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Indirect Reciprocity and the Evolution of Prejudicial Groups

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Prejudicial attitudes are widely seen between human groups, with significant consequences. Actions taken in light of prejudice result in discrimination, and can contribute to societal division and hostile behaviours. We define a new class of group, the prejudicial group, with membership based on a common prejudicial attitude towards the out-group. It is assumed that prejudice acts as a phenotypic tag, enabling groups to form and identify themselves on this basis. Using computational simulation, we study the evolution of prejudicial groups, where members interact through indirect reciprocity. We observe how cooperation and prejudice coevolve, with cooperation being directed in-group. We also consider the co-evolution of these variables when out-group interaction and global learning are immutable, emulating the possible pluralism of a society. Diversity through three factors is found to be influential, namely out-group interaction, out-group learning and number of sub-populations. Additionally populations with greater in-group interaction promote both cooperation and prejudice, while global rather than local learning promotes cooperation and reduces prejudice. The results also demonstrate that prejudice is not dependent on sophisticated human cognition and is easily manifested in simple agents with limited intelligence, having potential implications for future autonomous systems and human-machine interaction.

Prejudice is a human attitude involving generally negative and unsubstantiated prejudgement of others. When acted upon, this results in wide-ranging behaviours such as sexism, ageism and discrimination against sexual preference^{1–3} through to ethnic, racial, nationalistic and religious extremism^{4,5}, with bias and intergroup conflict characterised as a “problem of the century”⁶. Most recently, prejudice has been highlighted in connection to global political events: for example anti-immigration prejudice was a strong correlate of support for Brexit⁷.

The human disposition to categorize others through their group identity creates an opportunity for discrimination^{8–10}. As a consequence of in-group formation¹¹, which occurs through cultural or biological identification with others, or as a consequence of identity-less strangers mutually cooperating¹², bias can take hold in two ways. Through *in-group favoritism*^{13–16}, people prefer to help fellow group members, while *out-group prejudice*^{6,17,18} represents hostility to those beyond the in-group. These phenomena are easily triggered in human subjects under a wide range of transient experimental conditions^{8,13,16,19}. This has contributed to a misperception that positive discrimination to the in-group and negative discrimination to the out-group are inevitable²⁰.

Confusion arises between out-group prejudice and in-group favoritism because both concepts potentially reinforce the in-group, but as a consequence of different psychological mechanisms. While in-group favoritism is based on mutual attraction, out-group prejudice discounts the out-group by negatively accentuating differences. In-group favoritism does not depend on negatively biased attitudes, where as prejudice does. From a psychological perspective, this renders in-group favoritism insufficient to model prejudice. Consequently, understanding the separate roles of in-group and out-group discrimination is socially important⁶. In-group favoritism has received significant attention, but the evolution of out-group prejudice has received a more limited explicit focus.

Evolutionary game theory provides a powerful framework to examine the dynamics that can promote discriminatory behaviour^{14,15,21–25}. In particular, tag based models^{15,26–34} have shown that spontaneous cooperation can emerge from an agent’s donation being related to whether the recipient’s ‘tag’ is sufficiently similar to their own. Tags are arbitrary symbols upon which discrimination can be made, which must propagate with a behavioral strategy for cooperation to emerge. Groups of individuals can be defined through common tags where the model allows (e.g.¹⁵). This has established insights into in-group favoritism, particularly that the ability to

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discriminate between the in-group and out-group can actually promote cooperation, helping to explain why a predisposition toward in-group favoritism have evolved and can be easily triggered¹⁵.

Beyond tags, alternative models for studying the evolution of in-group favoritism are limited. Fu *et al.*¹⁴ provide an alternative generalised approach based on evolutionary set theory¹¹ that permits out-group as well as in-group interactions. Tag based models generally prohibit this, other than in^{33,34} where although explicit groups are not defined, the model allows individual probabilities of cooperation with dis-similar others to evolve. Fu *et al.*¹⁴ allow agents to move between sets, with successful sets attracting members and successful strategies gaining imitators. Agents can also differentiate between in-group and out-group strategies and conditions are determined under which preferential in-group cooperation is favoured by selection.

A further relevant consideration is so-called *parochial altruism*^{35–39}, where out-group discrimination has mainly been examined under coevolution with in-group favoritism. Both these costly discriminatory behaviours have been proposed as necessary for success in warfare³⁵, possibly promoting their coevolution³⁶. Parochial altruism is also observed as deeply embedded in human group behaviour^{37,39}, although further clarification is needed on the analysis of the selective mechanisms at work in current models³⁸.

While prejudice is common, its manifestation is fluid, indicating that culture and cultural evolution⁴⁰ must play an important role in the evolution of bias, through socially transmitted beliefs that help to create and sustain groups. In previous related models, we note that discrimination is considered independently from a group's identity. Typically, groups of individuals are modelled as a consequence of a common arbitrary tag, and evolution acts upon the agent's discriminatory strategy in association with that tag. However humans have the capacity to directly identify with a discriminatory attitude as a phenotypic tag in its own right. As such, a discriminatory attitude towards the out-group can provide a common defining feature for a group. In other words, prejudicial (or non-prejudicial) views can act to bind a group and define its boundary. We note that prejudicial feelings towards other groups have been predicted as a consequence of the perceived threat that they pose⁴¹. Also, at the extremes of group identity, common out-group prejudicial attitudes, from within a larger population, are a particular feature of homophilic attraction and group identity (e.g.^{42,43}).

Accordingly, in this paper we introduce and study the evolution of a new abstract class of group, the *prejudicial group*, defined by the common prejudicial disposition of its members towards the out-group. We assume that a population of agents is composed of sub-populations, each denoted SP_p , where the agents in SP_p have the common immutable trait t . A *prejudicial group* $G_{t,\alpha}$ within a sub-population SP_p represents the maximal subset of agents with a common prejudicial attitude (α) to the out-group. We use i to index the particular parameter values held by an agent i , with t_i indicating i 's trait and α_i indicating i 's prejudice level. Therefore $t_i = t$ and $\alpha_i = \alpha$ if and only if agent i is a member of $G_{t,\alpha}$. An out-group member is any agent not carrying both the prejudicial attitude value α and trait t . This arrangement gives a simple representation of features such as nationalism, or political, ideological, religious or extremist convictions within a sub-population. People who are less favourable to one out-group tend to be less favourable to other out-groups⁴⁴, and therefore we do not distinguish between them: an agent's prejudice level α_i is equally applied to all out-groups. The groups $G_{t,\alpha}$ partition the sub-population SP_p , so that every agent belongs to precisely one group. For experimental purposes we assume $\alpha \in \{0, 0.25, 0.5, 0.75, 1\}$.

Our aim is to observe how α_i evolves with cooperation, and to further understand the conditions that promote or impede α_i . We seek to achieve this in a context aligned with observed human behaviour. Across all species, only humans fully engage with indirect reciprocity^{23,45} making it an appropriate cooperative scenario to consider⁴⁶. Indirect reciprocity is commonly examined using the donation game, a special case of the mutual aid game⁴⁷, where agents choose whether or not to donate at cost c to a recipient who gains benefit $b > c > 0$, without the guarantee of future reciprocation.

Strategies for indirect reciprocity are generally driven by reputation^{46,48}, which acts as a currency to judge third party agents who may never be encountered again. While a range of evolutionary approaches to sustaining indirect reciprocity are known^{22,46,49,50}, the social comparison of reputation between a donor and the recipient has recently been developed²⁵, where the heuristic of donating to those with similar or higher reputation evolves to sustain cooperation. This is of high relevance to prejudice because social comparison is a widespread human disposition^{51–55} that plays a fundamental role in categorization^{8–10} and subsequent stereotyping¹⁸. Therefore we extend this model²⁵ to incorporate prejudicial attitudes against out-group agents, allowing agents to discount the reputation of out-group members by a factor of α_i when considering whether or not to donate.

The model we develop involves 100 agents, which are randomly selected to play the donation game 5000 times, and which constitutes one generation, before evolution of the agents' strategy. Reputation is central to the model, and *assessment rules* are applied to update a donating agent's reputation in light of their donation behavior immediately after each donation game. Assessment rules represent social norms, which humans are well-disposed to internalising and perpetuating^{56–58}. These enable the judgement of reward and penalty, which are a basis for modelling morality⁵⁹. Because prejudicial groups are defined by the common out-group prejudicial disposition of their members, it is appropriate to model an *in-group reputation* for each agent i , denoted r_i^G , as well as a *universal reputation* for agent i , denoted r_i^U , which is the hypothetical reputation in the absence of any prejudice or groups. This approach applies social norms both locally and globally.

Wide-ranging assessment rules have been previously studied^{22,60–64}, however standing⁶², with its origins in the work of Sugden⁶⁰, has emerged as one of the dominant approaches because it permits "legitimate shirking". Here, an agent's reputation is not reduced when there is a justified basis for defection (e.g., the potential recipient is a defector). We apply a generalised form of standing for both in-group and universal reputations, where a reputation is permitted to range between -5 and $+5$ in unit steps, as employed in⁴⁹. This choice is based on the analysis conducted in²⁵, where the moral conventions of judging, image scoring and standing were compared, allowing evolution to act upon all possible social comparison action rules. These results indicated that either

standing or judging are preferential rules, and this comes from their ability to ensure those agents who are limited in their cooperation are not rewarded.

