

1 **Why cooperation is not running away**

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14 **Abstract**

15 A growing number of experimental and theoretical studies show the importance of partner choice
16 as a mechanism to promote the evolution of cooperation, especially in humans. In this paper, we
17 focus on the question of the precise quantitative level of cooperation that should evolve under this
18 mechanism. Using a classic adaptive dynamics model, we first highlight the existence of an
19 apparent paradox. When individuals compete to be chosen by others, their level of investment in
20 cooperation evolves towards ever-higher values, a process called competitive altruism, or runaway
21 cooperation. Our model shows that, when individuals can easily choose their partners, this runaway
22 process leads to a profitless escalation of the level of cooperation, up to the point where the cost of
23 cooperation exactly cancels out its benefit. In other words, at first sight, under the effect of partner
24 choice we predict that cooperation should have no benefit at ESS:the evolutionary equilibrium.
25 Second, importing models from matching theory in economics we, however, show that, when
26 individuals can plastically modulate their choosiness in function of their own cooperation level,
27 partner choice stops being a runaway competition to outbid others, and becomes a competition to
28 form the most optimal partnerships. Assortative partner choice then leads to the evolution of the
29 socially optimum level of cooperation. This result could explain the observation that human
30 cooperation seems to be often constrained by considerations of social efficiency.

31

32 **Key words:** partner choice, biological markets, matching models, competitive altruism, human
33 cooperation

34

35 **1. Introduction**

36 Cooperation among non-kin constitutes a puzzle for evolutionary biologists, and a large body of
37 theoretical models, inspired by game theory, have been developed to solve it. The most commonly
38 accepted explanation is that cooperation can be enforced if it triggers a conditional response on the
39 part of others (West et al. 2007). Several enforcement mechanisms have been proposed: direct
40 reciprocity (Trivers 1971; Axelrod and Hamilton 1981; Lehmann and Keller 2006), indirect
41 reciprocity (Nowak and Sigmund 1998, 2005; Leimar and Hammerstein 2001), punishment (Boyd
42 and Richerson 1992; Boyd et al. 2003; Bowles and Gintis 2004) and partner choice (Bull and Rice
43 1991; Noë and Hammerstein 1994, 1995; Sachs et al. 2004). A growing number of experimental
44 studies support the idea that, among this set of mechanisms, partner choice is likely to be
45 particularly influential in nature, both in inter-specific and in intra-specific interactions (Bshary
46 and Schaffer 2002; Simms and Taylor 2002; Kiers et al. 2003, 2011; Fruteau et al. 2009; Schino
47 and Aureli 2009; Hammerstein and Noë 2016). Besides, partner choice is also believed to play a
48 major role in human cooperation, where friendships and coalitions are common (Barclay 2013,
49 2016; Baumard et al. 2013; and see Discussion).

50

51 The key idea of partner choice models is that, when one happens to be paired with a defecting
52 partner, one has the option to seek for another, more cooperative, partner present in the “biological
53 market” and interact with her instead of the defector. This possibility allows cooperators to
54 preferentially interact with each other, and, consequently, prevents any invasion by free-riders
55 (Eshel and Cavalli-Sforza 1982; Bull and Rice 1991; Noë and Hammerstein 1994, 1995; Ferriere
56 et al. 2002; Bergstrom 2003; Aktipis 2004, 2011; Sachs et al. 2004; Fu et al. 2008; Barclay 2011).

57

58 So far, the primary objective of most partner choice models has been to explain how *some*
59 cooperation can exist at all in an evolutionary equilibrium. On this ground, models have reached a
60 clear answer: partner choice can trigger the evolution of cooperation. In this paper, however, we
61 are interested in another issue that models generally consider with less scrutiny: that of
62 understanding the quantitative *level* of cooperation that should evolve under partner choice.

63

64 This analysis is crucial because the quantitative level of cooperation determines the “social
65 efficiency”, also called the Pareto efficiency, of interactions. Cooperating too little is inefficient
66 because individuals miss some opportunities to generate social benefits. But cooperation, as any
67 investment, is likely to have diminishing returns (Altmann 1979; Weigel 1981; Killingback and
68 Doebeli 2002). As a result, there is a “socially optimal” amount of cooperation, an intermediate
69 level where the sum of the helper and helpee’s payoff is maximized. Cooperating more than this
70 amount is hence also inefficient, because it increases more the cost of cooperation than it raises its
71 benefit. In the extreme, there is even a “wasteful” threshold beyond which the overall cost of
72 cooperation becomes larger than its benefit. If two partners cooperate more than this threshold, the
73 net benefit of their interaction is negative, that is they are both worst off than if they had not
74 cooperated at all.

75

76 Prima facie, partner choice appears to be a unidirectional pressure acting on the evolution of
77 cooperation, unlikely to generate an intermediate equilibrium. Competition to be chosen by others,
78 called “competitive altruism” (Roberts 1998; Hardy and Van Vugt 2006; Nesse 2009), should lead
79 to a runaway of cooperation, as it does in sexual selection (West-Eberhard 1983). In principle, this
80 runaway should proceed up to the point where the cost of investing into cooperation cancels out

81 the benefit of finding a partner (West-Eberhard 1979; Fisher 1999 p.152) that is up to the
82 “wasteful” threshold where cooperation becomes fruitless. Is competitive altruism, however,
83 balanced by opposite forces, leading to an evolutionary stabilization of cooperation below this
84 threshold? Is this level socially optimal, or does partner choice lead to the investment into
85 counterproductive forms of cooperation to out-compete others as it does in sexual selection?

86

87 ~~Most previous models~~ In the theoretical literature on partner choice ~~have not addressed, relatively~~
88 little attention has been given to these questions, ~~either because they have assumed that. First of~~
89 all, a large proportion of models consider cooperation ~~is~~ as an all-or-nothing decision and thus
90 cannot study its quantitative level (Eshel and Cavalli-Sforza 1982; Bergstrom 2003; Aktipis 2004;
91 Fu et al. 2008; Chen et al. 2009; Aktipis 2011; Suzuki and Kimura 2011; Sibly and Curnow 2012;
92 Campenni and Schino 2014; Izquierdo et al. 2014; Chen et al. 2016; Wubs et al. 2016), ~~or because~~
93 ~~they have studied the investment in.~~ Second, some models consider cooperation as a quantitative
94 trait but ~~without considering~~ do not entail diminishing returns, and are thus ill-suited to study the
95 social efficiency of cooperative interactions (Sherratt and Roberts 1998; ~~Ferriere et al. 2002~~; Foster
96 and Kokko 2006; Nesse 2009; Song and Feldman 2013)-

97 . Third, still other models consider cooperation as a quantitative trait with diminishing returns, but
98 they only focus on one side of the problem –the evolution of cooperation– considering the other
99 side –the strategy employed by individuals to choose their partner– as an exogenous parameter
100 (Wilson and Dugatkin 1997; Ferriere et al. 2002; Barclay 2011; Wild and Cojocaru 2016).

