We see variability in every tongue, and new
105 words are continually cropping up; but as there is a limit to the powers
106 of the memory, single words, like whole languages, gradually become
107 extinct. The survival or preservation of certain favoured words in the
108 struggle for existence is natural selection.” (Darwin 1871, p. 90)

109

110 Here, Darwin went further than merely applying the notion of common descent to
111 languages, as the linguists had done. He also applied his mechanism of natural selection
112 to language change. Similar parallels were drawn between biological evolution and
113 technological evolution by Augustus Pitt-Rivers around the same time (Pitt-Rivers 1875),
114 whose museum in Oxford was, and still is, innovative in displaying archaeological and
115 ethnographic items according to their presumed evolutionary relationships, rather than
116 their age or collector.

117

118 In an alternative universe, these strands of evolutionary thinking in the social sciences
119 would have matured into a quantitative and rigorous science of cultural evolution, in the

120 same way that evolutionary theory became established in the biological sciences via
121 population genetics models in the early 1900s and then the evolutionary synthesis in the
122 1940s (Mayr 1982). Sadly, cultural evolution instead took an unfortunate wrong turn. In
123 the late 1800s several anthropologists and sociologists devised schemes of cultural
124 evolution based not on Darwin's theory of descent-based trees and natural selection, but
125 rather on Herbert Spencer's progressive, ladder-like, unilinear theory of evolution
126 (Freeman 1974). These schemes, such as those of Morgan (1877) and Tylor (1871), saw
127 cultural evolution as the inevitable progress of entire societies along a sequence of fixed
128 stages of increasing advancement, starting at savagery and barbarism, and ending at
129 civilisation. 'Civilisation' typically resembled the Victorian English or American societies of
130 the schemes' authors.

131

132 The racist tones of these theories is obvious today but not unusual in that time of cultural
133 imperialism, and these Spencerian schemes were often used to justify the subjugation of
134 supposedly 'less evolved' societies by 'more evolved' ones, frequently mixed in with
135 ideas of eugenics. A later wave of anthropologists such as Franz Boas (Boas 1940; see H.
136 S. Lewis 2001) quite correctly rejected these progressive Spencerian theories not just
137 because of their political motivation but also, perhaps more importantly, because they
138 have little empirical basis. Entire societies simply do not fit into neat stages of increasing
139 complexity. For many socio-cultural anthropologists today, however, this association
140 between evolution and stage-like progression remains. It is worth emphasising that these
141 progressive Spencerian theories are not what is meant by 'cultural evolution' today, which
142 draws on Darwin's theory of evolution rather than Spencer's, the latter of which resembles
143 the development of an individual rather than the evolution of a population.

144

145 During the mid-twentieth century a few isolated scholars maintained that a properly
146 Darwinian theory of cultural evolution was viable, such as the psychologist Donald
147 Campbell (Campbell 1965). Richard Dawkins provoked interest but little actual empirical
148 research with his notion of the 'meme' in the final chapter of *The Selfish Gene* (Dawkins
149 1976), intended to illustrate the substrate-neutrality of his replicator-based theory of
150 evolution. However, just as evolutionary theory in the biological sciences only really
151 became useful once it had been formalised mathematically by population geneticists
152 such as Fisher, Haldane and Wright in the early 1900s, cultural evolution only really took
153 off once two pairs of scholars devised quantitative mathematical models of cultural
154 evolution in two books in the 1980s: one by Marc Feldman and Luigi Luca Cavalli-Sforza
155 (Cavalli-Sforza and Feldman 1981) and the other by Robert Boyd and Peter Richerson
156 (Boyd and Richerson 1985). These books were also notable in taking seriously the
157 differences between biological and cultural evolution, rather than simply importing
158 biological analogies to the cultural case, as perhaps both Campbell and Dawkins were
159 guilty of doing. The following section outlines the theoretical basis of cultural evolution as
160 presented in these books, and which has inspired much subsequent research.

161

162 **The theory of cultural evolution**

163 Many textbook definitions of evolution talk of changes in gene frequencies or require
164 Mendelian rules of genetic inheritance. While this is reasonable when one's focus is
165 exclusively on biological (i.e. genetic) evolution, Darwin's theory can quite easily be
166 formulated in a general, mechanism-neutral manner. After all, Darwin himself knew
167 nothing about genes or Mendelian inheritance when he wrote *The Origin*. Lewontin (1970)

168 expressed this generality by defining evolution as comprising three principles, each of
169 which were clearly specified in *The Origin*:

170

- 171 1. Different entities in a population vary in their characteristics (principle of variation)
- 172 2. These entities have different rates of survival and reproduction (principle of differential
173 fitness, or what Darwin called a 'struggle for existence')
- 174 3. There is a correlation between parent and offspring entities in those characteristics that
175 contribute to differential fitness (principle of inheritance)

176

177 Lewontin (1970) goes on to state that:

178

179 "It is important to note a certain generality in the principles. No
180 particular mechanism of inheritance is specified, but only a correlation
181 in fitness between parent and offspring. The population would evolve
182 whether the correlation between parent and offspring arose from
183 Mendelian, cytoplasmic, or cultural inheritance." Lewontin (1970, p.1).

184

185 The theory of cultural evolution holds that cultural change can be described by these
186 three general principles (Mesoudi et al. 2004), as Lewontin (1970) alludes to when he talks
187 of cultural inheritance¹. Thus, cultural traits (words, ideas, artefacts etc.) exhibit variation;
188 these variants have different rates of survival and reproduction; and they are transmitted

¹ Confusingly, the terms 'social learning', 'social transmission', 'cultural transmission', 'cultural inheritance' and variants thereof are used interchangeably within the field, to denote the passing of information non-genetically from one individual to another. Here I stick to the term 'social learning', although this may differ from cited sources.

189 from person to person via social learning mechanisms such as imitation or speech.

190

191 To give a concrete example, Lieberman et al. (2007) used vast quantitative databases of
192 English verb usage over the past 1200 years to show that, at any single point in time,
193 verbs have often varied in their past tense form, including regular (e.g. chided) and
194 irregular (e.g. chid, chode) forms (principle of variation), and that regular forms have
195 steadily displaced irregular forms particularly for those verbs that are infrequently used
196 (principle of differential fitness). Given that verb form is learned from others just like other
197 aspects of one's language (Harris 1995; Labov 1972), the principle of inheritance is also
198 observed. So this provides quantitative support for Darwin's informal suggestion in the
199 quote above that words vary, they compete for expression, and they are transmitted from
200 person to person. Thus, they evolve. Similar observations can be made for technology,
201 such as the replacement of traditional seed corn with hybrid seed corn in Iowa during the
202 1940s (Henrich 2001; Ryan and Gross 1943), or any number of other well-documented
203 examples of the diffusion of innovations (E. Rogers 1995) and changing frequencies of
204 archaeological artefacts such as pottery types (Shennan 2002).

