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The early evolution of cooperation in humans. On cheating, group identity and group size

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Abstract

The evolution of cooperation is difficult to understand, because cheaters — individuals who profit without cooperating themselves — have a benefit in interaction with cooperators. Cooperation among humans is even more difficult to understand, because cooperation occurs in large groups, making cheating a bigger threat. Restricting cooperation to members of one's own group based on some tag-based recognition of non-group members (allorecognition) has been shown to stabilise cooperation. We address how spatial structure and group size affect the opportunities for cheating such tag-based cooperation in a spatially explicit simulation. We show that increased group diversity, under conditions of limited dispersal, reduces the selective opportunities for cheaters. A small number can already be sufficient to keep cheating at a low frequency. We discuss how marginal additional benefits of increased group size, above the benefits of local cooperation, can provide the selective pressure to reduce the number of group identities and discuss possible examples.

Keywords

altruism, cooperation, allorecognition, cultural inheritance, human evolution, levels of selection, kin selection, reciprocal altruism.

1. Introduction

Humans in all cultures have a tendency to cooperate, although not unlimited, but typically with a subset of the population only. For example, in hunter-gatherer societies, game is shared between individuals, also with individuals that do not hunt themselves (Lewis et al., 2014). Communities tend to take care for sick, wounded, very young and very old people. Also warfare is characterised by cooperation among individuals who risk their lives to help the

1 group to which they belong, in the war against another group. The evolution 1
2 of such cooperative behaviour, i.e., behaviour that benefits other individuals, 2
3 is hard to understand. In a group of cooperators, ‘cheaters’, who do not co- 3
4 operate, but receive the cooperation by other individuals, will experience a 4
5 relative benefit. Cooperation in human societies is even harder to explain, as 5
6 it occurs in large groups. 6

7 Two main explanations have been proposed for the evolution of coopera- 7
8 tion: kin selection or inclusive fitness effects and reciprocal altruism (Hamil- 8
9 ton, 1964a, b; Trivers, 1971; [Axelrod & Dion, 1988](#)). Inclusive fitness effects 9
10 occur through interactions between genetically related individuals. Natural 10
11 selection not only occurs through the effect of a gene on its bearer’s fitness, 11
12 but also through its effect on other individuals carrying copies of that gene. 12
13 This can imply that a gene promoting a cooperative behaviour can be se- 13
14 lected via its positive effect on social partners, even if this behaviour has a 14
15 negative effect on its carrier’s fitness. In most social organisms, cooperation 15
16 occurs among genetically related individuals, and kin selection theory is the 16
17 most widely accepted one to explain the evolution of cooperation. 17

18 The second main category of explanation for the evolution of coopera- 18
19 tion, is for cooperation between unrelated social partners through reciprocal 19
20 altruism. Reciprocal altruism can evolve, if received help enhances the re- 20
21 cipient’s cooperativeness (Trivers, 1971). Reciprocity can generate stable 21
22 cooperation if costly help sufficiently increases the likelihood that donors 22
23 obtain fitness benefits in return for helping, provided that the benefits more 23
24 than compensate for the costs of initial investment (strictly speaking, recip- 24
25 eral altruism, therefore, is not true altruism as pointed out by West et al., 25
26 2007). This means that the benefit from being helped must on average ex- 26
27 ceed the cost of helping, and that social interactions should be sufficiently 27
28 frequent. 28

29 A crucial requirement shared by both types of explanations is that co- 29
30 operative individuals interact with cooperative individuals more than with 30
31 uncooperative individuals ([Fletcher & Doebeli, 2009](#)). Such positive assort- 31
32 ment can be achieved via recognition of relatives (kin recognition), previous 32
33 interactions with individuals (for generalized reciprocity (Taborsky, 2013); 33
34 for direct reciprocity ([Axelrod & Hamilton, 1981](#)); or, for indirect reciprocity 34
35 (Nowak & Sigmund, 1998)) or little migration resulting in high population 35
36 viscosity (Hamilton, 1964b; but see Queller, 1994; West et al., 2002), alone 36
37 or in combination. Various theoretical studies have addressed the evolution 37

1 of cooperation via positive assortment based on discernible phenotypic tags, 1
2 either genetically or culturally inherited ([Axelrod et al., 2004](#); [Hammond & 2](#)
3 [Axelrod, 2006](#); [Cohen, 2012](#); [Czaran, 2014](#)). 3

4 However, theoretical problems have been identified for the evolution of 4
5 cooperation based on these two types of tags, genetically and culturally in- 5
6 herited. First, if tags are genetically encoded, short-term selection will work 6
7 against the genetic diversity of tags. The common allele will always be 7
8 favoured, because it will receive more cooperation than rare alleles. There- 8
9 fore, tag-based cooperation ‘eats up’ the genetic variation upon which it 9
10 crucially relies, a prediction now known as ‘Crozier’s paradox’ ([Crozier, 10](#)
11 [1986](#); [Rousset & Roze, 2007](#); [Aanen et al., 2008](#); [Bastiaans et al., 2015](#)). 11
12 Recent simulations show that cheating can stabilise genetic kin recognition 12
13 ([Axelrod et al., 2004](#); [Czaran, 2014](#)). A problem for culturally inherited tags 13
14 is that they may be vulnerable to imitation and thus not reliable to base 14
15 cooperation on. However, some culturally inherited markers, such as lan- 15
16 guage and accent are hard to fake and hard to hide, and may thus be more 16
17 reliable tags ([Sigmund & Nowak, 2001](#); [Cohen, 2012](#)). Another possible ex- 17
18 ample of a hard-to-fake culturally inherited tag is religious membership. In 18
19 many cases, being or becoming a member encompasses costly behaviours 19
20 and rituals, which are not easy to fake for non-believers. These ‘tags’ may, 20
21 thus, reliably signal the presence of cooperative intention toward in-group 21
22 members, buffering religious groups against defection from freeloaders and 22
23 reinforcing cooperative norms ([Norenzayan & Shariff, 2008](#)). 23

