

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~~ Using a classic adaptive dynamics model ~~shows, we first show~~ that, when
22 ~~individuals can easily choose their partner~~ the cost of changing partner is low, this runaway process
23 ~~leads~~ can lead to a profitless escalation of ~~the level of~~ cooperation. In the extreme, when partner
24 choice is entirely frictionless, cooperation even increases up to the point a level where ~~the~~ its cost
25 ~~of cooperation exactly~~ entirely cancels out its benefit. ~~In other words~~ That is, at ~~first sight, under the~~
26 ~~effect of partner choice we predict that cooperation should have no benefit at the~~ evolutionary
27 equilibrium, individuals gain the same payoff than if they had not cooperated at all. Second,
28 importing models from matching theory in economics we, however, show that, when individuals
29 can plastically modulate their choosiness in function of their own cooperation level, partner choice
30 stops being a runaway competition to outbid others, and becomes a competition to form the most
31 optimal partnerships. ~~Assortative~~ In this case, when the cost of changing partner tends toward zero
32 partner choice ~~then~~ leads to the evolution of the socially optimum level of cooperation. This last
33 result could explain the observation that human cooperation seems to be often constrained by
34 considerations of social efficiency.

35

36

37 **Key words:** partner choice, biological markets, matching models, competitive altruism, human
38 cooperation

39

40 **1. Introduction**

41 Cooperation among non-kin constitutes a puzzle for evolutionary biologists, and a large body of
42 theoretical models, inspired by game theory, have been developed to solve it. The most commonly
43 accepted explanation is that cooperation can be enforced if it triggers a conditional response on the
44 part of others (West et al. 2007). Several enforcement mechanisms have been proposed: direct
45 reciprocity (Trivers 1971; Axelrod and Hamilton 1981; Lehmann and Keller 2006), indirect
46 reciprocity (Nowak and Sigmund 1998, 2005; Leimar and Hammerstein 2001), punishment (Boyd
47 and Richerson 1992; Boyd et al. 2003; Bowles and Gintis 2004) and partner choice (Bull and Rice
48 1991; Noë and Hammerstein 1994, 1995; Sachs et al. 2004). A growing number of experimental
49 studies support the idea that, among this set of mechanisms, partner choice is likely to be
50 particularly influential in nature, both in inter-specific and in intra-specific interactions (Bshary
51 and Schaffer 2002; Simms and Taylor 2002; Kiers et al. 2003, 2011; Fruteau et al. 2009; Schino
52 and Aureli 2009; Hammerstein and Noë 2016). Besides, partner choice is also believed to play a
53 major role in human cooperation, where friendships and coalitions are common (Barclay 2013,
54 2016; Baumard et al. 2013; and see Discussion).

55

56 The key idea of partner choice models is that, when one happens to be paired with a defecting
57 partner, one has the option to seek for another, more cooperative, partner present in the “biological
58 market” and interact with her instead of the defector. This possibility allows cooperators to
59 preferentially interact with each other, and, consequently, prevents any invasion by free-riders

60 (Eshel and Cavalli-Sforza 1982; Bull and Rice 1991; Noë and Hammerstein 1994, 1995; Ferriere
61 et al. 2002; Bergstrom 2003; Aktipis 2004, 2011; Sachs et al. 2004; Fu et al. 2008; Barclay 2011).

62

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

68

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

80

81 Prima facie, partner choice appears to be a unidirectional pressure acting on the evolution of
82 cooperation, unlikely to generate an intermediate equilibrium. Competition to be chosen by others,

83 called “competitive altruism” (Roberts 1998; Hardy and Van Vugt 2006; Nesse 2009), should lead
84 to a runaway of cooperation, as it does in sexual selection (West-Eberhard 1983). In principle, this
85 runaway should proceed up to the point where the cost of investing into cooperation cancels out
86 the benefit of finding a partner (West-Eberhard 1979; Fisher 1999 p.152) that is up to the
87 “wasteful” threshold where cooperation becomes fruitless. Is competitive altruism, however,
88 balanced by opposite forces, leading to an evolutionary stabilization of cooperation below this
89 threshold? Is this level socially optimal, or does partner choice lead to the investment into
90 counterproductive forms of cooperation to out-compete others as it does in sexual selection?

91
92 In the theoretical literature on partner choice, relatively little attention has been given to these
93 questions. First of all, a large proportion of models consider cooperation as an all-or-nothing
94 decision and thus cannot study its quantitative level (Eshel and Cavalli-Sforza 1982; Bergstrom
95 2003; Aktipis 2004; Fu et al. 2008; Chen et al. 2009; Aktipis 2011; Suzuki and Kimura 2011; Sibly
96 and Curnow 2012; Campennì and Schino 2014; Izquierdo et al. 2014; Chen et al. 2016; Wubs et
97 al. 2016). Second, some models consider cooperation as a quantitative trait but do not entail
98 diminishing returns, and are thus ill-suited to study the social efficiency of cooperative interactions
99 (Sherratt and Roberts 1998; Foster and Kokko 2006; Nesse 2009; Song and Feldman 2013). Third,
100 still other models consider cooperation as a quantitative trait with diminishing returns, but they
101 only focus on one side of the problem –the evolution of cooperation– considering the other side –
102 the strategy employed by individuals to choose their partner– as an exogenous parameter (Wilson
103 and Dugatkin 1997; Ferriere et al. 2002; Barclay 2011; Wild and Cojocaru 2016).

104
105 To our knowledge, only one existing model studies the joint evolution of cooperation and partner
106 choice in a quantitative setting with diminishing returns (McNamara et al. 2008). However,

107 McNamara et al. (2008) make two key assumptions that turn out to have important consequences:
108 (i) they assume that variability in the amount of cooperation is maintained owing to a very large
109 genetic mutation rate on this trait, which prevents natural selection to act efficiently, and (ii) they
110 restrict the set of possible strategies to choose one's partner in such a way that individuals can
111 never do so in an optimal manner.

112
113 In this paper, we build a model inspired by McNamara et al. (2008), in which a quantitative level
114 of cooperation expressed by individuals jointly evolves with a quantitative level of choosiness
115 regarding others' cooperation, while relaxing these two assumptions. First, we observe that ~~partner~~
116 ~~choice leads to a runaway of cooperation. When partner choice is cheap enough, it does create a~~
117 ~~competition to be chosen as a partner, leading leads~~ to a joint rise of both cooperation and
118 choosiness up to a level that depends on the efficiency of partner choice that is, in particular, on
119 the cost of changing partner. The more efficient is partner choice, the higher cooperation is at
120 evolutionary stability. Moreover, when the cost of changing partner is low, cooperation can rise
121 beyond its socially optimal level. In fact, in the limit where partner choice is entirely frictionless
122 (i.e. the cost of changing partner is zero), cooperation and choosiness rise up to the point "wasteful
123 threshold" where the cost of cooperation entirely cancels out its benefit. Individuals gain the same
124 payoff than if they had not cooperated at all. Hence, at first sight, our analyses show that partner
125 choice ~~is unlikely to explain~~generates no systematic trend toward the ~~evolution of a moderate and~~
126 ~~efficient~~socially optimal level of cooperation.

