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4   **Cultural Evolution: A Review Of Theory, Findings and Controversies**

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Abstract

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

Introduction

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

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

"The formation of different languages and of distinct species, and the

proofs that both have been developed through a gradual process, are

curiously parallel...We find in distinct languages striking homologies

due to community of descent. The frequent presence of rudiments,

both in languages and in species, is still more remarkable. Dominant

languages and dialects spread widely, and lead to the gradual

extinction of other tongues. A language, like a species, when once

extinct, never reappears. We see variability in every tongue, and new

words are continually cropping up; but as there is a limit to the powers

of the memory, single words, like whole languages, gradually become

extinct. The survival or preservation of certain favoured words in the

struggle for existence is natural selection." (Darwin 1871, p. 90)

Here, Darwin went further than merely applying the notion of common descent to

languages, as the linguists had done. He also applied his mechanism of natural selection

to language change. Similar parallels were drawn between biological evolution and

technological evolution by Augustus Pitt-Rivers around the same time (Pitt-Rivers 1875),

whose museum in Oxford was, and still is, innovative in displaying archaeological and

ethnographic items according to their presumed evolutionary relationships, rather than

their age or collector.

In an alternative universe, these strands of evolutionary thinking in the social sciences

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.

During the mid-twentieth century a few isolated scholars maintained that a properly

Darwinian theory of cultural evolution was viable, such as the psychologist Donald

Campbell (Campbell 1965). Richard Dawkins provoked interest but little actual empirical

research with his notion of the 'meme' in the final chapter of *The Selfish Gene* (Dawkins

1976), intended to illustrate the substrate-neutrality of his replicator-based theory of

evolution. However, just as evolutionary theory in the biological sciences only really

became useful once it had been formalised mathematically by population geneticists

such as Fisher, Haldane and Wright in the early 1900s, cultural evolution only really took

off once two pairs of scholars devised quantitative mathematical models of cultural

evolution in two books in the 1980s: one by Marc Feldman and Luigi Luca Cavalli-Sforza

(Cavalli-Sforza and Feldman 1981) and the other by Robert Boyd and Peter Richerson

(Boyd and Richerson 1985). These books were also notable in taking seriously the

differences between biological and cultural evolution, rather than simply importing

biological analogies to the cultural case, as perhaps both Campbell and Dawkins were

guilty of doing. The following section outlines the theoretical basis of cultural evolution as

presented in these books, and which has inspired much subsequent research.

The theory of cultural evolution

Many textbook definitions of evolution talk of changes in gene frequencies or require

Mendelian rules of genetic inheritance. While this is reasonable when one's focus is

exclusively on biological (i.e. genetic) evolution, Darwin's theory can quite easily be

formulated in a general, mechanism-neutral manner. After all, Darwin himself knew

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 inheritance[1]. Thus, cultural traits (words, ideas, artefacts etc.) exhibit variation;

188 these variants have different rates of survival and reproduction; and they are transmitted

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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

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

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

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 transformation[2].

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

A wealth of experimental studies demonstrate the existence of these cognitive biases

(incorporating guided variation and content biases). Several studies have used the

'transmission chain' method (Bartlett 1932; Mesoudi and Whiten 2008) which

experimentally simulates the transmission of cultural information along a chain of

individuals, much like the children's game Telephone. In the case of written material, for

example, each person reads and recalls from memory what the previous person recalled,

the new recall is given to the next person to remember, and so on along the chain.

Transmission chain studies have shown that certain kinds of information are preferentially

transmitted. A result replicated by several independent labs is that information about

social relationships is transmitted with higher fidelity than equivalent non-social

information (McGuigan and Cubillo 2013; Mesoudi et al. 2006; Reysen et al. 2011;

Stubbersfield et al. 2014), as predicted by social brain theories of the biological evolution

of primate cognition (Dunbar 2003). There is also experimental support for a bias for

emotionally salient disgust-inducing information (Eriksson and Coultas 2014; Heath et al.

2001). Xu et al. (2013), meanwhile, found that initially random colour terms transmitted

along chains of people gradually converged on those colour terms commonly seen across

actual societies, arguing that the innate features of our perceptual system makes certain

colours more salient and thus more likely to emerge through repeated transmission.

These would all be examples of biases in cultural evolution that have roots in biologically-

evolved features of individual human cognition and perception, resulting from naturally

selected adaptations for living in complex groups (social bias), protecting against disease

(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 one[3].

---

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

594

Controversies, criticisms and challenges

Despite the growth in cultural evolution research, the theory has also been much criticised

by both social and evolutionary scientists. In this section I explore these criticisms,

beginning with what I consider to be relatively minor issues of misunderstanding that have

been addressed in the literature, then moving on to more substantive challenges and

ongoing debates.

