

Dynamic-persistence of cooperation in public good games when group size is dynamic

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Abstract

The evolution of cooperation is possible with a simple model of a population of agents that can move between groups. The agents play public good games within their group. The relative fitness of individuals within the whole population affects their number of offspring. Groups of cooperators evolve but over time are invaded by defectors which eventually results in the group's extinction. However, for small levels of migration and mutation, high levels of cooperation evolve at the population level. Thus, evolution of cooperation based on individual fitness without kin selection, indirect or direct reciprocity is possible. We provide an analysis of the parameters that affect cooperation, and describe the dynamics and distribution of population sizes over time.

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1. Introduction

The study of cooperation between individuals of species has led to a variety of interesting proposed explanations. The theory of kin selection focuses on cooperation among individuals who are closely related genetically (Hamilton, 1964), whereas theories of direct reciprocity focus on the selfish incentives for cooperation in repeated interactions (Trivers, 1971; Axelrod, 1984). Theories of indirect reciprocity and costly signaling show how cooperation in larger groups can emerge when cooperators can build reputations (Alexander, 1987; Nowak and Sigmund, 1998; Lotem et al., 1999; Wedekind and Milinski, 2000; Leimar and Hammerstein, 2001; Zahavi, 1977; Gintis et al., 2001).

Empirical studies show evolution of cooperation among *Homo sapiens* (Kagel and Roth, 1995), other higher organisms (Dugatkin, 1997), and microorganisms (Travisano and Velicer, 2004). A recent study has shown that cooperative, isogenic-respirer strains of yeast can prosper

when mixed with “cheater”, respiro-fermenter strains in a spatially heterogeneous environment (MacLean and Gudelj, 2006). A basic model of biological cooperation must, therefore, not rely only on the high-level cognitive capacity of the individual agents.

Another line of explanation focuses on group selection (Wade, 1977, 1978; Wilson, 1983; Wright, 1945). A group that includes more altruistic agents derives higher average fitness for its members, which may lead to more offspring of agents in the successful group even though within each group the altruistic agents are less fit than their selfish neighbors. It is known that low demographic mobility is a crucial factor for the evolution of altruistic traits (Wright, 1945; Killingback et al., 2006).

Many models in the study of group selection build on the “haystack model” of Maynard Smith (1964). In haystack models, agents are divided into a number of groups in which games are played, and asexual reproduction takes place within each group. At the end of the reproductive phase there is a dispersal phase, where the entire population is pooled and new groups are randomly formed from the pooled population. For haystack models where the games are prisoner dilemmas, the only stable equi-

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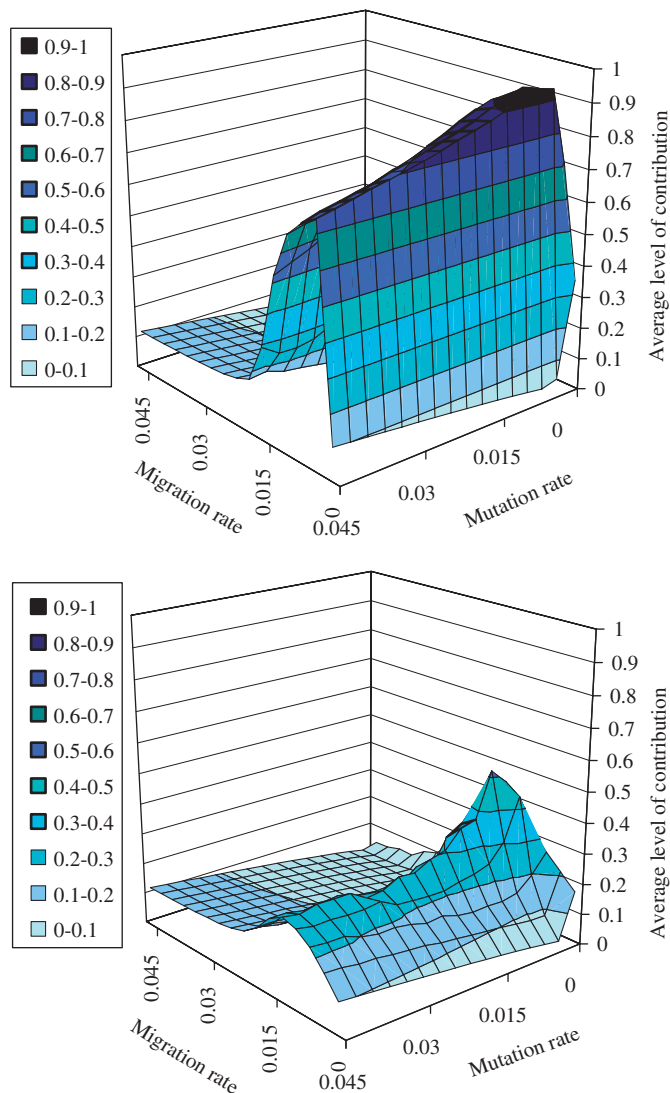