Both the in-group and universal reputations are conceptually simple but require a number of criteria to update them in light of the donation or defection behaviour by an agent i . Both types of reputation follow the principles of standing. Specifically, r_i^U and r_i^G are incremented when the donor i cooperates. For the universal reputation, if agent i defects on agent j , whose reputation is of relatively low standing (i.e., r_j^U is lesser than r_i^U), then this is deemed legitimate and i suffers no penalty to its reputation (i.e., r_i^U remains unchanged). However if i defects on agent j and this isn't deemed legitimate (i.e., r_j^U is the same or greater than r_i^U) then i 's universal reputation is decremented.

Concerning in-group reputation, when i and j belong to the same group G_{i,α_i} , the updating of r_i^G is analogous to updating the universal reputation, but through comparing r_i^G with r_j^G . However, when j is out-group, prejudice comes into play and i 's in-group reputation is compared with j 's universal reputation as discounted by i 's prejudice level. If i defects and j 's discounted reputation $r_j^U \cdot (1 - \alpha_i)$ is less than r_i^G then this is deemed legitimate by i 's in-group and i 's in-group reputation remains unchanged, otherwise r_i^G is decremented. Note that in-group reputation may deviate from universal reputation as a consequence of prejudice.

The donation behavior of each agent i (i.e., the action rule) is governed by a *social comparison heuristic*, denoted $H_i = (s_i, u_i, d_i, \alpha_i, P_i, S_i)$. Upon being selected to play, an agent i randomly determines its potential recipient j , using the probability S_i to determine whether j is selected from in-group (with probability $1 - S_i$ that i is selected from an out-group). Variables s_i, u_i, d_i and α_i allow a donor agent i to compare its reputation against that of the potential recipient j , and to make the donation decision.

An agent i plays a donation game by comparing its reputation against that of j , and three outcomes are possible. Assuming i and j are in the same group, these are similarity ($r_j^G = r_i^G$), upward self-comparison ($r_j^G > r_i^G$), or downward self-comparison ($r_j^G < r_i^G$). The reputation r_j^G is replaced with $r_j^U \cdot (1 - \alpha_i)$ in these comparisons when j is out-group to i . The binary variables from i 's social comparison heuristic govern whether or not i donates when similarity (s_i), upward comparison (u_i) or downward comparison (d_i) is observed by i in respect of j . On closure of a generation, a reproductive step conducts natural selection on the social comparison heuristics. Similar to approaches used in a spatial context (e.g.^{15,65}), we limit the opportunity for each agent's reproduction at an evolutionary step to be 10%. This controls potential genetic drift due to selection from within small sub-populations, and the reproductive step is repeated over 50,000 generations, unless otherwise stated. At each reproductive step, if selected to reproduce, an agent i chooses another agent's social comparison heuristic to copy. Based on the Island model^{49,66}, copying may be local (i.e., from within the in-group) with probability P_i or from the whole population (with probability $1 - P_i$). Agent i then selects a new social comparison heuristic with chance proportional to the relative fitness of the in-group members or the whole population, while further applying a random mutation to each element of the agent's new social comparison heuristic, at the rate of 1%²⁵. The fitness of an agent is taken as the cumulative difference between the benefits received and costs paid since the previous reproductive step. This genetic reproduction extends that applied in previous work²⁵, and follows the general approach of asexual reproduction⁴⁹.

Note that the reproductive process represents a way in which an agent i effectively learns from others, by probabilistic copying, based on the proportional fitness. P_i controls the extent to which this learning is in-group, where only the strategies (i.e., social comparison heuristics) of agents in the same group G_{i,α_i} are considered. When P_i is low, agent i has a greater chance of learning from beyond its own group, across the wider population. For various experiments P_i and S_i may be exogenously fixed, enabling the influence of these variables to be assessed. A summary of the key parameters is presented in Table 1. The subtle dynamics underlying donation and reputation systems impede formal analysis (such as evolutionary stable strategies), but as in wide ranging studies where this is also the case^{15,25,26,65,67}, we employ agent-based simulation. A summary of the pseudocode is also presented in Fig. 1.

Results

Firstly we investigate the emergence of prejudicial groups when all variables in an agent's social comparison heuristic are permitted to evolve. We partition the population into 5 equal sub-populations and consider evolution over 100,000 generations. Figure 2 shows how agents become in-group focussed in three dimensions. Natural selection of players focuses interactions on the in-group (high S_i), accompanied with the emergence of prejudice (presence of high α_i), which occurs within 10,000 generations. At the same time, in-group learning rapidly emerges (high P_i) - aligning a choice of strategy with in-group selection.

Prejudice enters the population through mutation. Agents with strategies that discount the out-group reduce their risk of making donations that may not be reciprocated. As the presence of prejudicial groups increases, agents with a non-prejudicial disposition or an out-group focus for interaction become more exposed to free-riding recipients, because reciprocation has a limited chance of occurring from prejudicial out-groups. This further promotes prejudice, with in-group learning (P_i) ensuring that agents avoid risking a strategy that has been successful in the context of a different group's behaviour. Interestingly, although considerable prejudice is evident, cooperation rapidly evolves, and the social comparison heuristic of $d_i = 0, s_i = 1$ and $u_i = 1$ dominates, consistent with previous research²⁵.

Prejudice and cooperation are often perceived as antagonistic forces. However the results show how cooperation coevolves with prejudice, specifically that prejudice discounts cooperation from the out-group and restricts it to the in-group. Figure 2 also shows that this doesn't come without a cost. Although S_i evolves to preference in-group selection of players for the donation game, opportunities to receive donations from an out-group are lost (Fig. 2(d)), with higher prejudicial groups proportionally contributing the most to this loss.

Parameter(s)	Description	Role in model	Subject to Natural Selection
u_i, d_i, s_i	Rules for i 's donation based on self comparison of the potential recipient j 's reputation, while applying prejudice if j is out-group	Governs i 's donation behaviour	Yes
α_i	Prejudice level of i	Defines the level by which i reduces the universal reputation of out-group agents. Used to define commonality with others to create an in-group G_{t_i, α_i}	Yes
t_i	Fixed trait held by i	Controls the sub-population to which i belongs	No
G_{t_i, α_i}	The in-group to which i belongs, defined by agents with both the same fixed trait and prejudice level as i	Defines the in-group boundary for i , determining whether or not i applies a prejudicial view of other agents	Yes, as a consequence of α_i evolving
S_i	The probability that i plays the donation game with a randomly chosen member of the in-group, rather than from an out-group	Governs how well-mixed the interactions are between agents in different groups	Optional – can evolve (Fig. 2) or exogenously fixed (all other Figs.)
P_i	The probability that i reproduces by selecting a social-comparison heuristic from in-group, rather than from the whole population	Governs how the in-group focused agents are, from learning by copying the social comparison heuristics of others	Optional – can evolve (Fig. 2) or exogenously fixed (all other Figs.)
r_i^U	Universal reputation for i	Status of the donation behaviour of i , based on generalised standing, assuming prejudice is not legitimate when considering the recipient's reputation	No
r_i^G	In-group reputation for i	Status of the donation behaviour of i , from the in-group perspective, which assumes that prejudice is applicable to out-group reputation	No
tp_i	total payoff for i	Accumulates costs and benefits from making and receiving donations	No

Table 1. Key parameters of the model for an agent i . Note that these parameters populate an agent's social comparison heuristic, denoted $H_i = (s_i, u_i, d_i, \alpha_i, P_i, S_i)$. Natural selection occurs with respect to P_i and S_i in Fig. 2, but P_i and S_i are exogenously fixed in all other Figures, as a means to consider scenarios where these variables are set by the external context.

The experiments reported in Fig. 2 allow natural selection to act on all variables in an agent's social comparison heuristic. However, two variables in particular are open to exogenous influence: the tendency for in-group interaction (S_i) and the extent of in-group learning (P_i) versus global learning. These factors abstractly reflect the pluralism of a society, being influenced by issues beyond the individual, such as social policy, government, historical conflict, culture, religion and the media. To further investigate the nature of prejudicial groups, we proceed by considering S_i and P_i as external variables that are set by context (i.e., specified and fixed by the experiment) rather than free to be chosen by natural selection. This allows observation of prejudicial groups assuming different pluralistic scenarios. In particular, it allows us to understand the role of interactions and social learning as variables that contribute to the emergence and mitigation of prejudice.

Cooperation, prejudice and pluralism. Figure 3 shows how prejudice and cooperation is sustained in terms of P_i and S_i when they remain fixed during the simulation, for all agents. This assumes that the extent of pluralism, in terms of interaction and learning, is set by the external context. Lower levels of in-group mixing are necessary to attain lower levels of average prejudice (Fig. 3a), and this is most effective when the chance of global learning is high (low P_i). Cooperation generally benefits from higher in-group mixing (Fig. 3b), which is compounded by increased global learning (low P_i). High in-group mixing reduces the opportunity for cooperation to be diminished by prejudice. The exception here are extreme circumstances (e.g., $S_i < 0.2$ and $P_i \leq 0.5$) where there is limited opportunity for a prejudicial group to gain utility from in-group interactions. The relationship between cooperation and prejudice is further mapped throughout the results.

Small mutations are sufficient to cause prejudicial groups. Susceptibility to prejudice can be considered by the extent to which a small chance of mutation in an agent's α_i value, given an initially non-prejudicial population ($\forall i, \alpha_i = 0$), is sufficient to trigger more widespread prejudicial attitudes in conditions where prejudice can emerge (Fig. 3a, $S_i \geq 0.2$). This can be examined by considering a population with low pluralism, such as one with little out-group interaction (e.g., $S_i = 0.8$) and high in-group learning (e.g., $P_i = 0.9$), consistent with Leimar *et al*⁴⁹.

