THE EVOLUTION OF COOPERATION AND DIVISION OF LABOUR IN STRUCTURED POPULATIONS – THREE INDIVIDUAL BASED MODELS

Thesis book

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Introduction

Major Evolutionary Transitions are often characterised by cooperation and division of labour on a given level of organisation which leads to the emergence of a higher level of evolutionary unit [13, 21]. Thus, understanding the evolution of cooperation and division of labour is of exceptional importance. It is especially so in the case of humans, where both cooperation and division of labour operates on numerous levels and on a remarkably large scale. But cooperation of this scale is not only a *result* of our singular evolutionary history, but presumably it is also among the primary *causes* of the unusual success of the *Homo sapiens* (see e.g. [4] or [11]). As all this was realised many decades ago, an immense body of literature accumulated in this research field. To give an idea about the wide range of the literature, on March 08 2018 the Web of Science found 24 531 titles including the term "cooperation", and 2287 titles including "division of labour". Yet, however extensive this literature is, it still cannot cover all the appearing questions in connection with such a complex problem. In my thesis I attempt to answer a number of untackled questions regarding the emergence and evolutionary role of cooperation and division of labour in structured populations, with special emphasis on human social groups. In my thesis I discuss three studies investigating different, but related problems, as follows:

1. How can cooperation invade variously viscous populations in characteristically different social situations?

2. How does division of labour emerge during cooperative task solving in social groups, and what are the evolutionary consequences?

3. How does food production and sedentism effect the appearance of division of labour and specialisation in human social groups?

Cooperation in the Volunteer's Dilemma Game

When studying the evolution of cooperation, two main questions arise: (i) whether cooperation can be evolutionarily stable, and (ii) whether it can spread when appearing as a rare mutant strategy [2]. For explaining the evolution of cooperation we have to find the answers to both of these questions. In the first study I ask how cooperators, as rare mutants, can invade a population of cheaters in characteristically different social dilemmas, that is, situations in which collective and private interest conflict with each other.

I compare two types of N-person social dilemmas, the most frequently studied N-person Prisoner's Dilemma (NPD) [10] and the less well-known, but biologically more adequate Volunteer's Dilemma (VD) games [1]. The difference between these two games is how the number of cooperators affects the benefit they provide their group with: while in the NPD the benefit increases linearly with the number of cooperators, the VD is characterised by a step function (see Fig. 1). Since many social situations are characterised by typically non-linear benefit functions (see e.g. [17] or [12]), the VD appears to be a better model to describe natural systems.
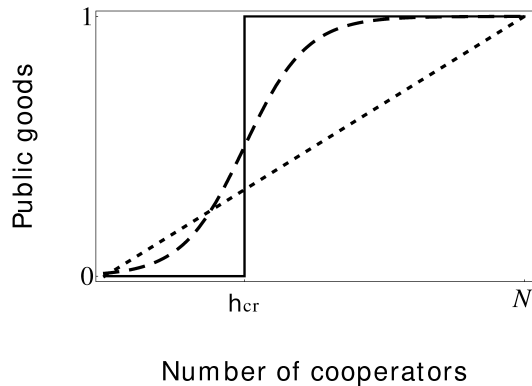

Figure 1: Schematic picture of the different benefit functions. A general saturating non-linear benefit function (dashed line), the linear NPD (dotted line) and the VD (continuous line).

In infinite, well-mixed populations of the NPD, cooperation disappears unless there is positive assortment or relatedness between cooperators [16]. In the VD, there is a parameter range, where a stable coexistence of cooperators and defectors is possible. However, even if coexistence is possible, the problem of how the rare mutant strategy can

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spread remains a problem in both games.

In this study, I was concerned with the likelihood of rare cooperators invading populations dominated by defection. I used models of cellular automata in which individuals played stochastic NPD and VD games, or a general saturating non-linear N-person game. I also studied the role of dispersal (or viscosity).

I considered a toroidal square lattice grid of L^2 (generally 100x100) nodes with at most one individual per grid point. Every individual interacted with its eight nearest neighbours. The modelled population was asexual with overlapping generations. I examined the effect of viscosity throughout three different settings: (i) The highly viscous case, in which there is no dispersal. (ii) The well-mixed case, in which each cycle is followed by an exchange of every individual with a randomly chosen other one. (iii) The variable mixing case, in which each cycle is followed by a given number of mixing steps, when two randomly chosen neighboring individuals change their position. In the invasion experiments, I modified the initial ratio of cooperators on a continuum from $1/L^2$ to 0.4. I measured the probability of a successful invasion as a function of the intial frequency of cooperators. Finally, I examined the role of the population size, using alternative grids with sizes varying between 50x50 and 250x250 grid points. With the help of the model I described above, I have got the following results.

