

Group formation and the evolution of sociality

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Abstract

In spite of its intrinsic evolutionary instability, altruistic behavior in social groups is widespread in nature, spanning from organisms endowed with complex cognitive abilities to microbial populations. In this study, we show that if social individuals have an enhanced tendency to form groups and fitness increases with group cohesion, sociality can evolve and be maintained in the absence of strong assortative mechanisms such as kinship or mutual recognition. When explicitly taken into account in a game-theoretical framework, the process of group formation qualitatively changes the evolutionary dynamics with respect to games played in groups of constant size. The evolutionary consequences of the rules underpinning the group size distribution are discussed for a simple model of microbial aggregation by differential attachment, indicating a way to the evolution of sociality under minimal hypotheses on reciprocal recognition.

1 **Keywords:** social dilemma; public goods games; evolution of altruism; group
2 size; assortative mechanisms

3 **1 Introduction**

4 The emergence and persistence of social ventures, where individuals concur to the
5 sustainment of a community at the cost of a personal investment, has been clas-
6 sically addressed in a game-theoretical framework. The evolution of cooperation
7 has been first formalized in the context of dyadic interactions, where the formation
8 of pairs and the accomplishment of the game are concomitant. When individuals
9 play in couple, several mechanisms have been shown to effectively promote co-
10 operation even for a Prisoner's Dilemma type of interactions, where it is always
11 in one own's interest to defect in a single round of the game. Cooperation may be
12 maintained if interacting individuals are genetically related (Hamilton, 1964) or if
13 a sufficient assortment between carriers of the cooperative gene is ensured, for in-
14 stance via the knowledge of the co-player's past behavior (Trivers, 1971; Axelrod
15 and Hamilton, 1981) or reputation (Nowak and Sigmund, 1998).

16 Those results have then been extended to games involving a number N of play-
17 ers, where the Public Goods Game plays the same prototypic role as the Prisoner's
18 Dilemma (Kollock, 1998). The PGG formalizes the so-called tragedy of the com-
19 mons (Hardin, 1968; Rankin et al., 2007), whereby cheaters who do not contribute
20 to the public goods are always better off, in a one-shot game, than cooperators that
21 pay a cost to sustain the collective enterprise.

22 Sociality, however, relates not only to the act of helping others, but also af-
23 fects the context where social games are played, among which the way groups
24 are formed in the first place. In extending the framework from two players to N -
25 players games, the processes that lead to group formation have often been over-
26 looked in holding the group size constant.

27 This assumption has been recently relaxed in different ways. Group size
28 variations can be externally forced by imposing bottlenecks that periodically in-
29 crease the variance among groups (Chuang et al., 2009), leading to a 'Simpson's
30 paradox' in which cooperation is disadvantaged locally but a winning strategy
31 on the whole (Wilson, 1975). They can also result from demographic fluctua-
32 tions (Hauert et al., 2006a) or facultative participation to the game (Hauert et al.,
33 2002a,b). The effect of a fixed group size distribution with binomial allocation
34 of individuals within groups has also been investigated in various types of games
35 and can either promote or hinder cooperation (Peña, 2011).

36 Group size can be directly affected by traits that co-evolve with cooperation.
37 Pfeiffer and Bonhoeffer (2003) illustrated how group clustering (defined in terms
38 of spatial proximity) is selected together with non-exploiting, cooperative behav-
39 ior if resources are sufficiently concentrated. Avilés et al. (Avilés, 2002; van Vee-
40 len et al., 2010) showed that grouping tendency and cooperativeness co-evolve in
41 the emergence of sizable and cooperative groups. This result relies on two fea-
42 tures of the model: on the one hand, while cooperation is costly, the ability to
43 join groups is not ; thus, as soon as some cooperators are present in the popula-
44 tion, individuals are better off in a group than alone, making the lonely lifestyle

45 unprofitable and the 'dispersed' population structure unstable. On the other hand,
46 the introduction of a hump-shaped fitness function implies from the start the exist-
47 tence of intermediate 'optimal' group sizes, at fixed average level of cooperation
48 within the group. The cheating load is then twofold: 'freeloaders' both hamper the
49 benefits retrieved from the group and crowd them uselessly. Powers et al. (2011)
50 similarly evidenced that inheritable aggregative features may evolve jointly with
51 cooperation. They let players have a clear-cut group size preference, whereby
52 groups form by gathering individuals sharing the same preference. In their model,
53 cooperation ends up being tightly linked with small group sizes that support it
54 more easily, even when direct selection pressures for large groups or weaker se-
55 lection against cooperation is applied.

