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CULTURAL EVOLUTION OF COOPERATION: THE INTERPLAY BETWEEN FORMS OF SOCIAL LEARNING AND GROUP SELECTION

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Abstract

The role of cultural group selection in the evolution of human cooperation is hotly debated. It has been argued that group selection is more effective in cultural evolution than in genetic evolution, because some forms of cultural transmission (conformism and/or the tendency to follow a leader) reduce intra-group variation while creating stable cultural variation between groups. This view is supported by some models, while other models lead to contrasting and sometimes opposite conclusions. A consensus view has not yet been achieved, partly because the modelling studies differ in their assumptions on the dynamics of cultural transmission and the mode of group selection. To clarify matters, we created an individual-based model allowing for a systematic comparison of how different social learning rules governing cultural transmission affect the evolution of cooperation in a group-structured population. We consider two modes of group selection (selection by group replacement or by group contagion) and systematically vary the frequency and impact of group-level processes. From our simulations we conclude that the outcome of cultural evolution strongly reflects the interplay of social learning rules and the mode of group selection. For example, conformism hampers or even prevents the evolution of cooperation if group selection acts via contagion; it may facilitate the evolution of cooperation if group selection acts via replacement. In contrast, leader-imitation promotes the evolution of cooperation under a broader range of conditions.

Introduction

The extension, degree and diversity of cooperation among unrelated individuals are key to the ecological success of humans. The term ‘cooperation’ refers to behaviours by which benefits arise from the interactions between individuals. Hence cooperative behaviour provides benefits at the group level. From the individual perspective, however, the evolutionary emergence and stability of cooperation is often puzzling. In particular, this holds for social dilemmas where performing a cooperative act is costly to the actor, and free-riding individuals can reap the benefits of cooperation without paying the costs.

In evolutionary biology, which is focused on genetic evolution, the evolutionary emergence and stability of cooperation is the subject of a considerable body of literature (Axelrod 1985; Lehmann and Keller 2006; Nowak 2006). Since the dawn of evolutionary theory, Darwin suggested that the evolution of cooperation might be explained by the differential performance of cooperative and non-cooperative groups in intergroup competition (Darwin 1859, 1871). Ever since then, this idea has been controversial (Maynard Smith 1964; Queller 1992; West et al. 2007*b*; Leigh 2010). Evolutionary models demonstrate that selection between groups can indeed favour cooperation, but only under a limited range of demographic conditions (Maynard Smith 1964; Leigh 1983; Lehmann and Keller 2006; Lehmann et al. 2006; Traulsen and Nowak 2006). The problem is that within-group processes are typically faster than between-group processes. The rapid spread of individually favoured strategies (like refraining from cooperation) within groups erodes intergroup variation and, as a consequence, undermines the effectiveness of selection at the group level.

It has been argued that when social strategies are transmitted culturally rather than genetically, group selection can favour the evolution of cooperation under less restrictive conditions. The transmission of cultural traits is mediated by various forms of social learning, some of which play a key role in theories of cultural group selection. In particular, conformism, which is the individual tendency to acquire locally common strategies (Boyd and Richerson 1985), can retard or prevent the spread of initially rare defective strategies (Henrich and Boyd 1998). By homogenizing behavioural strategies within groups, conformism changes the distribution of variation within and between groups, rendering cultural group selection a potentially efficient force

promoting the evolution of cooperation (Boyd and Richerson 1985, 2002; Bowles et al. 2003; Boyd et al. 2003, 2011; Henrich 2004; Guzmán et al. 2007; Scheuring 2009). Recent models, however, cast doubt on the facilitating role of conformism in the evolution of cooperation (Lehmann and Feldman 2008). These models indicate that conformism can even hamper the evolution of cooperation because it hinders the spread of *any* new strategy in a group. Some modelling studies suggest that other mechanisms of social learning, such as the tendency to follow a group leader are more efficient in promoting cooperation via cultural group selection (Cavalli-Sforza and Feldman 1981; Lehmann and Feldman 2008; Lehmann et al. 2008). The contrasting conclusions of different modelling studies by different schools of thought have led to an on-going debate on the role of cultural group selection. Part of the debate centres on the range of parameter values considered reasonable by different authors. Perhaps more importantly, comparison across models is hampered by the fact that the models differ in their basic assumptions on social learning and group selection (Boyd et al. 2011).