127
128 However, we then ~~resolve this apparent paradox by importing~~import tools from the economics
129 literature and ~~assuming~~assume that individuals can plastically modulate their choosiness in
130 function of their own cooperation level. This plasticity allows every individual to behave optimally

131 on the biological market, which did not occur in the first model. ~~Assortative~~In this second
132 approach, we show that assortative matching emerges. That is, more cooperative individuals are
133 also choosier and ~~leads to the evolution~~thus interact with more cooperative partners. As a
134 consequence of this assortment, and provided that partner choice is efficient levels of enough,
135 cooperation. ~~If the cost of changing partner is low enough, this process can even lead to the~~
136 ~~evolution of the~~ evolves to the socially optimal level ~~of cooperation,~~ where the mutual efficiency
137 of cooperation is maximised.

138

139 **2. Methods**

140 *2.1. Partner choice framework*

141 We model partner choice in an infinite size population using Debove et al. (2015a)'s framework.
142 Solitary individuals randomly encounter each other in pairs at a fixed rate β . In each encounter,
143 the two players decide whether they accept one another as a partner (see below how this decision
144 is made). If one of the two individuals (or both) refuses the interaction, the two individuals
145 immediately split and move back to the solitary pool. If both individuals accept each other, on the
146 other hand, the interaction takes place and lasts for an exponentially distributed duration with
147 stopping rate τ , after which the two individuals move back to the solitary pool again. The ratio β/τ
148 thus characterizes the “fluidity” of the biological market. If β is high and τ is low, individuals meet
149 each other frequently and interact for a long time. In such an almost frictionless market, partner
150 choice is almost cost-free so they should be choosy about their partner's investment in cooperation.
151 Conversely, if β/τ is low, individuals rarely meet potential partners and interact for a short time.
152 In such a market, on the contrary, individuals should accept any partner.

153

154 Regarding the encounter rate, here we assume that β is a fixed constant independent of the density
155 of available partners, an assumption called “linear search” that captures a situation in which already
156 paired individuals do not hinder the encounters of solitary individuals (Diamond and Maskin 1979).
157 In the Supplementary Information, however, using simulations we also analyse the model under
158 the assumption that β increases linearly with the proportion of solitary individuals in the
159 population, an assumption called “quadratic search” that corresponds to a situation in which
160 already matched individuals interfere with the encounters of solitary individuals (and that is also
161 equivalent to the classic mass-action kinetics used in mathematical epidemiology). In the paper,
162 we only describe the results obtained under linear search. The results obtained under quadratic
163 search are qualitatively similar (see the Supplementary Information).

164

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

174

175 When they are solitary, individuals gain a payoff normalized to zero per unit of time. When
 176 involved into an interaction, they gain a social payoff that depends on both partners' cooperation
 177 level. The cooperative interaction is a continuous prisoner's dilemma: making an investment brings
 178 benefits to the partner but comes at a cost to the provider. As stated in the introduction, we make
 179 the additional assumption that cooperation has diminishing returns (Altmann 1979; Weigel 1981;
 180 Killingback and Doebeli 2002). This induces the existence of an intermediate level of cooperation
 181 at which the sum of the partners' gains is maximized, the so-called "social optimum". An
 182 individual i paired with j gains the following social payoff $\Pi(x_i, x_j)$ per unit of time:

$$183 \quad \Pi(x_i, x_j) = x_j - cx_i^2$$

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

$$185 \quad \frac{x_j - cx_i^2}{\tau}$$

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

191
 192 Previous studies demonstrated that the existence of some variability among individuals is
 193 necessary to stabilize conditional cooperation (Ferriere et al. 2002; Foster and Kokko 2006;
 194 McNamara et al. 2008; McNamara and Leimar 2010; Song and Feldman 2013). If every possible
 195 partner is equally cooperative, then there is no need to be choosy with regard to the quality of one's
 196 partner, and choosiness cannot be evolutionarily stable. In order to capture the effect of variability
 197 in the simplest possible way, we assume that individuals do not perfectly control their investment

198 into cooperation (as in Song and Feldman 2013 and André, 2015 for instance). An individual's
199 actual cooperation level x_i is a random variable which follows a truncated to zero normal
200 distribution around the individual's gene value \bar{x}_i , with standard deviation σ . In what follows, we
201 call cooperation level the genetically encoded cooperation level that individuals aim for, and
202 "phenotypic cooperation" the actual level of cooperation that they express after phenotypic noise.

203 For the sake of simplicity, here, we assume that an individual's cooperation level is randomized at
204 every encounter. In the Supplementary Information, however, we also consider the alternative
205 assumption where phenotypic noise occurs only once at birth (see also section 3.1).

206

207 We are interested in the joint evolution of cooperation, and choosiness by natural selection. We
208 undertake and compare the consequences of two distinct assumptions. In a first approach, we
209 assume that both cooperation and choosiness are hard-wired traits, that is each individual is
210 characterized by a single level of cooperation \bar{x} and a single choosiness y , both expressed
211 unconditionally. In a second approach, we still assume that cooperation is a hard-wired trait, but
212 we consider that choosiness is a reaction norm by which individuals respond to their own
213 phenotypic cooperation.

214

215 *2.2. Hard-Wired choosiness*

216 Here, we assume that each individual is genetically characterized by two traits: his level of
217 cooperation \bar{x} and his choosiness y and we are interested in the evolution of these two traits by
218 natural selection. For this, we need to derive the fecundity of a rare mutant m playing strategy
219 (\bar{x}_m, y_m) in a resident population r playing strategy (\bar{x}_r, y_r) . The mutant fecundity is proportional

220 to her cumulative lifetime payoff G_m , which can be written as (see SI for a detailed analysis of the
221 model):

$$222 \quad G_m = \frac{\bar{\Pi}_m \alpha_m \beta}{\alpha_m \beta + \tau}$$

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

227
228 The evolutionary trajectory of the two traits (choosiness and cooperation) can be studied from the
229 analysis of the selection gradient on each trait:

$$230 \quad \left\{ \begin{array}{l} \frac{\partial G_m}{\partial \bar{x}_m} \Big|_{\substack{\bar{x}_m = \bar{x}_r \\ y_m = y_r}} \\ \frac{\partial G_m}{\partial y_m} \Big|_{\substack{\bar{x}_m = \bar{x}_r \\ y_m = y_r}} \end{array} \right.$$

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

234 [Table 1]

235

236

237 *2.3. Plastic choosiness*

238 Because cooperation is subject to phenotypic noise (i.e. one does not perfectly control one's own
239 level of cooperation), it could make sense, at least in principle, for individuals to adapt plastically

240 their degree of choosiness to the actual phenotypic cooperation that they happen to express. For
241 instance, it could make sense for those individuals who happen to be phenotypically more generous
242 to be also choosier, and vice versa. In our second model, we aim to explore the consequences of
243 this possibility. To do so, we assume that choosiness is not a hard-wired trait, but a plastic decision
244 that individuals take in function of their own phenotypic cooperation. An individual's "choosiness
245 strategy" is thus defined as a reaction norm rather than a single value.