Fig. 4. Average level of contribution x for different values of mutation (η) and migration (μ). Top figure without Eq. (5), lower figure including Eq. (5).

migrate as often as cooperators, but when they migrate into unpopulated groups, they are likely to die out rather than thrive as émigré groups of cooperators do.

When B is restricted (Fig. 4b), the levels of cooperation are smaller because it is harder for small groups (smaller than B individuals) to cooperate. Nevertheless, we get cooperation levels of more than 25% for small levels of migration. The cooperation level drops significantly with higher levels of mutation. For higher levels of mutation, there is a high probability that more selfish agents enter a group of cooperators and break down the cooperation.

Next we look at the relation between number of groups and migration rate (Fig. 5). A larger number of groups and smaller migration rates (but not zero) lead to higher values of cooperation. With more groups, there is a greater chance that a group of cooperators is isolated from less cooperative agents. Cooperation thrives when groups are

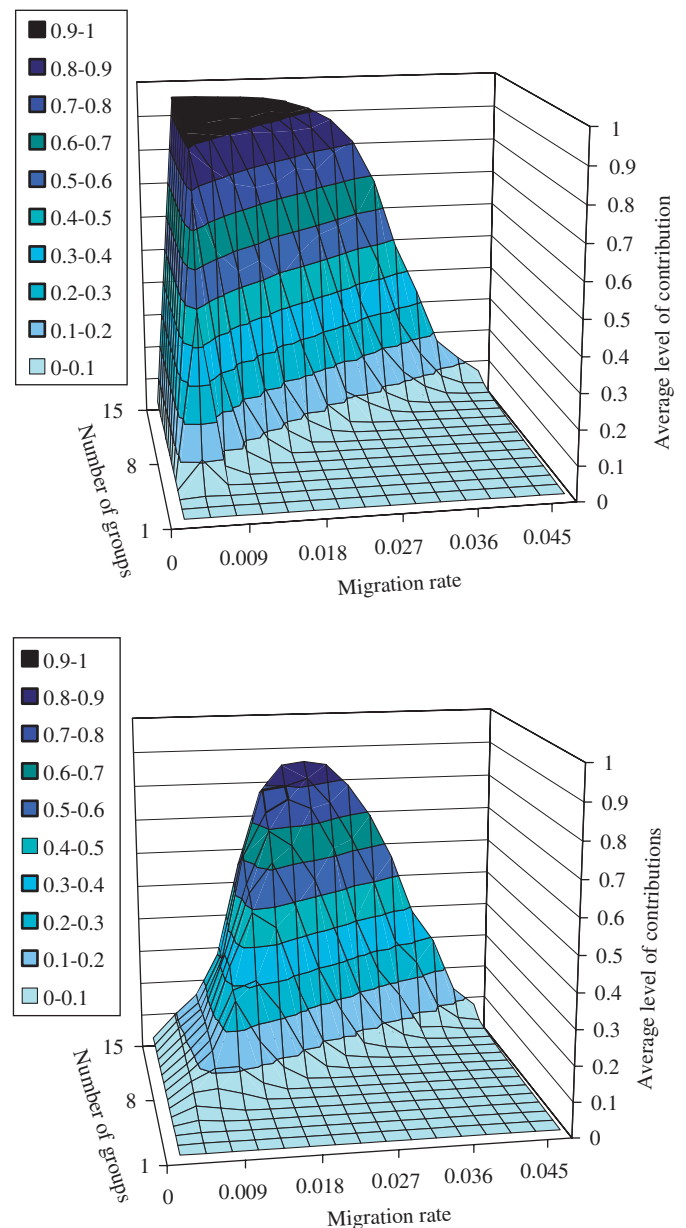


