

The Evolution of Altruism - Spatial Assortment in  
the Prisoner's Dilemma  
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## Abstract

At first glance the existence of altruism in nature seems paradoxical. In displaying an altruistic act, an individual incurs some cost to its own fitness. Natural selection favours the fittest individuals and one would expect that genes promoting altruism would be selected against. This report investigates the mechanisms that facilitates the evolution of altruism. Game theory is widely applied in the study of the evolution of altruism and cooperation. We review game theory concepts which occur regularly in the literature and which are important in the study of the evolution of cooperation. The Prisoner's Dilemma game captures the essence of altruism and is a model often employed in the theoretical study of cooperation.

The best strategy for both players in the single round Prisoner's Dilemma (PD) game is to defect, but having repeated rounds can lead to the evolution of cooperation. The mechanism by which cooperation is established in this scenario is known as direct reciprocity. Another mechanism which promotes the evolution of cooperation is the non-random interaction of players, called assortment. A couple of factors could influence the assortment of players, one of which is the spatial distribution of players.

A model is constructed in which the players in the PD are placed on a lattice. Each player adopts one of two strategies, pure cooperation or pure defection. The players propagate and die out in proportion to how well they do in playing the PD against their neighbours. The model is used to investigate the spatial dynamics of the players and the level of assortment achieved. A simple movement strategy is introduced, whereby players move if they encounter a defector. The effect of this movement on the assortment is investigated.

Our results show that by placing the players in the PD on lattice, enough assortment can be gained to allow the persistence of cooperation. An increase in the dispersal parameter leads to a decline in the success of cooperators and a loss in assortment. This suggests that the best movement strategy for cooperators is to have low dispersal rates, while defectors gain a big benefit from higher dispersal rates.

# 1 Introduction

## 1.1 Biological Background

Altruism is a phenomenon that is witnessed throughout the natural world. Altruism is defined as the behaviour of an organism that benefits another organism, with some cost to the benefactor [19]. The cost and benefit are measured in the contribution that is made to the organism's inclusive fitness.

At face value altruism seems to contradict the principles of Darwinian evolution. Evolution is the gradual change of organisms over many generations. Darwin proposed natural selection as the mechanism driving evolution: nature acts on pre-existing differences selecting the best adapted inheritable traits and passing these on to the next generation. The evolutionary fitness of an individual is measured by its ability to reproduce and pass on its genes. From a gene's point of view, in order to persist, it has to give its carrier some advantage over other individuals, allowing its carrier to be more successful at reproducing copies of itself. It seems that genes promoting altruism hold a cost to the bearer and should therefore be selected against, but, paradoxically, we find many examples of altruism being expressed in nature [19].

There are many cases of cleaning symbiosis in the ocean where one organism cleans another of ectoparasites, sometimes entering the gills and mouth of the host. There are more than 45 species of fish and six shrimp species known to be cleaners with many species of fish serving as hosts. It would seem the most beneficial to a host to be cleaned, and then make a meal of the cleaner once it has finished. However, host fish avoid eating cleaners, even going to great lengths to do so with a cost to itself.

Birds have calls designed to warn others against the presence of predators. The caller is incurring a cost to itself by exposing its location to any potential predators, whether detected or not. Nearby birds benefit from the caller's presence since their chances of escaping from predators are increased.

Many cases of altruism exist in humans: helping others in danger, sharing food, helping the vulnerable, sharing implements and sharing knowledge.

With ample evidence of altruism scientists have proposed a number of theories to explain these occurrences of altruism. Nowak and Sigmund [16] explore five current theories in good detail, namely kin selection, direct reciprocity, indirect reciprocity, graph selection and group selection.

**Kin Selection:** This theory was first proposed by Hamilton [8]. Kin selection occurs when evolution is driven by the interaction between related individuals. Cooperation occurs when a donor pays a cost,  $c$ , for a recipient to get a benefit,  $b$ . It is possible for natural selection to favour kin selection if the coefficient of genetic relatedness is greater than the cost/benefit ratio,  $r > c/b$ . Related individuals are more likely to have many genes in common. An act of cooperation while having a cost to one individual, may still benefit the set of genes.

**Direct Reciprocity:** Put forward by Trivers [19] as an alternative to kin

selection, direct reciprocity can explain cooperative situations where organisms are not related. The Prisoner's Dilemma (PD) is used as a tool for studying this kind of cooperation. Direct reciprocity is discussed further later on in this report.

**Indirect Reciprocity:** Nowak and Sigmund explain it as follows [16]: "Whereas direct reciprocity embodies the idea of you scratch my back I scratch yours, indirect reciprocity suggests that you scratch my back I scratch someone else's." Reputation plays a part in enforcing cooperation. Individuals are not directly punished in their act of defection, but may be punished later by a third party for a previous defection.

**Group Selection:** Selection not only acts on individuals but also on groups. A group of cooperators may be more successful than a group of defectors. Group selection is a controversial theory [14].

**Graph Selection:** Populations demonstrate a network-like structure with certain individuals interacting more with some than with others. Graph theory can be used to study the effect of this spatial structure on the emergence of cooperation.

An important tool for studying the evolution of cooperation is game theory. In the next section some background is given with regard to game theory and games that regularly occur in the study of the evolution of cooperation.

## 1.2 Mathematical Background

Game theory is widely applied in the investigation of the evolution of altruism and cooperation. Described very generally game theory is concerned with the behaviour of decision makers (players) whose decisions affect each other [4]. These interactions are analysed from a rational point of view. Fields where game theory is applied include economics, political science, tactic and strategic military problems, computer science and, as in this case, evolutionary biology. Games in game theory are played between two or more players where the score attained by each player is affected by the strategies of the other players and the player's own strategy. A very famous concept in game theory is the Nash Equilibrium.

**Definition 1. *Nash Equilibrium*** *In a game played by two or more players, a set of strategies is a Nash equilibrium if no player can do any better by changing its strategy while the other players keep the same strategy.*

Other areas where game theory have been applied in biology is the evolution of fighting behaviour in animals [18] and signalling interactions [7]. An important concept originally developed by Maynard Smith and Price [18], in evolutionary game theory is that of an evolutionary stable strategy or ESS.

**Definition 2. Evolutionary Stable Strategy (ESS).** An ESS is a strategy which, if adopted by a population of players, renders them immune to invasion by a rare mutant strategy.

Let  $S$  and  $T$  be two strategies and  $E(S, T)$  the pay-off strategy  $S$  receives after playing against strategy  $T$ . Then  $S$  is an ESS if either

$$E(S, S) > E(T, S) \text{ or}$$

$$E(S, S) = E(T, S) \text{ and } E(S, T) > E(T, T)$$

is satisfied.

ESS is a refinement of the Nash equilibrium. All ESSs are Nash equilibria, but a Nash equilibrium could exist which is not an ESS.

Next I introduce three games that are regularly applied in biology and the theory of evolution of cooperation. For each game the Nash equilibrium is given together with an example of an ESS. Although all three these games are closely related, each can be used as an analogy for a different set of interactions as witnessed in nature.

### 1.3 The Prisoner's Dilemma and Direct Reciprocity

The Prisoner's Dilemma (PD) is a game played by two players. Each player has the option to cooperate or defect. If both players cooperate, each player receives the reward,  $R$ . If both players defect they receive the punishment,  $P$ . If one player defects and the other cooperates, the cooperator receives the sucker's pay-off,  $S$ , and the defector receives the temptation,  $T$ . The pay-off is ranked  $T > R > P > S$ . Suppose you are playing the PD against an opponent whom you expect to defect, the best strategy is to defect also and minimize your loss, since  $P > S$ . Assuming that your opponent is going to cooperate, you can gain the maximum pay-off by defecting, since  $T > R$ . The best rational strategy and also the Nash equilibrium in the PD is for both players to defect, each getting reward  $P$ . If both players cooperated, they could have achieved a higher pay-off,  $R$ , and this is where the dilemma lies. The pay-off structure is also often represented in matrix form:

	C	D
C	R,R	S,T
D	T,S	P,P

If one considers a cooperating act by a player as a contribution to its opponent's fitness,  $b$ , with a cost  $c$  to its own, then the PD pay-off is given by the pay-off matrix

	C	D
C	b-c	-c
D	b	0



omitting the second entry since the scores are symmetric. To fulfil the pay-off structure of the PD it is required that  $c < b$ .

The PD with repeated rounds is known as the Iterated Prisoner's Dilemma (IPD). By having repeated rounds of the PD with players having to interact more than one round, it is possible for cooperation to develop [2]. In the IPD a player's strategy defines what his action will be in a particular round: defect or cooperate. In the case where the number of rounds are known, it is best to defect in the last round. But then, expecting your opponent to defect in the ultimate round, it is best to defect in the penultimate round. Then, by induction, it's best to defect every round. The investigation proceeds to a case where cooperation can emerge: the IPD where the number of rounds is unknown with the probability of having another round given by  $w$ .