In the theory of genetic evolution, there has been considerable confusion and debate around the meaning of ‘group selection’. Some authors even argue that this term should be abandoned altogether (West et al. 2007a), since group selection is a special case of a more general hierarchical theory of selection (Frank 1986). Yet the concept of group selection can be useful in the context of a group-structured population, since group traits may be an emergent property of the interaction of group members that cannot easily be reduced to individual-level traits (Okasha 2006; Simon et al. 2012). When talking about group selection, it is crucial to distinguish between two main modes, each representing different mechanisms that can have different effects on the outcome of evolution (West et al. 2007a). First, group selection can be driven by the differential extinction and colonization of patches, that is, the replacement of less successful groups by more successful ones (Maynard Smith 1964; Leigh 1983). This mode of group selection played a prominent role in the earliest discussions on group selection and is currently been referred to as ‘old’ group selection (West et al. 2007a) or multilevel selection 2 (Okasha 2006). We prefer to use a more descriptive term and will henceforth refer to ‘replacement group selection’ when group selection is driven by the replacement of less successful groups by more successful ones. Second, group selection can be driven by the differential production of individuals

migrating to and settling in other groups, that is, the ‘contagion’ of groups by individuals derived from other groups (Wilson 1975; Rogers 1990). This mode of group selection has been coined ‘trait-group’ selection (Wilson 1975), ‘new’ group selection (West et al. 2007a), or multilevel selection 1 (Okasha 2006). As a more descriptive term, we propose to call this mode ‘contagion group selection’. In the biological literature, the distinction between group selection by replacement and group selection by contagion, or the lack of it, has produced extensive discussion (Okasha 2004, 2006; West et al. 2007a, 2007b; Wilson 2007) and confusion (Wilson and Wilson 2007). Despite this, there have been very few attempts to compare the requirements for each of these processes to work (Lehmann et al. 2006; García and van den Bergh 2011).

In cultural evolution, the distinction between replacement and contagion group selection is as relevant as in biological evolution (Henrich 2004). Replacement group selection corresponds to the cultural take-over of whole groups by other more successful groups (Boyd et al. 2003; Traulsen and Nowak 2006; Guzmán et al. 2007). This may happen as a result of intergroup conflicts, where the winning group imposes their ‘culture’ upon subdued groups (Boyd et al. 2003; Traulsen and Nowak 2006; Guzmán et al. 2007). It may proceed in a more indirect way, if less successful groups tend to disband and go extinct, while well-performing groups bud off subgroups recolonizing empty patches (Soltis et al. 1995). Contagion group selection is mediated by the more gradual migration of cultural traits from one group to another. This may, for example, happen if the cultural traits observed in well-performing groups are preferentially imitated by the individuals of other groups, leading to the gradual introgression of group-beneficial strategies into less successful groups (Henrich and Gil-White 2001; Boyd and Richerson 2002; Lehmann et al. 2008). It is to be expected that, as in genetic evolution, the two modes of group selection have contrasting effects on the course and outcome of cultural evolution. Yet, systematic studies on these effects are currently lacking.

Before continuing it is important to clarify the meaning of the term ‘selection’ in the context of cultural evolution. We use a definition that is analogous to the usage of natural selection in genetic evolution, but somewhat more restricted than the definitions often given in the literature on cultural evolution (e.g. (Cavalli-

Sforza and Feldman 1981; Boyd and Richerson 1985). In genetic evolution, natural selection refers to the preferential transmission of alleles that enhance the ‘fitness’ of individuals, groups or other entities, that is, the ability of these entities to survive and reproduce. Darwinian fitness is often measured in payoffs that are acquired in interactions with others. Natural selection is an important driver of evolutionary change, but there are many other processes (including genetic drift and mutation pressure) leading to a change in allele frequencies. These processes differ from natural selection in that the evolutionary success of an allele is not related to the effect this allele has on the performance of the individuals, groups or other entities harbouring this gene. Similarly, in cultural evolution, various processes lead to changes in frequencies of cultural variants. In some of these processes, the evolutionary success of a cultural variant is related to the ‘performance’ of individuals, groups or other entities harbouring this variant. Examples include the preferential imitation of high-payoff individuals or the higher rate of cultural take-over from groups with superior organisation or technology. However, as in genetic evolution, the cultural transmission of a trait is not necessarily linked to the ‘performance’ of this trait, or to any of its inherent properties. Examples of forms of social learning that lead to cultural changes independent of payoffs include conformism-based learning (imitating traits that are locally most frequent), and status- or reputation-based learning (e.g. following a leader irrespective of intrinsic qualities of his/her cultural traits). To maintain consistency with genetic evolution, we interpret cultural change that is driven by performance- or payoff-based social learning as analogous to natural selection, while cultural change driven by other forms of transmission (such as conformism) does not fall into this category.

In this paper, we study three forms of social learning: payoff-based learning, conformism and leader imitation. Firstly, humans preferentially copy strategies from successful individuals (Henrich and Gil-White 2001; Lehmann et al. 2008; Kendal et al. 2009). In the context of a social dilemma, this social learning rule is expected to decrease rates of cooperation within groups since free-riding leads to higher payoffs. Secondly, under conformist learning individuals tend to adopt locally common strategies, thereby further increasing the frequency of those strategies in their groups. Thirdly, individuals may be inclined to follow a leader or a teacher in their group, so that the strategy of one influential individual tends to spread locally

(Cavalli-Sforza and Feldman 1981). Experimental results suggest that more than one of the abovementioned social learning rules can apply at the same time (Efferson et al. 2008; McElreath et al. 2008).

