Conformity in mate choice, the overlooked social component of animal and human culture

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ABSTRACT

Although conformity as a major driver for human cultural evolution is a well-accepted and

intensely studied phenomenon, its importance for non-human animal culture has been largely

overlooked until recently. This limited for decades the possibility of studying the roots of

human culture. Here, we provide a historical review of the study of conformity in both

humans and non-human animals. We identify gaps in knowledge and propose an evolutionary

25   route towards the sophisticated cultural processes that characterize humanity. A landmark in

26   the study of conformity is Solomon Asch's famous experiment on humans in 1955. By

27   contrast, interest in conformity among evolutionary biologists has only become salient since

28   the turn of the new millennium. A striking result of our review is that, although studies of

29   conformity have examined many biological contexts, only one looked at mate choice. This is

30   surprising because mate choice is probably the only context in which conformity has self-

31   reinforcing advantages across generations. Within a metapopulation, i.e. a group of

32   subpopulations connected by dispersing individuals, dispersers able to conform to the local

33   preference for a given type of mate have a strong and multigenerational fitness advantage.

34   This is because once females within one subpopulation locally show a bias for one type of

35   males, immigrant females who do not conform to the local trend have sons, grandsons, etc. of

36   the non-preferred phenotype, which negatively and cumulatively affects fitness over

37   generations in a process reminiscent of the Fisher runaway process. This led us to suggest a

38   sex-driven origin of conformity, indicating a possible evolutionary route towards animal and

39   human culture that is rooted in the basic, and thus ancient, social constraints acting on mating

40   preferences within a metapopulation. In a generic model, we show that dispersal among

41   subpopulations within a metapopulation can effectively maintain independent Fisher runaway

42   processes within subpopulations, while favouring the evolution of social learning and

43   conformity at the metapopulation scale; both being essential for the evolution of long-lasting

44   local traditions. The proposed evolutionary route to social learning and conformity casts

45   surprising light on one of the major processes that much later participated in making us

46   human. We further highlight several research avenues to define the spectrum of conformity

47   better, and to account for its complexity. Future studies of conformity should incorporate

48   experimental manipulation of group majority. We also encourage the study of potential links

49   between conformity and mate copying, animal aggregations, and collective actions.

50 Moreover, validation of the sex-driven origin of conformity will rest on the capacity of human

51 and evolutionary sciences to investigate jointly the origin of social learning and conformity.

52 This constitutes a stimulating common agenda and militates for a rapprochement between

53 these two currently largely independent research areas.

54

55 *Key words*: cultural evolution, conformity in humans, conformity in animals, sexual selection,

56 mate choice, Fisher Runaway Process.

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58 CONTENTS

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I. INTRODUCTION

Social learning is a form of learning that specifically uses information obtained from conspecifics or other animals or the products of their activities to gain information about the environment (adapted from Heyes, 1994). It has been recognized as a crucial learning process for the transmission and spread of adaptive behaviours within and among populations (Laland, 2004; Rendell *et al.*, 2011; Aplin *et al.*, 2015*b*). As such, social learning is the cornerstone of cultural traditions, since culture relies by definition on socially transmitted information (Boyd & Richerson, 2005).

A major form of social learning that is essential for the establishment of cultural traditions and social norms in humans is conformity (Boyd & Richerson, 1985; Henrich & Boyd, 1998). Several definitions of conformity (or conformist bias) have been used in the literature, depending on the field. They range from 'copy the majority', which is a simple positive frequency-dependent bias in learning (e.g. Laland, 2004) to 'Aschian conformity', where personal knowledge or preference is overridden by countervailing options performed by others (Asch, 1955). Perhaps the most popular and widespread definition of conformist bias or conformist transmission is defined as the *disproportionately likely* adoption of the most common variant within the local population (Boyd & Richerson, 1985). Conformity allows individuals easily to grasp local behaviours and norms. In turn, it can generate socially learned traditions that are both resistant to erosion and robust to invasion of alternative variants, potentially persisting over generations. Thus, conformity can produce a combination of within-group homogeneity and between-group heterogeneity (see discussion in Section III).

Because of its central role for the emergence and maintenance of culture, conformity has long been a major topic of research in human sciences (Boyd & Richerson, 1985; Banerjee, 1992; Bernheim, 1994; Aoki, Lehmann & Feldman, 2011; Merrell, 2011; Claidière & Whiten,

100   2012; Efferson *et al.*, 2016; Denton *et al.*, 2020). By contrast, the study of conformity in non-

101   human animals became a major topic in evolutionary sciences only recently (e.g. Whiten,

102   Horner & de Waal, 2005; Aplin *et al.*, 2015*b*; van Leeuwen *et al.*, 2015; Danchin *et al.*,

103   2018), and a synthesis between these two scientific domains is still lacking. Here, we review

104   the literature on conformity in both humans and non-human animals, thus drawing a link

105   between these two sides of the literature. This review allows us to identify gaps in knowledge

106   and suggest a general model for the evolution of social learning and conformity. Our review

107   further suggests that conformity in mate choice deserves closer attention as sexual selection is

108   a strong evolutionary force that has been largely overlooked up to now in this context. We

109   aim to inspire new research agendas in both human and non-human animals to determine in

110   which context, e.g. mate choice or foraging, the cognitive processes that underpin the

111   evolution of animal and human culture could have evolved and how they interact.

112

113 **II. EARLY DEFINITIONS: CONFORMITY OR POSITIVE FREQUENCY-**

114 **DEPENDENT LEARNING?**

115   In this section, we propose a brief history of the term 'conformity' pre-dating Boyd &

116   Richerson's (1985) definition of conformist transmission bias. Most uses of the term

117   'conformity' over this period would now be more accurately described as positive frequency-

118   dependent social learning [see Efferson *et al.* (2008) for a discussion around existing

119   definitions of conformity].

120   The influence of groups on individual behaviour first attracted attention in the early

121   twentieth century (Jenness, 1932; Sherif, 1935), but it was Asch (1955) who popularized the

122   term *conformity* itself. Using a simple 'visual judgement' task, Asch documented that people

123   were willing to abandon their own personal preferences (or convictions) when confronted

124   with a disagreeing majority opinion. He ascribed this behaviour to social pressure and called

125 this innate tendency to self-align on group opinion 'conformity'. Asch's findings became

126 momentous in developing the field of social psychology. They were replicated many times

127 across different age classes and cultures, even when factors such as group size, motivation,

128 task difficulty or relevance were varied (Baron, Vandello & Brunsman, 1996; Bond, 2005;

129 Bond & Smith, 1996; Griskevicius *et al*., 2006). Later, Latané's (1981) work on 'social

130 impact theory' provided a tentative conceptual framework for these findings. Drawing a

131 parallel with physics, Latané pictured social influence as a force emanating from the group,

132 and acting on individuals (e.g. peer pressure). The intensity of this force could depend on the

133 source group's size, its behavioural composition (the proportion of individuals performing the

134 various behaviours), its status (such as prestige), or its proximity in time and space to the

135 target individual (see also Latané & Wolf, 1981). Overall, social psychology had suggested a

136 proximate reason for 'conforming', namely that people inherently dislike going against the

137 majority.

138   Note that these early studies equated conformity with a linear increase in the likelihood of

139 adopting a behaviour as that behaviour becomes more common in the population – what today

140 is called positive frequency-dependent social learning. Conformist transmission bias as

141 defined by Boyd & Richerson (1985) is a particular case of this class of learning rules

142 (adoption of the most common variant needs to be disproportionately likely). Still, debates

143 from this early period may provide useful insights regarding positive frequency-dependent

144 social learning, and therefore, regarding conformist transmission bias in the Boyd &

145 Richerson sense.

146   One such example is the question of whether positive frequency-dependent social learning

147 arises because of normative or informational reasons. In Asch's studies, following the

148 majority was a response to peer pressure, but this does not have to be the case. Early on,

149 Deutsch & Gerard (1955) remarked that social psychology had focused mainly on a single

150   side of 'conformity' (here again understood as positive frequency-dependent social learning),

151   namely, the normative side. In what they called normative social influence (later also referred

152   to as *social* conformity; e.g. Coleman, 2004), the commonest behaviour defines a social norm.

153   If the norm is explicitly enforced, for instance by rewarding compliers and punishing non-

154   compliers, then individuals might adopt the normative behaviour through ordinary cognitive

155   mechanisms for avoiding social and environmental risks; in this case, conforming simply

156   means avoiding punishment. But individuals might also adopt the norm not because they

157   consciously try to avoid social risks, but because of specific preferences for conforming,

158   which might have proved adaptive over long timescales. In other words, the drive to conform

159   could be an individually optimized response to social incentives, but it could also be the result

160   of evolved, wired-in preferences. For now, the literature remains unclear on whether

161   normative conformity includes both these mechanisms, or just the latter (conforming because

162   of an evolved, intrinsic drive to do so, e.g. self-esteem concerns).

163   But Deutsch & Gerard (1955) described another driver of majority-following:

164   informational social influence (sometimes also called *instrumental* conformity; *cf*. Burdett *et*

165   *al*., 2016). In this case, the behaviour of the majority does not define a norm, but instead

166   reveals useful information about the environment. Take the example of durian (*Durio*

167   *zibethinus*), a tropical fruit with a distinctly unpleasant smell which is widely popular in

168   South-east Asia. The naïve tourist might be willing to try it despite the stench, not for fear of

169   social sanctions if he or she does not, but rather because he or she can *infer* from observing

170   the majority behaviour that the fruit is actually palatable. As pointed out by Cialdini &

171   Goldstein (2004) however, informational and normative conformity are actually interrelated –

172   for instance, from these definitions it is unclear whether an individual using social

173   information to navigate a social environment (e.g. to avoid punishment) is an example of

174   normative or informational conformity.