101

102 To our knowledge, only one existing model studies the joint evolution of cooperation and partner
103 choice in a quantitative setting with diminishing returns (McNamara et al. 2008). However,
104 McNamara et al. (2008) make two key assumptions that turn out to have important consequences:

105 (i) they assume that variability in the amount of cooperation is maintained owing to a very large
106 genetic mutation rate on this trait, which prevents natural selection to act efficiently, and (ii) they
107 restrict the set of possible strategies to choose one's partner in such a way that individuals can
108 never do so in an optimal manner.

109
110 In this paper, we build a model inspired by McNamara et al. (2008), in which a quantitative level
111 of cooperation expressed by individuals jointly evolves with a quantitative level of choosiness
112 regarding others' cooperation. ~~Analysing this model, while relaxing these two assumptions. First,~~
113 ~~we first confirm the existence of a paradox. Partner~~ observe that partner choice leads to a runaway
114 of cooperation. When partner choice is cheap enough, it does create a competition to be chosen as
115 a partner, leading to a ~~runaway~~ joint rise of both cooperation and choosiness up to the point where
116 the cost of cooperation entirely cancels out its benefit. Hence, at first sight, our analyses show that
117 partner choice is ~~unable~~ unlikely to explain the evolution of a moderate and efficient level of
118 cooperation.

119
120 However, we then resolve this apparent paradox by importing tools from the economics literature
121 and assuming that individuals can plastically modulate their choosiness in function of their own
122 cooperation level. This plasticity allows every individual to behave optimally on the biological
123 market, which did not occur in the first model. Assortative matching emerges and leads to the
124 evolution of efficient levels of cooperation. If the cost of changing partner is low enough, this
125 process can even lead to the evolution of the socially optimal level of cooperation where the mutual
126 efficiency of cooperation is maximised.

128 2. Methods

129 2.1. Partner choice framework

130 We model partner choice in an infinite size population using Debove et al. (2015a)'s framework.

131 Solitary individuals randomly encounter each other in pairs at a fixed rate β . In each encounter,

132 the two players decide whether they accept one another as a partner (see below how this decision

133 is made). If one of the two individuals (or both) refuses the interaction, the two individuals

134 immediately split and move back to the solitary pool. If both individuals accept each other, on the

135 other hand, the interaction takes place and lasts for an exponentially distributed duration with

136 stopping rate τ , after which the two individuals move back to the solitary pool again. The ratio β/τ

137 thus characterizes the “fluidity” of the biological market. If β is high and τ is low, individuals meet

138 each other frequently and interact for a long time. In such an almost frictionless market, partner

139 choice is almost cost-free so they should be choosy about their partner's investment in cooperation.

140 Conversely, if β/τ is low, individuals rarely meet potential partners and interact for a short time.

141 In such a market, on the contrary, individuals should accept any partner.

142

143 Regarding the encounter rate, here we assume that β is a fixed constant independent of the density

144 of available partners, an assumption called “linear search” that captures a situation in which already

145 paired individuals do not hinder the encounters of solitary individuals (Diamond and Maskin 1979).

146 In the Supplementary Information, however, using simulations we also analyse the model under

147 the assumption that β increases linearly with the proportion of solitary individuals in the

148 population, an assumption called “quadratic search” that corresponds to a situation in which

149 already matched individuals interfere with the encounters of solitary individuals (and that is also

150 equivalent to the classic mass-action kinetics used in mathematical epidemiology). In the paper,
151 we only describe the results obtained under linear search. The results obtained under quadratic
152 search are qualitatively similar (see the Supplementary Information).

153
154 Regarding the nature of the social interaction, we consider a quantitative version of the prisoner’s
155 dilemma in continuous time. Each individual i is genetically characterized by two traits: her
156 cooperation level x_i , and her choosiness y_i . Cooperation level x_i represents the quantitative amount
157 of effort that an individual i is willing to invest into cooperation. Choosiness y_i represents the
158 minimal cooperation level that an individual i is willing to accept in a partner, i.e. every potential
159 partner j with cooperation $x_j \geq y_i$ will be accepted, whereas every potential partner with $x_j < y_i$
160 will be rejected. Once an interaction is accepted by both players, at every instant of the interaction,
161 each player invests her effort x_i (see below for the payoff function), and the interaction lasts in
162 expectation for $1/\tau$ units of time, where τ is the stopping rate of the interaction.

163
164 When they are solitary, individuals gain a payoff Snormalized to zero per unit of time. When
165 involved into an interaction, they gain a social payoff that depends on both partners’ cooperation
166 level. The cooperative interaction is a continuous prisoner’s dilemma: making an investment brings
167 benefits to the partner but comes at a cost to the provider. As stated in the introduction, we make
168 the additional assumption that cooperation has diminishing returns (Altmann 1979; Weigel 1981;
169 Killingback and Doebeli 2002). This induces the existence of an intermediate level of cooperation
170 at which the sum of the partners’ gains is maximized, the so-called “social optimum”. An
171 individual i paired with j gains the following social payoff $\Pi(x_i, x_j)$ per unit of time:

$$\Pi(x_i, x_j) = x_j - cx_i^2$$

173 Hence, the expected payoff of an individual i paired with j is

$$174 \frac{x_j - cx_i^2}{\tau}$$

175 where individual i paired with τ is the stopping rate of the interaction. The socially optimal level
176 of cooperation is $\hat{x} = 1/2c$. Beyond this level, the net benefit of cooperation decreases. Eventually,
177 the interaction becomes entirely profitless, or even costly, if individuals invest more than the
178 “wasteful threshold” $x = 1/c$. We allow both cooperation and choosiness to take any positive real
179 value.

180

181 Previous studies demonstrated that the existence of some variability among individuals is
182 necessary to stabilize conditional cooperation (Ferriere et al. 2002; Foster and Kokko 2006;
183 McNamara et al. 2008; McNamara and Leimar 2010; Song and Feldman 2013). If every possible
184 partner is equally cooperative, then there is no need to be choosy with regard to the quality of one’s
185 partner, and choosiness cannot be evolutionarily stable. In order to capture the effect of variability
186 in the simplest possible way, we assume that individuals do not perfectly control their investment
187 into cooperation (as in Song and Feldman 2013 and André, 2015 for instance). An individual’s
188 actual cooperation level x_i is a random variable which follows a truncated to zero normal
189 distribution around the individual’s gene value \bar{x}_i , with standard deviation σ . In what follows, we
190 call cooperation level the genetically encoded cooperation level that individuals aim for, and
191 “phenotypic cooperation” the actual level of cooperation that they express after phenotypic noise.