To clarify matters and to help resolving the disagreements in the literature on the role of cultural group selection, we developed an individual-based model of cultural evolution in a group structured population. The model allows to consider various mixtures of social learning rules (payoff-based learning, conformism, leader imitation) in the context of two contrasting modes of cultural group selection (contagion versus replacement). For all combinations of settings, we systematically varied the strength of individual and group selection with the aim of elucidating whether, and under which conditions, cultural group selection favours the evolution of cooperation in a social dilemma.

The model

Overview

We simulate a metapopulation structured in m groups of n individuals each. Individuals face a social dilemma, modelled here as a public goods game. At each point in time, each has a pure strategy, ‘cooperate’ or ‘defect’. Cooperators contribute to the public good of their group at a cost. Defectors contribute nothing. All contributions to the public good yield a benefit that is distributed equally among all group members, irrespective of whether they have contributed to the public good or not. In our simulations of cultural evolution, payoffs acquired in the public goods game influence the probability that a strategy spreads due to payoff-based learning. In each time step of the simulation, one individual (‘focal’) is randomly sampled from the metapopulation to change its strategy by imitating one or more other individuals. Imitation can be based on payoffs, conformism to the majority, or following a leader. After each iteration, the payoff that individuals obtain from the game is updated. This stepwise procedure leads to an evolutionary dynamics in which the population can lose or gain one cooperator per iteration. We iterate this event-based process until cooperation has either been lost in the metapopulation or spread to fixation. Imitation of strategies can either occur within the focal individual’s group or in the context of a different group. The probability of occurrence of within and between group imitation events is given by the parameter γ that corresponds to the probability of a

group level event. Within-group imitation occurs either based on individual payoffs from the public goods game (with probability α) or based on another imitation rule (probability $1 - \alpha$). As alternatives to payoff-based learning, we consider conformism, leader-following and – as a standard of comparison – the imitation of a randomly chosen group member. As motivated in the introduction, we interpret changes in the frequency of strategies due to payoff differences as ‘selection’. Therefore, the parameter α that specifies the frequency of payoff-based imitation within groups represents the strength of individual selection. Between-group imitation occurs either randomly (with probability $1 - \beta$), or based on benefits of the public goods in the respective groups (probability β). The parameter β specifies the frequency of payoff-based imitation at the group level, and therefore the strength of group selection. Events involving different groups are implemented in two ways, reflecting two modes of group selection (contagion versus replacement). Figure 1 gives a graphical representation of the possible events that occur in a single iteration of the simulation. Details of the implementation of the imitation rules and modes of group selection are given below. First we examine scenarios where the metapopulation initially consists of one fully cooperative group and defectors in all the other groups. This is an assumption that has been adopted in several models of cultural group selection (Henrich and Boyd 2001; Boyd et al. 2003, 2011; Guzmán et al. 2007) and is based on the idea that cooperation gained a foothold and has spread to fixation in one group due to stochastic processes. Second, we contrast these scenarios with simulations that start with a whole metapopulation of defectors, allowing cooperation to arise spontaneously with a fixed probability (corresponding to a mutation in genetic evolution).

The public goods game

The social dilemma is modelled as a public goods game with discrete strategies. Cooperators contribute c units of their resources to a public good. Defectors do not contribute, avoiding the cost of cooperation. The total of investments is multiplied by $a > 1$, yielding the overall benefit $b = n_c \cdot a \cdot c$ to a group containing n_c cooperators. This benefit is distributed equally among the n members of the group, irrespective of their contribution. Accordingly, payoffs acquired by cooperators and defectors are $P_c = b/n - c$ and $P_d = b/n$, respectively. Since the payoff of a defector is always higher than that of a co-operator, within-group selection favours defection over cooperation.