Misunderstandings and clarifications

The following criticisms, in my view at least, have been addressed earlier in the article or

elsewhere in the literature, but it is worth highlighting them again as they represent

continued sources of misunderstanding.

- *Cultural evolution is not progressive:* As noted above, many social scientists still
  identify cultural evolution with progressive Spencerian theories, and reject modern
  cultural evolution by rejecting the notion of inevitable progress (e.g. Fracchia and
  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). Claidiere 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

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

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

The evolution of large-scale human cooperation

A fiercely debated question across the biological sciences concerns the evolutionary 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

learners do not learn from social learners because, by definition, they do not learn

socially. While this specific result may or may not be broadly applicable, it highlights the

possibility that cultural dynamics may be significantly altered when one assumes that

social learning can itself be socially learned.

Empirically, Mesoudi et al. (2015) showed that the tendency to engage in social learning in

an experimental artifact-design task varies cross-culturally, with participants from

mainland China more likely to use social information than participants from the UK and

Hong Kong, as well as Chinese immigrants living in the UK. Although further studies are

needed to explore the precise determinants of human social information use, these

results suggest that social learning tendencies are themselves learned from others; the

Western-style learning of Chinese immigrants and Hong Kong residents in particular

count against any genetic basis for learning style.

In the non-human literature, too, it has been argued that social learning can be explained

in terms of simple associative learning mechanisms, rather than dedicated genetically-

specified, domain-specific mechanisms (Heyes 2012; Heyes and Pearce 2015;

Leadbeater 2015). Recent studies have shown that social learning in rats can be

influenced by early developmental cues such as maternal care (Lindeyer et al. 2013), and

in bees by past learning histories (Dawson et al. 2013). However, while similar processes

may well operate in humans (Heyes 2012), it is difficult to explain the species differences

in cumulative cultural evolution described above without positing some kind of genetic

adaptation in the human lineage, perhaps involving the extent of imitation during

childhood (Lyons et al. 2007) or theory of mind (Tomasello et al. 2005).

851

Conclusions

In this paper I have provided an overview of contemporary cultural evolution research. The details of cultural micro-evolution are becoming increasingly better understood through a combination of theoretical models, lab experiments and field studies. These focus on pathways and biases in social learning, examining who people learn from, what they learn, and how learning transforms transmitted information. Macro-evolutionary studies are also proliferating, with sophisticated analyses of the evolution of languages, technology and social organisation giving valuable insights into broad patterns of cultural change through human history and prehistory.

Major progress is likely to occur through the linking of cultural micro and macroevolution, just as occurred in biology during the evolutionary synthesis. This is greatly facilitated by the quantitative models of cultural evolution that lie at the heart of the field, as the large-scale, population-level consequences of individual-level learning processes can be explored in a manner that verbal models do not allow. Thus we have seen links made from payoff bias and demography to patterns of cumulative cultural evolution, from transformative cognitive biases to cross-cultural universals such as colour terminologies and grammatical structure, and from conformist bias to large-scale cooperation.

Much of the work presented here is consistent with existing findings in the non-evolutionary social sciences: language phylogenies are broadly consistent with informal trees constructed by linguists, for example, while social learning biases such as conformity have precedent in the work of social psychologists. The added value of

viewing cultural change as an evolutionary process lies in (i) the application to cultural

datasets of quantitative methods already developed by biologists, such as phylogenetic

methods in linguistics, where previously inferences were subjective; (ii) the grounding of

human behaviour within a broader evolutionary framework, such as the use of formal

models to explore the adaptiveness of different social learning biases; and (iii) the linking

of micro- and macro-levels of explanation, which is inherent in Darwinian population

thinking but represents a perennial problem in the social sciences due to the lack of

quantitative methods for making this link, and the lack of communication between

disciplines that focus on the micro (e.g. psychology) and those that focus on the macro

(e.g. history or archaeology).

For evolutionary biologists, cultural evolution is significant for several reasons. First, the

existence of a second major evolutionary process that resembles genetic evolution but

differs from it in important ways may well provide valuable insights into the processes of

genetic evolution. Phylogenetic methods, for example, are now being developed in

parallel for both cultural and genetic data (Pagel 2009), and phenomena common to

cultural datasets such as cross-lineage borrowing is just as much a challenge for

biologists facing phenomena such as horizontal gene transfer. Second, social learning is

now recognised to be common across multiple taxa, not just humans. The existence of a

second inheritance system - and potentially a third, if one also includes transgenerational

epigenetic inheritance - means that standard explanations for phenotypic variation in

terms purely of the natural selection of genetically-inherited variation will not be sufficient

(Danchin et al. 2011). Finally, when considering explanations for human behaviour,

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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