We consider these fixed values for S_i and P_i . All agents are initially prejudice free ($\alpha_i = 0, \forall i$) and Fig. 4a shows the resultant prejudicial characteristics. Mutation at a rate of $\mu = 1/100$ creates prejudicial individuals relatively infrequently, but when a small number of such individuals occur with the same prejudice level, a non-trivial group can establish itself. Prejudicial individuals prosper by building a strong in-group reputation, while retaining resources rather than donating to the out-group. This limits their universal reputation and limits the extent of donations received from the out-group. When there is dominance of in-group interactions (e.g., $S_i = 0.8$), this is not an impediment to their payoff and it also reduces their costs.

Even when in-group mixing is lower (e.g., $S_i = 0.4$) it is still sufficient for prejudicial groups to establish themselves. Cooperation through in-group interaction involves social comparison heuristics with $s_i = u_i = 1$ and $d_i = 0$ emerging as prevalent, which limit an agent's exposure to those of lower standing within the group, offering relative protection against shirkers, consistent with previous findings²⁵. Non-prejudicial groups become relatively disadvantaged when prejudice is present, as they are susceptible to making out-group donations without reciprocation. This leads to the emergence of defection (i.e., $s_i = u_i = d_i = 0$) as the preferential strategy for these groups.

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1: set of agents  $N = 100$ ; number of traits  $t_n$ ; cost  $c = 0.7$ ; benefit  $b = 1$ ;
2: # Generate initial population of agents
3: for agent  $i \in N$  do
4:   Assign trait at random:  $i \leftarrow (t_i)$ ; Assign  $i$  to group:  $i \in G_{t_i, \alpha_i}$ ;
5:   Assign social-comparison-heuristic at random:  $H_i \leftarrow (s_i, u_i, d_i, \alpha_i, P_i, S_i)$ ;
6: # Perform Evolutionary Simulation
7: for number of generations  $M = 50,000$  do
8:   Initialise:  $tp_i \leftarrow 0$ ;  $r_i^G \leftarrow 0$ ;  $r_i^U \leftarrow 0$ ;
9:   for number of iterations  $m = 5,000$  do
10:    Select donor  $i \in N$  at random;
11:    Select recipient  $j$  at random from  $G_{t_i, \alpha_i}$  with probability  $S_i$ 
12:    else select  $j$  randomly from  $N - G_{t_i, \alpha_i}$ ;
13:    # Action Rules
14:    if  $j \in G_{t_i, \alpha_i}$  then  $i$  compares  $r_i^G$  with  $r_j^G$ 
15:    else  $i$  compares  $r_i^G$  with  $r_j^U \cdot (1 - \alpha_i)$ ;
16:     $s_i, u_i$  and  $d_i$  determine whether or not  $i$  donates to  $j$ ;
17:    if donation occurs then  $tp_i \leftarrow tp_i - c$ ;  $tp_j \leftarrow tp_j + b$ ;
18:    # Assessment Rules ( $r^U, r^G$  vary in the range  $[-5, 5]$ )
19:    if donation occurs then  $r_i^G \leftarrow \min\{r_i^G + 1, 5\}$ ;  $r_i^U \leftarrow \min\{r_i^U + 1, 5\}$ ;
20:    else
21:      if  $r_j^U \geq r_i^U$  then  $r_i^U \leftarrow \max\{r_i^U - 1, -5\}$ ;
22:      if  $j \in G_{t_i, \alpha_i}$  and  $r_j^G \geq r_i^G$  then  $r_i^G \leftarrow \max\{r_i^G - 1, -5\}$ ;
23:      if  $j \notin G_{t_i, \alpha_i}$  and  $r_j^U \cdot (1 - \alpha_i) \geq r_i^G$  then  $r_i^G \leftarrow \max\{r_i^G - 1, -5\}$ ;
24:    # Perform Reproduction
25:    for all agents  $i \in N$  do calculate fitness (Equation (1));
26:    for all agents  $i \in N$  do
27:      if agent  $i$  selected for reproduction (10% chance) then
28:         $i$  selects an agent to copy either from  $G_{t_i, \alpha_i}$  with probability  $P_i$ 
29:        or otherwise copying occurs from  $N$  with probability  $1 - P_i$ ;
30:      if  $i$  copies from  $G_{t_i, \alpha_i}$  then
31:         $j \in G_{t_i, \alpha_i}$  is copied with probability as defined in Equation (2)
32:      else  $j \in N$  is copied with probability as defined in Equation (3);
33:      Update social-comparison-heuristic:  $H_i \leftarrow (s_j, u_j, d_j, \alpha_j, P_j, S_j)$ ;
34:      Mutate each element of  $H_i$  with probability  $\mu = 0.01$ ; Update group  $G_{t_i, \alpha_i}$ ;

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Figure 1. Representation of the pseudocode for simulations, using parameters from Table 1, and supported by further description in the Methods Section.

High levels of out-group interaction suppress prejudice irrespective of global learning. When out-group interactions are high (i.e., S_i is fixed as low), agents become increasingly dependent on the out-group for donation of resources, and universal reputation becomes important. Agents discriminating through prejudice are less likely to make out-group donations, restricting their opportunity to build a high universal reputation that is attractive to out-group donors, impeding the payoff for prejudicial group members. This gives advantage to lower prejudice agents.

Figure 4b shows an example of the evolution of groups under high rates of out-group interaction ($S_i = 0.1$). In contrast to Figure 4a, which is exactly equivalent other than for the setting of S_i ($S_i = 0.9$), Figure 4b shows that extensive out-group interactions are sufficient to promote non-prejudicial groups that are more cooperative.

Even when opportunities for mixing are limited, prejudice can be mitigated through learning.

Societies which are in-group focused with their interactions can still mitigate prejudice through learning from the wider population. Figure 3a shows that for all S_i , when out-group learning increases (P_i is reduced), the average frequency of prejudice is diminished. This exposes agents to a wider range of strategies for selection. However reducing P_i also results in a greater variance in prejudice level frequency (S.D. in the range [0.3, 0.4] when $P_i = 0.3$, $P_i = 0.5$ and $S_i \geq 0.2$; S.D. in the range [0.003, 0.076] when $S_i < 0.2$; S.D. in the range [0.071, 0.18] when $P_i = 0.9$). This is consistent with the population structure having a lesser effect on impeding genetic drift⁴⁹, resulting in sporadic instances of highly prejudicial agents. This occurs alongside strategies in lower prejudice groups that are successful through maintaining a high universal reputation.

Widespread prejudice is challenging to reverse: trait diversity helps. For a fully prejudicial population, we consider the conditions required to reverse prejudice, focusing on the role of fixed traits as provided by sub-populations. In the initial population we assume that all agents are entirely prejudicial ($\alpha_i = 1 \forall i$) and we explore to what extent prejudice diminishes when the number of fixed traits (i.e., sub-populations) is varied, as shown in Figure 5. We exogenously control for S_i and P_i . From previous experimentation (Figure 3) prejudice