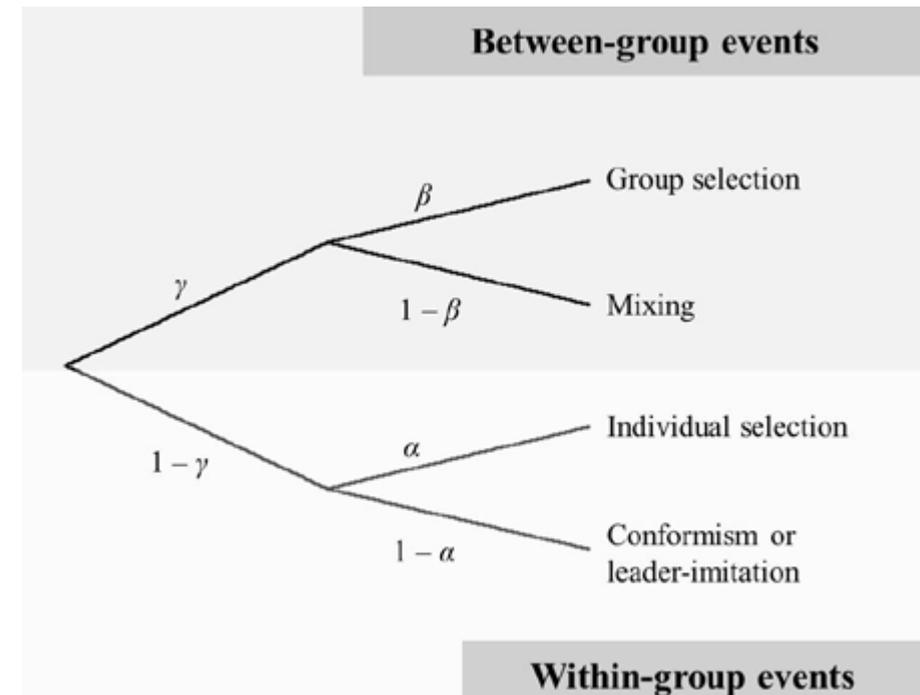


Figure 1. Structure of the event based-model. When an event occurs, a randomly chosen focal individual may change its strategy as a result of either between-group imitation (probability γ) or within-group imitation (probability $1 - \gamma$). In case of a within-group event, imitation is either based on the payoffs in the local public goods game achieved by a randomly chosen group member (probability α) or based on another form of social learning like conformism or leader-following (probability $1 - \alpha$). Accordingly, α reflects the strength of individual selection against cooperation. In case of a between-group event, imitation is either based on the comparison of the public-good benefits achieved in the focal individual’s group with those of another group (probability β) or by the random imitation of an individual from a foreign group (probability $1 - \beta$). Accordingly, β reflects the strength of group selection in favour of cooperation.

Within-group events

The focal individual can imitate a member of its own group with probability $1 - \gamma$. We consider four social learning rules determining this within-group imitation. With probability α , social learning is based on the payoffs acquired in the public goods game. With probability $1 - \alpha$, payoff-based imitation is complemented by either random imitation, conformism or leader-imitation. These four learning rules were implemented as follows:

- Payoff-based imitation: the payoff of the focal individual P_f is compared with the payoff P_m of a randomly chosen group member (the ‘cultural model’). The focal

individual switches its strategy to that of the cultural model when the perceived payoff difference $P_m - P_f + \varepsilon$ is positive, where the ‘noise’ term ε is drawn from a standard normal distribution.

- Random imitation: the focal individual switches its strategy to that of a randomly chosen group member. Random imitation corresponds to genetic drift in genetic models of evolution. It is included in our model as a benchmark to assess the effects of a decrease in the strength of individual selection α on the evolution of cooperation in the absence of conformism and leader-imitation.
- Conformism: the focal individual samples three randomly chosen models from its group and imitates the majority in that sample (Boyd and Richerson 1985). With only two strategies in our model, taking three models guarantees a majority in a sample of minimal size. This small sample size reflects limited availability of information (e.g. due to constraints on the time that individuals can spend sampling the behaviour of other group members), or limited cognitive capacities. Alternative implementations of conformism, including larger sample sizes, are discussed below.
- Leader-imitation: the focal individual imitates the ‘leader’ of its group. Each group has a leader, who is randomly chosen at the beginning of the simulation. The identity of the leader remains unchanged throughout a simulation run. Leaders may change their strategy by imitation, like any other member of their group by payoff-based imitation or between-group events. Leader-imitation homogenises strategies within groups, irrespective of their payoff or frequency.

Between-group events

Imitation based on between-group comparisons occurs with frequency γ . With probability $1 - \beta$, the focal individual imitates a randomly chosen individual from any group in the population. This process mimics the random migration of strategies or mixing of ideas between groups. With probability β , imitation is based on a measure of group performance, reflected in the acquired payoffs. In this case, the focal individual compares the per-capita benefit b_f/n from the public goods in its own group to the per-capita benefits b_m/n in a randomly chosen ‘model group’. The perceived benefit difference is $(b_m - b_f)/n + \varepsilon$, where the ‘noise’ term ε is again drawn from a standard normal distribution. We consider the following modes of group selection:

- Contagion-based group selection: if the perceived benefit difference is positive, the focal individual imitates a randomly chosen individual from the model group. The group of the focal individual is ‘contagioned’ with the strategy of the model group.
- Replacement-based group selection: if the perceived benefit difference is positive, with probability $1/n$ the strategies of all n members of the group of the focal individual are changed to the strategies in the model group. The group of the focal individual is replaced by the model group, so that the group of the focal is an exact copy of the model group. With probability $1 - 1/n$, no change does occur. We introduced the probability $1/n$ to compensate for the fact n group members change their strategies in case of group replacement. This allows a more direct comparison of contagion-based and replacement-based group selection, as the same number of individuals is expected to change in every time step.