175   Economists summarized the mechanisms and limitations of the informational channel in a

176 famous decision problem. Suppose that, on a night out and looking for a good dinner, you

177 stumble upon two adjacent restaurants. One is crowded, the other almost empty. Which

178 restaurant will you choose? First, you should realize that the behaviour of others probably

179 conveys information about quality. The safest choice is therefore to follow the 'wisdom of the

180 crowd' and go for the crowded restaurant (i.e. conform). However, sometimes the crowd is

181 wrong, as Banerjee (1992) and Bikhchandani, Hirshleifer & Welch (1992) pointed out.

182 Indeed, in this problem, the first few customers are pivotal in determining group behaviour: if

183 they choose the lower-quality restaurant, all subsequent customers will copy their mistake.

184 Such *informational cascades* were later observed in laboratory experiments with human

185 subjects (Anderson & Holt, 1997). What these studies emphasized is the fragility of mass

186 behaviour when it is driven by conformity, in the sense that it is susceptible to shifts when

187 accurate information is publicly released. Back to the restaurant example, it means that if

188 customers had had access to the restaurants' ratings on Yelp or Tripadvisor, then they could

189 have ignored the mistake of the first few customers and chosen the best restaurant instead

190 despite it being empty.

191   Economists also studied the normative channel. For instance, Bernheim (1994) considered

192 a population in which individuals must balance their self-interest with social esteem. Social

193 esteem is obtained by adhering to a group norm, but individuals vary in how their self-interest

194 aligns with this norm. Bernheim (1994) showed that individuals whose self-interest closely

195 aligns with the norm will conform to it in order to reap the social esteem benefits. On the

196 other hand, individuals whose self-interest departs a lot from the norm will ignore that norm,

197 but by doing so their behaviour flags them to the rest of society as undeserving of social

198 esteem. This model illustrates how reward and punishment can enforce conformity around a

199 social norm, even in the presence of individual heterogeneity. In a similar spirit, Kuran &

200   Sandholm (2008) studied how individuals with heterogeneous preferences behave in the

201   presence of coordination incentives; they also found that individuals tend to align their

202   behaviour with the social norm.

203   This informational *versus* normative dichotomy, together with the above studies by

204   economists, provides a convenient analytical structure for evolutionary biologists. They

205   suggest that any tendency towards positive frequency-dependent social learning should be

206   rooted in one of these two channels, i.e. that it should have normative or informational

207   benefits. However, informational and normative conformity are interrelated (David & Turner,

208   1996), and as such they are difficult to disentangle theoretically and empirically. This is

209   reflected in the research on individual differences in conformity. For example, DeYoung,

210   Peterson & Higgins (2002) looked at two personality types, namely *Stability* (emotional

211   stability, agreeableness and conscientiousness) and *Plasticity* (extraversion, openness), and

212   found that Stability is a positive predictor of conformity while Plasticity was negatively

213   correlated with conformity. Thus, strong conformists tend to be very stable but also less able

214   to adjust to novelty or change. This also suggests that positive frequency-dependent social

215   learning is not always the right answer to an environmental challenge, as we will see more in

216   detail below. Finally, as a particular case of positive frequency-dependent social learning,

217   conformist transmission in the Boyd & Richerson sense should also obey these insights.

218

219   **III. CONFORMITY EVOLVES: A BENEFICIAL BIAS?**

220   A few decades after Asch's experiments, biologists incorporated conformity into the study of

221   cultural evolution, i.e. the change of culture over time (Claidière & Whiten, 2012; Haun, van

222   Leeuwen & Edelson, 2013; van Leeuwen & Haun, 2013; Whiten, 2019, 2021) where culture

223   is the phenotypic variation that is inherited through social learning (Danchin *et al*., 2018).

224   Integrating socially transmitted information into a population genetics framework raised the

225   question of how individuals use social information to maximize fitness (Cavalli-Sforza &

226   Feldman, 1981; Boyd & Richerson, 1985). This predicts that such socially aware individuals

227   would be equipped with a wide range of social transmission biases that dictate whom they

228   copy and when (Feldman, Aoki & Kumm, 1996; Henrich & Boyd, 1998; Henrich &

229   McElreath, 2003; Laland, 2004; Enquist, Eriksson & Ghirlanda, 2007; Wakano & Aoki,

230   2007; Kendal, Giraldeau & Laland, 2009). For instance, individuals could preferentially copy

231   prestigious models (prestige bias), or models that look like themselves (similarity bias), or

232   even – our focus here – models that display the majority behaviour (conformist bias, or

233   *conformity* for short). A rigorous definition of conformity was established early on by Boyd &

234   Richerson (1985): an individual is *conformist* if it is more likely to adopt the majority

235   behaviour than if it copied a demonstrator picked at random (Morgan & Laland, 2012;

236   Muthukrishna, Morgan & Henrich, 2016; see Fig. 1). Given the right conditions, this 'over-

237   copy-the-majority' rule could be highly profitable.

238   Subsequent evolutionary models examined conditions favouring different learning biases.

239   Conformity's 'sweet spot' turned out to be a spatially variable environment with migration,

240   since conforming helps migrants to adopt the locally adaptive behaviour quickly (Boyd &

241   Richerson, 1985; Henrich & Boyd, 1998; reviewed in Aoki & Feldman, 2014). More

242   generally, conformists perform better when environmental change is slow, social learning is

243   easy (relative to individual learning), transmitted traits have high adaptive value, and fitness

244   payoffs vary greatly with space (Nakahashi, 2007; Kendal *et al.*, 2009).

245   Conformity adds robustness to the transmission process overall (Dindo, Whiten & de

246   Waal, 2009; Danchin *et al.*, 2018; Lachlan, Ratmann & Nowicki, 2018). A conformist learner

247   is unlikely to pick up a one-off behavioural mistake, since its decision is based on many

248   demonstrators. Yet this redundancy also dampens innovation (Sterelny, 2006), and in rapidly

249   changing environments it may cause a carryover of old behaviours that are no longer adaptive

250   if the individuals are not flexible enough to adapt at the same speed as the environment

251   changes (Aplin, Sheldon & McElreath, 2017). In the context of cultural evolution, this can in

252   turn slow down the response to environmental change and thus promote the maintenance of

253   outdated maladaptive behaviours (Whitehead & Richerson, 2009). In practice however, a mix

254   of conformity and individual learning may allow populations to switch to newly adaptive

255   behaviours. This was shown by Aplin *et al*. (2017) in an experimental study on great tits

256   (*Parus major*): by manipulating behaviour rewards, they documented that both individuals

257   and populations were able to move away from established, now-suboptimal behavioural

258   traditions. The takeaway message is that conformity can catalyse a behavioural change that is

259   initially driven by individual learning. A related point was made by Perreault, Moya & Boyd

260   (2012), in providing theoretical evidence that conformity is expected to be a universal feature

261   of social learning when individual learning is also in play.

262   Given the right conditions, conformity can stabilize any trait – adaptive or not (Laland,

263   1994). For example, in some models conformity can foster cooperation if interactions and

264   learning are spatially constrained in the population, thus giving rise to 'local clusters' of co-

265   operators (Peña *et al*., 2009; Mengel, 2009; Molleman, Pen & Weissing, 2013). Instead, in

266   large homogeneous populations, cooperation is diluted, and conformity can block its

267   evolution (Lehmann & Feldman, 2008; Molleman, Quiñones & Weissing, 2013). Similarly,

268   conformity can coevolve with other cultural or genetic traits such as altruism (Lehmann &

269   Feldman, 2008) or the ability to copy (Wakano & Aoki, 2007). Empirical studies to verify

270   these predictions remain needed, for instance to study how conformity interacts with group

271   size to affect traditions of cooperation.

272   Crucially, conformity can generate a stable combination of within-group homogeneity and

273   between-group heterogeneity. Indeed, conformity fixes a given group on a single socially

274   learned tradition that remains stable over generations, making the tradition resistant to erosion

275   and robust to invasion of alternative variants. Importantly, different groups can fix on

276   different traits depending on which trait is locally optimal, cultural drift or some specific

277   initial conditions. This is illustrated by patterns of tool use among chimpanzees (*Pan

278   troglodytes*) from the Taï National Forest (Ivory Coast). These chimpanzees crack *Coula

279   edulis* nuts with stone and/or wooden hammers and use roots as anvils. Which tools they use

280   depends on the community they live in, and is culturally transmitted. Despite high levels of

281   female intergroup migration, differences between neighbouring groups persist over time with

282   incoming females conforming to their new group-specific tradition (Luncz & Boesch*, 2014).

283

284   **(1) Looking for normative conformity in non-human animals**

285   All the evolutionary models mentioned above relate to *informational* benefits of conformity.

286   They depict cases where the majority behaviour is a local fitness-maximizing social cue.

287   Hence, predicting the evolutionary success or failure of conformity rests on the statistical

288   concept of *Bayesian inference*, as made explicit by Perreault *et al*. (2012). All models thus

289   follow more or less the same reasoning, at least implicitly. They (*i*) take a naïve individual

290   seeking the fitness-maximizing alternative amongst several behaviours; (*ii*) assume that the

291   best behaviour is selected for so that it increases in frequency; (*iii*) hence, conclude that the

292   most-displayed behaviour should be the best, provided that the demonstrator population had

293   enough time to undergo selection. Although this reasoning holds under many circumstances,

294   it may fail when the environment is too unstable for the demonstrator population to have

295   reached the best strategy.

