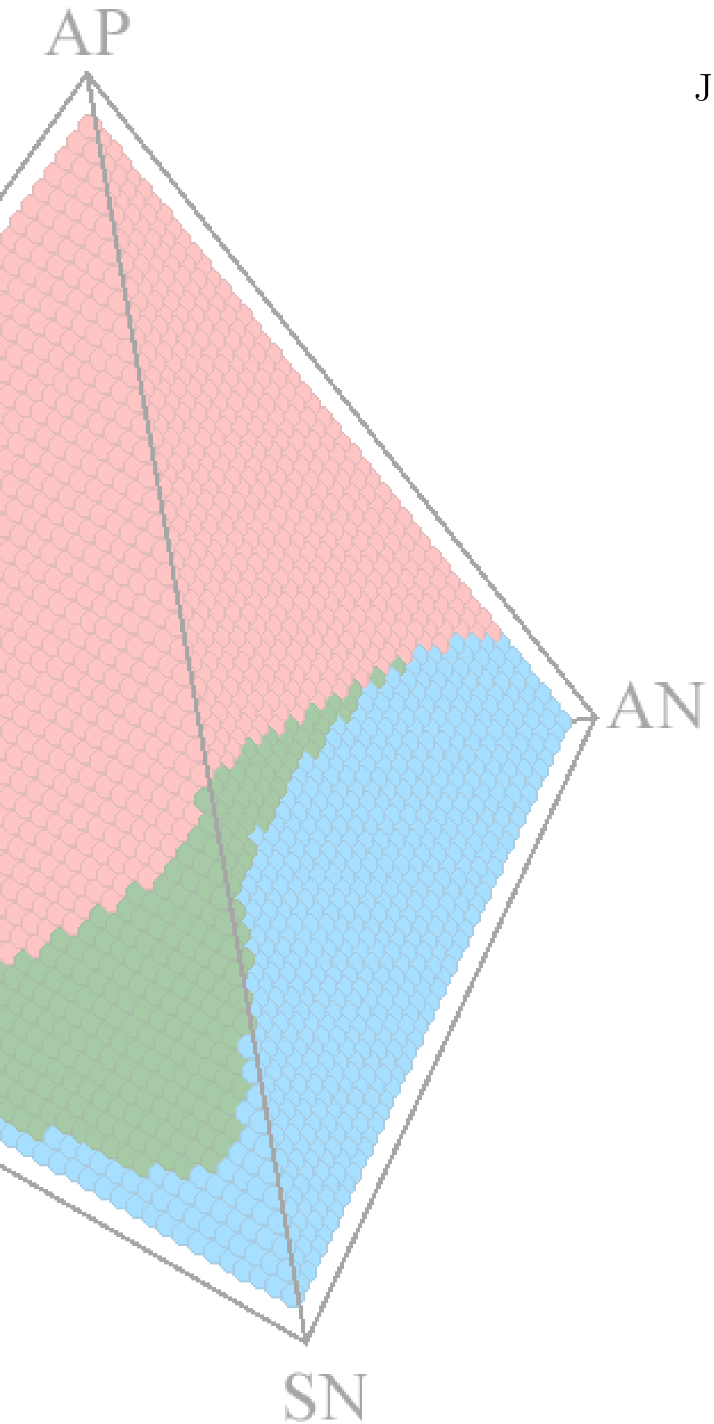
Evolution of altruistic punishment in heterogeneous populations

H.A. de Weerd

July 5, 2010



Supervisors:

Prof.dr. L.C. Verbrugge
Dr. H.B. Verheij

university of groningen

Contents

Abstract

Cooperation among animals as well as among humans represents one of the more enduring mysteries in biology and social sciences. Many different models have been proposed to answer the question of how altruistic cooperative behaviour could have evolved under the constant risk of exploitation by selfish individuals. One of the assumptions common to these models is that individuals are homogeneous: they have the same costs and benefits of cooperating with each other and punishing for selfish behaviour. Nevertheless, empirical research shows that human subjects adjust their expectations and actions based on individual differences. When the benefits for cooperating differ among the subjects that cooperate, subjects that enjoy a higher benefit are expected to contribute more, and are punished more severely if they fail to do so (Fisher et al., 1995; Reuben and Riedl, 2009).

In this research, we determine the effects of heterogeneity in the individual ability to punish for selfishness on the co-evolution of cooperation and punishment, and take a closer look at the resulting structure of the population in a simulated public goods game. To achieve this, the public goods game with voluntary participation (Brandt et al., 2006) is extended by separating the population into heterogeneous classes. Individuals within the same class are homogeneous, but between classes individuals may differ in the cost they pay for punishing, as well as the cost they inflict by punishing others.

The effects of introducing heterogeneity this way are compared across two population models that represent two different types of populations. An infinite and well-mixed population as used by Brandt et al. describes the way social insects such as ants and bees are organized. On the other hand, a spatially structured population in the form of a square lattice is related to the way social norms evolve and are maintained in a social network. We show that differences between individuals in a population can help or hinder altruistic efforts, depending on the way the population is structured.

In general, we find that heterogeneity in the effectiveness of punishment by itself has little to no effect on whether or not altruistic behaviour will stabilize in a population. In contrast, heterogeneity in the cost that individuals pay to punish for selfish behaviour allows altruistic behaviour to be maintained more easily by means of specialization between classes. Fewer punishers are needed to deter selfish behaviour, and the individuals that punish will mostly be the ones that pay a lower cost to do so. This effect is amplified when individuals that pay a lower cost for punishing inflict a higher punishment. However, when a lower cost for punishing is offset by a lower punishment inflicted on selfish individuals, altruistic behaviour becomes harder to stabilize in an infinite and well-mixed population.

When a population is spatially structured, it can take advantage of individual differences in a wider variety of cases by specialization between classes of individuals, such that punishment is mostly performed by the individuals that are best suited to do so. When altruistic behaviour is initially common, most of the punishment will eventually be carried out by the individuals that inflict the highest punishment, even if they pay a higher personal cost to do so. On the other hand, when selfish behaviour is initially common, a low cost of punishment is preferred and punishing behaviour will occur more frequently among individuals that pay the lowest cost, even at the expense of the punishment they inflict on selfish individuals. This way, a spatially structured population can avoid negative effects of heterogeneity in the ability to punish.

Chapter 1

Introduction

The question of how cooperation has evolved represents one of the more enduring mysteries in biology and social sciences. The paradox of cooperation is that although cooperation adds to the common good of a group of individuals, cooperating is an altruistic behaviour in the sense that contributing to the common good bears a higher cost than the individual returns. A rational individual would come to the selfish conclusion that the benefits are highest when everyone in the group cooperates, except for himself. A group of rational individuals would therefore be destined to never cooperate, even if the combined benefit of every single individual cooperating outweighs the cost of contributing. In game theory, this problem is commonly represented in the prisoner's dilemma. In this dilemma, two prisoners are interrogated separately on their involvement in a crime. Evidence in the case is so circumstantial it would only lead to a one year sentence for each of the two prisoners. Both of the prisoners are therefore offered a deal; if he confesses to the crime and testifies against the other prisoner, he will go free. This would make the case solid enough to get a six year sentence for the other prisoner. If both of them confess, both of them would get a five year sentence. Although the prisoners cannot communicate, it is assumed they know the other has been offered the same deal.

It is obvious in this case that it is for the common good of both prisoners to cooperate by not confessing. But individually, if a prisoner confesses while the other remains silent, his own sentence is reduced by one year. Similarly, if the same prisoner confesses when his fellow prisoner has confessed, his own sentence will be reduced by one year as well. Whatever the other would do, it serves the individual prisoner's interests best to defect and confess. Assuming both prisoners are rational, both would defect and receive a five year sentence, even though they would get a one year sentence each if they had cooperated with each other.

Even though cooperation seems to be destined to fail in theory, many social animals engage in cooperative action, ranging over a wide variety of activities such as foraging, signalling danger and defending the group from predators. One of the mechanisms that has been identified as being able to assist cooperation by preventing individuals from free-riding on the efforts of others is punishment. Punishment can provide the necessary incentive to stabilize cooperation in a group (Fehr and Gächter, 2002) or promote a social norm in human societies (Ostrom, 2000). But also in non-human species, punishment can be used to enforce a rule that is beneficial to the population in terms of evolutionary fitness. For example, in harems of red deer, the male punishes females who attempt to escape (Clutton-Brock and Parker, 1995). Also, workers of social insects punish workers that attempt to produce their own offspring (Monnin and Ratnieks, 2001). Once punishing has reached a reasonable foothold, it can stabilize virtually anything, whether it is cooperation or something else (Boyd and Richerson, 1992). However, until punishing has attained a reasonable foothold, punishing individuals are at a disadvantage since imposing a punishment is generally not free of cost. While there are relatively many defectors to be punished and few punishers to enforce cooperation, natural selection will eliminate the punishers in favour of the defectors.

Even in the light of costly punishment, experiments have shown that human subjects have a high willingness to sacrifice in order to punish selfish behaviour, even when there are no benefits for punishing (Fehr and Gächter, 2000). This is especially apparent in the ultimatum game, which is traditionally used in experiments involving human cooperation. In this experimental setup, a pair of volunteers is offered a sum of money. One of them is assigned the role of proposing how to divide the money among them. The other person can either accept the proposal, in which case the money is divided as suggested, or reject it, in which case neither of the participants receives any money. Since any sum of money is better than no money at all, the game-theoretically optimal strategy for the second player is to accept any offer in which he gets any money. However, in human experiments, participants often refuse low offers (Güth et al., 1982; Camerer and Thaler, 1995). Even when there is no repetition of the game, proposers often offer close to half the sum of money to the other person, while responders often reject offers of less than one third of the total sum (Bolton and Zwick, 1995; Henrich et al., 2001).

An N-person extension of the prisoner's dilemma, known as the public goods game (Kagel et al., 1995; Fehr and Gächter, 2002), has recently received more attention. In the public goods game, the game is played by $N > 2$ individuals, each of which received an initial capital. They may choose to keep that capital to themselves, or invest any part of it in a common pool. Once every player has decided how much to invest, the capital in the common pool is doubled, and divided equally among the players, irrespective of their investment. If every player invests their entire capital, each will end up with double their initial capital. However, each individual is faced with the temptation of exploiting the common pool. Since the return on the individual investment is negative, the game-theoretical dominant strategy is not to invest. But if none of the players invests, each will end up with half the capital they would have gained if everyone invested. In experiments with volunteers with actual economic incentive, human players do tend to invest a reasonable sum. Typically, in the first round, participants choose to invest at least half their capital. When the game is repeated over several rounds, the amount invested quickly declines until nobody invests anything, unless there is an opportunity to punish individuals for low investments (Fehr and Gächter, 2002).

The models that have been proposed to explain why cooperation persists and would even be able to invade in a population of selfish individuals, commonly make the assumption of homogeneity. Although individuals can use different strategies, the payoffs of an encounter between two individuals depend only on the strategy the individuals adopt. Individuals have the same cost of punishing, and the same benefit of their partner cooperating. By allowing for individual differences in these costs and benefits, individuals may have different opportunities. Empirical research shows that differences in marginal benefit from contributions to a public good changes the willingness to contribute and punish (Fisher et al., 1995; Reuben and Riedl, 2009). Subjects that enjoy a higher benefit not only tend to contribute more to the public good, but are also expected to do so, and are punished more severely by other players if they contribute less than their fair share.

In this research, we determine the effects of a heterogeneous population of individuals on the co-evolution of cooperation and punishment, and the resulting structure of the population in a simulated environment. Specifically, we investigate the effect of differences in the cost for punishing a co-player as well as the cost of being punished by another individual across two different population models. The first model assumes the public goods game is played in an infinite size and well-mixed population, where any pair of individuals are assumed never to encounter each other twice in the same setting. The second model imposes a spatial structure on the population in the form of a lattice, such that individuals only play the public goods game with a small selection of close neighbours. In both cases, the individuals share the common knowledge that the population is heterogeneous, but not how this affects the rewards.

The remainder of this master's thesis is structured as follows. Chapter 2 gives an overview of previous research into the public goods game. In particular, several extensions to the basic model are discussed that are also used in the current research. Chapter 3 will then derive the structure of the infinite population model. After that, chapter 4 discusses the lattice model, in which a spatial structure is imposed on the population. Chapter 5 lists the results of numerical simulations for both these models. Finally, chapters 6 and 7 provide a discussion of the results and directions for further research.

Chapter 2

Related research

In this chapter, we summarize the literature related to the current research, which served as the starting point of the models described in chapters 3 and 4. In the first part of this chapter, section 2.1 provides a general introduction into previous research aimed at explaining altruistic behaviour. In section 2.2 we will discuss an extension of the public goods game that allows individuals to forego participation in the game in return for a fixed payoff. Finally, section 2.3 is devoted to the concept of selfish punishment, in which the assumption that all punishers are altruistic is released.

2.1 Altruistic behaviour and punishment

Many species of animals are known to exhibit altruistic behaviour in the sense that individuals perform actions that are beneficial to the group, but costly to themselves. Social animals work together to provide shelter, protection, or food for the group, and cooperative behaviour has even been reported in micro-organisms (Hardin, 1968; Trivers, 1971; Colman, 1995; Dugatkin, 1997; Crespi, 2001). But even though altruistic behaviour appears regularly, it is not apparent how this could have evolved. The group as a whole benefits from altruistic behaviour, but individuals may profit by shirking their duties while enjoying the benefits provided by the work of others. If this benefit can be interpreted as evolutionary fitness, natural selection favours the selfish over the altruist.

The earliest models that tried to explain why altruistic behaviour would persist in a population when natural selection would favour selfishness depended on kin selection (Hamilton, 1964). This model suggests that altruistic behaviour will only be bestowed upon individuals that are close of kin, such as offspring, siblings or cousins. Cooperation would therefore benefit individuals that would most likely share part of the genetic code prescribing altruistic behaviour. Explaining altruistic behaviour with a selfish gene, however, does not explain why unrelated individuals or strangers would cooperate with one another.

Trivers (1971) showed that even without kinship, direct reciprocity could account for the success of cooperation. If interaction between a pair of individuals was repeated sufficiently often, cooperative strategies based on reciprocation could persist. The future rewards from continued cooperation would outweigh the immediate gain of selfishness. In a large tournament in which different strategies played the repeated prisoner's dilemma against random opponents, Axelrod and Hamilton (1981) found that on average, the highest score was not achieved by the strategy that always opted for the selfish choice, but by a strategy called tit-for-tat. This strategy cooperated with any strategy it had not encountered before, and afterwards copied the action its opponent had taken the last time they interacted. In effect, this caused tit-for-tat to reward strategies that showed altruistic behaviour before by cooperating again, and retaliate for being exploited by defecting during their next encounter. This strategy proved to be very effective as long as there was a sufficient number of individuals willing to cooperate, the probability of repeat encounters was high enough, and the memory was sufficiently large to recall the last action of all previously encountered individuals.

Direct reciprocity works when repeat encounters are likely, but fails if previous co-players are rarely met again. In the latter case, there is little or no opportunity to retaliate, and selfishness goes mostly unpunished. One way to deal with this issue and stabilize altruistic behaviour in a population is achieved by indirect reciprocity (Alexander, 1987). Rather than relying only on personal experience, in the system of indirect reciprocity individuals gain information about interactions that do not involve themselves, either through active exchange of information, or by passive observation. Individuals that base their actions on reputation of their co-player will then cooperate with co-players that have a good reputation, but will retaliate against co-players with a bad reputation. However, retaliating lowers the reputation score for an individual, which decreases the probability other individuals will cooperate with the retaliator in the future. Although it is possible to construct a system that can distinguish between selfish and retaliatory behaviour, such a system requires cognitive capabilities beyond the abilities of most animal societies.

Reciprocating strategies have been shown to stabilize cooperation in repeated two-player games such as the classic prisoner's dilemma (Nowak and Sigmund, 1998; Leimar and Hammerstein, 2001), but fail when cooperation in larger groups is examined (Boyd and Richerson, 1988). Retaliation for selfish behaviour occurs by withholding cooperation, which means individuals intending to retaliate against a particular selfish co-player will also harm all altruistic co-players in the group.

If individual defection may be observed, strong reciprocity or punishment can stabilize cooperation in a population (Sigmund et al., 2001; Boyd et al., 2003; Brandt et al., 2003; Fowler, 2005). Instead of withholding cooperative behaviour from co-players that previously defected, punishing individuals actively reduce the payoff received by selfish individuals at a personal cost to themselves. Note that doing so contributes to a second "public good"; by discouraging selfish behaviour, the entire population profits from the costly efforts of the punisher. From the viewpoint of an altruist that encounters a selfish individual, punishing the selfish individual would only further reduce their own payoff. As in the case of cooperation, it is in the best interest of the individual not to punish and only enjoy the benefits provided by the punishment inflicted by other individuals. Altruistic non-punishers that do contribute to the public good, but fail to punish, are therefore sometimes referred to as second-order free-riders.

Although punishment only lowers payoffs in the short run, punishing deters future occurrences of selfish behaviour. As such, punishment will stabilize altruistic behaviour once it has reached enough of a foothold in the population. However, the additional cost for punishing selfish behaviour makes it hard for altruistic punishment to invade a population of selfish individuals.