Initial conditions

In the first set of simulations, we initialise our population with one group composed of only cooperators and the other $m-1$ groups composed of only defectors. This choice of the initial state rests on the assumption that one group has shifted to a cooperative state due to stochastic effects (Boyd et al. 2003, 2011). The initial presence of strategic variation allows us to study the effect of transmission and selection without ‘mutation’. In the second set of simulations, we start with m groups of defectors (and no cooperators) to see if a stochastic group shift is likely to occur. To this end, we allow individuals to spontaneously change their strategy with probability μ . While we consider this second set of simulations - including spontaneous changes - more realistic, we include both sets to compare the effects of common settings used in the literature.

In all simulations, we track the evolution of cooperation by iterating the model for a maximum of 500 000 time steps (events). Simulation runs finished when either cooperation or defection had reached fixation in the population. Parameters (α , β , γ) were varied between 0 and 1 with steps of 0.1, and with steps of 0.01 for values under 0.1. Based on preliminary simulations runs, we chose to run 30 replicates for each parameter combination to assure that the results were robust to stochastic processes. In the results reported in the main text, we consider a metapopulation of

$m=50$ groups consisting of $n=20$ individuals, yielding a total population size of 1000 individuals. All figures shown below are based on the payoff parameters $a=3$ and $c=1$.

Results

For each parameter combination, we calculated the frequency of cooperation in the metapopulation at the final time step averaged across the 30 replicate simulations. Figure 2 gives an overview of the simulations that were initialised with one cooperative group. Each panel summarizes the outcome of cultural evolution as a function of the parameters α (strength of individual selection) and β (strength of group selection). The 24 small panels to the right correspond to the scenarios obtained by combining two modes of group selection (contagion-based versus replacement-based) with three alternatives to payoff-based imitation (random imitation R, leader-imitation L, conformism C) and four levels of γ (corresponding to the relative frequency of between-group events).

Selection strengths

As exemplified by the enlarged panel in Figure 2, the evolved frequency of cooperation decreased with the strength of individual selection (from left to right), while it increased with the strength of group selection (from bottom to top). In all scenarios considered, cooperation disappeared in case of weak group selection ($\beta \approx 0$) while it spread to fixation in case of strong group and weak individual selection ($\beta \approx 1, \alpha \approx 0$). This makes sense, since payoff-based imitation disfavors cooperation in case of within-group events, while it favors cooperation in case of between-group events. Strong individual selection ($\alpha \approx 1$; right-hand side of each panel) almost invariably lead to the disappearance of cooperation; only in case of strong ($\beta \approx 1$) replacement-based group selection it remained in the population and even spread to fixation.

The scenarios where payoff-based imitation is combined with random imitation (panel rows R) exemplify how a decrease in the strength of individual selection on its own may lead to the establishment of cooperation. The corresponding panels serve as a benchmark for the cases where payoff-based imitation is combined with leader-imitation (panel rows L) or with conformism (panel rows C). A comparison

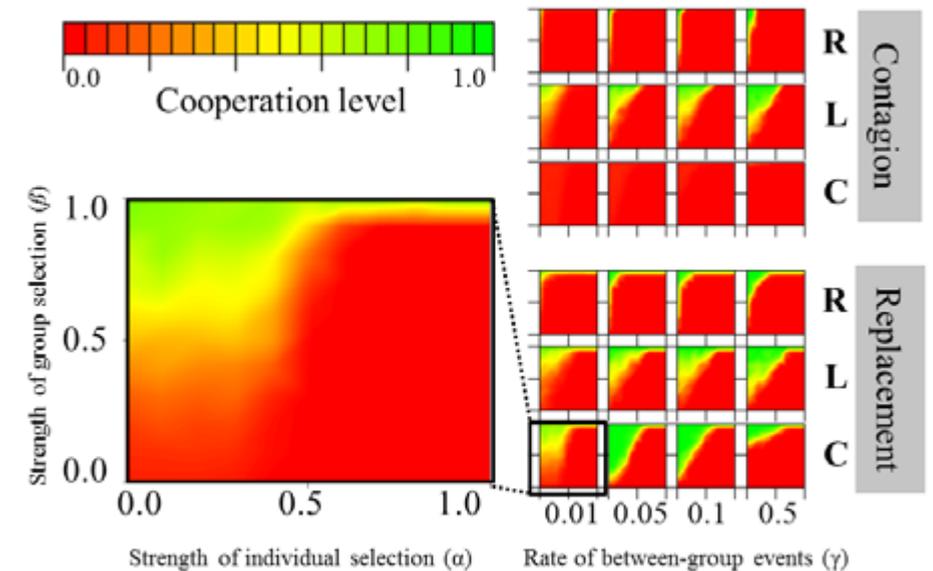


Figure 2. Evolution of cooperation under cultural group selection under various assumptions on social learning and the mode of group selection. Each panel depicts the evolved frequency of cooperation as a function of the rate α of payoff-based imitation within groups (a measure of the strength of individual selection) and the rate β of payoff-based imitation between groups (a measure of the strength of group selection). The six rows of panels present outcomes when within-group payoff-based learning is complemented (at rate $1-\alpha$) by either random imitation (R), leader-imitation (L), or conformism (C), under group selection by either contagion or replacement. The four columns of panels present varying frequencies of between-group events (γ) as opposed to within-group events. Values obtained from the simulations were interpolated to smoothen the plots.

