Evolution of stable reciprocity

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Human cooperation among non-kin has long been accepted as being based on reciprocity – the idea that we return help from individuals that we re-meet (Trivers, 1971). However, this paradigm has been challenged by Efferson et al. who make the bold claim that repeated interaction is insufficient to support cooperation (Efferson et al., 2024). The authors base their conclusion on a model in which cooperative partners use a novel function to determine their response. In their system, cooperation through repeated interaction breaks down. We point out here that the collapse of cooperation is not the result of the novel strategy set. Instead, it is a standard modelling result in which a cooperative environment allows drift towards unstable, undiscriminating strategies. Efferson et al.'s simulations are unusual in not allowing mutation from always cooperating to always defecting. We show how allowing full defectors into a cooperative environment provides selection for the maintenance of discrimination. Discriminating strategies resist invasion by strategies that exploit undiscriminating cooperation. In consequence, cooperation is stabilized. We conclude that Efferson et al.'s results can readily be explained by existing theory and that repeated interaction can support cooperation without additional processes such as between group competition.

Reciprocity is a classical explanation for cooperation involving repeated interactions despite each move offering a temptation to defect (Trivers, 1971). It works when discriminating strategies, most famously 'Tit-for-Tat' (Axelrod & Hamilton, 1981), cooperate with cooperators but defect on defectors. However, this scenario has an Achilles heel. If cooperative strategies are profitable over multiple rounds, all agents will tend to evolve to cooperate through some form of reciprocation. In this cooperative utopia, the discrimination that makes strategies like Tit-for-Tat successful in an uncooperative environment becomes redundant and unconditionally cooperative strategies can drift in by mutation ('indirect invasion' (van Veelen, 2012)). This paves the way for uncooperative strategies

to invade by exploiting the underlying naivety (Bendor & Swistak, 1995). Such dynamics "are the underlying basis for every model of cooperation" (Wahl & Nowak, 1999b).

Now, Efferson et al. have presented a model of repeated interactions in which cooperation collapses and have interpreted this as meaning that reciprocity cannot work on its own. They begin by describing a familiar scenario. In a cooperative population, individuals tend to start with high offers; this means there is little scope for escalation within a fixed endowment and consequently the parameters determining the degree of escalation in their model have little effect. Relieved from selection, the escalation parameters drift into a range where they are vulnerable to what they call 'ambiguous' strategies which engage in a form of 'short-changing' (Roberts & Sherratt, 1998). As a result, cooperation declines to low levels. However, the difference between Efferson et al.'s paper and previous work is that rather than offering the standard interpretation, the authors instead claim to have uncovered a flaw in the long-standing paradigm of repeated interaction as a pillar of cooperation. They further claim that uncovering this flaw was a consequence of modelling an 'extended' strategy space.

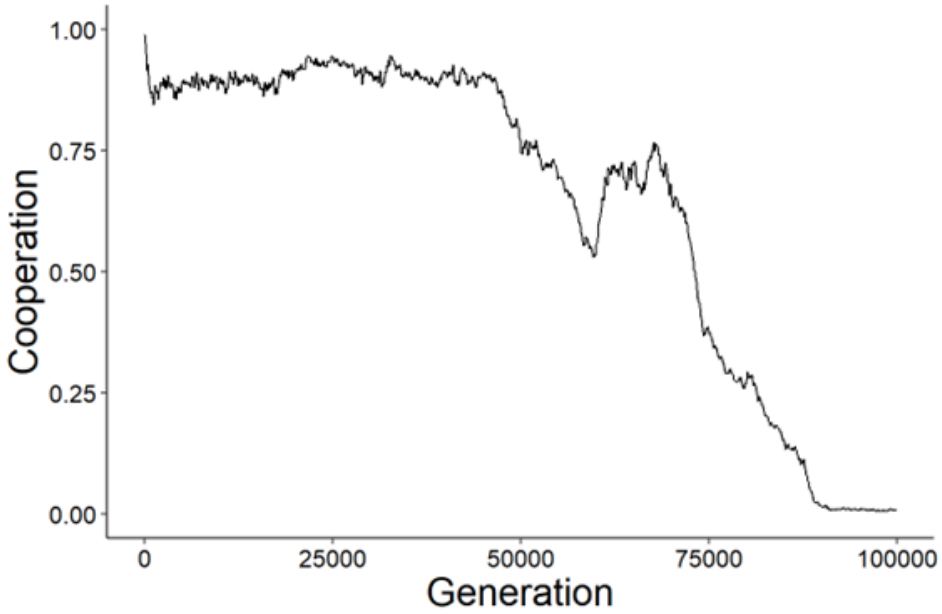
Here, we show how the breakdown of cooperation observed by Efferson et al. is an artefact of their decision not to expose full cooperators to mutant full defectors. It is customary to test cooperation against defection and so it is surprising that Efferson et al. did not include such a contest and allowed only local mutations that give a little bit more or less. We began by coding a simple model using their response function to replicate the collapse of cooperation reported in Efferson et al. (Figure 1a). Next, we ran the model with an additional mutation process in which a small proportion of offspring in each generation defected by giving nothing. This resulted in a high level of stable cooperation (Figure 1b). Similarly, introducing defection in the form of 'phenotypic defectors', which carry a cooperative genetic strategy yet defect due to being unable to cooperate (Lotem et al., 1999; Sherratt & Roberts, 2001) results in a high and stable level of cooperation (Figure 1c). As shown in Figure 1d, this is a quite different effect to that of introducing errors (e.g. Van Veelen 2012).