205

206 Beyond these three general principles derived from *The Origin*, no further assumptions
207 are made about the mechanisms by which the principles operate. We do not need to –
208 and often should not – impose mechanisms that are specific to biological evolution onto
209 cultural evolution. These might include the mechanisms of genetic inheritance, such as
210 the acquisition of information in equal contribution from two parents or the existence of
211 discrete units that are inherited in a particulate fashion, or the randomness of genetic
212 mutation with respect to fitness. In Mesoudi (2011a), I expressed this as follows: cultural

213 evolution is *Darwinian*, in that it comprises the three general principles of variation,
214 differential fitness and inheritance as laid out by Darwin in *The Origin*, but it is not *neo-*
215 *Darwinian*, in that it may not necessarily exhibit the specific mechanisms of genetic
216 inheritance, random mutation etc. that biologists subsequent to Darwin discovered and
217 that were integrated into evolutionary theory during the evolutionary synthesis.

218

219 Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) constructed
220 quantitative mathematical models of cultural evolution using the tools of population
221 genetics, and which clearly made this distinction. Cavalli-Sforza and Feldman (1981)
222 constructed models that explored the transmission of cultural traits not only from one's
223 biological parents (vertical social learning) but also from peers (horizontal social learning)
224 and from older unrelated members of the parental generation (oblique social learning).
225 They constructed models of cultural mutation, analogous to genetic mutation, where
226 novel cultural traits appear at random; cultural selection, analogous to natural selection,
227 where certain cultural traits are more likely to be learned and transmitted than others; and
228 cultural drift, an analogue of genetic drift, where cultural traits change in frequency due to
229 chance. They explored the consequences of migration and other demographic processes
230 for cultural diversity. They also modelled the evolution of continuous cultural traits,
231 abandoning the assumption of discrete replicators and particulate inheritance. Contrary to
232 Dawkins (1976), these models demonstrated that discrete replicators are not necessary
233 for evolution, all that is required is some form of variation, be it discrete or continuous,
234 and some form of inheritance, be it particulate or blending (Henrich and Boyd 2002).

235

236 Boyd and Richerson (1985) constructed models adding psychological realism to the

237 notion of cultural selection, modelling cases where people preferentially copy the traits of
238 successful or prestigious individuals (indirect or prestige bias), copy traits on the basis of
239 their popularity (frequency-dependent bias, with positive frequency-dependence called
240 conformity, and negative frequency-dependence called anti-conformity), or copy traits
241 based on their intrinsic characteristics (e.g. their memorability or usefulness, known as
242 direct or content bias). They also constructed models whereby individuals transform
243 cultural traits in particular, non-random directions ('guided variation', in contrast to
244 random genetic mutation). Finally, they explored the interaction between genetic and
245 cultural evolution, examining the conditions under which social learning might genetically
246 evolve, which led to analyses of specific cases of gene-culture coevolution (Feldman and
247 Laland 1996; Laland et al. 2010).

248

249 These models concern the equivalent of what biologists would call microevolution. The
250 following years saw the introduction of phylogenetic methods to reconstruct cultural
251 macroevolution, within anthropology (Mace and Pagel 1994), linguistics (Gray and
252 Atkinson 2003; Gray and Jordan 2000; Pagel 2009), and archaeology (O'Brien et al. 2001;
253 O'Brien and Lyman 2003). These focus less on the within-population mechanisms of
254 cultural microevolution, and more on reconstructing evolutionary relationships between
255 languages, artefacts and customs, given the insight that these traits are related by
256 evolutionary descent (Gray et al. 2007; Lipo et al. 2006; Pagel 2009). Just as in biology,
257 this concerns constructing the most likely evolutionary tree given the data, distinguishing
258 between homoplasies and homologies, and using trees to test hypotheses using the
259 comparative method controlling for the non-independence of data points due to common
260 descent (here, cultural rather than genetic descent). Also as in biology, initial use of

261 maximum parsimony has given way to more sophisticated Bayesian Markov Chain Monte
262 Carlo (MCMC) methods (Matthews et al. 2011; Pagel 2009).

263

264 In summary, cultural evolution theory rests on the principle that cultural change is
265 Darwinian, in that it exhibits variation, differential fitness and inheritance (Mesoudi et al.
266 2004). It does not, however, require that these processes follow neo-Darwinian principles,
267 such as particulate inheritance or random mutation (Mesoudi 2011a). Population-genetic-
268 like mathematical models have formalised the processes that are thought to drive cultural
269 microevolution, including psychological decision-making processes such as conformity or
270 memory biases, and demographic processes such as migration or drift. Phylogenetic
271 methods have been used to reconstruct cultural macroevolution based on the principle of
272 inheritance. Much subsequent work has been devoted to using lab experiments, field
273 studies of real-life populations, and historical/archaeological data to test the assumptions
274 and predictions of these theoretical models. The following section highlights some key
275 findings that have emerged from this theoretical foundation.

276

277 **Key findings in the field**

278 The following comprises a subjective selection of what I consider to be the major
279 advances in cultural evolution research in the last decade or so, although there is much
280 that I have not included due to space constraints. I have tried to select examples that
281 have been addressed using multiple methods (models, experiments, field studies,
282 historical analyses) and replicated by multiple independent labs. There is a tendency to
283 focus on humans, again because of space constraints, but many of the same findings
284 equally apply to non-human species. I start with key findings related to cultural

285 microevolution, and gradually move to cultural macroevolution.

286

287 *Social learning is payoff-biased and conformist*

288 Evolutionary models predict that social learners should be selective in when and who they

289 copy (Boyd and Richerson 1995; Enquist et al. 2007; Laland 2004), otherwise social

290 learning confers no adaptive benefits compared to asocial learning (A. R. Rogers 1988).

291 Two key social learning biases, first introduced and modelled by Boyd and Richerson

292 (1985), concern who one learns from. *Payoff bias* (also labelled *indirect bias*, *success bias*,

293 or *copy-successful-individuals*) involves copying individuals who demonstrate some

294 degree of success in terms of high or higher payoffs. Various forms of payoff bias have

295 been modelled, including copying the individual with the highest absolute payoff, copying

296 another individual if that other individual's payoff is higher than one's own, or copying in

297 proportion to the difference between own and other's payoffs (Schlag 1998), but they all

298 have in common some assessment of payoffs to behaviour. 'Payoff' may be defined

299 biologically (e.g. feeding or reproductive success) or culturally (e.g. wealth, social power),

300 which may or may not coincide.

301

302 An alternative is *conformist bias* (also labelled *positive frequency-dependent bias* or *copy-*

303 *the-majority*), which involves being disproportionately more likely to copy the most

304 common behaviour in the population irrespective of its payoff (Henrich and Boyd 1998).