24 These different means to restrict interactions to a subset of the population 24
25 put a limit to the size of cooperating groups. Several studies have demon- 25
26 strated that this is indeed the case (kin selection: [Czaran, 2014](#); reciprocal 26
27 altruism: [Boyd & Richerson, 1988](#)). Because of the limited group size, it is 27
28 generally assumed that many forms of cooperation in humans cannot be ex- 28
29 plained by current models of kin selection and reciprocity as cooperation 29
30 occurs in groups that extend the theoretically expected size by orders of 30
31 magnitude. However, it remains hard to judge this inference as group size 31
32 is rarely modelled separately, but only implicitly as a consequence of the 32
33 joint evolution of tag diversity and cooperation. In this manuscript, we first 33
34 explore the evolution of tag-based cooperation in a spatially structured en- 34
35 vironment. Next, we vary group size by varying the maximum number of 35
36 groups, and establish the importance of group size for the opportunities of 36
37 cheating. 37

2. Material and methods

2.1. The model

The model is a spatially explicit cellular automaton (CA) addressing the problem of evolving group discrimination as a means to avoid cheaters invade and eventually replace populations of cooperators.

The basic assumptions of the model are the following:

1. Spatial setup: A population of individuals (or that of highly coherent assemblies of individuals, like families) occupy an area represented by a 1000×1000 square lattice of residential units ('homes'). We attribute a toroidal topology to the area by assuming that the homes on the opposite edges of the lattice are neighbours, so that each home is equivalent to all the others, in terms of the number and the spatial configuration of neighbours (i.e., no edge effect confounds the dynamics). All homes are always inhabited, each by one individual (family).
2. Clan identity: The individuals (families) are assigned group ('clan') identities based on kinship; clans are defined by genetic relatedness which, in turn, determines the willingness of their members to cooperate — no cooperation between members of different clans occurs. Clan identities are directly inherited: the offspring belong to the clan of the parent, except for rare 'mutation' events whereby the progeny takes a random clan identity with probability μ_g .
3. Cooperating teams: Cooperation takes place in local teams composed of a focal individual (family) and its immediate neighbours belonging to its own clan, and it aims at harvesting some benefit — the cooperation payoff — that increases the fitness of the team as a whole. Cooperators also pay a fitness cost of cooperation individually. Observe that three nested levels of group identities are kept track of in the model: clans and teams are separate levels of interaction (besides the trivial population level): teams are cooperating units of individuals (families) within the clans, whereas clans are recognition units within the population.
4. Cooperators and cheaters: Cooperation is feasible only with clan-mates present in a team. Individuals can always discriminate members of other clans; therefore, teams of size 1 never attempt cooperation. Cooperators may mutate to cheaters (who do not cooperate even with their own clan-mates, thus they do not pay the cost but enjoy the benefit of cooperation)

with probability μ_c ; cooperation and cheating are also heritable traits. Cooperators cannot discriminate cheaters, so they attempt cooperation (and pay its cost) even if all other clan-mates are cheaters in the team, but cooperation increases team fitness only above $n = 1$.

5. Team fitness benefit of cooperation: The maximum size of a potentially cooperating team is 5 individuals (families), but, depending on the clan identities of the neighbours, it may be anything between 1 and 5 (0 is not feasible, since all homes, thus also the focal one, are inhabited). The per capita contribution $w(n)$ of cooperators to team fitness W_T follows a ‘diminishing returns’ pattern with increasing the number n of cooperators in the team:

$$w(n) = w_0 \times \left(1 + f \times \frac{n-1}{n} \right) \quad (n = 1-5),$$

$$w(0) = w_0,$$

where f determines the strength of the cooperative effect, and w_0 is the baseline fitness contribution of a solitary individual (family). Cheaters contribute w_0 each, so that the team fitness $W_T(n, m)$ of a team consisting of n cooperators and m cheaters becomes

$$\begin{aligned} W_T(n, m) &= mw_0 + nw(n) \\ &= mw_0 + nw_0 \times \left(1 + f \times \frac{n-1}{n} \right) \\ &= (n+m)w_0 + fw_0(n-1) \quad \text{for } n = 1-5 \end{aligned}$$

and

$$W_T(0, m) = mw_0,$$

which means that the team-fitness benefit of cooperation $fw_0(n-1)$ is a linear function of the number of cooperators.

6. Allocation of team benefits and cooperation costs to team members: The team fitness W_T is shared equally among the members of a team, irrespective of their actual contribution. Cooperators also pay an individual fitness cost of cooperation, c , which cheaters do not, therefore the actual fitness share of a cooperator is $\frac{W_T(n,m)}{n+m} - c$, whereas that of a cheater is $\frac{W_T(n,m)}{n+m}$ for $(n+m) > 1$, and it is always the baseline fitness w_0 for a solitary individual (family), i.e., for $(n+m) = 1$, irrespective of it being a cooperator or a cheater.

