

# Cultural transmission and biological markets

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## Abstract

Active cultural transmission of fitness-enhancing behavior can be seen as a costly strategy, one whose evolutionary stability poses a Darwinian puzzle. In this article, we offer a biological market model of cultural transmission that substitutes or complements existing kin-selection based theories for the evolution of cultural capacities. We explicitly formulate how a biological market can account for the evolution of deference and prestige-related phenomena, as well as how it can affect the dynamics of cumulative culture. We show that, under certain conditions, teaching evolves even when innovations are not sufficiently opaque and can be acquired by emulators via inadvertent transmission. Furthermore, teaching in a biological market is a precondition for enhanced individual learning abilities.

### *Keywords:*

Social learning, comparative advantage, teaching, deference, cumulative culture, partner choice

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## 1. Introduction

2     A certain view of cultural evolution sees cultural transmission as bringing  
3     a straightforward advantage to the group or the individual's kin. Hence, its  
4     evolution follows. However, if the active transmission of culture is such a  
5     successful strategy, then where is all the evidence of it in the animal kingdom?  
6     Although social learning and certain forms of animal traditions are common  
7     in many non-human species, active cultural transmission or teaching is a far  
8     rarer phenomenon (Boyd and Richerson, 1996; Thornton and Raihani, 2008).

9     On the production side of active cultural transmission, “natural pedagogy”  
10    —the dispositions and efforts of adults to make themselves easily  
11    understood by children and to thus facilitate the transmission of cultural  
12    knowledge— is certainly part of the human pattern of cultural transmission

13 (Hewlett et al., 2011), a good candidate for a universal trait of our species,  
14 and perhaps even a biological adaptation (Csibra and Gergely, 2009). Such  
15 considerations suggest a vertical-transmission view of the evolution of human  
16 culture, i.e: direct transmission from the parental generation to the genera-  
17 tion of siblings. Nonetheless, another view widely accepted among ethnogra-  
18 phers claims that adult-infant instruction is rare in hunter-gatherers groups  
19 (Atran and Sperber, 1991). Moreover, as several case studies in cultural  
20 transmission have indicated, non-vertical transmission —that is, transmis-  
21 sion to children from other children or slightly older individuals, as opposed  
22 to much older adults— is far more important for cultural transmission than  
23 assumed (Aunger, 2000; Morin, 2015). It has even been argued that non-  
24 vertical transmission might constitute the key component in children’s and  
25 young adults’ adoption of much of the cultural repertoire (Harris, 1998).

26 From a population genetics perspective, other considerations also counter  
27 the all-importance of vertical transmission in the evolution of culture. Cul-  
28 tural capabilities were plausibly “built for speed” and adaptability (Richerson  
29 and Boyd, 2000). However, pure vertical cultural transmission is more anal-  
30 ogous to genetic adaptation, and thus has fewer of those properties: it is  
31 more often subject to maladaptive lag and inertia than other forms of cul-  
32 tural transmission (McElreath and Boyd, 2008). In changing environments,  
33 *mother does not always know best*. The facilitation of cultural transmission  
34 via genetic relatedness, namely as a form of evolved nepotism, is possibly  
35 part of the picture yet can be easily exaggerated. There are conflicts of in-  
36 terests between parents and siblings (Trivers, 1974). In principle, parental  
37 manipulation could be selected for, which in return could prompt the evo-  
38 lution of devices that counteract the effects of vertical cultural transmission  
39 among siblings (Trivers, 2011).

40 Active cultural transmission is essentially problematic on the grounds of  
41 its cost-benefit structure. If what an individual learns is so useful in terms of  
42 fitness that acquiring it makes sense for other individuals, then why bother  
43 actively transmitting it? From the standard inclusive fitness perspective of  
44 evolution, it follows that traits that do not benefit kin need to benefit their  
45 carriers in order to evolve by way of natural selection (Dessalles, 2001, 2006).  
46 However, a great deal of cultural transmission is both not directed to kin and  
47 costly enough to pose a Darwinian puzzle. The question thus remains: Why  
48 transmit culturally?

49 Seemingly altruist cultural transmission of fitness-enhancing information  
50 yields a free rider problem structured similarly to the standard prisoner’s

51 dilemma. Briefly, since active cultural transmission of fitness-enhancing in-  
52 formation (“teaching”) is a form of cooperation, every individual would be  
53 better off if other individuals cooperate, while he or she does not cooperate.  
54 Therefore, all else being equal, a population of individuals capable of cultural  
55 transmission could be expected to evolve toward a sub-optimal equilibrium,  
56 one in which cultural transmission is simply not practiced.

57 The ethological definition of teaching characterized it as a form of altru-  
58 ism from early on (Caro and Hauser, 1992). In principle, ecological conditions  
59 linked to kin selection and alloparentality might have facilitated the evolu-  
60 tion of certain cultural capacities (Hrdy, 2009; Flinn and Ward, 2005). Thus,  
61 the immense majority of formal models which have been used to investigate  
62 the evolution of teaching have relied on genetic relatedness to explain its  
63 stability (Castro and Toro, 2014; Fogarty et al., 2011). Nevertheless, the  
64 abovementioned theoretical and empirical considerations largely justify the  
65 exploration of complementary, if not alternative, evolutionary pathways by  
66 which cultural capacities can reach an adaptive equilibrium in a given pop-  
67 ulation.

68 In this article, we analyze conditions of the evolution of cultural transmis-  
69 sion capacities in a biological market model. Originally proposed by behav-  
70 ioral ecologists Ronald Noë and Peter Hammerstein, biological markets arise  
71 when associations between biological individuals are sufficiently uncoerced  
72 that competition occurs not so much by force or its threat, as due to a need  
73 to offer more of what the choosing party “demands”. The idea of biological  
74 markets thus sheds light on certain selective mechanisms, namely market ef-  
75 fects in which “*members of one class can “force” members of another class*  
76 *to evolve traits that would have a negative effect on fitness in the absence of*  
77 *the cooperative interaction”* (Noë and Hammerstein, 1994, p. 2).