296   In the normative case, benefits instead occur when the population itself rewards a given

297   behaviour (the norm), or punishes non-compliers. Administering these rewards or

298   punishments is often costly, which impedes the evolution of such social machinery. However,

299   conformity can overcome this evolutionary obstacle so that hardwired conformity allows

costly social norms to evolve, implying that conformity might be responsible for the

emergence of a reward-and-punishment culture (Henrich & Boyd, 2001). Once established,

costly social norms can even coevolve with conformity (Gúzman, Rodríguez-Sickert &

Rowthorn, 2007) although such associations are harder to obtain than previously thought

(Van Cleve, 2016). Since conformity also accounts for the stable combination of intergroup

heterogeneity and intragroup homogeneity, it can in turn trigger cultural group selection

(Boyd & Richerson, 1985).

Until now, informational benefits have been the dominant explanation for conformist

behaviour in evolutionary biology (for an extended discussion see Claidière & Whiten, 2012).

Nonetheless, in a non-conformity context rewards or punishments for complying (or not) with

group-specific rules or norms have been documented in animals (Singh & Boomsma, 2015;

reviewed by Raihani, Thornton & Bshary, 2012) particularly in insects and non-human

societies where it seems to maintain intense levels of cooperation, suggesting the existence of

normative benefits in non-human animals. We thus suggest that the normative channel

deserves more attention.

(2) Viability of conformity in strategic settings

Is it always beneficial to copy the majority? As a preliminary answer to this question,

consider how you, as a conformist individual, might fare in the following three scenarios.

(1) Choosing between two plentiful food sources, each potentially healthy or

poisonous.

(2) Choosing between two identical but limited-supply food sources.

(3) Choosing between two paths to avoid a predator that preys preferentially on

smaller groups.

324   Scenario 1 is a straightforward win for informationally driven conformity: if a majority of

325   people feed from a given food source, it probably means that it is healthy, so conforming is a

326   good bet. That changes, however, in scenario 2: since the food sources are in limited supply,

327   the more individuals feed from one, the less food remains for you there. Here, conforming

328   will not work well: the situation calls for *not* copying the majority, and you would be better

329   off by taking the less-popular option. In scenario 3, conformity makes a comeback: the more

330   individuals take a given path, the less likely you are to be attacked by also taking that path

331   (Cresswell & Quinn, 2011). To improve your chances of survival you should learn which is

332   the safe way according to the number of individuals using it, i.e. copy the majority.

333   The crucial difference between these scenarios is how the behaviour of others affects your

334   fitness. In scenarios 2 and 3 the viability of each option depends on what others do – neither

335   option is intrinsically better independently of the actions of others. Economists call such

336   interactions *strategic*. In scenario 2, those you copy affect your fitness *negatively*. Such

337   behaviours are called *strategic substitutes*, which means that the attractiveness of an option

338   decreases as more individuals choose it (negative frequency dependence). In scenario 3, those

339   you copy affect your fitness *positively* – such behaviours are called *strategic complements*,

340   which means that the attractiveness of an option increases as more individuals choose it

341   (positive frequency dependence) (Bulow, Geanakoplos & Klemperer, 1985). Scenario 1 is

342   non-strategic as there *is* an intrinsically better option (the healthy one) and the behaviour of

343   others affects your fitness only insofar as it provides social information on what that better

344   option is.

345   These scenarios sketch a qualitative result: conformity seems to thrive only when

346   behaviours are strategic complements, or non-strategic. While a rigorous theoretical

347   exploration may be needed to confirm this simple intuition, it suggests that strategic

348   complements or substitutes may provide a useful lens to understand why conformity evolves

349 for some traits but not others. Further research is needed, both on theoretical and empirical

350 fronts, to investigate this potential link between conformity and strategic settings.

351

352 **(3) Information acquisition, the value of observations, and memory**

353 As a matter of fact, the classical formalisms used to model information acquisition largely are

354 idealized. Models commonly assume a simple group structure where individuals observe

355 *simultaneously everyone else* in their group, and then infer the majority behaviour from this

356 far-reaching, sweeping look. More realistically, observations in fact are gathered *sequentially*

357 from a *subset* of the whole population (Morgan, Acerbi & van Leeuwen, 2019), as in a recent

358 study on chimpanzees (Watson *et al.*, 2018). Organisms must deduce the majority behaviour

359 from such imperfect samples, probably by using individual learning and memory, which none

360 of the models of conformity to date has implemented. Different environments could promote

361 different ways to deal with information. In unstable environments for instance, older

362 observations may be discounted in favour of recent ones, since reliance on past observations

363 could cause deleterious behavioural inertia. Regarding the size of the sample of

364 demonstrators, Denton *et al.* (2020) showed that evolutionary dynamics can be more complex

365 than previously thought when there are more than three role models, as in Boyd &

366 Richerson's (1985) classical treatment.

367   Similar arguments hold for how to integrate space, prestige or other characteristics into the

368 evaluation of observation. Should an immigrant completely ignore information from its home

369 environment in favour of local practices? Should it give more weight to demonstrators like

370 itself? Is a prestigious demonstrator worth two, ten, or a thousand ordinary ones? Mesoudi

371 (2018) addressed similar questions by modelling immigrant conformist acculturation.

372 Basically, this comes down to studying the interaction between conformity and other biases,

373 such as prestige, success, locality, ethnicity, age, sex, etc. The core problem is to determine

15

374   the value of adding a single demonstrator into the decision process, based on that

375   demonstrator's personal characteristics relative to the observer. This is both a theoretical and

376   an empirical question that needs to be explored.

377   Finally, while most current studies concern binary choices, natural situations usually

378   involve many more options. Expanding the binary approaches would raise empirical

379   challenges (what would occur when the majority is still an absolute minority, as in a 40–30–

380   30 split?) and theoretical ones. A first unanswered problem is to devise a suitable learning

381   rule (an S-shaped probability, symmetric in all behaviours) when there are more than two

382   behaviours to choose from, or even when traits are continuous. These issues remain under-

383   explored for the moment, with a few exceptions (e.g. Nakahashi, Wakano & Henrich, 2012;

384   Mesoudi, 2018). In the next section we outline a possible step in this direction.

385

386   **(4) Conformity with more than two choices: a functional form and a statistical test**

387   The canonical mathematical model for conformist transmission is the sigmoid curve (Fig. 1,

388   red lines) proposed by Boyd & Richerson (1985) in their initial work on conformist

389   transmission and cultural evolution (Fig. 1A). Their model considers the case with two traits,

390   where learners are exposed to three demonstrators and exhibit a positive frequency-dependent

391   bias. If we call q the proportion of trait A in the population, and $1-q$ the proportion of trait B,

392   then Boyd & Richerson (1985) defined the probability p that an individual will adopt trait A

393   as

394    $$p(q) = q + Dq(1 - q)(2q - 1) \tag{1}$$

395   where D is a parameter between 0 and 1 that expresses the strength of the positive frequency-

396   dependent bias. This model conveniently encapsulates the essential feature of the conformist

397   bias, i.e. that an individual is disproportionately likely to adopt the majority variant. However,

398   as can been seen from Fig. 1A, it covers only a small fraction of all possible S-shaped curves.

399   In particular, it cannot account for very steep slopes around $p = 0.5$. This is because Boyd &

400   Richerson's learners only observe a small sample of demonstrators, preventing them from

401   accurately identifying the majority behaviour. Yet, empirical work has shown that individuals

402   can be surprisingly efficient in detecting majorities around 50%, leading to a sharp

403   behavioural response to demonstrator frequencies that can look more like a step function than

404   a mild sigmoid curve (Aplin *et al.*, 2017; Danchin *et al.*, 2018). Boyd & Richerson's (1985)

405   framework could in theory be extended to account for this, but it quickly becomes analytically

406   untractable when the number of demonstrators or traits becomes large. Therefore, does a

407   simple model exist which can accommodate these very steep slopes, and (ideally) that could

408   also be generalizable to the case with any number of traits?

409   One such model could be derived from McFadden (1973)'s discrete choice model, which

410   is commonly used in economics to describe consumer choices. The probability of adopting

411   trait A takes the logistic form

$$p(q) = \frac{q^\beta}{q^\beta + (1-q)^\beta},\qquad(2)$$

412   where β is a real-value parameter expressing the strength of the conformist bias. This model

413   can be micro-founded by considering that learners pick up the most common trait among a

414   large pool of observed demonstrators but may be subject to random errors. [Specifically, $p(q)$

415   takes this form when the learner chooses the trait j which maximizes $\ln(q_j) + \varepsilon_j$ where the ε_j

416   are independent and identically distributed Extreme Value Type-I, with β a scale parameter.]

417   In this case, the smoothness of the learning curve is a result of these behavioural errors, as

418   opposed to the Boyd & Richerson (1985) model where it comes from small sampling errors.

419   As can be seen from Fig. 1B, this alternative model is very comprehensive for describing

420   milder to stronger forms of conformity in Boyd & Richerson's sense. One can also show

421   numerically that these curves resemble those that can be obtained by extending Boyd &

422   Richerson's (1985) model to an arbitrary number of demonstrators. Furthermore, it also

423   accommodates other learning rules, which sometimes have been called 'weak conformity' and

424   'anti-conformity' (see Whiten, 2019). Specifically,

425   $\beta > 1$ corresponds to conformist transmission in Boyd & Richerson's (1985) sense;

426   $0 < \beta < 1$ corresponds to weak conformity;

427   $\beta < 0$ corresponds to anti-conformity.

428   These three cases also suggest a simple statistical test for conformity. Assuming that one

429   has data on individual behavioural responses as a function of demonstrators' behavioural

430   frequencies q, testing for whether these behavioural data exhibit conformity is then

431   straightforward: the data must fit the model for a value of β greater than 1. To test this, simply

432   note that

$$\ln\left(\frac{p(q)}{1-p(q)}\right) = \beta \ln\left(\frac{q}{1-q}\right), \tag{3}$$

433   i.e. that there is a linear relationship between the log odds of the response probabilities and the

434   log odds of the demonstrators' frequencies, with the associated slope being β. The value of β

435   can thus be obtained by performing a simple linear regression, since the log odds are

436   immediately available from the data. Whether this coefficient is significantly above 1 should

437   be evidence for conformist bias.