305 For example, if 6 out of 10 peers exhibit behaviour A rather than B, a conformist learner

306 would have a greater than 0.6 chance of adopting behaviour A (copying A with exactly 0.6

307 probability would describe an unbiased social learner, while copying A with less than 0.6

308 probability would be anti-conformist).

309

310 Subsequent experiments have shown that people employ both of these social learning
311 strategies, as predicted, but that payoff bias is typically preferred to conformity. McElreath
312 et al. (2008) found this using a simple two-option task of planting wheat or potatoes
313 where one gave higher yields, Morgan et al. (2011) using various tasks including mental
314 rotation and perceptual judgements, and Mesoudi (2011b) using a more complex artifact-
315 design task. In each of these, participants could employ trial-and-error asocial learning, or
316 use some form of social learning. A notable recent study by Molleman et al. (2014) found
317 that participants were more likely to employ payoff bias in a two-option task where one
318 option always has a higher payoff, but more likely to use conformity in social dilemma,
319 coordination and evasion games where payoffs depend on other participants' behaviour.

320

321 Less research has examined these biases outside the lab, in natural settings, but findings
322 generally reflect the experimental results. Henrich and Henrich (2010) showed that
323 pregnant women in Fijian fishing villages preferentially acquire adaptive food taboos from
324 locally prestigious unrelated older women, consistent with prestige bias. Beheim et al.
325 (2014) analysed records of opening moves of professional players of the popular East
326 Asian board game Go, showing the preferential copying of the moves of successful
327 players. These findings fit with data from sociology on the diffusion of innovations (E.
328 Rogers 1995) showing that innovations often spread via successful or high status 'change
329 agents', and sociolinguistics (Labov 1972) showing that dialect change spreads via the
330 imitation of successful or prestigious individuals. Perhaps mirroring the experimental
331 results, conformity in the sense modelled by Boyd and Richerson (1985) has received less
332 clear non-experimental support. Henrich (2001) argued that long-tailed S-shaped

333 diffusion curves of technological innovations are indicative of conformity, but such curves
334 may also be consistent with other underlying learning biases (Kandler and Steele 2009).

335

336 The predictions derived from evolutionary models are not specific to humans. Indeed,
337 recent experiments show just as good evidence for payoff bias and conformity in fish,
338 birds and mammals. Pike et al. (2010) showed that nine-spined sticklebacks abandoned a
339 food patch they had previously learned was optimal when they observed a demonstrator
340 feeding at a higher-payoff patch. Conformity has been demonstrated in stickleback (Pike
341 and Laland 2010) and great tits (Aplin et al. 2014), with an individual fish or bird
342 disproportionately more likely to feed at a location where a majority of other individuals
343 had fed. These studies with phylogenetically diverse species show that adaptive social
344 learning rules likely evolved independently in response to particular ecological conditions
345 rather than exclusively in our own species' recent ancestors. Indeed, chimpanzees are
346 surprisingly reluctant to switch to higher-payoff behaviours (Marshall-Pescini and Whiten
347 2008; although see Yamamoto et al. 2013) and while they do exhibit social learning, and
348 this is sometimes labelled 'conformity' (e.g. Whiten et al. 2005), conformity has not been
349 demonstrated in chimpanzees in the specific sense of being disproportionately more
350 likely to copy the majority (van Leeuwen and Haun 2013).

351

352 Why are these social learning strategies important? A key advantage of Darwinian
353 population thinking is that we can extrapolate from small-scale individual-level decisions
354 to large-scale population-level patterns. It has been argued (Boyd and Richerson 1995;
355 Enquist and Ghirlanda 2007; Henrich 2004; Mesoudi 2011c) that payoff-biased social
356 learning is a crucial component of *cumulative cultural evolution*, whereby beneficial traits

357 are selectively preserved and built upon over successive generations (Tomasello 1999). It
358 is not difficult to see why: only payoff bias will drive populations to selectively preserve
359 and build upon beneficial traits. It has also been argued that some forms of payoff-bias,
360 particularly ones that use more indirect measures of success like prestige, can generate
361 prestige hierarchies as people pay costs in terms of deference or material goods in
362 exchange for access to skilled people's knowledge (Henrich and Gil-White 2001). While
363 broadly adaptive, this may misfire when the sources of prestige are disconnected from
364 the sources of success (Atkisson et al. 2011), and may lead to runaway selection for
365 excessive indicators of success (Boyd and Richerson 1985). Conformity, meanwhile, has
366 been suggested as a means to maintain between-group cultural variation, given that it
367 forces migrants to adopt the majority behaviour of their new group (Henrich and Boyd
368 1998). Some have suggested that selection may then act on these homogenous cultural
369 groups, favouring the emergence of group-level adaptations (Henrich and Boyd 2001).

370
371 *Cognitive biases can drive cultural evolution towards cultural attractors*

372 A general principle of biological evolution is that inheritance alone does not cause
373 evolutionary change, except in rare cases such as meiotic drive. This is formalised in the
374 Hardy-Weinberg principle, as well as the Price equation (Price 1970), where for biological
375 systems the component that specifies evolutionary change due to transmission is
376 typically set to zero.

377
378 In cultural evolution, however, transmission is not necessarily unbiased in this manner.
379 People typically transform cultural information they receive from others in non-random
380 directions due to the structure and function of cognition. This was formalised by Boyd

381 and Richerson (1985) in their models of ‘guided variation’, where an individual acquires a
382 cultural trait from another individual, then modifies that trait in some non-random manner,
383 before passing it on to another individual. The same process has been modelled using a
384 Bayesian framework, where cognitive (or ‘inductive’) biases form the priors that people
385 use when making inferences about culturally acquired information (Griffiths et al. 2008;
386 Kirby et al. 2007). A group of cognitive anthropologists led by Dan Sperber (Boyer 1998;
387 Claidière and Sperber 2007; Sperber 1996) have also emphasised the importance of this
388 individual transformation due to cognitive biases, with Sperber coining the term ‘cultural
389 attractor’ to describe a representation that is particularly likely to result from this individual
390 transformation².

391

392 Closely related, but formally distinct, are content biases (Henrich and McElreath 2003).
393 These occur not via the transformation of information by individuals, but when individuals
394 preferentially select certain cognitively appealing traits, without any modification or
395 transformation. Content biases are therefore selection-like, because they change trait
396 frequencies rather than the traits themselves. Both content biases and guided variation
397 are likely to involve the same cognitive operations, but as Boyd and Richerson (1985)
398 showed, they have different evolutionary dynamics: the strength of selection-like content
399 biases, like selection in general, depends on the amount of variation in the population,
400 while the strength of guided variation depends only on individual features of cognition
401 rather than populational characteristics.