78 Along with other ecological forces, part of the evolutionary rationale of  
79 active cultural transmission might be a result of biological markets. Models  
80 and hypotheses akin to biological markets have already found applications in  
81 other arenas of evolutionary psychology, including the psychology of coop-  
82 eration and mutualism (Frank, 1988; Baumard, 2010; André and Baumard,  
83 2011). To our knowledge, Henrich and Gil-White (2001) first proposed that  
84 cultural abilities and knowledge could enter into a market-like exchange of  
85 what they called “information goods” and “prestige”. Based on previous an-  
86 thropological observations (Barkow et al., 1975), they formulated a theory of  
87 human hierarchies, in which dominance and prestige hierarchies both differ  
88 and mix in the context of human hierarchical strategies. In humans, hier-

89 archical status is attainable not only by use of force (i.e: the “dominance”  
90 strategy) or power, but also by demonstration of expertise in certain cultural  
91 domains, an ability that when is socially acknowledged is usually referred as  
92 “prestige” (Cheng et al., 2013). Since status tends to be associated with re-  
93 productive success and survival of the individual (Marmot, 2004), and since  
94 the use of force by way of sheer dominance was probably selected against  
95 during the evolution of our species (Boehm, 1999), pursuing competence and  
96 prestige might have been an advantageous reproductive strategy of primary  
97 importance in the history of our species. In what follows, we incorporate ex-  
98 plicitly the modeling of that ecological force into the study of the evolution  
99 of cultural transmission.

## 100 2. Model 1: Absence of teaching

101 To present our modeling, as well as to underscore the necessity of intro-  
102 ducing a perspective focused on biological markets, we begin by considering  
103 a simple producer/scrounger scenario with frequency dependence based on  
104 previous attempts at capturing basic processes in the evolution of social learn-  
105 ing such as the influential pioneering work of anthropologist Alan Rogers (  
106 Rogers, 1988; Boyd and Richerson, 2004, for a review, see Aoki and Feldman,  
107 2014) .

108 We first suppose a minimal case in which there is no active teaching.  
109 Agents in the population can follow one of several strategies, each of which  
110 has the same baseline fitness,  $W_0$ , in addition to the frequency-dependent  
111 fitness based on characteristics of the strategy. The strategies reproduce in  
112 the next generation with probability proportional to the fitness: if at time  
113  $t$  there are  $n_I$  individuals with strategy  $I$  of fitness  $W_I$ , then the number of  
114 individuals with strategy  $I$  at time  $t + 1$  will be  $\frac{n_I \times W_I}{\sum_j n_j \times W_j}$ . Such an idealiza-  
115 tion represents either the result of genetic evolution in an haploid panmictic  
116 asexual population or the dynamics resulting from social learning focused on  
117 the relative success of other strategies in the population.

118 In the simplest preliminary form of that scenario, a part of the popula-  
119 tion follows the strategy of individual learning. Those agents bear a cost  $a$   
120 of learning individually. (This is a usual assumption in this type of models.  
121 Such a cost could represent either the cost of committing costly errors while  
122 learning by oneself, or the opportunity cost of investing time in individual  
123 learning, instead of something else.) At the same time, the strategy of in-  
124 dividual learning also yields a benefit  $\alpha$ . To simplify, we suppose here that

125 agents who learn individually always discover an innovation of fitness value  
 126  $\alpha$ . In the online appendix we show that if hiding the innovation is costly,  
 127 then actively hiding individually acquired innovations is not an evolutionary  
 128 stable strategy. Since this finding or discovery is partially observable, it is  
 129 possible that other agents in the group will attempt to copy the solution  
 130 by following a social learning strategy. We call agents who use that lat-  
 131 ter strategy “emulators”, and the process of social learning without evolved  
 132 transmission of fitness enhancing behavior “inadvertent social transmission”.

133 To begin, we assume two conditions: First, only rarely does inadvertent  
 134 social transmission produce perfect copies of behavior. Emulators who adopt  
 135 the solution discovered by other agents thus benefit to the degree of  $f \times \alpha$   
 136 in which  $f < 1$  is a transformation or “loss factor” associated with social  
 137 learning (see Enquist et al., 2007 on the maladaptiveness of social learning).  
 138 Second, we suppose that the easiness of social learning is directly propor-  
 139 tional to the number of individual learners (Pagel, 2012). In our model, we  
 140 codify that constraint by imposing a limited number of social learners  $N_p$   
 141 who can learn socially from a given individual learner. That condition is  
 142 ecologically plausible, at least for a wide range of learning processes used to  
 143 acquire certain techniques. Furthermore, it is easy to imagine that only a  
 144 finite number of agents can have access to a given individual learner for the  
 145 behavior to be adopted<sup>1</sup>.

146 The average fitness of an agent who learns socially is then dependent of  
 147 the frequency of those who learn individually and that by the following rule:

$$W_S = W_0 + f \times \alpha \times \text{Min}(1, N_p \times \text{freq}_I / \text{freq}_S) \quad (1)$$

148 where  $\text{freq}_X$  is the proportion of strategy  $X$  in the population ( $I$  for  
 149 individual learning,  $S$  for social learning), and  $\text{Min}$  denotes a selection of the  
 150 minimal value between 1 and the effective proportion of emulators that can  
 151 acquire the behavior given the number of individual learners in the population  
 152  $N_p \times \text{freq}_I / \text{freq}_S$ .