192

193 We are interested in the joint evolution of cooperation, and choosiness by natural selection. We
194 undertake and compare the consequences of two distinct assumptions. In a first approach, we
195 assume that both cooperation and choosiness are hard-wired traits, that is each individual is

196 characterized by a single level of cooperation \bar{x} and a single choosiness y , both expressed
197 unconditionally. In a second approach, we still assume that cooperation is a hard-wired trait, but
198 we consider that choosiness is a reaction norm by which individuals respond to their own
199 phenotypic cooperation.

200

201 *2.2. Hard-Wired choosiness*

202 Here, we assume that each individual is genetically characterized by two traits: his level of
203 cooperation \bar{x} and his choosiness y and we are interested in the evolution of these two traits by
204 natural selection. For this, we need to derive the fecundity of a rare mutant m playing strategy
205 (\bar{x}_m, y_m) in a resident population r playing strategy (\bar{x}_r, y_r) . The mutant fecundity is proportional
206 to her cumulative lifetime payoff G_m , which can be written as (see SI for a detailed analysis of the
207 model):

$$208 \quad G_m = \frac{\bar{\Pi}_m \alpha_m \beta + S\tau}{\alpha_m \beta + \tau}$$

209 with α_m the mean probability for an encounter between the mutant and a resident to be mutually
210 accepted, and $\bar{\Pi}_m$ the mutant mean social payoff (see Table 1 for a list of the parameters of the
211 model). This expression is similar to the classical sequential encounter model of optimal diet
212 (Schoener 1971).

213

214 The evolutionary trajectory of the two traits (choosiness and cooperation) can be studied from the
215 analysis of the selection gradient on each trait:

216

$$\left\{ \begin{array}{l} \frac{\partial G_m}{\partial \bar{x}_m} \Big|_{\substack{\bar{x}_m = \bar{x}_r \\ y_m = y_r}} \\ \frac{\partial G_m}{\partial y_m} \Big|_{\substack{\bar{x}_m = \bar{x}_r \\ y_m = y_r}} \end{array} \right.$$

217 We could not derive an analytical expression of the evolutionarily stable strategy. However, we
 218 numerically computed the selection gradient on each trait, in order to study the evolutionary
 219 trajectories.

220

[Table 1]

221

222

223 *2.3. Plastic choosiness*

224 Because cooperation is subject to phenotypic noise (i.e. one does not perfectly control one’s own
 225 level of cooperation), it could make sense, at least in principle, for individuals to adapt plastically
 226 their degree of choosiness to the actual phenotypic cooperation that they happen to express. For
 227 instance, it could make sense for those individuals who happen to be phenotypically more generous
 228 to be also choosier, and vice versa. In our second model, we aim to explore the consequences of
 229 this possibility. To do so, we assume that choosiness is not a hard-wired trait, but a plastic decision
 230 that individuals take in function of their own phenotypic cooperation. An individual’s “choosiness
 231 strategy” is thus defined as a reaction norm rather than a single value.

232

233 Our aim in this second model is to study the joint evolution of cooperation \bar{x} on one hand, and of
 234 the “choosiness strategy” $y(x)$, defined as the shape of a reaction norm, on the other hand. One
 235 facet of this problem, therefore, consists in seeking for the equilibrium choosiness strategy in a
 236 situation where both one’s own quality (one’s phenotypic cooperation level) and the quality of

237 one's prospective partners vary. Matching theory, a branch of micro-economics, provides tools to
238 resolve this problem. Here we briefly explain this approach, and show how it applies to our
239 problem.

240
241 In a first category of approaches, called matching models, changing partner is assumed to be
242 entirely cost-free (Gale and Shapley 1962; Becker 1973). That is to say, agents have an infinite
243 amount of time available to find each other. In this setting, theory shows that there is a unique
244 equilibrium choosiness strategy: an individual with phenotypic cooperation x should only accept
245 to interact with individuals with at least the same phenotypic cooperation level x , i.e. the
246 equilibrium reaction norm is the identity function. This equilibrium strategy leads to a strictly
247 positive assortative matching in which individuals are paired with likes.

248
249 The second category of approaches, called search and matching models, accounts for frictions in
250 the matching process, i.e. incorporates an explicit cost for changing partner (Chade et al. 2017).
251 These models actually correspond exactly to our own partner choice framework. Individuals
252 randomly encounter each other at a given rate and, when an individual refuses an interaction, she
253 has to wait for some time before encountering a new partner. Unfortunately, the equilibrium
254 choosiness reaction norm $y^*(x)$ cannot be analytically derived in these models. However, Smith
255 (2006) has shown that a mathematical property of the social payoff function $\Pi(x_i, x_j)$ allows
256 predicting the shape of this reaction norm. If the social payoff function $\Pi(x_i, x_j)$ is strictly log-
257 supermodular, then $y^*(x)$ is strictly increasing with x . If this is the case, the more an individual
258 invests into cooperation, the choosier she should be. This equilibrium is called a weakly positive
259 assortative matching. Log-supermodularity is defined as the following: $\Pi(x_i, x_j)$ is strictly log-

260 supermodular only if $\Pi(x_i, x_j) \Pi(x_k, x_l) > \Pi(x_i, x_l) \Pi(x_k, x_j)$ for any investments $x_i > x_k$ and
261 $x_j > x_l$.

262
263 Matching and search and matching models are, however, only interested in characterizing the
264 equilibrium choosiness strategy of individuals, assuming a given, fixed, distribution of cooperation
265 levels. As a result, matching models can offer an insight into the evolution of choosiness, but not
266 into the joint evolution of choosiness and cooperation. To study this joint evolution in the case
267 where choosiness is a reaction norm, and not a single value, we developed individual-based
268 simulations.

269

270 *2.4. Individual-based simulations*

271 In addition to our analytical models, we run individual-based simulations coded into Python. We
272 simulate the joint evolution of cooperation and choosiness in a population of N individuals, with
273 the same lifespan L . A Moran evolution process is applied with mutations occurring at rate μ .
274 Mutant genes are drawn from a normal distribution around the parent's gene value, with standard
275 deviation σ_{mut} . Large effect mutations are implemented with probability μ_l . They do not alter the
276 equilibrium result and they allow to speed up the joint evolution process. We run long enough
277 simulations for both choosiness and cooperation to stabilize. In contrast with previous papers
278 (Sherratt and Roberts 1998; Foster and Kokko 2006; McNamara and Leimar 2010), here we
279 consider a continuous rather than discrete trait space, because Sherratt and Roberts (1998) have
280 shown that too much discretization can produce undesirable consequences when studying a joint
281 evolution process.

282

283 We run simulations both under the assumption that choosiness is hard-wired, and under the
284 assumption that it is a reaction norm. In the second case, we test two types of reaction norms. First,
285 we consider polynomial functions, the coefficients of which evolve by natural selection. Second,
286 we consider step functions with evolving coefficients coding for the value of choosiness for each
287 interval of cooperation. In the initial generation, all reaction norms are set to a constant zero
288 function, so that individuals are never choosy at initiation.