2.2 Voluntary participation

Until a reasonable foothold is reached, exploitation by selfish individuals generally causes cooperators and punishers to be eliminated from the population. Several structures for allowing cooperation and punishment to evolve have been proposed. Hauert et al. (2002b) have shown that voluntary participation in the public goods game can prevent the dead-lock situation in which all individuals are defectors. In this model, individuals would choose between entering the public goods game as a cooperator or defector, or become a "loner" and settling for an autarkic way of life. The payoff of the loner is assumed to be higher than a group consisting only of defectors, but lower than a group consisting entirely of cooperators. By allowing individuals to withdraw from the game, the size of the group becomes dynamic. Hauert et al. show that in small groups, cooperation yields the highest payoff, drawing more individuals towards the game. As the group grows in size, the public goods are distributed among more players, and therefore the returns for the individual on his or her own investment decrease. This favours defection, which in turn lowers the return on the public goods game, causing people to withdraw again. Therefore, instead of converging to situation in which every individual is a defector, the population proportion of cooperators and defectors oscillates. Hauert et al. (2002a) refined this model by preventing groups of size one, which would let players play the public goods game by themselves to receive a higher payoff than loners. Hauert et al. argued that when the returns on the public goods game are at least twice the investment, their results still hold.

Fowler (2005) extended this idea of voluntary participation to allow for punishment, and claimed that allowing individuals the choice of entering the public goods game would always lead to a situation

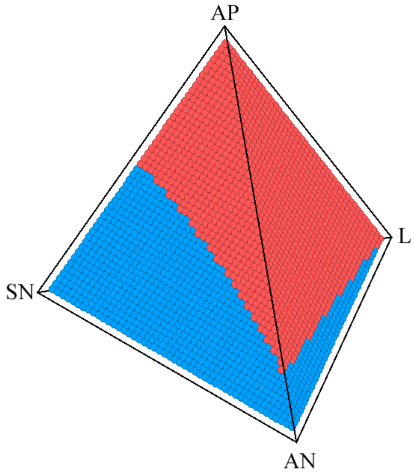


Figure 2.1: (Reconstruction of figure 2 by Brandt et al. (2006)). Replicator dynamics in the interior of the state space. Each corner represents one of the pure strategies cooperator (AN), punisher (AP), defector (SN) and loner (L). Initial states indicated by red dots eventually lead to a population of punishers (AP) and cooperators (AN), while blue dots indicate initial states that lead to periodic oscillations in loners (L), defectors (SN) and cooperators (AN).

in which punishment could invade and take over. Each population without punishers would converge to a population of only loners, which could be invaded by a single altruist or punisher. Brandt et al. (2006), however, argued that this model should be modified on two points. First, they incorporated the refinements proposed by Hauert et al. (2002a), such that whenever an individual is the only one interested in participating in the public goods game, that player will be forced to be a loner as well. Second, the model used by Fowler allowed punishers to punish for second-order free-riding. That is, punishers imposed a fine not only on defectors for their failure to cooperate, but also on non-punishing cooperators for their failure to punish defectors. Brandt et al. pointed out that this model let punishers impose fines for second-order free-riding even when there were no defectors in which case failure to punish would be impossible to detect. They showed that in their modified model, punishment would not always be the end state of the population. Only when the proportion of punishers is high enough, the population will eventually converge to an all-punisher population. In other cases, the proportion of punishers will drop to zero, and other population proportions would oscillate. Figure 2.1 shows the relation between the initial configuration and the eventual fate of the population. Red dots indicate states that lead to final state on the AP-AN edge. That is, when the initial proportion of loners and altruistic punishers is high enough, the population will eventually consist only of altruistic individuals. Blue dots, on the other hand, lead to the oscillating orbits in the AN-SN-L plane. This means that for blue dots, punishment will be selectively eliminated from the population.

In finite populations, cooperation and punishing seems to be favoured when participation in the public goods game is voluntary (Hauert et al., 2007, 2009). In the limit of rare mutations, a system consisting of cooperators, defectors and loners will be a population of cooperators roughly 40% of the time, while being a population of loners roughly 50% of the time. When punishing is introduced as well, the system typically spends around 80% of the time in the state of all punishers for large populations (Hauert et al., 2009). Punishing for second-order free-riding turns out to have little effect on this result.

2.3 Selfish punishment

In most research into altruistic behaviour and punishment, punishers are assumed to be altruistic. That is, in the two-stage game that is played, punishers are assumed to cooperate in the first round, and punish in the second. The effects of selfish punishers, a type of individual that does not cooperate in the first round, but does punish all other individuals that did not cooperate in the first round, is usually ignored.

However, since altruistic cooperation is beneficial to selfish as well as to altruistic individuals, defectors do have an incentive to punish the selfishness of others. An experiment by Falk et al. (2005) shows that the proportion of human subjects that punish defectors, even though they themselves defected in the first round, is surprisingly high. However, Falk et al. (2005) attribute this to spiteful behaviour, since in their experimental setup, punishment could also be used as a cheap way to reduce the payoff of others.

Sigmund et al. (2001) investigated replicator dynamics for rewards and punishment in repeated two-player games, in which they allowed selfish players to punish for failure to cooperate. However, since selfish punishment is a self-limiting strategy, their conclusions were mainly limited to the other strategies.

On the other hand, Nakamaru and Iwasa (2006) argue that selfish punishers are an important aspect in the evolution of punishment, because selfish punishment can represent a division of labour: part of the population contributes by being altruistic in the first round, while other individuals punish for selfish behaviour. This way, the cost of punishment can then be "paid for" by the altruistic players. In their research, the assumption that all punishers are altruistic is released altogether to study the co-evolution of altruistic behaviour and punishment on a range of models. They investigate a repeated two-player game in which the total payoff determines either the rate of survival (viability model) or rate of reproduction (fertility model). Furthermore, they compare the differences in these two models of a well-mixed population with the results on a lattice-based world. In the latter case, individuals within the population are assumed to have a spatial location, while interactions are limited to a local neighbourhood. Unlike well-mixed populations, in which interactions are randomized through the entire population, interactions in lattice-based worlds are always between the same individuals. For other game-theoretical games, it has been shown that incorporating a spatial structure in this way can allow local clusters of altruistic individuals to survive against defectors where they would not survive in a well-mixed population (Nowak and May, 1993; Lindgren and Nordahl, 1994; Killingback and Doebeli, 1996). Nakamaru and Iwasa argue that selfish punishment locally decreases the fitness of selfish individuals, encouraging altruistic behaviour. One of their main conclusions is that the presence of selfish punishers encourages the evolution of altruistic punishment.

Eldakar et al. suggest cooperation can be encouraged by selfishness as well (Eldakar et al., 2007; Eldakar and Wilson, 2008). They argue that unlike altruistic punishers, who contribute to the common good and are therefore at a double disadvantage to selfish non-punishers, selfish punishers use the advantage they have over altruistic individuals to punish those that do not cooperate. Their conclusions are similar to those of Nakamaru and Iwasa (2006); where second-order free-riding discourages punishment, selfish punishers can successfully discourage selfishness when the size of the group playing the public goods game is small enough. However, when the cost for punishing decreases, the use of punishment can increase until it is used as a form of spite. Instead of punishing for selfish behaviour, punishment is then used indiscriminately in order to gain an advantage in fitness over other individuals.

Even though selfish punishment might seem like a hypocritical strategy that is limited to humans, forms of selfish punishment have been observed in non-human species as well. In populations of the tree wasp *Dolichovespula sylvestris*, some of the workers that restrict reproduction of other workers by destroying worker-laid eggs or attacking egg-laying workers laid eggs themselves (Wenseleers et al., 2005).

Chapter 3

Infinite population model

To determine the effect of heterogeneity of individuals on the evolution of altruistic behaviour and punishment, we have constructed two models of the public goods game. In this chapter, we will construct a model based on the assumption of an infinite sized, well-mixed population of individuals. As a starting point, we use the model introduced by Brandt et al. (2006), which already allows for voluntary participation. This model is extended by also allowing for selfish punishment. Once we have derived the payoff functions for a population of homogeneous individuals, we then adapt the model to allow for a population that consists of M heterogeneous classes of individuals in section 3.3.

3.1 Basic infinite population model

In the infinite population model, we follow Brandt et al. (2006). Their model is an extension of the basic public goods model, in which players may choose not to share in the public good and instead receive a fixed payoff. We further extend their model to allow for selfish punishment. Individuals that decide to play the game have the choice of being either altruistic or selfish, as well as the choice whether or not they will punish co-players for not being altruistic. These choices are independent in our case. That is, a punisher is not forced to be altruistic, creating an additional strategy of the selfish punisher, similar to Eldakar and Wilson (2008). Therefore, the population is divided into five different classes of individuals: the loners x_L, altruistic non-punishers or cooperators x_{AN}, selfish non-punishers or defectors x_{SN}, altruistic punishers x_{AP} and selfish punishers x_{SP}, where $x_L, x_{AN}, x_{SN}, x_{AP}, x_{SP}$ refer to the fraction of the population adopting their respective strategy. Note that individuals only play pure strategies. We assume the public goods game is not played by the entire population simultaneously. Instead, the game is played by a random sample of N individuals. The expected payoffs of each of the strategies are calculated accordingly.

When a random sample of size N is drawn, the public goods game is played by all the individuals in this group except for the loners. Loners refuse to play the game and instead of sharing in the public goods, they receive a fixed payoff σ. They have no share in the public good, but they also do not contribute to it, and are not punished for failing to contribute.

An altruistic individual chooses to invest an amount c in the public goods. The total amount contributed in the public goods across all of the N individuals is multiplied by a factor $r > 1$ before it is distributed among all individuals playing the game, whether they are altruistic or selfish, but excluding the loners. That is, in a group of $n_A := N(x_{AP} + x_{AN})$ altruistic individuals and $n_L := Nx_L$ loners, the public goods yield the non-loners a benefit of $rc\frac{n_A}{N-n_L}$ at a cost c to each of the altruistic individuals. However, there is an exception to this rule. When the group consists of $N-1$ loners, the only individual willing to participate in the public goods game is forced to be a loner as well. Furthermore, it is assumed that $(r-1)c > \sigma > 0$, such that a loner receives a better payoff than a group of selfish individuals that receive 0 payoff, but worse than a group of altruistic individuals, where each individual receives $(r-1)c$.

After all contributions have been made and the public good is shared, punishing individuals punish the selfish individuals. Selfish individuals in this setting are individuals that choose to participate in the public goods game, but do not contribute to the public good. Punishers inflict a cost $\beta > 0$ to each selfish individual at a personal cost of $\gamma > 0$. Punishers may also punish individuals that fail to punish selfish participants. In this context, altruistic non-punishers are also termed second-order free-riders, since they do contribute to the public good, but do not contribute to the punishment system. Note that this type of punishment is meant to encourage altruistic non-punishers to start punishing selfish individuals. In this sense, there is no incentive for selfish punishers to punish for second-order free-riding. Selfish punishers want to encourage altruistic behaviour, but discourage other individuals from punishing. Therefore, only altruistic punishers punish for second-order free-riding. Altruistic punishers incur a fraction $0 \leq \alpha \leq 1$ of the cost they incur to selfish individuals to the second-order free-riders. That is, at a cost of $\alpha\gamma$ to themselves, they lower the payoff of altruistic non-punishers by $\alpha\beta$. However, when there are no selfish individuals in the group, none of the participants to the public goods game will punish, and altruistic non-punishers can therefore not be detected. Second-order free-riding is therefore only punished if there is at least one altruistic punisher, one altruistic non-punisher, and at least one selfish individual present in the group.

3.2 Calculation of payoffs

Evolution in well-mixed, infinite populations is traditionally studied using replicator dynamics (Taylor and Jonker, 1978; Nowak and Sigmund, 2004). In this section, we will derive the payoffs of the different strategies using replicator dynamics. The results are first derived for a homogeneous population, and then adapted to support our model of a heterogeneous population.

For a homogeneous population, the frequencies of each of the different strategy types determine the current state of the population, such that $x_{AN} + x_{AP} + x_{SN} + x_{SP} + x_L = 1$. The state space is therefore effectively limited to the convex hull of a set of five points, each representing one of the pure strategies. That is, the state space of all possible strategies is the simplex

$$S_5 = \left\{ x \in \mathbb{R}^5_+ \,\middle|\, \sum_{i=1}^{5} x_i = 1 \right\}.$$

Individuals within the population interact in groups of size N, which are randomly sampled according to a multinomial distribution. Under replicator dynamics, strategies that perform better than average within the population will increase in frequency, while strategies that perform poorly relative to others will become less abundant. This idea is captured in the replicator dynamics differential equation

$$\dot{x}_i = x_i(P_i - \bar{P}), \tag{3.1}$$

where P_i represents the expected payoff of strategy i and $\bar{P} = \sum_j x_j P_j$ represents the population average payoff.

The intuition behind replicator dynamics is that occasionally, and independently of the group sampling, a randomly chosen player A compares its expected payoff with that of another player B (randomly chosen within the entire population). If the strategy adopted by player B results in a higher expected payoff than the expected payoff for player A, player A will adopt the strategy of B with a probability proportional to the difference in their expected payoffs. In the remainder of this section, we will derive the expected payoff of playing any of the strategies in a group of N individuals drawn from an infinite and well-mixed population.

First, loners refuse to participate in the public goods game and receive a fixed payoff σ instead, irrespective of the strategies of other individuals. Their payoff is independent of the sampling, or the structure of the population:

$$P_L = \sigma.$$

In other cases, the payoff depends on the number and strategy of other players. First of all, when any individual is in a group along with $N - 1$ loners, there will be no public goods game and the individual will be forced to be a loner as well, receiving payoff σ. The probability of this occurring in our setting of an infinite, well-mixed population is x_L^{N-1}. Following Hauert et al. (2002a), the probability of forming a public goods game with $S-1$ out of the $N-1$ co-players under the multinomial sampling is

$$\binom{N-1}{S-1}(1-x_L)^{S-1}x_L^{N-S},$$

and the probability that m of these players are altruistic is

$$\binom{S-1}{m}\left(\frac{x_{AP}+x_{AN}}{1-x_L}\right)^m\left(\frac{x_{SP}+x_{SN}}{1-x_L}\right)^{S-1-m}.$$

The individual share of the public good in a group of $S \geq 2$ individuals, of which m are altruistic, is $rc\frac{m}{S}$. Since a selfish individual does not contribute to the public goods, the expected return on the public goods for selfish players in a group of S participants is

$$\frac{rc}{S}\sum_{m=0}^{S-1} m\binom{S-1}{m}\left(\frac{x_{AP}+x_{AN}}{1-x_L}\right)^m\left(\frac{x_{SP}+x_{SN}}{1-x_L}\right)^{S-1-m} = \frac{rc}{S}(S-1)\frac{x_{AP}+x_{AN}}{1-x_L}.$$

From this, it follows that the expected return on the public goods game for a selfish individual is

$$rc\frac{x_{AP}+x_{AN}}{1-x_L}\sum_{S=2}^{N}\left(1-\frac{1}{S}\right)\binom{N-1}{S-1}(1-x_L)^{S-1}x_L^{N-S}.$$

Using the fact that for $S=1$, $1-\frac{1}{S}=0$, and the fact that $\frac{N}{S}\binom{N-1}{S-1}=\binom{N}{S}$, the expected return on the public goods for selfish players simplifies to

$$rc\frac{x_{AP}+x_{AN}}{1-x_L}\left(1-\frac{1-x_L^N}{N(1-x_L)}\right).$$

The return on the public good is slightly different for altruistic individuals, who invest an amount c in the public goods game. Note that this contribution also increases their total share of the public goods game by $\frac{rc}{S}$, where S is the number of non-loner individuals in the group. Therefore, using the same reasoning as before, the expected difference in the return on the public good between selfish and altruistic individuals is:

$$\begin{aligned} cF(x_L) &:= c\sum_{S=2}^{N}\left(1-\frac{r}{S}\right)\binom{N-1}{S-1}(1-x_L)^{S-1}x_L^{N-1} \\ &= c\left((1-x_L^{N-1})-\frac{r}{N(1-x_L)}(1-x_L^N-N(1-x_L)x_L^{N-1})\right) \\ &= c\left(1+x_L^{N-1}(r-1)-\frac{r}{N}\frac{1-x_L^N}{1-x_L}\right). \end{aligned}$$

Next, selfish individuals are punished by punishing individuals at a cost of $\beta > 0$ to the selfish individual and $\gamma > 0$ to the punisher. The expected punishment to selfish individuals is therefore $\beta(N-1)(x_{SP}+x_{AP})$. Note that there is no difference in the expected amount of punishment received by selfish punishers and selfish non-punishers, since neither selfish non-punishers nor selfish punishers will punish themselves. Moreover, since the population is assumed to be infinite and well-mixed, the strategies of the individuals in the group are independent. Similar to the cost of being punished, the cost of punishing is $\gamma(N-1)(x_{SN}+x_{SP})$ for both altruistic and selfish punishers.