153 If  $N_p \times \text{freq}_I > \text{freq}_S$ , then all emulators can find a model to copy

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<sup>1</sup>Mathematically, this condition helps to prevent singularities: without it, a single learning agent suffices in order for all social learners in a large population to be able to acquire the innovation ( $N_{pop} \gg 1$ ). However, the number of social learners would abruptly collapse (and become 0) when the proportion of individual learners decreases from  $1/N_{pop}$  to 0. It is not incoherent to state that social learning is facilitated when the proportion of individual learners in the population is greater.

154 and their fitness will therefore equal  $W_S = W_0 + f \times \alpha$ . In the opposite  
 155 case, certain emulators can learn from a model but not all of them. The  
 156 probability of learning socially is then  $N_p \times freq_I / freq_S$ . If  $f \times \alpha < \alpha - a$ ,  
 157 then the individual learning strategy is always more advantageous than the  
 158 social learning one. At the same time, if  $f \times \alpha > \alpha - a$ , then the number of  
 159 social learners will tend to increase until  $f \times \alpha \times N_p \times freq_I / freq_S = \alpha - a$ ,  
 160 that is, to the point at which both strategies have the same fitness. At that  
 161 equilibrium, it is the case that:

$$freq_I = \frac{\alpha - a}{f \times \alpha \times N_p + \alpha - a}. \quad (2)$$

### 162 **3. Model 2: Teaching in a biological market**

#### 163 *3.1. Analytical model*

164 A crucial feature of model 1 is that there is a maximum number  $N_p$  of  
 165 emulators which can learn at a given time from one individual learner. At the  
 166 equilibrium, not all emulators have the same kind of access to an individual  
 167 learner. This is why there can be a market, the individual learners offering a  
 168 privileged access to their skills (“selling”) in exchange for biological services.  
 169 To introduce the possibility of teaching, we assume that agents who learn  
 170 individually—with a frequency in the population  $freq_I$ —can also follow a  
 171 strategy by which they actively teach the acquisition of their technique. In  
 172 addition to the cost of individual learning  $a$ , such a strategy will have a cost  
 173  $t$  linked to teaching. As with the previous model, we assume that there is a  
 174 maximum  $N_t$  of individuals who can at once learn from a single teacher as  
 175 “apprentices<sup>2</sup>”.

176 Another assumption of our model is that social learners who acquire the  
 177 technique directly from the teacher will reproduce a perfectly efficacious copy  
 178 of the teacher’s innovation. Although admittedly an idealization, the point  
 179 is simply that, for this modality of technological learning, social learning  
 180 without a teacher sometimes tends to produce a less fit solution than were  
 181 there a teacher-apprenticeship relationship. Thus, if there is a teacher, then  
 182 the fitness value of the socially learned technique becomes  $\alpha$  instead of  $f \times \alpha$ .

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<sup>2</sup>We make no assumption concerning the specific social configuration of the teacher-apprentice relationship, except that there is some nonzerosumness or collaboration in the basic terms described in the model.

183 However, individuals who learn socially from a teacher will recompense the  
 184 teacher via deference and prestige mechanisms that have a cost  $m$  and that  
 185 return  $m \times g$  to the teacher. It seems reasonable to assume that most of the  
 186 time  $g > 1$ , however our model does not strictly depend on that assumption.

187 For deference to evolve in social learning, its cost  $m$  must be less than  
 188 the cost of individual learning  $a$ . Consequently, at its greatest value  $m$  is  
 189 equal to  $a$ . For the evolution of teaching, the cost  $t$  of teaching thus has to  
 190 be inferior to  $N_t \times g \times a$ .

191 Calculating the equilibrium state of the system is not straightforward, as  
 192 both  $freq_S$  relative to  $freq_I$  and the value of  $m$  may evolve. Additionally, it  
 193 could be that not all the individual have the same preference  $m$ .

194 One method is to look at the evolution of the frequencies and of  $m$  in-  
 195 dependently. We can start assuming that all the individuals in a population  
 196 have a fixed preference  $m$ . We can write the fitness values for the teach-  
 197 ers and apprentices and obtain their equilibrium frequencies for which their  
 198 fitnesses are equal. Then, we assume that the frequencies are fixed, the  
 199 whole population has still this preference  $m$ , except that there are mutants.  
 200 If  $N_t freq_I < freq_S$ , not all apprentices are matched with a teacher, and  
 201 thus a mutant apprentice with a slightly higher  $m$  will be favored, and thus  
 202 the preference  $m$  of the apprentices will evolve towards higher values, thus  
 203 allowing the preference of the teachers  $m$  to also evolve towards higher val-  
 204 ues. Conversely, if  $N_t freq_I > freq_S$ , not all teachers are paired with  $N_t$   
 205 apprentices, thus  $m$  is driven to decrease for the teachers, which then leads  
 206 to a decrease in  $m$  for the apprentices. The next step is to study the effect  
 207 of the change in  $m$  on the frequencies. For the initial  $m$ , the frequencies  
 208 were such that apprentices and teachers had the same fitness. If  $m$  increases  
 209 (respectively decreases), then teachers are less (respectively more) fit than  
 210 apprentices, then the teacher's frequency decreases (resp. increases). Thus  
 211 the equilibrium point is:

$$N_t freq_I = freq_S, \quad (3)$$

212 which is equivalent to:

$$freq_I = \frac{1}{1 + N_t} \quad (4)$$

213 and:

$$m = m_{eq} = \frac{a + t}{N_t \times g + 1} \quad (5)$$

214 in which  $m_{eq}$  is the value of  $m$  at equilibrium.