- 1 7. Local and global dispersal: Individuals (families) produce offspring 1
2 in proportions of their individual fitness (which consists of their share 2
3 of the team fitness in each generation, and possibly the fitness cost of 3
4 cooperation in the case of cooperating individuals). The vast majority 4
5 of the offspring remains close to their parents (i.e., within a distance D 5
6 from them), but a small fraction g of the offspring disperses far away, 6
7 attempting to occupy randomly chosen homes within the lattice. 7
- 8 8. Population dynamics: Each home is assigned to a single individual (family) 8
9 in each generation, even if more offspring from the last generation 9
10 claims for it. The candidates compete for the homes with chances of 10
11 winning proportional to their fitness. Obviously, the offspring of a parent 11
12 (family) have the best chances to occupy homes within the local dis- 12
13 persal distance D of their parents; the remote colonisation probability 13
14 depends on the rate of global dispersal g . Thus the outcome of competi- 14
15 tion for a home depends on the fitness of the individuals claiming it, and 15
16 the distances of the targeted home from those of their parents. The local 16
17 outcomes add up to constitute the next generation. 17

19 3. Results 19

20 Our simulations demonstrate that group (clan) identity, i.e., the ability to dis- 20
21 tinguish ‘self’ from ‘other’ can reduce the frequency of cheaters. However, 21
22 the stabilisation of cooperation via clan identity works only under conditions 22
23 of limited dispersal, combined with a low rate of global dispersal (see be- 23
24 low). Starting from a single clan of cooperating individuals and allowing for 24
25 heritable changes (‘mutations’) in cooperation strategy (from ‘cooperator’ to 25
26 ‘cheater’ or vice versa within the same clan) and in clan identity (from coop- 26
27 erator to cooperator or cheater to cheater of a different clan) we have run the 27
28 simulations for 10 000 generations, systematically exploring the influence of 28
29 different model parameters modifying one parameter at a time, relative to a 29
30 basic set of feasible parameter values producing the dynamics and the lattice 30
31 pattern shown on Figure 1. Figure 2 is a summary of all simulated parameter 31
32 settings. 32

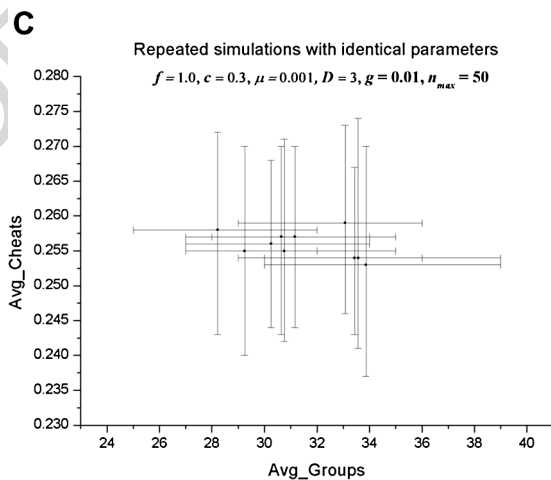
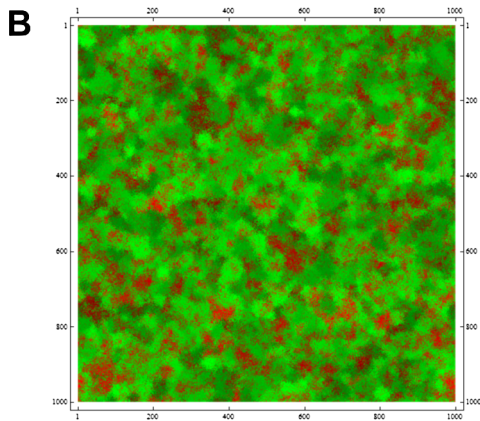
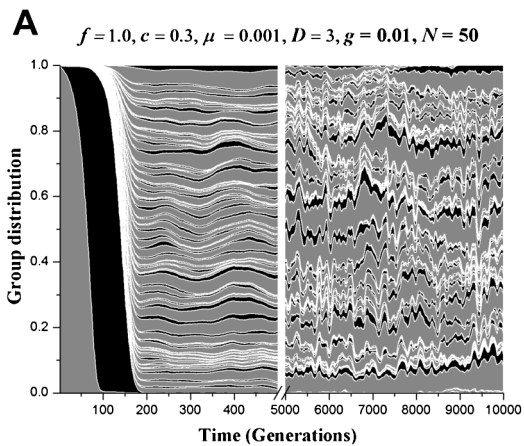
33 3.1. Role of the number of clan identities 33

34 The most important question we wish to answer is whether the system is 34
35 capable of maintaining cooperation in spite of the substantial fitness ad- 35
36 vantage that cheaters are supposed to enjoy in a predominantly cooperating 36
37 37

1 population. As expected, a single clan of cooperators ($N = 1$) cannot resist 1
2 the selection pressure of its own cheaters if cooperation is costly and clan 2
3 identity cannot be changed: the equilibrium proportion of cooperators in the 3
4 stationary population of a single clan is negligibly small. Increasing the number 4
5 of possible clan identities (N) allows for the coexistence of cheaters and 5
6 cooperators — the higher N is, the less the proportion of cheaters in the station- 6
7 ary population (Figure 3A). The mechanism ensuring coexistence is the 7
8 fugitive behaviour of cooperators: In a resident population of cheaters be- 8
9 longing to clan A the cooperators of another clan B are at an advantage: they 9
10 can cooperate among themselves and harvest the benefits thereof, but the 10
11 cheaters of clan A cannot exploit their cooperation. As soon as the cheaters 11
12 of clan B show up in teams of B cooperators (due to mutation or global 12
13 dispersion) cheaters invade the spatially contiguous patch of the cooperator 13
14 population. If most clan B cooperators belong to a single patch, the takeover 14
15 by the cheaters eradicates almost all cooperators of the clan from the pop- 15
16 ulation, but if the clan is spatially fragmented into more patches, then the 16
17 cooperators in other patches remain safe until hit by another cheating mutant. 17
18 The recruitment of new clans proceeds until the invasion of cheaters into the 18
19 cooperator patches of the same clan becomes as fast as the invasion of coop- 19
20 erators into cheater patches of other clans, i.e., until cooperator and cheater 20
21 fitnesses become equal. As the number of different clans increases average 21
22 patch size decreases. Smaller cooperator patches persist longer, because they 22
23 are hit less often by mutant or migrant cheaters of the same clan. At the same 23
24 time, increasing N allows for the spatial isolation of different patches of a 24
25 clan: the four-colour map theorem (Appel & Haken, 1977) ensures that each 25
26 clan can be fragmented so that every patch of a certain clan is surrounded 26
27 by patches of other clans, if $N \geq 4$. As soon as the fragmentation effect sets 27
28 in, the proportion p of cheaters falls dramatically within the population, and 28
29 increasing N further does not have a substantial effect on the stationary pro- 29
30 portion p (cf., Figure 3A). This explains the phase transition-like fall of p 30
31 with increasing N at about $N = 5$. 31