Like in altruistic behaviour, in the one-round PD a player gains most by not being an altruist and defecting. The defectors exploits others exhibiting altruism, the cooperators. The PD is therefore a good analogy for investigating cooperation and establishing under which conditions cooperation could evolve.

For a strategy to be evolutionary viable, it has to meet all three of the following criteria [2] [1]:

- Robustness: Can the strategy survive in an environment with a variety of more or less complicated strategies?
- Stability: Once established in a population, can the strategy resist invasion by another mutant strategy?
- Initial viability (invasiveness): Can the strategy get a foothold in a non-cooperative environment?

Axelrod and Hamilton [2] set up a tournament to investigate how well strategies fared when competing in a mixed population of different strategies, playing the IPD. Professional game theorists were invited to submit their strategies into the competition. In the tournament each strategy played against every other strategy round-robin style. The strategy scoring the highest average over all the rounds was the winner. The results from the tournament were used to establish that Tit for Tat (TFT) is indeed an evolutionary viable strategy, fulfilling all three requirements.

### **Tit for Tat**

A player using Tit for Tat cooperates on the very first round and on subsequent rounds merely mirrors its opponent's move on the previous round. If its opponent cooperated in the preceding round then Tit for Tat will cooperate in the current round and a defection the preceding round will be met with a defection in the current round.

The tournament showed Tit for Tat's success, winning the round robin style tournament by out competing 14 other strategies. In a second tournament with 62 entries Tit for Tat was once again the winner. To test the

robustness of TFT, an alternative version of the tournament was tested, where strategies advance to the next round in proportion to how well they did. Tit for Tat out-competed all the other strategies. Can TFT survive in a world of meanies? Axelrod and Hamilton [2] discuss how kin selection and clustering can help to get Tit for Tat established in a non-cooperative environment. Once established, TFT can resist intrusion by clusters of other strategies. Although IPD is not strictly an evolutionary stable strategy, it can resist invasion by a large variety of strategies [12].

Axelrod [1] calls a strategy collectively stable if the conditions  $E(S, S) \geq E(T, S)$  is satisfied. This is a relaxation of Maynard Smith's [14] requirements for a strategy to be an ESS. Axelrod [1] proved the following theorem.

**Theorem 1.** *Tit for Tat is a collectively stable strategy in the Iterated Prisoner's Dilemma provided that*

$$w \geq \max \left( \frac{T - R}{R - S}, \frac{T - R}{T - P} \right)$$

with  $w$  the probability that the interaction between two players will continue to another round of the IPD.

This demonstrates that it is possible for cooperation to emerge as direct reciprocity.

#### 1.4 Hawk Dove

The Hawk-Dove game, also called the chicken or the snowdrift game is similar to the PD but with a different pay-off structure. The game is played between two players. A player can use one of two strategies: it can be a hawk and fight for the resource, or merely use threat displays, playing 'dove'. If both players play hawk they fight until one is injured. When a hawk plays a dove the dove backs off and the hawk gains the resource. Two doves reach a tie and share the resource. The pay-off is structured  $T > R > S > P$  with pay-off matrix

	Hawk	Dove
Hawk	P,P	T,S
Dove	S,T	R,R

If one's opponent plays hawk then it is best to play dove, and if your opponent plays dove it is best to play hawk. The hawk-dove game has two Nash equilibrium states (H,D) and (D,H). If both players play different strategies a player can't improve his outcome by switching strategies while the other stays the same. The ESS for the Dove Hawk game is a mixed strategy where each player chooses either strategy with some probability. The hawk dove game arises when the cost,  $c$ , associated with a cooperating act outweighs the benefit  $b$  ( $c > b$ ).

## 1.5 Public Goods

Again there are two possible strategies, cooperate (C) or defect (D). The Public Goods game is played by  $N$  players. A cooperative act by a player contributes a benefit  $b$  to the public with a cost  $c$  to the player itself, it is usually assumed that the contribution to the public good exceeds the cost,  $b > c$ . A defection by a player adds nothing to the public good with no cost to itself. At the end of the round the total contribution of all the players is then redistributed equally among all the players in the group. In a group with  $k$  cooperators and  $N - k$  defectors the pay-off for a cooperator is  $kb/N - c$  and a defector  $kb/N$ . Defectors receive a higher pay-off than cooperators, which is the basic dilemma of altruism. Only one evolutionary stable strategy exists, and that is to defect.

Meerkats take turns to stand guard while other members of the group forages, an example of the Public Goods game in nature.

## 1.6 Assortment

Assortment has come forward as an important factor in the evolution of cooperation. [5] [17] [6]. In a well mixed population cooperation has little chance of succeeding, but if the encounters between players are non-random and strategy tend to interact more with strategies of their own kind, cooperation is capable of becoming fixed in a population.

### 1.6.1 Generalised Assortment

A framework for investigating assortment was created by Eshell and Cavalli-Sforza [5]. Two strategies  $S_1$  and  $S_2$  are considered. The expected pay-off for a strategy occurring with frequency  $x$  is given by  $V_i(x)$  and  $V_{ij}$  represents the pay-off received by strategy  $i$  after encountering strategy  $j$ . The probability that an individual with strategy  $S_i$  encountering an individual with strategy  $S_j$  is given by  $u_{ij}$ .

The expected pay-off an individual with strategy  $S_i$  will receive is given by

$$V_i(x) = u_{i1}(x)V_{i1} + u_{i2}(x)V_{i2} \quad (1.1)$$

Assuming that the expected number of encounters per individual is independent of its strategy we have that the proportion of encounters of which the second individual is using strategy  $S_1$  is equal to the frequency of that strategy:

$$xu_{11} + (1 - x)u_{21} = x$$

This together with the fact that  $u_{i1} + u_{i2} = 1$  allows us to write all the

probabilities  $u_{ij}$  in terms of  $u_{11}$

$$\begin{aligned} u_{11} &= \frac{x(1 - u_1)}{1 - x} \\ u_{12} &= 1 - u_{11} \\ u_{22} &= \frac{1 - 2x + xu_1}{1 - x} \end{aligned}$$

as long as  $x \neq 1$ . Substituting these back into the payment functions (1.1):

$$\begin{aligned} V_1(x) &= V_{12} + (V_{11} - V_{12})u_{11}(x) \\ V_2(x) &= V_{22} + (V_{21} - V_{22})\frac{x}{1 - x}(1 - u_{11}(x)) \end{aligned}$$

To study the evolutionary viability of a strategy it is assumed that the frequency of a strategy in the next generation is proportional to the success it achieved in the previous generation. If the frequency of strategy  $S_1$  was  $x$  this generation, then in the next generation its frequency is given by

$$x' = \frac{xV_1}{xV_1 + (1 - x)V_2} \quad (1.2)$$

Eshell and Cavalli-Sforza introduced a simple method for measuring assortment. Let  $m$  denote the proportion of the population that meets the same strategy and  $1 - m$  the proportion of the population that meets randomly. The frequency of meetings between individuals who both have strategy  $S_1$  is given by

$$P_{11} = (1 - m)x^2 + mx$$

and the probability that an individual with strategy  $S_1$  meets another individual practising the same strategy is given by

$$u_{11} = \frac{P_{11}}{x} = m + (1 - m)x \quad (1.3)$$

Note that in the case where strategies meet randomly, the probability of meeting a certain strategy is given by its frequency  $u_{i1} = x, u_{i2} = x - 1$ , which is equivalent to setting  $m = 0$  in equation 1.3 and substituting back for the other probabilities.

By doing a stability analysis for equation (1.2) at the fixed point  $x = 0$  it is possible to find the requirements for a strategy  $S_1$  to be viable and evolutionary stable. The details of the linear stability analysis is shown on page 8. The results show that

$$mV_{22} + (1 - m)V_{21} > V_{11} \quad (1.7)$$

is a sufficient requirement for a strategy  $S_1$  to be evolutionary stable and the requirement

$$mV_{11} + (1 - m)V_{12} > V_{22} \quad (1.8)$$

is sufficient for  $S_1$  to establish itself in a population dominated by another strategy  $S_2$ , which reduces to  $V_{22} < V_{12}$  in the absence of assortment,  $m = 0$ .

### Stability Analysis

$$x' = f(x) \quad (1.4)$$

$$f(x) = \frac{xV_1}{xV_1 + (1-x)V_2}$$

$$f'(x) = \frac{V_1V_2 - x(1-x)(V_1'V_2 - V_1V_2')}{(xV_1 + (1-x)V_2)^2} \quad (1.5)$$

A fixed point is a point,  $x^*$ , such that  $f(x^*) = x^*$ . There exist at least two fixed points in equation (1.4) namely;  $x = 0$  and  $x = 1$ . For a fixed point to be linear stable it is required that  $|f'(x)| < 1$ .