246
247 Our aim in this second model is to study the joint evolution of cooperation \bar{x} on one hand, and of
248 the "choosiness strategy" $y(x)$, defined as the shape of a reaction norm, on the other hand. One
249 facet of this problem, therefore, consists in seeking for the equilibrium choosiness strategy in a
250 situation where both one's own quality (one's phenotypic cooperation level) and the quality of
251 one's prospective partners vary. Matching theory, a branch of micro-economics, provides tools to
252 resolve this problem. Here we briefly explain this approach, and show how it applies to our
253 problem.

254
255 In a first category of approaches, called matching models, changing partner is assumed to be
256 entirely cost-free (Gale and Shapley 1962; Becker 1973). That is to say, agents have an infinite
257 amount of time available to find each other. In this setting, theory shows that there is a unique
258 equilibrium choosiness strategy: an individual with phenotypic cooperation x should only accept
259 to interact with individuals with at least the same phenotypic cooperation level x , i.e. the
260 equilibrium reaction norm is the identity function. This equilibrium strategy leads to a strictly
261 positive assortative matching in which individuals are paired with likes.

262

263 The second category of approaches, called search and matching models, accounts for frictions in
264 the matching process, i.e. incorporates an explicit cost for changing partner (Chade et al. 2017).
265 These models actually correspond exactly to our own partner choice framework. Individuals
266 randomly encounter each other at a given rate and, when an individual refuses an interaction, she
267 has to wait for some time before encountering a new partner. Unfortunately, the equilibrium
268 choosiness reaction norm $y^*(x)$ cannot be analytically derived in these models. However, Smith
269 (2006) has shown that a mathematical property of the social payoff function $\Pi(x_i, x_j)$ allows
270 predicting the shape of this reaction norm. If the social payoff function $\Pi(x_i, x_j)$ is strictly log-
271 supermodular, then $y^*(x)$ is strictly increasing with x . If this is the case, the more an individual
272 invests into cooperation, the choosier she should be. This equilibrium is called a weakly positive
273 assortative matching. Log-supermodularity is defined as the following: $\Pi(x_i, x_j)$ is strictly log-
274 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
275 $x_j > x_l$.

276
277 Matching and search and matching models are, however, only interested in characterizing the
278 equilibrium choosiness strategy of individuals, assuming a given, fixed, distribution of cooperation
279 levels. As a result, matching models can offer an insight into the evolution of choosiness, but not
280 into the joint evolution of choosiness and cooperation. To study this joint evolution in the case
281 where choosiness is a reaction norm, and not a single value, we developed individual-based
282 simulations.

283

284 2.4. Individual-based simulations

285 In addition to our analytical models, we run individual-based simulations coded into Python. We
286 simulate the joint evolution of cooperation and choosiness in a Wright-Fisher population of N
287 individuals, with the same lifespan L . ~~A Moran evolution process is applied with mutations~~
288 ~~occurring and non-overlapping generations. Mutations occur~~ at rate μ . ~~Mutant and mutant~~ genes
289 are drawn from a normal distribution around the parent's gene value, with standard deviation σ_{mut} .
290 Large effect mutations are implemented with probability μ_l . They do not alter the equilibrium
291 result and they allow to speed up the joint evolution process. We run long enough simulations for
292 both choosiness and cooperation to stabilize. In contrast with previous papers (Sherratt and Roberts
293 1998; Foster and Kokko 2006; McNamara and Leimar 2010), here we consider a continuous rather
294 than discrete trait space, because Sherratt and Roberts (1998) have shown that too much
295 discretization can produce undesirable consequences when studying a joint evolution process. In
296 the Supplementary Information, we also present additional simulations based on a Moran process
297 with overlapping generations, where the lifespan of individuals is determined by a constant
298 mortality rate (see also section 3.1; McNamara et al. 2008).

299
300 We run simulations both under the assumption that choosiness is hard-wired, and under the
301 assumption that it is a reaction norm. In the second case, we test two types of reaction norms. First,
302 we consider polynomial functions, the coefficients of which evolve by natural selection. Second,
303 we consider step functions with evolving coefficients coding for the value of choosiness for each
304 interval of cooperation. In the initial generation, all reaction norms are set to a constant zero
305 function, so that individuals are never choosy at initiation.

306

307

308 **3. Results**

309 *3.1. Hard-wired choosiness*

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

313

314 When phenotypic cooperation is variable, however, the evolutionarily stable strategy cannot be
315 formally derived. We therefore ~~studied~~study the joint evolutionary dynamics of cooperation and
316 choosiness by plotting numerically the selection gradients acting on both traits (~~Fig. In Figure 1~~),
317 we show the evolutionary dynamics of cooperation, choosiness, and average payoff, in a case
318 where partner choice is very effective. When starting from an initially selfish population, ~~we~~
319 ~~showed that a runaway occurs:~~ cooperation and choosiness jointly ~~evolve up to very high values,~~
320 ~~largely beyond~~rise above zero (Fig. 1a). At first, this leads to an increase of the net social payoff
321 (Fig. 1b) because cooperation is efficient (that is, the marginal benefit of increasing cooperation
322 for the helpee is larger than its marginal cost for the helper). At some point, however, cooperation
323 reaches the socially optimal level. ~~At evolutionary equilibrium, both traits are in~~ where the net
324 payoff of individuals is maximized. Beyond this level, the marginal cost of increasing cooperation
325 is larger than the marginal benefit, but the evolutionary runaway of cooperation and choosiness
326 does not stop. Cooperation keeps on rising toward higher values, thereby decreasing the net payoff
327 (Fig. 1b). Eventually, cooperation and choosiness stabilize when cooperation is so high, and

328 therefore so inefficient, that its cost entirely cancels out its benefit (the so-called “wasteful
329 threshold”). That is, at ESS, individuals gain the same payoff than if they had not cooperated at all.
330 This runaway process, however, only occurs if partner choice is very efficient. If partner choice
331 has more frictions, the rise of cooperation and choosiness halts at an intermediate level between 0
332 and the wasteful threshold. In Figure 2, we plot the level of cooperation (Fig. 2a), the level of
333 choosiness (Fig. 2b) and the average payoff (Fig. 2c) reached at evolutionary stability, in function
334 of the efficiency of partner choice (that is, in function of the parameter β controlling the fluidity
335 of the social market and the parameter σ controlling the extent of phenotypic variability). As
336 partner choice becomes more efficient, the evolutionarily stable cooperation and choosiness
337 monotonously rise from zero up to the wasteful threshold (Fig. 2a, b). Accordingly, the net payoff
338 obtained by individuals at evolutionary stability varies with the efficiency of partner choice in a
339 non-monotonous way. Increasing the efficiency of partner choice has first a positive and then a
340 negative effect very close on payoff (Fig. 2c). In the extreme, when partner choice is frictionless,
341 cooperation and choosiness increase up to the “wasteful threshold” $x = 1/c$ at which cooperation
342 is entirely profitless. ~~In fact (as was shown in Fig. 1). Note that, in this case, choosiness is even~~
343 slightly larger than the “wasteful threshold” at equilibrium because, due to phenotypic variability,
344 some individuals cooperate beyond $x = 1/c$ which makes it adaptive to request ~~high values of~~
345 ~~cooperation. We then tested the robustness of this result under a range of parameter values (Fig. 2)~~
346 ~~varying the parameter β (controlling the fluidity of the social market) and the parameter σ~~
347 ~~(controlling the extent of phenotypic variability in cooperation). When the market is very fluid~~
348 ~~(large β) and phenotypic variability is large enough (large σ), individuals are very choosy at the~~
349 ~~evolutionary equilibrium (Fig. 2a, b), to the point where they only accept partners with a~~
350 ~~cooperation level higher than $x = 1/c$, that is the precise level at which the cost of cooperation for~~