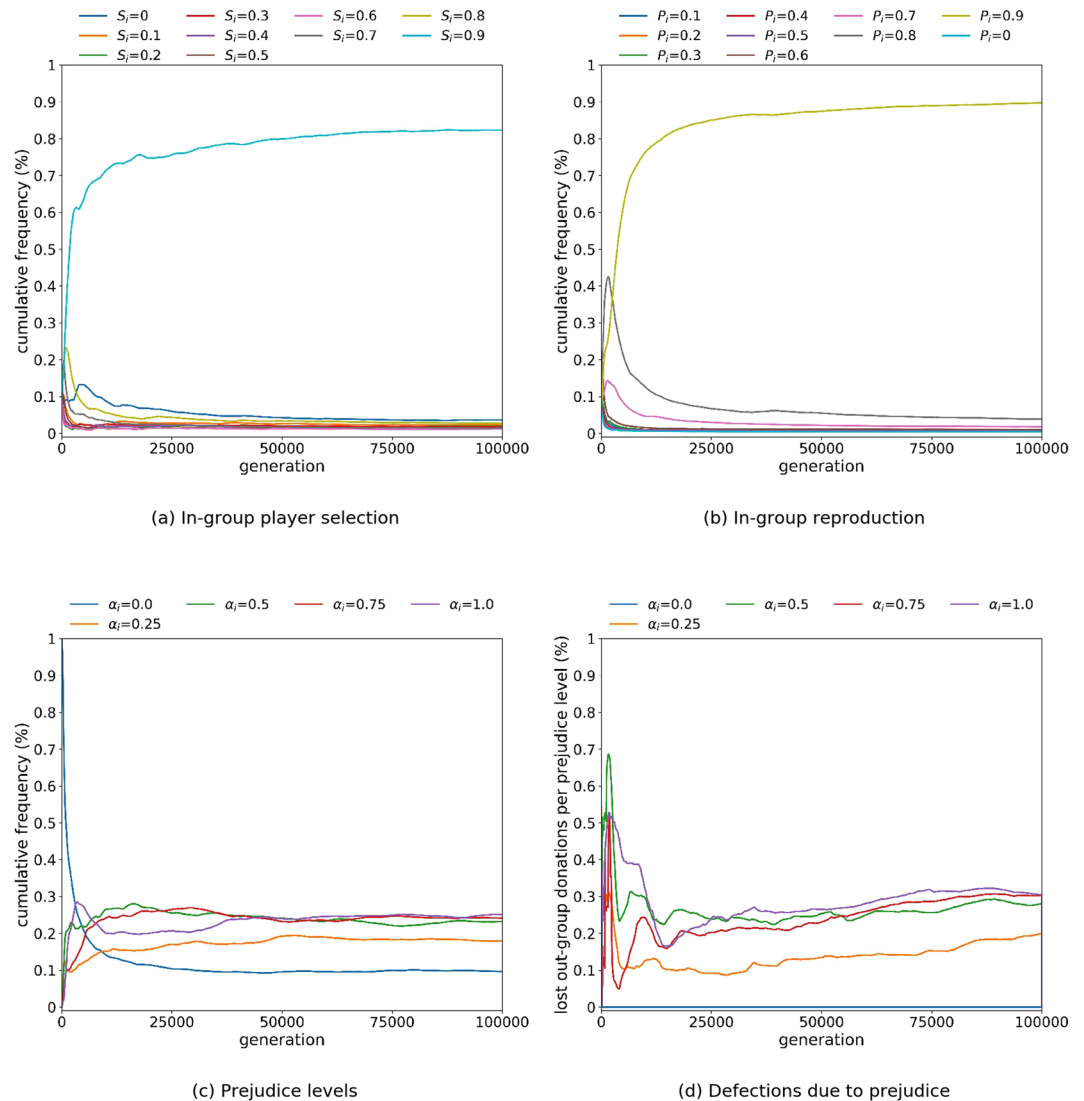


Figure 2. Evolution of 100 agents with 5 equal-size sub-populations over 100,000 generations. Initial conditions: d_i, s_i, u_i, S_i and P_i are randomly selected and $\alpha_i = 0 \forall i$. S_i and P_i are permitted to evolve in the range $\{0, 0.1, \dots, 0.9\}$. The cumulative proportion of agents by values of S_i, P_i and α_i is shown in (a), (b) and (c) respectively. (d) Shows the cumulative proportion of out-group defections that occur as a consequence of prejudice. In the absence of prejudice, this additional proportion of out-group donations would have occurred.

mitigation is most likely to occur under conditions of high out-group mixing (e.g., $S_i < 0.2$). Figure 5a shows that as the number of fixed traits increases, the average level of agent prejudice decreases, but this requires very high out-group mixing ($S_i = 0.1$). Figure 5b shows the cumulative frequency of prejudicial attitudes as the number of fixed traits increase.

Throughout, we evenly split in-group and global learning ($P_i = 0.5$) for all agents. A mutation rate of $\mu = 1/100$ is adopted, being sufficient to trigger the infrequent coexistence of non-prejudicial agents, which form a non-trivial group. When these conditions are present with a single sub-population (i.e., one fixed trait), members of the non-prejudicial group are initially unable to receive donations from any out-group interactions. This constraint is removed when two sub-populations (i.e., two fixed traits) are introduced.

This effect generalises: if we consider a fixed number of total non-prejudicial agents at a particular point in time, as the number of fixed traits (i.e., sub-populations) increase, the non-prejudicial agents can occur with different traits. Therefore the number of non-prejudicial out-group members increase. This means that each non-prejudicial agent has a greater chance of receiving a donation from a non-prejudicial out-group member, increasing the payoff for non-prejudicial agents. As a result, increasing the number of traits promotes lower prejudice.

Prejudice emerges more easily when group sizes are imbalanced. Previous work concerning the analysis of intolerance under economic stress⁶⁸ identified that it is easier for intolerance to emerge in minorities (i.e., when groups have different sizes). This involved consideration of the leading eight strategies⁵⁰ over two

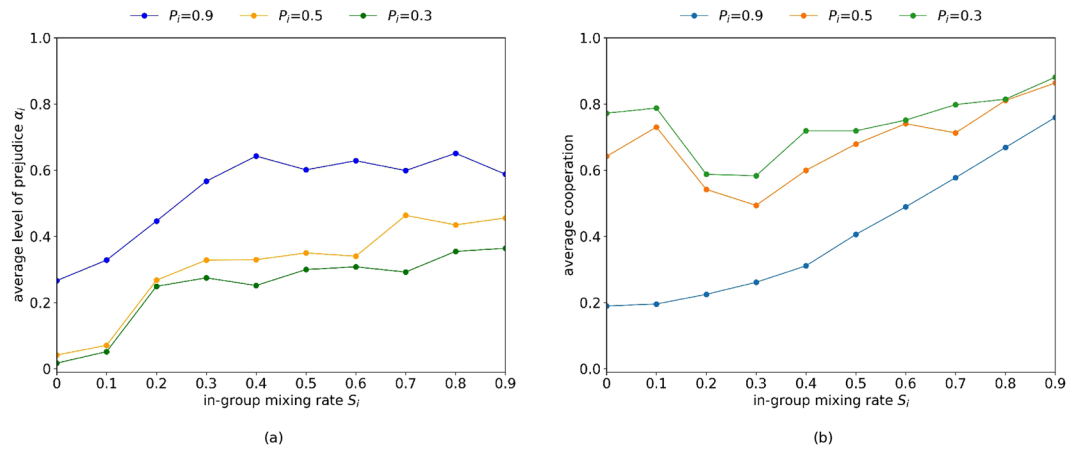


Figure 3. (a) The average level of prejudice vs. in-group mixing for different in-group learning rates and (b) the average cooperation vs. in-group mixing for different in-group learning rates. S_i and P_i are a-priori fixed for all agents, and results represent the average of 10 randomly seeded runs, each conducted for 50,000 generations. Initial configuration involves $\alpha_i = 0, \forall i$. Mutation applied at the rate $\mu = 1/100$ to each variable d_i, s_i, u_i and α_i . Five equally sized sub-populations are assumed.

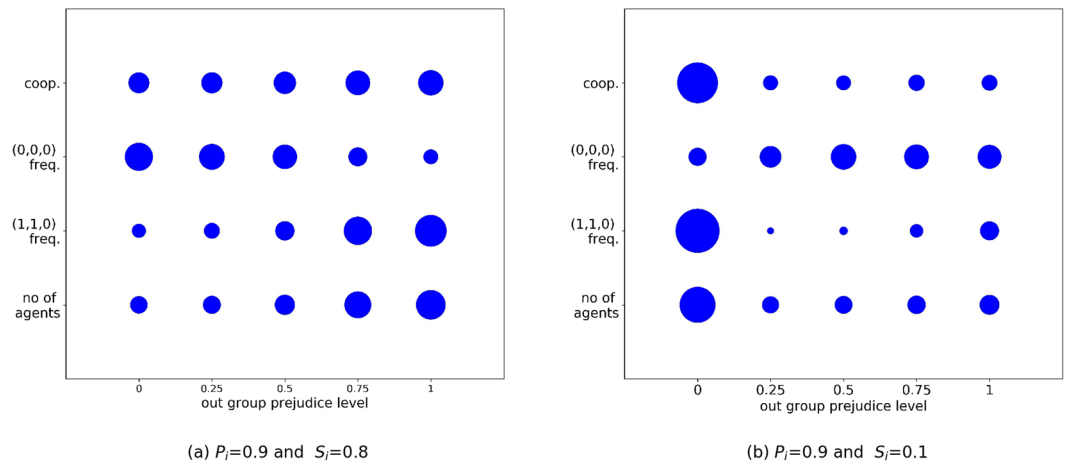


Figure 4. The relative cumulative frequency of agents' characteristics by prejudice level. Characteristics concern number of agents (no of agents); instances of the dominant cooperative social comparison heuristic $s_i = u_i = 1$ and $d_i = 0$ ((1,1,0) freq.); instances of the defection social comparison heuristic $s_i = u_i = d_i = 0$ ((0,0,0) freq.); instances of cooperation (coop). All simulations assume five sub-populations (i.e., 5 traits). (a) $P_i = 0.9$ and $S_i = 0.8$; (b) $P_i = 0.9$ and $S_i = 0.1$, fixed for all agents over 50,000 generations. The circles represent the relative proportions of agents with those characteristics across ten randomly seeded runs. Starting configurations involve all agents having zero prejudice ($\forall i, \alpha_i = 0$).

groups. We investigate the extent to which difference in group size has a similar effect in the context of prejudicial behaviours.

In Figure 6 we examine the evolution of two non-prejudicial groups, each involving a different fixed trait. Using two scenarios, we compare the effect of varying the initial group size, evenly splitting the agents in one scenario and splitting them 90/10 in the other. Group evolution is particularly sensitive to the extent of in-group learning (P_i), and a degree of out-group interaction has to be present for effects to be observed. Figure 6 shows that when P_i allows a mix of learning from the in-group and the wider population (e.g., $P_i = 0.5$), imbalance in group size leads to significantly greater prejudice. This is because any economic advantage from being prejudicial has a greater chance of been copied in-group in a smaller group, purely as a consequence of the smaller group size. Consequently prejudicial views rapidly spread in the smaller sub-population, creating prejudicial groups. The presence of global learning then promotes prejudice in the larger sub-population involving the other trait. This is not seen when the initial sub-groups have the same size.