- **1.1** I have shown that in the VD, unlike the NPD, the coexistence of cooperators and defectors is typical. Furthermore, the game with the general saturating benefit function is characteristically different from the NPD, but similar to the VD.

- **1.2** In agreement with the replicator dynamics of the VD, the invasion of cooperators in a well-mixed population is only possible if their initial concentration exceeds a critical threshold.

- **1.3** In a viscous population, I have found that instead of the initial concentration, the initial number determines the success of invasion. In this case, even a single mutant cooperator can invade with a high probability, because the local density of cooperators exceeds the critical threshold.

VÁSÁRHELYI, ZS & SCHEURING, I Invasion of cooperators in lattice populations: Linear and non-linear public good games. *BioSystems*, 113(2):81–90, 2013.

Division of labour in a collective task

Behavioural differences among conspecifics of the same population have been reported from all kinds of living organisms, from bacteria to vertebrates, including humans [7, 8, 20, 9, 6]. Interestingly, the adaptive value of individual variation in animal personality, especially in humans, is still the subject of debate [19, 14]. There are several approaches to explaining the ultimate causes of human and animal personality variation (see e.g. Wolf et al. [22], Nettle [15], or Bergmüller and Taborsky [3]), however, the possibility that selection for cooperation can also play a role in causing or maintaining this diversity, had not yet received proper attention.

I propose that division of labour (DL) between socially related conspecifics can cause and maintain variation in behaviour through negative frequency dependent selection that continuously decreases a phenotype's benefit as its frequency increases. Selection thus creates diversity, by favouring the rare, acting on preferences and skills, that is, on personality traits. In the second study I analysed a strategic model that studied the effect of DL on heritable behavioural differences.

I considered a large well-mixed population, where members of small groups solve a collective task. Solving this task produces a common good for the group which is distributed among the members after performing the task. Individuals can choose between two kinds of subtasks, before entering a group. The abilities to perform the two subtasks are not independent, and are in negative trade-off. Individuals are characterised by two heritable traits: the probability of choosing the subtasks, and the cost assigned to these. The population is asexual, and occasional mutations occur in both traits. I consider two different benefit sharing systems. In the first, sharing is equal. In the second, the sharing is frequency dependent: those who chose the scarcer subtask, get more. My main interest is whether DL emerges as a result of an evolutionary branching into two subpopulations specialised for the two subtasks.

A mathematical analysis of this model revealed two numerically testable predictions. (i) If the trade-off is convex betwen the costs, DL is likely to appear in the population, especially with the unequal benefit sharing system. (ii) The homogeneous population specialised to one of the subtasks is in a stable state, that is, in such a population DL will never appear. I have tested these predictions numerically, and studied a further extension with social control and varying population sizes, too. By social control I meant that there
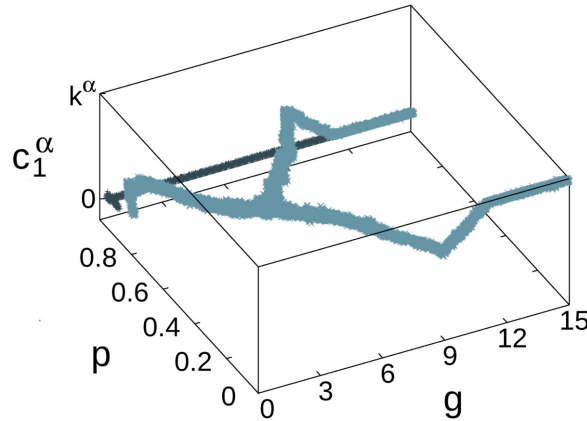
Figure 2: The impact of the initial trait values on branching. The plot shows two runs of 10^4 generations from different initial states.

is a social pressure on every individual not to get specialised, or more practically, to carry out both subtasks with nonzero probability. My main results are as follows.

- **2.1** I have shown that SDL and specialisation can emerge in a population frequently facing a collective task, especially with a convex trade-off between the costs of different subtasks.

- **2.2** SDL and specialisation proved to be much more probable in the case of a benefit sharing system that takes into account the individual's relative value to its group.

- **2.3** The numerical model confirmed that though the local mathematical analysis can predict the global behaviour, in the case of rare mutant strategies, the population never reaches the branching point, where specialisation could appear (see Fig. 2).

- **2.4** Finally, I have shown that branching is seriously hindered by both social control and a small population size in the model.

VÁSÁRHELYI, ZS, MESZÉNA, G & SCHEURING, I Evolution of heritable behavioural differences in a model of social division of labour. *PeerJ*, page 977, 2015.

Food production and behavioural diversity

Agriculture and sedentary life changed human societies immensely. The most striking features of typical pre-agricultural societies include the absence of leadership, strong hierarchy, and permanent homes [5], all of which are present in post-agricultural societies. The third study is concerned with two further outcomes of food production: food storage and social division of labour (SDL), DL within sex and age groups.

