The Good, the Bad and the Stochastic: How Living in Groups Innately Supports Cooperation

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Abstract

Based on theoretical considerations and computer simulations, I show that living in groups brings advantages for cooperative traits through purely stochastic effects that result from the division of a population into groups. These advantages can be sufficient to compensate individual selection pressures that may be associated with the cooperative traits. In more complex agent-based simulation models, this effect combined with some migration between the groups leads to stable dynamic equilibria between cooperative and defective replicators in the population.

Introduction

A central question in evolutionary biology since Charles Darwin is how cooperative traits emerge and prevail, although they can entail costs and disadvantages for the cooperative actors. However, countless examples in biology, from bacterial colonies to insect states and human societies, demonstrate that there must be ways and means for the evolution of traits that are “for the good of the group“.

Nowak (2012) lists five mechanisms for the evolution of cooperation: direct and indirect reciprocity as well as spatial selection, multi-level selection, and kin selection. A rather controversial mechanism is multi-level selection, an enhanced group selection, which aims to explain that there are different levels on which natural selection works. Some concepts and models show that group and multi-level selection might work (Wilson 1975, Traulsen & Nowak 2006, Wilson&Wilson 2008), but there are also strong opposing views.

Maynard Smith & Szathmáry (1996) argue that in the “Trait Group Model” (Wilson 1975) the frequency of altruistic replicators can only increase if altruistic replicators come together non-randomly or if there are synergistic effects on fitness (Fig. 1). Representatives of group and multi-level selection, however, argue that competition between groups would be necessary that group selection takes place (Wilson&Wilson 2008).

Based on some calculations and multi-agent simulations, however, I come to the conclusion that cooperative features alone achieve advantages through the division of a population into groups and through purely stochastic effects that occur. These effects can be sufficiently large to compensate intrinsic selection pressures that may be associated with the cooperative trait.

As a further consequence, under suitable circumstances, the migration of individuals leads to stable dynamic equilibria between cooperative (***C***) and defective (***D***) traits in the population.

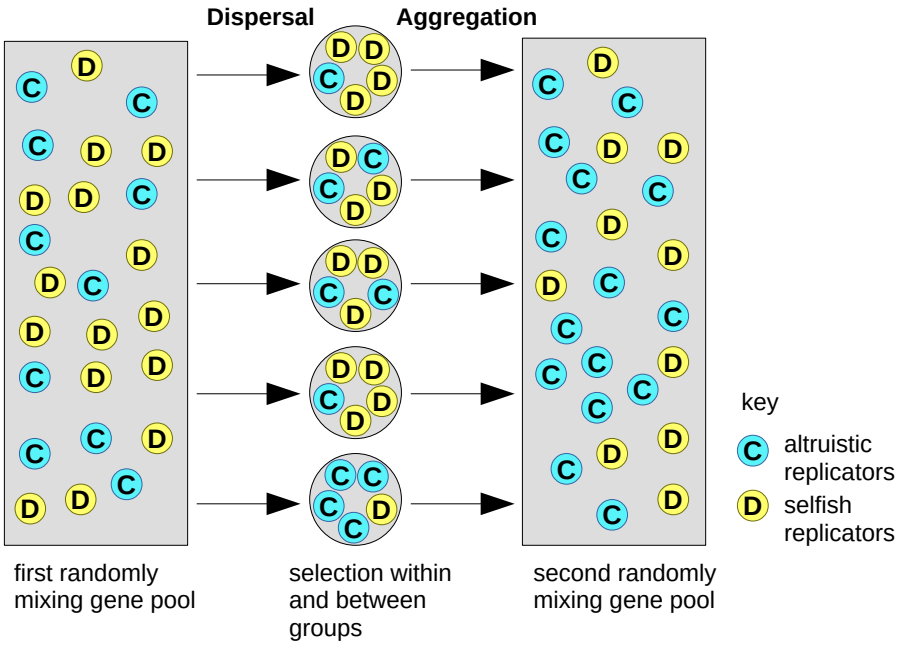

Figure 1: Description and criticism of Wilson's "trait group" model from Maynard Smith and Szathmáry (1996), they wrote: "If there is to be an increase in the frequency of altruisitc replicators, as shown, then either (1) altruistic replicators must assort together non-randomly or (2) there must be synergistic fitness effects, so that a group of altruistic replicators contributes disproportionately to the next generation."