215 By extension, another condition for the evolution of teaching is that  $\alpha >$   
 216  $m_{eq}$  : an apprentice has to gain more through the acquired technique than  
 217 the cost of deference. That condition is really constraining for teaching only  
 218 at very high values of  $a$  or  $t$ . It is most reasonable that  $g$  is at least equal to  
 219 1, and  $N_t$  at least equal to 1. Thus for instance, if  $a$  and  $t$  remain less costly  
 220 than  $\alpha$ , then that condition is filled.

221 An interesting property of  $m_{eq}$  is that it is the  $m$  value maximizing the  
 222 fitness of the population (see appendix). The evolutionary stable equilibrium  
 223 is also the state of the system with the highest fitness. In our model, the  
 224 so-called Rogers’ paradox (Aoki and Feldman, 2014) does not occur.

225 We considered here that all social learners have the same preference  $m$ ,  
 226 with  $m > 0$ , i.e. the social learners reward their teachers. But, there could  
 227 be a distribution of preferences  $m$  in the population, and as in model 1, there  
 228 could also be social learners (the “emulators”) who only try to copy without  
 229 being taught, provided that  $f \times \alpha \geq \alpha - m$  (when  $m = m_{eq}$  (5), this condition  
 230 is equivalent to  $f > 1 - \frac{a+t}{(N_t \times g + 1) \times \alpha}$ ). Interestingly, the presence of these emu-  
 231 lators does not modify neither the equilibrium between the frequencies of the  
 232 individual learning and apprentice strategies, nor the evolution of  $m$ . Even  
 233 when  $f \times \alpha > \alpha - m$ , apprentices are not driven to extinction by emulators.  
 234 In other words, teaching may evolve even if social learning without teaching  
 235 (“inadvertent social transmission”) is still an available and profitable strat-  
 236 egy in the population. We can calculate the expected frequency of emulators:  
 237 their frequency increases until there are not enough individual learners, so  
 238 that  $f \times \alpha N_p \text{freq}_I / \text{freq}_{emul} = \alpha - m$ . This ultimately leads to:

$$\text{freq}_I = \frac{1}{1 + N_t + \frac{f \times \alpha \times N_p}{\alpha - m_{eq}}} \quad (6)$$

239 Even if deference is relatively costly, the apprentice strategy can be on par  
 240 with the emulator strategy, because it enables a better access to individual  
 241 learners who are a source of innovation. In fact, both strategies could still  
 242 coexist with  $f = 1$  — albeit the larger  $f$ , the smaller the frequency of the  
 243 apprentice strategy. As a result, the assumption that  $f < 1$  is not necessary.

### 244 3.2. Simulation

245 The analytical calculations assumed mostly homogeneous  $m$  preferences,  
 246 and evolution of the frequencies and  $m$  were considered separately. But both  
 247 will actually evolve simultaneously, and if  $m$  mutates when the strategy is

$t <$ $N_t \times g \times a$	$f > 1 - \frac{m_{eq}}{\alpha}$	Teaching and emulating (5) $m = m_{eq} = \frac{a+t}{N_t \times g + 1}$ (6) $freq_I = \frac{1}{1 + N_t + \frac{f \times \alpha \times N_p}{\alpha - m_{eq}}}$
	$f < 1 - \frac{m_{eq}}{\alpha}$	Teaching (5) $m = m_{eq} = \frac{a+t}{N_t \times g + 1}$ (4) $freq_I = \frac{1}{1 + N_t}$
$t >$ $N_t \times g \times a$	$f > 1 - \frac{a}{\alpha}$	Emulating no $m$ (2) $freq_I = \frac{\alpha - a}{\alpha(1 + fN_p) - a}$
	$f < 1 - \frac{a}{\alpha}$	Individual learning only No $m$ $freq_I = 1$

Table 1: Summary analytical regimes

248 reproduced, preferences of teachers and apprentices cannot be exactly equal,  
 249 because a mutation towards a slightly higher  $m$  for a teacher or a slightly  
 250 lower  $m$  for an apprentice would lead to the inability to enter in a teaching  
 251 relationship, thus decreasing the second-generation fitness.

252 To check that the system converges towards our analytical results, we  
 253 coded an agent-based simulation. Each individual  $j$  is either an individ-  
 254 ual learner or a social learner, and attributes the reservation value  $m_j$  to  
 255 teaching. Random pairs are formed between social learners who have not  
 256 yet acquired the skill, and individual learners who have not yet taught to  
 257  $N_t$  social learners. If for a given pair, the reservation value  $m$  is smaller for  
 258 the social learner, nothing occurs. But in the opposite case, the individual  
 259 learner teaches the skill to the social learner at a price  $m$  which is taken as  
 260 the average between the  $m$  values of the two individuals. (Any intermediate  
 261 value between the two values would give similar results, see supplementary  
 262 figure 12 in appendix.) This method of estimating the actual exchange value  
 263 of  $m$  builds on the natural idea that there will be some form of bargaining  
 264 between the two individuals. Pairs are formed until there is no possible ad-  
 265 ditional interaction. Then the population is renewed, with new strategies  
 266 taken at random proportionally to their fitness in the previous round, and  
 267 the values  $m_i$  attributed to teaching in these strategies are copied with small  
 268 random errors (to allow for the evolution of  $m$ ). The frequencies of the differ-  
 269 ent strategies and the average value of  $m$  tend to the state defined in equation