$x=0$

Substituting  $x = 0$  into (1.5) we have  $f'(0) = \frac{V_1}{V_2}$ . Thus for the fixed point  $x = 0$  to be linearly stable it is required that  $V_1(0) < V_2(0)$ . For random encounters this simplifies to

$$V_{12} < V_{22}$$

Taking assortment into account we have

$$V_1(0) = V_{11} + (1-m)V_{12}$$

$$V_2(0) = V_{22}$$

and the requirement for stability becomes

$$mV_{11} + (1-m)V_{12} < V_{22} \quad (1.6)$$

At the point  $x = 0$  the population consist entirely of strategy  $S_2$ . If the point  $x = 0$  is linearly stable it implies that strategy  $S_2$  is an evolutionary stable strategy and cannot be invaded by strategy  $S_1$ . If the inverse of inequality (1.6) is satisfied, then the frequency of  $S_1$  will initially increase in a population consisting of mostly  $S_2$ . We did not assume any difference between strategy  $S_1$  and  $S_2$ , therefore by simply renaming the strategies in (1.6) we can find the condition for  $S_1$  to be an ESS. For  $S_1$  to be viable and ESS the two in inequalities must be satisfied

$$mV_{11} + (1-m)V_{12} > V_{22}(\text{Initial viability})$$

$$mV_{22} + (1-m)V_{21} > V_{11} \text{ (ESS)}$$

**Table 1**

In the Prisoner's Dilemma let  $S_1$  be the strategy that always cooperates and  $S_2$  the strategy which always defects. Using the pay-off values for the PD as introduced in section 1.3 and scaling the values to ensure they are positive results in

$$\begin{aligned} V_{21} &= b + c \\ V_{11} &= b \\ V_{22} &= c \\ V_{12} &= 0 \end{aligned}$$

with  $b > c > 0$ . It is clear that  $V_{22} > V_{12}$  and hence it is impossible for cooperation to increase in a population dominated by defectors in the absence of assortment. Using the pay-off values with equation 1.7 results in the requirement  $mb > c$  for cooperation to be an ESS. This rule is similar to the Hamiltonian rule for kin selection but with  $m$  the measure of assortment replacing relatedness parameter  $r$ .

### 1.6.2 Assortment in the Public Goods game

Fletcher [6] explores how assortment leads to the evolution of altruism in the Public Goods game.

Consider a group of  $N$  interacting players. In section 1.5 we have shown that it is not possible for a cooperator to do better than a defector. The solution can be found by considering the entire population consisting of interacting groups each of size  $N$  [6].

Let  $e_C$  denote the average number of cooperators in the  $N - 1$  interacting partners in the interacting group of a focal C individual. The pay-off a C individual receives from his group is  $e_C b/N$ , adding the benefit from its own act of cooperation,  $b/N - c$ , results in the total pay-off  $e_C b/N + b/N - c$ . Similarly let  $e_D$  be the average number of cooperators in the interacting environment of a focal D individual. The average pay-off received by a D individual is  $e_D * b/N$ . For strategy C to be evolutionary viable it is required that

$$\frac{(e_C + 1)b}{N} - c > \frac{e_D b}{N} \quad (1.9)$$

Rearranging this equation the relative assortment necessary for the evolution of altruism is given by

$$e_C - e_D > \frac{cN}{b} - 1 \quad (1.10)$$

Lets assume that interacting groups are formed at random from a large population with the frequency of cooperators in the population given by  $p$ . The distribution of different compositions of interacting groups is given by the binomial. It follows that  $e_C = e_D = p(N - 1)$ . From this and (1.10) it follows

that cooperators will do better than defectors if  $b/N - c > 0$ . Rearranging equation 1.9 generates a Hamilton rule for the Public Good game

$$\frac{e_C - e_D + 1}{N} b > c$$

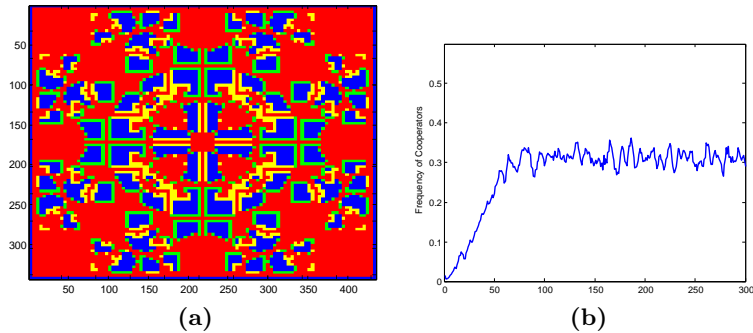
The role of 'relatedness' is played by  $r = \left(\frac{e_C - e_D + 1}{N}\right)$ . In the case of extreme assortment each cooperator is interacting only with cooperators and a defector only with defectors, thus  $e_C = N - 1$  and  $e_D = 0$  and we have  $r = 1$ . In the case of negative assortment cooperators are spread through the entire population so that  $e_C = 0$  and  $e_D = 1$  with  $r = 0$ . If  $b > c$  altruism will always evolve if  $r = 1$  and never evolve if  $r = 0$ . This treatment of  $r$  does not require that individuals are related, but rather here  $r$  is interpreted as a measure of assortment.

### 1.6.3 Assortment and the Iterated Prisoner's Dilemma

How can assortment be applied to direct reciprocity? Rankin and Toborsky [17] investigated the effect of assortment using the IPD as the analogy for cooperation. The model considers an infinite population with three strategies: pure defectors, pure cooperators and generalised reciprocators. General reciprocators cooperate if they were helped in the previous round, and defect if their opposite player defected in the previous round. A generalised reciprocator can therefore be considered to be in one of two states at any particular time, either cooperative or defecting. Assortment is specified in the same manner as by Eshell and Cavalli-Sforza [5]. The parameter  $m$  is the proportion of interactions of a strategy with its own type. The proportion of random interactions is given by  $1 - m$  and the probability that a specific strategy interacts with its own type is given by  $P = m + x(1 - m)$ , where  $x$  is the frequency of the strategy in the population.

## 1.7 Aims

In this report we investigate the conditions under which cooperation can evolve. Cooperation does not fare well in well mixed populations, assortment has been shown to promote the evolution of cooperation. Here we investigate the contribution to assortment by spatial structure. We address the questions: How much assortment does the spatial PD game achieve? What is the effect of movement on assortment?



**Figure 1:** Nowak and May’s [15] version of the spatial PDG. a) The game is played on a 99 by 99 lattice, each site playing against itself and its eight neighbours. We set  $b = 1.9$ . Blue represents cooperators, red defectors, yellow and green represents sites that are changing. A yellow site is a cooperator in this round, but was a defector the previous. A green site is a cooperator which was previously a defector. Initially the entire lattice is inhabited by cooperators except for a single defector site in the centre of the lattice. The results are interesting chaotic patterns, a snapshot shown here after round 400. b) The frequency of cooperators for a lattice with sites initially being C or D at random with equal probability. The value tends to 0.318.

## 2 Mathematical Models

In this section we present two mathematical models. The first model incorporates spatial dynamics into PD. This model shows that cooperators can persist for the certain parameter values. The second model demonstrates how the PD can be incorporated in a metapopulation model with the colonisation and extinction rates of local populations proportional to the pay-off received after playing the PD against neighbouring populations.

### 2.1 Deterministic Spatial Games

Nowak and May [15] took the players in the PD and put them on a lattice, introducing a spatial dimension to the PD. Players have no memory and can choose only one of two strategies, it either cooperates or defects regardless of previous interactions. Each round the player at a site plays the PD against each of its neighbours. A player’s neighbourhood could include itself. The scores of these games are summed to give a player its score for that round. The next round a player adopts the strategy that fared the best in that player’s neighbourhood. The scoring is simplified so that  $T = b, R = 1, S = 0$  and  $P = 0$ . Nowak and May [15] found that even in this simplistic situation cooperation can persist. The qualitative behaviour of the system depends on the value of  $b$ . For certain values the spatial distribution of cooperators and defectors undergo chaotic behaviour, never reaching a steady state (see Figure 1a).



## 2.2 Levins Model

The Nowak and May Model has some limitations. The model does not take local extinction into account and neglects how the PD game affects population dynamics. As a result we introduce the spatial PD game into a well defined structured (metapopulation) model.