351 ~~the helper entirely cancels out its benefit for the helpee (Fig. 2c). Individual based simulations~~
352 ~~confirm these results (see SI). Cooperation can have some positive social payoff at equilibrium~~
353 ~~only provided that partner choice is inefficient (β and σ are both low). In this case, cooperation~~
354 ~~can reach any level below the wasteful threshold depending on the parameter combination (Fig.~~
355 ~~2a, c). Thus, there is no reason for cooperation to specifically stabilize at the socially optimal~~
356 ~~level.~~ higher values of cooperation. In fact, when phenotypic variability is too high (large σ),
357 individuals are so choosy at evolutionary equilibrium that the equilibrium level of cooperation is
358 reduced (Fig. 2a). These results have been confirmed in individual-based simulations (see SI).

359
360 ~~This~~ The runaway process can be understood intuitively. In any population, some individuals
361 cooperate more than average, in particular owing to phenotypic variability. As a result, if partner
362 choice is sufficiently fluid, it is adaptive to accept only these hyper-generous partners. Hence,
363 choosiness increases by natural selection beyond the average cooperation level. In turn, this favours
364 individuals who cooperate more than average, i.e. the mean level of cooperation increases by
365 natural selection, etc. ~~Like in sexual selection, if switching partner is cheap enough,~~ The extent to
366 which this process can go on until depends, however, on the efficiency of partner choice owing
367 to the existence of a trade-off between the cost ~~of cooperating becomes larger than the~~ and benefit
368 of ~~being chosen as a partner, i.e. until individuals cooperate precisely~~ choosiness. The runaway
369 process stops at the “wasteful threshold” point where the expected benefit of finding a better
370 partner is not worth the risk of remaining alone.

371

372 [Figure 1]

373 [Figure 2]

374

375 -In our model so far, the cost and benefit of switching partner are only determined by two
376 parameters (the market fluidity, β/τ , and the amount of phenotypic variability, σ). Under more
377 realistic biological assumptions, however, the cost of rejecting a partner should also depend on
378 other parameters. For instance, one could model mortality as a stochastic process. The risk of dying
379 while searching for a new partner would then constitute a supplementary cost of choosiness
380 (McNamara et al. 2008). In the Supplementary Information, we develop a model based on a Moran
381 process where individuals are subject to a constant mortality rate. As expected, ceteris paribus, the
382 runaway process results in lower levels of cooperation and choosiness at evolutionary equilibrium
383 when the mortality rate is high. Cooperation, however, still rises beyond the socially optimal level,
384 even up to the wasteful threshold, if β is large and if the mortality rate is not too high.

385

386 Also, in our model, so far, we assume that an individual's phenotypic level of cooperation is
387 randomized in every encounter. The distribution of cooperative types in the solitary population is
388 thus a fixed and exogenous property. To test the robustness of our results, in the Supplementary
389 Information, we analyse an alternative case where the phenotypic level of cooperation of an
390 individual is randomized only once, at birth. In this case, the distribution of cooperative types in
391 the solitary population is not an exogenous, fixed, property. More cooperative individuals are less
392 likely to be solitary than average because they are rapidly accepted as partners (McNamara et al.
393 2008). Hence, the population of solitary individuals tends to be biased toward selfish phenotypes.
394 As a result, the cost of being choosy is larger. Yet, in SI we show that the runaway process still
395 occurs in this case, including up to the "wasteful threshold", as long as partner choice is efficient
396 enough.

397

398 Note that Ferriere et al. (2002) and Wild and Cojocaru (2016, inspired by Barclay 2011) also
 399 showed that partner choice could, under some circumstances, drive the evolution of cooperation
 400 up to a “wasteful threshold”. However, in both models, the choosiness strategy was fixed, and not
 401 necessarily optimal; it did not evolve jointly with cooperation. The present results are thus more
 402 robust and general.

403

404 *3.2. Plastic choosiness*

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

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

413

414 We first show that our production function Π is strictly log-supermodular. Indeed
 415 $\Pi(x_i, x_j) \Pi(x_k, x_l) > \Pi(x_i, x_l) \Pi(x_k, x_j)$ is equivalent to

$$416 \quad (x_i - x_k)(x_j - x_l)(x_i + x_k) > 0$$

417 which is true for all $x_i > x_k \geq 0$ and $x_j > x_l$. Accordingly, search and matching models show that
 418 the optimal choosiness strategy is an increasing reaction norm, i.e. more phenotypically
 419 cooperative individuals should also be choosier, leading to a positive assortative matching at

420 equilibrium (phenotypically generous individuals are matched with other generous individuals, and
421 vice versa).

422 [Figure 3]

423
424 Individual-based simulations confirm this result. Fig. 3 shows the reaction norm at evolutionary
425 equilibrium in these simulations: choosiness is strictly increasing, at least around the levels of
426 phenotypic cooperation that are actually present at equilibrium. Outside this range, selection is
427 very weak on the reaction norm, and we observe larger confidence intervals. As expected, when
428 the market tends to be frictionless, the reaction norm becomes very close to the identity function,
429 that is to a strict positive assortative matching (Fig. 3a and b, orange dashed line).

430

431 [Figure 4]

432

433 Importantly, the evolution of a plastic rather than hard-wired choosiness strategy has a key
434 consequence regarding the evolution efficiency of cooperation. ~~When choosiness is plastic,~~
435 ~~cooperation stabilizes at a level largely below the wasteful threshold (Fig. evolutionary~~
436 ~~equilibrium. In 4).~~ ~~As a result, in~~ contrast with the hard-wired case, ~~at the evolutionary equilibrium,~~
437 ~~cooperation has a strictly positive net benefit. What is more, when choosiness is plastic cooperation~~
438 ~~never rises above the socially optimal level. As the efficiency of partner choice (that is, market~~
439 ~~fluidity) increases, the level of cooperation at evolutionary stability increases but, at most, it~~
440 ~~reaches the socially optimal level and never more (Fig. 4). In particular, when partner choice is~~
441 ~~large (partner change has a small cost), very efficient,~~ cooperation evolves precisely towards the
442 socially optimal level, i.e. the level that maximizes the net total payoff of individuals ($\hat{x} = 1/2c$).