In-group mixing and global learning both promote cooperation, but with opposing implications for prejudice. Other than for the extreme circumstances (e.g., $S_i < 0.2$ and $P_i \leq 0.5$) where there is limited opportunity for a prejudicial group to gain utility from in-group interactions, attaining cooperation invokes

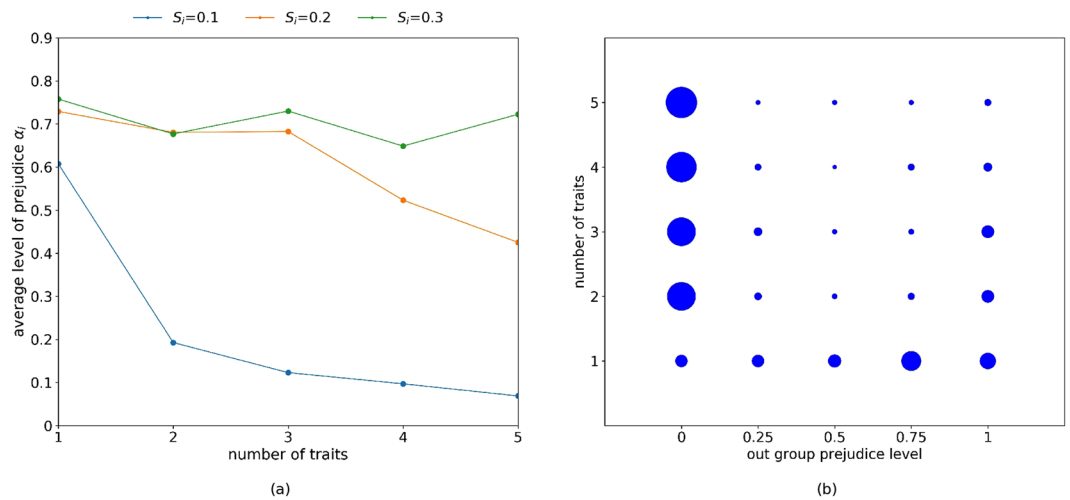


Figure 5. (a) Average level of prejudice as a function of the number of traits (sub-populations) with $P_i = 0.5$ after 50,000 generations. (b) The cumulative distribution of instances of agent's prejudice level by number of fixed traits. The circles represent the relative cumulative frequency over ten randomly seeded runs with $P_i = 0.5$ and $S_i = 0.1$, using 50,000 generations per run. The starting configuration involves all agents being fully prejudicial ($\alpha_i = 1, \forall i$), and equally distributed over the number of sub-populations involved.

prejudice in some form. We explore this by exogenously controlling for S_i and P_i , and examining how prejudice and cooperation co-evolve. Figure 7 shows cooperation as a function of prejudice from two perspectives. Figure 7a shows that increasing in-group interactions promotes cooperation while also increasing prejudice and Figure 7b shows that greater levels of global learning promote cooperation, while also reducing prejudice.

These results implicitly show the roles of S_i and P_i : in combination, they provide a trade-off in how cooperation can be achieved and show the role of interaction and learning in sustaining group attitudes. In terms of cooperation, high in-group mixing (high S_i) can be compensated for through high levels of out-group learning (high P_i), and vice-versa. For example consider a total cooperation level of 0.7 in Figure 7b. This can be achieved with high out-group mixing (e.g., $S_i \in [0, 0.1]$) and medium in-group learning (e.g., $P_i = 0.5$), which is accompanied by low prejudice levels ($\alpha_i \in [0, 0.1]$). Similar levels of cooperation can be attained with medium in-group mixing (e.g., $S_i \in [0.2, 0.7]$) and low in-group learning (e.g., $P_i = 0.3$), which is accompanied by medium prejudice levels ($\alpha_i \in [0.3, 0.4]$). Furthermore, we can achieve the same cooperation with high in-group mixing (e.g., $S_i \in [0.8, 0.9]$) and high in-group learning (e.g., $P_i = 0.9$), which is accompanied by high prejudice levels ($\alpha_i \in [0.6, 0.7]$) which reflect the in-group focus.

Note that all results involve a cost-to-benefit (c/b) ratio of 0.7. This is chosen based on analysis of the evolution of cooperation and social comparison²⁵. This c/b ratio has been adopted because it is relatively conservative, in the sense that donation is a relatively costly action. Using a lower c/b ratio means that at the reproduction stage, less impact from defectors is apparent, because lower costs are incurred from donation to them. Therefore prejudicial strategies, that seek to benefit by not donating, provide less of an advantage. This means that alternative lower c/b ratios result in lower prejudice overall, if applied in this model.

Discussion

The model we have introduced allows computational exploration of how attitudes towards the out-group, not just behaviours, are sustained and evolve. In particular, the results provide insight into the origins of prejudicial groups as a consequence of natural selection. The model addresses the commonality of prejudicial attitudes as a phenotypic tag that identifies an ideological group. This allows a simple representation through which discriminatory (or non-discriminatory) groups may emerge within a sub-population, enabling modelling of concepts such as nationalism. The model complements previous work⁶⁸ that has analytically studied the emergence of intolerance based on the leading eight donation strategies.

Our general approach involves an agent's prejudice creating a differential between the reputations of the in-group and those of the out-group. In addition, prejudice provides a basis for an "in-group" to form in the first place, from a common prejudicial disposition. This is a new relationship between out-group discrimination and in-group formation, which is a key aspect of the model, as seen in elements of human behaviour. Note that in-group favoritism could also take hold in prejudicial groups. However, to isolate factors, we have considered the effects of a negative prejudicial bias, but additionally, a positive reputational bias aligned with in-group favoritism could be added. This would further promote the differential between in-group and out-group reputation. Considering the effects of in-group favoritism in prejudicial groups, beyond creating a reputation differential, is possible future work.

The model is based on indirect reciprocity^{22,49,62,69}, a form of cooperation that strongly identifies with human behavior as compared to most other species. Indirect reciprocity is generally sustained by agents acting in response to the reputation of a third party²³. In our model, agents undertake self-comparison of their reputation against that of the potential recipient, whose reputation is discounted by prejudice if they are out-group. Strategies

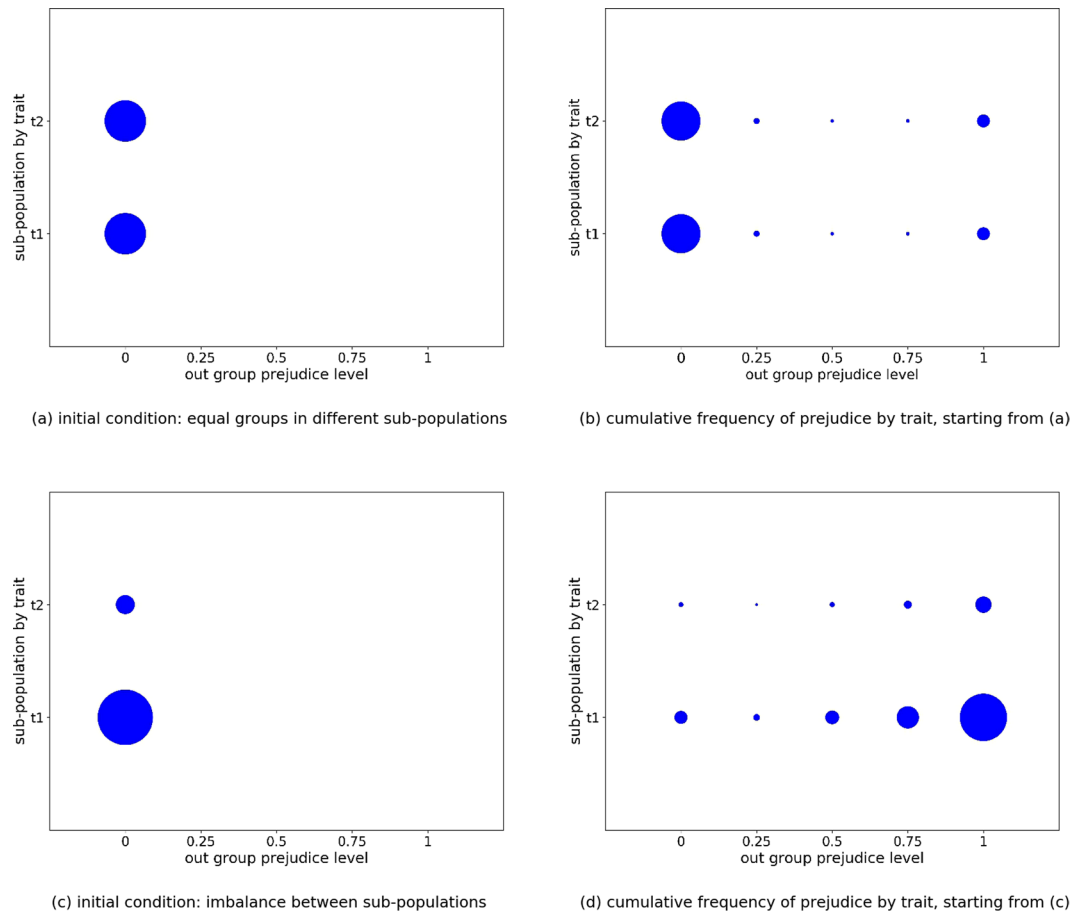


Figure 6. The relative cumulative frequency of agent's prejudice levels by trait, in a population of 100 agents and two traits. $P_i = 0.5$ and $S_i = 0.5$ are fixed for all agents, with simulations carried out using 50,000 generations. Initially all agents i have $\alpha_i = 0$. The circles represent the relative proportions of agents with those particular characteristics, accumulated over ten randomly seeded runs (see (b) and (d)). Two alternative starting configurations are employed: an equal split between sub-populations (see (a)) and a 90/10 imbalance between sub-populations (see (c)).

for donation evolve based on self-comparison, alongside the evolution of an agent's prejudice level, and an agent's variables concerning the probabilities of in-group interaction and in-group (verses global) learning. At face value, the action rules that we adopt, based on social comparison, differ from the seminal work identifying the “leading eight”⁵⁰. However in previous work we identified their close relationship with our approach²⁵. The social norms (assessment rules) we employ are based on a generalisation of standing^{60,62}, that are effective in supporting cooperation²⁵. However, we note that alternative assessment rules, particularly within the context of extreme prejudicial groups, could be applied within our overall modelling framework.

While in-group favoritism has been studied through explicit models¹⁴ and as a consequence of the “green beard” effect in tag-based models^{15,26–32}, out-group prejudice has received little explicit investigation, with it being easily conflated with in-group favoritism. To the best of our knowledge, only in^{33,34} are tag-based models presented that involve parameters to discount others based on dis-similarity, although prejudicial groups are not defined. Assignment errors often feature in tag-based (and other) models, which generally hinder the evolution of global cooperation levels and cooperation between individuals with different tags. It is possible that prejudice could be expressed through larger assignment errors, but forming groups on that basis would require them to be public. However this is an interesting possible future research direction.