The Levins model captures the idea of a metapopulation's persistence as a stochastic balance between local extinctions and recolonisation of empty habitat patches. A good description of the model is given in [9] which I summarise here. The metapopulation is considered as a population of local population inhabiting an infinitely large patch network. The metapopulation size,  $P(t)$ , is measured as the fraction of habitat patches occupied at time  $t$ . Each local population in the metapopulation has identical dynamics. Extinctions occur independently at each patch at a rate  $e$ . The existing populations contribute equally to the pool of migrants at a rate  $c$ . The migrants spread out across the entire patch network and colonise empty patches in proportion to how many empty patches there are. The rate of change in  $P$  is given by

$$\frac{dP}{dt} = cP(1 - P) - eP$$

The system has a non trivial equilibrium at  $P = 1 - e/c$ . The model assumes that colonisation is not affected by distance and that there are infinitely many patches. This seems contradictory as movement of most organisms are restricted in space. What the model in fact assumes is that all patches are equally connected to other patches, also known as the mean-field assumption. The mean-field approximation of interactions assumes that the players are well mixed. Hui and McGeoch [10] presented a spatial PD model based on Levins' [11] patch occupancy model. Each site in the patch occupancy model is considered to be player in the PD. Players can be considered or populations. A simplified PD game with  $T = b, R = 1, U = -1$  and  $S = -b(b > 1)$  is used.  $P_C$  is the fraction of patches occupied by cooperators and  $P_D$  the fraction occupied by defectors and the total fraction occupied is then given by  $P = P_C + P_D$ . The colonisation rate and the extinction rates are considered to be correlated to the pay-off received in the PD to reflect the gain or loss in an entity's fitness due to the outcome of the PD. Each player is equally likely to play with any other player, therefore the mean pay-off for a cooperator is  $w_C = P_C - bP_D$  and  $w_D = bP_C - P_D$  for a defector. The colonisation rate is positively correlated to the pay-off and the extinction rate negatively:

$$c_\Omega = \alpha \frac{b + w_\Omega}{2b} \text{ and } e = \beta \frac{b - w_\Omega}{2b}$$

The parameters  $\alpha$  and  $\beta$  represents the maximum colonisation and extinction rates and  $\Omega$  takes on the value  $C$  or  $D$ .

The differential equations

$$\frac{dP_C}{dt} = c_C P_C (1 - P) - e P_C \quad (2.1)$$

$$\frac{dP_D}{dt} = c_D P_D (1 - P) - e P_D \quad (2.2)$$

describe the system. Substituting all the variables back and solving for the steady states, one can calculate the non-trivial steady state

$$P_C = 0$$
$$P_D = \frac{1}{2} \left( \frac{\beta}{\alpha} + b + 1 - \sqrt{\left(\frac{\beta}{\alpha}\right)^2 + 4b \left(\frac{\beta}{\alpha} - 1\right)} \right)$$

The mean field approximation fails to show the persistence of cooperation, contrary to the findings using a cellular automaton model. Clearly the distribution of cooperators and defectors must be important.

### 3 A Spatially Explicit Model

In order to demonstrate the importance of spatial dynamics we construct spatially explicit model. We use the model to investigate the assortment achieved by placing players on a spatial grid. Movement is incorporated and its effect on assortment studied.

#### 3.1 Model Description

The model constructed is a stochastic cellular automaton model. The PD is played on a square lattice occupied by cooperators and defectors. A site's neighbourhood is taken as the classic Von Neumann neighbourhood, the four adjacent sites. Each site on the lattice can be in one of three states: 1) it is occupied by a cooperator - C, 2) it is occupied by a defector - D or 3) the cell is empty - E. During one iteration (or generation) of the simulation each site on the lattice is visited and updated according to a set of transition rules, Figure 2. During an iteration the sites are visited in a random order, known as asynchronous updating. Updating the lattice asynchronously captures the effect of continuous time. Periodic boundary conditions are used in order to minimise the effect of boundary conditions on the dynamics of the system. Large lattices with periodic boundaries approximate an infinite lattice.

The transition rules for a site occupied by a player is set out by the following steps:

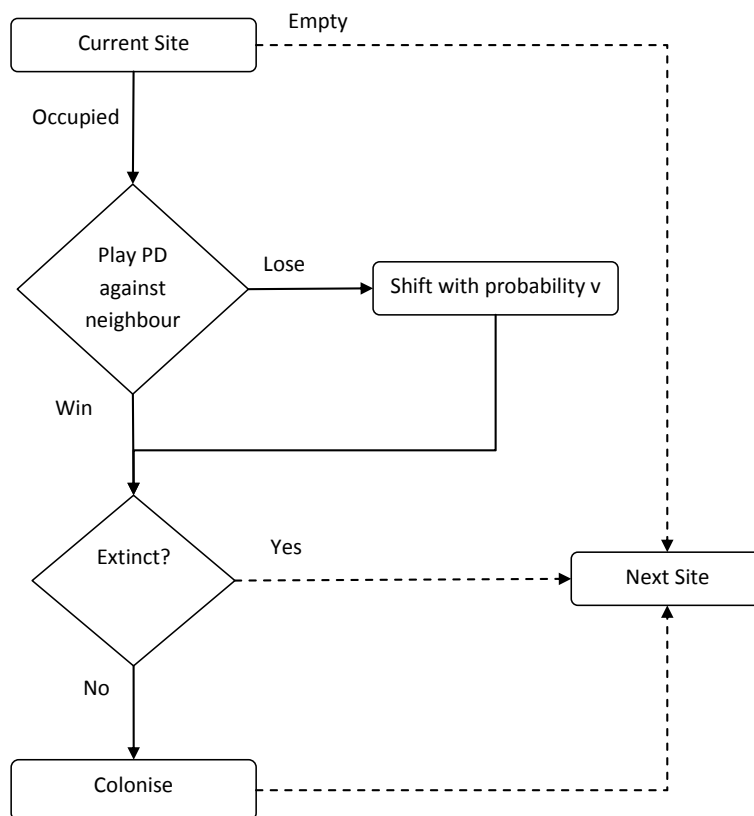
1. The PD is played against a random neighbour, the opponent. A player's fitness is determined by the pay-off.
2. The player goes extinct with probability  $e$ . If a player goes extinct step 3 and 4 are skipped and the simulation continues to the next site.
3. If the opponent is a defector the player moves with probability  $v$  to a random empty site in its neighbourhood.
4. Each neighbouring cell is colonised with probability  $u/4$

In the next section these rules are described in more detail and the method for calculating the colonisation and extinction rates  $u$  and  $e$  are given.

##### 3.1.1 Transition Rules

If the site is occupied by a player, the player the PD against one of its neighbours chosen randomly from its neighbourhood. The score attained in the PD is used to determine the occupant's fitness. The pay-off scheme used is  $T = b, R = b - c, P = 0, S = -c$  or represented in matrix form:

	C	D
C	b-c	-c
D	b	0



**Figure 2:** A flow diagram of the simulation at a single site. A 'lose' in the PD refers to a player playing against a defector. A 'win' represents a player playing against an empty site or a cooperator. During an iteration of the simulation each site on the lattice is visited in a random order.

The colonisation and extinction rates,  $c$  and  $u$ , are taken to be proportional to the pay-off in the PD game with maximum colonisation and extinction rates  $\alpha$  and  $\beta$ . For variables we let subscript  $i$  take on value C or D. The pay-off,  $V_i$ , a player receives has the bounds  $-c < V < b$ . To ensure that  $0 < u_i < \alpha$  while being proportional to  $V_i$ , we scale  $V_i$  so that

$$u_i = \alpha \frac{c + V_i}{b + c}$$

The extinction rate is negatively correlated to the pay-off

$$\begin{aligned} e_i &= \beta \left(1 - \frac{c + V_i}{b + c}\right) \\ &= \beta \frac{b - V_i}{b + c} \end{aligned}$$

We let  $N_C$  and  $N_D$  indicate the strategy of the opponent. If the opponent is a cooperator we have  $N_C = 1$  and  $N_D = 0$  and visa versa for a defector. When the opponent is an empty cell  $N_C = N_D = 0$ . The colonisation and extinction rates are given by

$$\begin{aligned} u_C &= \alpha \frac{c + (b - c)N_C - cN_D}{b + c} \\ e_C &= \beta \frac{b - (b - c)N_C + cN_D}{b + c} \\ u_D &= \alpha \frac{c + bN_C}{b + c} \\ e_D &= \beta \frac{b - bN_C}{b + c} \end{aligned}$$

Next it is determined whether or not the player goes extinct, a player goes extinct with probability  $e_i$ . If the player goes extinct the simulation continues to the next site. If the occupant does not go extinct, it colonises its neighbouring sites. Each neighbouring site is colonised with probability  $u_i/4$ . The parameter  $u$  can thus be interpreted as the average number of offspring a site will generate.

To apply movement a win-stay lose-move principle is applied. If a site player plays against a defector it will try and move away. After playing against a defector a player will move with probability  $v$  before colonising its new neighbouring sites. Movement is in a random direction to an empty cell. If a player played against a cooperator it will stay where it was and colonise its neighbours. Whether or not a player move is independent of its own strategy, it only depends on its opponent's strategy.

The model is developed using MATLAB [13], the code for the model and simulations can be found in Appendix B.