443

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

452

453 **4. Discussion**

454 Most theoretical works on the evolution of cooperation by partner choice aim at explaining how
455 *some* cooperation can be evolutionarily stable. They do not aim at understanding which specific
456 quantitative *level* of cooperation should evolve. In this paper, we have raised this second question
457 and. We have considered a model where cooperation has diminishing returns, such that the most
458 efficient level of cooperation (the level that maximises social welfare) is intermediate. We have
459 investigated whether partner choice can account for the evolution of an ~~intermediate and~~ efficient
460 level of cooperation in this case. In this aim, we have modelled, both numerically and with
461 individual-based simulations, the joint evolution of two traits: cooperation, the effort invested into
462 helping others, and choosiness, the minimal level of cooperation that an individual is willing to
463 accept in a partner.

464

465 In a first model, we have found that the mechanism of partner choice ~~seems to be an unlikely~~
466 ~~explanation for the evolution of an efficient level of cooperation. entails no systematic force~~
467 ~~favouring an efficient level of cooperation. On the contrary, when partner choice is effective~~
468 ~~enough, the level of cooperation increases evolutionarily toward very large values, beyond the~~
469 ~~socially optimal level. In the extreme, when partner choice is very effective, cooperation even~~
470 ~~increases up to a level where its cost entirely cancels out its benefit. That is, at evolutionary~~
471 ~~equilibrium, individuals gain the same payoff than if they had not cooperated at all.~~

472
473 To understand intuitively, consider a population with a given distribution of cooperation levels,
474 with some particularly generous individuals, some particularly stingy individuals, and a given
475 mean cooperation level. In such a population, provided that the variability of cooperation is
476 sufficiently large and the market sufficiently fluid, it is always adaptive to accept only partners that
477 are slightly better than average (McNamara et al. 2008). Hence, natural selection favours
478 individuals with a choosiness always slightly larger than the average cooperation level. In turn, this
479 choosiness selects for mutants whose cooperation level is larger than the mean, which leads to a
480 gradual increase in cooperation. ~~This runaway process drives cooperation up to the point where~~
481 ~~interactions become totally profitless because the cost of cooperation entirely cancels out its~~
482 ~~benefits (Figs. 1 and 2). Thus, partner choice prompts~~Importantly, this runaway process has no
483 particular reason to stop when cooperation is maximally efficient. Rather, it stops when the cost of
484 searching for more generous individuals exceeds the benefit of interacting with them (Fig. 2). As
485 long as partner choice is effective (i.e. the cost of searching is low), it is always worth trying to
486 find a better than average partner, irrespective of whether the current mean level of cooperation is
487 below or beyond the socially optimal level. Hence, partner choice can prompt individuals to invest
488 into counterproductive forms of cooperation to outbid others, leading to an eventually fruitless

489 arms race. ~~For low values of phenotypic variability and market fluidity, still, our model predicts~~
490 ~~that cooperation can reach levels where the social payoff is positive because the runaway process~~
491 ~~stops before it reaches the wasteful threshold (Fig. 2). Nevertheless, there is no evolutionary~~
492 ~~pressure driving cooperation specifically towards the socially optimal level.~~

493

494 In a second approach, in line with matching models from the economic literature, we have designed
495 a model in which choosiness is implemented as a reaction norm to the individual's own cooperation
496 level (see Section 2.3), the shape of which evolves by natural selection. In this case, both our
497 analytical model and complementary individual-based simulations show that the evolutionarily
498 stable reaction norm is a monotonously increasing function of cooperation (Fig. 3). This implies
499 that more generous individuals are also choosier, leading to a positive assortative matching:
500 generous individuals tend to interact with other generous individuals, and vice versa. Furthermore,
501 if the biological market is fluid enough (i.e. if the cost of changing partner is low), this positive
502 assortative matching becomes very close to a perfect matching in which individuals with a given
503 level of cooperation always interact with other individuals with the exact same level (Fig. 3a and
504 b).

505

506 In this case, and in sharp contrast with the model in which choosiness is a hard-wired trait,
507 cooperation does not reach the counterproductive level where its cost cancels out its benefit when
508 partner choice is very cheap (Fig. 4). More precisely, when the market is very fluid, the
509 evolutionarily stable cooperation becomes very close to the social optimum, i.e. the amount of
510 cooperation that maximizes the sum of the partners' payoffs. This can also be understood
511 intuitively. Because of the strict assortment between cooperative types, individuals with a given
512 cooperation level interact with other individuals with the exact same level. Hence, pairs of

513 individuals become the effective units of selection, like if interactions occurred among genetic
514 clones (Eshel and Cavalli-Sforza 1982; Wilson and Dugatkin 1997; Aktipis 2004; Akçay and Van
515 Cleve 2012). Consequently, the socially optimal level of cooperation is favoured.

516
517 Hence, the fruitless runaway of cooperation that occurs in a model with hard-wired choosiness is
518 a consequence of the assumption that individuals cannot optimally adapt their degree of choosiness
519 to local circumstances. If individuals are allowed to behave optimally, which entails in the present
520 case to adapt plastically their choosiness to their own generosity, then partner choice looks less
521 like a competition to outbid others, and more like a competition to form efficient partnerships with
522 others, which leads to a very different outcome regarding the net benefits of cooperation.

523
524 Wilson and Dugatkin (1997) already discussed the consequences of assortative matching for the
525 evolution of socially efficient levels of cooperation. However, they did not explicitly model a
526 partner choice strategy, let alone the evolution of this strategy, but merely assumed that assortment
527 occurs in one way or another. In contrast, here, we have studied the joint evolution of choosiness
528 and cooperation, showing how a positive assortative matching can emerge from a simple partner
529 choice mechanism.

530
531 In another related work, using individual-based simulations McNamara et al. (2008) also observed
532 a form of assortative matching in the joint evolution of cooperation and choosiness. ~~The~~
533 differenceOne of the main differences with the present approach, however, is that they assumed
534 that the variability of cooperation is maintained at the genetic level, via a high mutation rate, rather
535 than at the phenotypic level. Under this assumption, negative selection on inefficient mutants
536 (either too choosy or too generous) generates linkage disequilibrium between cooperation and

537 choosiness, resulting in a positive assortative matching. For this reason, their work is more similar
538 to our second model where choosiness is plastic than to our first model where choosiness is hard-
539 wired. In McNamara et al. (2008)'s simulations, however, in contrast with our results, cooperation
540 never reaches the socially optimal level (in the model where they consider a payoff function with
541 diminishing returns). In a complementary analysis (see SI), we showed that this iscould be a
542 consequence of their assumption that the genetic mutation rate is very high, which prevents natural
543 selection from fully optimizing social strategies.