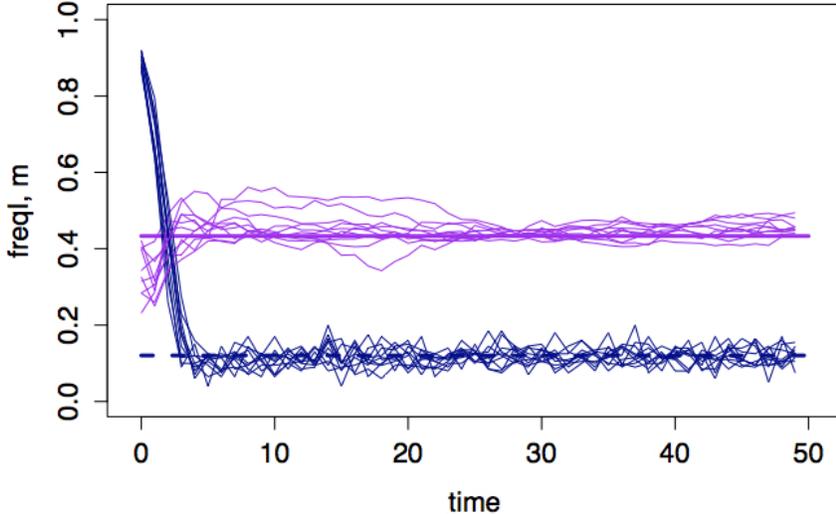


Figure 1: Simulation example. Frequency of individual learners (dark blue) and mean  $m$  values of interactions (light purple) for 10 different simulations, as a function of time (in generations). The horizontal thicker lines represent the predicted values of the frequency of individual learners (dark blue dashed line) and  $m$  (light purple solid line). For a population of 200 individuals, with  $N_t = 2$ ,  $N_p=5$ ,  $W_0=0.01$ ,  $\alpha=1$ ,  $a=0.8$ ,  $f=1$ ,  $g=1$ ,  $t=0.5$ , and  $\delta m=0.02$ . At the beginning of the simulations: 90% of the population are individual learners, a random  $m$  value is attributed to each individual, taken from a uniform distribution between 0 and 1.

270 (6) and (5), albeit with fluctuations around these values (see figure 2, and  
 271 supplementary figures 2 to 13 in appendix). Having validated the results, we  
 272 can now discuss them.

### 273 3.3. Results

274 As confirmed by the numerical simulations, there are four different regimes,  
 275 as summarized in table 1. Teaching is a stable strategy if the cost of teach-  
 276 ing  $t$  is smaller than  $N_t \times g \times a$ . Teaching is clearly facilitated when there  
 277 are more potential apprentices ( $N_t$ ) (Table 1 and supplementary figure 2),  
 278 receiving deference provides a higher gain ( $g$ ) (Table 1 and supplementary  
 279 figures 5 and 9), and if learning the technique individually is costly ( $a$ ) (Table  
 280 1 and supplementary figures 3 and 7). Interestingly, this condition does not  
 281 depend on the characteristics of inadvertent social transmission ( $N_p$  and  $f$ )  
 282 (Table 1 and panels B and C of figure 2). Profiting of “inadvertent social

283 transmission” by emulators is a stable strategy if the loss in the technique  
284 value  $(1 - f)\alpha$  is smaller than the cost of retributing a teacher ( $m_{eq}$ ) if there  
285 is teaching (Table 1 and figure 2C), or smaller than the cost of learning the  
286 technique individually ( $a$ ) if there is no teaching (Table 1 and supplementary  
287 figure 7).

288 In the case of teaching, the value of the deference  $m$  at equilibrium in-  
289 creases with  $a$ ,  $t$ , and decreases with  $N_t$  and  $g$  : deference has to be higher  
290 to offset a higher cost of individual learning and teaching, and the higher  
291 the number of apprentices per teacher and the higher the factor  $g$ , the less  
292 the deference cost per apprentice (table 1 and figures). The frequency of the  
293 teachers is such that there are  $N_t$  apprentices per teacher. If there are no  
294 emulators, then the teachers frequency depends only on  $N_t$ . The teachers fre-  
295 quency is lower when there are emulators. It depends on  $a$ ,  $t$ ,  $g$  only through  
296 its dependence on  $m$  (table 1 and figure 2D). It decreases with  $f$  and  $N_p$  :  
297 the more the emulators, the fewer the teachers and apprentices (table 1 and  
298 panels B and C of figure 2). It is maximum for some intermediate value of  
299  $N_t$  (table 1 and figure 2A).

300 Another result is that, under a biological market of the type described  
301 here, for individual learning to be beneficial, it is sufficient that the cost of  
302 individual learning  $a$  is smaller than  $\alpha \times (N_t g + 1) - t$ , which, except when  
303  $t$  is large and  $N_t$  is small, is likely much larger than  $\alpha$ . Hence, there are  
304 investments in skills for which benefits would not be sufficient in themselves,  
305 which thus become attractive because of the extra incentive linked to the  
306 sociability of teaching.

#### 307 4. Model 3: Cumulative culture

308 Previous research has shown that social learning *per se* does not auto-  
309 matically lead to cumulative culture, that is, sustained evolution of ever  
310 increasingly adaptive cultural techniques (Enquist and Ghirlanda, 2007). In  
311 model 2, we have shown that the market for deference and prestige supports  
312 increased costs of innovations. Accordingly, we believe that taking those  
313 sorts of biological markets seriously can shed light on ecological forces active  
314 in the evolution of cumulative culture.