### 3.2 Methods of Analysis

Let  $P_C$  and  $P_D$  represent the fraction of sites occupied by cooperators and defectors respectively. The total fraction of sites occupied, or population density,

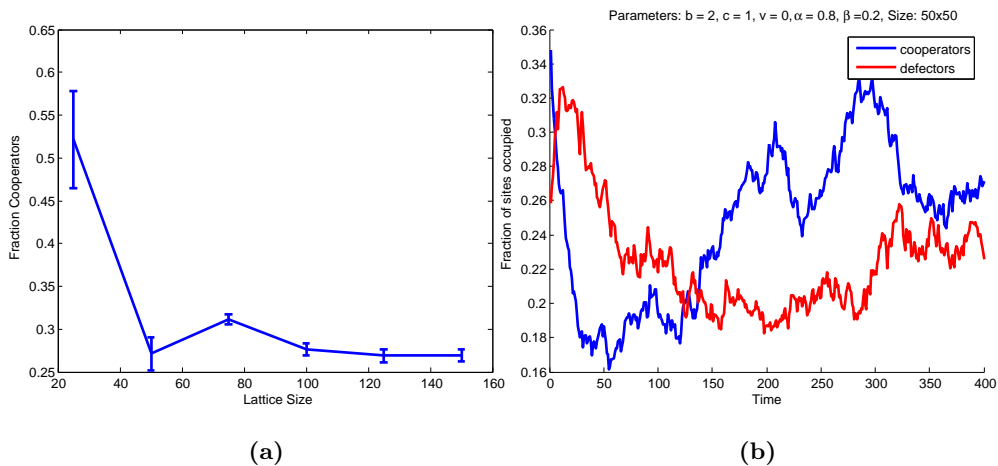
is given by  $P = P_C + P_D$ . Sensitivity analysis is done by varying parameters values and measuring the effect on the steady-state values of  $P_C$  and  $P_D$ . The starting state of the lattice is such that each site on the lattice is in one of the three states with equal probability, cooperators and defectors are thus distributed randomly across the lattice.

To measure the equilibrium values of  $P_C$  and  $P_D$  the model is run for a number of generations and the average is taken over the last 100 generations. Initially it was thought that 300 generations was sufficient for equilibrium to be reached, but upon later investigation it was found that it could take up to 700 generations before equilibrium is reached, Figure 5. The consequence is that most measurements were done from generation 350 to 450 with the exception of later results, Figure 6, which was measured from generation 700 to 800. The running time of the model for 800 generations is between two and three minutes, making analysis over a wide range of parameter values time intensive. The assortment of cooperators,  $Q_{CC}$ , is measured as the probability that a randomly chosen neighbour of a cooperator is also a cooperator and similarly  $Q_{DD}$  is the assortment of defectors. Large population densities cause an increase in the measured assortment. To correct for the contribution to assortment by population size we measure the relative assortment  $R_{ii} = Q_{ii}/P_i$ ,  $i = C, D$  which is a measure of the degree of clustering in the population.

## 4 Results

### 4.1 Habitat Size

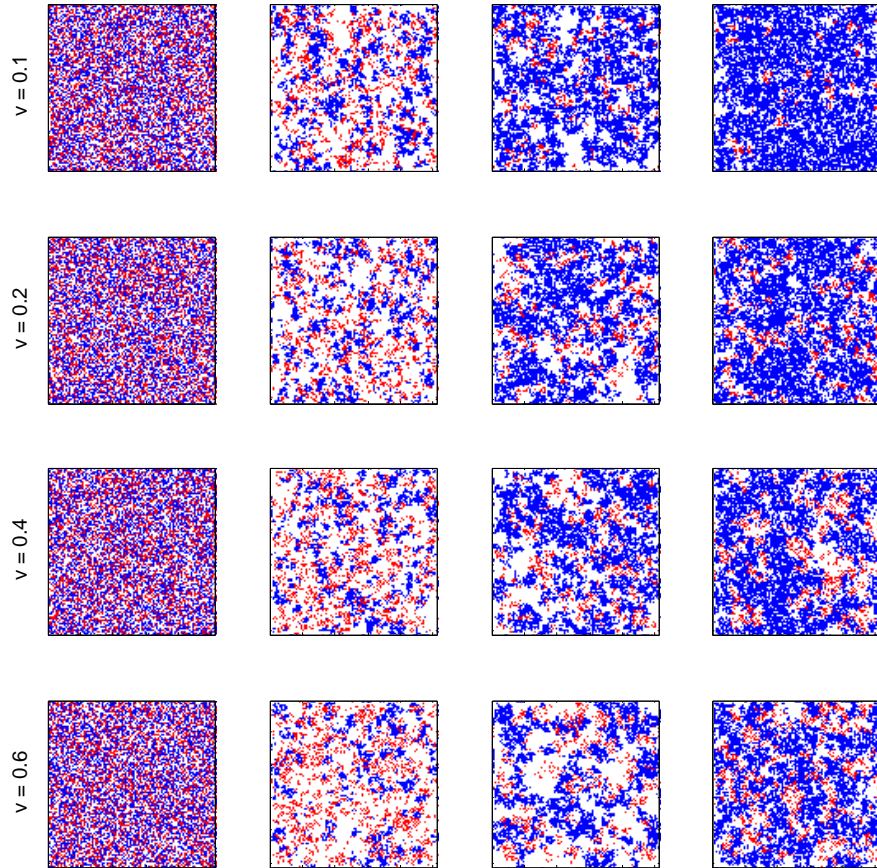
The equilibrium values were examined to determine the effect that lattice size has on the dynamics of the system. The steady state values of the fraction of sites occupied by cooperators is measured for different lattices, Figure 3. The parameter values were set to  $\alpha = 0.8, \beta = 0.2, b = 2$  and  $c = 1$ . For these parameter values square lattices with size less than  $50 \times 50$  are very sensitive to stochastic effects and don't reach equilibrium but have fluctuating numbers of cooperators and defectors. Lattices of size 100 exhibit similar steady state values. From these results it was decided to run all further analyses for lattices of size  $100 \times 100$ . The size of the lattice has a big influence on the running time of simulation, the chosen value is a compromise between efficiency in modelling time and minimising boundary effects.



**Figure 3:** a) The steady state values for the fraction of cooperators occupying lattices of different sizes. b) Lattices smaller than  $50 \times 50$  are susceptible to stochastic effects and don't reach equilibrium, but rather display chaotic characteristics. Lattices of size  $100 \times 100$  and greater reached similar equilibrium points.

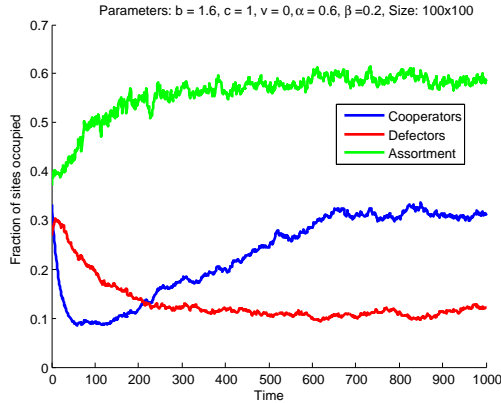
### 4.2 Spatial Dynamics

Cooperators score well when interacting with other cooperators. Cooperators organise themselves into cluster, maximising their pay-off. Defectors do best when they are surrounded by cooperators. Starting with a random grid, cooperators do not fare well and their numbers decrease drastically. Aggregation of cooperators tend to do better, and small clusters of cooperators will survive. These clusters will then grow until the system has reached equilibrium.