Besides punishing selfish individuals, altruistic punishers also impose a fine on non-punishing individuals for failing to punish selfish individuals. Selfish punishers are assumed not to fine non-punishers, since it is not in their interest to encourage punishing. The fine for failing to punish is a fraction $0 < \alpha < 1$ of the punishment for selfishness. However, this kind of punishment can only be enforced when there is at least one selfish individual, one altruistic non-punisher and one altruistic punisher in the group. That is, altruistic punishers have an expected additional cost of

$$\alpha\gamma x_{AN}(N-1)G(x_{SN}+x_{SP}), \text{ where } G(x_S) := (1-(1-x_S)^{N-2})$$

to punish non-punishers. Altruistic non-punishers, on their part, suffer a cost of

$$\alpha\beta x_{AP}(N-1)G(x_{SN}+x_{SP})$$

for not punishing selfish individuals when they were present in the group.

Combining the costs and benefits yields the following payoffs for the five strategies:

$$\begin{aligned}
P_L &= \sigma \\
P_{AN} &= \sigma x_L^{N-1} + rc(x_{AP}+x_{AN})B(x_L) - cF(x_L) - \alpha\beta(N-1)x_{AP}G(x_{SP}+x_{SN}) \\
P_{SN} &= \sigma x_L^{N-1} + rc(x_{AP}+x_{AN})B(x_L) - \beta(N-1)(x_{AP}+x_{SP}) \\
P_{AP} &= \sigma x_L^{N-1} + rc(x_{AP}+x_{AN})B(x_L) - cF(x_L) - \gamma(N-1)(x_{SN}+x_{SP}) - \\
&\qquad \alpha\gamma(N-1)x_{AN}G(x_{SP}+x_{SN}) \\
P_{SP} &= \sigma x_L^{N-1} + rc(x_{AP}+x_{AN})B(x_L) - \gamma(N-1)(x_{SN}+x_{SP}) - \beta(N-1)(x_{AP}+x_{SP})
\end{aligned}$$

where

$$\begin{aligned}
B(x_L) &= \frac{1}{1-x_L}\left(1-\frac{1-x_L^N}{N(1-x_L)}\right) \\
F(x_L) &= 1 + x_L^{N-1}(r-1) - \frac{r}{N}\frac{1-x_L^N}{1-x_L} \\
G(x_S) &= 1-(1-x_S)^{N-2}
\end{aligned}$$

3.3 Extension by heterogeneous population

We further extend the model outlined in sections 3.1 and 3.2 to allow for a heterogeneous population. In our case, the population is assumed to consist of M classes of individuals, which occur at a fixed ratio within the population. That is, although evolutionary dynamics affects the frequencies at which the different strategies occur within each class, this has no effect on the relative frequency of the different classes within the population. Each class of individuals occurs at a constant frequency $0 < f_i < 1$ $(1 \leq i \leq M)$, such that $\sum_i f_i = 1$. Furthermore, the class of an individual only affects its ability to punish. The costs and benefits of participating in the public goods game, as well as the loner payoff, are the same for all individuals in the population.

Whenever an individual of class i $(1 \leq i \leq M)$ punishes a selfish individual for failure to contribute to the public good, the punisher inflicts a cost β_i to the punished individual at a personal cost of γ_i, independent of the class the punished individual belongs to. As before, the punishment for second-order free-riding is fraction α of the punishment for selfishness, such that altruistic punishers pay a personal cost of $\alpha\gamma_i$ to incur a cost of $\alpha\beta_i$ on altruistic non-punishers. In this model, the class of the punisher determines the cost for punishing (γ_i) as well as the effectiveness of punishment (β_i). Note that the class of the punished individual does not change these costs.

When adding heterogeneous individuals to the model, the model description of section 3.2 changes. Instead of a single population of homogeneous individuals, effectively there now are M populations. The proportion of individuals adopting a certain strategy can be different for each of class of individuals. To accommodate for this, let $x_{i,AN}, x_{i,AP}, x_{i,SN}, x_{i,SP}$ and $x_{i,L}$ be the fraction of altruistic non-punishers, altruistic punishers, selfish non-punishers, selfish punishers and loners of class i ($1 \leq i \leq M$) respectively, such that

$$x_{i,AN} + x_{i,AP} + x_{i,SN} + x_{i,SP} + x_{i,L} = f_i \qquad \text{for all } 1 \leq i \leq M, \text{ and}$$

$$x_s := \sum_{i=1}^{M} x_{i,s} \qquad \text{for all strategies } s \in \{AN, AP, SN, SP, L\}.$$

The class of an individual does not affect the returns on the public good, but it does change the cost of punishing and being punished. For punishing individuals, the parameter γ_i indicating the cost for punishing is dependent on the individual's class $1 \leq i \leq M$. Similarly, for individuals being punished, the cost of being punished β_i depends on the class of the punisher $1 \leq i \leq M$. This results in the following expected payoffs for each of the strategies:

$$\begin{aligned}
P_{i,L} &= \sigma \\
P_{i,AN} &= \sigma x_L^{N-1} + rc(x_{AP} + x_{AN})B(x_L) - cF(x_L) - \alpha G(x_{SP} + x_{SN}) \sum_{j=1}^{M} \beta_j (N-1) x_{j,AP} \\
P_{i,SN} &= \sigma x_L^{N-1} + rc(x_{AP} + x_{AN})B(x_L) - \sum_{j=1}^{M} \beta_j (N-1)(x_{j,AP} + x_{j,SP}) \\
P_{i,AP} &= \sigma x_L^{N-1} + rc(x_{AP} + x_{AN})B(x_L) - cF(x_L) - \gamma_i (N-1)(x_{SN} + x_{SP}) - \\
&\quad \alpha \gamma_i (N-1) x_{AN} G(x_{SP} + x_{SN}) \\
P_{i,SP} &= \sigma x_L^{N-1} + rc(x_{AP} + x_{AN})B(x_L) - \gamma_i (N-1)(x_{SN} + x_{SP}) - \\
&\quad \sum_{j=1}^{M} \beta_j (N-1)(x_{j,AP} + x_{j,SP}).
\end{aligned}$$

The auxiliary functions B, F and G do not change, and are repeated here for convenience only:

$$\begin{aligned}
B(x_L) &= \frac{1}{1 - x_L} \left(1 - \frac{1 - x_L^N}{N(1 - x_L)} \right) \\
F(x_L) &= 1 + x_L^{N-1}(r - 1) - \frac{r}{N} \frac{1 - x_L^N}{1 - x_L} \\
G(x_S) &= 1 - (1 - x_S)^{N-2}.
\end{aligned}$$

Chapter 4

Lattice model

In the previous chapter, we derived a model for playing the public goods game under the assumption of an infinite size, well-mixed population of individuals. From simulations with repeated pairwise interactions between individuals, such as the prisoner's dilemma or the ultimatum game, it is known that including spatial structure to the model of the population can have strong effects on the evolution of cooperation (Nowak and May, 1993; Lindgren and Nordahl, 1994; Killingback and Doebeli, 1996). The spatial structure allows altruistic individuals to persist by clustering together, thereby locally avoiding exploitation from selfish individuals.

Punishment also generally performs better on spatially structured worlds than on models that consider groups or populations as a whole. However, neighbours on a lattice compete with each other for the opportunity to reproduce, which also encourages spiteful behaviour. This kind of behaviour allows an individual to pay a cost to damage others, similar to punishing, but with the intention of causing a fitness advantage for the punishing individual rather than discouraging a certain behaviour.

In this chapter, we will derive a model for playing the public goods game in a spatially structured environment, and extend it to allow for heterogeneous classes of individuals.

4.1 Spatial models

There are different ways of introducing a spatial structure into a population model. One of the more common approaches is to organize the individuals of a population on a square lattice. Interactions between individuals are then limited to include only those within a certain neighbourhood on the lattice. In general, periodic boundaries are assumed to prevent edge effects. That is, the lattice represents a torus, such that the left edge of the lattice is connected to the right edge, and the top edge is connected to the bottom.

The size of the interaction neighbourhood affects the eventual state of the population. Ifti et al. (2004) show that in the Continuous Prisoner's Dilemma, in which cooperation is measured as an amount invested in cooperation rather than a binary choice, smaller neighbourhoods tend to favour cooperation, while cooperation becomes unsustainable when the interactions are possible over larger distances.

Similar to the limited range of interaction, individuals on a lattice can only compare their fitness to the fitness of other individuals in a local neighbourhood. This means that individuals can only change their strategy to a strategy that is present in their learning neighbourhood. Typically, the learning neighbourhood is the same as the interaction neighbourhood, although this is not required. Ifti et al. (2004) report that when the learning and interaction neighbourhood differ in size, the final state of any population playing the Continuous Prisoner's Dilemma game is zero cooperation. Even though we use a different model than Ifti et al., we choose to keep the interaction and learning neighbourhood of equal size. That is, every individual will compare its fitness only with individuals it played the public goods game with during that round.

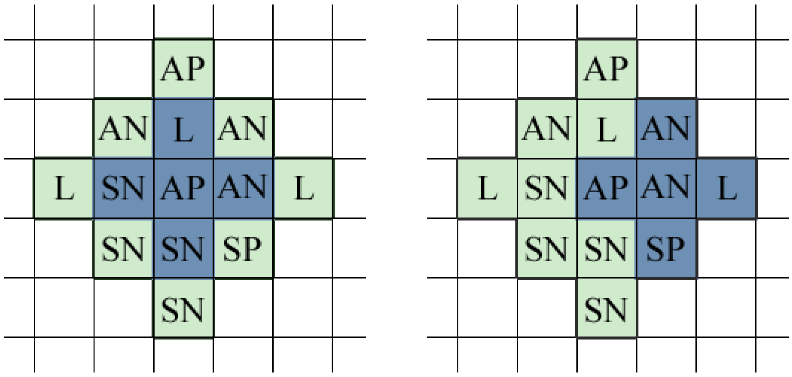


Figure 4.1: Interaction neighbourhood in the lattice-based world. Each individual hosts a public goods game that includes the individual itself as well as its four neighbours, indicated by the darker blue areas. Each individual is therefore invited to five separate public goods games, which expands the individual's interaction neighbourhood to include all the individuals in the light green area.

A lattice is not the only way to model spatial structure. Instead of the rigid placement of individuals on a discrete lattice, individuals may be randomly placed on a continuous torus shaped world, thereby creating differences in the distances between neighbouring individuals. Interactions and learning would then occur between individuals within a certain distance. Other models of spatial structure include graphs that represent dynamic social distances. In this case, the interaction neighbourhood can change over time, based on social interactions between individuals. In general, heterogeneity in the connectivity of individuals increases the success of cooperation (Santos et al., 2006; Gómez-Gardeñes et al., 2007; Poncela et al., 2007). When individuals differ in the amount of interactions they engage in, it is easier for a cooperation strategy to gain enough of a foothold to locally outperform selfish behaviour.

In order to keep the results of the spatially structured world comparable to the results of the infinite well-mixed population model, we chose to organize the individuals on a square lattice with periodic boundaries. This way, the shape of the neighbourhood is not influenced by the edges of the lattice. This ensures that, similar to the infinite population model of chapter 3 in which the group size N was fixed, the number of individuals invited to participate in the public goods is fixed as well.

4.2 The homogeneous lattice-based model

To investigate the effects of the spatial structure, we let the public goods game be played on a regular square lattice, similar to Hauert et al. (2002b). To remove the edge effects of the lattice, we assume periodic boundaries. However, instead of the chess king's neighbourhood proposed by Hauert et al., in our model each of the individuals interacts with each of its four neighbours[1], as indicated by the blue cross in figure 4.1. That is, each of the public goods games played has a maximum of five participants if none of them chooses to be a loner. Also, since each of the individuals "hosts" one game, each individual plays the public goods game a total of five times. The game is divided into discrete rounds. After each round, all individuals simultaneously update their strategy by adopting the strategy that yielded the highest fitness within a local neighbourhood.

The shape of the interaction neighbourhood is illustrated by the light green area in figure 4.1. Note that the participants in the interaction neighbourhood differ in the influence they have on the individual's fitness. Each of the eight direct neighbours[2] of the individual participates in two of the five games the individual is invited to, while the remaining four indirect neighbours only participate in one of these games each.

In each of the games for which there are at least $N-1$ loners, the payoff for each individual is σ. In

[1] This type of neighbourhood is also known as a von Neumann neighbourhood
[2] This type of neighbourhood is also known as a Moore neighbourhood

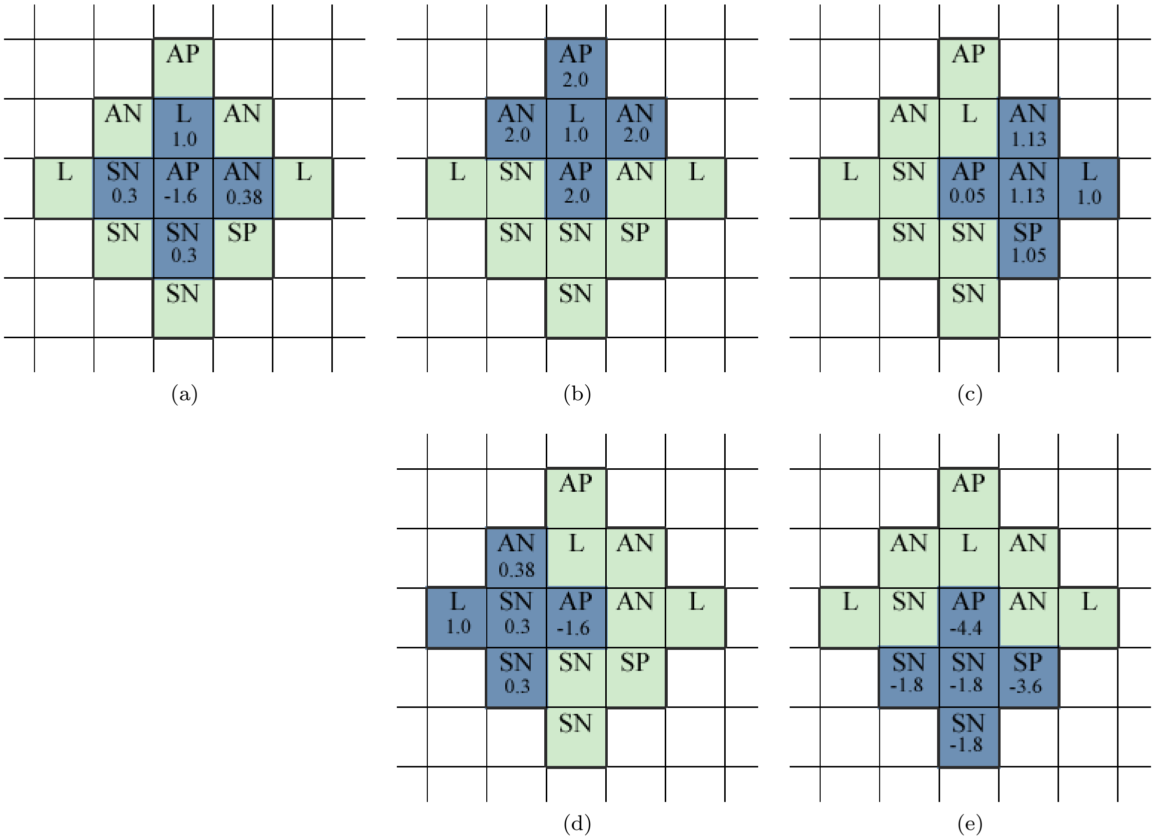


Figure 4.2: Example of individual payoffs for playing the public goods game. Each individual plays five different games, each with a different group. The fitness of an individual is defined as the sum of the payoffs over these five games.

any other case, the payoff P_s of an individual adopting strategy s in a homogeneous population is given by

$$\begin{aligned}
P_L &= \sigma \\
P_{AN} &= rc\frac{n_{AP}+n_{AN}}{N-n_L} - c - \alpha\beta n_{AP} G^*(n_{SN}+n_{SP}) \\
P_{SN} &= rc\frac{n_{AP}+n_{AN}}{N-n_L} - \beta(n_{AP}+n_{SP}) \\
P_{AP} &= rc\frac{n_{AP}+n_{AN}}{N-n_L} - c - \gamma(n_{SN}+n_{SP}) - \alpha\gamma n_{AN} G^*(n_{SN}+n_{SP}) \\
P_{SP} &= rc\frac{n_{AP}+n_{AN}}{N-n_L} - \gamma(n_{SP}+n_{SN}-1) - \beta(n_{AP}+n_{SP}-1),
\end{aligned}$$

where n_s is the number of individuals in the interaction neighbourhood that have adopted strategy s, and $G^*(n) = 1$ if $n > 0$ and 0 otherwise. Note that unlike in the infinite population model of chapter 3, the payoff of a selfish punisher is not necessarily lower than that of a selfish non-punisher.