32 3.2. Role of the fitness cost of cooperation 32

33 Allowing for many clan identities (at fixed $N = 50$) and changing the actual 33
34 fitness cost of cooperation c from low to high values has a consistent effect 34
35 (Figure 4): (1) At low cooperation cost ($c = 0.1$) cheaters cannot invade the 35
36 cooperating community, and new ‘mutant’ clans do not increase to signifi- 36
37 cant sizes either. The selective force keeping new clans at check is that the 37



1 average team size, and thus the average fitness of the resident, cooperating 1
 2 clan is larger than that of a new mutant clan. (2) At intermediate cooperation 2
 3 costs ($0.2 < c < f/2 = 0.5$ for $f = 1$) cheaters can invade the cooperating 3
 4 population, which responds to the invasion of cheaters by evolving new clans 4
 5 of cooperators. The number of clans increases until the average fitness of 5
 6 cooperators and cheaters becomes equal, and the population settles at a sta- 6
 7 tionary cooperator/cheater ratio. Increasing cooperation costs also increases 7
 8 the equilibrium number of clans maintained, because high cost means fast 8
 9 takeover of cooperators' patches by cheaters, from which the only escape for 9
 10 cooperators is to change clan identity and start a new cooperators' patch 10
 11 before cheaters eradicate them. Essentially, cooperators defend themselves by 11
 12 changing clan identity, but at high cooperation costs the takeover of cheaters 12
 13 is much faster than the formation of new cooperating patches. (3) Obviously, 13
 14 at fitness costs of cooperation higher than the fitness benefit thereof (i.e., for 14
 15 $c > f/2 = 0.5$) cheaters take over, but the number of clans remains high due 15
 16 to the high number of quickly failing initiations of new cooperating clans. 16
 17 The overall effect is a lot of very fragmented clans with a marginal fraction 17
 18 (about 0.5–1.0%) of cooperators in each. Note that solitary cooperators are 18
 19 selectively neutral against the cheaters of other clans, because they do not 19
 20 even attempt to cooperate alone, therefore they do not pay the (high) coop- 20
 21 eration cost, but they are immediately selected against when they occur in 21
 22 the same team and start to cooperate with each other. Once a clan consists 22
 23 of cheaters and solitary cooperators, the group size levelling effect of 'mu- 23
 24 tations' sets in: since larger clans produce more individuals of other clans 24
 25 25
 26

27 **Figure 1.** Simulations with the basic parameter setting as specified: f , cooperation fitness 27
 28 advantage parameter; c , cooperation fitness cost; $\mu = \mu_g = \mu_s$, mutation rates; D , local 28
 29 dispersal distance; g , proportion of globally dispersed offspring; N , maximum number of clans. 29
 30 (A) The dynamics of clan and strategy distributions. Grey bands indicate proportion of coop- 30
 31 erators, black bands above grey ones the proportion of cheaters of the same clan as the 31
 32 cooperators below. (B) The spatial pattern of cooperation and cheating in the 10 000th 32
 33 generation. Shades of green indicate cooperators of different clans, shades of red cheaters of 33
 34 different clans. (C) The average number of clans (Avg_Groups) and the average cumulated 34
 35 proportion of cheaters (Avg_Cheats) of the last 1000 generations in 10 replicate runs of the 35
 36 simulation program, replicates differing only in random number seeds. Vertical and hori- 36
 37 zontal bars indicate the ranges of change in the corresponding variable during the last 1000 37
 38 generations. This figure is published in colour in the online edition of this journal, which can 38
 39 be accessed via <http://booksandjournals.brillonline.com/content/journals/1568539x>. 39

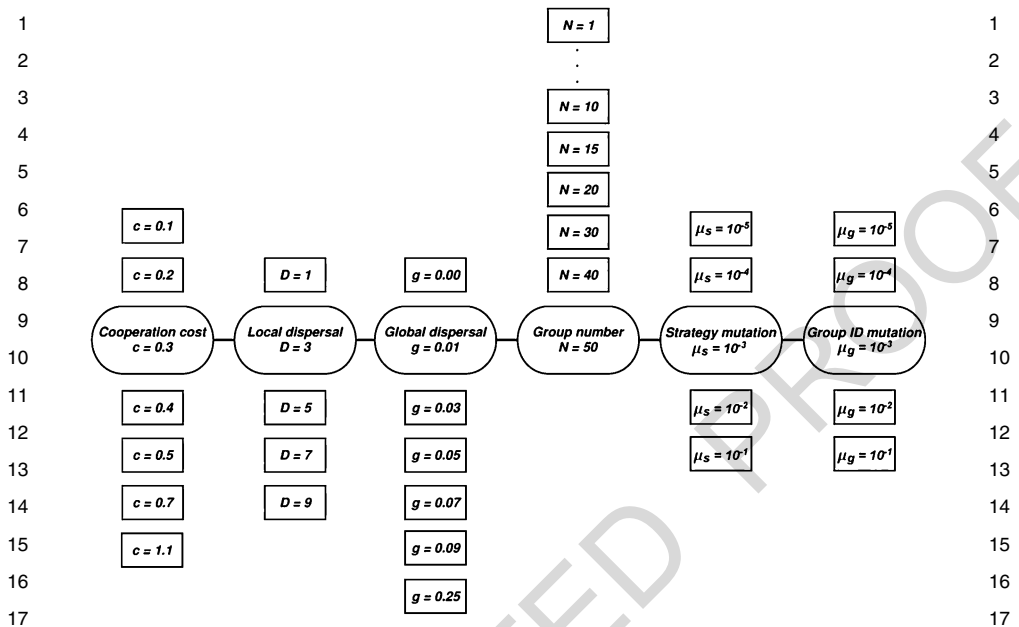


Figure 2. Parameter settings of the simulations performed. Oval boxes, the basic parameter set; rectangular boxes, alternative values of the parameter in the corresponding oval box. Parameters have been changed one at a time, except for the two mutation rates which have been changed both simultaneously and separately.

than small ones, clan sizes tend to become equal. This is what maintains clan diversity at high cooperation cost.