About the stochastic advantage of being cooperative in the group

The basic assumption of the following considerations is a population of cooperative individuals with trait ***C*** and selfish defectors with trait ***D***, who are divided into random groups. The cooperators each provide the contribution $b=1$ to their group, the contribution of defectors is $b=0$. The sum of contributions is divided equally in the group, regardless of whether it is ***D*** or ***C***. Consequently in a group with only ***C***, each member receives the individual benefit $B_i=1$, in a ***D*** only group there is nothing to distribute, the benefit is $B_i=0$, and in mixed groups the individual benefit payoff lies in between.

For example, Fig. 2 shows a population of 5 cooperators and 5 defectors (written as 5C5D for short). As a single group there are thus 5 contributions from ***C*** and none from ***D***, the overall benefit is therefore 5. Divided by 10, each individual receives the benefit $B_i=0.5$. The total benefit for each trait is therefore $B_C=B_D=2.5$ for both the 5 ***C*** and the 5 ***D***.

Let us now divide the 5C5D population into two groups, for example into the most likely combination 3C2D and 2C3D. The group 3C2D achieves the group benefit $B_1=3$ through the 3 cooperators. Divided among the five members, each individual in this group receives $B_i=3/5$. The other group (2C3D) has two cooperators therefore the group benefit is only $B_2=2$, which is $B_i=2/5$ per member.

The total benefit for trait ***C*** is $B_{C1}=3\cdot3/5$ from group 3C2D and $B_{C2}=2\cdot2/5$ from group 2C3D, i.e. $3\cdot3/5 + 2\cdot2/5 = 13/5$.

In contrast, the overall benefit for ***D*** is $B_{D1}=2\cdot3/5$ from group 3C2D and $B_{D2}=3\cdot2/5$ from group 2C3D, so $2\cdot3/5 + 3\cdot2/5 = 12/5$.

This means that simply by dividing the population in two groups, the overall benefit for trait ***C*** has increased from 5/2 to 13/5 and that for ***D*** has decreased from 5/2 to 12/5. Specifically, the factors are 1.04 for ***C*** and 0.96 for ***D*** related to the population 5C5D.

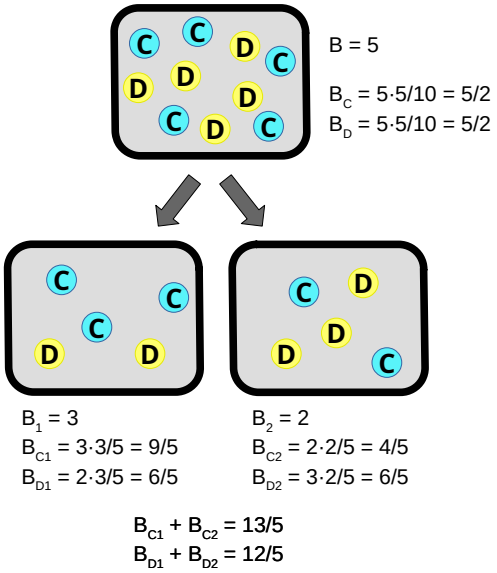

*Figure 2: Distribution of the group benefits for **C** and **D**. After splitting into two groups, the total benefit for trait **C** is greater and for **D** less than before.*

Figure 3 shows the benefit factors for a number of grouping combinations for two differently composed populations of 10 individuals, respectively. It is obvious that the more the ***C:D*** ratio in the group deviates from that in the population, the more the factors deviate from one. The benefit payoff can even be a multiple for ***C*** and it can also be completely eliminated for ***D***, as in the case of 3C0D: 0C7D, where the trait ***C*** has a benefit of three. Compared to 9/10 in the undivided 3C7D population, this gives a factor of 3.333. However, ***D*** does not achieve any benefit, since it only occurs in the ***D***-only group.