Figure 4.2a shows an example for a homogeneous population using the parameter values used in Brandt et al. (2006), that is $c = \sigma = \gamma = 1.0, \alpha = 0.1, r = 3.0$ and $\beta = 1.2$. The figure shows the five games the central individual plays each round. The darker blue areas indicate the individuals that are invited to play a public goods game. If we consider figure 4.2a, the game is played by a loner (L), an altruistic non-punisher (AN), an altruistic punisher (AP) and two selfish non-punishers (SN). The loner in this example refuses to participate in the public goods game and therefore receives the loner payoff

$\sigma = 1.0$. The remaining four individuals each share equally in the public good. Of these four individuals, the two altruistic individuals each pay a contribution $c = 1.0$ units to the public good, which makes the total return on the public good $2rc = 6.0$. Since there are four participants, the individual return of each of the participants is 1.5 units.

After the public good has been distributed, each punisher, indicated by the letter P, punishes each of the selfish individuals. The only exception to this is that an individual will not punish itself. That is, a selfish punisher (SP) will receive less punishment than a selfish non-punisher (SN) in the same game. In the example shown in figure 4.2, there is one punisher that punishes both selfish individuals. The punisher thereby reduces its score by $2\gamma = 2.0$ to incur a cost of $\beta = 1.2$ to each of the selfish individuals.

Finally, if there were any selfish individuals, altruistic punishers punish altruistic non-punishers for not punishing the selfish individuals. This punishment is a fraction $\alpha = 0.1$ of the punishment for selfish behaviour. That is, in our example, the altruistic punisher pays another $\alpha\gamma = 0.1$ units in order to punish the single altruistic non-punisher for $\alpha\beta = 0.12$ units.

The final payoff for each individual in this game is listed in figure 4.2a. Note that this game is hosted by the central individual. This individual is also invited to join the games hosted by each of its neighbours. The payoffs for each of these four games are shown in figures 4.2b-4.2e. The total fitness for an individual is the sum of the payoffs over the five games an individual will play. That is, for the central individual shown in figure 4.2, the total fitness is -5.55.

4.3 Spatial learning and heterogeneity of individuals

The model described in the previous section involves a population of homogeneous individuals. However, the model can be easily extended to allow for M heterogeneous classes of individuals. To this end, define $n_{i,s}$ as the number of individuals in the interaction neighbourhood of class i that have adopted strategy s, and let

$$n_s := \sum_{i=1}^{M} n_{i,s} \qquad \text{for all strategies } s \in \{AN, AP, SN, SP, L\}.$$

In each of the games for which there are at least two individuals that are not loners, the payoff $P_{i,s}$ of an individual of class i and adopting strategy s is given by

$$\begin{aligned}
P_{i,L} &= \sigma \\
P_{i,AN} &= rc\frac{n_{AP}+n_{AN}}{N-n_L} - c - \alpha G^*(n_{SN}+n_{SP})\sum_{j=1}^{M}\beta_j n_{j,AP} \\
P_{i,SN} &= rc\frac{n_{AP}+n_{AN}}{N-n_L} - \sum_{j=1}^{M}\beta_j(n_{j,AP}+n_{j,SP}) \\
P_{i,AP} &= rc\frac{n_{AP}+n_{AN}}{N-n_L} - c - \gamma_i(n_{SN}+n_{SP}) - \alpha\gamma n_{AN}G^*(n_{SN}+n_{SP}) \\
P_{i,SP} &= rc\frac{n_{AP}+n_{AN}}{N-n_L} - \gamma_i(n_{SP}+n_{SN}-1) - \sum_{j=1}^{M}\beta_j(n_{j,AP}+n_{j,SP}) + \beta_i,
\end{aligned}$$

where $G^*(n) = 1$ if $n > 0$ and 0 otherwise.

However, the lattice-based setup proposed in the previous section causes a problem in learning. In the well-mixed infinite population model that we discussed in chapter 3, individuals were assumed to learn only from other individuals of the same class. Since interactions occur on a global scale in the infinite population model, this learning can take place even when a particular class is rare. However, in the spatial setting, interactions are localized. If a particular class of individuals is rare, such an individual may have little or no other individuals of the same group among the twelve individuals in its learning neighbourhood. Note that our model does not provide a solution to this problem.

Chapter 5

Simulation results

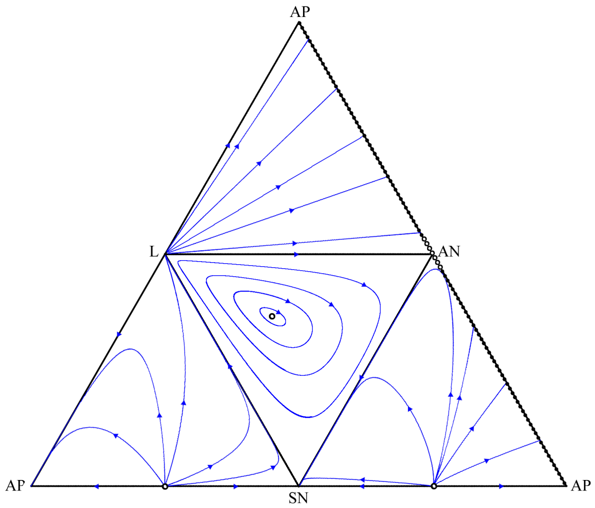
In this section, we present simulation results of our Java implementation of the models discussed in the previous chapters. The results for the infinite and well-mixed population model derived in chapter 3 are presented in sections 5.1 and 5.2, for a homogeneous and heterogeneous population respectively. Section 5.3 is devoted to simulation results of the lattice model described in chapter 4 for a homogeneous population, while section 5.4 shows how heterogeneity in the individual ability to punish affects these results. Finally, section 5.5 explains the role of the selfish punisher in the lattice model.

5.1 Infinite homogeneous population model

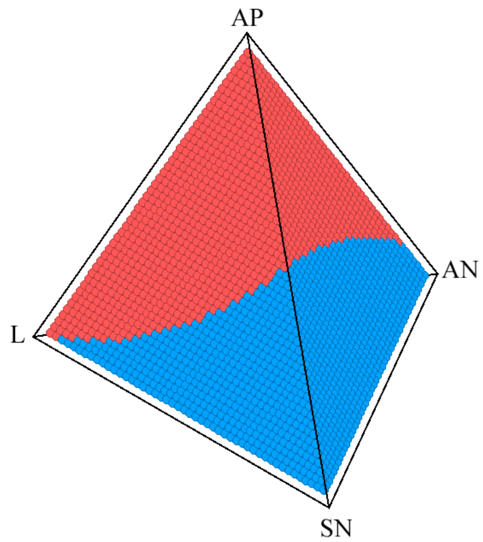
To determine the effects of heterogeneity of individuals within a population on the behaviour of a well-mixed infinite population, the model outlined in chapter 3 has been implemented in Java. Note that one of the immediate effects of this model is that selfish non-punishers will always have a higher expected payoff than selfish punishers. That is, in the infinite population model selfish punishment is self-destructive, and the proportion of selfish punishers will therefore always tend to zero over time. Because of this, as well as to improve representation of the results, we will assume $x_{i,SP} = 0$ for all groups i throughout this section.

Following Brandt et al. (2006), we use the parameter setting $c = \sigma = \gamma = 1.0, \beta = 1.2, \alpha = 0.1, r = 3.0, N = 5$ for simulations in the interior of the simplex. Note that for $M = 1$, the model can be rewritten to match the one described by Brandt et al.. In this situation, the population is homogeneous, and can therefore serve as a baseline comparison for different forms of heterogeneity. The results for the homogeneous population are shown in figure 5.1. Since we ignore the effects of selfish punishment, the configuration of strategies within the population can be represented as a point in the simplex S_4; the convex hull of the pure strategies AN, SN, L and AP. Each point p within the simplex represents a configuration for which the relative frequency of each strategy is proportional to the distance of p to the corresponding corner. Note that compared to the figure by Brandt et al, the simplex we present here is rotated such that the AP-SN-L plane is visible and the AP-AN-L plane is blocked from view.

The behaviour of the population on the surface of the simplex, where only three out of five strategies are present in the population, is still mathematically tractable. The results are presented in figure 5.1a. A point is *stationary* when the replicator dynamics given by equation 3.1 result in $\dot{x}_i = 0$ for all strategies. When the population reaches a stationary point, the proportions adopting the different strategies no longer change over time. There are several stationary points on the surface of the simplex, indicated by circles in figure 5.1a. On the SN-AP edge, there is a stationary point in which the advantage of selfish behaviour is compensated by the cost of being punished. In this point, only selfish non-punishers and altruistic punishers exist in the population, and the payoff they get for playing the public goods game is exactly the same. Although this point is stationary, it is *unstable* in the sense that deviations in the population proportions from the exact stationary point may lead the population away from the stationary point. This effect is indicated by the blue arrows leading away from the point. Unstable stationary points are indicated by the open circles in figure 5.1a.



(a) Surface of the simplex S_4. Open circles indicate unstable stationary points, while closed circles indicate stable stationary points. The AP-AN edge consists entirely of stationary points. Blue lines indicate trajectories.



(b) Interior of the simplex S_4. Each dot represents an initial configuration that is either drawn to the plane defined by $x_{AP} = x_{SP} = 0$ (blue dots) or to the AP-AN edge (red dots).

Figure 5.1: Surface (a) and interior (b) of the simplex S_4 defined by $x_{SP} = 0$.

In contrast to unstable stationary points, any small deviation in the population proportions of *stable* stationary points will not cause the population to move away from the stationary point. These points are indicated by closed circles in figure 5.1a. A stationary point is called *asymptotically stable* when small deviations from the point lead the population back to the stationary point. For this to happen, the blue arrows in figure 5.1a should be pointed towards a stationary point. Although this appears to be true for some of the points on the AP-AN edge, none of these points are asymptotically stable, since failure to punish cannot be detected when there are no selfish individuals. That is, small deviations in the number of altruistic punishers and altruistic non-punishers on the AN-AP edge will lead the population into a different stationary point, and not back to the original one. Therefore, none of these points are asymptotically stable. However, as reported by Brandt et al., the points for which

$$\frac{c}{N\beta}\frac{N-r}{N-1} < x_{AP} \leq 1$$

are stable. In these cases, enough altruistic punishers are present in the population to prevent invasion by selfish individuals.

Finally, there is one stationary point in the AN-SN-L plane. In this case, there are no more punishers in the population, while the proportions of loners, altruistic non-punishers and selfish non-punishers stay constant over time as their fitness payoffs $P_{AN} = P_{SN} = P_L = \sigma$ are the same. Around this point in the AN-SN-L plane, individuals are endlessly locked in a game of rock-paper-scissors (Nowak, 2006), where each of the three strategies altruistic non-punisher, selfish non-punisher and loner is continuously overtaken by one of the other two strategies. When the population consists mostly of altruists, they are exploited by selfishness. This in turn leads to individuals refusing to join the game and settle for the loner payoff. However, as the effective group size decreases, the opportunity for altruists to work together increases. This effect can be seen as the periodic orbits in the AN-SN-L plane in figure 5.1a.

There are no further stationary points in the interior of the simplex defined by $x_{SP} = 0$. Similar to Brandt et al, we find that any point in the interior of the simplex is drawn to either one of two *attractors*. That is, given enough time, any population will eventually settle into one of two possible situations. Which situation the population will end up in is only determined by the initial proportions of the different strategies. Since the interactions between the proportions of the four strategies (excluding selfish punishment) are no longer mathematically tractable, figure 5.1b shows the results of numerical simulations. Each dot indicates an initial state of the population in the interior of the simplex. That is, for each dot in figure 5.1b, each of the proportions x_{SN}, x_{AN}, x_{AP} and x_L is non-zero. The colour of the dot indicates the final destiny of the population. The first possibility, indicated by blue dots in figure 5.1b, is the set of periodic orbits in the plane $x_{AP} = x_{SP} = 0$. In this case, all punishers are eliminated from the population, and the population settles in one of the orbits in the AN-SN-L plane. The second attractor is the AP-AN edge, in which the population only consists of altruistic individuals. The initial states that end up in this situation are indicated by red dots in figure 5.1b. Brandt et al. report that as a rule of thumb, the fraction of initial states leading to a state which includes punishers is

$$\frac{1}{\beta+\gamma}\left(\beta - \frac{N-r}{N-1}\frac{1}{N}\right),$$

corresponding to the fraction of punishers in the stationary point on the AP-SN edge.

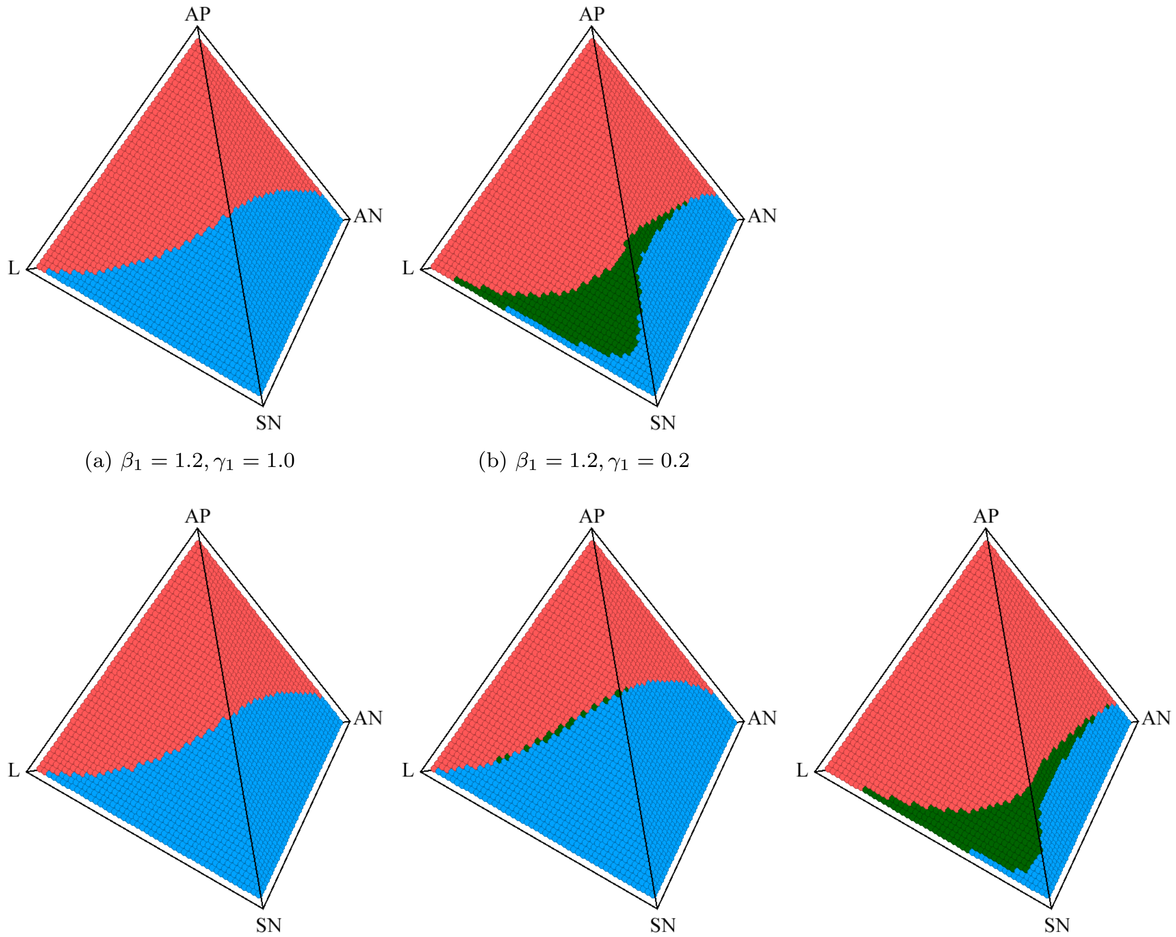
5.2 Infinite heterogeneous population model

To determine the effects of heterogeneity, we introduced the heterogeneous classes of individuals as described in chapter 3.3. That is, the population is subdivided into $M > 1$ classes such that the return on punishment β_i and the cost of punishment γ_i are homogeneous within a class, but heterogeneous across classes. For our simulation, the number of classes was limited to $M = 2$. To make the results better comparable to the baseline behaviour of the homogeneous infinite population model, the average values $\bar{\beta}$ and $\bar{\gamma}$ were fixed such that the average effectiveness of punishment and average cost of punishing are the same for the homogeneous and the heterogeneous populations in the initial configuration. Figure 5.2 shows simulation results in the case each class represents half the population, and the initial configuration of strategies is constant across classes. That is, for each strategy $s \in \{SN, AN, SP, AP, L\}$, $x_{1,s} = x_{2,s}$ at the beginning of the simulation. This way, the results can be presented in a simplex similar to the homogeneous case described in chapter 5.1. Like before, initial configurations for which the entire population is drawn to the AP-AN edge are represented by a red point in figure 5.2. Similarly, a blue point indicates that an initial configuration is drawn to the AN-SN-L plane. A new situation arises when for some initial configuration, different classes of individuals within the population are drawn to different attractors. In figure 5.2, such initial configurations are indicated by a green point.

For completeness, figure 5.2a shows the situation of a population consisting of two homogeneous classes. Conceptually, this setup should produce the same results as a population consisting of only one class of homogeneous individuals, although numerical simulation could introduce some differences. Instead of a single homogeneous population, the population is divided into two classes consisting of indistinguishable individuals that can only learn from other individuals in the same class. However, since the initial state of each class is the same, both classes react exactly the same.