Fig. 5. Average level of contribution x for different values of migration (μ) and number of groups (M). Top figure without Eq. (5), lower figure including Eq. (5).

well insulated by low migration rates, which prevents too much homogeneity among the groups. When homogeneity is too high, the population is essentially a single group rather than a collection of independent groups. Again, a restricted B (Fig. 5b) leads to lower but still significant levels of cooperation.

When we focus on the effect of mutation and number of groups (Fig. 6), we observe less sensitivity to variations in mutation rate and relatively more sensitivity to variations in the number of groups. There is a large difference between constrained and unconstrained multiplier levels of B . When unconstrained, more than five groups can lead to

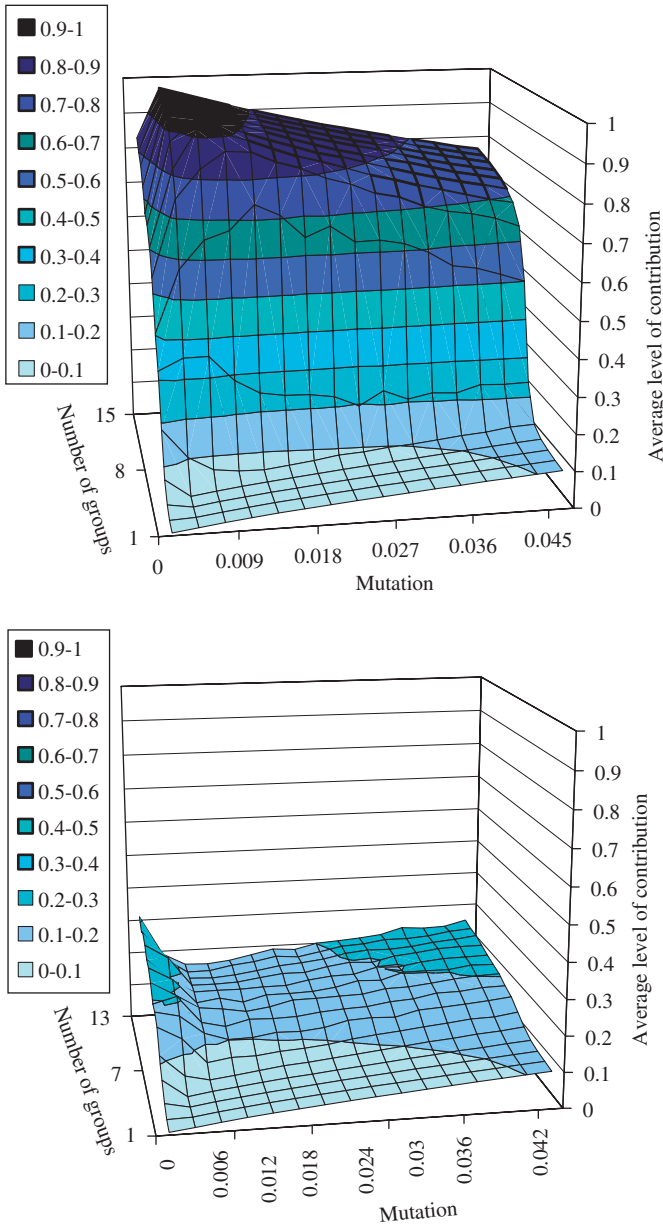


Fig. 6. Average level of contribution x for different values of mutation (η) and the number of groups (M). Top figure without Eq. (5), lower figure including Eq. (5).

high levels of contribution irrespective of the mutation rate because groups are not significantly affected by variations in mutation levels.