across panel rows reveals that the effects of leader-imitation and conformism, while clearly present, only marginally expand the parameter range for the establishment of cooperation. In case of contagion-based group selection, conformism even leads to a reduction in the parameter range allowing for the evolution of cooperation. In that sense, conformism can hamper the evolution of cooperation by cultural group selection.

Group selection by contagion

When group selection is based on contagion, only leader-imitation favours the evolution of cooperation, whereas conformism has a detrimental effect. It is easy to understand why conformism hampers the spread of cooperation: even if some individuals get ‘contagioned’ by a cooperative strategy (by imitating an individual from a group with high public-goods benefits), this strategy cannot get a foothold

in the local group since within-group payoff comparisons act against cooperation while within-group conformism tends to weed out cooperation as long as it is rare. In contrast, leader-imitation can promote the evolution of cooperation provided that group selection is strong enough to overcome the effects of individual selection.

Group selection by replacement

Under group selection by replacement, both conformism and leader-imitation widen the scope for cooperation (Figure 2). In contrast to the contagion scenario, conformism can promote cooperation here. This is even the case when group selection is relatively weak (low values of β), particularly when within-group events are based on considerable frequencies of conformism (say, $\alpha < 0.4$). Note that conformism favours cooperation most when rates of between-group events (γ) are relatively low. This effect is also exemplified by Figure 3. When between-group events are rare, conformism can prevent defectors from invading in cooperative groups and facilitate the evolution of cooperation under group replacement (Figure 3, right panel). This effect breaks down if between-group events are too frequent. All else being equal, the impact of group selection increases with γ . However, beyond a certain level of γ , within-group dynamics is too slow for conformism to prevent the spread of defectors that are introduced by random mixing between groups. When conformism is infrequent, variation between groups breaks down, weakening the potential of group selection to promote cooperation. While the effect of conformism on the evolution of cooperation is strongly dependent on the mode of group selection, leader-imitation has similar effects under contagion- and replacement-based group selection (Figure 2, panel rows L, Figure 3). In contrast to conformism, leader-imitation promotes cooperation more strongly under increasing rates of between-group events (Figure 2, panel rows L; Figure 3). The arrival of migrants from other groups does not diminish the homogenising power of leader-imitation.

Spontaneous emergence of cooperation

All results reported so far were obtained from simulations initialised with one group of cooperators. We relaxed this assumption by initialising the population with only defectors and allowed individuals to spontaneously switch their strategy by innovation. In this scenario, conformism does not promote the evolution of cooperation. Even under group selection by replacement, conformism impedes the