To determine the effects of heterogeneity, we first consider the situation in which the cost of punishing γ_i is taken to be heterogeneous across classes, but the effectiveness of punishment β_i is constant across classes. In this case, payoffs are dependent on the individual's class, since selfish and altruistic punishers of class 1 will pay a lower cost for punishing selfishness ($\gamma_1 = 0.2$) than individuals adopting the same strategy in class 2 ($\gamma_2 = 1.8$) . Although each class of individuals still has the same two attractors as in the case of the homogeneous population, different classes may be drawn to different attractors. Individuals of class 1 may find it lucrative to punish in the sense that punishing reduces the fitness of selfish individuals more than it reduces the fitness of the punishers themselves, while for class 2 the penalty incurred for selfishness may be too low when offset to the costs of inflicting such a penalty. As an additional effect, for any class that settles on the AP-AN edge, as long as there are selfish individuals in the population, failure to punish can be identified and second-order free-riding may be punished accordingly. In effect, this causes the entire class to tend to either pure altruistic punishment or pure altruistic non-punishment, depending on the abundance of selfishness and subsequent cost of punishing.

Similarly, any class that settles on the AN-SN-L plane will not follow a periodic orbit while there are punishing individuals present in the population. Under the influence of these punishers, the payoff for selfishness is reduced, which prevents individuals from switching their altruistic non-punisher strategy to



(a) $\beta_1 = 1.2, \gamma_1 = 1.0$ (b) $\beta_1 = 1.2, \gamma_1 = 0.2$

(c) $\beta_1 = 0.3, \gamma_1 = 1.0$ (d) $\beta_1 = 0.3, \gamma_1 = 0.2$ (e) $\beta_1 = 2.1, \gamma_1 = 0.2$

Figure 5.2: Interior of the simplex S_4 defined by $x_{SP} = 0$ for five different settings: (a) homogeneous classes, (b) low cost, (c) low returns, (d) low returns and low cost, and (e) high returns and low cost. To improve comparability across situations, the average values $\bar{\beta}$ and $\bar{\gamma}$ over the two classes of individuals are fixed. Blue dots indicate initial configurations of the population for which individuals of both classes are drawn to the plane $x_{AP} = x_{SP} = 0$, while configurations drawn to the AP-AN edge are marked by red dots. When classes are drawn to different attractors, the corresponding point in the figure is green.

a selfish non-punisher strategy. If this reduction is sizeable enough, the class will tend to pure altruistic non-punishers. Figure 5.2b shows the effect of heterogeneous cost of punishment on the final state of the population. The green dots indicate initial configurations for which class 1, having the lower cost of punishment $\gamma_1 = 0.2$, is drawn to the AP-AN edge, while the higher cost of punishment $\gamma_2 = 1.8$ causes all altruistic punishers to disappear from class 2. In the simulation, each of these situations resulted in a population of only altruists, under the influence of the altruistic punishers of class 1. In effect, in these cases the burden of punishing selfishness is carried by the individuals best suited for the task in the sense that they are the more efficient punishers. Note that this is not a division of labour as suggested by Nakamaru and Iwasa (2006), since the punishers themselves are still altruistic.

One effect that appears in figure 5.2b is that under heterogeneous classes, an initial configuration will end up in an end state without punishers more readily when the proportions of selfish non-punishers and altruistic non-punishers are balanced. This is due to the fact that altruistic non-punishers will contribute to the common good, which helps selfish non-punishers and altruistic punishers equally in terms of fitness, but altruistic punishers are still forced to punish the altruistic non-punishers for second-order free-riding. In effect, altruistic non-punishers discourage altruistic behaviour this way.

When instead of the cost of punishing γ_i we consider the situation in which the returns on punishment β_i vary across classes, the picture changes. Note that changes in β_i only affect the payoff of selfish individuals and, more importantly, uniformly so for all classes. In this case the payoff of an individual only depends on the strategy it adopts, and is independent of its class. Therefore, the results for this heterogeneous population model are similar to the homogeneous population model. Whether an individual will be drawn to a final state with only altruistic individuals (the AP-AN edge) or tend to a solution without punishers (the AN-SN-L plane) is also independent of class. There is no configuration which leads to different classes being drawn to different attractors. Moreover, if the initial proportions of strategies are the same for each class, the population as a whole will react exactly the same as a homogeneous class of individuals with $\beta = \sum f_i\beta_i$, where f_i denotes the relative frequency of individuals belonging to class i. This result is shown in figure 5.2c. Even though the two classes in this simulation differ in the effectiveness of their punishment ($\beta_1 = 0.3$ and $\beta_2 = 2.1$), since their (weighted) average effectiveness is the same as the case with homogeneous classes shown in figure 5.2a, there are no real differences between the figures.

Even though heterogeneity in the returns on punishment β_i between classes does not influence the behaviour of the population by itself, it does change the behaviour of the population when the cost of punishing γ_i is also heterogeneous. Figure 5.2d shows that the interaction between the two types of heterogeneity can deter altruistic punishment. In this situation, class 1 inflicts a low punishment at a low cost ($\gamma_1 = 0.2$ and $\beta_1 = 0.3$), while class 2 inflicts high punishment at a high cost ($\gamma_1 = 1.8$ and $\beta_1 = 2.1$). When classes differ in the level of punishment they inflict this way, figure 5.2d shows that the proportion of final states that include punishers falls below the baseline performance of the homogeneous population. In an infinite and well-mixed population, punishing at different levels hinders the co-evolution of altruistic behaviour and punishment.

Figure 5.2e shows that the interaction between heterogeneity in cost for and returns on punishment can work both ways. When class 1 has a lower than average cost of punishment $\gamma_1 = 0.2$ and also a higher than average returns on punishment $\beta_1 = 2.1$, this increases the proportion of initial configurations for which the final state includes punishers. This effect is stronger than the separate effect of heterogeneity in the costs for punishing.

5.3 Homogeneous lattice model

It is known from game-theoretical games such as the prisoner's dilemma that introducing spatial structure into the model of a population can have a powerful effect on the behaviour of the individuals. Even without the help of punishing individuals, small clusters of altruistic non-punishers already provide enough of an advantage to prevent them from copying selfish behaviour (see among others Nowak and May, 1993; Lindgren and Nordahl, 1994; Killingback and Doebeli, 1996). The basic public goods model we use as a starting point is no exception. In this section we show the results of our Java implementation of the lattice based model described in chapter 4. All results in this section are obtained by simulation

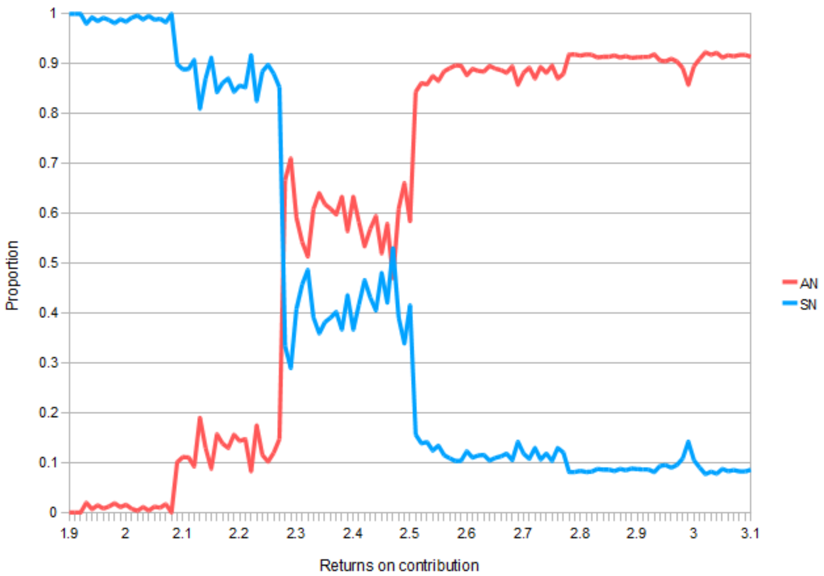


Figure 5.3: Effect of the value of returns on contribution (r) on the proportions of altruistic non-punishers (AN) and selfish non-punishers (SN). The initial distribution of strategies was randomized for each run. The final proportions were determined after 500 rounds of lead time and averaged over 200 runs, for every 0.01 change of r in the range $1.9 \leq r \leq 3.1$.

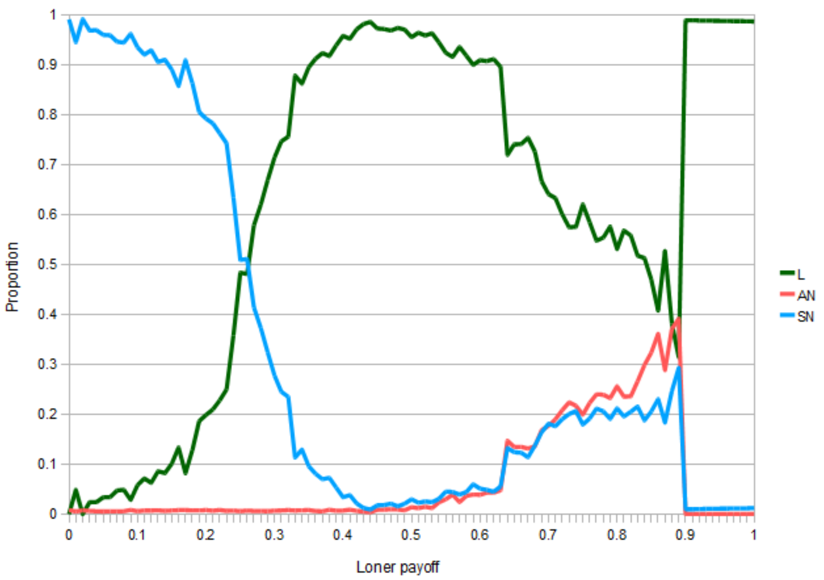


Figure 5.4: Effect of the value of loner payoff (σ) on the proportions of loners (L), altruistic non-punishers (AN) and selfish non-punishers (SN). The initial distribution of strategies was randomized for each run. The final proportions were determined after 500 rounds of lead time and averaged over 200 runs, for every 0.01 change of σ in the range $0 < \sigma \leq 1.0$.

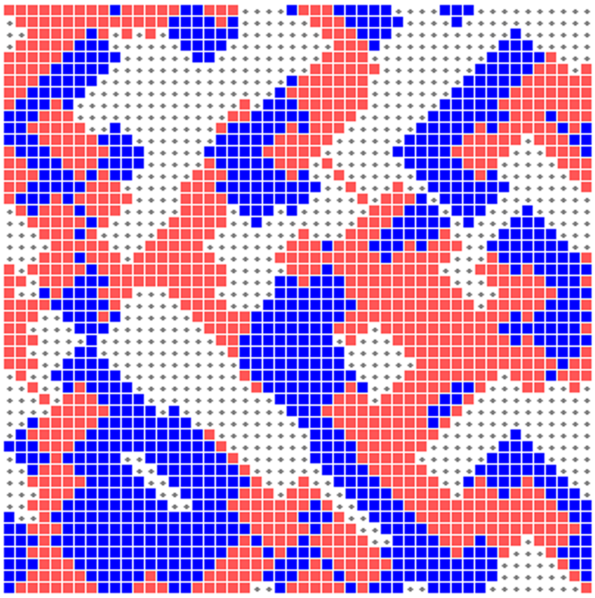


Figure 5.5: Typical results of a population with $r = 2.0$, $c = 1.0$ and $\sigma = 0.8$. Selfish non-punishers (red) exploit altruistic non-punishers (blue), until their payoff decreases below the loner (white) payoff.

on a 50 by 50 lattice with periodic boundaries.

One of the effects of spatial structure is that due to localized interactions, selfish individuals can no longer exploit distant altruistic individuals, which encourages altruistic behaviour. Figure 5.3 shows this result by showing the proportion of altruistic and selfish individuals for different levels of the return on contribution r. In this setting, every individual is randomly assigned the strategy of altruistic or selfish non-punisher, after which the proportions of the two strategies after a 500 round lead-in time was determined. Figure 5.3 shows these proportions averaged over 200 runs, for every 0.01 change of r in the range $1.9 \leq r \leq 3.1$.

In the infinite population model, altruistic non-punishers cannot survive in the absence of loners and punishers, no matter how high the return on contribution. Figure 5.3 shows that in the lattice model, sufficiently dense clusters of altruistic non-punishers can withstand an invasion of selfish non-punishers for $r > 2.1$. For $r > 2.28$, altruistic non-punishers can even outperform selfish non-punishers in terms of fitness, and will reliably represent over 80% of the population for $r > 2.5$. For the purposes of comparing the effects of heterogeneity on the behaviour of a population on a lattice, we therefore set the return on contribution $r = 1.9$ instead of using $r = 3.0$ as in the setting of an infinite size population.

To make sure the public good remains competitive, the loner payoff σ should be lower than the maximum payoff for altruistic individuals $(r - 1)c$. For $r = 1.9$ and $c = 1.0$, figure 5.4 shows the proportions of loners, altruistic non-punishers and selfish non-punishers as a function of the loner payoff σ. As before, the results are averaged over 200 runs. In each of these runs, the population was randomly initialized and given 500 rounds of lead time before the proportions of the three strategies were determined. This process was repeated for every 0.01 change in σ in the range $0 < \sigma \leq 1.0$. Note that the value $\sigma = 0$ was omitted for display purposes.

For $\sigma \geq 0.9$, altruistic behaviour is at a disadvantage to a loner, which means the population will eventually end up in the situation of 100% loners. Although some individuals may adopt a non-loner strategy in this situation, none of them will have any other non-loner individual in their interaction neighbourhood, and they are therefore forced to play as a loner as well.

Another discrete step in the graph appears around $\sigma = 0.63$. To avoid artefacts caused by either one of these steps, a loner payoff of $\sigma = 0.75$ was chosen for the public goods game simulations. Figure 5.5 shows a typical result of this parameter setting when there are no punishers. As in the case with the infinite population model, altruistic individuals, selfish individuals and loners are locked in an infinite game of

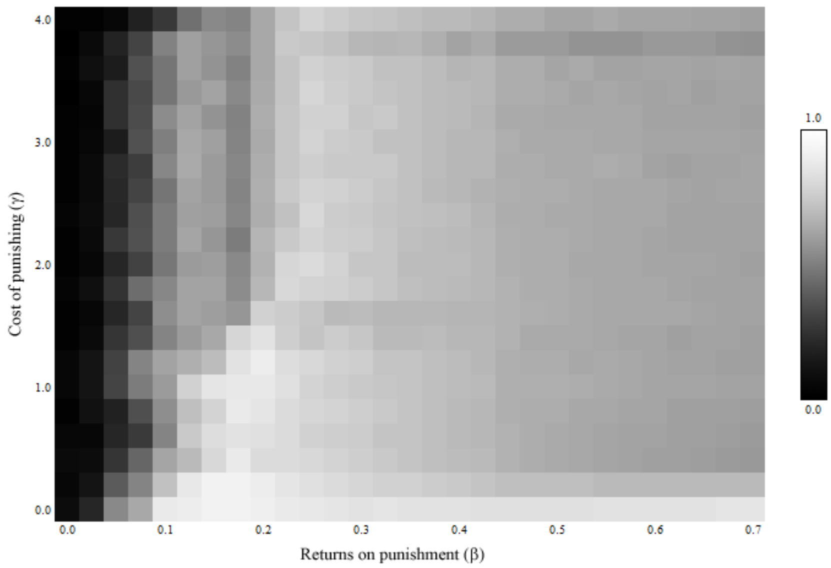


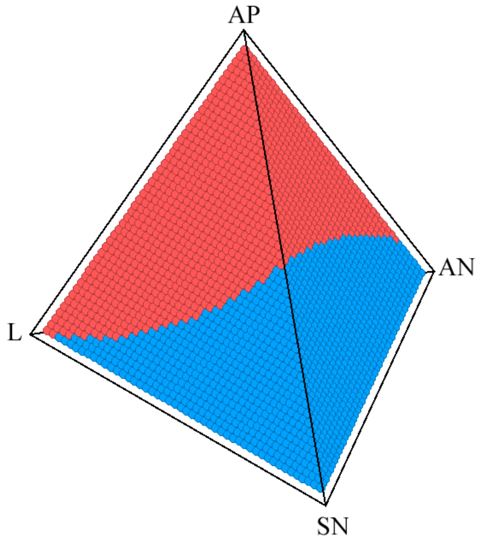
Figure 5.6: Effect of the values of the returns on punishment β and cost of punishing γ on the proportion of altruistic punishers. The initial distribution of strategies was randomized for each run, such that AP and SN represent 40% of the population each, and AN and L represent 10% each. The final proportions were determined after 500 rounds of lead time and averaged over 200 separate runs, for every 0.025 change of β in the range $0 \leq \beta \leq 0.7$ and every 0.2 change of γ in the range $0 \leq \gamma \leq 4.0$.

rock-paper-scissors. Selfish individuals exploit the altruistic non-punishers, but the popularity of their strategy quickly causes individuals in their interaction neighbourhood to adopt the selfish non-punisher strategy as well, sharply reducing their payoff. This leaves all selfish non-punishers open to become a loner. In the absence of selfishness, the payoff of altruistic non-punishers increases, tempting the loners to rejoin the public goods game. Unlike the infinite population model, in which the initial configuration of strategies determines which periodic orbit the population will eventually reach, the initial state of the population has little effect on the eventual proportions of strategies in the lattice model. Typically, in the first rounds after initialization of the population, most of the altruistic and selfish individuals are replaced by loners, after which remaining clusters of altruists start expanding and the situation of figure 5.5 appears.