289

290

291 **3. Results**

292 *3.1. Hard-wired choosiness*

293 Without variability in cooperation ($\sigma = 0$), there is no selective pressure to be choosier and,
294 therefore, to be more cooperative. The only Nash equilibrium is $(\bar{x}, y) = (0, 0)$, see SI for a
295 demonstration.

296

297 When phenotypic cooperation is variable, however, the evolutionarily stable strategy cannot be
298 formally derived. We therefore studystudied the joint evolutionary dynamics of cooperation and
299 choosiness by plotting numerically the selection gradients acting on both traits (Fig. 1). When
300 starting from an initially selfish population, we showed that a runaway occurs: cooperation and
301 choosiness jointly evolve up to very high values, largely beyond the socially optimal level. At
302 evolutionary equilibrium, both traits are in effect very close to the “wasteful threshold” $x = 1/c$
303 at which cooperation is entirely profitless. In fact, choosiness is even slightly larger than the
304 “wasteful threshold” at equilibrium because, due to phenotypic variability, some individuals

305 cooperate beyond $x = 1/c$ which makes it adaptive to request high values of cooperation. We
306 ~~test then tested~~ the robustness of this result under a range of parameter values (Fig. 2). ~~The~~ varying
307 the parameter β ~~controls~~ (controlling the fluidity of the social market ~~(the larger is β , the less costly~~
308 ~~it is to change partner)~~ and the parameter σ ~~controls~~ (controlling the ~~width~~ extent of ~~the~~ phenotypic
309 variability ~~of in~~ cooperation ~~).~~ When the market is very fluid (large β) and phenotypic variability
310 is large, enough (large σ), individuals are very choosy at the evolutionary equilibrium, (Fig. 2a, b),
311 to the point where they only accept partners with a cooperation level higher than $x = 1/c$, that is
312 the precise level at which the cost of cooperation for the helper entirely cancels out its benefit for
313 the helpee (Fig. 2b). ~~Individual based simulations confirm these results (see SI). 2c~~. ~~Individual-~~
314 based simulations confirm these results (see SI). Cooperation can have some positive social payoff
315 at equilibrium only provided that partner choice is inefficient (β and σ are both low). In this case,
316 cooperation can reach any level below the wasteful threshold depending on the parameter
317 combination (Fig. 2a, c). Thus, there is no reason for cooperation to specifically stabilize at the
318 socially optimal level.

319

320 This runaway process can be understood intuitively. In any population, some individuals cooperate
321 more than average, in particular owing to phenotypic variability. As a result, if partner choice is
322 sufficiently fluid, it is adaptive to accept only these hyper-generous partners. Hence, choosiness
323 increases by natural selection beyond the average cooperation level. In turn, this favours
324 individuals who cooperate more than average, i.e. the mean level of cooperation increases by
325 natural selection, etc. Like in sexual selection, if switching partner is cheap enough, this process
326 can go on until the cost of cooperating becomes larger than the benefit of being chosen as a partner,
327 i.e. until individuals cooperate precisely at the “wasteful threshold”.

328

329

[Figure 1]

330

[Figure 2]

331

332 Note that [Ferriere et al. \(2002\)](#) and Wild and Cojocaru (2016, inspired by Barclay 2011) also
 333 showed that partner choice could, under some circumstances, drive the evolution of cooperation
 334 up to a “wasteful threshold”. However, in ~~their model~~ [both models](#), the choosiness strategy was
 335 fixed, and not necessarily optimal; it did not evolve jointly with cooperation. The present results
 336 are thus more robust and general.

337

338 *3.2. Plastic choosiness*

339 Here, an individual’s choosiness is a reaction norm to her own phenotypic cooperation, and we
 340 used search and matching models (see Section 2.3) to derive the two following predictions
 341 regarding the evolutionarily stable reaction norm:

- 342 i. If the social payoff function is strictly log-supermodular, an individual’s optimal
 343 choosiness is a strictly increasing function of her own cooperation (weakly positive
 344 assortative matching).
- 345 ii. If the market fluidity β/τ is high, the reaction norm should be close to $y^*(x) = x \ \forall x$
 346 (strictly positive assortative matching).

347

348 We first show that our production function Π is strictly log-supermodular. Indeed

349 $\Pi(x_i, x_j) \Pi(x_k, x_l) > \Pi(x_i, x_l) \Pi(x_k, x_j)$ is equivalent to

350

$$(x_i - x_k)(x_j - x_l)(x_i + x_k) > 0$$

351 which is true for all $x_i > x_k \geq 0$ and $x_j > x_l$. Accordingly, search and matching models show that
352 the optimal choosiness strategy is an increasing reaction norm, i.e. more phenotypically
353 cooperative individuals should also be choosier, leading to a positive assortative matching at
354 equilibrium (phenotypically generous individuals are matched with other generous individuals, and
355 vice versa).

356 [Figure 3]

357
358 Individual-based simulations confirm this result. Fig. 3 shows the reaction norm at evolutionary
359 equilibrium in these simulations: choosiness is strictly increasing, at least around the levels of
360 phenotypic cooperation that are actually present at equilibrium. Outside this range, selection is
361 very weak on the reaction norm, and we observe larger confidence intervals. As expected, when
362 the market tends to be frictionless, the reaction norm becomes very close to the identity function,
363 that is to a strict positive assortative matching (Fig. 3a and b, orange dashed line).

364
365 [Figure 4]

366
367 Importantly, the evolution of a plastic rather than hard-wired choosiness strategy has a key
368 consequence regarding the evolution of cooperation. When choosiness is plastic, cooperation
369 stabilizes at a level largely below the wasteful threshold (Fig. 4). As a result, in contrast with the
370 hard-wired case, at the evolutionary equilibrium, cooperation has a strictly positive net benefit.
371 What is more, when market fluidity is large (partner change has a small cost), cooperation evolves
372 precisely towards the socially optimal level, i.e. the level that maximizes the net total payoff of
373 individuals ($\hat{x} = 1/2c$).

374

375 This result can also be understood intuitively. In the first model where choosiness was hard-wired,
376 it was adaptive to increase one's cooperation level beyond the population mean because, by doing
377 so, an individual could switch from "being rejected by everyone", to "being accepted by everyone".
378 The runaway process, therefore, proceeded until cooperation had no benefit at all. In contrast, in
379 the present model where choosiness is plastic, increasing one's cooperation level is beneficial
380 because it allows one to *access better partners*. Hence, this is useful only provided the benefit of
381 accessing a higher quality partner is larger than the cost of being more cooperative. As a result,
382 cooperation only rises up to the social optimum, where its net benefit is maximized.

383

384 **4. Discussion**

385 Most theoretical works on the evolution of cooperation by partner choice aim at explaining how
386 *some* cooperation can be evolutionarily stable. They do not aim at understanding which specific
387 quantitative *level* of cooperation should evolve. In this paper, we have raised this second question
388 and investigated whether partner choice can account for the evolution of an intermediate and
389 efficient level of cooperation. In this aim, we have modelled, both analytically numerically and with
390 individual-based simulations, the joint evolution of two traits: cooperation, the effort invested into
391 helping others, and choosiness, the minimal level of cooperation that an individual is willing to
392 accept in a partner.