56 In line with these studies, we address here the evolution of aggregative traits in
57 a context that is dynamically shaped by the traits themselves. Such traits require
58 an individual investment and produce collective benefits, and can therefore be re-
59 garded as a cooperative strategy once individuals have been distributed in groups
60 by the aggregation process. The quest for simple mechanisms allowing grouping
61 to evolve is of particular relevance to understand how sociality can be maintained
62 in microorganisms, where individuals interact in clusters of many individuals, a
63 setting that is recognized as unfavorable to social ventures. We assume that indi-
64 viduals have different tendencies to form cohesive aggregates, and that group co-
65 hesion itself is a common good. In our model, individuals are thus endowed with
66 a unique gene that codes for a costly trait (coined hereafter 'sociality'). The social
67 trait promotes aggregative cohesion during both the group formation process and

68 the reproductive stage, where the fitness is the individual payoff in a PGG. The
69 outcome of the social interaction is hence considered to hinge upon the physical
70 properties of the groups: more cohesive groups are fitter than groups fragilized by
71 looser attachment of the individuals they are composed of. This setting is relevant
72 at least for several microbial organisms usually taken as examples of primitive
73 social behavior (Crespi, 2001; West et al., 2006; Smukalla et al., 2008; Nanjudiah
74 and Sathe, 2011), where physical stickiness is coupled to cooperative behavior
75 once aggregates are formed.

76 To evolve, an altruistic trait must ultimately entail some kind of assortment be-
77 tween its bearers (Fletcher and Doebeli, 2009). When the gene giving rise to such
78 assortment also codes for cooperative behavior, they are framed under the term of
79 greenbeards (Gardner and West, 2010). This general definition actually brings
80 together very different mechanisms able to generate assortment, including direct
81 recognition of others' traits and segregation in response to environmental features.
82 Here, we will consider an instance of the latter, where assortment is an emergent
83 property of the interactions among individual players. The environment is in this
84 case shaped by the group formation process and therefore changes jointly with
85 the frequency of the social strategy. We present a model showing that the rise of
86 sociality can stem from merely quantitative differences in the probabilities of at-
87 tachment, so that even mechanisms that do not produce assortment within groups
88 of fixed size can lead to the evolution of sociality if group sizes are distributed.

89 In section 2, we describe the evolutionary consequences of group formation
90 schemes where social and asocial individuals differ quantitatively in their ability

91 to aggregate. Group formation is considered a 'black box' generating the group
92 size distributions experienced by players. The average fitness advantage of so-
93 cial players is related to the distribution of group sizes players of each strategy
94 belong to. We derive the condition for sociality to outcompete asociality under
95 the assumption that no nepotistic grouping between social individuals generates
96 assortment a priori. In section 3, we apply the results of section 2 to a toy model
97 based on differential attachment and show that full sociality in a population can be
98 attained, along with sizeable average group sizes, as soon as a threshold frequency
99 of socials is overcome. We also stress the role of lonely individuals, usually ne-
100 glected when fixed group sizes are considered, in the balance of benefits and costs
101 of the social game. We eventually point out that our mechanism does not condemn
102 large social groups, and may thus be relevant to account for sociality in microor-
103 ganisms. Different interaction rules leading to non-zero a priori assortment are
104 briefly addressed by numerical simulation. In section 4, we discuss the implica-
105 tions of our results for biological systems and the perspectives in elucidating the
106 mechanistic basis of group formation processes.

107 **2 Rooting payoffs in the group formation process**

108 In this work, we want to address the emergence and maintainance of social be-
109 havior in organisms whose life cycle consists of a phase of aggregation, a phase
110 of differential reproduction that modifies the frequencies of each type in the fol-
111 lowing generation, and a dispersal phase (see Fig. 1). This requires resolving a

112 process, group formation, that happens on a time scale much faster than evolu-
113 tionary changes. Our working assumption is that sociality consists primarily in a
114 quantitative difference in the ability to aggregate, that affects both the group for-
115 mation phase and the competitive success of aggregates. Once groups are formed,
116 their cohesion constitutes a public good, so that fitter groups are those comprising
117 a larger fraction of cohesive individuals.