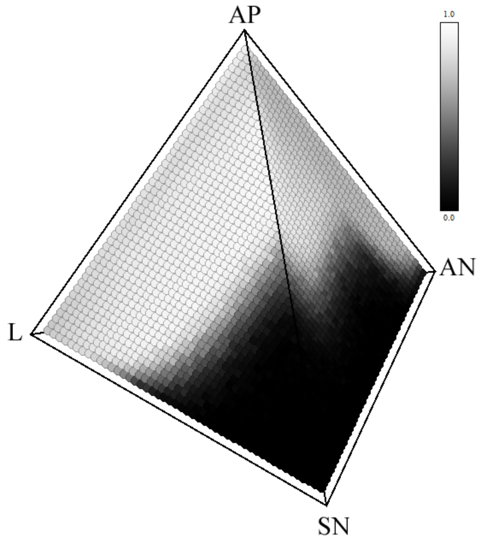
It is well known from research on two-person games such as the prisoner's dilemma (Nowak and May, 1993) and hawks and doves (Killingback and Doebeli, 1996) that punishing is much more efficient on a lattice than in an infinite and well-mixed population. Because of the local interactions, once a cluster of altruistic punishers has appeared, it can easily grow. The interior of the cluster contains no selfish individuals, which means the altruistic punishers enjoy the full benefit of their mutual cooperation, without the burden of having to punish for selfishness. Meanwhile, on the edge of the cluster, selfish behaviour is punished, causing the payoff for selfishness to decrease. Even though punishment is costly, as long as the high payoff of other altruistic punishers in the interior of the cluster is higher than the payoff of the punished selfish individuals, the individuals on the edge will not change their strategy.

Figure 5.6 shows that this effect also holds for the public goods game. The figure shows the proportion of altruistic punishers after 500 rounds of the public goods game as a function of the return on punishment β and the cost for punishing γ. In this setting, populations were initialized on a 50 by 50 lattice such that approximately 40% of the population started as altruistic punisher, 40% started as selfish non-punisher, and the remaining 20% consists of loners and altruistic non-punishers. The proportion of altruistic punishers was recorded after 500 rounds of play, and was averaged over 200 separate runs. Only when the return on punishment fell short of 0.2 did the proportion of altruistic punishers drop below 50%.

As shown by figure 5.6, the co-evolution of altruistic behaviour and punishment is largely insensitive of the cost of punishing. The reason behind this is that due to the synchronous updating, altruistic



(a) Infinite population model. Each dot represents an initial configuration that is either drawn to the plane defined by $x_{AP} = x_{SP} = 0$ (blue dots) or to the AP-AN edge (red dots).



(b) Lattice model. The brightness of each dot indicates the proportion of altruistic individuals (AN and AP) after 200 rounds in the entire population. Proportions are averaged over 200 separate runs.

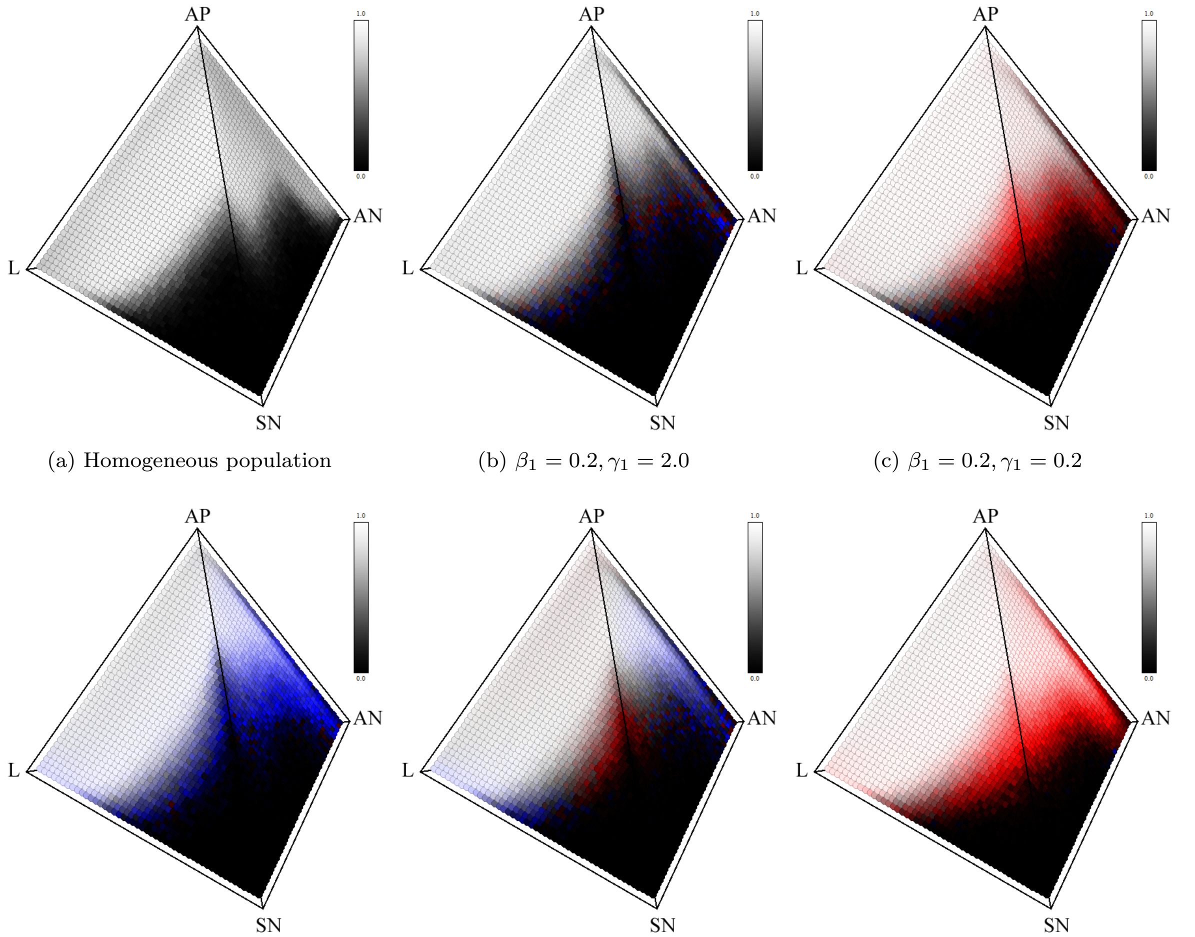
Figure 5.7: Interior of the simplex S_4 defined by $x_{SP} = 0$ for (a) the infinite and well-mixed population model and (b) the lattice model, both for a homogeneous population.

individuals expand in clusters. Altruistic punishers at the edge of such a cluster are forced to punish many selfish individuals outside of the cluster, sharply reducing their fitness. However, punishers need not reduce the fitness of selfish individuals below that of their own. When the fitness of the selfish individuals is lower than the fitness of any other altruistic punisher deeper in the cluster, where there are few selfish individuals to punish, altruistic punishers at the edge of the cluster will not change their strategy.

The parameters used for the lattice model and a homogeneous population are $N = 5, \sigma = 0.75, c = 1.0, r = 1.9, \alpha = 0.1, \gamma = 2.0$ and $\beta = 0.2$. Note that these parameters are less favourable for altruistic individuals and punishers when compared to the parameter setting for the infinite and well-mixed population of section 5.1 ($N = 5, c = \sigma = \gamma = 1.0, r = 3.0, \beta = 1.2, \alpha = 0.1$). Figure 5.7 shows the results of a homogeneous population for the infinite and well-mixed population model and the lattice model side by side. Figure 5.7a is repeated from section 5.1. In this figure, red dots indicate initial situations that eventually end up in a state in which every individual is altruistic, whereas blue dots indicate such a situation will never occur. Figure 5.7b shows the results for a lattice model, where the brightness of each dot indicates the proportion of individuals that are altruistic after 200 rounds of playing the public goods game, where brighter dots indicate more altruistic individuals in the population. For the lattice model, the results are averaged over 200 separate runs. Even though the parameters are less favourable for the lattice model, the results compare reasonably well to the results for the infinite and well-mixed population model. This parameter setting will therefore be used as the base scenario for determining the effects of heterogeneity in the next section.

5.4 Heterogeneous lattice model

To determine what the effects are of introducing heterogeneity into the lattice population, we characterize the end state of the population by the proportion of individuals that have adopted an altruistic (either punishing or non-punishing) strategy. Figure 5.8 summarizes the results for the simulations in six different settings. In every setting, the brightness of a dot represents the average proportion of altruistic individuals 200 rounds after initialization. Lighter dots indicate that a larger proportion of the population



(a) Homogeneous population (b) $\beta_1 = 0.2, \gamma_1 = 2.0$ (c) $\beta_1 = 0.2, \gamma_1 = 0.2$

(d) $\beta_1 = 0.05, \gamma_1 = 2.0$ (e) $\beta_1 = 0.05, \gamma_1 = 0.2$ (f) $\beta_1 = 0.35, \gamma_1 = 0.2$

Figure 5.8: Interior of the simplex S_4 defined by $x_{SP} = 0$ for six different settings: (a) single homogeneous population, (b) homogeneous classes, (c) low cost, (d) low returns, (e) low returns and low cost, and (f) high returns and low cost. To improve comparability across situations, the average values $\bar{\beta}$ and $\bar{\gamma}$ over the two classes in situations (b) to (f) are fixed. The brightness of the dots indicates the proportion of altruistic individuals (AN and AP) after 200 rounds in the entire population. The colour of the dots shows the relative proportion of altruistic punishers across both classes, where a red dot indicates most altruistic punishers are of class 1, while blue indicates most altruistic punishers are of class 2. A more saturated colour indicates a larger difference in the proportion of altruistic punishers between class 1 and 2. Proportions are averaged over 200 separate runs.

has adopted an altruistic strategy. The differences between classes is illustrated by the colour of a dot. Red dots indicate that the majority of the altruistic punishers are of class 1, while blue dots indicate that class 2 holds most of the altruistic punishers. When the number of altruistic punishers is divided equally between classes, the dot appears grey in figure 5.8.

The results in figure 5.8 are obtained by averaging over 200 runs. In every setting the parameter values $\sigma = 0.75, c = 1.0$ and $r = 1.9$ were fixed. Furthermore, the average value of the return on punishment and the cost of punishing were constant across the simulation runs such that $\bar{\beta} = 0.2$ and $\bar{\gamma} = 2.0$. As for the results of the infinite population model, the position of the dot determines the relative frequencies of the strategies such that each corner of the simplex represents an initial state where every individual adopts the strategy indicated by the corresponding label. Note that figure 5.8 shows the interior of the simplex, such that the proportion of strategies other than selfish punisher is non-zero for each of the dots.

Figure 5.8a shows the results for a single homogeneous population. In contrast with the infinite population model, separating the homogeneous population into two homogeneous classes does have an effect on the results for the lattice model. Figure 5.8b shows that when individuals only learn from part of the individuals in their interaction neighbourhood, altruistic behaviour will fail more often to stabilize in the population. The fact that there is no inter-class learning favours selfish behaviour by allowing it to exploit altruistic individuals without causing those individuals to become selfish as well. This breaks up the cluster structure that greatly benefits altruistic punishers in the lattice.

The introduction of two homogeneous classes does not cause great variation in the number of altruistic punishers between classes. This is as expected, since there are no differences in the individual abilities between the two classes. Figure 5.8b shows mostly grey dots, with some more colour in the dark grey area in which altruistic behaviour mostly fails. In this area, altruistic punishment regularly disappears from one or both classes because of an unfavourable initial situation. The red and blue dots in this area therefore indicate that one of the classes had a higher proportion of altruistic punishers over 200 separate runs by random chance.

The results when heterogeneity in the cost of punishing γ_i is introduced, while the effectiveness of punishment β_i remains constant across classes are shown in figure 5.8c. The proportion of altruistic individuals appears to be fairly insensitive to changes in the cost of punishing in figure 5.6, but heterogeneity in the cost of punishing does provide an opportunity for altruistic behaviour to evolve. However, this effect is fairly limited compared to the differences in costs between classes ($\gamma_1 = 0.2$ against $\gamma_2 = 3.8$). The advantage for altruistic behaviour in the case of heterogeneous cost of punishing may result in specialization between classes. As indicated by the predominantly red colour in figure 5.8c, whenever the population does not end up in a state of all altruists or no altruists, punishment is mainly performed by class 1, the class paying the lowest cost for punishing. Note however that the effect is stronger when the initial configuration is close to the AP-SN edge, where the colour is the brightest red. When the initial configuration includes more altruistic non-punishers or loners, the colour remains more grey, indicating that the distribution of altruistic punishers over the two classes is more equalized.

When instead of the cost of punishing γ_i, the returns on punishment β_i are taken to be heterogeneous across classes, figure 5.8d shows that heterogeneity has little effect on the evolution of cooperation. The population is slightly more likely to end up in a state with mostly altruistic individuals when the initial proportion of altruists is high, and slightly less likely to end up in such a state when selfish individuals and loners are more common in the initial configuration of strategies. However, the changes in the structure of the population are more pronounced. The majority of punishment is performed by the class of individuals with the highest returns on punishment. As opposed to the case where the cost of punishing is taken to be heterogeneous, classes that differ in the returns on punishment show the most specialization when altruists dominate the initial configuration, while the colour in figure 5.8d remains more grey when there are many loners and selfish non-punishers.

The differences in specialization effects may be caused in part by punishing for second-order free-riding. When altruists are rare, the additional punishment for failure to punish discourages both altruistic non-punishers and altruistic punishers. In figure 5.8d, the higher punishment inflicted by class 2 aggravates the discouraging effect, which makes it harder for altruistic behaviour to stabilize. The punishment for second-order free-riding is less of an issue when altruists are common, since it is compensated by the higher returns on the public good. In this case, a higher punishment is preferred to discourage selfishness more effectively.

Since heterogeneity in the cost for punishing has a positive effect on the proportion of altruistic individuals in the end state of the lattice-based population, and heterogeneity in the returns on punishment does not have a clear positive or negative effect, this leaves us with the issue of how these effects interact. Figure 5.8e shows the results when individuals of class 1 can only inflict low punishment at a low cost ($\gamma_1 = 0.2$ and $\beta_1 = 0.05$) while individuals of class 2 inflict high punishment at a high personal cost ($\gamma_2 = 3.8$ and $\beta_2 = 0.35$). Compared to the situation in which only the cost for punishing is heterogeneous, altruistic behaviour has a slightly harder time to stabilize in the population. Unlike the situation for the infinite and well-mixed population however, this type of heterogeneity still represents a beneficial effect for altruistic behaviour compared to the homogeneous classes.

The case of low punishment at a low cost and high punishment at a high cost also exhibits an interesting pattern of specialization between classes in the lattice-based population, combining the separate specialization effects of heterogeneity in cost for punishing and those of heterogeneity in returns on punishment. In the combined setup, which class contains most of the altruistic punishers in the final state depends on the initial configuration of strategies in the population. When altruistic non-punishers are initially rare, punishment is carried out by the class with the lowest cost, as illustrated by the red colour along the AP-SP edge in figure 5.8e. On the other hand, when altruistic non-punishers are more common in the initial layout, the class with the highest returns on punishment ends up carrying out most of the punishment.