3.3. Role of mutation rate

New clans and cheaters are, in the first place, supplied by ‘mutation’, i.e., by some individuals changing their inherited clan identities or cooperation strategies. Therefore, the rate of mutation is an important determinant of the actual dynamics of clan diversity and cooperation. Obviously, zero mutation rates would allow no change, but very low mutation rates ($\mu = 10^{-5}$) are sufficient to initiate the increase in clan number and to set the balance of cooperation and cheating in the population, if the other parameters allow for it. The simultaneous increase of both mutation rates (i.e., that of clan identity and of cooperation strategy) has a substantial effect on clan diversity — the equilibrium number of clans steeply increases with μ —, but the average equilibrium frequency of cheaters admits just a marginal increase at the same time, with decreasing fluctuations. Very low mutation rates (i.e., $\mu = 10^{-5}$)

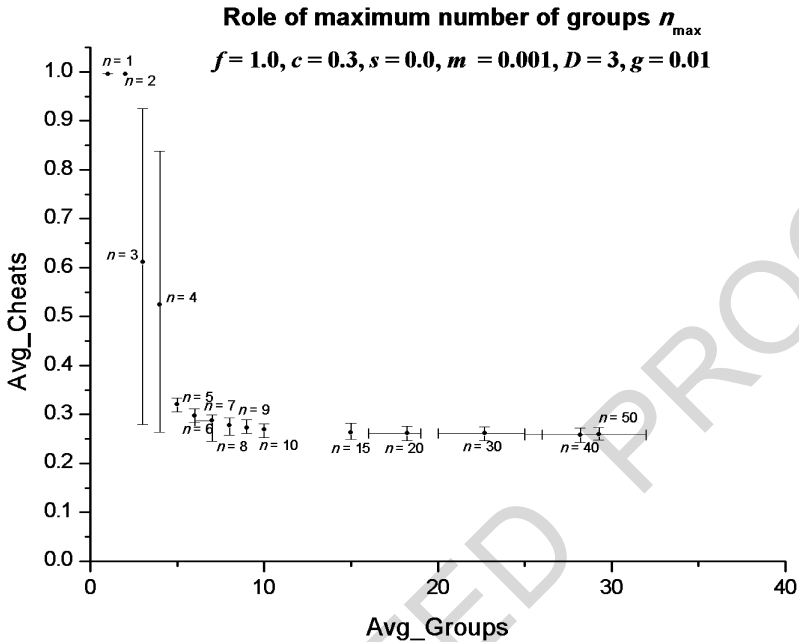


Figure 3. The role of the maximum number of clan identities for the average cumulated proportion of cheaters (Avg_Cheats) during the last 1000 generations of the simulations. Vertical and horizontal bars indicate the ranges of change in the corresponding variable during the last 1000 generations.

induce high amplitude oscillations in cheater frequency, indicating that the population dynamical time-scale of the system is much faster in this case than the ‘evolutionary’ scale on which new strategies appear. If ‘mutations’ to cheating are rare, and the dynamics of the population is relatively fast, then cheating individuals will take over (percolate) within large, coherent patches of their own ‘susceptible’ (cooperating) clan, after which they will be locally driven extinct by cooperators of different clans. This upswing-downswing dynamics is of high amplitude, if mutations to cheating are rare, because cooperating patches may grow large before being hit by a cheating mutant, and the large cheater patches thus established fall deep after they have taken over. This is an aspect of the role of the inherent randomness of evolutionary processes in shaping cooperation patterns (Hadzibeganovic et al., 2015).

Independently varying the two mutation rates explains why simultaneous mutation rate increase has no consistent effect on cheater proportion: more frequent mutations to cheating increase the proportion of cheaters,

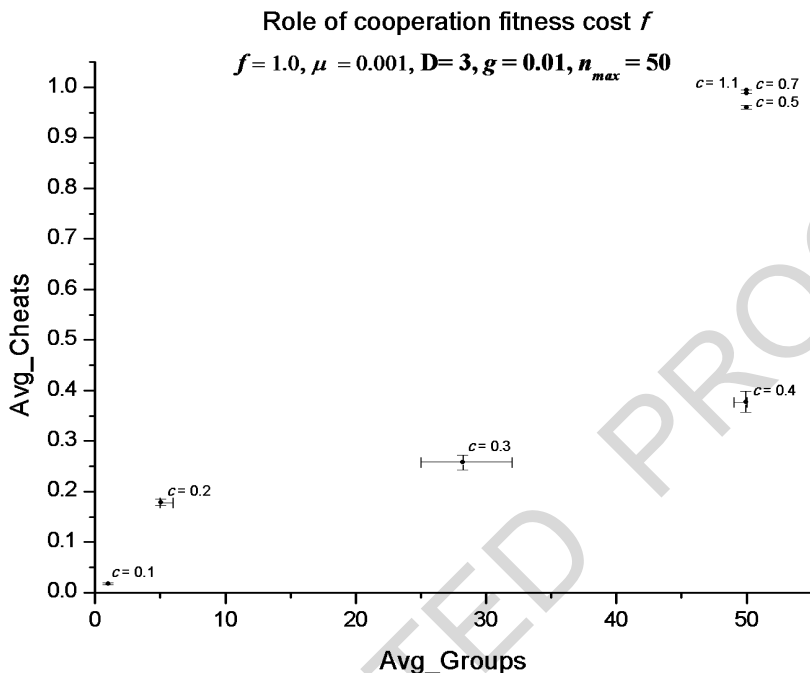


Figure 4. The role of the fitness cost of cooperation for the average cumulated proportion of cheaters (Avg_Cheats) during the last 1000 generations of the simulations. Vertical and horizontal bars indicate the ranges of change in the corresponding variable during the last 1000 generations.