² Some of this latter school (e.g. Claidiere, Scott-Phillips and Sperber 2014) have argued that the existence of these transformative processes requires a major revision of the standard approach to cultural evolution presented in this article; I deal with this critique separately in a later section.

402

403 A wealth of experimental studies demonstrate the existence of these cognitive biases
404 (incorporating guided variation and content biases). Several studies have used the
405 'transmission chain' method (Bartlett 1932; Mesoudi and Whiten 2008) which
406 experimentally simulates the transmission of cultural information along a chain of
407 individuals, much like the children's game Telephone. In the case of written material, for
408 example, each person reads and recalls from memory what the previous person recalled,
409 the new recall is given to the next person to remember, and so on along the chain.

410

411 Transmission chain studies have shown that certain kinds of information are preferentially
412 transmitted. A result replicated by several independent labs is that information about
413 social relationships is transmitted with higher fidelity than equivalent non-social
414 information (McGuigan and Cubillo 2013; Mesoudi et al. 2006; Reysen et al. 2011;
415 Stubbersfield et al. 2014), as predicted by social brain theories of the biological evolution
416 of primate cognition (Dunbar 2003). There is also experimental support for a bias for
417 emotionally salient disgust-inducing information (Eriksson and Coultas 2014; Heath et al.
418 2001). Xu et al. (2013), meanwhile, found that initially random colour terms transmitted
419 along chains of people gradually converged on those colour terms commonly seen across
420 actual societies, arguing that the innate features of our perceptual system makes certain
421 colours more salient and thus more likely to emerge through repeated transmission.
422 These would all be examples of biases in cultural evolution that have roots in biologically-
423 evolved features of individual human cognition and perception, resulting from naturally
424 selected adaptations for living in complex groups (social bias), protecting against disease
425 (disgust bias), and innate features of our perceptual systems (colour perception).

426

427 Other transmission chain studies have shown how the structure of cognition shapes
428 culturally transmitted information as a result of repeated transmission. Mesoudi and
429 Whiten (2004) showed that detailed descriptions of events become systematically
430 'schematized' during transmission, i.e. low-level details such as names and dates are lost
431 as material is transformed into more generic higher-level knowledge. Similar effects have
432 been found for gender and racial stereotypes (Kashima 2000; Martin et al. 2014), with
433 stereotype-inconsistent information gradually transformed into simpler, stereotype-
434 consistent information. Kirby et al. (2008) showed how a similar process can shape
435 grammatical features of languages, by demonstrating that artificial languages transmitted
436 along chains of people gradually become more learnable, and in so doing come to
437 possess features of actual languages, such as compositionality, that are typically thought
438 of as innate.

439

440 Transmission chain experiments have also been performed with non-human species
441 (Whiten and Mesoudi 2008). Interestingly, similar inductive biases to those observed by
442 Kirby et al. (2008) have been shown in songbirds, where repeated learning constraints
443 generate structure in songs in the same way that repeated learning constraints generate
444 structure in languages (Feher et al. 2009).

445

446 As noted previously, Darwinian population thinking allows us to link individual-level biases
447 to population-level patterns. The cognitive biases discussed in this section are consistent
448 with certain patterns of cultural diversity observed in ethnographic and historical records
449 (Sperber and Hirschfeld 2004). An individual-level disgust bias may therefore explain the

450 prevalence of disgusting information in real-life urban legends (Heath et al. 2001), while
451 near-universal aspects of grammar and colour terminology can be explained in terms of
452 repeated transmission constraints (Kirby et al. 2008; Xu et al. 2013). A key finding of many
453 of these studies is that weak individual biases can be easily magnified at the population
454 level, in a way that could not be anticipated by focusing on individual cognition alone.

455

456 *Demography can influence the evolution of cultural complexity*

457 Cavalli-Sforza and Feldman (1981) explored how demographic factors such as population
458 size and migration can influence cultural evolution just as they can influence biological
459 evolution. In the last decade this has been pursued further, primarily in the
460 historical/archaeological study of past cultural change, where the influence of changing
461 demography can be observed over long time periods.

462

463 Henrich (2004) presented Tasmania as an example of the influence of demography on
464 cultural evolution. When Tasmanian settlers became cut off from the Australian mainland
465 around 10,000 years ago, they lost many complex tools and skills including winter
466 clothing, fishing spears and boomerangs. Henrich (2004) argued that this loss of complex
467 culturally-transmitted traits was due to the reduced effective population size that occurred
468 following isolation from the mainland population. In smaller populations, there are fewer
469 skilled individuals from whom to learn, and fewer individuals to make rare beneficial
470 modifications.

471

472 To formalise this, Henrich (2004) introduced an influential model linking population size to
473 cultural complexity. The latter he defined in abstract terms designed to represent a

474 quantitative measure of skill in some task, such as basket-weaving ability or stone tool
475 production accuracy. In the model, each new generation acquires the skill of the most-
476 skilful member of the previous generation (i.e. they exhibit payoff biased social learning)
477 with some error. This error has two components, one that determines the loss of skill due
478 to imperfect copying, and one that represents attempts to improve the skill. Complexity
479 increases with population size because the more individuals there are, the more likely
480 someone is to make an improvement without significant transmission error (see also
481 Kobayashi and Aoki 2012; Mesoudi 2011c; Vaesen 2012).

482

483 Shennan (2001) and Powell et al. (2009) applied similar models directly to archaeological
484 data regarding Palaeolithic Europe, showing that the appearance and disappearance of
485 complex technological and social traits such as abstract art, the bow and musical
486 instruments all coincide with changes in population density. Other studies have used
487 repeated founder effect models to explain declining diversity in Acheulean handaxes with
488 distance from an East African origin (Lycett and von Cramon-Taubadel 2008), shown that
489 island population size predicts the size and complexity of fishing technology in the Pacific
490 (Kline and Boyd 2010), and found that across Polynesian languages new words are more
491 likely to be gained by larger populations and existing words are more likely to be lost in
492 smaller populations (Bromham et al. 2015). Not all studies have found a link between
493 population size and cultural complexity, however: Collard et al. (2013), for example, did
494 not find a link in populations of North American hunter gatherers. More mobile hunter-
495 gatherers may experience fewer cultural benefits from large population sizes than
496 sedentary agriculturalists.