544

545 Some scholars have already imported principles from matching theory into evolutionary biology,
546 especially in the field of sexual selection. Johnstone et al. (1996) and Bergstrom and Real (2000)
547 have used matching models, respectively with and without search frictions, to shed light on mutual
548 mate choice. Both works focused on the evolution of choosiness with a given, fixed distribution of
549 individual's quality. As we have previously shown, the intensity of assortment may have a dramatic
550 impact on the evolution of the chosen trait (cooperation, in our case). For instance, further models
551 could investigate the precise limits of the runaway processes that occur on weaponry, or on
552 ornamental traits, in sexual selection. More generally, matching models could be helpful to analyse
553 a large variety of biological markets (Noë and Hammerstein 1994, 1995; Hammerstein and Noë
554 2016), including inter-specific mutualisms, such as mycorrhizal symbiosis or plant-rhizobia
555 relationships (Simms and Taylor 2002; Kiers et al. 2003, 2011).

556

557 As for the human case in particular, several lines of evidence suggest that partner choice is a likely
558 candidate as a key driving force in the evolution of cooperation. Numerous experimental studies
559 have shown that human beings indeed do choose their social partners in function of their
560 cooperative reputation (Barclay and Willer 2007; Sylwester and Roberts 2010, 2013; Barclay 2013,

561 2016; Baumard et al. 2013; Raihani and Smith 2015; Barclay and Raihani 2016; Efferson et al.
562 2016; Stovel and Chiang 2016; Wu et al. 2016). Anthropological observations show that defection
563 in traditional societies is mostly met with a passive abandon rather than with more defection in
564 return (see Baumard et al. 2013 for a review). Also, several theoretical studies have shown that
565 partner choice can account for the evolution of other important properties of human cooperation,
566 such as the fact that its benefits are often shared in proportion to everyone's respective effort in
567 producing them (Chiang 2008; André and Baumard 2011*a*, 2011*b*; Debove et al. 2015*a*, 2015*b*,
568 2017; Takesue 2017).

569
570 Regarding the quantitative level of cooperation, observations show that humans have precise
571 preferences regarding the amount of effort that shall be put into helping others. Daily life contains
572 ample examples of these preferences. For instance, we hold the door for others in subway stations,
573 but only when they are sufficiently close to the door already, not when they are very far from it.
574 And this is true quite generally. As experiments in real settings demonstrate, we have preferences
575 for specific amounts of cooperation, neither too little, nor too much (Santamaria and Rosenbaum
576 2011; Lange and Eggert 2015). Sometimes this preference is expressed in a purely quantitative
577 manner. At other times, the same preference is expressed in a more qualitative way, determining
578 the kinds of cooperative action that we are willing, or unwilling, to perform. In any case, our
579 investment in helping is quantitatively bounded. Moreover, the precise level of effort we are willing
580 to put in cooperation seems to be constrained by considerations of social efficiency. Individuals
581 help one another only when it is mutually advantageous, that is when the cost of helping is less
582 than the benefit of being helped. Additionally, recent evolutionary modellings of risk pooling have
583 revealed the socially optimal nature of helping behaviours (Cronk 2007; Aktipis et al. 2011, 2016;

584 Campenni and Schino 2014; Hao et al. 2015). They have shown that people's systems of mutual
585 help correspond to the most efficient systems of risk pooling in a volatile environment.

586
587 In this paper, we have shown that partner choice can foster the evolution of such an intermediate
588 and efficient amount of cooperation, neither too little nor too much. But we have also shown that
589 the precise evolutionarily stable amount of cooperation should depend on the fluidity of the
590 biological market, and can range from a very low level of cooperation, up to the socially optimal
591 level (Fig. 4). A number of anthropological studies suggest that contemporary hunter-gatherer
592 societies exhibit high levels of spatial mobility (Baumard et al. 2013; Lewis et al. 2014). Therefore,
593 it seems plausible that biological markets were highly fluid in the social structure that our ancestors
594 experienced. Our model predicts that, in this case, the amount of effort invested into cooperation
595 should become very close to the social optimum. Therefore, partner choice can account for the
596 evolution of human preferences concerning social efficiency.

597
598 One could wonder, however, whether other models than partner choice could account for the
599 evolution of a socially optimal level of cooperation as well. The most influential model on the
600 evolution of quantitative cooperation among non-kin is the continuous version of the iterated
601 prisoner's dilemma (Roberts and Sherratt 1998; Wahl and Nowak 1999*a*, 1999*b*; Killingback and
602 Doebeli 2002; Lehmann and Keller 2006; André and Day 2007; André 2015). In this game, André
603 and Day (2007) have shown that the only evolutionarily stable level of investment is the one that
604 maximises the total benefit of the interaction, i.e. that natural selection does eventually favour the
605 socially optimal amount of cooperation (see also Binmore 1990; Fudenberg and Maskin 1990;
606 Robson 1990 and Binmore and Samuelson 1992 in a discrete version of the iterated prisoner's
607 dilemma). Yet, in this approach, selection for efficient cooperation is only a second-order force,

608 which plays a significant role only because André and Day (2007) assumed the absence of other
609 first-order effects. For instance, a slight cognitive cost of conditional behaviour would have
610 prevented the evolution of efficient cooperation in their model. In another related study, Akçay and
611 Van Cleve (2012) have shown that socially optimal cooperation is favoured when individuals play
612 a specific class of behavioural responses to others' cooperative actions. They have also shown that,
613 for a specific case of their model, ~~a moderate level of genetic~~ these behavioural responses can
614 evolve by natural selection under low levels of relatedness ~~can favour the evolution of the socially~~
615 ~~optimal amount of cooperation by first-order selective effects in the continuous prisoner's~~
616 ~~dilemma. In contrast~~ Here, we have shown that, under the effect of partner choice, efficient
617 cooperation is favoured by first-order selective effects even in the total absence of genetic
618 relatedness. This occurs because, unlike reciprocity, partner choice is a *directional* enforcement
619 mechanism. Whereas reciprocity merely stabilizes any given level of cooperation (a principle
620 called the folk theorem, see Aumann and Shapley 1994; Boyd 2006), partner choice directionally
621 favours the most efficient level.

622

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

631

632

633 **Acknowledgements**

634 This work was supported by ANR-10-LABX-0087 IEC and ANR-10-IDEX-0001-02 PSL. This is
635 contribution 2018-XXX of the Institut des Sciences de l'Evolution de Montpellier (UMR CNRS
636 5554). We thank the Recommender, Erol Akçay, and two anonymous reviewers for very helpful
637 comments on previous versions of this paper.