This result illustrates how allowing a small proportion of individuals that always defect has the paradoxical effect of increasing cooperation. Analytically, this has long been understood: discriminators do better against those who always defect because they suffer less exploitation than unconditional cooperators (Sherratt & Roberts, 2001). These discriminating strategies form the basis of stable cooperation, in contrast to the unstable cooperation of undiscriminating strategies. Thus, paradoxically, defection allows cooperation. Whilst one can discuss the merits of assuming local mutation versus mutation to giving nothing, the point is that the results presented by Efferson et al are fragile with respect to one of the key parameters of their model (such as group size, number of interactions etc.) whose effects they did not examine.

Efferson et al.'s results are not novel, nor are they the consequence of using a continuous model (see also (Roberts & Sherratt, 1998; Wahl & Nowak, 1999a, 1999b)) or what they refer to as an expanded strategy set. The significance of their work is that in purportedly demonstrating the fragility of cooperation through repeated interactions, it promoted the role of between-group competition as a decisive process in human social evolution. Others, showing a surprising lack of awareness of the literature on models of cooperation, have gone on to interpret the flawed models as demonstrating the role of cultural-group selection in human uniqueness (Mathew, 2024). In fact, we cannot draw any such conclusions from Efferson et al.'s work.

Figure 1. Evolutionary dynamics of cooperation: (a) replicating Efferson *et al.*'s model including their assumption that mutation in the parameters of the reciprocal response function are restricted to small increments of the 1 unit of endowment per round; (b) with an additional mutation process giving a 1% chance that the offspring will always defect; (c) with 2% 'phenotypic defectors' (which always defect regardless of the genetic strategy they carry; and (d) where agents make implementation errors on 2% of moves. In each case, points are plotted every 100 generations and are the medians of 10 simulations. Cooperation is the proportion of the endowment donated to the partner.