497

498 Recently, the link between population size and cultural complexity has been explored
499 experimentally. Henrich's (2004) original model contained certain assumptions concerning
500 the micro-level link between demography and complexity (e.g. payoff-biased social
501 learning), but large-scale archaeological studies such as Powell et al. (2009) can only test
502 the outcome of this model, not the validity of the mechanisms. Derex et al. (2013),
503 Muthukrishna et al. (2014) and Kempe and Mesoudi (2014) all found that, as predicted,
504 larger groups containing more individuals from whom to learn supported higher levels of
505 cultural complexity in various tasks, including designing computerised fishing nets, knot-
506 tying, and completing jigsaw puzzles. While Derex et al. (2013) and Muthukrishna et al.
507 (2014) showed that Henrich's (2004) payoff-biased mechanism works, Kempe and
508 Mesoudi (2014) showed that the effect can also be seen when people integrate the
509 solutions of other people into a single solution (a kind of 'blending inheritance'). Further
510 work is needed to delineate the precise micro-evolutionary mechanisms that support the
511 macroevolutionary link between population size and cultural complexity.

512

513 *Phylogenetic methods can reconstruct language macroevolution*

514 As noted previously, another major strand of cultural evolution research has applied
515 phylogenetic methods to reconstruct the evolutionary relationships between culturally-
516 transmitted traits, based on the principle of inheritance. Much of this work has focused on
517 reconstructing language evolution (Pagel 2009). While historical linguists before Darwin
518 were constructing language family trees based on the assumption of common descent,
519 this endeavour continued largely separately from evolutionary science throughout the
520 20th century, resulting in trees based on the subjective judgement of linguists as to what
521 languages were most similar, and what changes were most likely (McMahon and

522 McMahon 2003).

523

524 In the last decade, sophisticated phylogenetic methods developed in evolutionary biology
525 have been applied to the many language datasets already assembled by linguists, in
526 many cases resulting in significant advances in our understanding of language evolution.

527 A good example is the origin of the Indo-European language family, described as “the
528 most intensively studied, yet still the most recalcitrant, problem of historical linguistics”
529 (Diamond and Bellwood 2003, p. 601). Two major hypotheses proposed by linguists are
530 the “steppe hypothesis”, that Indo-European languages originated in the Pontic-Caspian
531 steppe region (modern Kazakhstan) with the expansion into Europe of seminomadic
532 Kurgan horsemen around 5000-6000 years ago, and the “Anatolian hypothesis”, which
533 posits an older origin around 8000-9500 years ago in Anatolia (modern Turkey) and a
534 spread associated with farming. Both hypotheses are consistent with the archaeological
535 record, and are fiercely argued over amongst historical linguists (Diamond and Bellwood
536 2003).

537

538 Building on an earlier phylogenetic analysis (Gray and Atkinson 2003), Bouckaert et al.
539 (2012) used spatially-explicit Bayesian phylogenetic (i.e. phylogeographic) methods to
540 test these hypotheses. Cognates (homologous words) from 103 extinct and extant Indo-
541 European languages were used to infer the most likely phylogeny given known past and
542 present geographic ranges, with language range modelled as evolving over time along the
543 branches of the phylogeny. Bouckaert et al. (2012) found strong support for the Anatolian
544 hypothesis: the estimated posterior distribution of the root of the Indo-European
545 phylogeny was located in Anatolia and dated to 7,000-10,500 years ago. This conclusion

546 was robust to several different assumptions about the spread of the languages, such as
547 the likelihood of migration across water bodies (although see Chang et al. (2015) for an
548 alternative conclusion).

549

550 Similar phylogenetic analyses have been applied to the spread of Austronesian languages
551 across the Pacific (Gray et al. 2009; Gray and Jordan 2000). These suggest an origin
552 around 5,500 years ago in Taiwan with a subsequent series of rapid expansion pulses
553 interspersed by settlement pauses (the “pulse-pause” hypothesis), rather than an
554 alternative “slow-boat” hypothesis that posits an earlier origin in Wallacea (modern-day
555 Sulawesi) around 13-17,000 years ago. Moreover, internal branch lengths were used to
556 identify the specific pulses and pauses in the Austronesian expansion, which were then
557 linked to the emergence of specific technologies such as outrigger canoes that allowed
558 migration from Taiwan to the Philippines (Gray et al. 2009).

559

560 *The comparative method can test functional hypotheses about cultural evolution*

561 Biologists typically use phylogenies not simply to reconstruct the past, but also to test
562 functional hypotheses about evolution by comparing traits across different species. This
563 comparative method (Felsenstein 1985; Harvey and Pagel 1991) uses phylogenies to
564 correct for the non-independence of data due to shared descent when comparing across
565 species. The comparative method can also be used in cultural evolution, comparing traits
566 across different societies and using language phylogenies to control for non-
567 independence due to descent (Mace and Pagel 1994). Although anthropologists have
568 long been aware of this problem of non-independence (known as ‘Galton’s Problem’, after
569 Francis Galton pointed it out in 1889), during the 20th century socio-cultural

570 anthropologists abandoned the practice of comparing across societies in order to test
571 functional hypotheses, preferring to describe individual societies within interpretivist or
572 post-modern frameworks.

573

574 Galton's problem was therefore left for biologists to solve, but since Mace and Pagel
575 (1994) the comparative method as developed in biology has also been applied to cultural
576 datasets. For example, Holden and Mace (2003) showed that, in 68 Bantu-speaking sub-
577 Saharan African societies, the introduction of cattle-keeping in formerly horticulturalist
578 societies led to a shift from matrilineal to patrilineal wealth inheritance. This shift makes
579 functional sense because, in these societies, cows are more useful to sons than
580 daughters, and therefore lead to more male-biased parental investment. Cows are more
581 useful to sons because grooms must pay bridewealth to the bride's family in order to
582 marry. Once cows are being kept, then wealth can be accumulated in the form of herd
583 size, and families with larger herds can offer a larger bridewealth.

584

585 A similar comparative phylogenetic analysis was conducted by Currie et al. (2010) for
586 changes in political complexity in Austronesian-speaking societies in the Pacific over the
587 last 5,500 years, given the newly available Austronesian language phylogenies discussed
588 above (Gray et al. 2009). Ethnographic data was used to classify societies based on the
589 number of hierarchical decision-making levels, from one (an egalitarian society with no
590 leaders), to more than two levels (what ethnographers define as 'states'). Currie et al.
591 showed that the best-fitting model of political evolution is one where complexity
592 increases incrementally by one level at a time (precluding leaps from, say, one level to
593 three), but with the possibility of sudden collapses from any level down to one³.

³ Earlier I discussed 19th century progressive Spencerian theories of cultural evolution.

594

595 **Controversies, criticisms and challenges**

596 Despite the growth in cultural evolution research, the theory has also been much criticised
597 by both social and evolutionary scientists. In this section I explore these criticisms,
598 beginning with what I consider to be relatively minor issues of misunderstanding that have
599 been addressed in the literature, then moving on to more substantive challenges and
600 ongoing debates.

601

602 *Misunderstandings and clarifications*

603 The following criticisms, in my view at least, have been addressed earlier in the article or
604 elsewhere in the literature, but it is worth highlighting them again as they represent
605 continued sources of misunderstanding.