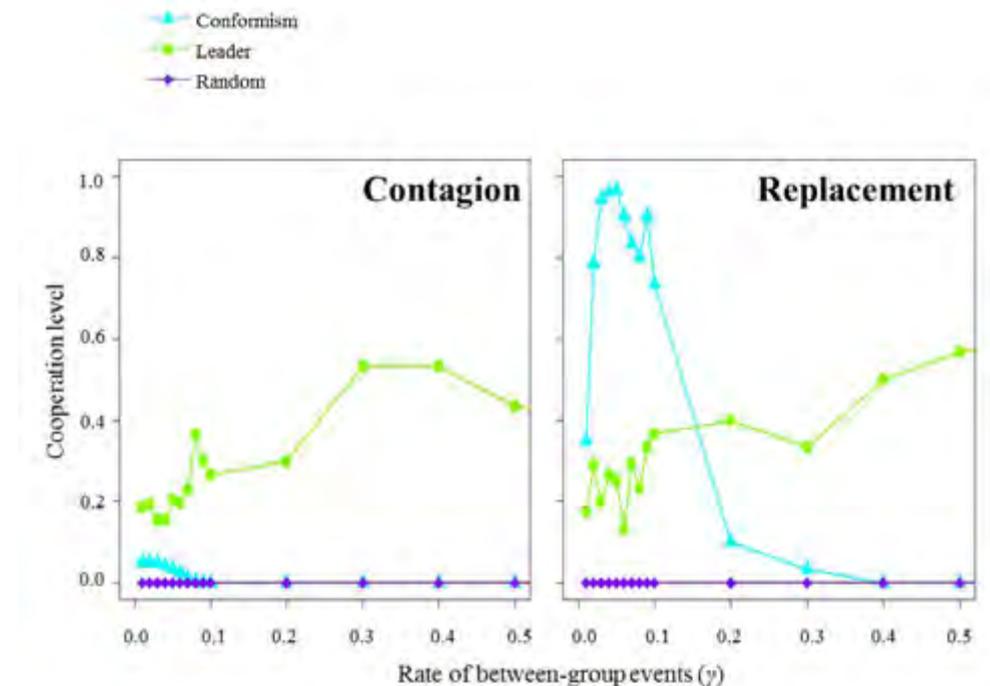


Figure 3. Increasing the frequency γ of between-group events hinders cooperation under conformism and promotes cooperation under leader-imitation. Both graphs are based on $\alpha=0.2$ and $\beta=0.5$. For low rates of between-group events, simulations with conformism do not always reach fixation within $5 \cdot 10^6$ time steps.

evolution of cooperation, preventing the spread of any new strategy that arises by innovation (Figure 4). For leader-imitation, the initial conditions do not influence the outcome of cultural evolution qualitatively.

Robustness of results

In addition to the simulations reported above, we ran numerous other simulations. Changing the payoff parameters in the public goods game, the distribution of individuals over groups (e.g. $m=10$, $n=100$; $m=40$, $n=25$) and the total population size (with $n=20$ and $m=500$) only had a small quantitative effect but did not change our conclusions. In contrast to the findings reported by Boyd and colleagues (2011), the outcome of cultural group selection was also not affected when we considered a spatially explicit model with stepping-stone migration on a torus (Boyd and Richerson 2002). More localized migration only slows down the speed of evolution, but does not change the outcome in a qualitative way.

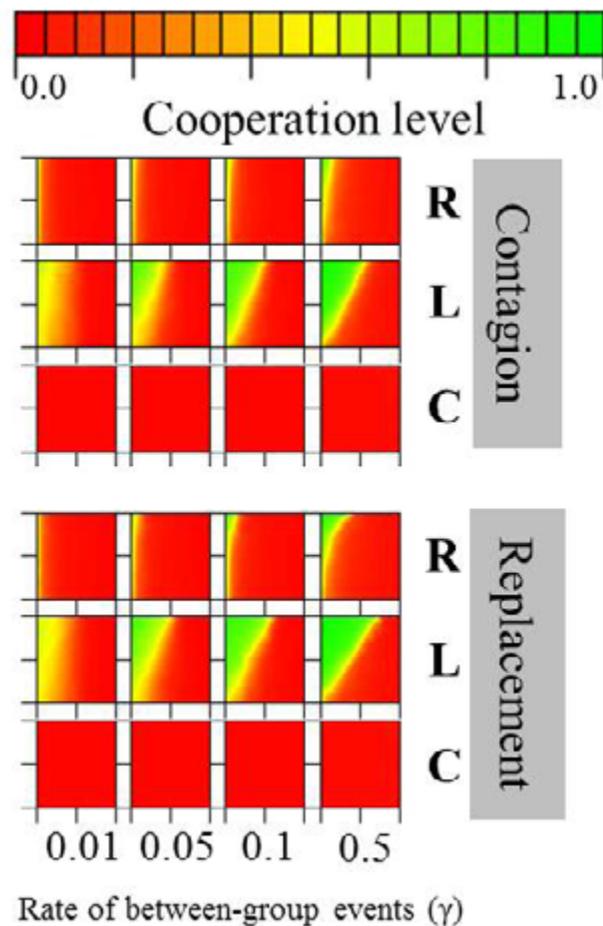


Figure 4. Outcome of cultural group selection when cooperation was initially absent and could only arise by spontaneous ‘mutation’ (innovation). Panels as in Fig 2. Per event, the focal individual spontaneously changes its strategy with probability $\mu=0.01$. Values obtained from the simulations were interpolated to smoothen the plots.

In our implementation of conformist learning, an individual samples only three models in its group (Boyd and Richerson 1985). Increasing the size of this sample strengthens conformist effects, leading to more efficient within-group homogenization of behaviour (simulation data not shown). Moreover, alternative approaches to modelling the effects conformism on the cultural evolution of social behaviour yield results in line with the findings reported here (Molleman and Weissing in press), suggesting that our simulation results are robust to changes in the way conformism is implemented.