315 Until now, we have considered the skill to be fixed. Here, however, we  
316 consider a different model, in which the skill of value  $\alpha$  can be improved by  
317  $\delta\alpha$  with probability  $\epsilon$  when effort  $r$  is invested into innovation. We consider  
318 that at each time step, a new individual enters the population of size  $N$ ,

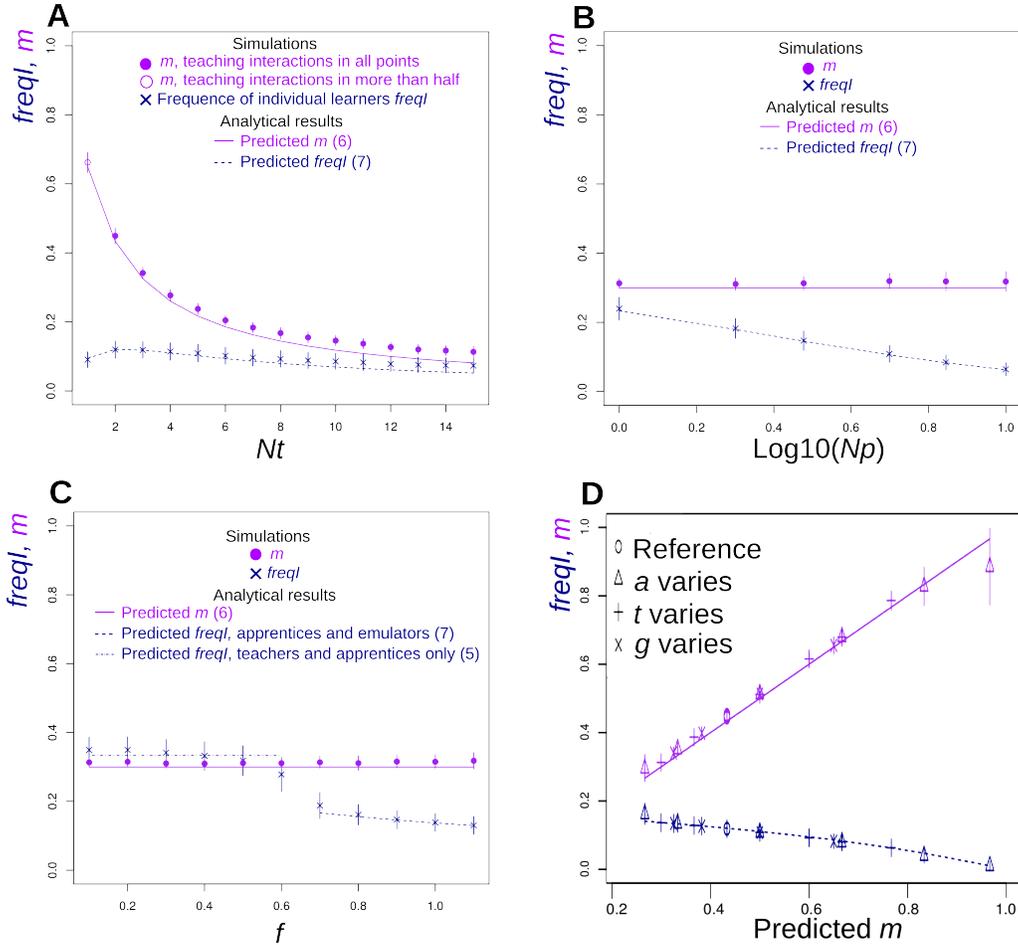


Figure 2: Dependence of the frequency of individual learners (dark blue) and average value of  $m$  in exchanges (light purple) with the different parameters. Results from simulations (symbols) taken averaged on 10 simulations, for generations 100 to 200 (see supplementary figure 1), and errors-bars represent the standard deviation. Theoretical curves :  $m$  (5) (solid purple lines),  $freq_I$  with teachers, apprentices, and emulators (6) (dashed blue), with teachers and apprentices only (4) (dot-dashed blue), with individual learners and emulators only (2) (dotted blue). For all the simulations, the population is taken as 200 individuals, with the base fitness  $W_0 = 0.01$ , the technique benefit  $\alpha = 1$ , the typical mutational change on  $m$   $\delta_m = 0.02$ , and when the interaction happens,  $m$  is taken as the average between the preferences of the two individuals ( $coefshare = 0.5$ ). Initially 50% of the population are individual learners, with for all individuals,  $m$  taken at random between 0 and 1. Except if stated otherwise, the other parameters are  $N_t = 2$ ,  $N_p = 3$ ,  $a = 0.8$ ,  $t = 0.5$ ,  $f = 1$ ,  $g = 1$ . Panel A: dependence on  $N_t$ . Panel B: dependence on  $N_p$  ( $t = 0.1$ ,  $f = 0.9$ ). Panel C: dependence on  $f$  ( $t = 0.1$ ). For panels A, B and C,  $freq_I$  in simulations is represented by triangles, and  $m$  in simulations is represented by a filled circle when there are exchanges in all the points used for computing the average values, and an empty circle when there are points for which there has not been any exchanges (but at least for half the points;  $m$  values for which there are exchanges in less than half the simulation points are not represented). Panel D: as the dependence of  $freq_I$  on  $t$ ,  $g$  and  $a$  is predicted to occur only through the value of  $m$  when there are teachers, apprentices and emulators, we represent the values of  $m$  and  $freq_I$  as a function of the predicted  $m$  for the points predicted to be within this regime. Supplementary figures 3, 4 and 5 show the dependence for each parameter individually.

319 whereas the “oldest” individual dies. The entrance can represent either a  
 320 birth — more realistically a child’s coming of age and being prepared for the  
 321 apprenticeship — or a migration. If there is no active teaching, then the  
 322 new individual copies the best skill in the population, of value  $\alpha(T)$ , but not  
 323 perfectly. The individual will thus have a skill of value  $f \times \alpha(T)$ , in which  
 324  $T$  represents the moment in time when the technique is copied by the newly  
 325 arrived agent. We assume that individuals can recognize the best skill, and  
 326 access the value of parameters  $r$ ,  $\delta\alpha$  and  $\epsilon$ , as well as that innovation can  
 327 occur only after the new individual entered the group and acquired its skill.  
 328 This latter assumption represents the idea that some periods are more prone  
 329 to innovation than others. The new individual can then decide whether to  
 330 invest in innovation depending on whether  $\epsilon \times \delta\alpha > r$ . If  $\epsilon \times \delta\alpha < r$ , then no  
 331 innovation is ever made, and, provided that  $f < 1$ , the skill will be completely  
 332 lost in the population over time. If  $\epsilon \times \delta\alpha > r$ , the skill will be improved  
 333 upon by  $\delta\alpha$  per each  $1/\epsilon$  new individuals on average. Population size matters  
 334 (Kline and Boyd, 2010): if  $1/\epsilon > N$ , then the innovations will not occur often  
 335 enough to preserve the skill in the population. If  $1/\epsilon < N$ , then the value  
 336 of the skill over time will tend toward the point at which the imperfect copy  
 337 and the innovation compensate:  $\alpha = \delta\alpha/(1 - f)$ .