438   A convenient feature of this model is that it can be easily extended to any number of traits,

$$p_i(q) = \frac{q_i^{\beta}}{\sum_j q_j^{\beta}}, \tag{4}$$

439   where q is now a vector of population shares q_j for each trait j. A corresponding statistical test

440   can then be derived from the following equality, valid for any two traits A and B:

$$\ln\left(\frac{p_A(q)}{p_B(q)}\right) = \beta \ln\left(\frac{q_A}{q_B}\right). \tag{5}$$

441   Lastly, both Boyd & Richerson's (1985) mathematical model and the one we propose

442   above fail to account for individual departures from unanimous majorities (i.e. a few learners

443   picking up trait B when 100% of demonstrators show trait A; see Fig. 1A). Yet, such

444   occurrences were documented as early as Asch (1955) and have been corroborated in many

445   animal studies of conformity (e.g. Pike & Laland, 2010; Battesti *et al*., 2015; Aplin *et al*.,

446   2017; Danchin *et al*., 2018). This phenomenon could for instance be evidence of major

447   cognitive limitations, or of important heterogeneities within populations regarding learning

448   rules. In any case, this feature seems ubiquitous and may lead to false negatives when using

449   the statistical test suggested above. However, a simple extension of the model above can

450   address it. Consider that the learner chooses a trait at random with probability α, and chooses

451   a trait using the conformist rule $p(q)$ above with probability $1 - α$. In the case with two traits,

452   the probability of adopting trait A becomes

$$p'(q) = \frac{\alpha}{2} + (1-\alpha)\frac{q^\beta}{q^\beta + (1-q)^\beta}. \tag{6}$$

453   Once again, one can estimate this equation on behavioural data and check whether $\beta > 1$ for

454   evidence of conformist transmission in Boyd & Richerson's (1985) sense.

455

456   **IV. CONFORMITY IN NON-HUMAN ANIMALS**

457   **(1) Behavioural ecology**

458   Boyd & Richerson's (1985) conformist transmission model has recently attracted a lot of

459   attention in behavioural ecology (e.g. Brown & Laland, 2002; Pike & Laland, 2010; Nelson &

460   Poesel, 2014; Aplin *et al*., 2015*b*, 2017; Battesti *et al*., 2015; Danchin *et al*., 2018; Lachlan *et*

461   *al*., 2018; Ayoub, Armstrong & Miller, 2019), the domain of evolutionary sciences that

462   studies the evolution of behaviour (Davies & Krebs, 1984; Danchin, Giraldeau & Cézilly,

463   2008). However, although conformity in humans rapidly attracted attention, it remained

464   largely overlooked in non-human animals for a long time, with the first studies of animal

465   conformity being published in the early 2000s, more than 50 years after Asch's studies.

466   Although non-human animal conformity is now becoming a hot topic, the junction with the

467   domain of human conformity remains to be made to allow the full study of the evolutionary

468   origins of human conformity.

469   In the non-human animal literature, conformity is often defined as 'behaving like, or

470   copying, the majority' which is in many cases a simplification of Boyd & Richerson's (1985)

471   'disproportionate likelihood of adopting the majority strategy' definition. At the very least,

472   this broader definition raises several important issues that are also subject to recent debate.

473   First, the definition 'copy the majority' does not specify whether the majority concerns the

474   larger number of individuals performing a behaviour or whether it concerns the behaviour that

475   is most frequently displayed (van Leeuwen *et al*., 2015). Indeed, it is interesting to notice that

476   this is not specified in Boyd & Richerson's (1985) model either. From an evolutionary

477   standpoint, the majority should refer to the number of individuals performing a behaviour.

478   This allows an outsider to grasp easily what is the appropriate behaviour under given

479   circumstances. Otherwise, there might be only a few individuals over-displaying a given

480   behaviour, making it the most frequent, but not the one adopted by the majority of individuals

481   in the population (van Leeuwen *et al*., 2015; Acerbi *et al*., 2016). However, in some cases, it

482   can also be beneficial if the behaviour with the highest frequency is adopted; namely when

483   particularly highly skilled or successful individuals perform one behaviour especially

484   frequently. For example, when great tits trained to open a puzzle box to get a food reward

485   were released into the wild, these few skilled individuals frequently opened the slider of the

486   puzzle box in a specific way and this technique was adopted by other individuals in the

487   population. Thus, conforming with respect to the frequency of options performed may be as

488   adaptive as conforming with respect to the majority of individuals (Aplin *et al*., 2015*a*).

489   Similarly, models showed that both the number of individuals and the frequency of the

490   behaviour can lead to the same sigmoidal conformity curve (Smaldino, Aplin & Farine,

491   2018). It is likely that if at the beginning the most frequent behaviour is copied, soon a

492   majority of individuals in the population will also exhibit this behaviour. Second, this

493   simplified definition of 'copy the majority' is sometimes used only for cases where an

494   individual performing behaviour A *changes* to behaviour B to follow the majority (e.g.

495   Cialdini & Goldstein, 2004; Cherng *et al*., 2014; Haun, Rekers & Tomasello, 2014). For

496   example, wild male vervet monkeys (*Chlorocebus pygerythrus*) that migrate to a new group

497   will abandon personal foraging preferences in favour of the new group norms (van de Waal,

498   Borgeaud & Whiten, 2013). This restriction that behaviour A must first be learned before

499   switching to B seems unnecessarily restrictive as even naïve individuals can show conformist

500   behaviour after observing others. Last but not least, it is important to focus on the fact that

501   frequency-dependent copying *without* disproportionately likely copying of the most common

502   variant cannot foster stable local traditions in which all group members adopt the same

503   behaviour. This is illustrated in Fig. 1A where Boyd & Richerson's (1985) definition of

504   conformity corresponds to the grey areas, while the common broader definition of conformity

505   would also consider strategies in the white areas as conformist, despite the fact that such

506   strategies would invariably rapidly drive populations towards a stable equilibrium with no

507   majority (i.e. at 0.5). Thus, the 'disproportionate likelihood of adopting the majority strategy'

508   is crucial to study and compare conformity both in non-human animals and humans.

509   Although research on non-human animal conformity is relatively recent, there is some

510   evidence for conformity in several taxa from insects to great apes and in various contexts

511   including foraging, song learning, problem-solving tasks, tool use and mate choice (Table 1).

512   Unfortunately, these studies use very different kinds of definition of conformity ranging from

513   a 'copy the majority' rule, over Aschian conformity where a personal preference/behaviour is

514   replaced by the majority preference/behaviour to Boyd & Richerson's (1985) definition of

515   conformist transmission. Thus, the field would benefit from clearer definition and consistent

516   use of terminology to allow for comparisons across species and studies. More generally,

517   Table 1 does not include the well-studied phenomena of herding or shoaling and other

518   processes of collective behaviour [for instance, coloniality in birds (e.g. Siegel-Causey &

519   Kharitonov, 1990; Buckley, 1997; Danchin & Wagner, 1997; Danchin, Boulinier & Massot,

520   1998; Dukas & Edelstein-Keshet, 1998; Rolland, Danchin & de Fraipont, 1998; Doligez *et*

521   *al*., 1999, 2003; Barta & Giraldeau, 2001; Brown & Bomberger Brown, 2001; Serrano *et al*.,

522   2001; Boulinier *et al*., 2002; Doligez, Danchin & Clobert, 2002; Eberhard, 2002; Parejo *et al*.,

523   2007; Varela, Danchin & Wagner, 2007)] that are not usually called conformity, despite the

524   fact that such processes can be envisioned as forms of conformity in space as long as they

525   involve social learning, which was clearly suggested by several authors from both

526   observational and experimental data (Danchin *et al*., 1998; Boulinier *et al*., 2002; Doligez *et*

527   *al*., 2002, 2003; Parejo *et al*., 2007).

528   All these considerations suggest that there is probably more evidence for the existence of

529   informational conformity in animals than usually thought. This vast breadth of taxonomies

530   and contexts (Table 1) raises the question of the evolutionary origin of conformity. In itself,

531   this breadth suggests convergent selection for conformity rather than a homologous capability

532   (Laland, Atton & Webster, 2011). However, we are still lacking a general framework by

533   which conformity may have emerged in the first place during the course of evolution.

534

535   **(2) Conformity in mate choice and the Fisher runaway process**

536   Our review of the literature on non-human animal conformity has revealed a quasi-absence of

537   evidence for conformity in the context of mate choice (Table 1, with the nuance we introduce

538   in Section V). The only clear example of conformity in mate choice in any animal including

539   humans is a study in fruit flies (*Drosophila melanogaster*) where females develop mating

540   preferences for a certain male phenotype in a conformist manner (Danchin *et al*., 2018). In

541   that study, as long as there was a majority of demonstrator females copulating with males of a

542 given phenotype, observer females copied this choice and developed a similarly significant

543 bias for males of that specific phenotype whatever the level of majority in the population. As

544 a result, the response function of observer females followed a step function (as the green

545 dotted curve of Fig. 1B), with females learning equally well to prefer the most commonly

546 chosen male colour whatever the level of majority, which in that study varied experimentally

547 from 100% to only 60%. However, a certain number of individuals did not copy the majority

548 for whatever reason (e.g. being anti-conformists or individual learners). A simple model also

549 suggested that this strong conformity in mate choice might generate surprisingly long-lasting

550 traditions of preferring one male phenotype at the local scale (Danchin *et al*., 2018).