118 We assume that individuals are either social or asocial, these two strategies
119 being genetically encoded. A social individual pays a cost c for being more
120 aggregation-prone. Asocial individuals do not pay this cost and have a lower
121 probability of aggregating. After group formation has occurred, both social and
122 asocial players can be found inside a group or can remain alone. For the sake of
123 generality, we do not explicit the grouping process, but characterize it by its out-
124 come: the distributions $d_s(n)$ and $d_a(n)$ ($n \in \mathbb{N}^*$) of group sizes in which social
125 (resp. asocial) individuals are found. During group formation, assortment may be
126 generated within groups. For instance, processes leading to positive within-group
127 assortment of social individuals may rely on preferential interactions (Wilson and
128 Dugatkin, 1997), or on a probability to join a group proportional to the number of
129 social players it contains (Avilés, 2002). In this section, we point out that whereas
130 some kind of assortment is necessary for sociality to evolve, no preferentially as-
131 sortative feature needs to be assumed a priori as soon as the group size is not fixed;
132 as such, it is compatible with the scenario where groups form by random and blind
133 interaction processes.

134 Once groups are assembled, social players contribute b to a linear public goods

135 game (PGG), whereas asocial players do not contribute. When found within a
136 group of size n with m social players, all individuals thus gain bm/n irrespective
137 of their strategy. Different choices of the gain function (notably accounting for
138 discount or synergy, as in Hauert et al. (2006b); Archetti and Scheuring (2010))
139 are possible, but we opt here for the standard linear formulation, so as to focus
140 only on the nonlinearities generated by the aggregation process. In particular,
141 we stress that this formulation does not impose an *a priori* preference for a given
142 group size, since the payoff only depends on the proportion and not on the absolute
143 number of social players. We refer to Avilés (2002) for a model where the payoff
144 is maximal at intermediate group sizes.

145 We now focus on the aggregation stage, considering that the frequency of
146 strategies does not change during group formation. Let us compute the average
147 payoff of each (social or asocial) strategy in a population where a fraction x of
148 individuals is social and a fraction $(1-x)$ is asocial. After the aggregation process,
149 social and asocial players belong to groups of variable sizes. A PGG is played
150 within each group, and the resulting average payoffs for both types conditions the
151 evolution of their frequencies at the next generation.

152 We first consider groups of size n ($n \geq 2$). Following Fletcher and Doebeli
153 (2009), we split the payoff of each player in a part due to self and an other due to
154 the interaction environment, that depends only on the composition of the group.
155 The payoff due to self is $b/n - c$ for a social player, who pays a cost $-c$ for
156 sociality and gets a share b/n of its own contribution to the common goods; for
157 an asocial player, who does not contribute to the PGG, it is 0.

158 For a linear PGG, the payoff due to the interaction environment is proportional
 159 to the average number $e_s(n)$ (resp. $e_a(n)$) of social individuals among the $n - 1$
 160 coplayers of a social (resp. asocial) player, so that the average payoffs of social
 161 individuals in a group of size n is:

$$P_s(n) = \frac{b}{n} e_s(n) + \frac{b}{n} - c \quad (1)$$

162 and for asocial ones:

$$P_a(n) = \frac{b}{n} e_a(n) \quad (2)$$

163 Considering all possible group sizes, the payoff for social and asocial indi-
 164 viduals is obtained as an averaged sum of these payoffs, weighted by the group
 165 size distributions $d_s(n)$ and $d_a(n)$. In doing this, one has to consider separately
 166 the contribution of lonely individuals, who do not engage in a PGG, and whose
 167 payoffs are $-c$ for socials and 0 for asocials.

168 Since evolutionary consequences are measured in terms of relative advantages,
 169 we only display here the difference in the average payoff of social and asocial
 170 individuals:

$$\begin{aligned} \Delta P(x) &= -c d_s(1) + \sum_{n \geq 2} [d_s(n) P_s(n) - d_a(n) P_a(n)] \\ &= -c + \sum_{n \geq 2} \frac{b d_s(n)}{n} + \sum_{n \geq 2} \frac{b}{n} [d_s(n) e_s(n) - d_a(n) e_a(n)] \quad (3) \end{aligned}$$

171 This formula is composed of three terms: the cost to the individual for its in-

172 vestment in a social action, which is payed also when the social player remains
173 alone; the marginal gain for being social, averaged over groups of all sizes; and a
174 third term combining the effect of within-group assortment to that of differential
175 allocation in groups. While the second term necessarily declines when groups of
176 larger size form in the population, the third term allows for different repartitions
177 between groups (d_s and d_a) to compensate for unfavorable average interaction
178 environment within groups of a given size. This compensatory effect may in prin-
179 ciple even overcome negative within-group assortment (i.e. $e_a(n) > e_s(n)$).