338 For active teaching, when the new individual enters the population, many  
 339 potential teachers are available, meaning that there will be active teaching  
 340 as long as  $m \times g > t$ . Due to competition among teachers,  $m$  will tend  
 341 to  $t/g$ . If  $t/g < (1 - f)\alpha$ , then the new individual will prefer to learn the  
 342 technique via active teaching instead of emulation, and thus end up learning  
 343 the best skill  $\alpha$  of the population. At that point, when choosing whether to  
 344 invest in innovation, the individual will compare the investment cost  $r$  not  
 345 only with the direct benefit ( $\epsilon \times \delta\alpha$ ), but also the direct benefit plus the  
 346 benefit expected from teaching the innovation to the rest of the population.  
 347 Since the new individual has a monopoly on the skill, other individuals in  
 348 the population will recompense his or her teaching by a maximum of  $m =$   
 349  $(1 - f)(\alpha + \delta\alpha)$ , or even more if  $N > N_p$ . Thus, the benefit expected from  
 350 teaching is  $Min(N, N_t)g(1 - f)(\alpha + \delta\alpha) - t$ .

351 In sum, populations with active teaching differ from those with only “in-  
 352 advertent” social learning (emulation) in two ways. Because the skill can be  
 353 learned more accurately, cumulative innovations are facilitated and the value  
 354 of the skill can continue to increase. Furthermore, innovation is favored since  
 355 its benefits might also derive from deference and prestige. Accordingly, in  
 356 biological markets evolved teaching has the double effect of promoting cu-

357 mulative culture, but also, and importantly, enhancing individual learning.

## 358 5. Discussion and conclusions

359 Modeling evolutionary social dynamics offers proof of the internal consistency of hypothesized evolutionary selective pressures (McElreath and Boyd, 360 2008). The models presented here thus corroborate the logical soundness of 361 some intuitions previously formulated in purely verbal arguments (Henrich and Gil-White, 2001), as well as develop a well-articulated mathematical 362 framework that adds to the paucity of models of the evolutionary milestone 363 that is the evolution of teaching (Kline, 2015). 364

365 Reciprocity-based models are not usually well equipped to accommodate 366 hierarchies and asymmetries as the ones that we describe in our model 2. Besides, reciprocity-based cooperation models usually focus more on the partner 367 control aspect of repeated interactions than on partner choice, outside options, and active discrimination. We have shown that market effects can 368 account for relevant dimensions of the sociability of teaching, such as the 369 propensity to transmit fitness-enhancing information, as well as the evolution of deference and prestige. We believe that these important aspects of 370 human social learning are better studied focusing on the supply and demand 371 demographic dynamics of a biological trade, rather than on the standard 372 reciprocity mechanism. 373

374 We have provided a partner-choice model of the evolution of teaching that 375 focuses on the functional aspects of teacher-apprentice cooperation. This account cannot be per se an exhaustive evolutionary characterization of the 376 emergence of teaching. Teaching is, after all, a complex ethological category 377 that subsumes different —and presumably related— types of phenomena 378 (Kline, 2015). Moreover, the models presented are not intended to be so 379 much a realistic depiction of the actual evolutionary process, as an exploration of general ecological conditions for the evolution of teaching. However 380 our work nevertheless points to possible evolutionary pathways, which perhaps 381 because they had not been mathematically modeled, had not received 382 much attention. One such possible paleoanthropological pathway is that the 383 structure of communication and nonzerosumness inherent in the form of the 384 basic apprenticeship system described here might have preceded —instead 385 of followed— the evolutionary emergence of modern (i.e. Middle Paleolithic) 386 human inventiveness (McBrearty and Brooks, 2000). 387 388 389 390 391

392 We have additionally shown that teaching can evolve under certain con-  
393 ditions. First, individual learning or learning without relying on others’  
394 experience is costly. Second, certain techniques are constrained in terms of  
395 the number of individuals who can socially learn the technique from a single  
396 expert. Under those conditions, demographic dynamics could force social  
397 learners, who want to acquire the adaptive behavior discovered by individual  
398 learners, to pay a price in the form of deference. Furthermore, albeit unneces-  
399 sary, the evolution of teaching is facilitated if, for learning certain techniques,  
400 social learning without explicit teaching —“eavesdropping” (Danchin et al.,  
401 2004)— yields an imperfect copying in which adaptive value can be lost. Cru-  
402 cially, genetic relatedness and parent-offspring nepotism (Castro and Toro,  
403 2004) are not strictly necessary, either.

404 An important point that emerges from our work is that evolved teach-  
405 ing might be the mother of invention. In other terms, natural pedagogy  
406 and communication skills may precede, and not necessarily follow, the ap-  
407 pearance of complex forms of culture. This dynamic runs counter to the  
408 perspective sometimes advanced holding that teaching evolved as a response  
409 to increasingly complex for novices, “opaque” cultural forms (Caldwell, 2015;  
410 Gergely and Csibra, 2006). According to that evolutionary hypothesis, com-  
411 plex cumulative culture necessarily preceded evolved teaching. However, as  
412 we show here, teaching might constitute an evolutionarily stable strategy  
413 even if the existing cultural forms are not opaque enough for novices: teach-  
414 ing could evolve when inadvertent social transmission (i.e. social learning  
415 without teaching) remains a thriving strategy in the population.