638

639

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853 **Tables**

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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
$\Pi(x_i, x_j)$	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

856

Figures

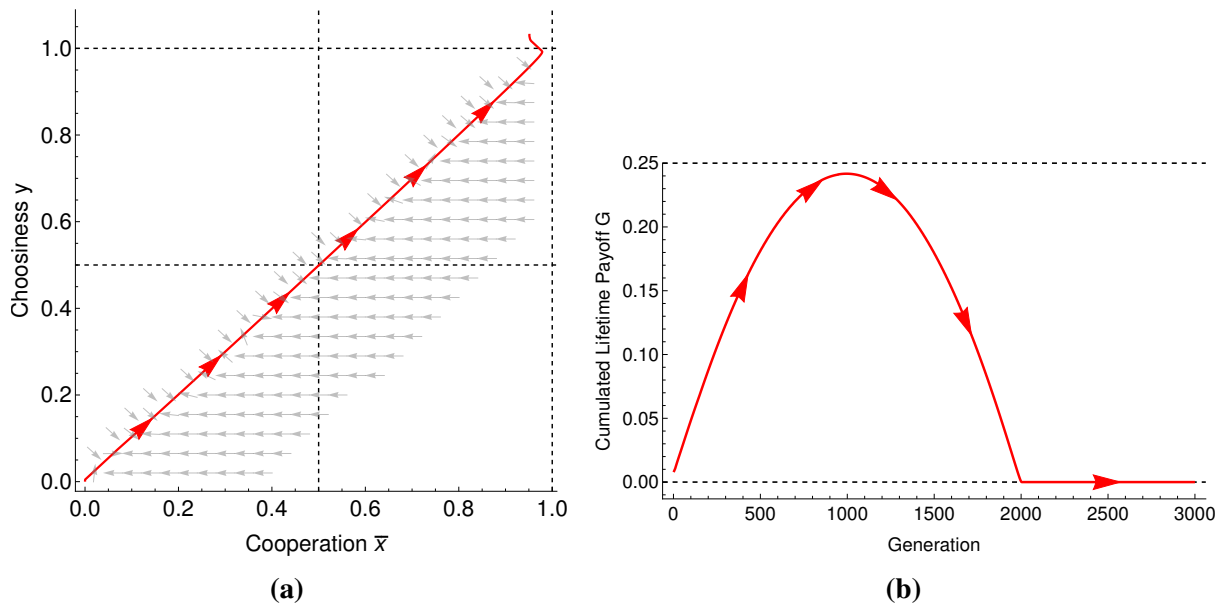
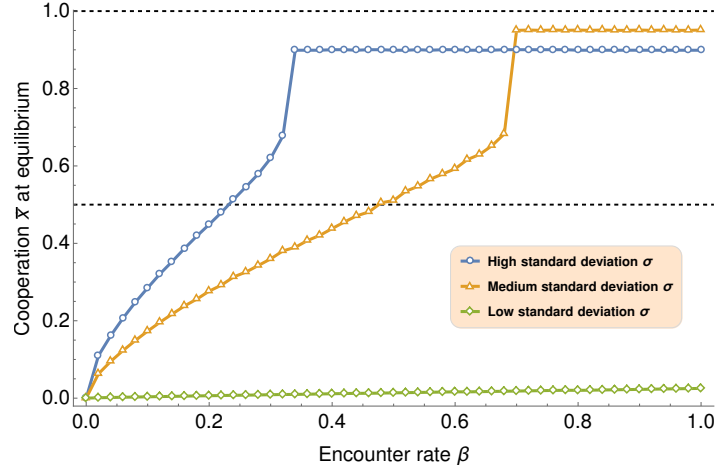
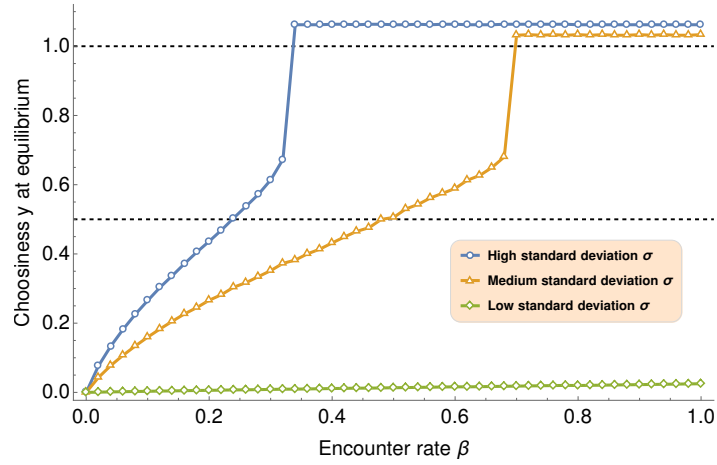


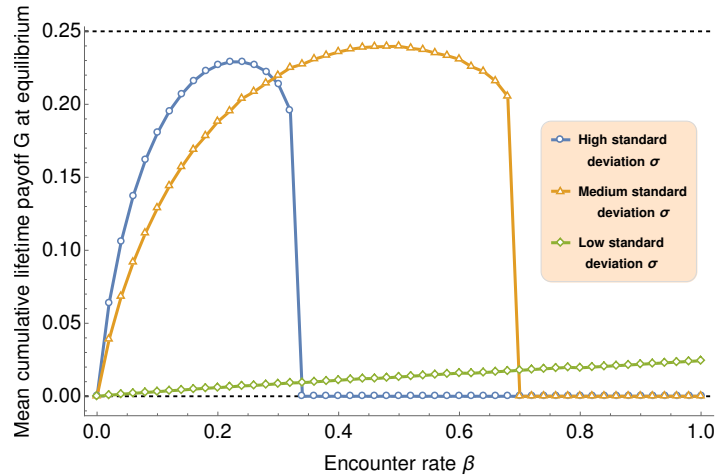
Figure 1. Analytical and numerical results with hard-wired choosiness. (a) The grey arrows show the vector field of the selection gradient on both cooperation and choosiness. The red arrows show an evolutionary trajectory starting from an initial selfish population $(\bar{x}, y) = (0, 0)$. (b) The red arrow shows the corresponding evolution of the cumulative lifetime payoff G for a resident individual. Parameters are $c = 1$; $\sigma = 0.025$; $\beta = 1$; $\tau = 0.01$. 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 with hard-wired choosiness. Equilibrium values are shown for (a) cooperation, (b) choosiness and (c) cumulative lifetime payoff as a function of the encounter rate β to manipulate the market fluidity, and for three values of the standard deviation $\sigma = 0.0001; 0.01; 0.02$ respectively for low, medium and high phenotypic variability. Other parameters are the same as in Fig. 1

