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Original Article

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.

1. Introduction

The extension, degree and diversity of cooperation among unrelated individuals are keys 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 are 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 are the subjects of a considerable body of literature (Axelrod, 1985; Lehmann & 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 (Leigh, 2010; Maynard Smith, 1964; Queller, 1992; West, Griffin, & Gardner, 2007a). Evolutionary models demonstrate that selection between groups can indeed favour cooperation, but only under a limited range of demographic conditions (Lehmann & Keller, 2006; Lehmann, Perrin, & Rousset, 2006; Leigh, 1983; Maynard Smith, 1964; Traulsen & 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 & Richerson, 1985), can retard or prevent the spread of initially rare defective strategies (Henrich & 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 (Bowles, Choi, & Hopfensitz, 2003; Boyd, Gintis, Bowles, & Richerson,

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2003; Boyd, Richerson, & Henrich, 2011; Boyd & Richerson, 1985, 2002; Guzmán, Rodríguez-Sickert, & Rowthorn, 2007; Henrich, 2004; Scheuring, 2009). Recent models, however, cast doubt on the facilitating role of conformism in the evolution of cooperation (Lehmann & 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 & Feldman, 1981; Lehmann, Feldman, & Foster, 2008; Lehmann & Feldman, 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 have been considerable confusion and debate around the meaning of 'group selection'. Some authors even argue that this term should be abandoned altogether (West, Griffin, & Gardner, 2007b), 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, Fletcher, & Doebeli, 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., 2007b). 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 (Leigh, 1983; Maynard Smith, 1964). 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., 2007b) 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 (Rogers, 1990; Wilson, 1975).This mode of group selection has been coined 'trait-group' selection (Wilson, 1975), 'new' group selection (West et al., 2007b), 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 & Wilson, 2007). Despite this, there have been very few attempts to compare the requirements for each of these processes to work (García & van den Bergh, 2011; Lehmann et al., 2006).

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; Guzmán et al., 2007; Traulsen & Nowak, 2006). This may happen as a result of intergroup conflicts, where the winning group imposes their 'culture' upon subdued groups (Boyd et al., 2003; Guzmán et al., 2007; Traulsen & Nowak, 2006). 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, Boyd, & Richerson, 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 (Boyd & Richerson, 2002; Henrich & Gil-White, 2001; 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. (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981). 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 & Gil-White, 2001; Kendal, Giraldeau, & Laland, 2009; Lehmann et al., 2008). 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 & Feldman, 1981). Experimental results suggest that more than one of the abovementioned social learning rules can apply at the same time (Efferson, Lalive, Richerson, McElreath, & Lubell, 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