606

- 607 • *Cultural evolution is not progressive*: As noted above, many social scientists still
608 identify cultural evolution with progressive Spencerian theories, and reject modern
609 cultural evolution by rejecting the notion of inevitable progress (e.g. Fracchia and
610 Lewontin 1999). As noted, this represents a misunderstanding of modern cultural

Currie et al.'s (2010) analysis presents an interesting empirical test of a version of those claims that societies increase in complexity, although it should be noted that (i) Currie et al.'s analysis is an empirical test, whereas Tylor and Morgan offered little empirical support for their progressive schemes; (ii) Currie et al. precisely defined 'complexity' in terms of political hierarchy, whereas Tylor and Morgan were vague and conflated social organisation, technology and many other traits into a single scheme; and (iii) Currie et al. showed that cultural evolution is not *inevitably* progressive, in that societies often lost social hierarchical levels.

611 evolution theory, which is not Spencerian or progressive.

- 612 • *Culture is too complex for simple models:* Modern cultural evolution research is
613 often criticised on the grounds that the population-genetic-style models at the core
614 of the field are inappropriate for capturing the complexity of cultural phenomena
615 (Fracchia and Lewontin 1999). Largely this represents a misunderstanding of the
616 use of formal models. Just as in biology (Servedio et al. 2014), models are not
617 intended to simulate all aspects of reality, nor are they arguments that the real
618 world really is simple; they are used to formalise the logic of verbal arguments
619 about a complex world (Richerson and Boyd 1987).
- 620 • *Culture cannot be divided into memes:* It is common for cultural evolution to be
621 rejected on the grounds that culture cannot be divided into discrete units of
622 inheritance (e.g. Bloch 2000). As noted above, this again rests on a
623 misunderstanding: Darwinian evolution does not require discrete replicators, and
624 many cultural evolution models assume the blending inheritance of continuously
625 varying cultural traits (Henrich and Boyd 2002).
- 626 • *Biological evolution branches, cultural evolution blends:* A critique of cultural
627 phylogenetics is that while biological macroevolution is a process of population
628 fissioning into distinct lineages, cultural macroevolution frequently involves cross-
629 lineage exchange via migration or trade, thus invalidating phylogenetic methods
630 (Moore 1994). This distinction is unfounded: biological systems also feature cross-
631 lineage exchange in the form of horizontal gene transfer (Syvanen 2012), and
632 empirical tests demonstrate that many cultural datasets show just as strong
633 phylogenetic signal as biological datasets (Collard et al. 2006). Moreover,
634 Bayesian-MCMC methods can explicitly detect and handle cross-lineage

635 borrowing (Matthews et al. 2011).

636

637 *Is culture proximate or ultimate?*

638 Cultural evolution researchers are sometimes accused of making overblown claims about
639 the causal role of culture in explaining human behaviour (Dickins and Rahman 2012; El
640 Mouden et al. 2014; Scott-Phillips et al. 2011). This is typically placed within the context
641 of the proximate-ultimate distinction (Mayr 1961; Tinbergen 1963). Proximate (or “how”)
642 causes of biological phenomena are immediate mechanisms and triggering stimuli, while
643 ultimate (or “why”) causes concern the evolutionary history and function of a trait. For
644 example, proximate causes of birdsong might include the anatomical features that allow
645 birds to sing, or the presence of a rival bird. Ultimate causes of birdsong might include
646 descent from an ancestral lineage in which birdsong was present, and the selection
647 pressures that gave rise to and maintain birdsong. Biological phenomena can be
648 simultaneously explained at both proximate and ultimate levels.

649

650 How does culture fit into this scheme? Researchers coming from sociobiology and
651 evolutionary psychology have typically argued that culture is proximate: a mechanism set
652 up by genes to maximise inclusive fitness (Dickins and Rahman 2012; El Mouden et al.
653 2014; Scott-Phillips et al. 2011). There is merit in this argument: after all, the capacity for
654 culture evolved genetically because it increased inclusive fitness, as explored by
655 numerous gene-culture coevolution analyses (Boyd and Richerson 1985, 1995). Moreover,
656 many of the cognitive biases discussed above have putative inclusive fitness benefits,
657 such as keeping track of social relationships (Mesoudi et al. 2006) and learning about
658 disease-carrying substances (Eriksson and Coultas 2014).

659

660 Others (myself included) have argued that non-genetic forms of inheritance such as
661 cultural evolution can additionally constitute ultimate causes of behaviour and thus
662 require a rethinking of the original proximate-ultimate scheme (Danchin et al. 2011; Laland
663 et al. 2011; Mesoudi et al. 2013). For a non-cultural species, the original scheme is fairly
664 straightforward: ultimate historical causes involve genetic lineages connected via genetic
665 descent, and ultimate selective causes involve the natural selection of genetic variation.
666 For a cultural species such as ours, however, ultimate historical causes may also involve
667 cultural lineages connected via cultural descent, and ultimate selective causes may also
668 involve the cultural selection of cultural variation.

669

670 For example, the question “why does a person living in England speak English, and a
671 person living in France speak French?” cannot satisfactorily be answered in terms of
672 genetic differences or natural selection; it must be answered in terms of cultural descent
673 (being descended from a cultural lineage of English or French-speakers on the tips of the
674 Indo-European language phylogeny), and in terms of cultural selection (the
675 microevolutionary processes that caused the languages to change and diversify over
676 time, which might include both selection-like social learning biases and cultural drift). In
677 cases of gene-culture coevolution, culturally transmitted traits such as dairy farming have
678 caused the spread of genes such as lactose tolerance (Laland et al. 2010), again blurring
679 a simple framework in which natural selection of genes is the ultimate cause of
680 evolutionary change.

681

682 While to some extent these issues are merely semantic (i.e. how different researchers

683 define 'proximate' and 'ultimate'), definitional and theoretical frameworks are important
684 because they guide the research questions that are asked. At the heart of this debate is
685 the extent to which culture is under genetic control: if culture is proximate then it should
686 be under tight genetic control, always (or almost always) resulting in behaviour that
687 maximises inclusive genetic fitness. If cultural evolution can also play an ultimate role,
688 then it may drive behaviour to novel equilibrium that are not necessarily genetically
689 optimal, or predictable from evolutionary models containing purely genetic inheritance.

690

691 *The relative influence of transformative and selective processes*

692 Earlier I noted that cultural evolution differs from biological evolution in that whereas
693 genetic inheritance does not in itself generate evolutionary change (except in unusual
694 cases such as meiotic drive or imprinting), cultural inheritance (i.e. social learning) itself
695 may do so, through the individual transformation of information. This difference has
696 inspired some researchers to suggest an alternative framework for modelling and
697 understanding cultural change, one based on 'cultural attraction' (Claidière et al. 2014;
698 Claidière and Sperber 2007; Sperber 1996).