416 Undoubtedly, access to various forms of social learning cannot be con-  
417 trolled in a way to give rise to biological exchange markets: “eavesdropping”  
418 or inadvertent social facilitation could be the most frequent form of social  
419 learning in nature, perhaps even in humans. Nonetheless, in humans, im-  
420 portant forms of technique acquisition can be reasonably controlled, even  
421 monopolized to some extent. For instance, ethnographic studies of stone-  
422 tool production (Stout et al., 2002) confirm that adult acquisition of certain  
423 sophisticated skills can be perceived as a form of transferable intellectual  
424 property. Such capacity for transmission is endowed with a form of author-  
425 ity often safeguarded and administered in a teacher-apprentice system via  
426 manifestations of personal commitment. In more modern settings, partner  
427 choice has widely been observed to be crucial to acquiring competence within  
428 organizations (Blau, 1964).

429 In contrast to nonhuman social learning, certain forms of human social

430 learning are characterized by both the sophistication of cognitive mechanisms  
431 at work and the important constitutive role played by collaboration and  
432 nonzerosumness. These characteristics eventually give rise to apprenticeship  
433 structures (Waal, 2001; Sterelny, 2012). In this article, we have shown how  
434 those behavioral strategies can attain evolutionary equilibrium and persist  
435 in a population.

436 Naturally, not all forms of cultural diffusion rely on competence-based  
437 partner choice, a point that can hardly be overemphasized. However, some  
438 forms of human social learning depend far more on competence-based partner  
439 choice than others. Indeed, that aspect can help to explain the existence  
440 of several interesting regularities in the human psychology of competence  
441 assessment, admiration, and deference (Fessler, 2006).

442 At the proximate level, hierarchical tendencies of this sort are not entirely  
443 specific to humans. In fact, other animals have been observed to behave in  
444 ways consistent with the predictions of biological markets. In particular, non-  
445 human primates, such as chimpanzees (*Pan troglodytes*), have demonstrated  
446 an ability to discriminate possible partners based on their abilities (Melis  
447 et al., 2006). Experimental studies have furthermore shown how different  
448 species of primates can temporarily align their hierarchical behavior after  
449 individuals in their group have acquired some valuable cultural competence  
450 (see Stambach (1988) for interesting work on Rhesus macaques). Grooming  
451 behavior has been shown to adapt to the supply and demand characteristics  
452 of a biological market in which at least one individual in a group has learned  
453 to use a tool to obtain a valuable shareable food (Fruteau et al., 2009).  
454 Indeed, it has even been suggested that, for some species, grooming could be  
455 a form of proto-currency in primate exchange markets (Barrett and Henzi,  
456 2006).

457 In humans, considerable evidence points to the existence of both compe-  
458 tence assessment and prestige-signaling behavior, the latter being a form of  
459 communicating that one excels in a given domain (Tracy and Matsumoto,  
460 2008). Although the human ability to detect competence in given domains is  
461 certainly far from perfect (Mauboussin, 2012), it nevertheless works in a sat-  
462 isfying manner in many settings. Competence is assessed through both fast  
463 and slow processes of cognition. And quick it can be: in adults, judgments of  
464 competence can be made in as little as 100 milliseconds and those judgments  
465 are sometimes highly persistent and difficult to override (Fiske et al., 2007).  
466 Early on, children also begin to pay special attention to individuals judged  
467 as competent in a given domain (Keil et al., 2008). The current consensus

468 maintains that children commonly use two different pathways to judge the  
469 reliability of an informant: one related to trust and benevolence, the other  
470 to competence and ability (Mascaro and Sperber, 2009; Harris, 2012).

471 Clearly, we have just scratched the surface of what biological trade models  
472 could offer for the modeling of social learning dynamics. It would be inter-  
473 esting to further explore the evolutionary dynamics linked to maladaptive  
474 biases in the human psychology of competence and prestige detection. For  
475 instance, we have not explored here the complex dynamics that could follow  
476 if social learners were to adopt the techniques and behaviors of other social  
477 learners who no longer track the environment through individual learning  
478 and innovation, yet might receive some form of social reward due to further  
479 transmitting a highly prized form of “knowledge”, even if it is directly ineffec-  
480 tual. Moreover, the amount of effort that cultural models put into teaching  
481 their apprentices, even if not genetically related to them, the diminishing  
482 fitness values of the technology if shared, or the reliability of the deference  
483 provided by the apprentices are all interesting features where genetic conflict  
484 and partner choice could be modeled fruitfully. We hope to encourage further  
485 work in this area.

486 Regarding important aspects of the evolution of cultural transmission,  
487 we have suggested that the partner-choice framework (Nesse, 2009) is bet-  
488 ter equipped than other theoretical frameworks that rely exclusively on ei-  
489 ther partner control or nepotistic genetic relatedness (Noë and Voelkl, 2013).  
490 The free-rider problem of fitness-enhancing cultural transmission, and cul-  
491 tural parental manipulation are largely by-passed by evolutionary systems  
492 such as those described in this article. Nearly a century ago, Lev Vigotsky  
493 characterized human social learning as an eminently cooperative activity.  
494 Biological market models can incorporate nonzerosumness of human social  
495 learning while at once accommodating important findings of the anthropol-  
496 ogy of deference and prestige, and revealing surprising evolutionary processes  
497 that lead to cumulative culture.

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499 None

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506 **Data availability**

507 An online appendix including further analytic details, supplementary fig-  
508 ures, and simulation code is provided.

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