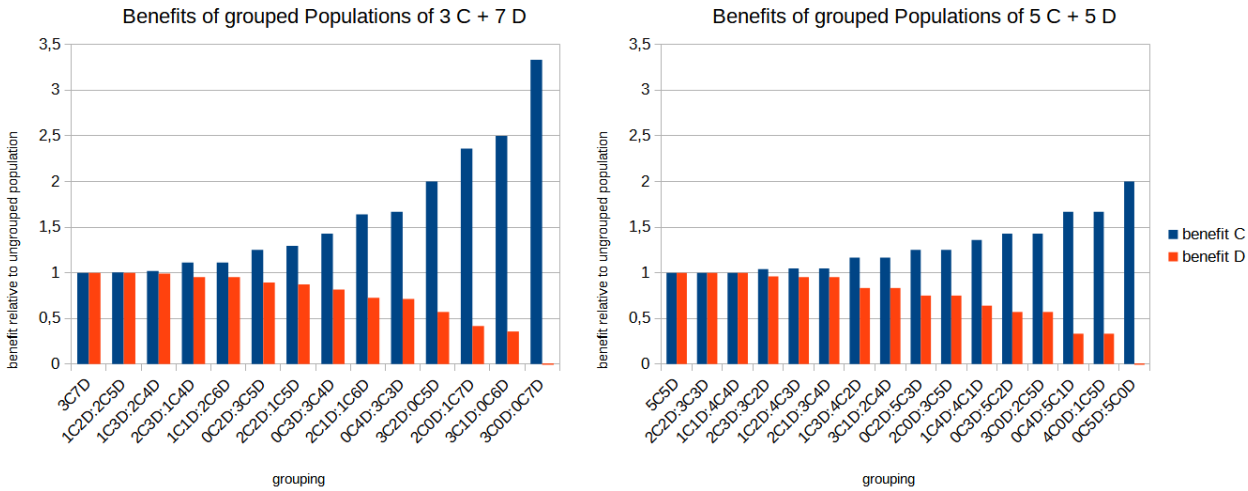

*Figure 3: Calculated benefit factors for traits **C** and **D** for various group divisions, each related to the undivided population. Details in text.*

In addition, one can see that through any grouping, feature ***C*** never has a disadvantage and ***D*** never has an advantage. Both can achieve a factor of 1 only if the groups have the same symmetry (***C:D***-ratios) as the population (e.g. the two groups 2C2D: 3C3D related to 5C5D). Further simulated results for different group sizes and ***C:D*** ratios are shown in Fig. 4.

Since this effect occurs with every split into smaller groups, ***C*** should tend towards smaller groups, and ***D*** towards larger groups. This is likely to be counteracted by pressures from the advantages and disadvantages of group size ("group effects"). However, I will not go into further detail here, but rather explicitly define the maximum group sizes in my models. Up to this specified size, I treat all groups equally, provided they consist of at least two members.