When we look at the trade-off between migration and B , we see that for higher levels of B it is easier to establish high levels of cooperation in the unrestricted case (Fig. 7a). This is not surprising given that higher values of B mean that there is a relatively strong benefit for cooperation compared to the benefit for free-riding.

When B is restricted, we see that cooperation does not appear beyond a certain level of B . The reason for this is that small groups ($N_G < B$) do not benefit from high values of B since they are cut off to $B = N_G$. This will benefit

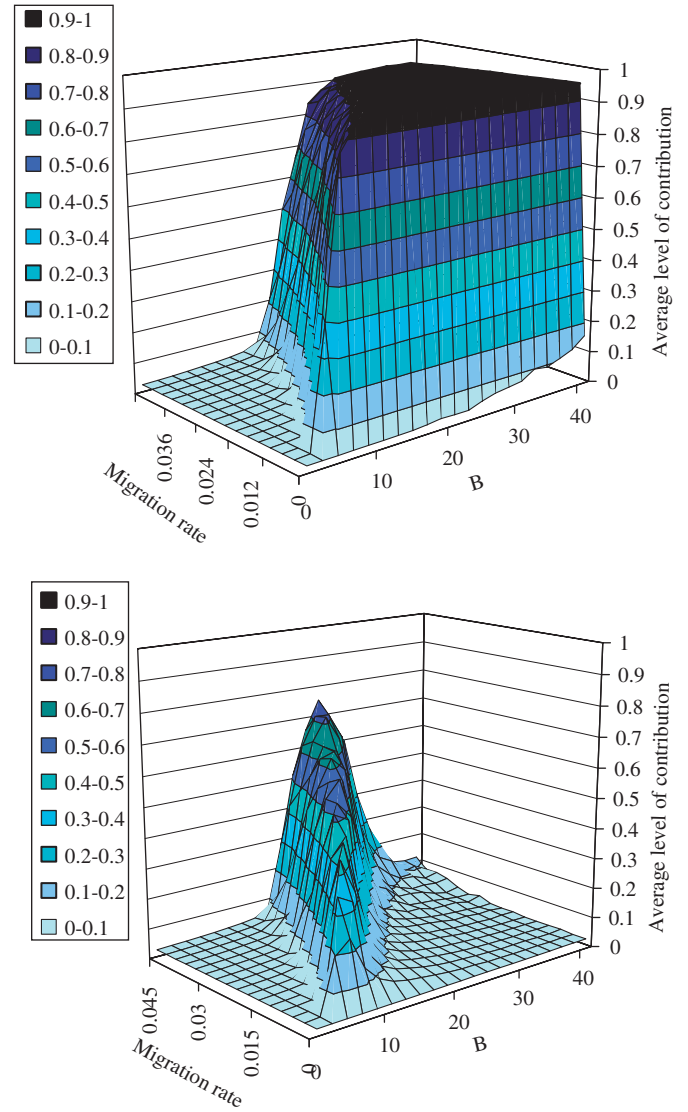


Fig. 7. Average level of contribution x for different values of migration (μ) and B . Top figure without Eq. (5), lower figure including Eq. (5).

larger groups, but these are also likely to be the groups that have defectors. When B is not restricted, a collapse of a populous group leads to small groups that all benefit from the large values of B , and new cooperative groups emerge. When B is restricted, the collapse of a large group will bring the population back to a number of small groups that each depends upon the existence of sufficient cooperation to grow again. Thus, with a restricted B (according to Eq. (5)) and a low migration rate, there is only a small probability that cooperative agents move to other (smaller) groups at a sufficient rate for new cooperative groups to become established before the larger groups collapse due to invasion and propagation of selfish agents.