551   The *Drosophila* result on conformity calls for an evolutionary explanation. Interestingly,

552 conformity in the context of mate choice is reminiscent of the well-known Fisher runaway

553 process (Fisher, 1930). According to this process, both male traits and female preferences are

554 supposed to be under genetic control. Under such conditions, as soon as females develop

555 some preference, females tend to mate with their preferred male phenotype, which

556 automatically generates a correlation between the male trait and the female preference. This

557 generates a linkage disequilibrium of purely statistical nature (Bailey & Moore, 2012). This

558 statistical linkage participates in what we now call 'inclusive heritability', i.e. parent–

559 offspring resemblance due to genetic or non-genetic information being transferred from

560 parents to offspring (Danchin & Wagner, 2010; Danchin *et al*., 2011). Such resemblance can

561 involve DNA sequence variation (which is probably partly valid for the male trait) but could

562 also result from the cultural transmission of female preference. What matters is that females

563 transmit their preference to their daughters, and fathers their trait to their sons, so that the

564 information responsible for the two traits (e.g. male trait A, and the preference for A) are

565 transmitted jointly. Hence, the female trait becomes statistically associated with the male trait,

566 producing a self-reinforcing process called the Fisher runaway process. Based on this

567 understanding of the Fisherian process, we now propose and provide a generic model for a

568 possible two-step evolutionary scenario rooted in this process, which unfolds at two different

569 spatial scales.

570   Let us first imagine an ancestral metapopulation with two heritable male phenotypes A

571 and B with equal fitness (as is the case, for instance, in Danchin *et al.*, 2018). There is no

572 initial female preference for one of these male phenotypes, but some inclusively heritable

573 variation in females' tendency to copy others (due to the inheritance of genetic or non-genetic

574 information). In a given subpopulation, chance may sometimes lead to more females mating

575 with, for instance, A males. As soon as such a majority becomes detectable, copier females

576 tend to mate more often with A males. As a result, they will tend to have A sons and

577 daughters that tend to copy the choices of their elders, implying that they reject B males (left

578 panel, Fig. 2). At the scale of the subpopulation, because of the Fisher runaway process, this

579 reinforces both the proportion of A males and the tendency socially to learn to prefer A males.

580 On the other hand, females of the initial subpopulation choosing B males (i.e. mostly non-

581 copiers) would have B sons and mostly non-copier daughters that mate randomly with A and

582 B males. So, at the beginning, while copier females tend to amplify the proportion of A males

583 and the tendency to copy, non-copier females produce sons in proportion to the frequency of

584 each male type in the subpopulation, while producing non-copier daughters. Thus, non-copier

585 females do not affect the proportion of male types.

586   Thus, at the scale of the subpopulation, locally both the proportion of A males and of

587 copier females slowly increase at a rate that accelerates with the proportions of copier females

588 in a kind of snowball effect. As a result, non-copier females mating with B males will have B

589 sons that will be more and more socially unsexy over the course of generations. On the other

590 hand, copier females mating with A males are more and more favoured (Fig. 2, left panel). In

591 summary, at the local scale, this process transitorily selects for A males, and for social

592 learning in mate choice. This process, however, is transitory because social learning becomes

593 neutral after the local disappearance of the B male phenotype (see simulations in Section VI).

594 Note that even if the two male phenotypes initially did not differ in terms of fitness, the trait

595 soon quits neutrality because of the social transmission of mating preferences in females. This

596 is the runaway process.

597   Now, this logic unfolding within a single subpopulation should simply transitorily select

598 for females preferring A males. Nonetheless, that transitory phase probably generated a

599 correlation between male trait and female preference for it. As this correlation is likely to

600 persist for some time after the disappearance of B males, this implies that if dispersing B

601 males enter that local population the Fisher runaway process will immediately resume. In fact,

602 at the scale of a metapopulation, which consists of subpopulations connected by dispersing

603 individuals, in some subpopulations selection would favour females mating with A by chance

604 (Fig. 2, left panel), and in other subpopulations females mating with B males (Fig. 2, right

605 panel). In such a system, dispersal hampers the local evolution of a heritable preference for A,

606 and favours conformity, as immigrants detecting the local preference and conforming to it

607 have higher fitness (Fig. 2, right panel and Section VI). Hence, it is the spatial structure of the

608 metapopulation with individuals dispersing among subpopulations that generates selection for

609 the more integrated rule of 'mate with males of the *locally* preferred phenotype', i.e. for

610 conformity.

611   Note that this process is superficially similar to a process by which conformity could arise

612 for foraging preferences, but it is different at a deeper level as in the latter case conformity

613 evolves due to natural and not sexual selection as proposed above. Suppose that in the first

614 subpopulation fruit C is nutritious and fruit D is poisonous, while in the second subpopulation

615 there is fruit E, resembling C, that is poisonous and fruit F, resembling D, that is nutritious. A

616 preference for C and a preference for copying the majority would be equally adaptive in the

617   first subpopulation, just as a preference for F and a preference for copying the majority would

618   be equally adaptive in the second subpopulation. However, for dispersers between the two, a

619   preference for copying the majority would continue to be adaptive, while a preference for C,

620   translated to the second environment, might be fatal, as would a preference for F, translated to

621   the first environment. So, conformity would be more adaptive on average than either direct

622   nutritious preference.

623   Unlike the Fisher process, though, this process would not be self-reinforcing – conformity

624   would not become more adaptive as it became more common in the population. In addition,

625   its adaptive value would depend on the absence of consistency in the nutritious value of

626   foraging preferences across environments. This may be true in some ecologies but lacks the

627   general autocatalytic runaway character of the Fisher process at the metapopulation scale,

628   which is independent of other characteristics of the environment.

629   In view of the generality of the Fisher runaway process in sexually reproducing

630   organisms, and in view of its autocatalytic properties, we should expect conformity in mate

631   choice to be far more common than usually understood. In other words, it should have

632   evolved very early in evolution, soon after the moment when sexually reproducing organisms

633   developed enough cognitive capacities to detect the local majority. This raises the question of

634   the links between mate copying and conformity.

635   Mate copying is a special case of social learning in the context of mate choice in which

636   females build their own preference from observations of another female choosing between

637   male phenotypes. Mate copying can be performed in a conformist manner (Danchin *et al*.,

638   2018), i.e. over-copying what is preferred by the majority on one hand, and on the other hand

639   conformity in mate choice can be the result of positive frequency-based mate copying.

640   Unfortunately, very few studies of mate copying have tested whether it is performed also in a

641   conformist fashion, precluding us from studying the links between these two processes. In

642   fact, most studies on mate copying use only a single demonstration for practical reasons

643   (reviewed in Varela, Matos & Schlupp, 2018), thus preventing us from talking about the

644   majority. We suggest that mate copying experiments may in fact constitute a specific test of

645   conformity in which the experimental design limits itself to a sample size of demonstrators of

646   1. As animals have been selected to conform in mate choice (as we developed above), as soon

647   as they see one demonstration, they may interpret it as a majority preference in the

648   population, because chance makes it more likely that this single observation represents the

649   local majority. But the smaller the majority the higher the risk of opting for the locally non-

650   preferred male phenotype (which corresponds to the black random copying line in Fig. 1B). In

651   nature, however, by observing multiple matings, observer females can considerably increase

652   the quality of their assessment of the local majority and thus can considerably increase their

653   chance of building a preference for the majority male phenotype.

654   This reasoning would suggest that the rather large literature on mate-copying experiments

655   may reveal the existence of conformity in mate choice in the many concerned species. Hence,

656   we can predict that a quick way to increase the evidence for conformity in non-human

657   animals would be to test for conformity in species known to preform mate copying by simply

658   adapting the experimental design in order to be able to show multiple demonstrations in order

659   to manipulate the majority as in the testing of Danchin *et al*. (2018)'s criterion 5. If, as we

660   predict, many such studies provide evidence for conformity in sex, this would support the idea

661   that mate copying and conformity are tightly linked, and that mate copying and conformity in

662   mate choice are two faces of the same coin that jointly accelerate and maintain the evolution

663   of local traditions for preferring a specific male phenotype over generations. Thus, future

664   studies should systematically test for conformity in mate copying. It is thus of prominent

665   importance to design experiments that manipulate the level of majority in order to study the

666   response function of conformity in mate choice in a wide range of species.

667

V. FROM FISHER TO CULTURE

Beyond the fact that the existence of conformity in numerous animal taxa generates a

continuum from non-human animals to humans, it is necessary to integrate some of the major

consequences of the evolutionary scenario presented in the previous section in terms of its

potential to foster cultural transmission in general and in humans in particular.

As discussed above, the first step in this evolutionary pathway unfolds locally and

temporarily favours social learning (Step 1 of Fig. 3). Similarly, the second component results

from individuals dispersing among subpopulations within the metapopulation, which

stabilizes social learning and leads to the evolution of conformity (Step 2 of Fig. 3). Thus, in

highly mobile species, conformist mate choice might have fostered the development of a kind

of 'conformist module' for detecting the majority and following it in order to mate

preferentially with the locally preferred male phenotype. These two first steps are detailed in

the previous section and should foster the emergence of local traditions in mating preferences

(Step 3 of Fig. 3). In view of the generality of the Fisher runaway process and of the scenario

proposed in Section IV.2, these capacities probably evolved as soon as sexually reproducing

ancestral species acquired the capacity to detect the majority, so that they should be present in

a vast array of species.