**Figure 4:** *The spatial dynamics of the stochastic model. Blue sites indicate cooperators, red sites defectors and white sites are empty patches. The probability of moving after playing against a defector,  $v$ , is varied from 0.1 to 0.6 and snapshots of the lattices are taken after 0, 50, 150 and 300 iterations. Other parameter values are  $c = 0.4, b = 1, \alpha = 0.7$  and  $\beta = 0.2$*





**Figure 5:** *The fraction of cooperators and defectors over time. The green line indicates the assortment,  $Q_{C/C}$ , the probability that a randomly chosen neighbour of a cooperator is also a cooperator. The other parameter values are  $b = 1.8, c = 1, v = 0, \alpha = 0.6$  and  $\beta = 0.2$ .*

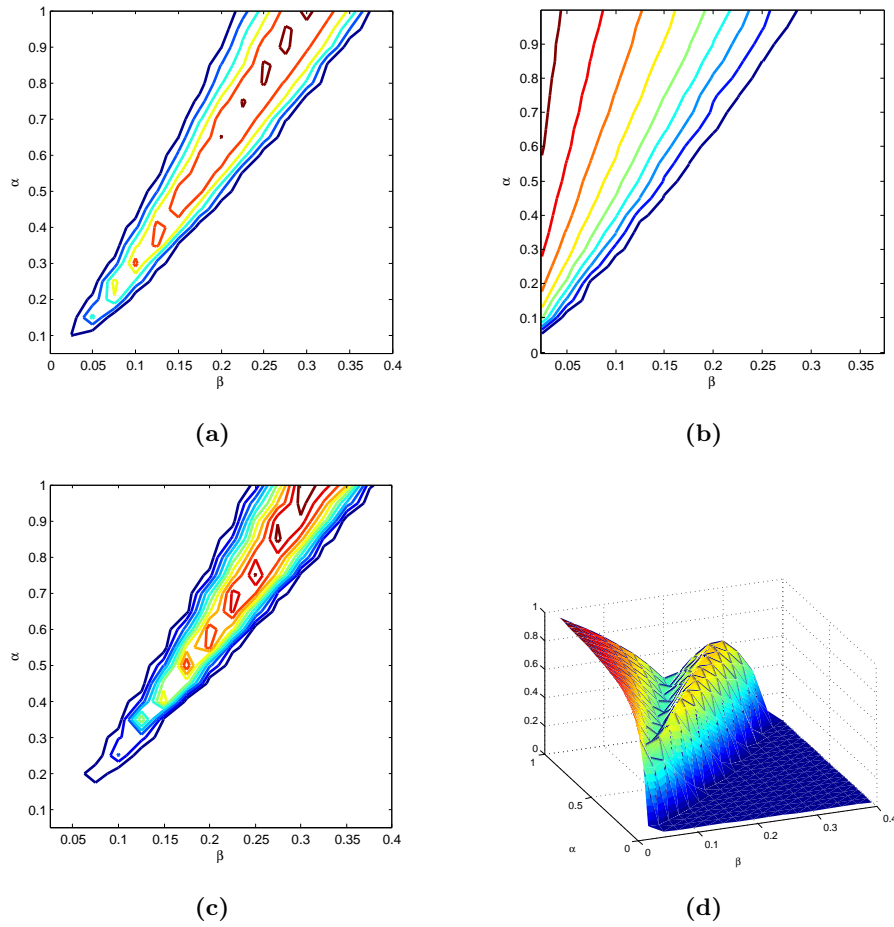
### 4.3 Temporal Dynamics

In an environment with randomly spaced cooperators and defectors, cooperators do not fare well, Figure 5. Initially there is a small rise in the number of defectors as they exploit cooperators. But as the number of cooperators dwindle, defectors fare worse since less of their interactions are with cooperators and more are with empty sites and other defectors. Isolated cooperators will tend to die out, while clustered cooperators will survive, and cluster size will increase. At point a balance is reached between the exploitation of cooperators by defectors and the fitness gain of clustering by cooperators. Depending on the parameters set there are four possible equilibrium states: no survival by either the cooperators or the defectors, defectors die out and cooperators persist, cooperators die out and defectors persist, both cooperators and defectors persist together.

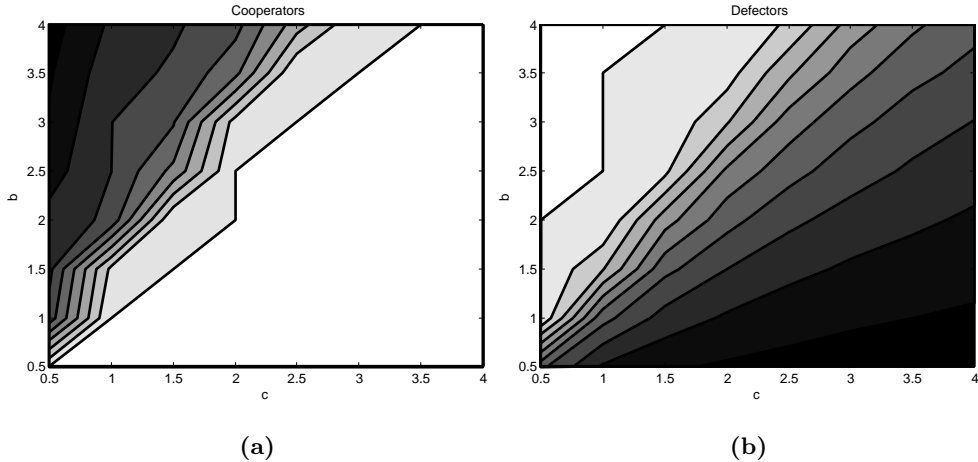
### 4.4 Sensitivity Analysis

Considering the colonisation rate, when  $\alpha = 0$  no colonisation takes place, when  $\alpha = 1$  each player can at best reproduce 1 copy of itself. For the extinction rate when  $\beta = 0$  players don't die out, but when  $\beta = 1$  every round every player will certainly go extinct. Figure 6 shows the result of varying  $\alpha$  in the bound (0 1) and  $\beta$  (0 0.4). Only a narrow region in the parameter space allows for the existence of cooperators. Defectors perform better by being able to survive over a wider region. The size of the total population forms a ridge in the area where cooperators do well. A larger population can be maintained when cooperators are doing well, even for low parameter values. In contrast cooperators require a large colonisation rate and small extinction to maintain the same population size when defectors outnumber cooperators.

The values for the PD game also play a big role on the steady state dy-



**Figure 6:** A contour plot showing how the fraction of a) cooperators and b) defectors at steady state vary for different values of  $\alpha$  and  $\beta$ . Fixed parameter values are  $b = 2, c = 1, v = 0$ . c) Increasing  $v = 0.2$  has no effect on the result for defectors but reduces the parameter space where cooperation is feasible. d) The total population density.



**Figure 7:** The influence of pay-off values in the PD on a)cooperator density  $P_C$  and b) defector density  $P_D$ . The values of cost  $c$  and benefit  $b$  are varied while other parameter are fixed:  $\alpha = 0.6, \beta = 0.2$  and  $v = 0$ .

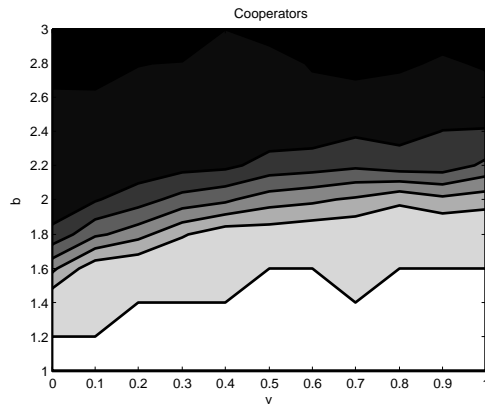
namics as shown in Figure 7 and 8. The cost-benefit ratio determines how much a cooperator loses out when being exploited by a defector. If the cost of cooperating is small when compared to the benefit, defectors gain very little by exploiting cooperators. But if the cost associated with cooperating is large, defectors gain a big advantage exploiting cooperators. In Figure 7 it is clear that as  $b/c$  increases cooperators do better. The contour lines seem to have equations  $b = a c$  with  $a$  some constant. Examining the model with movement we see that increase in  $b/c$  increases  $P_C$  at steady state, while increase movement probability  $v$  reduces the success of cooperators, Figure 8.

#### 4.5 Assortment

In the previous section on assortment it has been shown that enough assortment can lead to cooperators out-competing defectors. Starting from a random lattice one witnesses cooperators forming clusters, Figure 4. Small clusters of cooperators that arose by chance due to the starting grid, can do quite well relative to defecting neighbours and isolated neighbours. The isolated cooperators, easily exploited by defectors, will die out. The small clusters persist and grow leading to an increase in assortment over time, Figure 5.

Introducing movement influences the assortment of cooperators and defectors. With an increase in dispersal ability,  $v$ , results in a decrease in assortment, Figure 9b. Increasing  $v$  results in a lower number of cooperators and an increase in defectors. Defectors thus gain the most from increases dispersal ability, this becomes clear when one plots the relative assortment  $R_{ii}$ , Figure 9c.