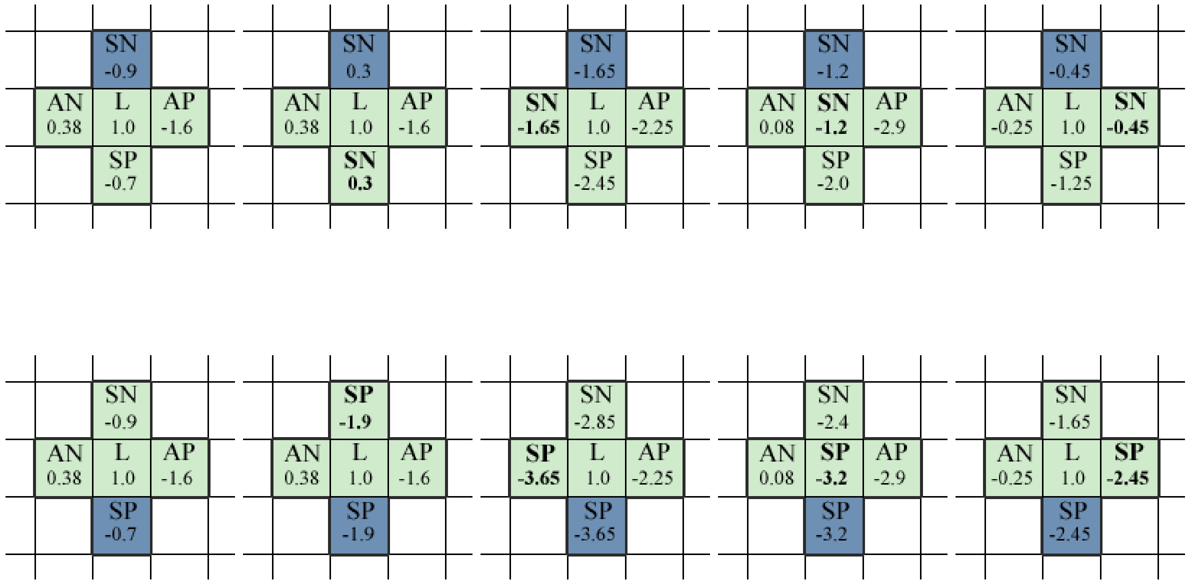
Finally, figure 5.8f shows that when one group is strictly better at punishing ($\beta_1 > \beta_2$ and $\gamma_1 < \gamma_2$), this results in an advantage for altruistic behaviour that is stronger than in the situation in which only the cost for punishing is heterogeneous. Moreover, the population exhibits a high degree of specialization, where almost all punishment is carried out by the efficient punishers. This specialization is mostly independent of the initial configuration of strategies. Only when there is a moderate proportion of loners in the initial configuration, the final distribution of altruistic punishers is more equalized.

5.5 Selfish punishment on a lattice

Up to now, the influence of selfish punishment in the lattice model was ignored. The reason for this is that in order to allow for comparability between the infinite population model and the lattice model, the parameter setting for the lattice model was manipulated such that the returns on punishment β_i were lower than the cost of punishing γ_i. Under these conditions, a selfish punisher will always have a lower payoff than a selfish non-punisher in the same group. The selfish punisher punishes any other selfish individual, inflicting a cost β_i, but at a cost γ_i to itself, reducing the payoff of the selfish punisher more than it reduces the payoff of the selfish non-punisher.

However, even when selfish punishers are efficient punishers in the sense that the returns outweigh the costs, in a homogeneous population, selfish punishment barely has a chance of survival. To show this, consider how the payoffs of selfish punishers and selfish non-punishers change at the end of a round. First, consider the selfish non-punisher. If the selfish non-punisher has a particularly high fitness, some of the individuals in the interaction neighbourhood may change their strategy to selfish non-punisher as well. The effects are illustrated in the top row of figure 5.9, but they hold in general. When an altruistic individual imitates the strategy of a selfish non-punisher, this will result in a loss of $\frac{rc}{m}$ for the original selfish non-punisher, where m is the number of non-loner individuals in the group. Similarly, when a loner imitates the selfish individual, this will reduce the share of the public good to the original selfish non-punisher and decrease its payoff. On the other hand, when a punishing individual imitates the strategy of a selfish non-punisher, this will result in a β gain in payoff for the original selfish non-punisher, since it will no longer be punished. A selfish non-punisher's payoff can therefore increase if its strategy is imitated by punishing individuals.

In contrast, if a selfish punisher has a fitness high enough to encourage other individuals to become selfish punishers, the payoff of the selfish punisher will always go down. This effect is illustrated in the bottom row of figure 5.9. The selfish punisher not only has the disadvantages of the selfish non-punisher, but also the added disadvantage that every individual that imitates the selfish punisher will punish it,



(a) (b) (c) (d) (e)

Figure 5.9: Effects of imitation of selfish behaviour on the payoff of the individuals in a group. Figure (a) shows the original situation, whereas figures (b)-(e) show the effect of a single imitation of a selfish strategy on the payoffs. The strategy that is imitated is indicated by the blue colour, while the individual that changes strategy is printed in bold. Parameters were set to $c = \sigma = \gamma = 1.0, \alpha = 0.1, r = 3.0$ and $\beta = 1.2$.

inflicting a cost β, and has to be punished at a personal cost γ. Also note that selfish non-punishers and selfish punishers have the same maximum payoff from a single game, which is $\frac{4}{5}rc$ when the individual plays with a group of only altruistic non-punishers. However, the minimum payoff for a single game, when the individual plays with a group of only selfish punishers, is -4β for a selfish non-punisher, but $-4\beta - 4\gamma$ for a selfish punisher who is forced to punish each of its co-players.

Figure 5.9 illustrates the effects of imitating a selfish non-punisher (top row) or selfish punisher (bottom row) on the payoffs for each individual. In this figure, the parameter setting $c = \sigma = \gamma = 1.0, \alpha = 0.1, r = 3.0$ and $\beta = 1.2$ was used. Compared to the original situation shown in figure 5.9a, the payoff for the selfish non-punisher increases when its behaviour is imitated by the selfish punisher (figure 5.9b) or the altruistic punisher (figure 5.9e). When a selfish punisher is imitated (bottom row of figure 5.9), the payoff for the selfish punisher will always go down. The figure also illustrates how the payoff for selfish punishers decreases more quickly than that of a selfish non-punisher. Even though the payoff for the selfish punisher is slightly higher than the payoff for the selfish non-punisher in the initial situation, whenever a selfish strategy is imitated, the payoff for the selfish punisher is the lower of the two.

Compared to altruistic punishers, selfish punishers are initially at an advantage as selfish punishers do not contribute to the public good and therefore enjoy a higher payoff. However, altruistic punishers support one another by contributing to the public good, sacrificing part of their fitness to increase the fitness of other altruistic punishers in their interaction neighbourhood. Selfish punishers on the other hand not only fail to support one another, they also punish other selfish punishers, which quickly dissipates any advantage over altruistic punishers. As an effect, selfish punishers never stabilize on a lattice.

Chapter 6

Discussion

Most models concerned with the question of how altruistic and punishing behaviour may have evolved assume that the population consists of homogeneous individuals. Each individual in the population has the same costs and benefits of cooperating, as well as the same costs and effectiveness of punishing for selfish behaviour. In this master's thesis, we investigated the effects of heterogeneity on the co-evolution of altruistic behaviour and punishment. In particular, we determined how individual differences in the cost inflicted by punishment and the personal cost at which punishment may be performed influence the conditions under which altruistic behaviour can stabilize in a population, as well as the resulting structure of altruistic punishers in the population. To achieve this, we separated the population into two classes such that individuals are homogeneous within each class, but may differ in the cost they pay to punish for selfishness and the cost punishers inflict on selfish individuals between classes. Furthermore, we compared these results for two population models: an infinite size population and a spatially structured population. Based on the results listed in chapter 5, heterogeneity of individuals may certainly have an effect on the co-evolution of altruistic behaviour and punishment. In this section, we will discuss these results and relate our findings to results of other research as well as naturally occurring situations.

The infinite population model described in chapter 3 models a well-mixed and infinite sized population, which represents any sufficiently large population in which individuals are very unlikely to encounter the same co-player twice in the setting of a public goods game over the course of their lifetime. The infinite population model may therefore describe the public goods game in a large colony of social insects, such as ants, bees or wasps. In these societies, workers generally exhibit altruistic behaviour by sacrificing most or all of their direct reproduction to help rear the offspring of the queen (Oster and Wilson, 1979). Interestingly, in some species of social insects, infertile workers can still lay haploid eggs destined to be males (Wenseleers et al., 2005). There is an evolutionary incentive to do so, in the sense that workers are more related to their own sons than sons of their queen mother and sons of their sister workers. The reward for such behaviour is therefore an increase in their inclusive fitness, that is the probability of their genes surviving. Natural selection would therefore favour the social insect that lays its own eggs. However, workers lay eggs at the expense of performing their duties to the colony. Punishment for this selfish behaviour takes the form of queen and worker policing, in which worker-laid eggs are destroyed, effectively removing all benefits from the selfish behaviour.

Even though workers, queens and males in a colony of social insects represent morphologically different castes that perform different tasks, the homogeneous infinite population model can be used to model the interactions between the workers of large colonies. However, some colonies of social insects exhibit a further subdivision of the worker caste (Oster and Wilson, 1979) up to a point where a heterogeneous infinite population model would fit the situation better. For example, leaf-cutting ant workers exhibit a 200-fold variation in body mass (Wilson, 1980), while in weaver ants of the genus *Oecophylla*, workers show a clear bimodal size distribution, with almost no overlap in size between minor and major workers (Hölldobler and Wilson, 1990). In cases like these, morphologically different workers typically perform different tasks depending on their physical traits. In general, the minor workers stay in the nest to tend to the queen and her brood, while major workers perform the more dangerous tasks of foraging and defending the colony.

We have shown that for the infinite population model, a population can take advantage of heterogeneity in the ability to punish for selfish behaviour by specialization. When the cost for punishing is differentiated, punishing co-players for selfish behaviour can be justifiable by some class of individuals, while it may be too expensive for another class. Moreover, heterogeneity in the cost for punishing makes it easier for altruistic behaviour to evolve; a lower proportion of altruistic punishers is needed to ensure that a population will end up in a state without selfish individuals. In situations in which the difference in cost is high, or when there are many individuals exhibiting selfish behaviour, this may lead to a clear specialization. Altruistic punishers disappear from the class with the highest cost for punishing, which leaves the class with the lowest cost for punishing with the responsibility of enforcing altruistic behaviour through punishment. For social insects, the model therefore predicts that when individual differences in the costs of punishing are sufficiently high, these differences will cause a division of labour in the population.

The infinite and well-mixed population proved insensitive to heterogeneity in the returns on punishment. When controlled for the average value, variations in the returns on punishment across classes of individuals do not change the way altruistic behaviour and punishment co-evolve. However, variations in the returns on punishment do interact with heterogeneity of punishing cost. If some class of individuals can inflict high punishment, doing so at a low cost increases the chances for altruistic behaviour to stabilize. If, on the other hand, high punishment can only be achieved by a high cost, the combined effect will make it harder for the population to stabilize altruistic behaviour than in the case of a homogeneous population. The model therefore predicts that large differences in the level of punishment are rare in social insects, and that when individuals that pay a lower cost for punishing for selfishness also inflict a higher punishment, these individuals are likely to become solely responsible for punishing.

As an alternative to the well-mixed infinite population model, the lattice model described in chapter 4 represents a different kind of population. Where the infinite population model represents a large population in which individuals are unlikely to meet the same co-player twice in the setting of a public goods game, the lattice model represents a relatively small population with a rigid interaction structure. Individuals only interact with a small selection of other individuals, and always in the same groups. The lattice model can therefore be used to model individuals that are arranged in a strict geographical structure, but also social connections between individuals. In the latter interpretation, the lattice-based population can be used to model the evolution and enforcing of social norms, in which the payoff of the public goods game is interpreted as a personal utility rather than evolutionary fitness. Note that this utility is not necessarily an external reward: experiments reveal that children show a strong tendency to help others at a very young age, even in the absence of material or social rewards (Tomasello, 2009). In fact, Warneken and Tomasello (2008) show that providing a reward for helping diminishes the children's motivation to help in the future.

Social norms are customary rules of behaviour that people will conform to given the expectation others will conform to it too (Lewis, 1969; Bicchieri, 2006). The individuals in our model have no way of explicitly forming expectations about the actions of others. They simply imitate the strategy of the individual with the highest payoff. The implicit expectation is that imitating the most successful strategy will raise their own payoff. In the setting of the public goods game, altruistic strategies yield the highest payoff when they are used by everyone else in the interaction neighbourhood. Altruistic punishment can therefore become a social norm, since individuals prefer to imitate the altruistic behaviour on the condition that everyone else is an altruistic punisher.

As expected from results of two-player games (Nowak and May, 1993; Lindgren and Nordahl, 1994; Killingback and Doebeli, 1996), altruistic behaviour and punishment in the public goods game can evolve more easily on a lattice than in the infinite and well-mixed population. Because of the localized interactions, altruists are at a lower risk of being exploited by selfish individuals, while punishers only punish selfish individuals which they will encounter again in the public goods game. Moreover, if selfish behaviour is highly profitable, some of the altruistic individuals that the selfish individual has interacted with will imitate the strategy, withholding cooperation the next round. In this sense, the lattice structure provides a form of direct reciprocity.

We have shown that in a lattice-based population, heterogeneity in the returns on punishment by itself has little effect on whether or not altruistic behaviour will stabilize. Differentiation in the cost of punishing does have a positive effect for altruistic behaviour, although the effect does not seem to be as pronounced as in the case of the infinite and well-mixed population. However, heterogeneous classes within a population on a lattice readily specialize such that punishment is carried out by the class of individuals best suited for the task, whether this is because they enjoy a higher return on punishment or because they pay a lower cost for punishing. When a class of individuals combines both benefits to their ability to punish, inflicting a higher punishment at a lower cost, punishment becomes the almost sole responsibility of this class. Compared to the homogeneous case, heterogeneity of this kind has a clear positive effect on the evolution of altruistic behaviour in the sense that fewer punishers are needed in the initial configuration to reliably stabilize altruistic behaviour in the entire population. As with the infinite and well-mixed population, the combined effect of heterogeneity in the costs of punishing and the returns on punishment is stronger than the separate effects.

The ability of the lattice model to specialize is best illustrated in the case where the two heterogeneous classes differ in their level of punishment, such that one class inflicts high punishment at a high cost, while the other inflicts a lower punishment at a lower cost. In this case, which class will specialize into becoming the class of punishing individuals depends on the initial proportions of strategies. When altruistic behaviour is already common, the class that inflicts high punishment will contain most altruistic punishers. On the other hand, if altruistic behaviour is less common, and punishers are faced with more selfish individuals to punish, the class enjoying a lower cost for punishing will take over the responsibility of punishing.

In the interpretation of social norms that are maintained by a group of people, the lattice model predicts that punishment will be carried out either by the ones paying the lowest personal cost or the ones inflicting the highest punishment. When there is a choice between low punishment at a low cost and high punishment at a high cost, the level of punishment depends on the popularity of the social norm. When a social norm is popular in the sense that many people adhere to it, the model predicts that violation of the norm will be punished severely, even if it comes at a high personal cost to the punishers. When only few people adhere to the norm in the initial situation, punishment for violating it will be lower. Note however that this choice in the level of punishment is not made individually in our model. Individuals may choose whether or not they punish for selfish behaviour, while the level of punishment is entirely determined by their individual abilities.

The specialization that occurs in the lattice-based population shows some similarities with experimental results on the bystander effect. In general, bystanders are slower to help and help less often during an emergency situation when other bystanders are present (Latane and Darley, 1968). However, experimental research has shown that this bystander effect does not occur when subjects consider other bystanders to be unable to help (Bickman, 1971). Moreover, when subjects consider themselves to be more competent in dealing with the emergency, the presence of other bystanders does not inhibit helping either (Pantin and Carver, 1982; Cramer et al., 1988). In naturally occurring situations, bystanders that intervene in a crime generally describe themselves as being physically strong and appear to act out of a sense of capability through training experience or personal strength (Huston et al., 1981). On the other hand, preschoolers are less likely to respond to the distress of one of their peers when a competent adult caregiver is present (Caplan and Hay, 1989). This sense of responsibility, where emergencies and norm violations are handled by the individual most competent to complete the task, also appears in the lattice-based population. Our results show that even if the individual abilities of others are not observable, norm violation will be punished by the individuals best suited for the task. However, if none of these individuals are present in the group playing the public goods game, norm violation is likely to go unpunished.

Although both the infinite population model and the lattice-based population model can take advantage of heterogeneity in the cost for punishing, there are striking differences between the two models. When classes of individuals differ in the level of their punishment, such that some class inflicts low punishment at a low cost, while another inflicts high punishment at a high personal cost, a lattice-based population can take advantage of these differences by specialization. The same structure of classes of individuals within an infinite and well-mixed population is detrimental to the co-evolution of altruistic behaviour and punishment. In this case, a larger proportion of punishers is needed to stabilize altruistic behaviour.

Note that in our analysis, individual changes in the returns on and costs for punishing do not affect the share of the public good the punisher is entitled to. An individual that can punish with unusually high effectiveness has no more benefits from punishing than others: the increased effect of discouraging selfish behaviour is of no greater advantage to them than to others. In nature, dominant animals in a social group are more likely to punish for failure to contribute to the public good, but they commonly gain a disproportionate share of reproduction. This is not simply the right of the strongest, since subordinates are known to challenge a dominant animal if it takes more than its fair share (Clutton-Brock and Parker, 1995). In effect, the dominant animal has a strategy that is in between that of an altruistic punisher and a selfish punisher. This additional immediate benefit of punishing for selfish behaviour ensures that the punishing individuals have higher stakes in stabilizing cooperation in the population.

In our model such additional advantages do not exist. The effects of heterogeneity of the effectiveness of punishment and the resulting structure of the population are purely caused by differences in the abilities to punish. Based on these differences, individuals may pay a lower personal cost for punishing, but the act of punishing always represents a short-term loss in fitness for the punisher.