393

394 In a first model, we have found that the mechanism of partner choice seems to be incompatible
395 with an unlikely explanation for the evolution of an efficient level of cooperation. To understand
396 intuitively, consider a population with a given distribution of cooperation levels, with some
397 particularly generous individuals, some particularly stingy individuals, and a given mean
398 cooperation level. In such a population, provided that the variability of cooperation is sufficiently
399 large and the market sufficiently fluid, it is always adaptive to accept only partners that are slightly
400 better than average (McNamara et al. 2008). Hence, natural selection favours individuals with a
401 choosiness always slightly larger than the average cooperation level. In turn, this choosiness selects
402 for mutants whose cooperation level is larger than the mean, which leads to a gradual increase in
403 cooperation. This runaway process drives cooperation up to the point where interactions become
404 totally profitless because the cost of cooperation entirely cancels out its benefits (Figs. 1 and 2).
405 Thus, partner choice prompts individuals to invest into counterproductive forms of cooperation to
406 outbid others, leading to an eventually fruitless arms race. For low values of phenotypic variability
407 and market fluidity, still, our model predicts that cooperation can reach levels where the social
408 payoff is positive because the runaway process stops before it reaches the wasteful threshold (Fig.
409 2). Nevertheless, there is no evolutionary pressure driving cooperation specifically towards the
410 socially optimal level.

411
412 However, in a second approach, in line with matching models from the economic literature, we
413 have designed a model in which choosiness is implemented as a reaction norm to the individual's
414 own cooperation level (see Section 2.3), the shape of which evolves by natural selection. In this
415 case, both our analytical model and complementary individual-based simulations show that the
416 evolutionarily stable reaction norm is a monotonously increasing function of cooperation (Fig. 3).
417 This implies that more generous individuals are also choosier, leading to a positive assortative

418 matching: generous individuals tend to interact with other generous individuals, and vice versa.
419 Furthermore, if the biological market is fluid enough (i.e. if the cost of changing partner is low),
420 this positive assortative matching becomes very close to a perfect matching in which individuals
421 with a given level of cooperation always interact with other individuals with the exact same level
422 (Fig. 3a and b).

423
424 In this case, and in sharp contrast with the model in which choosiness is a hard-wired trait,
425 cooperation does not reach the counterproductive level where its cost cancels out its benefit when
426 partner choice is very cheap (Fig. 4). More precisely, when the market is very fluid (~~partner choice~~
427 ~~is very cheap~~), the evolutionarily stable cooperation becomes very close to the social optimum,
428 i.e. the amount of cooperation that maximizes the sum of the partners' payoffs. This can also be
429 understood intuitively. Because of the strict assortment between cooperative types, individuals
430 with a given cooperation level interact with other individuals with the exact same level. Hence,
431 pairs of individuals become the effective units of selection, like if interactions occurred among
432 genetic clones (Eshel and Cavalli-Sforza 1982; Wilson and Dugatkin 1997; Aktipis 2004; Akçay
433 and Van Cleve 2012). Consequently, the socially optimal level of cooperation is favoured.

434
435 Hence, the fruitless runaway of cooperation that occurs in a model with hard-wired choosiness is
436 a consequence of the assumption that individuals cannot optimally adapt their degree of choosiness
437 to local circumstances. If individuals are allowed to behave optimally, which entails in the present
438 case to adapt plastically their choosiness to their own generosity, then partner choice looks less
439 like a competition to outbid others, and more like a competition to form efficient partnerships with
440 others, which leads to a very different outcome regarding the net benefits of cooperation.

441

442 Wilson and Dugatkin (1997) already discussed the consequences of assortative matching for the
443 evolution of socially efficient levels of cooperation. However, they did not explicitly model a
444 partner choice strategy, let alone the evolution of this strategy, but merely assumed that assortment
445 occurs in one way or another. In contrast, here, we have studied the joint evolution of choosiness
446 and cooperation, showing how a positive assortative matching can emerge from a simple partner
447 choice mechanism.

448
449 In another related work, using individual-based simulations McNamara et al. (2008) also observed
450 a form of assortative matching in the joint evolution of cooperation and choosiness. The difference
451 with the present approach, however, is that they assumed that the variability of cooperation is
452 maintained at the genetic level, via a high mutation rate, rather than at the phenotypic level. Under
453 this assumption, negative selection on inefficient mutants (either too choosy or too generous)
454 ~~creates~~ generates linkage disequilibrium between cooperation and choosiness, resulting in a
455 positive assortative matching. In McNamara et al. (2008)'s simulations, however, in contrast with
456 our results, cooperation never reaches the socially optimal level- (in the model where they consider
457 a payoff function with diminishing returns). In a complementary analysis (see SI), we showed that
458 this is a consequence of their assumption that the genetic mutation rate is very high, which prevents
459 natural selection from fully optimizing social strategies.

460
461 Some scholars have already imported principles from matching theory into evolutionary biology,
462 especially in the field of sexual selection. Johnstone et al. (1996) and Bergstrom and Real (2000)
463 have used matching models, respectively with and without search frictions, to shed light on mutual
464 mate choice. Both works focused on the evolution of choosiness with a given, fixed distribution of
465 individual's quality. As we have previously shown, the intensity of assortment may have a dramatic

466 impact on the evolution of the chosen trait (cooperation, in our case). For instance, further models
467 could investigate the precise limits of the runaway processes that occur on weaponry, or on
468 ornamental traits, in sexual selection. More generally, matching models could be helpful to analyse
469 a large variety of biological markets (Noë and Hammerstein 1994, 1995; Hammerstein and Noë
470 2016), including inter-specific mutualisms, such as mycorrhizal symbiosis or plant-rhizobia
471 relationships (Simms and Taylor 2002; Kiers et al. 2003, 2011).

472
473 As for the human case in particular, several lines of evidence suggest that partner choice is a likely
474 candidate as a key driving force in the evolution of cooperation. Numerous experimental studies
475 have shown that human beings indeed do choose their social partners in function of their
476 cooperative reputation (Barclay and Willer 2007; Sylwester and Roberts 2010, 2013; Barclay 2013,
477 2016; Baumard et al. 2013; Raihani and Smith 2015; Barclay and Raihani 2016; Efferson et al.
478 2016; Stovel and Chiang 2016; Wu et al. 2016). Anthropological observations show that defection
479 in traditional societies is mostly met with a passive abandon rather than with more defection in
480 return (see Baumard et al. 2013 for a review). Also, several theoretical studies have shown that
481 partner choice ~~is able to explain~~can account for the evolution of other important properties of
482 human cooperation, such as the fact that its benefits are often shared in proportion to everyone's
483 respective effort in producing them (Chiang 2008; André and Baumard 2011a, 2011b; Debove et
484 al. 2015a, 2015b, 2017; Takesue 2017).