When we vary the number of agents N in the simulation, we increase the number of time steps to $2000 * (1000/N)$ in order to derive comparable results with the other figures. With a smaller number of time steps, the populations

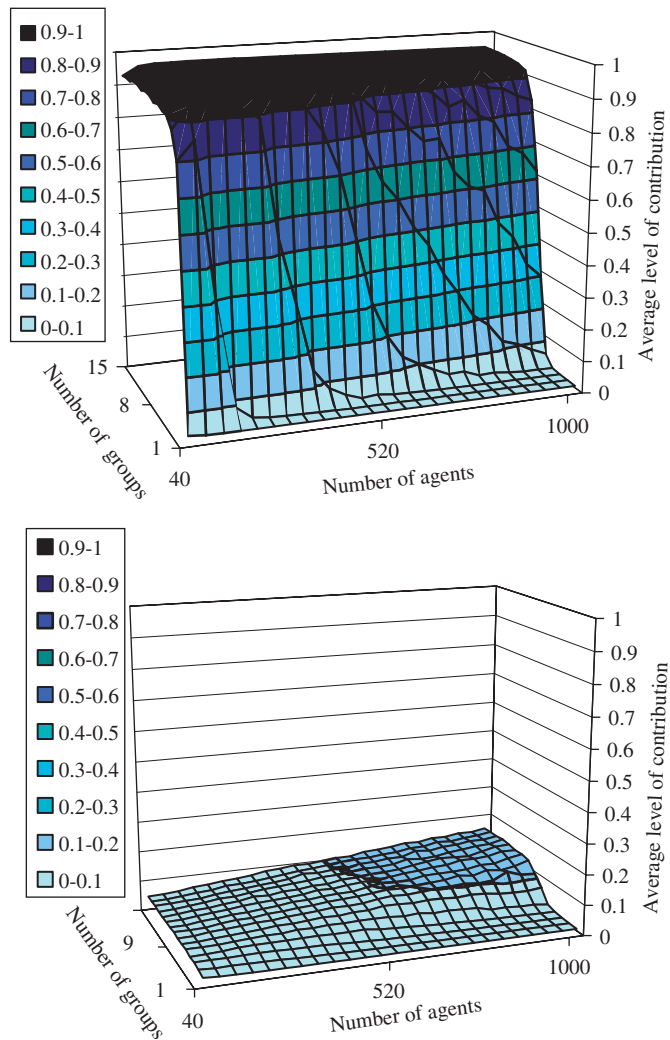


Fig. 8. Average level of contribution x for different values of number of agents (N) and the number of groups (M). Top figure without Eq. (5), lower figure including Eq. (5).

would experience less migration and mutation than the reference situation. Fig. 8 shows the trade-off of cooperation between different numbers of agents and groups. A large number of groups is beneficial for establishing high levels of cooperation because more groups lead to fewer opportunities for cooperative groups to be invaded by less cooperative agents. When the number of agents increases, more groups are necessary to derive the same level of cooperation. This relation is roughly linear, indicating that the level of cooperation achieved in a population is a function of the ratio of the population to the number of groups. It is harder to attain groups of cooperators for a restrictive B since small groups are also prone to the social dilemma that benefits selfish agents in cooperative groups.

4. Discussion

We introduced a simple model that leads to the evolution of high levels of cooperation without kin selection,