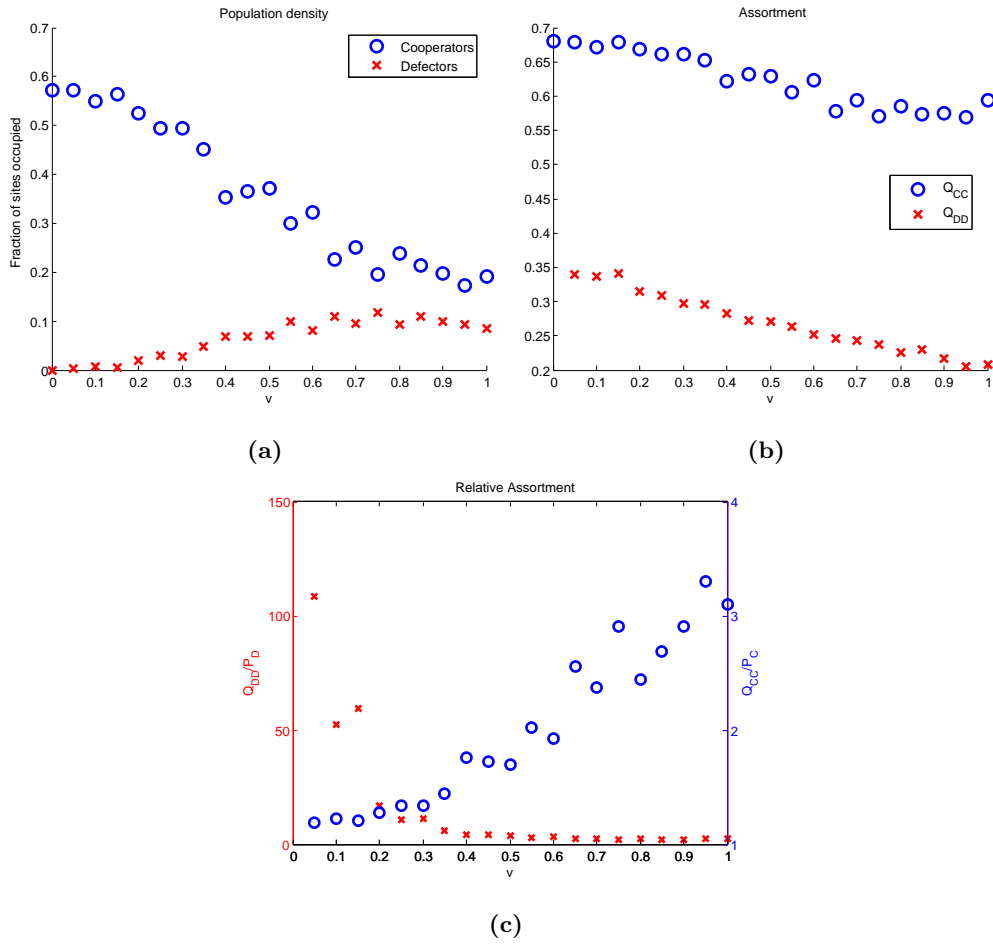
A defector wants to move away from other defectors as quickly as possible since they could gain more by finding and playing against cooperators. Cooperators gain the most from forming large clusters. Once a cooperator is



(a)

**Figure 8:** Varying the cost-benefit ratio  $b/c$  and the probability of moving  $v$  and their influence on  $P_C$ . Here  $\alpha = 0.6$  and  $\beta = 0.2$ .

in a cluster, it will lose by moving away. Its best strategy is to stay put. Defectors gain from low dispersal, offspring staying close to their parent and then playing the PD against each other, whereas defectors gain from high dispersal abilities.



**Figure 9:** The effect of  $v$ , the probability of moving, on the survival of cooperators. a) The fraction sites occupied by cooperators and defectors at steady state as a function of  $v$ . b) Assortment of cooperators,  $Q_{CC}$ , decreases as  $v$  increases,  $Q_{CC}$  is the probability that a randomly chosen neighbour of a cooperators is also a cooperators. c) The relative assortment measured as  $Q_{ii}/P_C$ .

## 5 Discussion

Even though at first glance altruism seems to contradict natural selection and evolution, upon deeper investigation one can find mechanisms that promote the evolution of altruism. It is necessary to first describe an altruistic situation formally before analysis can take place. Game theory has emerged as the leading framework for studying cooperation. Here three games were presented that resemble interactions in nature: the Prisoner's Dilemma, Hawk-Dove, and Public Goods game. In the single round versions of these games the best rational strategy is for players to defect, or the case of Hawk-Dove to play a mixed strategy. Players could have attained a higher score if they cooperated.

Trivers [19] constructed a model for altruism based on the IPD and used his model to show that direct reciprocity favours the evolution of cooperation. Having repeated rounds of the PD makes it possible for cooperation to evolve as long as the probability of having another round is large enough. In the IPD Tit for Tat is a very successful strategy. It can resist invasion by a mutant strategy and fares well in a population with a mixture of strategies [2]. Tit for Tat also encourages other players to cooperate, because it is quick to punish defecting moves and rewards cooperative ones. A strategy cannot do any better than Tit for Tat and is better off cooperating from the start.

In the PD, Hawk-Dove and Public Goods games, when interactions among strategies are random, cooperative strategies fare poorly [5] [17] [6]. Eshell [5] considered a population consisting of players that could adopt one of two strategies. The frequency of each strategy increased or decreased in the population according to its success. It was shown that under an altruistic pay-off strategies can't exist in the population in the absence of assortment. But if a large enough proportion of a player's interaction is with players with the same strategy, altruism can evolve. The same principle can be applied to the public goods game, Fletcher and Doebeli [6] does a similar analysis for the public goods game and again find that with enough assortment cooperation is a viable strategy.

What mechanisms promote assortment? Spatial structure makes it possible for strategies to assort. Playing the PD on a square lattice showed how assortment arises through the self organisation of cooperators. Clusters of cooperators have a higher pay-off and are able to out compete defectors. In nature animals and organisms tend to move around unless it is prevented by some barrier. In nature populations tend to occupy their maximum possible range, individuals migrate between populations, whole populations migrate with season, all examples of movement and dispersal. It therefore makes sense to include movement in modelling the population dynamics. Here we included a simple win-stay, lose-shift type movement, where after losing movement takes place with some probability. This type of movement decreases the assortment of cooperators and defectors and negatively affects the success of cooperators. Defectors gain more from increased dispersal. This leads to the question: What would be the optimal movement strategy for a player to adopt? The

results suggest that it is best for cooperators to have low dispersal, ensuring cooperators stay densely clustered. While defectors gain fitness when adopting a high dispersal rate, spreading out and reducing interaction with other defectors while increasing the likelihood of meeting a cooperator.

There are other factors that could lead to assortment. Populations are often structured, with individuals interacting more with some individuals than others. The ability of players to discriminate between different strategies and actively searching out other players with similar strategies would also increase assortment.

## 5.1 Limitations and Future Directions

There remains a number of unexplored dynamics and extension one could consider for the model we constructed:

- We only investigated two strategies, pure defectors and pure cooperators. One could consider more complex strategies. An example is the generalised reciprocator as modelled by Rankin et. al. [17].
- The additive pay-off matrix where cooperators contribute some benefit  $b$  with a cost  $c$  was chosen for the PD. One could consider other pay-off matrices and explore how it affects the dynamics.
- The influence of different lattice structures and neighbourhoods.

Many theories and examples have been proposed in the literature to explain altruism, there is a need to unify these theories and tease apart the differences and similarities as done by Fletcher and Doebelli [6]. They present assortment as a more generalised theory for the evolution of cooperation.

Our model showed that a specific dispersal strategy does not benefit all players equally, therefore a increase in dispersal rate we saw a decrease in the survival of cooperators. What would be the optimal strategy for a player to adopt? In the study of evolution of dispersal strategies [3] one could consider the effect that cooperative games have on the success of different strategies.

Defectors have an element of predators to them, seeking out and exploiting cooperators, the prey. Could one gain some understanding by incorporating models for cooperation with predator-prey models?

## 5.2 Conclusions

In this report we showed that even though altruism seems to contradict the principles of evolution by natural selection, there are mechanisms which makes the evolution of altruism possible, direct reciprocity as an example. Assortment has recently come forward as strong contender as a generalised theory explaining the evolution of cooperation. We showed that by placing players in PD on a lattice enough assortment can be gained for cooperation to persist and even out compete defectors. A simple win-stay, lose-shift strategy gave

defectors and advantage, indicating that higher dispersal rate benefit defectors while low dispersal rates favour cooperators.



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# Appendices

## A Acronyms

**ALLD** The strategy in the Iterated Prisoner's Dilemma which defect every round.

**ALLC** The strategy in the Iterated Prisoner's Dilemma which cooperates every round.

**ALT** The strategy in the Iterated Prisoner's Dilemma which alternates defection and cooperation.

**C** The strategy where the player cooperates in the game being considered. Usually paying some cost.

**CA** Cellular automaton

**D** The strategy where the player defects in the game being considered. The defector usually pays no cost, but gains the benefit when another player cooperates.

**IPD** Iterated Prisoner's Dilemma.

**PD** Prisoner's Dilemma.

**TFT** A strategy in the Iterated Prisoner's Dilemma. The strategy cooperates on the first round and on subsequent rounds plays the same strategy its opponent played in the previous round.

## B Code

All source code was developed in MATLAB [13] specifically for this project. The programme is divided among three files: *PDCAmove.m*, *assortment.m* and *run.m*. The essence of the CA model is contained in the function *PDCAmove*. This function calls the function '*assortment*' to calculate assortment of cooperators and defectors on the lattice. The script file *run.m* generates the results and figures for the CA model used in this report.