180 The “interaction neighborhoods” $e_s(n)$ and $e_a(n)$ are in general different, e.g.
181 if assortative mechanisms such as peer or group recognition are involved in the
182 process of group formation. In these cases, the local environment of a social player
183 is enriched in social players compared to that of an asocial one ($e_s(n) > e_a(n)$).
184 When only one group size is present in the population, from eq. 3 one immedi-
185 ately retrieves the condition for the evolution of sociality found in (Fletcher and
186 Doebeli, 2009). If group formation is governed by an extreme recognition process
187 leading socials to form groups only with their kind ($e_s(n) = n - 1$ and $e_a(n) = 0$
188 for all n), the condition $\Delta P(x) > 0$ reduces to $b/c > 1/(1 - d_s(1))$. This can be
189 as small as 1 if all social individuals end up in a group, thus yielding the necessary
190 assumption for sociality to possibly evolve.

191 When groups of different size are present, sociality can however thrive even in
192 the absence of such within-group assortment, i.e. when $e_s(n) = e_a(n)$ for all $n \geq$
193 2. In this case of random within-group repartition, the interaction neighborhoods

194 are equal:

$$e_s(n) = e_a(n) = (n - 1) p(s|n) \quad (4)$$

195 with $p(s|n)$ the fraction of social players within groups of size n . Given the dis-
196 tributions $d_s(n)$ and $d_a(n)$, this fraction is:

$$p(s|n) = \frac{d_s(n) x}{d_s(n) x + d_a(n) (1 - x)}. \quad (5)$$

197 In this case, eqs. 3, 4 and 5 thus yield:

$$\Delta P(x) = -c + \sum_{n=2}^{+\infty} \frac{b}{n} \left[(n - 1) \frac{(d_s(n) - d_a(n))x}{(d_s(n) - d_a(n))x + d_a(n)} + 1 \right] d_s(n) \quad (6)$$

198 We have explicitated the dependence of the payoff difference upon the fraction
199 x of social players to remind that the population composition and the aggregation
200 rules, which together determine the distributions d_s and d_a , are held fixed during
201 group formation.

202 The fraction of social players will increase in the next generation whenever
203 $\Delta P(x)$ is positive, and the evolutionary equilibria x_{eq} of the system are those
204 such that $\Delta P(x_{eq}) = 0$. As exemplified by a toy model in the next section,
205 sociality may be favored as soon as the distributions $d_a(n)$ and $d_s(n)$ seen by the
206 two strategies differ sufficiently. In the following, we will consider that selection
207 is weak enough to guarantee a small change in frequencies from one generation to
208 the next. The evolutionary dynamics is in this case approximated by a continuous-

209 time replicator equation (Taylor and Jonker, 1978; Schuster and Sigmund, 1983):

$$\dot{x} = x(1-x)\Delta P(x), \quad (7)$$

210 where the aggregation phase occurs infinitely fast with respect to evolutionary
211 changes. If the time-scales of aggregation and evolution were not separated, the
212 evolutionary dynamics would be more correctly described by a discrete-time repli-
213 cator equation that displays a potentially much more complex behavior (Villone
214 et al., 2011).

215 In the next section, we illustrate our conclusions through a toy model with an
216 explicit mechanism of aggregation underpinning different group size distributions
217 for the two strategies. This mechanism is chosen such that it creates no within-
218 group assortment. We can thus apply the equations derived in this section to study
219 the evolutionary dynamics of the social strategy along with that of the group size
220 distributions.

221 **3 Group formation by differential attachment**

222 In this section we apply the results of section 2 to an illustrative model where
223 group formation is based on simple hypotheses regarding individual interactions.
224 We show that the evolution of social behavior can be produced by an increase in
225 individual 'stickiness', and clarify the mechanism giving rise to assortment at the
226 population level even in the absence of peer recognition. A social individual pro-

227 duces a costly 'glue' that increases its chances to attach to any individual it comes
228 in contact with. At the same time, he enhances overall group cohesion to a higher
229 extent than an asocial individual more loosely glued to its group. This is consis-
230 tent with our assumption that sociality entails differences both in the process of
231 group formation, and in the contribution to group welfare. The following scheme
232 for group formation is deliberately crude so as to remain analytically tractable and
233 make the conditions for evolution of social attachment explicit. It is nonetheless
234 an example of the evolution of social behavior via a biologically plausible mech-
235 anism of 'blind' interactions among unrelated individuals, where assortment is an
236 emergent property of the group formation process.