485
486 Regarding the quantitative level of cooperation, observations show that humans have precise
487 preferences regarding the amount of effort that shall be put into helping others. Daily life contains
488 ample examples of these preferences. For instance, we hold the door for others in subway stations,
489 but only when they are sufficiently close to the door already, not when they are very far from it.

490 And this is true quite generally. As experiments in real settings demonstrate, we have preferences
491 for specific amounts of cooperation, neither too little, nor too much (Santamaria and Rosenbaum
492 2011; Lange and Eggert 2015). Sometimes this preference is expressed in a purely quantitative
493 manner. At other times, the same preference is expressed in a more qualitative way, determining
494 the kinds of cooperative action that we are willing, or unwilling, to perform. In any case, our
495 investment in helping is quantitatively bounded. Moreover, the precise level of effort we are willing
496 to put in cooperation seems to be constrained by considerations of social efficiency. Individuals
497 help one another only when it is mutually advantageous, that is when the cost of helping is less
498 than the benefit of being helped. Additionally, recent evolutionary modellings of risk pooling have
499 revealed the socially optimal nature of helping behaviours (Cronk 2007; Aktipis et al. 2011, 2016;
500 Campenni and Schino 2014; Hao et al. 2015). They have shown that people's systems of mutual
501 help correspond to the most efficient systems of risk pooling in a volatile environment.

502

503 In this paper, we have shown that partner choice can foster the evolution of such an intermediate
504 and efficient amount of cooperation, neither too little nor too much. But we have also shown that
505 the precise evolutionarily stable amount of cooperation should depend on the fluidity of the
506 biological market, and can range from a very low level of cooperation, up to the socially optimal
507 level (Fig. 4). A number of anthropological studies suggest that contemporary hunter-gatherer
508 societies exhibit high levels of spatial mobility (Baumard et al. 2013; Lewis et al. 2014). Therefore,
509 it seems plausible that biological markets were highly fluid in the social structure that our ancestors
510 experienced. Our model predicts that, in this case, the amount of effort invested into cooperation
511 should become very close to the social optimum. Therefore, partner choice can account for the
512 evolution of human preferences concerning social efficiency.

513

514 One could wonder, however, whether other models ~~on the evolution of cooperation can~~ than partner
515 choice could account for the evolution of a socially optimal level of cooperation as well. The most
516 influential model on the evolution of quantitative cooperation among non-kin is the continuous
517 version of the iterated prisoner's dilemma (Roberts and Sherratt 1998; Wahl and Nowak 1999a,
518 1999b; Killingback and Doebeli 2002; Lehmann and Keller 2006; André and Day 2007; André
519 2015). In this game, André and Day (2007) have shown that the only evolutionarily stable level of
520 investment is the one that maximises the total benefit of the interaction, i.e. that natural selection
521 does eventually favour the socially optimal amount of cooperation (see also Binmore 1990;
522 Fudenberg and Maskin 1990; Robson 1990 and Binmore and Samuelson 1992 in a discrete
523 version of the iterated prisoner's dilemma). Yet, in this approach, selection for efficient cooperation
524 is only a second-order force, which plays a significant role only because André and Day (2007)
525 assumed the absence of other first-order effects. For instance, a slight cognitive cost of conditional
526 behaviour would have prevented the evolution of efficient cooperation in their model. In another
527 related study, Akçay and Van Cleve (2012) have shown that ~~some, for a specific case of their~~
528 model, a moderate level of genetic relatedness ~~is required for~~ can favour the evolution of the
529 socially optimal amount of cooperation ~~to be favored~~ by first-order selective effects in the
530 ~~continuous~~ continuous prisoner's dilemma. In contrast, under the effect of partner choice, efficient
531 cooperation is favoured by first-order selective effects even in the absence of genetic relatedness.
532 This occurs because, unlike reciprocity, partner choice is a *directional* enforcement mechanism.
533 Whereas reciprocity merely stabilizes any given level of cooperation (a principle called the folk
534 theorem, see Aumann and Shapley 1994; Boyd 2006), partner choice directionally favours the most
535 efficient level.

536

537 One limit of our model is that we did not introduce an explicit mechanism for reputation. We
538 simply assumed that, in a way or another, individuals have reliable information regarding the
539 cooperation level of others, but we did not model the way in which they obtain this information.
540 Costly signalling theory proposes that some cooperative behaviours are costly signals of an
541 individual's quality or willingness to cooperate (Leimar 1997; Gintis et al. 2001; André 2010;
542 Barclay 2015; Bird and Power 2015; Bliege Bird et al. 2018). Such signals could, in theory, be far
543 from socially efficient (Gintis et al. 2001). However, further analyses are needed to rigorously
544 model signalling in the context of a biological market.

545

546

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551

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765

766 **Tables**

767

768

Table 1: Parameters of the model

| Parameter | Definition |
|-----------------|---|
| \bar{x}_i | Cooperation level of individual i (mean value before applying noise) |
| y_i | Choosiness of individual i |
| σ | Standard deviation of the phenotypic cooperation distribution |
| β | Encounter rate |
| τ | Split rate |
| S | Solitary gain per unit of time |
| $\Pi(x_i, x_j)$ | Social payoff of an individual i matched with a partner j |
| c | Cost of cooperation |
| α_i | Mean probability for an individual i to interact when she encounters a resident |
| $\bar{\Pi}_i$ | Mean social payoff for an individual i interacting with a resident |
| G_i | Cumulative lifetime payoff of an individual i |