whereas more frequent clan identity mutations help cooperators to escape exploitation by cheaters of their own clans, which decreases overall cheater frequency (Figure 5A, B); the two effects cancel each other when both mutation rates increase simultaneously. Very high mutation rates (i.e., $\mu = 0.1$) induce phase transition-like shifts in the corresponding directions: extremely frequent strategy switches ($\mu_s = 0.1$) to cheating abruptly pushes the number of clans down to $N = 1$ and increases the proportion of cheaters to about 60%. On the other hand, $\mu_g = 0.1$ abolishes cheaters almost completely, keeping the number of clans at its possible maximum ($N = 50$).

3.4. Role of dispersal

Dispersal (i.e., the spatial distance between the homes of parents and offspring) is determined by two parameters in the model: D , the maximum distance of locally dispersed offspring from the parent, and g , the proportion of offspring dispersed globally within the lattice at random. The success

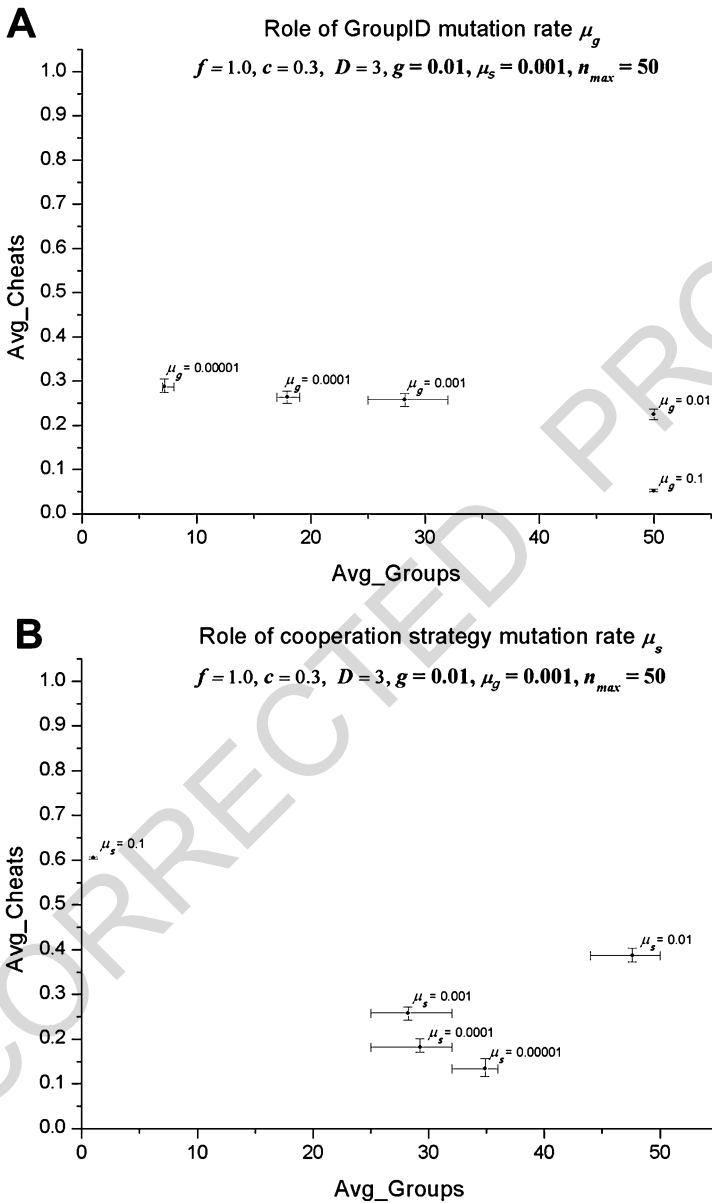


Figure 5. The role of mutation rates for the average cumulated proportion of cheaters (Avg_Cheats) during the last 1000 generations of the simulations. (A) The role of the mutation rate to new clans; (B) the role of the rate of strategy mutations. Vertical and horizontal bars indicate the ranges of change in the corresponding variable during the last 1000 generations.

1 of an invading clan depends on its ability to place cooperating individuals 1
2 into cheater patches of other clans, and the ability of the propagule to colo- 2
3 nize that patch. Delegating propagules to suitable places partly depends on 3
4 global dispersal (besides clan identity mutations); therefore, increasing g is 4
5 advantageous for cooperation in this respect. However, large g is also ad- 5
6 vantageous for cheaters to spread and find exploitable cooperator patches of 6
7 their own clan. The net effect of increasing the proportion of globally dis- 7
8 persed offspring seems to be beneficial for cooperators at very low g values 8
9 ($0 < g < 0.03$), with the proportion of cheaters, as well as the number of 9
10 different clans decreasing, but increasing global dispersal further is deleter- 10
11 ious: average cheater frequency as well as the amplitude of fluctuations in 11
12 clan size, clan number and cheater frequency all increase with $g > 0.03$ (Fig- 12
13 ure 6A), and all these effects tend to destabilize the population. The average 13
14 number of clans increases with global dispersal at the higher g region, again 14
15 due to the self-defence mechanism of cooperators trying to avoid extinction. 15

16 Local dispersal maintains the coherence of locally cooperating teams. 16
17 Therefore, keeping D small is obviously advantageous for cooperation, and 17
18 too large D values have an effect similar to large global dispersion: they 18
19 induce high amplitude fluctuations in clan size, clan number and cheater 19
20 frequency and increase the average incidence of cheating, while average clan 20
21 number does not consistently change with increasing D (Figure 6B). 21