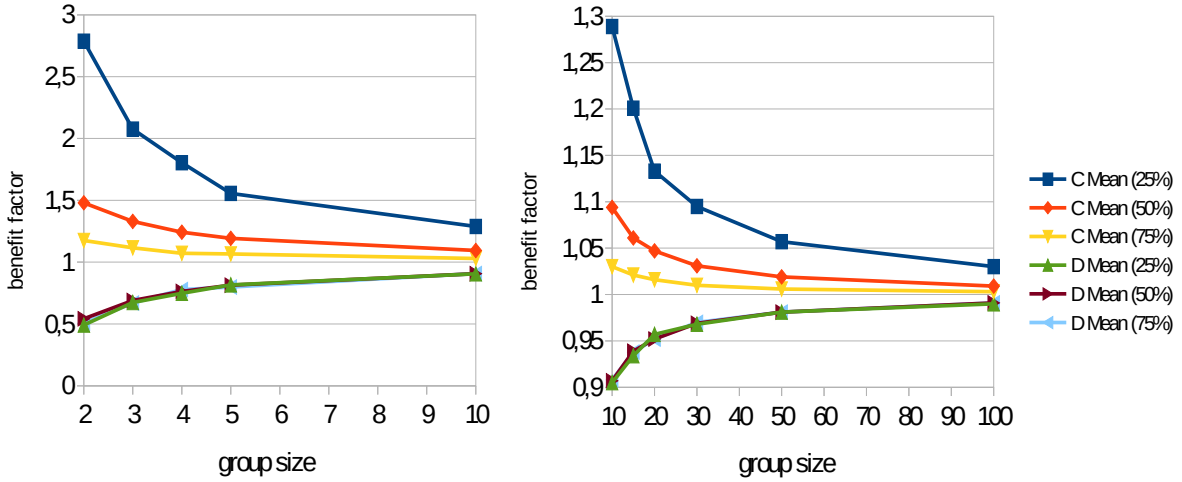

*Figure 4: Simulated benefit factors for various group sizes and ratios of **C** and **D**. For 16 groups of according group sizes and with 25%, 50%, and 75% of **C** in the population, the mean benefit factor of **C** and **D** has been determined from 100 simulation runs each. The plots show the results: In general, the smaller the group, the greater are both the advantages for **C** and the disadvantages for **D**. In addition, the smaller the proportion of **C** in the population, the greater are the benefits for **C** (25% > 50% > 75%). However, this ratio is irrelevant for **D**. Note that the diagram has been split at group size of 10 for better scaling.*

From grouping effect to system dynamics

I will demonstrate how these advantages from the group formation for cooperators (***C***) and the disadvantages for defectors (***D***) affect the dynamics of the trait distribution in the population by using increasingly complex simulation models.

When the payoff equals the odds to survive and survivors replicate

In my models, the benefit is transferred directly to the probability of survival or mortality. For a group of defectors (***D***) only, this means that every group member is eliminated in the next step. In a ***C***-only group, everyone survives. In a mixed group like C3D2, each member survives with $p=3/5$ (mortality is $p=2/5$), in a group C2D7 it would be $p=2/9$ (and mortality $p=7/9$). Under this assumption, the number of ***C*** in the (full) group is always equal to the number of survivors. But whoever survives is random and independent of trait ***C*** or ***D***.

In the following multi-agent simulations, there are 16 groups consisting of *n* randomly set replicators ***C*** and ***D***. In each step (= generation) the replicators are eliminated with the probability described above. Then the remaining group members replicate proportionally and inherit their trait ***C*** or ***D*** until their group is full again, i.e. there are 5 members. Finally group mortality comes back into play and so on.

Fig. 5 shows a typical development of such a population in a multi-agent simulation. After less than 10 generations, all defectors disappear and there are only groups with cooperators as well as extinct groups.