699

700 Two definitions of 'cultural attraction' exist in the writings of Sperber and colleagues
701 (Acerbi and Mesoudi in press). In some publications (e.g. Claidière and Sperber 2007),
702 cultural attraction equates to individual transformation, and seems equivalent to guided
703 variation as modelled by Boyd and Richerson (1985). Claidière and Sperber (2007), for
704 example, present a model in which a cultural trait - cigarette smoking - is influenced by
705 both cultural attraction, where people are individually more likely to decide to either
706 smoke zero or 25 cigarettes a day due to the initial unpleasantness and addictiveness of

707 smoking, and cultural selection, which takes the form of a model-based bias wherein
708 people are more likely to copy 10-cigarette-a-day smokers. As one might expect, the final
709 distribution of cigarette smoking depends on the relative strength of cultural attraction
710 (guided variation) and cultural selection (model-based bias).

711

712 As noted, this sense of cultural attraction seems synonymous with Boyd and Richerson's
713 (1985) guided variation, and transformative processes have been much studied in the field
714 using transmission chain methods. There does not seem to be any major disagreement
715 here, and indeed Sperber and colleagues have made a valuable contribution in
716 highlighting the importance of transformative processes. One might argue about the
717 relative strength of transformative and selective processes in cultural evolution, and this is
718 an empirical question that cannot be addressed through modelling alone. Experimental
719 studies are beginning to examine this (Eriksson and Coultas 2014), but more field and
720 historical studies are needed. It is likely that for certain domains where there are strong
721 cognitive constraints or biases, then individual transformation will dominate, such as the
722 case of colour terminology studied by Xu et al. (2013). In other domains, particularly those
723 involving complex, novel or rapidly changing cultural traits, there are unlikely to be any
724 innate cognitive or perceptual biases operating, and cultural traits may be so 'cognitively
725 opaque' (Csibra and Gergely 2009) - i.e. cannot be easily reconstructed or understood -
726 that individual transformation would be unlikely to result in beneficial modification any
727 more than chance (Boyd et al. 2011). This likely includes complex technologies that have
728 accumulated over multiple generations and that were shown above to appear and
729 disappear with demography, such as fishing hooks, bows, and modern technology such
730 as computers and spacecraft. Here, selection-like processes such as payoff-biased social

731 learning, plus random cultural mutation, are likely to be more important than individual
732 transformation.

733

734 Elsewhere (e.g. Claidière et al. 2014), cultural attraction appears to become synonymous
735 with the broad process of cultural evolution. Claidiere et al. (2014), for example, argue that
736 “cultural evolution is best described in terms of a process called cultural attraction ...,
737 which is populational and evolutionary, but only selectional under certain circumstances.”
738 (Claidière et al. 2014, p. 2). Here, cultural selection is described as a “special case” of
739 cultural attraction, which subsumes both transformative and selective processes. This
740 broader sense of cultural attraction seems to be redundant, and confusingly redefines the
741 notion of cultural attraction (Acerbi and Mesoudi in press). Claidiere et al. (2014) present
742 evolutionary causal matrices, a modelling scheme which they argue better represents
743 cultural change compared to existing ‘selectional’ models, but it is unclear how useful
744 these are compared to the already established models of Cavalli-Sforza and Feldman
745 (1981), Boyd and Richerson (1985) and many others, which as we have seen are not, in
746 fact, exclusively selectional and also include transformative processes.

747

748 *What underlies cumulative cultural evolution?*

749 Many species possess social learning, defined as the transmission of information non-
750 genetically from one individual to another (Galef and Laland 2005). Many species also
751 exhibit cultural traditions, defined as group differences generated by social learning
752 (Lycett et al. 2007; Whiten et al. 1999). Only humans, however, appear to possess
753 *cumulative* cultural evolution, defined as the accumulation of beneficial modifications over
754 successive generations (Dean et al. 2014). Different groups of chimpanzees may differ in

755 their nut-cracking behaviour (Whiten et al. 1999), but there is no sense in which nut-
756 cracking has accumulated over successive generations such that it is beyond the
757 inventive capacity of a single chimp. Aspects of human culture, such as spacecraft,
758 quantum physics, and financial markets, are the cumulative product of countless
759 individuals over many generations.

760

761 There is ongoing comparative, experimental and modelling work trying to explain this
762 difference between humans and other species. An initial suggestion that non-human
763 species lack high-fidelity imitation, i.e. the copying of motor actions (Tomasello et al.
764 1993), failed to find support when chimpanzees were shown able to faithfully transmit
765 behaviours through captive groups (Horner et al. 2006). Recent work has instead
766 implicated multiple factors as being jointly necessary. A recent experimental study
767 pointed to a suite of socio-cognitive abilities, including imitation, verbal instruction and
768 cooperation, that permitted human children to solve cumulative tasks that chimpanzees
769 and capuchins failed (Dean et al. 2012). Theoretical models linked to comparative data
770 suggest that transmission fidelity and population size are jointly necessary for cumulative
771 cultural evolution (Kempe et al. 2014). Certainly, if the confluence of multiple social,
772 cognitive and demographic factors was necessary for the evolution of cumulative cultural
773 evolution, then this may well explain its rarity in nature. Future comparative work will
774 provide a better understanding of these factors.

775

776 *The evolution of large-scale human cooperation*

777 A fiercely debated question across the biological sciences concerns the evolutionary
778 basis of cooperation (Abbot et al. 2011; Nowak et al. 2010). Human large-scale

779 cooperation between unrelated individuals has come under particularly intense scrutiny.
780 Boyd and Richerson (1985), alongside their general models of cultural evolution, also
781 presented a theory of cultural group selection to explain human cooperation. In their
782 original formulation, social learning biases such as conformity generate within-group
783 cultural homogeneity and between-group cultural variation. If this group-level cultural
784 variation persists in the face of migration, if groups vary in altruistic cultural traits which
785 benefit the group but are costly to the individual, and if selection acts at the level of the
786 group such as via their differential extinction, then this process of cultural group selection
787 may favour altruistic cultural norms (Boyd and Richerson 2009). Empirical support for the
788 cultural group selection hypothesis includes behavioural economic games which show
789 cooperation in one-shot, anonymous interactions with no possibility of reciprocity, and
790 between-group cultural variation in the extent of this cooperative behaviour (Henrich et al.
791 2005).

792

793 Cultural group selection has been criticised along with other theories of group (or
794 multilevel) selection (e.g. Wilson and Wilson 2007) by proponents of kin selection (West et
795 al. 2007, 2011). The latter argue that all human cooperation, like non-human cooperation,
796 ultimately has selfish benefits to the individual, even if these benefits also occur to those
797 individuals' groups. Cooperation in one-shot anonymous games is argued to be an
798 artifact of the unfamiliarity of such situations (West et al. 2007).