237 This model reflects some features of social microbes that are able to produce
238 adhesive proteins at their surface. Although in some cases adhesion proteins are
239 strain-specific and allow to recognize other bearers by direct matching, we can
240 imagine that, in the early stages of social evolution, cells might have been en-
241 dowed with generic adhesion-enhancing properties. In this case, one can regard
242 'stickiness' as an a priori property of a subpopulation of cells, that is energetically
243 costly and entrains higher group-level productivity (e.g. in the search for prey,
244 protection against predators, dispersal efficiency) since aggregates composed of a
245 higher proportion of adhesive cells are more cohesive.

246 This model mirrors the properties of, for instance, social amoebas and bacte-
247 ria. These microbes are thought to possess inheritable social strategies, whereby
248 cells have different propensity to sacrifice for the others, participating to the con-
249 struction of the dead tissues of a fruiting body rather than becoming spores. The

250 success of the genes that are passed on to the following generation is hence de-
251 termined by the composition of the spore pool in all the groups (fruiting bodies)
252 that are formed within the population at the aggregation stage of the life cycle.
253 Enhanced probabilities to end up in the stalk of the mushroom are moreover often
254 found associated to a higher stickiness (Strassmann and Queller, 2011).

255 **3.1 A toy model for differential attachment**

256 We consider an infinite population composed of a fraction x of social and a frac-
257 tion $(1 - x)$ of asocial individuals that differ in their attachment abilities. At each
258 generation, aggregates form from sets of T individuals that are randomly drawn
259 from the population pool. Group formation in each set is nucleated by one indi-
260 vidual, named *recruiter*, that is chosen at random within the set. The remaining
261 $(T - 1)$ individuals are sequentially given one possibility to attach to the recruiter
262 and hence to join the group. This one-shot adhesion step leaves some players
263 outside the groups. Such lonely individuals are commonly observed in microor-
264 ganisms (see for instance Smukalla et al., 2008) and will play a central role in the
265 emergence of sociality in our model. Attachment probabilities are fixed for any
266 couple of strategies: the probability of adhesion between two social individuals (a
267 social individual and an asocial individual; two asocial individuals) is denoted by
268 π_{ss} (resp. π_{as} ; π_{aa}).

269 Social individuals attach more efficiently, so that $\pi_{ss} \geq \pi_{as} \geq \pi_{aa}$. Moreover,
270 we choose these probabilities such that the two strategies have equal expectations
271 on the proportion of socials among the players they attach to. This hypothesis

272 reflects the requirement that interactions are not assortative *a priori*, unlike when
 273 social individuals recognize and select groups that are composed of a larger frac-
 274 tion of social players. For a given composition of the population, the condition for
 275 'blind interaction' reads:

$$\frac{x\pi_{ss}}{x\pi_{ss} + (1-x)\pi_{as}} = \frac{x\pi_{as}}{x\pi_{as} + (1-x)\pi_{aa}}, \quad (8)$$

276 that is verified for every x when:

$$\pi_{as} = \sqrt{\pi_{ss}\pi_{aa}} \quad (9)$$

277 When $\pi_{as} \leq \sqrt{\pi_{ss}\pi_{aa}}$, the expected proportion of social co-players is higher
 278 for social than for asocial individuals, i.e. positive assortment among socials
 279 would occur if the interactions were only pair-wise. On the other hand, $\pi_{as} \geq$
 280 $\sqrt{\pi_{ss}\pi_{aa}}$ would denote prior negative assortment in a dyadic context. In our an-
 281 alytical calculation, we will choose attachment probabilities satisfying eq. 9, but
 282 we will relax this assumption at the end of the section and consider rules of at-
 283 tachment generating non-null prior assortment.

284 **3.2 Group size distributions and payoff difference**

285 In the SI, we analytically derive the size distributions for social and asocial types
 286 given the previously described mechanism for group formation. These distribu-
 287 tions are illustrated in Fig. S1. They are the superposition of a component in $n = 1$

288 (players remaining alone) and of two binomial distributions of respective averages
 289 $T Q_s(x) = T [x\pi_{ss} + (1 - x)\pi_{as}]$ and $T Q_a(x) = T [x\pi_{as} + (1 - x)\pi_{aa}]$. Their
 290 relative weights depend on the social type: social individuals are less often alone
 291 than asocials. Increasing the fraction of social individuals, the two nonsingular
 292 distributions displace towards higher group sizes.