The results in this work allow us to observe how prejudicial groups and cooperation co-evolve. Prejudice and cooperation are often considered to be opposing forces. However we find that they are concurrently sustained, but with significant structural consequences for the population. Prejudice directs cooperation into “islands”⁴⁹ represented by groups holding the same out-group attitude. Thus prejudicial groups promote assortment with potential cooperators⁷⁰, or at least reduce the risk of assortment with those of a perceived threat to defection⁴¹. While prejudice acts to reduce the risk of donating to groups that may not reciprocate, cooperation evolves in-group. This is combined with agents preferring to play the donation game in-group, and with learning at the evolutionary step predominantly copying in-group strategies, consistent with observations from the origins of the human population (e.g., $P_i = 0.9$)⁴⁹. Also consistent with previous findings²⁵, the dominant heuristic of donating to those

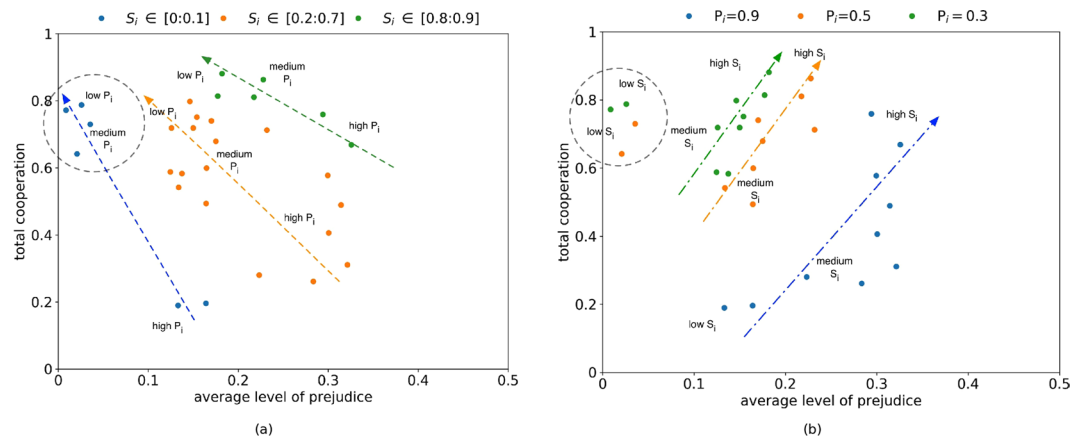


Figure 7. Total cooperation as a function of the average level of prejudice. Calculations are the result of 10 randomly seeded runs. Note that (a) and (b) show the same data points, but referenced by different parameters. (a) For fixed values of P_i ($P_i = 0.3, 0.5, 0.9$), the effects of varying S_i are indicated. (b) For low, medium and high values of S_i , the effects of varying P_i are indicated.

with similar or greater reputation levels sustain cooperation emerges in-group. Although prejudice results in lost opportunities to receive out-group donations, this is mitigated through in-group cooperation.

Beyond the economics of payoff, it is important to note that in-group cooperation in lieu of cooperation across the wider population can have significant negative societal implications, occurring as a consequence of the resultant disconnected social network structure. When cooperation is restricted in-group, such groups tend to become increasingly isolated, interacting and learning predominantly from their own members. This disrupts social and cultural connectivity, supporting the “filter bubble” problem where isolated in-group communication affirms and reinforces the group’s own perspective without exposure to wider discourse^{71,72}. Structurally, an in-group focus can also diminish the potential benefit from weak ties⁷³, which impedes a wide range of societal and economic issues. For example, individuals may become restricted in their opportunity to create or exploit social capital from bridging⁷⁴, limiting social mobility for group members⁷⁵. More generally, the diversity of individuals’ relationships is strongly correlated with the economic development of communities⁷⁶. In the context of organisational innovation, actors who can exploit weak ties have a greater source for ideas⁷⁷, thereby exploiting diversity. We also note that strong external cultural factors can contribute to the tendency for agents to engage in out-group interaction and global learning, which may be slow to change, effectively being fixed over long durations.

Analysis of the leading eight donation strategies under two sub-populations⁶⁸ shows that once intolerance invades one (or both) sub-populations, it becomes difficult to counter. Consistent with this, our results highlight that random instances of prejudice in agents are sufficient for prejudicial groups to become more widespread. After prejudicial groups become manifested in a sub-population, prejudicial attitudes spread as a means to prevent exploitation from the out-group. As a consequence, reversing prejudice is a significant challenge, and multiple factors have influence. Firstly, sub-population diversity increases the opportunity to counter prejudice, enabling out-group cooperation with non-prejudicial groups. Also societies based on high levels of out-group interaction and high levels of global learning provide mitigation. Critically, we also find that in-group mixing and global learning both promote co-operation, but with opposing implications for prejudice. This is the first known characterisation of such a relationship. Notably high levels of cooperation are possible, but with completely different interaction and learning behavior from agents.

An interesting feature of this study concerns the minimal cognitive ability of the agents involved. This decouples prejudice from the psychological and social capabilities that are distinctive in humans^{78–80}, and through which prejudice is frequently explained in society. This is significant because research^{10,81–85} on how inter-group contact leads to attitude change is dependent on sophisticated cognition. In particular, the nature of contact through relationships, as perceived through higher order cognition, predicts prejudice in humans^{86–88}. However, our model shows that prejudicial groups can easily manifest themselves through natural selection, as applied to agents with primitive cognitive abilities. Furthermore, we note that the pluralistic nature of the environment, in terms of embedded dispositions for out-group mixing, global learning, and the diversity of sub-populations, significantly influence how prejudicial groups evolve.

The findings of our research are also interesting in the context of machines and autonomous systems⁸⁹, in particular for scenarios involving one-shot interactions and learning, where collectively, devices need to sustain cooperation by periodically benefiting from the resources of others, while not necessarily encountering them again. Examples of these scenarios are currently being considered in the context of future communications^{90,91} and may also emerge in future human-machine interaction⁹². Our study highlights the scope for prejudice to emerge in populations of autonomous machines that have simple cognitive abilities, such as being driven by local interactions and the assessment of others. This reaffirms that the distributed collective intelligence of machines is also a social endeavour, and it is potentially susceptible to prejudicial phenomena as seen in the human population.

Methods

We extend a framework concerning the evolution of indirect reciprocity from the social comparison of reputation²⁵. The model involves a population of 100 agents, composed of sub-populations, each denoted SP_i , where the agents in SP_i are given a common immutable trait t . Each agent belongs to precisely one sub-population (see Agents and Groups Section). We vary the number of sub-populations for different experiments. Agents are randomly selected to play the donation game (see Action Rules Section), and the donor agent's reputations are updated (see Assessment Rules Section). After 5000 donation games, which constitutes one generation, natural selection is performed (see Selection and Reproduction Section). This cycle is repeated for 50,000 generations unless otherwise stated. All results represent an average of 10 randomly seeded runs. We assume that all agents commence with zero prejudice ($\alpha_i = 0$), unless otherwise stated. Information on accessing data supporting the results is available⁹³. A summary of the related pseudocode is presented in Figure 1.

Agents and Groups. Each agent i is represented by a *social comparison heuristic* denoted $(s_i, u_i, d_i, \alpha_i, P_i, S_i)$. These are acted upon by evolution at the end of each generation, and they govern the donation and reproductive behavior of each individual. Each agent i remains in its original sub-population throughout the simulation, but may move between the prejudicial groups within that sub-population, as a consequence of the reproductive step.

Binary variables s_i , u_i and d_i concern an agent's action rules, which are well-understood in isolation²⁵. These variables (action rules) are randomly initialised. α_i represents the agent's out-group prejudice level, where $\alpha_i \in \{0, 0.25, 0.5, 0.75, 1\}$. The prejudice level for an agent i is denoted α_i . We set $\alpha_i = 0$, for all agents i , at the start of each generation, unless otherwise stated. S_i and P_i range in the set $\{0, 0.1, \dots, 0.9\}$ unless the experiment fixes S_i and P_i . t_i denotes the particular trait of the sub-population to which i belongs.

A *prejudicial group* $G_{t,\alpha}$ is the maximal subset of agents with the same trait t and prejudice level α . Therefore prejudicial groups partition each sub-population. An out-group member to $G_{t,\alpha}$ is any agent not carrying both the prejudicial attitude α and trait t . Agent i belongs to group $G_{t,\alpha}$ if and only if $t_i = t$ and $\alpha_i = \alpha$.

The variable S_i controls the selection of i 's potential recipient j for each donation game, determining the chance that j is selected from in-group. P_i determines the chance that i 's social comparison heuristic evolves based on the in-group (referred to as in-group learning), as compared to evolutionary influence from the whole population⁴⁹. In numerous experiments we keep S_i and P_i fixed, to understand their effect on the evolution of prejudicial groups.

Each agent maintains two reputations that are used to represent i 's reputation from an in-group perspective (r_i^G) and a universal perspective that assumes no prejudice (r_i^U). Reputations vary between -5 and $+5$ in integer steps^{25,49}.