However, the story does not end there. We have detailed above that there is some

theoretical and empirical evidence that conformity is potent in fostering a cultural process

(Fisher, 1930; Sterelny, 2006; Efferson *et al*., 2008; Laland *et al*., 2011; Danchin *et al*., 2018;

Lachlan *et al*., 2018). Like norms or punishment, conformity can play the role of a 'repair

mechanism' to maintain an existing preference/behaviour. Thus, once acquired and potent, the

conformity module may have percolated to other contexts such as foraging, problem solving,

tool use, etc. (Step 4 of Fig. 3). Alternatively, cognitive processes involved in copying

692   foraging behaviour may have been subsequently co-opted for use in mate choice. Some

693   mechanisms, however, do not seem easily co-opted from foraging to mate choice – for

694   instance, the pheromone trails that yield conformity in ant foraging (Sumpter & Beekman,

695   2003). Another alternative is that conformity emerged independently in foraging and mate

696   choice within lineages. Further studies are needed to rule out the different possibilities.

697   Nonetheless, as in this scenario initial fitness benefits accrue from reproduction, it predicts

698   that social learning should remain efficient during the whole reproductive period, which

699   appears consistent with some non-human animal and human studies.

700   The evolution of a conformity module that expanded to other contexts then may have

701   fostered the emergence of local traditions in many domains of behaviour (Step 5 of Fig. 3).

702   This pathway would thus imply that all the reported cultural processes, whatever the domain

703   involved, would find their origin in mate choice and sexual reproduction in the first ancestors

704   that acquired the capacity to detect and comply with the majority, which must have produced

705   the initial trigger of the Fisher runaway process.

706

707   **VI. A GENERIC MODEL OF THE EVOLUTION OF CONFORMITY**

708   We investigated the verbal model that we developed above using simulations of population

709   dynamics, in order to explore whether conformity can indeed evolve *via* such a mechanism

710   (Figs 4 and 5). Consider a group of individuals, with the same number of males and females.

711   There are two diallelic genes (or two non-genetic inclusively heritable variants). The first one,

712   with variants A and B, is expressed in males only and is neutral for fitness. The second one,

713   with variants C and c, is expressed in females only: females c mate randomly, while females

714   C use the logistic conformist learning rule described in Section III.4. without associated cost.

715   The strength of this conformist rule is expressed by the parameter β. Initially, the two

716   inclusively heritable types of variants are neither physically nor statistically linked so that

717   they vary independently from each other. Each female has two offspring, one male and one

718   female that inherit the traits from their parents.

719   The metapopulation is composed of several such groups. In each new generation, a

720   random fraction d of the offspring migrates to another randomly chosen subpopulation on one

721   of the spots left vacant by other migrants (males take male spots and females take female

722   spots to prevent sex bias in groups). Initially, alleles A and B are randomly allocated in the

723   meta-population in 50:50 proportions. Alleles C and c are also randomly allocated, with an

724   initial proportion $q0$ of allele C. We explored the effect of the dispersal rate d and of the

725   conformity strength parameter β on the proportion of A and B males and of C and c females

726   (Fig. 4), taking the initial proportion of $q0$ of conformists and the recombination rate r fixed

727   ($q0 = r = 0.2$).

728   Simulations show that conformity can indeed evolve under the sole effect of the Fisher

729   runaway process unfolding independently in every subpopulation (Fig. 4). This happens in a

730   particular region of the parameter space, namely, when the dispersal rate d is not too high

731   compared to the conformity strength parameter β. A likely explanation is that when the

732   dispersal rate is too high, the spatial structure of the population becomes less relevant.

733   However, more theoretical work is needed to understand the precise role of each parameter in

734   the evolution of conformity *via* the Fisher runaway process.

735   Our simulation results mirror those of Somveille *et al.* (2018), who study the effect of

736   similar parameters in a computational model of the emergence of local traditions. Similarly,

737   they find that local traditions emerge when the dispersal rate is not too high compared to the

738   strength of conformity. The difference with our model is that they consider conformity as a

739   common feature of all individuals and study the consequences on behaviour adoption. By

740   contrast, we study whether conformity can evolve in the first place through the Fisher

741   runaway process. In our case, local traditions emerge because conformity has been able to

742   evolve. Our goal here is not to illustrate all the properties of this simple model but rather to

743   show that under some parameter values, conformity does evolve under the sole effect of the

744   Fisher runaway process unfolding independently in every subpopulation.

745   As an illustration, we also show how the population dynamics unfold for a set of

746   parameters for which conformity evolves (Fig. 5) and compare this to the case wherein the

747   population is spatially unstructured. For these parameter values, conformity evolves readily in

748   metapopulations, and leads to among-group diversity on the male phenotype. When the

749   population is unstructured however (the same number of individuals but no subgroups and

750   therefore no migration), male diversity is quickly lost, and conformity becomes neutral.

751

752   **VII. CONCLUSIONS**

753   (1) The strength of our proposed pathway rooted in mate choice and runaway sexual selection

754   is that it explains the evolution of social learning and conformity, as well as culture.

755   (2) One of the major challenges therefore for empirical studies of social learning is to find out

756   whether the detection of majority behaviour in mate copying preceded (in evolutionary time)

757   the detection of majority behaviour in other contexts such as foraging and to what extent it

758   evolved analogously or homologously. For that goal we will need to determine in a large

759   range of species the shape of the response function of conformity in mate choice, and other

760   contexts with experiments manipulating the level of majority. Altogether, this provides a rich

761   agenda for future research.

762   (3) In the expectation of such information, the tentative model we propose and simulate here

763   for the evolution of conformity, and all its cultural evolution consequences, casts surprising

764   light on one of the major processes that has participated in making us humans. Sex might play

765   a bigger role than previously thought in the long-run development of cultural traditions.

766

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1107 Table 1. Reported examples of conformity in the animal kingdom. We include only instances

1108 when the authors explicitly referred to conformity (see Section IV.1 for comments on this

1109 choice).

Context	Species	Working definition used	References
cooperation	ant (*Paratrechina longicornis*)	"conformist group members align their actions with those of their neighbours" (p. 2)	Gelblum *et al.* (2015)
oviposition site	fruit fly (*Drosophila melanogaster*)	"the tendency to disproportionately adopt the most commonly encountered social information" (p. 84)	Battesti *et al.* (2015)
mate choice	fruit fly (*Drosophila melanogaster*)	"an exaggerated tendency to copy the majority" (p. 362)	Danchin *et al.* (2018)
shoaling	mosquitofish (*Gambusia holbrooki*)	No clear definition	Herbert-Read *et al.* (2013)
	guppy (*Poecilia reticulata*)	"positive frequency-dependent social learning" (p. 917) "many animals are disproportionately likely to adopt via social learning the behaviour of the majority" (p. 41) "strong compulsion for individuals within social groups to remain in close contact and look and behave similarly" (p. 95)	Day *et al.* (2001); Brown & Laland (2002); Brown & Irving (2014)
	rummy-nose tetra (*Hemigrammus rhodostomus*)	"tendency to follow the majority of their neighbours nonlinearly" (p. 1)	Lecheval *et al.* (2018)
personality	solitary crab (*Carcinus maenas*)	"animals compromise their own behaviour to the level of a certain behaviour displayed by another individual or a group" (p. 131)	Fürstbauer & Fry (2018)
	Eurasian perch (*Perca fluviatilis*)	"behaving uniformly" (p. 501) No clear definition	Hellström *et al.* (2011); Magnhagen (2012)
	Gouldian finch (*Erythrura gouldiae*)	"individuals will tend to synchronize their behaviour in time and space, altering their behaviour in line with their group mates, and potentially suffering consensus costs" (p. 26)	King *et al.* (2015)

	marmoset (*Callithrix jacchus*)	no clear definition	Koski & Burkart (2015)
song	white-crowned sparrow (*Zonotrichia leucophrys*)	"when a young pupil models its song(s) on those of one or more tutors" (p. 433) "disproportionate tendency to copy the most common behavioural variant" (p. 1742)	Nelson & Poesel (2009); Nelson & Poesel (2014)
	swamp sparrow (*Melospiza georgiana*)	"disproportionate tendency to copy the majority" (p. 2)	Lachlan *et al.* (2018)
	Indo-Pacific bottlenose dolphin (*Tursiops aduncus*)	"being increasingly likely to adopt the most frequent behaviour" (p. 6)	Cantor & Whitehead (2013)
	humpback whale (*Megaptera novaeangliae*)	"being increasingly likely to adopt the most frequent behaviour" (p. 6)	Cantor & Whitehead (2013)
	sperm whale (*Physeter macrocephalus*)	"learn preferentially the most common codas" (p. 1)	Cantor *et al.* (2015)
tool use	Japanese macaque (*Macaca fuscata*)	"immature individuals should adopt the same type of stone-directed activities as most of the older group members" (p. 124)	Leca *et al.* (2010)
	chimpanzee (*Pan troglodytes*)	"a powerful tendency to discount personal experience in favour of adopting perceived community norms" (p. 738) no clear definition "personal knowledge was dropped in order to adopt the behaviour of the group" (p. 650)	Whiten *et al.* (2005); Whiten *et al.* (2007); Luncz & Boesch (2014)
foraging	nine-spined stickleback (*Pungitius pungitius*)	"positive frequency dependent social learning where the probability of acquiring a trait increases disproportionately with the proportion of other individuals performing it" (p. 466)	Pike & Laland (2010)
	threespined stickleback (*Gasterosteus aculeatus*)	No clear definition No clear definition	Webster & Hart (2006); McDonald *et al.* (2016)