293 Knowing the group size distributions emerging from the aggregation process,
 294 the payoff difference $\Delta P(x)$ can be computed for a given composition of the
 295 population. Figure 2 shows such payoff difference obtained by substituting eqs. 1
 296 and 2 in the SI in eq. 6. $\Delta P(x)$ is displayed for different values of the game
 297 parameters b and c and the aggregation parameters π_{ss} , π_{aa} and T . The advantage
 298 of social over asocial players increases monotonically with x , and is zero at most
 299 at one (unstable) equilibrium x^* .

300 **3.3 Evolutionary dynamics and effect of the parameters**

301 The internal equilibrium x^* exists in a large region of the parameters space. In
 302 this region, the evolutionary dynamics ruled by the replicator equation (eq. 7)
 303 is bistable, with two additional stable monomorphic equilibria of full asociality
 304 $x = 0$ and full sociality $x = 1$. Sociality invades as soon as x is larger than the
 305 threshold value x^* . Once established, full sociality is stable against the invasion
 306 by asocials. This scenario is qualitatively different from the case of one single
 307 group size, where the evolutionary dynamics can only lead to full asociality for
 308 linear PGG.

309 Figure 3 recapitulates the evolutionary dynamics by displaying the threshold

310 frequency x^* for sociality to invade. Figure 3a confirms that sociality evolves more
311 easily the bigger the difference between social and asocial individuals' attachment
312 probabilities. Figure 3b shows that the threshold frequency x^* decreases, as one
313 would expect, as b/c increases. The region where sociality is evolutionary stable is
314 larger than the region where the social behaviour implies direct benefits, i.e. when
315 the marginal gain of a social individual is larger than c (Wilson, 1979; Pepper,
316 2000). We refer to section 2 of the SI for the definition and calculation of the
317 condition that delimits such region where sociality trivially evolves. Figure 3
318 shows that sociality evolves and is maintained in the population for a wide range
319 of nontrivial parameters, that is even when it is an essentially altruistic act.

320 The threshold x^* increases with T , consistently with the common claim that
321 the evolution of altruism is easier in small groups (Olson, 1971). However, when
322 $T \rightarrow +\infty$, it converges to a value $x^* < 1$ (Fig. 2c), meaning that there exist a crit-
323 ical initial frequency of social individuals such that sociality will invade whatever
324 is the maximal group size.

325 The fact that x^* is always positive means that, in general, an infinitesimal ini-
326 tial load of social players, as is generated by extremely rare random mutations, is
327 not sufficient for sociality to evolve in the first place. However, when the threshold
328 is low, numerous mechanisms can lead the frequency of the social strategy over
329 the threshold, e.g. random fluctuations due to finite-size effects, non-infinitesimal
330 mutation rates or incomplete reshuffling from one generation to the next. Numer-
331 ical simulations show that in finite populations subjected to a small mutation rate
332 the evolution of sociality is indeed easier than analytically expected.

333 Figure 4 displays the coupled dynamics of the social strategy and of the group
334 size distributions in a numerical simulation of a large population (see section 3 of
335 the SI for details on the algorithm). Initially, only asocial individuals are present
336 in the population, and the threshold is reached thanks to random mutations. As the
337 frequency of social individuals increases, groups of progressively larger size form
338 and concomitantly the fraction of lonely individuals decreases. The difference
339 between the distributions for social and asocial individuals is enhanced by the fact
340 that the balance between the solo and group components of these distributions is
341 affected in opposite directions by the evolutionary dynamics.

342 When all players are social, a fraction $1 - \pi_{ss}$ of individuals remains alone,
343 while the others belong to groups binomially distributed around an average size
344 $T\pi_{ss}$. Notice that the group size at the social equilibrium is not influenced by
345 the parameters b and c defining the public goods game, but only by parameters
346 determining the group formation process. In particular, the average group size
347 arising in fully social populations linearly depends on the maximal possible group
348 size T . Although higher cooperation levels are believed to occur more easily in
349 small groups, group formation by differential attachment thus does not impose
350 an a priori burden on large groups. This suggests that unsophisticated interaction
351 rules may be relevant in explaining how sociality is maintained in the microbial
352 world, where social aggregates are commonly composed of a large number of
353 cells, e.g. thousands of them in flocculating yeast (Smukalla et al., 2008), or up to
354 10^5 in *D. discoideum* (Tang et al., 2002).