Action Rules. In each generation we perform 5000 random agent selections where each selected agent plays the donation game. Within a particular generation, assume that agent $i \in G_{t_i, \alpha_i}$ is selected to play with j . The probability that j is selected from the in-group is S_i . Otherwise j is selected from the out-group. Whether or not i donates is governed by s_i , u_i and d_i , upon i comparing its reputation with that of j . If j is in-group ($j \in G_{t_i, \alpha_i}$) then i compares r_i^G with r_j^G . Otherwise, when j is out-group, i compares r_i^G with $r_j^U \cdot (1 - \alpha_i)$, which is j 's reputation discounted by i 's prejudice.

Upon comparison, r_i^G is either the smaller reputation (upward self-comparison from i), the greater reputation (downward self-comparison from i) or the comparison is equal (similarity). The binary variables from i 's social comparison heuristic govern whether or not i donates in the presence of similarity (s_i), upward self-comparison (u_i) or downward self-comparison (d_i). When $i \in G_{t_i, \alpha_i}$, $\mathbb{1}_{G_{t_i, \alpha_i}} = 1$, and i is selected to play in-group, no cost is incurred and no donation is made.

The act of donation from agent i to j results in an economic transaction, with cost c to i and benefit b to j . From previous experimentation²⁵ we assume a c/b ratio of 0.7. Within a generation, each agent i tracks its accumulation of benefits received less costs from donations (tp_i).

Assessment Rules. Assessment rules are implemented immediately after action rules (i.e., after a donation game between agents i and j). Both the universal and in-group reputations are updated, based on generalised standing²⁵. Standing follows the principle that donations increment reputation, and defection reduces reputation, unless there is a legitimate reason. In this case we adopt the reason to be that an agent determines the recipient's reputation as less than their own.

Both r_i^U and r_i^G are incremented when the donor i cooperates. To update r_i^U , if agent i defects on j then r_i^U is decremented unless $r_j^U < r_i^U$ (i.e., j is perceived to be less cooperative and of lower standing), in which case the universal reputation r_i^U remains unchanged. An exactly analogous process is applied to update r_i^G when i and j are in-group. When j is out-group to i and agent i defects on j , then r_i^G is decremented unless $r_j^U \cdot (1 - \alpha_i) < r_i^G$ (i.e., j is perceived to be less cooperative and of lower standing than i , while also taking into account i 's out-group prejudice). At the beginning of a new generation, the in-group and universal reputations of all agents are reset to zero and reputations are assumed to be public, visible to all agents.

Selection and Reproduction. Each reproductive step occurs after 5000 randomly selected agent pairs have played the donation game (one generation). To counter potential genetic drift in small sub-populations, an agent's chance of reproduction, at the reproductive step, is limited to 10%, which is similar to approaches applied in a spatial context (e.g.^{15,65}). The reproductive step is repeated after each of 50,000 generations, unless otherwise stated.

At a reproductive step, all agents are considered for reproduction. If agent i is successful (10% chance), it copies the social comparison heuristic of another agent; otherwise agent i carries forward its current social comparison heuristic to the next generation.

To perform reproduction, the total payoff for an agent during a generation, denoted tp_i , is defined as: the total benefit received from donations to i , less the total cost i has incurred in making donations. We let tp^* denote the lowest negative value of total payoff across all agents i , in the current generation, with $tp^* = 0$ if such a negative value of tp^* doesn't exist. Then the fitness f_i for an agent i during a generation is defined as

$$f_i = tp^* + tp_i + \delta \quad (1)$$

where δ is a small constant. Throughout we apply $\delta = 1$. Note that tp^* and δ ensure that fitness is non-zero, while tp_i provides a relative weighting based on payoff.

If agent i goes forward to update its social comparison heuristic, then agent i selects an agent j from which to copy, using relative fitness. Copying takes place from either the in-group (i.e., locally) with probability P_i , or from the whole population with probability $1 - P_i$. This follows the Island model principle^{49,66}, with Islands corresponding to prejudicial in-groups. If an agent $i \in G_{t_i, \alpha_i}$ copies a social comparison heuristic from the in-group, then the probability of copying the social comparison heuristic of agent $j \in G_{t_i, \alpha_i}$ is:

$$\frac{f_j}{\sum_{k \in G_{t_i, \alpha_i}} f_k} \quad (2)$$

Alternatively if an agent $i \in G_{t_i, \alpha_i}$ copies a social comparison heuristic from the whole population of agents, denoted N , then the probability of copying the social comparison heuristic of agent $j \in N$ is:

$$\frac{f_j}{\sum_{k \in N} f_k} \quad (3)$$

A random mutation to each element of the agent's new social comparison heuristic (unless, in the case of S_i and P_i , they are fixed by the experiment), at the rate of 1% across each variable²⁵. This general clonal approach to reproduction is dependent on a single parent and is commonly used in previous studies on indirect reciprocity based on evolutionary simulation^{22,24,25,49}.

References

- Rudman, L. A., Moss-Racusin, C. A., Phelan, J. E. & Nauts, S. Status incongruity and backlash effects: Defending the gender hierarchy motivates prejudice against female leaders. *J. Exp. Soc. Psychol.* **48**, 165–179 (2012).
- Nelson, T. D. *Ageism: Stereotyping and prejudice against older persons*. (MIT press, 2004).
- Herek, G. M. Confronting sexual stigma and prejudice: Theory and practice. *J. Soc. Issues* **63**, 905–925 (2007).
- Bar-Tal, D. & Teichman, Y. *Stereotypes and prejudice in conflict: Representations of Arabs in Israeli Jewish society*. (Cambridge University Press, 2005).
- Bobo, L. Group conflict, prejudice, and the paradox of contemporary racial attitudes. In *Eliminating racism*, 85–114 (Springer, 1988).
- Fiske, S. T. What we know now about bias and intergroup conflict, the problem of the century. *Curr. Dir. Psychol. Sci.* **11**, 123–128 (2002).
- Meleady, R., Seger, C. R. & Vermue, M. Examining the role of positive and negative intergroup contact and anti-immigrant prejudice in brexit. *Br. J. Soc. Psychol.* (2017).
- Tajfel, H., Billig, M. G., Bundy, R. P. & Flament, C. Social categorization and intergroup behaviour. *Eur. journal social psychology* **1**, 149–178 (1971).
- Turner, J. C., Hogg, M. A., Oakes, P. J., Reicher, S. D. & Wetherell, M. S. *Rediscovering the social group: A selfcategorization theory*. (Basil Blackwell, 1987).
- Dovidio, J. F., Gaertner, S. L. & Validzic, A. Intergroup bias: status, differentiation, and a common in-group identity. *J. personality social psychology* **75**, 109 (1998).
- Tarnita, C. E., Antal, T., Ohtsuki, H. & Nowak, M. A. Evolutionary dynamics in set structured populations. *Proc. Natl. Acad. Sci.* **106**, 8601–8604 (2009).
- Gray, K. *et al.* The emergence of “us and them” in 80 lines of code: Modeling group genesis in homogeneous populations. *Psychol. science* **25**, 982–990 (2014).
- Balliet, D., Wu, J. & De Dreu, C. K. Ingroup favoritism in cooperation: A meta-analysis (2014).
- Fu, F. *et al.* Evolution of in-group favoritism. *Sci. reports* **2**, 460 (2012).
- Hammond, R. A. & Axelrod, R. Evolution of contingent altruism when cooperation is expensive. *Theor. population biology* **69**, 333–338 (2006).
- Yamagishi, T., Jin, N. & Kiyonari, T. Bounded generalized reciprocity: Ingroup boasting and ingroup favoritism. *Adv Gr Process.* **16**, 161–197 (1999).
- Allport, G. W. *The nature of prejudice*. (Cambridge/Reading, MA: Addison-Wesley, 1954).
- Fiske, S. T. Stereotyping, prejudice, and discrimination at the seam between the centuries: Evolution, culture, mind, and brain. *Eur. J. Soc. Psychol.* **30**, 299–322 (2000).
- Efferson, C., Lalive, R. & Fehr, E. The coevolution of cultural groups and ingroup favoritism. *Sci.* **321**, 1844–1849 (2008).
- Brewer, M. B. The psychology of prejudice: Ingroup love and outgroup hate? *J. social issues* **55**, 429–444 (1999).
- Smith, J. M. *Evolution and the Theory of Games*. (Cambridge university press, 1982).
- Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity by image scoring. *Nat.* **393**, 573–577 (1998).
- Nowak, M. A. Five rules for the evolution of cooperation. *science* **314**, 1560–1563 (2006).
- Nowak, M. A. & Sigmund, K. The dynamics of indirect reciprocity. J. theoretical. *Biol.* **194**, 561–574 (1998).
- Whitaker, R. M., Colombo, G. B., Allen, S. M. & Dunbar, R. I. A dominant social comparison heuristic unites alternative mechanisms for the evolution of indirect reciprocity. *Sci. Reports* **6** (2016).
- Riolo, R. L., Cohen, M. D. & Axelrod, R. Evolution of cooperation without reciprocity. *Nat.* **414**, 441 (2001).