a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Cooperation
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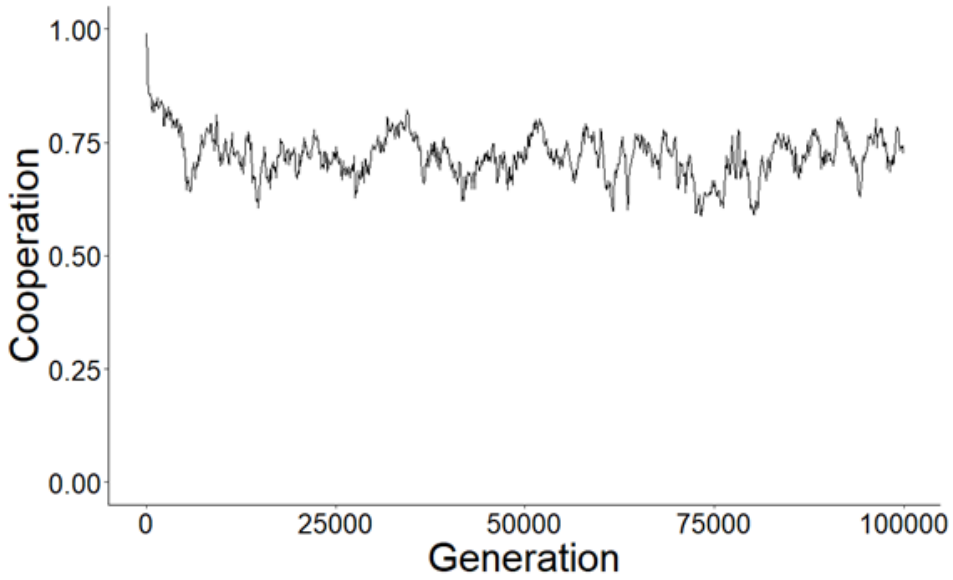
b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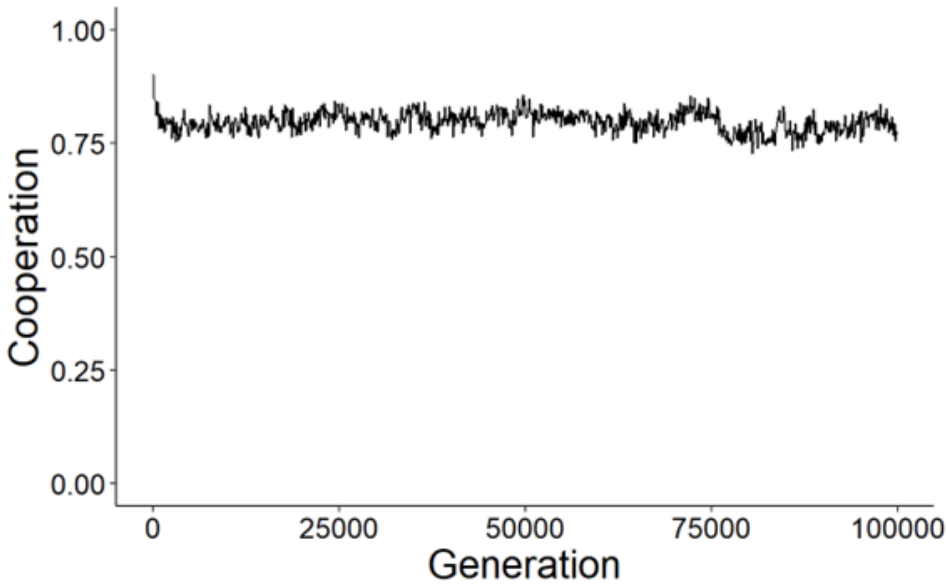
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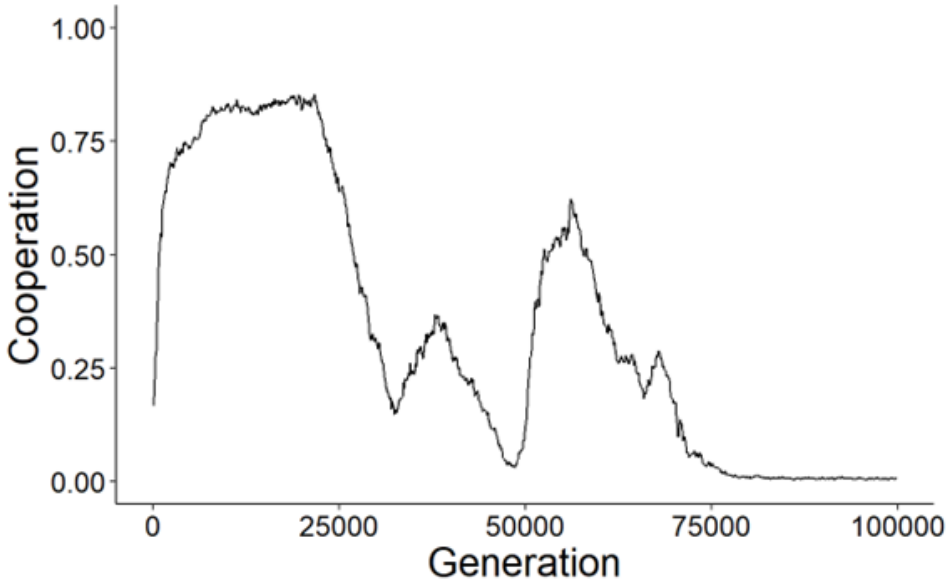
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Methods

Simulation methods were based on those described in Efferson et al. and were coded independently in Microsoft Visual C. Simulations were initialized by setting up a population of 100 individuals. Play involved selecting every possible pair in turn (100*99/2 = 4950 pairings) and then for each pair, playing an iterated asynchronous continuous Prisoner's Dilemma game for 100 rounds. On the first move, the leader was determined randomly. The leader donated part of its 1 unit of endowment according to its genetic strategy x, which was in increments of 0.01 between 0 and 1. The follower donated according to its response rule $(d\text{-}a)x$, where a and d were the left and right intercepts of a linear function of x. In subsequent rounds, both partners used this function to determine their response based on what their partner had donated. At the end of the full set of interactions, reproduction was proportional to payoffs and resulted in replacing the population of N=100 individuals.

During reproduction, mutation occurred. Mutation in Efferson et al. was implemented by adding or subtracting small increments to a strategy. This was implemented here by allowing the genetic strategies to increase or decrease in steps of 0.01 with probability 0.02 within the bounds of 0 to 1. However, this meant that in a cooperative environment, cooperators were not tested against defectors but just against those giving slightly less. To make the model more biologically realistic I added a second mutation process in which there was a 0.01 probability of each of the response parameters mutating to zero, thereby implementing an 'always defect' strategy. Phenotypic defectors were implemented by replacing the genetic strategy with a phenotypic strategy of always defecting for 2% of individuals in each generation. Execution errors were implemented by replacing 2% of responses with random responses.

Simulations began with full cooperation given by x=1, a=0, d=1. Simulations ran for 100,000 generations of strategy evolution. Cooperation was calculated as the average proportion of the 1 unit of endowment invested, averaged over the 4950 pairings * 100 rounds * 2 in a pair = 990,000 moves in each of 100,000 generations.

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