Discussion

The last years have seen a debate about the role of social learning in the evolution of cooperation by cultural group selection. On the one hand, it has been argued that a social learning rule like conformism favours the evolution of cooperation (Boyd and Richerson 2002; Boyd et al. 2003, 2011; Choi and Bowles 2007). This argument is based on the idea that conformism reduces behavioural variation within groups, thereby increasing the effects of variation between groups (Henrich and Boyd 1998). As a result, cultural group selection could potentially be an important factor facilitating the evolution of cooperation. On the other hand, recent theoretical work has challenged this argument, showing by means of example models that conformism does often not favour the evolution of cooperation (Lehmann and Feldman 2008; Lehmann et al. 2008). Our systematic comparison indicates that the contrasting conclusions reflect the specific combination of social learning rules and mode of group selection assumed in the models underlying these conclusions. Under group selection by contagion, individuals from cooperative groups are imitated more and defector groups get ‘contagioned’ by cooperative strategies. Conformism hinders the evolution of cooperation in this scenario: uncommon behaviours are strongly selected against and rare cooperators contagioning defector groups are disfavoured by both payoff-based imitation and conformism. When cooperative groups can replace less cooperative groups, conformism can promote the evolution of cooperation, provided that initially one group in the population consists of cooperators (Boyd et al. 2003).

Our results contrast with previous models in terms of the facilitating effects of conformism on the evolution of human cooperation (Boyd, Richerson, & Henrich, 2011; Boyd et al., 2011; Boyd & Richerson, 1985; Henrich & Boyd, 1998, 2001). However, one could think of scenarios in which conformism could have a positive influence on cooperation in a more indirect way. For instance, conformism might homogenize groups with respect to various norms and habits and thereby increase social cohesion. As a consequence, trust may build up among group members more easily, potentially facilitating cooperation. Secondly, conformism may have positive effects on cooperation when payoffs of behaviour vary spatially. Conformist learning can help newcomers to adopt locally beneficial strategies, allowing them to coordinate with resident individuals, and adapt to local equilibria (Boyd & Richerson, 1985). Therefore, it is possible that under these different conditions conformism plays a

more prominent role in the evolution of social behaviours. Further theoretical work is needed to clarify these issues.

Earlier studies (Lehmann and Feldman 2008; Lehmann et al. 2008) arrived at the conclusion that leader-imitation is more efficient than conformism in establishing cooperation through cultural group selection. Our results are in line with this conclusion. In fact, imitating a group leader can promote the evolution of cooperation irrespective of the mode of group selection. However, the way that leadership is implemented in these models as well as ours, is a simplification that is certainly quite unrealistic. Leaders are most likely not chosen at random, but they emerge in the interaction between individuals (e.g. (Weissing 2011)). Becoming a leader or a follower and accepting the leadership of somebody else will often be the outcome of a game with strategies and payoffs that are quite unrelated to the public goods game considered here. Leadership and followership can also be institutionalized, again associated with costs and benefits that are not necessarily congruent with those of the underlying public goods game. Accordingly, leaders and followers will often be motivated by incentives that are not conceptualized in our simple model. It is easy to imagine situations where leader-imitation is an even more potent force in bringing about cooperation than in our model (e.g. if institutions reward leaders on the basis of group benefits). However, in other situations leader-imitation might actually hamper the evolution of cooperation (e.g. if the leader has to be paid from public-good benefits). Clearly more refined models of leadership are required to really judge the role of leader-imitation for the evolution of cooperation.

In total, we conducted more than $4 \cdot 10^9$ simulations, each simulation running for up to $5 \cdot 10^5$ time steps. Yet, even an extensive study like this can only address few potential interactions between social learning rules and modes of cultural group selection. For example, we assessed the effects of only two imitation rules (conformism and leader-imitation). There may be many other rules potentially reducing variation within groups (Laland 2004; Rendell et al. 2011), and the way this reduction comes about could interact with the mode of group selection in unexpected ways (witnessed by the effects of conformism reported here). Also, different modes of group selection are by no means mutually exclusive, and may act simultaneously and interactively (Okasha 2006). In our model, payoff-based imitation is error prone, but we did not

systematically investigate the implications of various error rates and degrees of noise. For simplicity, we assumed that the errors associated with the measurement of payoff differences are equally large when imitation occurs within or between groups. In many situations it is more plausible to assume that the success of individuals from other groups is harder to assess than the payoffs of group members.

Models studying the evolution of social learning mainly focus on contexts in which outcomes of behaviour are independent of the behaviour of others (Boyd and Richerson 1985). The same is true for most (McElreath et al. 2005, 2008; Efferson et al. 2008) but not all (Traulsen et al. 2010) experimental work investigating how humans use social information to determine their behavioural strategies. Our understanding of the cultural evolution of cooperation would benefit from theory that predicts which forms of social learning are adaptive in contexts where outcomes of behaviour also depend on the strategic choices of others. Confronting humans with such contexts under controlled laboratory conditions could then test if humans indeed use these social learning rules in decision making in cooperative interactions. Also, studying cooperation should not restrict itself to social dilemmas. Human cooperation comes in many different forms and flavours; the public goods game modelled here represents only one specific context in which humans cooperate. Exploring the effects of various social learning rules on the cultural evolution of social behaviour in other games, such as coordination games and evasion games, presents an interesting venue of research for the future.