|	zebrafish (*Danio rerio*)	"copy the majority strategy" (p. 1519) "individuals will appear to disproportionately copy the most common behavioural choice demonstrated by their group" (p. 164)	Zala *et al.* (2012); Ayoub *et al.* (2019)
	great tit (*Parus major*)	"individuals to disproportionately adopt the most frequent local variant when first acquiring an innovation, and continuing to favour social information over personal information" (p. e5) "disproportionate tendency to copy the most common behavioural variant" (p. 7830)	Aplin *et al.* (2015*a*); Aplin *et al.* (2017)
	Norway rat (*Rattus norvegicus*)	"changing one's behaviour to match that of others" (p. 769)	Jolles *et al.* (2011)
	Indo-Pacific bottlenose dolphin (*Tursiops aduncus*)	"being increasingly likely to adopt the most frequent behaviour" (p. 6)	Cantor & Whitehead (2013)
	humpback whale (*Megaptera novaeangliae*)	"being increasingly likely to adopt the most frequent behaviour" (p. 6)	Cantor & Whitehead (2013)
	redfronted lemur (*Eulemur rufifrons*)	"adoption of the group's norm, despite being in principle able to behave differently, or overriding of individually learned by socially acquired information" (p. 506)	Schnoell & Fichtel (2012)
	capuchin monkey (*Cebus apella*)	"conform to the foraging preferences of their closest social partners, despite having the knowledge of alternative techniques" (p. 4) no clear definition no clear definition	Dindo *et al.* (2009); Crast *et al.* (2010); Franz & Matthews (2010)
	white-faced capuchin monkey (*Cebus capucinus*)	"the tendency for individuals to preferentially exhibit behavioural alternatives that they witness most frequently in their peers, or to exhibit the behaviours that are performed by peers who are considered most prestigious or successful, or those peers with whom they have the highest quality social relationships" (p. 706)	Perry (2009)

	vervet monkey (*Chlorocebus pygerythrus*)	"conformity to local behavioural norms" (p. 483)	van de Waal *et al.* (2013)
	chimpanzee (*Pan troglodytes*)	"follow-the-majority (= the number of animals in a group performing a specific behaviour increases, so does the likelihood of a naïve individual adopting that same behaviour, thus driving the preservation)" (p. 1195)	Hopper *et al.* (2011);
		"the increased likelihood for learners to end up not with the most frequent behavior but rather with the behavior demonstrated by most individuals" (p. 727)	Haun *et al.* (2012);
		"foregoing a pre-existing behaviour in favour of adopting one demonstrated by a majority of conspecifics" (p. 407)	Watson *et al.* (2018)

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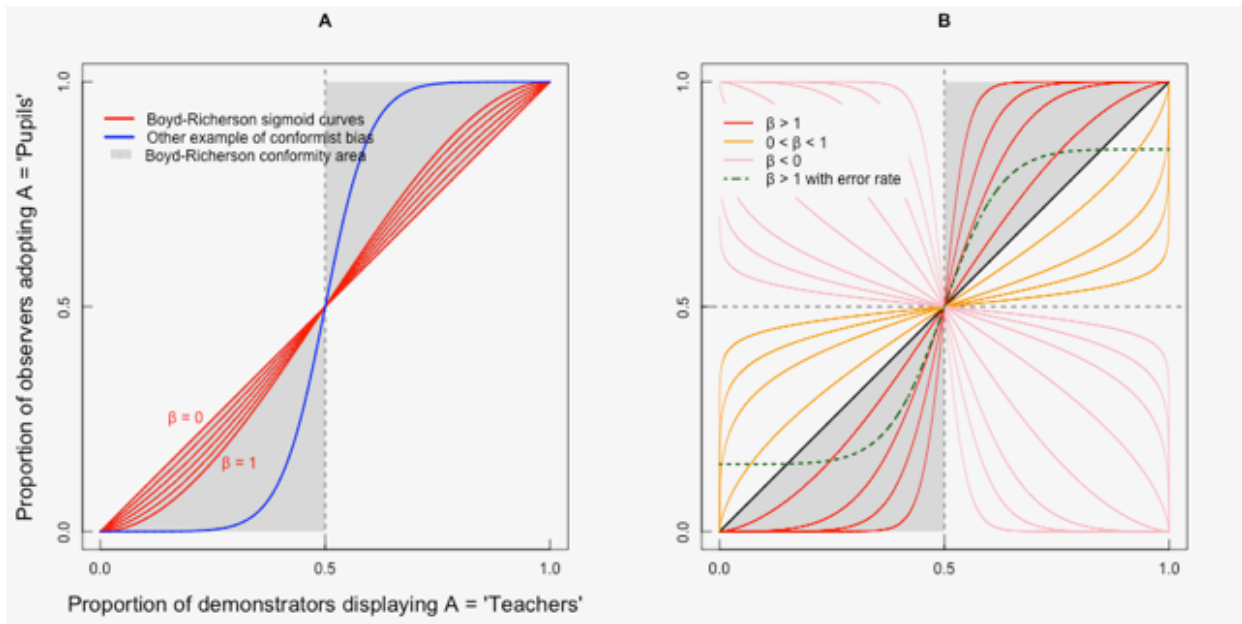
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1114   **Fig. 1.** An alternative functional form for conformity. Both graphs depict the relationship

1115   between the proportion of demonstrators adopting one option (*x*-axis) and the probability that

1116   an observer subsequently adopts that option (*y*-axis; in a case with two options). On the left

1117   (A) we show Boyd & Richerson's (1985) definition of conformist bias. The grey areas

1118   correspond to conformity: observers are *disproportionately likely* to adopt the majority

1119   behaviour, i.e. more than under random matching. The red lines correspond to Boyd &

1120   Richerson's (1985) mathematical definition of conformist bias: they only cover a small part of

1121   the area designated for conformity. The blue line corresponds to a conformist learning rule

1122   that cannot be approached by Boyd & Richerson's (1985) definition. On the right (B) we

1123   show learning rules associated with the logistic expression from Section III.4. This expression

1124   is flexible enough to cover Boyd & Richerson's conformist bias or 'hyper-conformity' (red

1125   lines), as well as 'weak conformity' (orange lines) and 'anti-conformity' (pink lines). Using

1126   an error rate (green dashed line) it can also approximate empirical patterns of behaviour [here
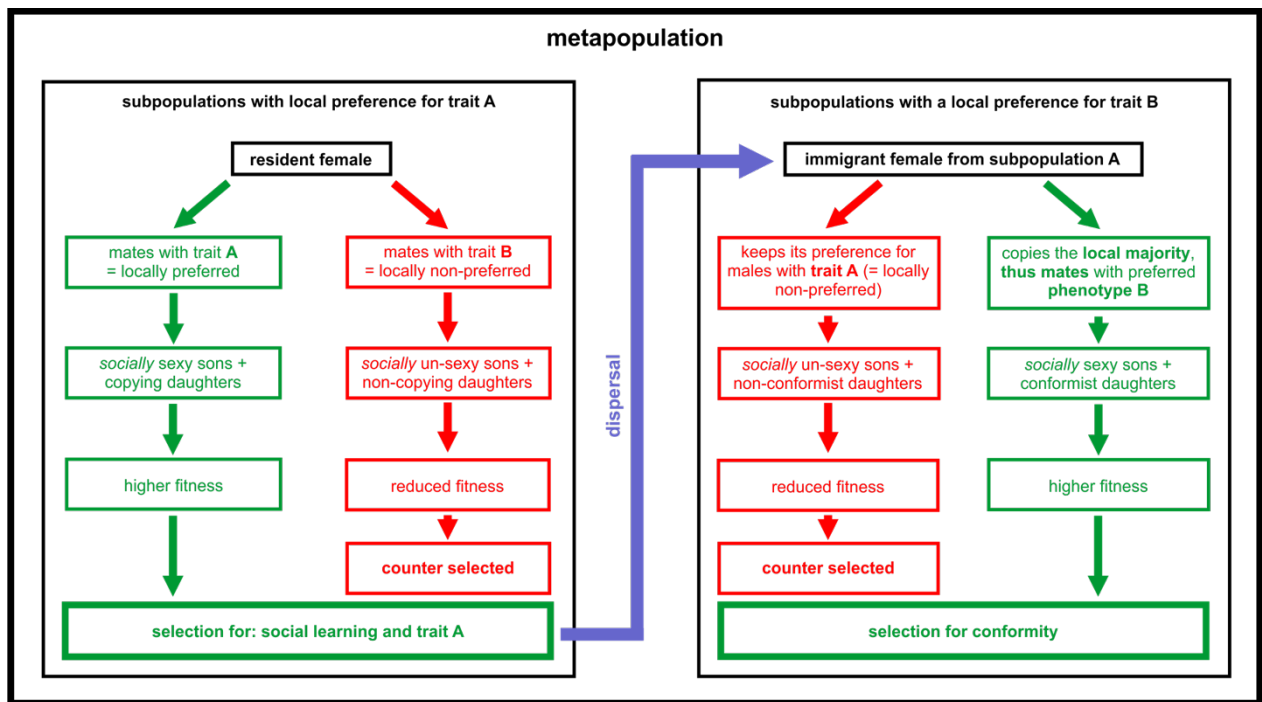
1127   that of Danchin *et al*. (2018) in the fruit fly] whereby individuals depart from unanimous
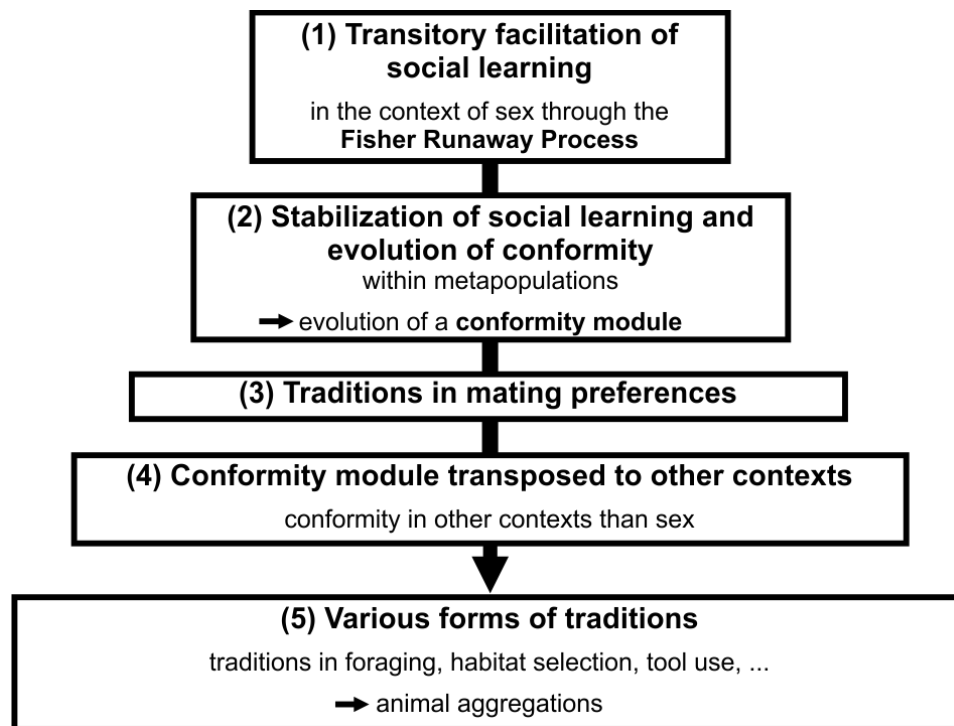
1128   majority behaviour. In effect, perfect conformity when getting close to 100% adopting the