769

Figures

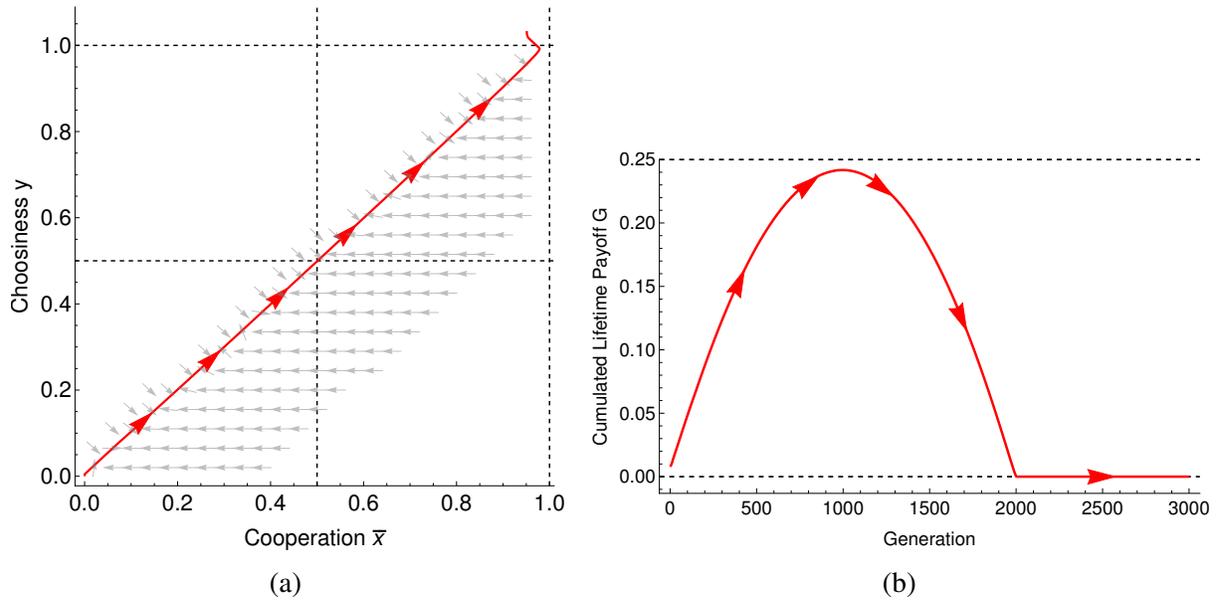
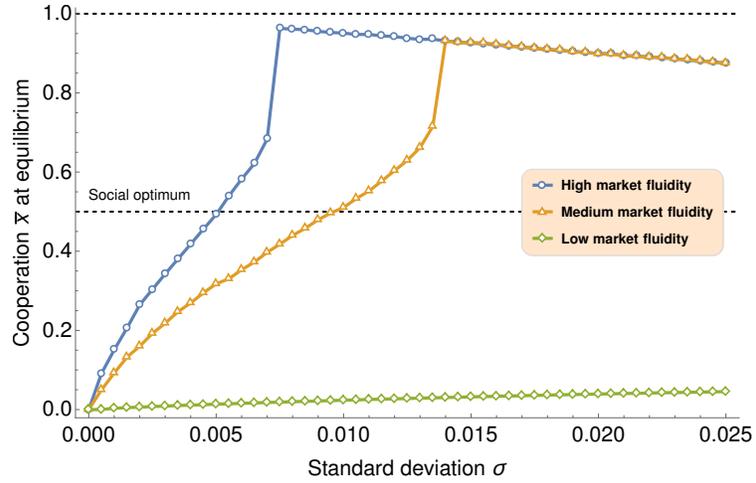
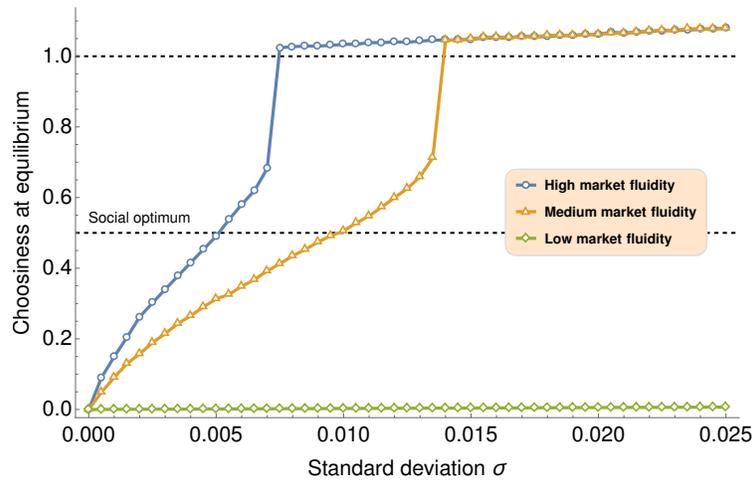


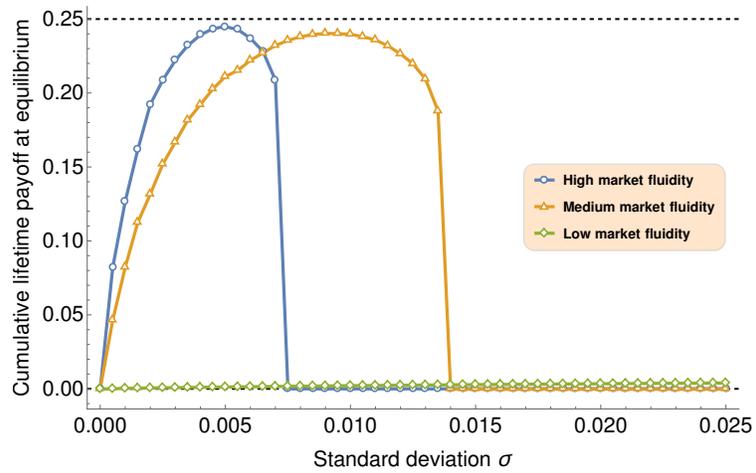
Figure 1: Analytical and numerical results. **(a)** In grey, the vector field of the selection gradient. In red, the evolutionary trajectory starting from an initial selfish population $(\bar{x}, y) = (0, 0)$. Parameters are $c = 1$; $\sigma = 0.025$; $\beta = 1$; $\tau = 0.01$. **(b)** The corresponding evolution of the cumulative lifetime payoff G for a resident individual. The socially optimal solution is $\hat{x} = 1/2$ and the interaction becomes profitless if both individuals invest $x = 1$.



(a)



(b)



(c)

Figure 2: Analytical results for a range of parameters. Equilibrium value for (a) cooperation, (b) choosiness and (b) cumulative lifetime payoff as a function of the standard deviation σ and three values of the encounter rate $\beta = 0.001; 0.5; 1$ respectively for low, medium and high market fluidity. Other parameters are the same as in Fig. 1