27. Roberts, G. & Sherratt, T. N. Behavioural evolution (communication arising): Does similarity breed cooperation? *Nat.* **418**, 499 (2002).
28. Hales, D. Cooperation without memory or space: Tags, groups and the prisoner's dilemma. In *International Workshop on Multi-Agent Systems and Agent-Based Simulation*, 157–166 (Springer, 2000).
29. Jansen, V. A. & Van Baalen, M. Altruism through beard chromodynamics. *Nat.* **440**, 663 (2006).
30. Traulsen, A. & Nowak, M. A. Chromodynamics of cooperation in finite populations. *PLoS One* **2**, e270 (2007).
31. Masuda, N. & Ohtsuki, H. Tag-based indirect reciprocity by incomplete social information. *Proc. Royal Soc. Lond. B: Biol. Sci.* **274**, 689–695 (2007).
32. Antal, T., Ohtsuki, H., Wakeley, J., Taylor, P. D. & Nowak, M. A. Evolution of cooperation by phenotypic similarity. *Proc. Natl. Acad. Sci.* **106**, 8597–8600 (2009).
33. Colman, A. M., Browning, L. & Pulford, B. D. Spontaneous similarity discrimination in the evolution of cooperation. *J. Theor. Biol.* **299**, 162–171 (2012).
34. Houy, N. Evolution of cooperation with similarity to an archetype. *J. theoretical biology* **332**, 78–88 (2013).
35. Choi, J.-K. & Bowles, S. The coevolution of parochial altruism and war. *science* **318**, 636–640 (2007).
36. Bowles, S. Being human: Conflict: Altruism's midwife. *Nat.* **456**, 326–327 (2008).
37. Bernhard, H., Fischbacher, U. & Fehr, E. Parochial altruism in humans. *Nat.* **442**, 912 (2006).
38. Rusch, H. The evolutionary interplay of intergroup conflict and altruism in humans: a review of parochial altruism theory and prospects for its extension. *Proc. Royal Soc. Lond. B: Biol. Sci.* **281**, 20141539 (2014).
39. Abbink, K., Brandts, J., Herrmann, B. & Orzen, H. Parochial altruism in inter-group conflicts. *Econ. Lett.* **117**, 45–48 (2012).
40. Lumsden, C. J. & Wilson, E. O. *Genes, mind, and culture: The coevolutionary process*. (World Scientific, 1981).
41. Cottrell, C. A. & Neuberg, S. L. Different emotional reactions to different groups: a sociofunctional threat-based approach to “prejudice”. *J. personality social psychology* **88**, 770 (2005).
42. Atran, S. The devoted actor: unconditional commitment and intractable conflict across cultures. *Curr. Anthropol.* **57**, S192–S203 (2016).
43. Sheikh, H., Gómez, Á. & Atran, S. Empirical evidence for the devoted actor model. *Curr. Anthropol.* **57**, S204–S209 (2016).
44. Duckitt, J. A dual-process cognitive-motivational theory of ideology and prejudice. *Adv. experimental social psychology* **33**, 41–113 (2001).
45. Yoeli, E., Hoffman, M., Rand, D. G. & Nowak, M. A. Powering up with indirect reciprocity in a large-scale field experiment. *Proc. Natl. Acad. Sci.* **110**, 10424–10429 (2013).
46. Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity. *Nat.* **437**, 1291–1298 (2005).
47. Panchanathan, K. & Boyd, R. Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nat.* **432**, 499–502 (2004).
48. Fehr, E. Human behaviour: don't lose your reputation. *Nat.* **432**, 449–450 (2004).
49. Leimar, O. & Hammerstein, P. Evolution of cooperation through indirect reciprocity. *Proc. Royal Soc. Lond. B: Biol. Sci.* **268**, 745–753 (2001).
50. Ohtsuki, H. & Iwasa, Y. The leading eight: social norms that can maintain cooperation by indirect reciprocity. *J. Theor. Biol.* **239**, 435–444 (2006).
51. Festinger, L. A theory of social comparison processes. *Hum. relations* **7**, 117–140 (1954).
52. Buunk, A. P. & Gibbons, F. X. Social comparison: The end of a theory and the emergence of a field. *Organ. Behav. Hum. Decis. Process.* **102**, 3–21 (2007).
53. Suls, J. M. & Miller, R. L. *Social comparison processes: Theoretical and empirical perspectives*. (Hemisphere, 1977).
54. Suls, J. & Wheeler, L. *Handbook of social comparison: Theory and research*. (Springer Science & Business Media, 2013).
55. Fiske, S. T. & Taylor, S. E. *Social cognition: From brains to culture* (Sage, 2013).
56. Chudek, M. & Henrich, J. Culture-gene coevolution, norm-psychology and the emergence of human prosociality. *Trends Cogn. Sci.* **15**, 218–226 (2011).
57. Rand, D. G. & Nowak, M. A. Human cooperation. *Trends Cogn. Sci.* **17**, 413–425 (2013).
58. De Waal, F. B. & Luttrell, L. M. Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? *Ethol. Sociobiol.* **9**, 101–118 (1988).
59. Alexander, R. D. *The biology of moral systems*. (Transaction Publishers, 1987).
60. Sugden, R. *The economics of rights, co-operation and welfare*. (Blackwell Oxford, 1986).
61. Wedekind, C. & Milinski, M. Cooperation through image scoring in humans. *Sci.* **288**, 850–852 (2000).
62. Panchanathan, K. & Boyd, R. A tale of two defectors: the importance of standing for evolution of indirect reciprocity. *J. Theor. Biol.* **224**, 115–126 (2003).
63. Brandt, H. & Sigmund, K. The logic of reprobation: assessment and action rules for indirect reciprocation. *J. Theor. Biol.* **231**, 475–486 (2004).
64. Ohtsuki, H. & Iwasa, Y. How should we define goodness?—reputation dynamics in indirect reciprocity. *J. Theor. Biol.* **231**, 107–120 (2004).
65. Axelrod, R. M. *The evolution of cooperation*. (Basic books, 2006).
66. Wright, S. Isolation by distance. *Genet.* **28**, 114 (1943).
67. Axelrod, R. An evolutionary approach to norms. *Am. political science review* **80**, 1095–1111 (1986).
68. Martinez-Vaquero, L. A. & Cuesta, J. A. Spreading of intolerance under economic stress: Results from a reputation-based model. *Phys. Rev. E* **90**, 022805 (2014).
69. Boyd, R. & Richerson, P. J. The evolution of indirect reciprocity. *Soc. Networks* **11**, 213–236 (1989).
70. Fletcher, J. A. & Doebeli, M. A simple and general explanation for the evolution of altruism. *Proc. Royal Soc. Lond. B: Biol. Sci.* **276**, 13–19 (2009).
71. Bozdag, E. & van den Hoven, J. Breaking the filter bubble: democracy and design. *Ethics Inf. Technol.* **17**, 249–265 (2015).
72. Pariser, E. *The filter bubble: What the Internet is hiding from you*. (Penguin UK, 2011).
73. Granovetter, M. S. The strength of weak ties. *Soc. networks* **347–367** (1977).
74. Lin, N. Building a network theory of social capital. In *Social capital*, 3–28 (Routledge, 2017).
75. Dominguez, S. & Watkins, C. Creating networks for survival and mobility: Social capital among african-american and latin-american low-income mothers. *Soc. problems* **50**, 111–135 (2003).
76. Eagle, N., Macy, M. & Claxton, R. Network diversity and economic development. *Sci.* **328**, 1029–1031 (2010).
77. Ruef, M. Strong ties, weak ties and islands: structural and cultural predictors of organizational innovation. *Ind. Corp. Chang.* **11**, 427–449 (2002).
78. Barton, R. A. & Dunbar, R. I. Evolution of the social brain. *Machiavellian intelligence II: Extensions evaluations* **2**, 240 (1997).
79. Dunbar, R. I. The social brain hypothesis. *Evol. Anthropol.* 178–190 (1998).
80. Dunbar, R. I. & Shultz, S. Evolution in the social brain. *science* **317**, 1344–1347 (2007).
81. Tajfel, H. Social psychology of intergroup relations. *Annu. review psychology* **33**, 1–39 (1982).
82. Pettigrew, T. F. Intergroup contact theory. *Annu. review psychology* **49**, 65–85 (1998).
83. Pettigrew, T. F. & Tropp, L. R. Does intergroup contact reduce prejudice? recent meta-analytic findings. *Reducing prejudice discrimination* **93**, 114 (2000).

84. Brewer, M. B. & Kramer, R. M. The psychology of intergroup attitudes and behavior. *Annu. review psychology* **36**, 219–243 (1985).
85. Brown, R. & Hewstone, M. An integrative theory of intergroup contact. *Adv. experimental social psychology* **37**, 255–343 (2005).
86. Paolini, S., Harwood, J. & Rubin, M. Negative intergroup contact makes group memberships salient: Explaining why intergroup conflict endures. *Pers. Soc. Psychol. Bull.* **36**, 1723–1738 (2010).
87. Barlow, F. K. *et al.* The contact caveat: Negative contact predicts increased prejudice more than positive contact predicts reduced prejudice. *Pers. Soc. Psychol. Bull.* **38**, 1629–1643 (2012).
88. Graf, S., Paolini, S. & Rubin, M. Negative intergroup contact is more influential, but positive intergroup contact is more common: Assessing contact prominence and contact prevalence in five central european countries. *Eur. J. Soc. Psychol.* **44**, 536–547 (2014).
89. Sabater, J. & Sierra, C. Review on computational trust and reputation models. *Artif. intelligence review* **24**, 33–60 (2005).
90. Allen, S. M., Chorley, M. J., Colombo, G. B. & Whitaker, R. M. Opportunistic social dissemination of micro-blogs. *Ad Hoc Networks* **10**, 1570–1585 (2012).
91. Chun, Y. J. *et al.* Device-to-device communications: A performance analysis in the context of social comparison-based relaying. *IEEE Transactions on Wirel. Commun.* **16**, 7733–7745 (2017).
92. Crandall, J. W. *et al.* Cooperating with machines. *Nat. communications* **9**, 233 (2018).
93. Colombo, G. Evolutionary simulation of prejudicial groups. <https://doi.org/10.17035/d.2018.0054105515> (2018).

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R.M.W. and D.G.R. are the principal investigators responsible for securing and managing the funding and research. All authors contributed to the model and experimental design. G.B.C. led the implementation of the simulations. All authors contributed to the analysis, writing and reviewing the manuscript.

Additional Information

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