In this study I discussed an individual based model that attempts to study the connections between the appearance of food production, human social division of labour and behavioural diversity. I have two main settings representing different social and ecological environments: the ones before, and after the adoption of agriculture.

I consider a sexually reproducing, well-mixed group. In each time frame, individuals choose between $N_T \geq 2$ different tasks, and they spend their time with that particular task or activity. Being engaged in a task increases the payoff of the actor but tasks differ in the sense that they require and improve different skills. When someone spent a round with task j, this will not only gain her payoff, but also improve her effectiveness in solving task j. Individuals increase their expertise in one or more tasks during their lifetime. The more someone chooses a task, the more her expertise will grow in it, but the limit and speed of this increase depends on genetic factors. An individual's genetics consists of a quantitative genetic background (talent or affinity) for each task. I imagine this talent or affinity to be coded by a large number of genes, similarly to how personality or behavioural traits are coded by numerous genes [18].

At the end of each round payoffs are assigned to individuals according to their expertise in that round's task. Occasionally, individuals have a choice to update their task choice strategy by imitating others. The purpose of such imitation is to copy successful strategies, but we assume that one is only willing to copy a strategy that is not too different from her own. At the end of a generation's time (that includes a number of imitation phases, too), individuals are assigned into pairs and sexual reproduction takes place.

I have examined the above model framework with two different fitness calculating procedures, the pre-Neolithic or *subsistence*, and the Neolithic or *producer* case. In the subsistence setting, because of the special ecological environment, individuals are better off when they have some expertise in all activities. In the producer setting, having a general knowledge or experience is no longer a necessity, individuals are free to specialise.
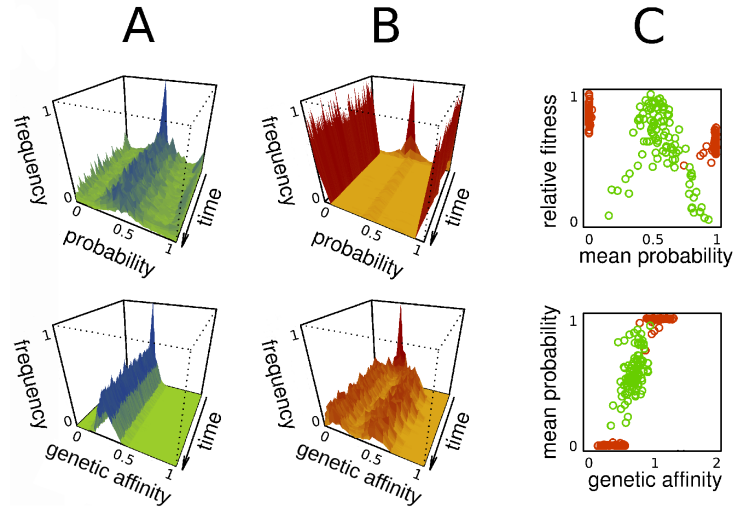
Figure 3: Summary of the basic results in both settings. The figure shows the task choice probabilities (top row) and the distribution of the genetics (bottom row) for one task throughout all generations. Greenish colours represent the subsistence, reddish the producer case.

I have studied both settings with 2, 3 and 4 tasks. I have also studied the effect of the group size, the role of frequency dependence and the strength of assortativity during imitation and reproduction. My main results are as follows.

- **3.1** When food storage and/or trade becomes available, behavioural specialisation and large-scale division of labour is likely to appear (see Fig. 3).

- **3.2** I have shown that in the producer case both phenotypic and genetic specialisation is possible, if scarcer goods are more valuable.

- **3.3** As the number of tasks increase, an ever larger group is necessary for specialisation.

- **3.4** Although phenotypic specialisation is often present, genetic specialisation requires strong assortativity both during imitation and mate choice.

VÁSÁRHELYI, ZS & SCHEURING ,I Behavioural specialisation during the neolithic – An evolutionary model. *Submitted*

Related publications

- Vásárhelyi, Zs and Scheuring I Invasion of cooperators in lattice populations: Linear and non-linear public good games. *BioSystems*, 113(2):81–90, 2013.
- Vásárhelyi, Zs, Meszéna, G, and Scheuring, I Evolution of heritable behavioural differences in a model of social division of labour. *PeerJ*, page 977, 2015.
- Vásárhelyi, Zs and Scheuring, I Behavioural specialisation during the Neolithic – An evolutionary model. Submitted.

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- Scheuring, I, Vásárhelyi, Zs Ásóbot, házityúk, benzinkút: az emberi evolúció ökológiája, *Természet Világa*. In press 2018.

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