22 Thus, the two dispersal mechanisms (local and global) seem to have similar 22
23 dynamical effects, essentially due to the level of population mixing in 23
24 space they imply. It is well known that cheaters can benefit from popula- 24
25 tion mixing (Nowak & Sigmund, 2004), although highly viscous population 25
26 structures prevent the emergence of cooperative strategies due to local com- 26
27 petition (cf., Queller, 1994; West et al., 2002), but it is slightly different in 27
28 this model than in classical cooperator-cheater games: since solitary cooper- 28
29 ators do not attempt to cooperate, they do not pay the cost of cooperation and 29
30 therefore they are not selected against in pure cheater teams of other clans. 30
31 This explains the relatively high tolerance level of cooperators to increased 31
32 mixing either at high g or at high D ; the same argument applies at high rates 32
33 of mutation to cheating (at $\mu_s = 0.1$, see above). 33

34 4. Discussion 34

35 36 The evolution of cooperation provides a problem for evolutionary biology 36
37 (Sachs et al., 2004; Lehmann & Keller, 2006; West et al., 2007). Why would 37

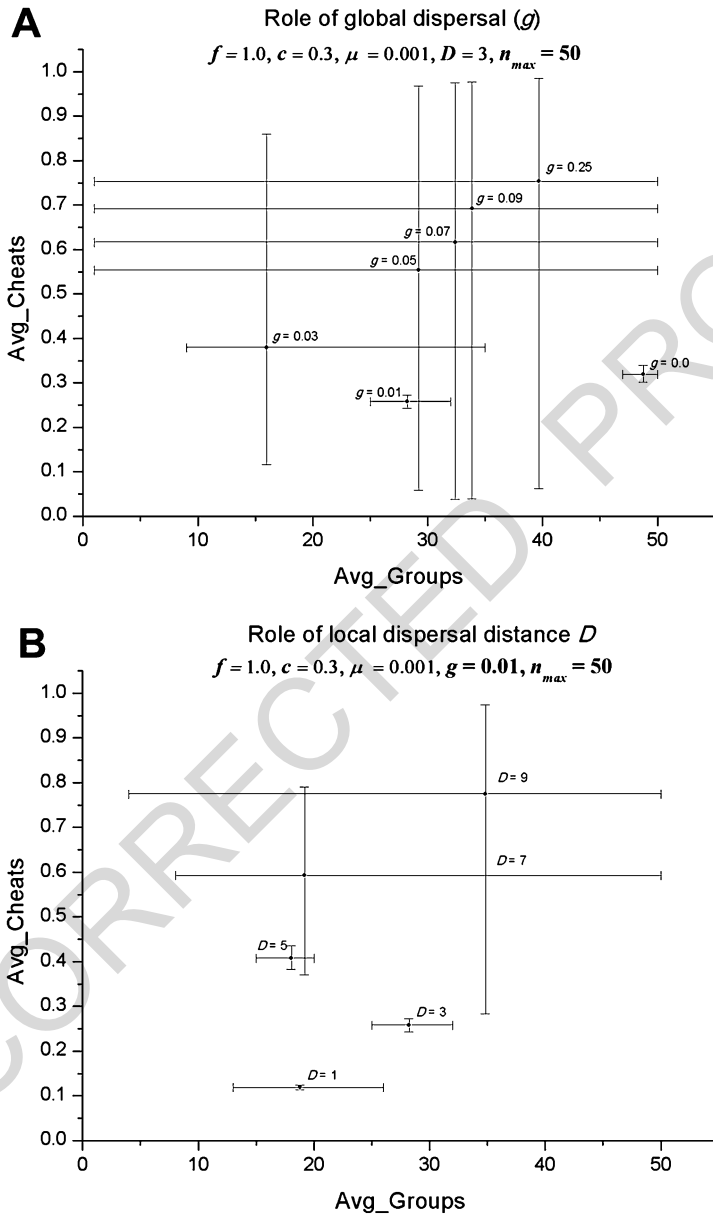


Figure 6. The role of dispersal for the average cumulated proportion of cheaters (Avg_Cheats) during the last 1000 generations of the simulations. (A) The role of global dispersal (g); (B) the role of local dispersal (D). Vertical and horizontal bars indicate the ranges of change in the corresponding variable during the last 1000 generations.

1 an individual provide a costly benefit to another individual, if it can also save 1
2 this cost and profit from the help provided by others? The two main classes 2
3 of explanation, i.e., kin selection and reciprocity, both depend on limiting 3
4 interactions to a subset of the population, which has a higher probability to 4
5 employ the cooperative behaviour ([Fletcher & Doebeli, 2009](#)). This positive 5
6 assortment can be achieved in various ways, such as recognition of previ- 6
7 ous behaviour ([Axelrod & Hamilton, 1981](#)), limited dispersal resulting in a 7
8 viscous population structure (Hamilton, 1964b; but see [Queller, 1994](#); [West](#)
9 [et al., 2002](#)), kin recognition (Hamilton, 1964b) or recognition of culturally
10 inherited tags ([Hammond & Axelrod, 2006](#); [Ihara, 2011](#); [Cohen, 2012](#)). 10