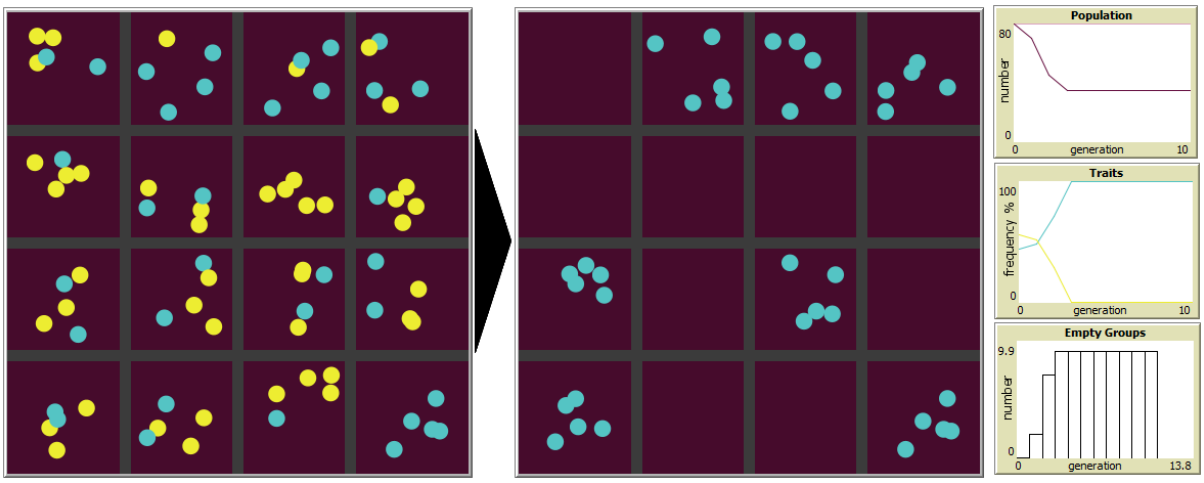

*Figure 5: Development over 10 generations without migration: there are only cooperators left, all defectors are extinct and about half of the groups are extinguished. Left: At the beginning with random distribution. Right: After 10 generations there are only cooperators and extinct groups. Cooperators **C** blue, defectors **D** yellow; 16 groups with 5 individuals each. The diagram right above: Population size in each generation; middle: traits plot shows the relative frequency of **C** (blue line) and **D** (yellow) over the generations; bottom plot shows the number of empty groups in each generation. This and the following simulation models I have created in the modeling environment Netlogo (Wilensky, 1999).*

The groups are firmly defined in my models and best understood as territories that are appropriately occupied or not. If empty or not fully occupied groups are allowed to be populated with migrating offspring from full groups, then all groups are occupied with cooperators ***C*** within a few generations (see Fig. 6).

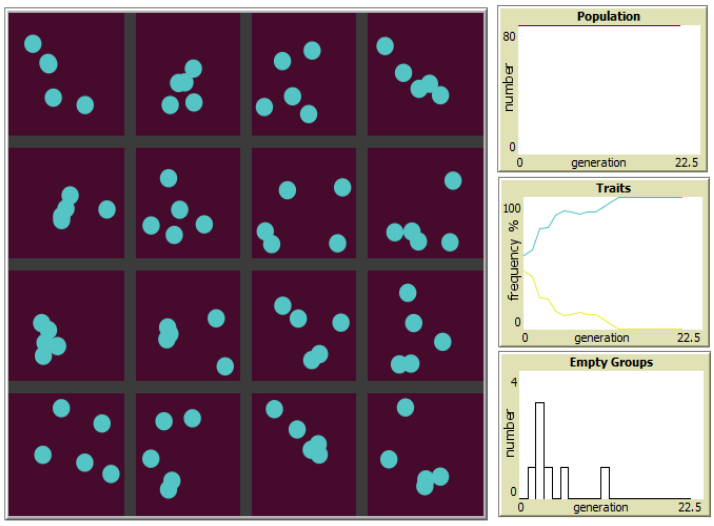

*Figure 6: Development of a random distribution after 20 generations with migration results in a population of cooperators **C** only, all groups are full and all **D** are extincted. Cooperators C blue, defectors D yellow; 16 groups with a maximum of 5 individuals each. The diagram above: Population is maximum over the time; middle: Traits plot shows increasing frequency of **C** (blue line) and decreasing **D** (yellow) until only **C** remains; bottom plot shows the number of empty groups in each generation*

Models with mutation and trait specific selection pressures

I also considered mutation for more realistic situations. Thus, with a certain probability *m*, a descendant has a different trait than its producer, i.e. ***C*** instead of ***D*** or vice versa. As a result, a trait alone cannot be eradicated. In the simulations, a stable dynamic equilibrium between ***C*** and ***D*** is usually established.

For more realistic simulations I also introduced different selection pressures on the two traits, whereby a greater selection pressure on ***C*** is of course the more interesting case, since cooperation usually entails a certain additional effort or risk for those acting in this way. I incorporated this into the simulations in the form of different intrinsic mortality rates for ***C*** and ***D***. These are completely independent of the group or other influences.

The process is now as follows: The individuals surviving the "group selection" (corresponding to the stochastic effects described above) and "individual selection" (corresponding to the intrinsic mortality rates of their traits) each produce asexually *N* offspring with a mutation rate of *m*. The offspring first fill their own group up, and if it is full, they wander off into empty or not yet full groups. When all groups are full, the excess offspring are eliminated. Then the cycle starts all over again with the selection.