perceptible markers of cooperation, indirect or direct reciprocity, or agents with cognitive abilities. Providing agents the opportunity to be divided into groups with modest migration between groups is sufficient for the evolution of cooperation in public good games. Our model differs from other approaches such as kin selection in subdivided populations (Maynard Smith, 1964), trait-group selection (Wilson, 1975), correlated markers (Burtsev and Turchin, 2006), and spatial public good games (Szabo and Hauert, 2002). Kin selection cannot explain our results because the agents do not differentially act in a manner that benefits other agents that are genetically similar. Our model is different from trait selection because groups are not assumed to have equal densities and mutation of cooperation levels and migration across groups are allowed. In models that use correlated markers (Burtsev and Turchin, 2006), cooperation has been shown to evolve provided that agents are capable of perceiving heritable external markers of other agents that may be correlated with a cooperative disposition. Our simple agents develop cooperation despite the absence of sensitivity to any markers. Finally, our model is different from spatial public good games, since no explicit spatial structure is assumed in which agents have fixed positions and interact only with their neighbors (Szabo and Hauert, 2002). Our model provides one mechanism for group selection (Wilson, 1983), or more generally, multi-level selection, in which alleles spread in a population because of the benefits they bestow on groups. This multi-level selection occurs even though each agent's reproduction rate depends only its individual fitness, because individual fitness depends upon the group's overall cooperation level.

Our paper resembles the modeling and results of Killingback et al. (2006) in a number of ways. Both of our models incorporate a public good problem with a total population divided into multiple groups, resource sharing within groups, competition for reproduction by agents across all groups, and parametric manipulation of the group benefit for cooperation, migration rate, and mutation rate. There are nevertheless important differences between our study and Killingback et al. (2006). We considered two types of public good games, and analysed in greater detail the temporal dynamics and the sensitivity of the level of cooperation to individual parameters and their interactions. The two types of games we distinguish are with a public good multiplier independent of group size, as also used by Killingback et al. (2006), and a stricter condition that the value of the public good multiplier always leads to a conflict between individual and group interests. This latter condition is particularly important because it shows that cooperation can emerge in a public good problem even when agents always face a social dilemma. Killingback et al.'s explanation of their results was that "reproduction in groups, combined with dispersal between groups, results in variations in group size, and for groups of sufficiently small size, the public goods game is

no longer a social dilemma” (p. 1480). We agree that the formation of small groups is the crucible for the emergence of cooperation, but argue that this can occur even when there is always a true social dilemma. It requires that mutation is not too fast, otherwise cooperation levels degrade before new pioneering colonies of cooperators can be formed. It also requires that migration be fast enough to regularly create clusters of cooperative pioneers, but not so fast as to constantly expose these colonies to less cooperative invaders.

Within these constraints, robust cooperation is reliably achieved. The fundamental mechanism is that once a particular cooperation level is achieved in a population, only newly forming groups that happen to have cooperation levels higher than this will thrive. As long as their group grows before they are invaded by defectors (how long they have to grow is determined jointly by migration and mutation rates), the agents that migrate out of the group to form new groups will possess this new, higher value of cooperation. In this manner, cooperation ratchets upwards in the population while ratcheting downwards within each of the groups. As noted by Killingback et al. (2006), the upward trend in population-wide cooperation is consistent with downward trends in each group, and is an example of Simpson’s paradox. The resolution to the paradox stems from the highly unequal population sizes in the groups. As the cooperation level in a group decreases its global competitiveness and population size also decreases, with the result that newly founded cooperative groups will rapidly increase their relative share of the total population.

Our systematic analysis of the parameter space shows that a small level of migration is important, as well as more than a handful of groups. Interestingly, the optimal rate of migration for achieving cooperation is between 0% and 1%. Although no cooperative group is ever stable, a sufficient chance of migration of cooperative agents leads to frequent enough creations of new cooperative groups to stabilize the level of cooperation within the whole population. The higher the value of the public good multiplier, the higher the level of migration that is required to form larger groups that can match this multiplier.

Our model also relates to the firm model of Axtell (1999). In this model Axtell define firms as a number of agents who are located in a group and who develop a “public” good, production, that is shared among all participants. Firms form, and as more defectors enter who free-ride on the more active agents, the more altruistic agents move out of the group. With this model he simulates the sizes of firms existing in a population, and is able to relate his simple model to observed firm distributions in the USA. The distribution of firm sizes is similar to the unconstrained situation shown in Fig. 2.

In sum we provided a simple mechanism which explains how agents without comprehensive cognitive abilities can evolve to cooperate in various public good games given the right group structure.

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