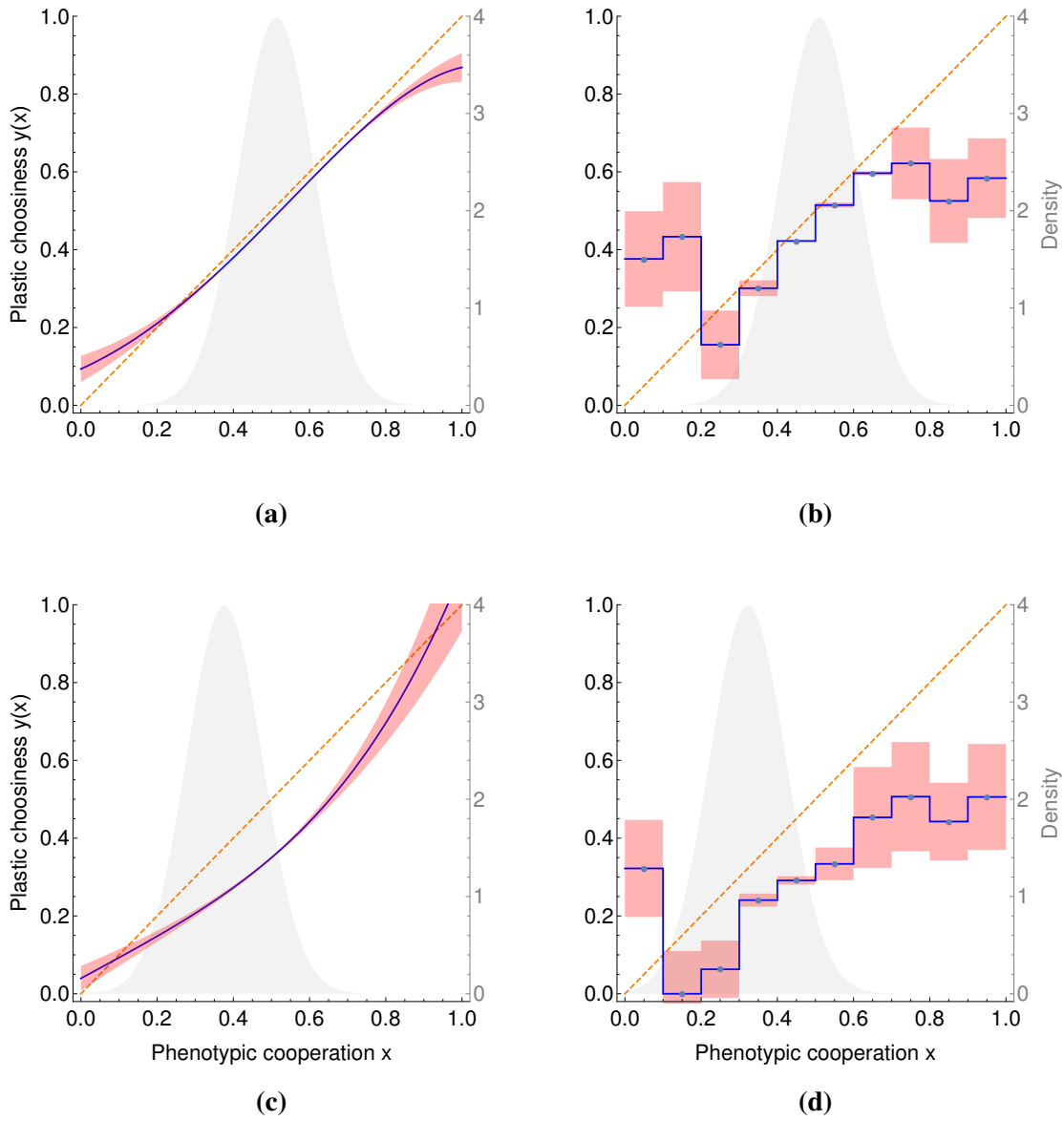


Figure 3. Plastic choosiness at the equilibrium. The equilibrium reaction norms over 30 simulations are shown in blue, and the corresponding 99% confident intervals are shown in red with **(a-b)** high market fluidity $\beta = 1$, **(c-d)** low market fluidity $\beta = 0.01$, **(a-c)** a polynomial reaction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

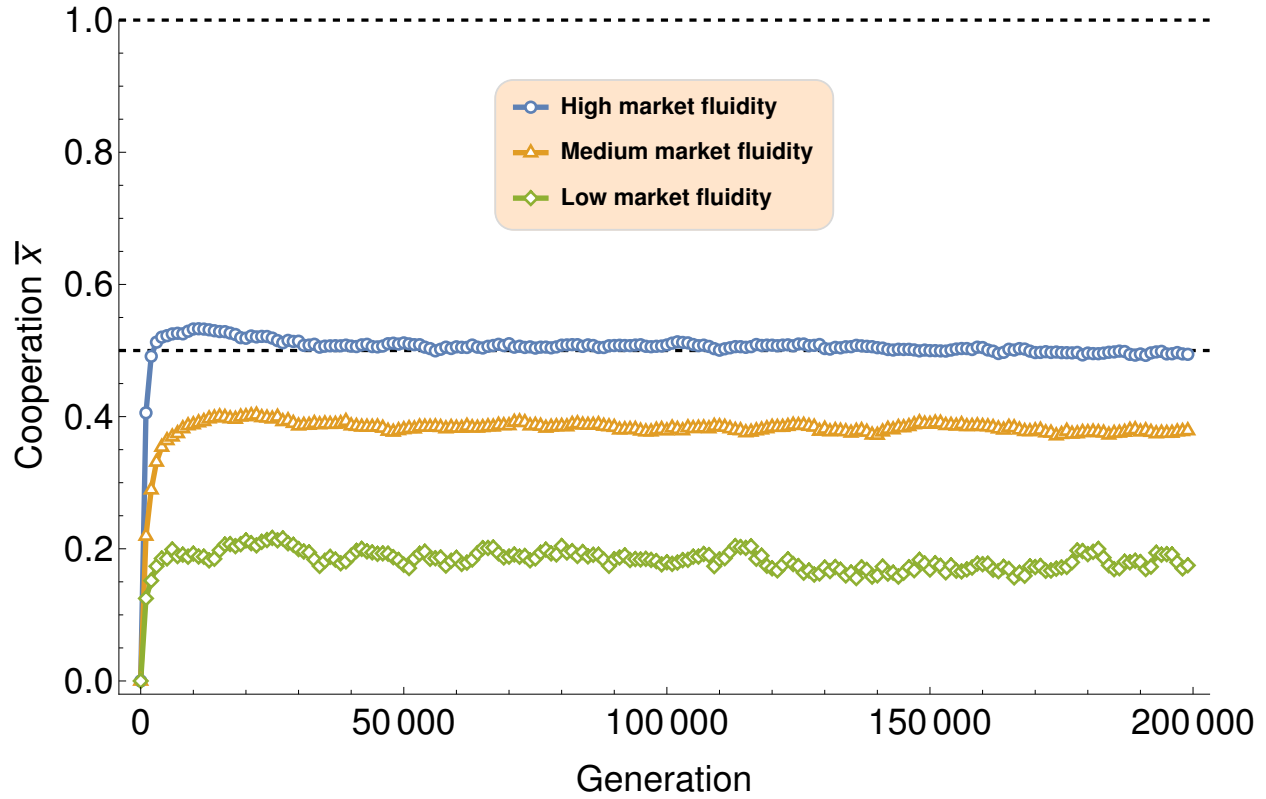


Figure 4. Evolution of cooperation for a polynomial reaction norm. The average cooperation over 30 simulations is shown for three values for the encounter rate $\beta = 0.001; 0.01; 0.1$ respectively for low, medium and high market fluidity. Other parameters are the same as in Fig. 3. The socially optimal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