11 Our simulations consider the importance of group identity in a popu- 11
12 lation of varying viscosity for the evolutionary stability of cooperation in 12
13 small neighbourhoods. The model is abstract, focusing on local cooperation 13
14 based on broadcasted group (clan) identity but neglecting factors of coop- 14
15 eration obviously important in any actual human population, like past or 15
16 expected reciprocities, punishments or rewards, and even less aware of hier- 16
17 archically organized and institutionalized forms of cooperation characteristic 17
18 of modern human societies. By constraining cooperation to small, personally 18
19 connected and genetically related ‘teams’ of individuals (families) the sce- 19
20 nario of this model applies best to prehistoric, early human communities. 20
21 This narrative fits best to the primary motivation of this study: to explain the 21
22 selective forces driving the early evolution of group discrimination. We have 22
23 assumed that cooperation is a fixed strategy directed to clan-mates only, and 23
24 that clan identity is specified by a tag, in most likelihood culturally inherited 24
25 with a high fidelity. Accordingly, we ask questions regarding the possibil- 25
26 ities of maintaining cooperation through rigid group discrimination in the 26
27 simplest possible social setup devoid of subtle social control mechanisms. 27

28 Our results demonstrate that variation in group identity is an efficient 28
29 means to disfavour selection of cheating behaviour. At the same time, focus- 29
30 ing on the maintenance of tag diversity, the recurrent threat of cheating via 30
31 mutation favours tag diversity, and solves [Crozier’s paradox \(Crozier, 1986\)](#). 31
32 However, the efficiency of selection against cheating is conditional on lim- 32
33 ited dispersal. Similar group identity and limited dispersal both increase the 33
34 probability that cooperative individuals interact. In most human populations 34
35 and for most possible kinds of group identity, group identity and philopatry 35
36 are linked, so this seems a reasonable assumption. The ability to recognize 36
37 group identities, and to favour one’s own group is widespread in humans and 37

1 an innate tendency to favour in-groups seems to be universal for our species 1
2 (cf., LeVine, 1972). 2

3 Other studies have also demonstrated that limiting cooperation to a sub- 3
4 set of the population by genetically or culturally inherited tags may stabilise 4
5 cooperation (cf., Hammond & Axelrod, 2006; Ihara, 2011; [Cohen, 2012](#)). 5
6 However, various problems have been identified questioning the importance 6
7 of such tag-based cooperation. Recently various theoretical studies have 7
8 demonstrated that tag-based cooperation may be evolutionarily stable ([Axel- 8
9 rod et al., 2004](#); Hammond & Axelrod, 2006). Our simulations confirm these 9
10 results, but the consequences of group discrimination strongly depend on 10
11 other parameters, most notably dispersal. We have systematically discussed 11
12 the roles of all model parameters in the Results. 12

13 Our model differs in several respects from that of a seemingly similar 13
14 model by Hammond & Axelrod (2006). First, in our simulations, the number 14
15 of group identities could evolve up to varying maxima, whereas in Hammond 15
16 and Axelrod's model the maximum number of groups was four (recall that 16
17 we find a phase-transition-like increase of cooperation in the model with 17
18 more than four clans). Furthermore, in our model, cooperative and cheating 18
19 interactions can occur only between individuals of the same group; solitary 19
20 individuals of different groups had the same base fitness. This means that 20
21 cheaters cannot cheat individuals from a different group. In contrast, in the 21
22 HA model, the payoffs of cooperative and defecting strategies could vary 22
23 with the group identities of the players. 23

24 A different type of model has considered the ability to recognize cheating 24
25 as a stabilizing factor of cooperation (cf., Sibly & Curnow, 2012). Our study 25
26 does not assume recognition of a behaviour, but just of a group, irrespective 26
27 of the behaviour of its members. Group recognition probably requires less 27
28 cognitive abilities, and may thus be an easier (and probably also earlier) route 28
29 to the evolution of cooperation than recognition of behaviours. 29

30 It has been pointed out that group identities must be sufficiently stable 30
31 to prevent the emergence of cheaters ([Cohen, 2012](#)). This is true for more 31
32 sophisticated forms of cheating if group identities can be chosen, for example 32
33 based on a high frequency of cooperators in a group. In our simulations, this 33
34 was not the case, and a high mutation frequency of group identity disfavoured 34
35 cheaters rather than favouring them. 35

36 Varying the maximum number of groups (Figure 3B) revealed that a 36
37 smaller number than the numbers of groups we reach in many of our sim- 37
ulations is sufficient to maintain cheaters at a low frequency. Without an

1 inherent fitness advantage of larger groups — i.e., a fitness component that 1
2 is independent of cooperation — the number of groups would increase and 2
3 average group size would decrease almost indefinitely (down to the size of 3
4 cooperating teams), because smaller groups of cooperators are hit by cheat- 4
5 ing mutants less often. However, the phase transition-like drop of cheater 5
6 frequency with increasing the number of possible groups shows that the fit- 6
7 ness advantage of further discrimination of groups has only a marginal fitness 7
8 advantage above a typically small number of groups (about 7 in the case of 8
9 Figure 3B). 9

10 If we assume additional marginal benefits of larger group size, i.e., benef- 10
11 its that extend the benefit of local cooperation, we have two counteracting 11
12 selective pressures on group size: local interactions maintaining high group 12
13 diversity and thus small group size to avoid the risk of cheaters, and increased 13
14 group size to harvest the benefit thereof. These two counteracting selective 14
15 pressures could maintain a relatively small number of large groups, as seen 15
16 in many examples of human cooperation. Additional benefits seem plausible, 16
17 for example larger groups may have an advantage in occasional self-defence, 17
18 or have a higher genetic diversity, or share facilities above the level of the 18
19 local neighbourhood. Many forms of cooperation in human societies are 19
20 organised both locally and more globally. Systems theory has proven that 20
21 loosely coordinated assemblies of tightly coordinated (local) groups can be 21
22 extremely resistant to external perturbations (cf., connective stability: Sil- 22
23 jak, 1972) — a theoretical prediction that seems to be applicable to many of 23
24 our social structures. For example, religious groups are organised locally (in 24
25 parishes, congregation, or mosques) and organized in larger entities nation- 25
26 ally or internationally (dioceses, synods, movements). Provided that local 26
27 groups are sufficiently small, and isolated from other such groups, coopera- 27
28 tion may be stable, even though the many local groups of a particular kind 28
29 together are large. 29

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