799

800 Cultural group selection is an elegant theory that fits with many findings from across the
801 social and behavioral sciences (Richerson et al. 2015). Of the few empirical studies that
802 have aimed to directly test its underlying assumptions, some have found support (Bell et

803 al. 2009) while others have not (Lamba 2014; Lamba and Mace 2011). It is also worth
804 noting that prominent cultural evolution researchers remain sceptical of the specific
805 theory of cultural group selection (Lehmann et al. 2008). No doubt future empirical tests
806 will further clarify the nature of human cooperation.

807

808 *Are social learning biases learned or innate?*

809 Many gene-culture coevolutionary models have looked at the evolution of social learning,
810 and of different social learning biases such as payoff or conformist biases. These models
811 typically assume that such capacities are genetically-specified, and examine when each
812 would be favoured by natural selection. To pick one example of many, Enquist et al.
813 (2007) assume in a model of the evolution of social learning that “Which [learning]
814 strategy is used is genetically determined for each individual” (p.6).

815

816 It is possible, however, that the degree of social learning employed by an individual is
817 itself learned, either individually or socially. To an extent, models such as those of Enquist
818 et al. (2007) do not require social learning to be genetically-specified in order for the
819 insights of their models to be valid: social learning could equally be acquired from others
820 culturally, without perhaps altering the results of the model. On the other hand, given the
821 known differences between the dynamics of genetic and cultural inheritance, this may not
822 necessarily be the case. In subsequent models, Enquist and colleagues explored this
823 further (Acerbi et al. 2009; Ghirlanda et al. 2006), showing that when the tendency to
824 engage in social learning can itself be socially learned, this gradually reduces individuals’
825 reliance on social information. This is because while social learners may learn from non-
826 social learners to become non-social learners, the reverse is less likely: non-social

827 learners do not learn from social learners because, by definition, they do not learn
828 socially. While this specific result may or may not be broadly applicable, it highlights the
829 possibility that cultural dynamics may be significantly altered when one assumes that
830 social learning can itself be socially learned.

831

832 Empirically, Mesoudi et al. (2015) showed that the tendency to engage in social learning in
833 an experimental artifact-design task varies cross-culturally, with participants from
834 mainland China more likely to use social information than participants from the UK and
835 Hong Kong, as well as Chinese immigrants living in the UK. Although further studies are
836 needed to explore the precise determinants of human social information use, these
837 results suggest that social learning tendencies are themselves learned from others; the
838 Western-style learning of Chinese immigrants and Hong Kong residents in particular
839 count against any genetic basis for learning style.

840

841 In the non-human literature, too, it has been argued that social learning can be explained
842 in terms of simple associative learning mechanisms, rather than dedicated genetically-
843 specified, domain-specific mechanisms (Heyes 2012; Heyes and Pearce 2015;
844 Leadbeater 2015). Recent studies have shown that social learning in rats can be
845 influenced by early developmental cues such as maternal care (Lindeyer et al. 2013), and
846 in bees by past learning histories (Dawson et al. 2013). However, while similar processes
847 may well operate in humans (Heyes 2012), it is difficult to explain the species differences
848 in cumulative cultural evolution described above without positing some kind of genetic
849 adaptation in the human lineage, perhaps involving the extent of imitation during
850 childhood (Lyons et al. 2007) or theory of mind (Tomasello et al. 2005).

851

852 **Conclusions**

853 In this paper I have provided an overview of contemporary cultural evolution research.

854 The details of cultural micro-evolution are becoming increasingly better understood

855 through a combination of theoretical models, lab experiments and field studies. These

856 focus on pathways and biases in social learning, examining who people learn from, what

857 they learn, and how learning transforms transmitted information. Macro-evolutionary

858 studies are also proliferating, with sophisticated analyses of the evolution of languages,

859 technology and social organisation giving valuable insights into broad patterns of cultural

860 change through human history and prehistory.

861

862 Major progress is likely to occur through the linking of cultural micro and macroevolution,

863 just as occurred in biology during the evolutionary synthesis. This is greatly facilitated by

864 the quantitative models of cultural evolution that lie at the heart of the field, as the large-

865 scale, population-level consequences of individual-level learning processes can be

866 explored in a manner that verbal models do not allow. Thus we have seen links made

867 from payoff bias and demography to patterns of cumulative cultural evolution, from

868 transformative cognitive biases to cross-cultural universals such as colour terminologies

869 and grammatical structure, and from conformist bias to large-scale cooperation.

870

871 Much of the work presented here is consistent with existing findings in the non-

872 evolutionary social sciences: language phylogenies are broadly consistent with informal

873 trees constructed by linguists, for example, while social learning biases such as

874 conformity have precedent in the work of social psychologists. The added value of

875 viewing cultural change as an evolutionary process lies in (i) the application to cultural
876 datasets of quantitative methods already developed by biologists, such as phylogenetic
877 methods in linguistics, where previously inferences were subjective; (ii) the grounding of
878 human behaviour within a broader evolutionary framework, such as the use of formal
879 models to explore the adaptiveness of different social learning biases; and (iii) the linking
880 of micro- and macro-levels of explanation, which is inherent in Darwinian population
881 thinking but represents a perennial problem in the social sciences due to the lack of
882 quantitative methods for making this link, and the lack of communication between
883 disciplines that focus on the micro (e.g. psychology) and those that focus on the macro
884 (e.g. history or archaeology).

885

886 For evolutionary biologists, cultural evolution is significant for several reasons. First, the
887 existence of a second major evolutionary process that resembles genetic evolution but
888 differs from it in important ways may well provide valuable insights into the processes of
889 genetic evolution. Phylogenetic methods, for example, are now being developed in
890 parallel for both cultural and genetic data (Pagel 2009), and phenomena common to
891 cultural datasets such as cross-lineage borrowing is just as much a challenge for
892 biologists facing phenomena such as horizontal gene transfer. Second, social learning is
893 now recognised to be common across multiple taxa, not just humans. The existence of a
894 second inheritance system - and potentially a third, if one also includes transgenerational
895 epigenetic inheritance - means that standard explanations for phenotypic variation in
896 terms purely of the natural selection of genetically-inherited variation will not be sufficient
897 (Danchin et al. 2011). Finally, when considering explanations for human behaviour,
898 biologists sometimes consider 'culture' to be a vague and imprecise notion, instead

899 defaulting to explaining patterns of human behaviour in terms of genes and natural
900 selection even where this is inappropriate. The work reviewed here should hopefully put
901 rest to that feeling, by presenting a coherent evolutionary science of culture that is just as
902 rigorous as evolutionary biology.

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