355 **3.4 Other rules for group formation**

356 So far, we have assumed that players undergo blind interactions whereby individ-
357 uals attach, according to their strategies, with probabilities π_{aa} , π_{as} and π_{ss} in geo-
358 metric progression, ensuring no a priori assortment. However, other formulations
359 of the adhesion probability, reflecting different settings of pairwise interactions,
360 can be contemplated, and will in general result in non-random assortment within
361 groups of fixed size. In these cases, eq. 6 does not hold any longer, but the pay-
362 off difference can anyway be numerically computed by repeatedly simulating the
363 aggregation process.

364 Figure 5 displays the difference in payoff between social and asocial players
365 for the two cases where the attachment probabilities take up their extreme values:
366 $\pi_{as} = \pi_{ss}$ and $\pi_{as} = \pi_{aa}$. In these model configurations, it is the asocial (resp.
367 social) coplayer that takes the lead in deciding the outcome of binary interactions.
368 The first rule, where the asocial-social attachment probability is maximal, reduces
369 the threshold for sociality to spread in the population. At the same time, the fully
370 social equilibrium is destabilized: when chances to encounter a social individ-
371 ual are high, sociality becomes a 'wasted investment' and asociality is favored
372 again. The resulting evolutionarily stable equilibrium is polymorphic: the social
373 and asocial strategies coexist. On the contrary, when the social-asocial attachment
374 probability is minimal, the invasion barrier x^* is more difficult to reach compared
375 with null a priori assortment. However, the fact that asocials are more efficiently
376 segregated when the population is largely social, makes the fully social equilib-
377 rium even more stable with respect to larger attachment probabilities. Any other

378 choice for π_{as} such that $\pi_{aa} \leq \pi_{as} \leq \pi_{ss}$ leads to thresholds x^* between those two
379 extremal values. Therefore, the potential for social behavior to become stable in
380 the population is not challenged by the amount of a priori assortment generated
381 by the attachment rules.

382 **4 Discussion**

383 **4.1 Social groups formation and evolution**

384 In this work, we address the coupling between the process of group formation
385 and the evolutionary dynamics of individual 'social' traits that affect both aggre-
386 gation propensity and group cohesion, e.g. cell-to-cell adhesiveness. In addition
387 to entailing a different contribution to group welfare, such traits underpin a dif-
388 ference in expected group size distributions. This difference ultimately generates
389 assortment at the population level even in the absence of preferentially directed
390 interactions based on peer recognition. Rather, we evidence that, whenever the
391 size of groups is not fixed, simple non-assortative rules can still generate average
392 local environments that favor the evolution of sociality even when it is not associ-
393 ated to direct benefits. We have illustrated our claim via a toy model where groups
394 form by blind interactions among individuals with different attachment abilities,
395 stemming for instance from signalling or due to the production of a costly glue.
396 In this deliberately simple setting, we showed that even when attachment rules are
397 indiscriminate toward the strategies of partners (and groups of any size are ran-
398 domly assorted), social individuals fare better than asocials thanks to the distinct

399 allocations of the two type in group of various sizes and in particular to differ-
400 ent chances of ending up alone. The emergent population structure gives rise to
401 a Simpson's paradox where one strategy's advantage is reversed when one goes
402 from the group to the population level. This has already been related to the evolu-
403 tion of cooperation when group size changes in time (Hauert et al., 2006a; Chuang
404 et al., 2009). It is noteworthy that in our toy model there is no intrinsic limitation
405 to the size of the evolutionarily viable groups, contrary to most previous models
406 of N -players games (e.g. Matessi and Jayakar, 1976; Powers et al., 2011). This
407 suggest that sociality in large groups, such as in microbial communities, can be
408 sustained with unsophisticated mechanisms that do not require information trans-
409 fer between partners.

410 **4.2 Aggregative sociality in microorganisms**

411 In the microbial world, the formation of biofilms and their cohesion are reckoned
412 to be beneficial to cells in many respects (Velicer, 2003). In several microor-
413 ganisms, the same costly individual traits that support the stability of groups may
414 enhance the probabilities for cells to be part of them in the first place. Velicer and
415 Yu featured costly 'stickiness' as an adaptive prerequisite in swarming microor-
416 ganisms (Velicer and Yu, 2003). In *D. discoideum*, the production of cell-adhesion
417 molecules required for the aggregation cycle is thought to reduce the chances to
418 become a spore: more adhesive strains are primarily found in the dead tissues of
419 the fruiting body (Ponte et al., 1998; Strassmann and Queller, 2011). Myxobacte-
420 ria form multicellular aggregates as well, that enhance survival by decreasing pre-