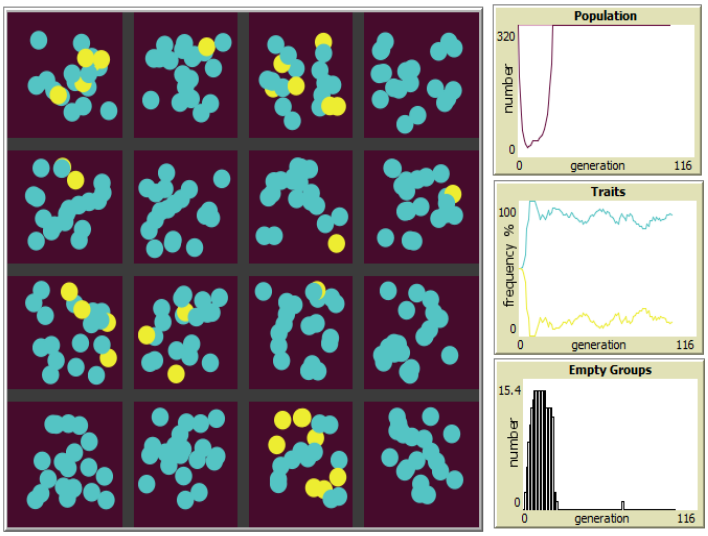

Figure 7: Stable steady state with mutation and different selection pressures over 100 generations. Cooperators C blue, defectors D yellow. 16 groups with a maximum of 20 individuals each. Offspring per survivor N=1; Mutation rate m=0.02; Mortality for C 25%, for D 20%. The traits diagram shows the relatively stable distribution of >80% C (blue) and <20% D (yellow) over the generations. The population decreases sharply after the start with the random population, but soon reaches the maximum size again and then remains at this level.

As a typical result for a wide range of parameters, stable equilibria are established with this model. In addition to the stochastic grouping effect, the flow of offspring from the more prosperous groups with a lot of benefit, that is with many ***C***, supports the cooperators. For example, around 80% of the population in Fig. 7 consist of cooperators, although their intrinsic mortality is 5% higher than that of the defectors.

If values are too extreme, such as very different or high mortality rates for ***C*** and ***D***, the whole population quickly collapses and dies out. Values in the marginal area, however, can lead to more or

less regular to chaotic fluctuations in the distribution of ***C*** and ***D*** as well as in population size, which can persist over hundreds or even thousands of generations (Fig. 8).

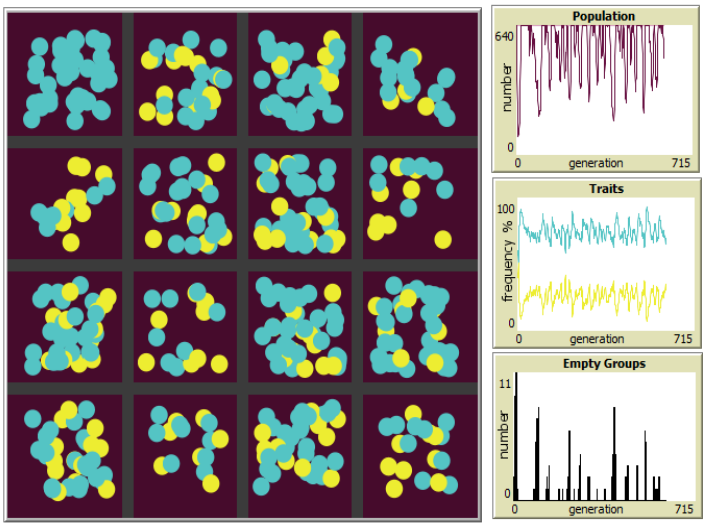

*Figure 8: "Turbulent" (chaotic?) steady state over 600 generations as simulation outcome for larger groups and with greater differences between selection pressures for **C** and **D**. Cooperators **C** blue, defectors **D** yellow. 16 groups with a maximum of 50 individuals each. Offspring per survivor N=1; Mutation rate m=0.02; Mortality for C 25%, for D 15%. "Traits" diagram shows strong fluctuations of **C** and **D**, and also the population size and number of empty groups vary greatly, almost to extinction.*

In addition to this simple, asexual model, I have also examined simulations with sexual reproduction, with and without generation overlap, and others with graduated features instead of the binary C vs. D. In all of them, stable equilibria as described above were found over wide value ranges.