1129   majority behaviour is highly unlikely in actual organisms.

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Fig. 2. Social learning and conformity in mate choice are produced by the Fisher runaway process within metapopulations. As females are usually the choosy sex, we illustrate that option. In some subpopulations, the majority of females mate with males of trait A while in others they prefer males of trait B. Costly options (mating with the locally non-preferred male phenotype) are shown in red and beneficial options (mating with the locally preferred male phenotype) are in green. Within subpopulations this selects for one male phenotype and social learning (left panel), but at the scale of a metapopulation dispersal leads to selection for 'copy the majority', that is for conformity (right panel).

(1) Transitory facilitation of social learning

in the context of sex through the
Fisher Runaway Process

(2) Stabilization of social learning and evolution of conformity
within metapopulations
➡ evolution of a **conformity module**

(3) Traditions in mating preferences

(4) Conformity module transposed to other contexts
conformity in other contexts than sex

(5) Various forms of traditions
traditions in foraging, habitat selection, tool use, ...
➡ animal aggregations

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1141 **Fig. 3.** A tentative evolutionary pathway towards culture. From the Fisher runaway process in

1142 the context of mate choice to social learning, conformity, traditions in sexual preferences,

1143 various forms of traditions including aggregated behaviour, and culture.
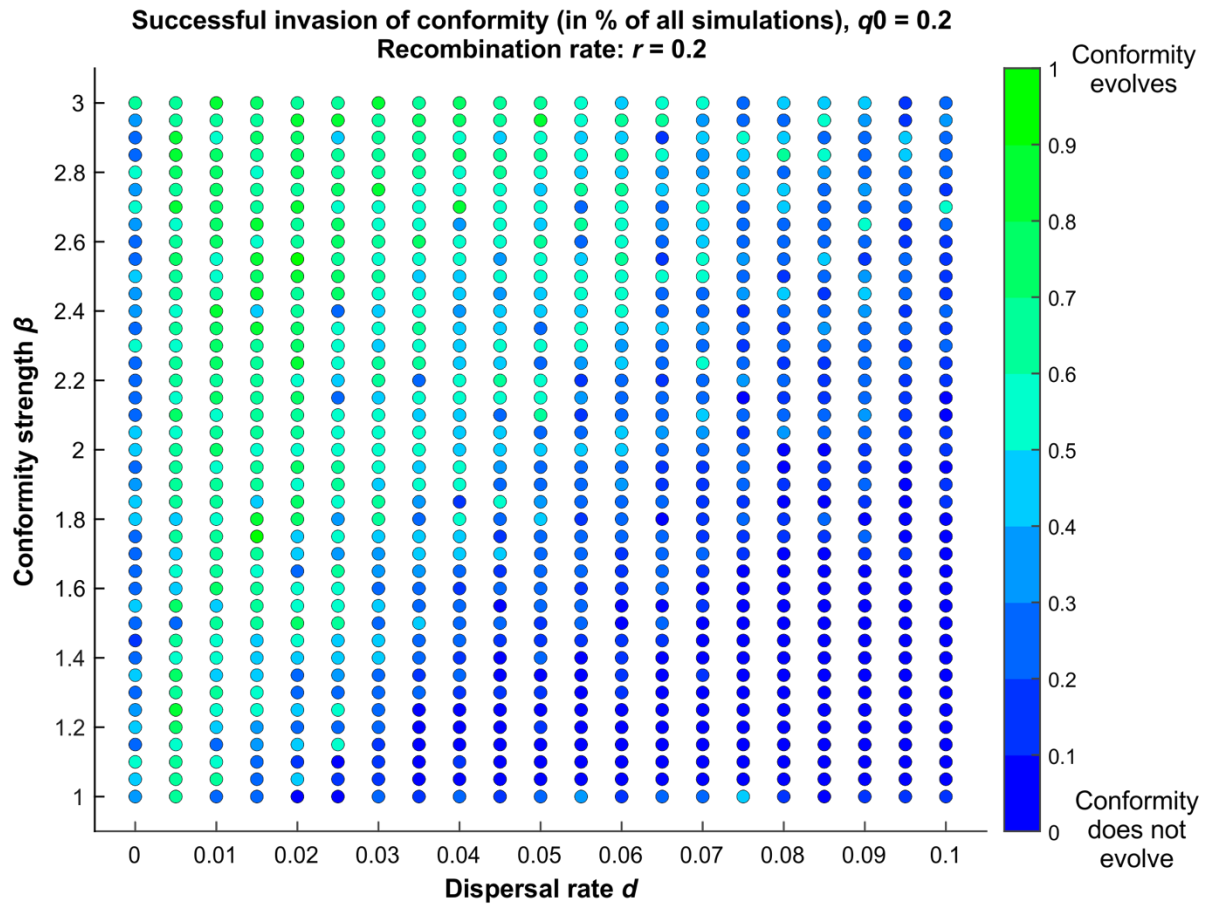
Fig. 4. Evolution of conformity in spatially structured metapopulations for different parameter values. Each point is obtained using 20 simulation runs of the evolution of conformity in a population of non-copiers. Males express either trait A or B. Females are conformist or pick a male randomly. The initial fraction of conformist females is $q0 = 0.20$. The recombination rate is fixed at $r = 0.20$. Conformity evolves when the dispersal rate d is not too high compared to the strength of conformity β. The code for this model is available at

https://github.com/antoine-jacquet/project-conformity
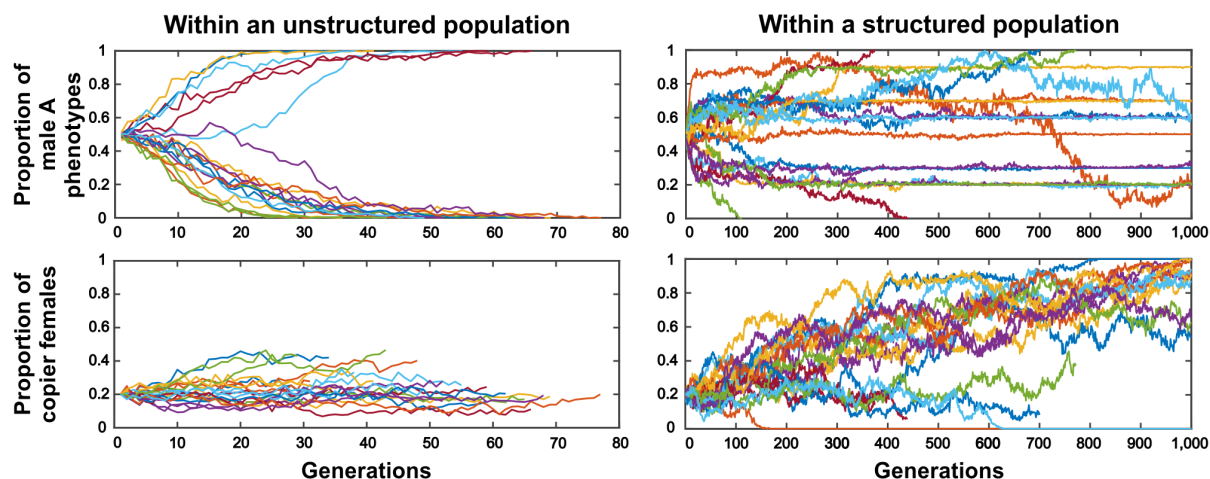
Fig. 5. Conformity evolves in spatially structured metapopulations. In a simple simulation model, we found that dispersal among subpopulations within a metapopulation can favour the evolution of social learning and conformity, which are well known to be essential traits for the evolution of long-lasting local traditions, the main marker of a cultural process. Graphs obtained in simulations of the evolution of conformity in a population of non-copiers for the set of parameter values: $\beta = 2.8$, $d = 0.02$, $q0 = 0.20$, $r = 0.20$ (see Fig. 4 for the definitions of these variables). Males express either trait A or B. Females are conformist or pick a male randomly. Lower graphs show dynamics of the conformity allele. Upper graphs show male trait dynamics. Left-hand graphs depict the dynamics within unstructured populations. Male diversity is rapidly lost, and conformity remains neutral. Right-hand graphs depict the dynamics within structured metapopulations. Male diversity is maintained both among and very often within subpopulations, and conformity can evolve.