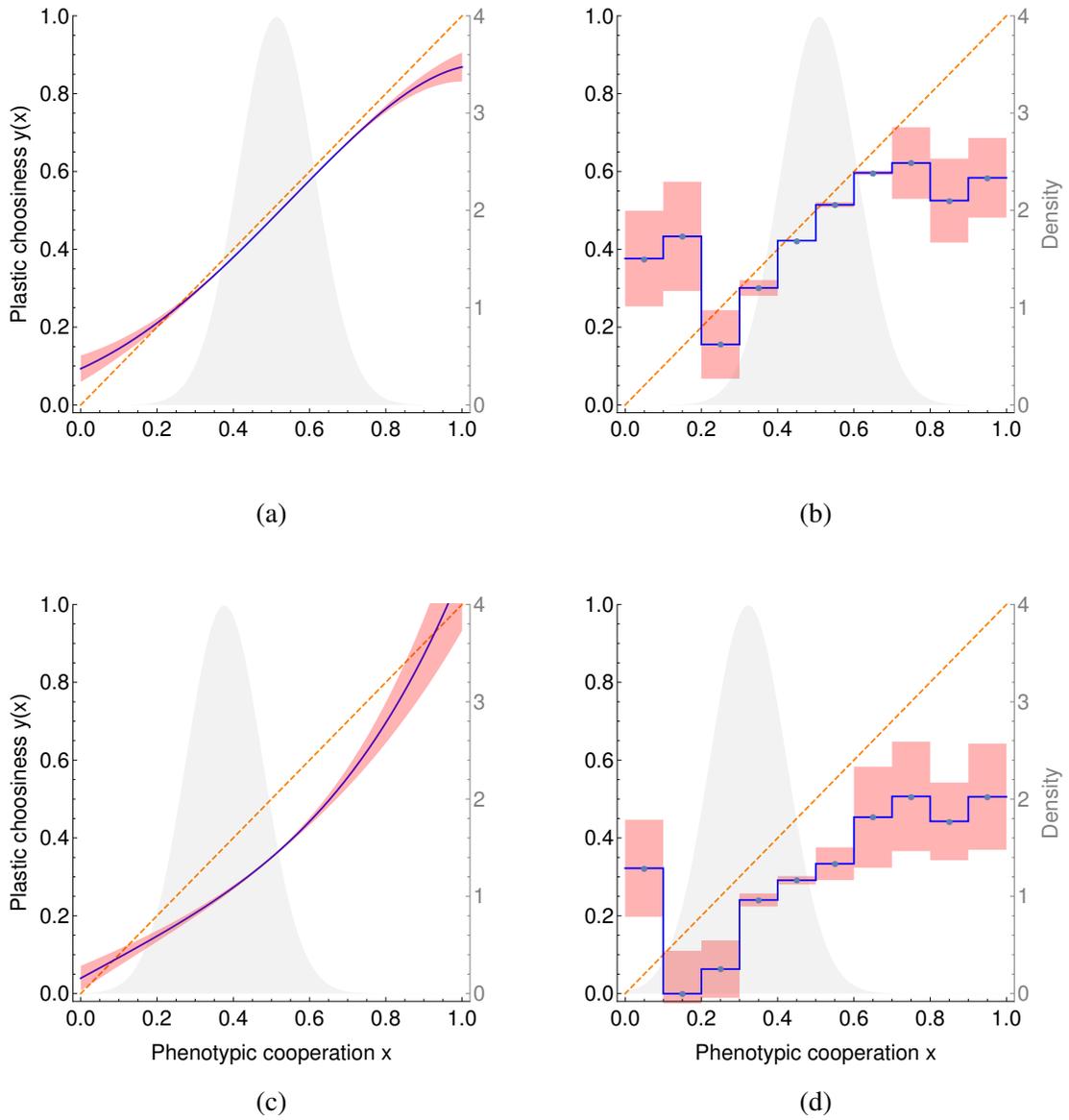


Figure 3: Plastic choosiness at the equilibrium. In blue, plastic choosiness at the equilibrium over 30 simulations. 99% confident interval in red. The orange dashed line is the optimal reaction norm for a frictionless matching market (strong form of positive assortative matching). In grey the distribution of phenotypic cooperation at equilibrium. **(a-b)** High market fluidity $\beta = 1$. **(c-d)** Low market fluidity $\beta = 0.01$. **(a-c)** Polynomial norm. **(b-d)** Discrete norm. Parameters are $c = 1$; $\sigma = 0.1$; $\tau = 0.01$; $\mu = 0.001$; $\sigma_{mut} = 0.05$; $\mu_l = 0.05$; $N = 300$; $L = 500$.

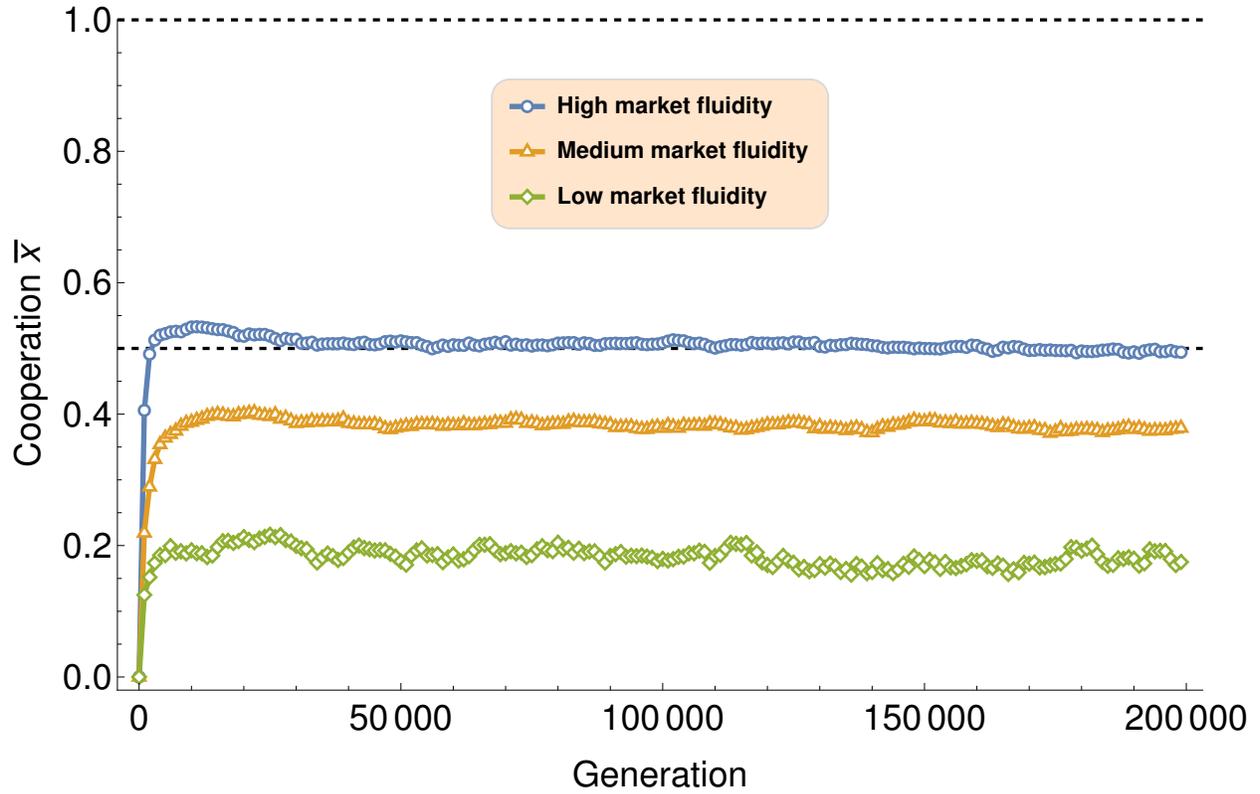


Figure 4: Evolution of cooperation for a polynomial reaction norm. Mean over 30 simulations. Parameters: there are three values for the encounter rate $\beta = 0.001; 0.01; 0.1$ respectively for low, medium and high market fluidity. Other parameters are the same as in Fig. 3. The socially optimal solution is $\hat{x} = 1/2$ and the interaction becomes profitless if both individuals invest $x = 1$.