Wilson's trait group model and the grouping effect

Finally, I want to come back to Wilson's trait group model and its review in Maynard Smith & Szathmáry (1996). In Tab. 1, I demonstrate how this stochastic grouping effect affects and solves the example of the trait group model shown in Fig. 1. With the same first gene pool and the same group division, as shown in Fig. 1, this effect results in three cooperators ***C*** (altruists) more and three defectors ***D*** (egoists) less in the second gene pool (13C12D) than in the first (10C15D). These are two ***C*** fewer and two ***D*** more than shown in the fictitious second gene pool of Fig. 1 with 15C10D, but nevertheless cooperation has increased significantly! This just happens at random, without synergistic effects, and also without competition between groups.

Table 1: Stochastic redistribution of altruistic (C) and egoistic (D) replicators through group formation using the example of the scheme shown in Fig. 1. Again, the assumption is that every altruist (C) makes the contribution b=1 to the group benefit, egoists contribute nothing (b=0) and the sum of a group's benefits directly determines its survival rate. As result, the gene pool changes from 10C15D to 13C12D, so there are three more altruists in the second gene pool than in the first, and accordingly three less egoists.

First gene pool	**Groups**	**Second gene pool**
10C15D i.e. the overall benefit is ... B=10 *… devided in …* B_C=4 B_D=6	1C4D: B_{C1}=1/5 and B_{D1}=4/5	The benefit B=10 is now divided in … $B_C=\sum B_{Cn}=26/5$ $B_D=\sum B_{Dn}=24/5$ If the trait benefit correlates with survival, then the proportional replication up to the initial populations (N = 25) results in … **13C12D**
	2C3D: B_{C2}=4/5 and B_{D2}=6/5	
	2C3D: B_{C3}=4/5 and B_{D3}=6/5	
	1C4D: B_{C4}=1/5 and B_{D4}=4/5	
	4C1D: B_{C5}=16/5 and B_{D5}=4/5	

Conclusion

In this study I tried to show that dividing a population of cooperators and defectors into random groups strengthens the cooperators through purely stochastic effects, almost like being taken by the invisible hand of Adam Smith. These advantages can, to a certain extent, compensate the selection pressure that may be associated with the cooperative trait.

Despite this grouping effect, each group can still be unstable and quickly disappear on its own, especially when there is a high proportion of defectors or the selection pressure against cooperators is very high. However, if low-individual groups are provided with emigrating offspring from prospering groups, which mainly consist of cooperators, a dynamic equilibrium will usually be established between the groups, and thus the system - the population - regulates itself. In other words, no further mechanism like reciprocity, kin selection, etc. is required in this concept to explain the emergence and maintenance of a stable cooperative trait in the population.

Alarm signals within animal groups, for example, could be easily explained with this grouping effect, since a signal like “Watch out, predator!” has a direct influence on the group's mortality. As long as the signaling does not exceed a certain risk for the emitter, it will be established and maintained in the population. Groups can also go beyond species boundaries, so that the grouping effect can also provide an explanation for mutualism. More important is that the groups are not too large, but even with group sizes of 100 individuals and a 1:1 ratio of ***C:D***, the payoff factors are still about +1% for ***C*** and -1% for ***D*** under the conditions given in Fig. 4.

Finally, how is this grouping effect to be classified in terms of evolutionary theory? Is this actually group or multi-level selection, because the effect only comes through the grouping and thereby changes the constraints for the selection? There is no competition between groups, which is usually seen a the basis for group selection. It is an emergent effect, since grouping per se leads to new properties and probabilities that the parts themselves do not have. So it's a new level after all? But isn’t it also a kind of genetic drift, since grouping causes a random change in the gene frequencies and thus a change in the payoffs, and consequently in fitness? Questions that I leave open here.

Acknowledgments

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