421 dation and favoring dispersal (Shimkets, 1986a,b). Both agglutination and social
422 cohesion are mediated in these bacteria by the production of a costly extracellular
423 matrix of fibrils, increasing at the same same time cell adherence and enabling
424 collective gliding (Velicer and Yu, 2003). Mutations that affect a gene located at
425 a single locus impair fibril binding and result in both lower cell-cell adhesion and
426 cohesion of aggregates (Shimkets, 1986b). In *S. cerevisiae*, an adhesion protein
427 expressed by a social gene (FLO1) prompts individuals to form flocs that pro-
428 vide them with enhanced resistance to chemical stresses (Smukalla and al., 2008).
429 When this strain is mixed with non-flocculating variants, heterogeneous aggre-
430 gates still contain a majority of FLO1⁺ cells, while individuals outside groups
431 are more often FLO1⁻, thus denoting assortment emerging from mere different
432 adhesive abilities.

433 Although the processes involved in group formation become more complex as
434 the cognitive abilities of players increase, our general conclusions might be also of
435 interest for higher organisms that interact via mechanisms parallel to physical ad-
436 hesiveness. For instance, Dunbar interpreted grooming in monkeys as a behavior
437 likely to provide higher grouping opportunities as well as cement social bond-
438 ing once the group is formed (Dunbar, 1993), and further extended the argument
439 to humans, based on the presumed genetic foundations of language (Pinker and
440 Bloom, 1990). Even if we have focused here on an aggregation mechanism that
441 is more promptly related to social microorganisms, our conclusions hold in general
442 for any inheritable trait, not necessarily involving physical adhesion, that plays a
443 role both in group formation and group cohesion.

444 **4.3 Non-nepotistic greenbeards?**

445 In our model, assortment is generated among carriers of the social gene alone, and
446 does not involve the whole genome. Therefore, sociality here pertains to green-
447 beard mechanisms as termed by the recent classification of Gardner and West
448 (Gardner and West, 2010; West et al., 2007). In their review, the authors stressed
449 that such genes need not code for conspicuous traits as was posited in the origi-
450 nal formulations (Hamilton, 1964; Dawkins, 1976). We argue that assortment at a
451 single locus does not require nepotistic behavior of the gene towards other carriers
452 neither, at least not in the usual sense imposed by dyadic or fixed- N frameworks.
453 Indeed, assortment may mechanistically occur even when social individuals inter-
454 act with each type in the same proportions as asocial individuals, provided they
455 do it more often. A blind increase in the propensity to interact can thus have the
456 same effect as preferentially directed interactions with peer discrimination, that
457 may be more demanding on the cognitive level. This might be of interest for the
458 interpretation of social behavior in organisms where the existence of recognition
459 mechanisms is not straightforward. More in general, it might be useful to disen-
460 tangle more explicitly greenbeard mechanisms that rely on active sorting of inter-
461 action partners from passive, indiscriminate mechanisms generating assortment
462 with weaker requirements (Eshel and Cavalli-Sforza, 1982). Such differentiation
463 would echo and complement that of 'obligate' vs. 'facultative' greenbeards for-
464 mulated in the case of dyadics interactions (Gardner and West, 2010).

465 **4.4 Toward a re-evaluation of the group formation step**

466 We have stressed that the process of group formation can play an essential role in
467 the unfolding of the evolutionary dynamics of social traits. A complete account of
468 the evolution of cooperative groups requires to trace back the entire process lead-
469 ing to their formation. The toy model used here is a useful tool for illustrating our
470 conclusion in a simple and extreme setting. It is however missing many features
471 of actual biological systems. One could instead wish to predict, based on indi-
472 vidual properties of physical attachment, the group size dynamics and the degree
473 and nature of assortment between the social and asocial types in a more realis-
474 tic aggregation model. This requires to further specify the mechanism of group
475 formation, and notably explicit the individual rules of interaction and the topol-
476 ogy structuring individual encounters. For organisms moving on a plane, such as
477 cells gliding on a surface, grouping patterns and the resulting group size distri-
478 butions have been mimicked by models based on simple rules (e.g. Okubo, 1986;
479 Vicsek et al., 1995; Bonabeau et al., 1999). Recently, social games have been
480 implemented in explicit schemes of aggregation for self-propelled particles inter-
481 acting locally with their neighbors (Chen et al., 2011). The way aggregative traits
482 themselves can be sustained in a landscape shaped by a realistic group formation
483 process however is still to be explored. Yet, the propensity to seek interactions,
484 before that of behaving altruistically once the interaction is established, may be
485 the very first, and a prerequisite, of all social actions.

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