Chapter 7

Conclusions and future work

In this master's thesis, we have examined the question of how individual differences affect the co-evolution of altruistic behaviour and punishment. In previous research, populations of individuals are commonly assumed to be homogeneous, such that the benefits and costs for cooperating and punishing are the same for every individual. We extended the public goods game with voluntary participation of Brandt et al. (2006) by separating the population into two classes such that individuals within the same class are homogeneous, but differ in their ability to punish across classes. By manipulating the cost individuals pay for punishing others, as well as the cost inflicted by punishment, we have shown how heterogeneity between individuals can affect the co-evolution of altruistic behaviour and punishment and the structure of the resulting population.

In the setting of an *infinite and well-mixed* population, individuals that meet in a public goods game are unlikely to meet each other again in their lifetime. Heterogeneity in the cost for punishing in this setting can make it easier for altruistic behaviour to stabilize; a lower proportion of punishers is needed to ensure the population ends up in a state with only altruistic individuals. In contrast, introducing individual differences in the effectiveness of punishment has no influence on whether or not altruistic behaviour will stabilize in an infinite population by itself. However, when combined with heterogeneity in the cost of punishing such that individuals that inflict high punishment do so at a lower cost, individual differences in the effectiveness of punishment can amplify the positive effect on the evolution of altruistic behaviour. For the infinite and well-mixed population, the interaction between heterogeneity of cost for punishing and heterogeneity of returns on punishment can work both ways. When individuals differ in the level of punishment, such that some individuals inflict a low punishment at a low personal cost, while others inflict high punishment at a high personal cost, altruistic behaviour can become harder to stabilize.

In addition to the infinite and well-mixed population, we also investigated the effects of heterogeneity in the individual abilities to punish in a *lattice-based* population. In this setting, individuals are assigned a spatial location on a grid, and only play the public goods game within a local neighbourhood. As in the infinite population model, we found a positive effect of heterogeneity in the cost for punishing that was amplified when individuals that inflict high punishment pay a low cost to do so. In contrast with the infinite population model, we found heterogeneity in the returns of punishment makes it slightly easier to stabilize altruistic behaviour when it is common in the initial situation, but slightly harder when altruistic behaviour is initially rare. This result becomes even more clear when individuals differ in their level of punishment. When altruistic behaviour is initially common, individuals that inflict high punishment at a high cost will perform most of the punishment. However, when altruistic behaviour is initially rare, punishment becomes the responsibility of individuals that inflict low punishment at a low cost.

A number of issues are left open for further research. In our models, we assumed the population consisted of two separate classes, where the heterogeneity was limited between classes, while individuals within the same class were homogeneous. Although this setup can be used to describe some cases in nature, such as the bimodal size distribution of workers in weaver ants (Hölldobler and Wilson, 1990), individuals in general have continuously distributed abilities.

In the models we discussed, altruistic non-punishers are punished for second-order free-riding when they could have punished a selfish individual but failed to do so. In the infinite and well-mixed population model, punishing for second-order free-riding is needed to prevent altruistic punishers from disappearing from the population entirely. As long as there are selfish individuals, the additional costs for punishing them causes altruistic punishers to have a lower fitness than altruistic non-punishers. By also punishing for second-order free-riding, altruistic punishers can have a higher fitness than altruistic non-punishers, encouraging more altruistic individuals to punish as well. However, punishing for second-order free-riding is generally found to have little effect in spatially structured populations. It remains an open question whether punishing for second-order free-riding influences the specialization effects in the lattice-based population, especially in the case where individuals differ in the level of their punishment.

The differences between the infinite and well-mixed population and the lattice-based population are quite large. In the infinite population model there are no repeat encounters. A pair of individuals that meet in the setting of the public goods game never meet each other in the same setting again. On the other hand, individuals in the lattice-based population only interact with the same twelve neighbours, playing the same five public goods games every round. However, the public goods game is well suited for an intermediate form, in which co-players are selected at random from a local neighbourhood, combining elements of both population models.

The simplified representation of individuals raises another issue. Each individual adopts one strategy and uses that strategy in all the games it plays. Individuals cannot take advantage of past experience when they encounter a co-player they have met before, which is particularly relevant in the lattice-based population. This simplified representation precludes the emergence of the hierarchical structure that is commonly found in animal societies. Research on dominance relations in competitive environments has resulted into models that allow for these hierarchical structures, such as DomWorld (Hemelrijk, 1999, 2000, 2002). Future research could shed light on how these competitive hierarchical structures affect cooperative efforts.

In our model of the public goods game, altruistic behaviour is represented as a binary choice; individuals either invest in the public good, or not. In practice, the amount invested in the public good may be chosen from a continuous range of possibilities, depending on individual abilities. Empirical research has shown human subjects readily accept individual differences and adjust their expectations, punishing only when they believe their co-players invested less than their fair share (Fisher et al., 1995; Reuben and Riedl, 2009). In our models, we have shown that a sense of "fairness" does seem to emerge in the lattice model, in the sense that punishment is carried out by individuals that are best suited for the task. This specialization occurs even in the absence of personal benefits. Whether this primitive form of a "fairness" principle also emerges in a more complex setting where cooperative behaviour is not simply a binary choice is a question for future research.

As a final note, in the models presented here we assume no mistakes are made in determining which individual has the highest payoff and in performing the actions associated with the strategy an individual has adopted. The effect of noise and mistakes on the evolution of altruistic behaviour has been researched extensively (see among others Foster and Young, 1990; Fudenberg and Maskin, 1990; Fudenberg and Harris, 1992; Blume, 2003). Especially in spatial games, introducing noise or mistakes benefits can greatly influence the evolution of altruistic behaviour. In the lattice-based population, altruistic behaviour benefits from local clusters of altruists. Random influences caused by noise and mistakes break up these clusters, allowing selfish individuals to exploit the altruists more easily. The addition of noise also prevents blinkers, in which a cluster of selfish individuals alternates between two states indefinitely (Killingback and Doebeli, 1996). Most of these effects are based on breaking up the symmetric expansion of successful strategies due to the synchronous updating in the lattice model (Nowak, 2006). However, in our setup of heterogeneous classes, expansion of successful strategies is no longer completely symmetric. We therefore expect noise and mistakes to have less of an impact on the evolution of altruistic behaviour than in a homogeneous lattice-based population.

Noise and mistakes may have an effect on the observed specialization effects. By preventing the population from settling in a stable state, the addition of noise may make specialization between classes more pronounced. The precise effects of errors in perception, in which the individual with the highest fitness is identified incorrectly, and implementation error, in which the individual performs a different strategy than the one it adopted, remain an issue for further research.

Bibliography

Alexander, R.D. 1987. ***The biology of moral systems***. Aldine Transaction.

Axelrod, R. & WD Hamilton 1981. The evolution of cooperation. ***Science***, 211(4489): 13–90.

Bicchieri, C. 2006. ***The grammar of society***. Cambridge University Press.

Bickman, L. 1971. The effect of another bystander's ability to help on bystander intervention in an emergency* 1. ***Journal of Experimental Social Psychology***, 7(3): 367–379.

Blume, L.E. 2003. How noise matters. ***Games and Economic Behavior***, 44(2): 251–271.

Bolton, G.E. & R. Zwick 1995. Anonymity versus punishment in ultimatum bargaining. ***Games and Economic Behavior***, 10(1): 95–121.

Boyd, R., H. Gintis, S. Bowles, & P.J. Richerson 2003. The evolution of altruistic punishment. ***Proceedings of the National Academy of Sciences***, 100(6): 3531–3535.

Boyd, R. & P.J. Richerson 1988. The evolution of reciprocity in sizable groups. ***Journal of Theoretical Biology***, 132(3): 337–356.

Boyd, R. & P.J. Richerson 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. ***Ethology and sociobiology***, 13(3): 171–195.

Brandt, H., C. Hauert, & K. Sigmund 2003. Punishment and reputation in spatial public goods games. ***Proceedings of the Royal Society of London. Series B: Biological Sciences***, 270(1519): 1099–1104.

Brandt, H., C. Hauert, & K. Sigmund 2006. Punishing and abstaining for public goods. ***Proceedings of the National Academy of Sciences***, 103(2): 495–497.

Camerer, C. & R.H. Thaler 1995. Anomalies: Ultimatums, dictators and manners. ***The Journal of Economic Perspectives***, 9(2): 209–219.

Caplan, M.Z. & D.F. Hay 1989. Preschoolers' responses to peers' distress and beliefs about bystander intervention. ***Journal of Child Psychology and Psychiatry***, 30(2): 231–242.

Clutton-Brock, T.H. & G.A. Parker 1995. Punishment in animal societies. ***Nature***, 373(6511): 209–216.

Colman, A.M. 1995. ***Game theory and its applications in the social and biological sciences***. Garland Science.

Cramer, R.E., M.R. Mcmaster, P.A. Bartell, & M. Dragna 1988. Subject competence and minimization of the bystander effect. ***Journal of Applied Social Psychology***, 18(13): 1133–1148.

Crespi, B.J. 2001. The evolution of social behavior in microorganisms. ***Trends in Ecology & Evolution***, 16(4): 178–183.

Dugatkin, L.A. 1997. ***Cooperation among animals: An evolutionary perspective***. Oxford University Press, USA.

Eldakar, O.T., D.L. Farrell, & D.S. Wilson 2007. Selfish punishment: Altruism can be maintained by competition among cheaters. ***Journal of Theoretical Biology***, 249(2): 198–205.

Eldakar, O.T. & D.S. Wilson 2008. Selfishness as second-order altruism. ***Proceedings of the National Academy of Sciences***, 105(19): 6982–6986.

Falk, A., E. Fehr, & U. Fischbacher 2005. Driving forces behind informal sanctions. ***Econometrica***: 2017–2030.

Fehr, E. & S. Gächter 2000. Cooperation and punishment in public goods experiments. ***American Economic Review***: 980–994.

Fehr, E. & S. Gächter 2002. Altruistic punishment in humans. ***Nature***, 415(6868): 137–140.

Fisher, J., R.M. Isaac, J.W. Schatzberg, & J.M. Walker 1995. Heterogenous demand for public goods: behavior in the voluntary contributions mechanism. ***Public Choice***, 85(3): 249–266.

Foster, D. & P. Young 1990. Stochastic evolutionary game dynamics*. ***Theoretical Population Biology***, 38(2): 219–232.

Fowler, J.H. 2005. Altruistic punishment and the origin of cooperation. ***Proceedings of the National Academy of Sciences***, 102(19): 7047–7049.

Fudenberg, D. & C. Harris 1992. Evolutionary dynamics with aggregate shocks* 1. ***Journal of Economic Theory***, 57(2): 420–441.

Fudenberg, D. & E. Maskin 1990. Evolution and cooperation in noisy repeated games. ***The American Economic Review***, 80(2): 274–279.

Gómez-Gardeñes, J., M. Campillo, LM Floría, & Y. Moreno 2007. Dynamical organization of cooperation in complex topologies. ***Physical Review Letters***, 98(10): 108103.

Güth, W., R. Schmittberger, & B. Schwarze 1982. An experimental analysis of ultimatum bargaining. ***Journal of Economic Behavior & Organization***, 3(4): 367–388.

Hamilton, WD 1964. The genetical evolution of social behaviour. II* 1. ***Journal of theoretical biology***, 7(1): 17–52.

Hardin, G. 1968. The tragedy of the commons. ***Science***, 162(3859): 1243–1248.

Hauert, C., S. De Monte, J. Hofbauer, & K. Sigmund 2002a. Replicator dynamics for optional public good games. ***Journal of Theoretical Biology***, 218(2): 187–194.

Hauert, C., S. De Monte, J. Hofbauer, & K. Sigmund 2002b. Volunteering as red queen mechanism for cooperation in public goods games. ***Science***, 296(5570): 1129–1132.

Hauert, C., A. Traulsen, H. Brandt, M.A. Nowak, & K. Sigmund 2007. Via freedom to coercion: the emergence of costly punishment. ***Science***, 316(5833): 1905–1907.

Hauert, C., A. Traulsen, H. Brandt, MA Nowak, & K. Sigmund 2009. Public goods with punishment and abstaining in finite and infinite populations. ***Biological Theory***, 3(2): 114–122.

Hemelrijk, C.K. 1999. An individual–orientated model of the emergence of despotic and egalitarian societies. ***Proceedings of the Royal Society of London. Series B: Biological Sciences***, 266(1417): 361.

Hemelrijk, C.K. 2000. Towards the integration of social dominance and spatial structure. ***Animal Behaviour***, 59(5): 1035–1048.

Hemelrijk, C.K. 2002. Despotic societies, sexual attraction and the emergence of male 'tolerance': an agent-based model. ***Behaviour***, 139(6): 729–747.

Henrich, J., R. Boyd, S. Bowles, C. Camerer, E. Fehr, H. Gintis, & R. McElreath 2001. In search of homo economicus: Behavioral experiments in 15 small-scale societies. ***The American Economic Review***, 91(2): 73–78.

Hölldobler, B. & E.O. Wilson 1990. ***The ants***. Belknap Press.

Huston, T.L., M. Ruggiero, R. Conner, & G. Geis 1981. Bystander intervention into crime: A study based on naturally-occurring episodes. ***Social Psychology Quarterly***, 44(1): 14–23.

Ifti, M., T. Killingback, & M. Doebeli 2004. Effects of neighbourhood size and connectivity on the spatial continuous prisoner's dilemma. ***Journal of Theoretical Biology***, 231(1): 97–106.

Kagel, J.H., A.E. Roth, & J.D. Hey 1995. ***The handbook of experimental economics***. Princeton University Press Princeton, NJ.

Killingback, T. & M. Doebeli 1996. Spatial evolutionary game theory: Hawks and Doves revisited. ***Proceedings: Biological Sciences***, 263(1374): 1135–1144.

Latane, B. & J.M. Darley 1968. Group inhibition of bystander intervention in emergencies. ***Journal of Personality and Social Psychology***, 10: 215.

Leimar, O. & P. Hammerstein 2001. Evolution of cooperation through indirect reciprocity. ***Proceedings of the Royal Society of London. Series B: Biological Sciences***, 268(1468): 745.

Lewis, D.K. 1969. ***Convention: A philosophical study***. Harvard University Press.

Lindgren, K. & M.G. Nordahl 1994. Evolutionary dynamics of spatial games. ***Physica D: Nonlinear Phenomena***, 75(1-3): 292–309.

Monnin, T. & F.L. Ratnieks 2001. Policing in queenless ponerine ants. ***Behavioral Ecology and Sociobiology***, 50(2): 97–108.

Nakamaru, M. & Y. Iwasa 2006. The coevolution of altruism and punishment: Role of the selfish punisher. ***Journal of Theoretical Biology***, 240(3): 475–488.

Nowak, M.A. 2006. ***Evolutionary dynamics: Exploring the equations of life***. Harvard University Press.

Nowak, M.A. & R.M. May 1993. The spatial dilemmas of evolution. ***International Journal of Bifurcation and Chaos***, 3: 35–35.

Nowak, M.A. & K. Sigmund 1998. The dynamics of indirect reciprocity. ***Journal of Theoretical Biology***, 194(4): 561–574.

Nowak, M.A. & K. Sigmund 2004. Evolutionary dynamics of biological games. ***Science Signaling***, 303(5659): 793–799.

Oster, G.F. & E.O. Wilson 1979. ***Caste and ecology in the social insects***. Princeton University Press.

Ostrom, E. 2000. Collective action and the evolution of social norms. ***The Journal of Economic Perspectives***: 137–158.

Pantin, H.M. & C.S. Carver 1982. Induced Competence and the Bystander Effect1. ***Journal of Applied Social Psychology***, 12(2): 100–111.

Poncela, J., J. Gómez-Gardeñes, LM Floría, & Y. Moreno 2007. Robustness of cooperation in the evolutionary prisoner's dilemma on complex networks. ***New Journal of Physics***, 9(184): 1–14.

Reuben, E. & A. Riedl 2009. Enforcement of contribution norms in public good games with heterogeneous populations. ***Research Memoranda***, 29: 1–25.

Santos, FC, JM Pacheco, & T. Lenaerts 2006. Evolutionary dynamics of social dilemmas in structured heterogeneous populations. ***Proceedings of the National Academy of Sciences***, 103(9): 3490–3494.

Sigmund, K., C. Hauert, & M.A. Nowak 2001. Reward and punishment. ***Proceedings of the National Academy of Sciences***, 98(19): 10757–10762.

Taylor, P.D. & L.B. Jonker 1978. Evolutionary stable strategies and game dynamics. ***Mathematical Biosciences***, 40(1-2): 145–156.

Tomasello, M. 2009. ***Why we cooperate***. MIT Press.

Trivers, R.L. 1971. The evolution of reciprocal altruism. ***The Quarterly Review of Biology***, 46(1).

Warneken, F. & M. Tomasello 2008. Extrinsic rewards undermine altruistic tendencies in 20-month-olds. ***Developmental psychology***, 44(6): 1785–1788.

Wenseleers, T., A. Tofilski, & FLW Ratnieks 2005. Queen and worker policing in the tree wasp Dolichovespula sylvestris. ***Behavioral Ecology and Sociobiology***, 58(1): 80–86.

Wilson, E.O. 1980. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: Atta). ***Behavioral Ecology and Sociobiology***, 7(2): 143–156.