### Core programme

```
function [fracCoop, fracDefect, assort] = PDCAmove(b,c,v,time,N,...
                                                alpha,beta,frame)

startTime = clock;

%CA value definitions
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% 0 - empty %
% 1 - Cooperator %
% -1 - Defector %
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

%Initialise some paramters
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
assort = 0;
dim1 = N + 2;
dim2 = N + 2;
total = N^2;
if ~exist('alpha','var'), alpha = 0.7; end
if ~exist('beta','var'), beta = 0.2; end
drawLattice = false;

%Payoff Structure
T = b;
R = b-c;
P = 0;
S = -c;

%Initial Conditions
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%Random
M = rand(dim1,dim2);
GAME = zeros(dim1,dim2);
GAME = GAME - 1 * (M < 0.333);
GAME = GAME + 1 * (M > 0.666);

%GAME = -1* ones(dim1,dim2);
%GAME(20:26,20:26) = 1;
%GAME(70:76,70:76) = 1;
%Boundary conditions
```

```

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
GAME(:,1) = GAME(:,dim2-1);
GAME(:,dim2) = GAME(:,2);
GAME(1,:) = GAME(dim1-1,:);
GAME(dim1,:) = GAME(2,:);
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

if drawLattice
    %Show starting state:
    currentFrame = frame*4 - 3;
    subplot(4,1,currentFrame);
    cMap = [1 0 0;1 1 1;0 0 1;];
    colormap(cMap);
    image(GAME + 2* ones(dim1,dim2));
    axis image;
    set(gca,'XTickLabel',{ })
    set(gca,'YTickLabel',{ })
    ylabel(['v = ', num2str(v)])
    %movieM = getframe;
    %im = rgb2ind(movieM.cdata,256,'nodither');
    %title('time = 0')
end

for t = 1:time
    %Capture movie
    %movieM(t) = getframe;
    %im(:, :, 1, t) = rgb2ind(movieM(t).cdata, cMap, 'nodither');

    randSort = randperm(total);

    for pos = randSort
        i = mod(pos-1,N) + 2;
        j = ceil(pos/N)+ 1;
        if GAME(i,j)  $\neq$  0

            neighbours = [GAME(i-1,j),GAME(i+1,j),GAME(i,j-1),...
                GAME(i,j+1)];
            index = [i-1,i+1,i,i;j,j,j-1,j+1];

            %Choose random neighbour
            opp = randperm(4);
            k = index(1,opp(1));
            l = index(2,opp(1));
            numCoop = (GAME(k,l) == 1);
            numDef = (GAME(k,l) == -1);
            %Determine each site's fitness
            if GAME(i,j) == 1
                pay = (S*numDef + R*numCoop);
            else
                pay = (P*numDef + T*numCoop);
            end
            e = beta * (b - pay) / (b + c) ;
            u = alpha * (pay + c) / (b + c);

            if rand < e
                GAME(i,j) = 0;

```



```

GAME(1,:) = GAME(dim1-1,:);
GAME(dim1,:) = GAME(2,:);
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

%Calculate output values
fracCoop(t) = sum(sum(GAME(2:(N+1),2:(N+1)) == 1))/total;
fracDefect(t) = sum(sum(GAME(2:(N+1),2:(N+1)) == -1))/total;
[assort(1,t),assort(2,t)] = assortment(GAME);

if drawLattice
    if t == 100 || t == 500 || t == 999
        currentFrame = currentFrame + 1;
        subplot(4,1,currentFrame)
        cMap = [1 0 0;1 1 1;0 0 1];
        colormap(cMap);
        image(GAME + 2* ones(dim1,dim2));
        axis image;
        set(gca,'XTickLabel',{})
        set(gca,'YTickLabel',{})
        %title(['time = ',num2str(t)])
    end
end
end

endTime = clock;
duration = endTime - startTime
%imwrite(im,cMap,'test.gif','DelayTime',0,'LoopCount',inf)
end

```

## Measuring assortment

```

function [vC vD] = assortment(GAME)
temp = size(GAME);
N = temp(1);
Cplayers = 0;
Dplayers = 0;
coopNeigh = 0;
defNeigh = 0;

for i = 2:(N-1)
    for j = 2:(N-1)
        if GAME(i,j) == 1
            Cplayers = Cplayers + 1;
            neighbours = [GAME(i-1,j),GAME(i+1,j),GAME(i,j-1),
                ...GAME(i,j+1)];
            coopNeigh = coopNeigh + sum(neighbours == 1);
        end
        if GAME(i,j) == -1
            Dplayers = Dplayers + 1;
            neighbours = [GAME(i-1,j),GAME(i+1,j),GAME(i,j-1),
                ...GAME(i,j+1)];
            defNeigh = defNeigh + sum(neighbours == -1);
        end
    end
end

```

```

        end
    end
    if Cplayers == 0
        vC = 0;
    else
        vC = coopNeigh / (Cplayers * 4);
    end
    if Dplayers == 0
        vD = 0;
    else
        vD = defNeigh / (Dplayers * 4);
    end
end
end

```

## Model Analysis

```

%Author: Martijn van der Merwe
%The Evolution of Cooperation
%Model Analysis

clc
clear all
c = 1;
b = 2;
v = 0;
time = 450;
PDCAmove(b,c,v,time,N);

%Testing lattice size
size = [25 50 75 100 125 150]
for i = 1:6
    i
    N = size(i);
    [fracCoop fracDefect] = PDCAmove(b,c,v,time,N);
    result(i,:) = fracCoop(350:450);
    resultMean(i) = mean(fracCoop(350:450));
    resultStd(i) = std(fracCoop(350:450));
end

figure
errorbar(size,resultMean,resultStd)
xlabel('Lattice Size')
ylabel('Fraction Cooperators')

%Spatial dynamics
N = 100;
v = [0.1 0.2 0.4 0.6];
i = 1;
for i = 1:4
    [fracCoop fracDefect] = PDCAmove(b,c,v(i),time,N,i);
end

%Sensitivity

```



```

%alpha beta
c = 1;
b = 2;
v = 0;
time = 800;
N = 100;
alphaA = 0.05:0.05:1;
betaA = 0.025:0.025:0.4;

for i = 1:length(alphaA)
    for j = 1:length(betaA)
        [fracCoop fracDefect] = PDCAmove(b,c,v,time,N,...
            alphaA(i),betaA(j));
        resultC(i,j) = mean(fracCoop(700:800));
        resultD(i,j) = mean(fracDefect(700:800));
    end
end

[X,Y] = meshgrid(betaA,alphaA);
contour(X,Y,resultC,'LineWidth',2)
xlabel('\beta')
ylabel('\alpha')
axis equal
axis square
figure
contour(X,Y,resultD,'LineWidth',2)
xlabel('\beta')
ylabel('\alpha')
axis equal
axis square
save('sensAlphaBetaV0')

%Sensitivity
%b c %
N = 100;
alpha = 0.6;
beta = 0.2;
bA = 0.5:0.5:4
cA = 0.5:0.5:4
v = 0;
time = 450;

for i = 1:length(bA)
    for j = 1:length(cA)
        bA(i)
        cA(j)
        [fracCoop fracDefect] = PDCAmove(bA(i),cA(j),v,time,...
            N,alpha,beta);
        resultC(i,j) = mean(fracCoop(350:450))
        resultD(i,j) = mean(fracDefect(350:450));
    end
end

[X,Y] = meshgrid(cA,bA);
contourf(X,Y,ones(size(resultD))-resultC,'LineWidth',2)
colormap('hot')

```

```

xlabel('c')
ylabel('b')
title('Cooperators')
figure
contourf(X,Y,ones(size(resultD))-resultD,'LineWidth',2)
colormap('hot')
xlabel('c')
ylabel('b')
title('Defectors')

%Sennsitivity b/c versus v
N = 100;
alpha = 0.6;
beta = 0.2;
c = 1;
bA = 1:0.2:3;
vA = 0:0.1:1;
time = 450;

for i = 1:length(bA)
    for j = 1:length(vA)
        bA(i)
        vA(j)
        [fracCoop fracDefect] = PDCAmove(bA(i),c,vA(j),time,N,...
            alpha,beta);
        resultC(i,j) = mean(fracCoop(350:450))
        resultD(i,j) = mean(fracDefect(350:450));
    end
end

[X,Y] = meshgrid(vA,bA);
contourf(X,Y,ones(size(resultD))-resultC,'LineWidth',2)
colormap('hot')
xlabel('v')
ylabel('b')
title('Cooperators')
figure
contourf(X,Y,ones(size(resultD))-resultD,'LineWidth',2)
colormap('bone')
xlabel('v')
ylabel('b/c')
title('Defectors')

%Temporal Dynamics
N = 100;
alpha = 0.6;
beta = 0.2;
c = 1;
b = 1.6;
v = 0;
time = 1000;
[fracCoop fracDefect, assort] = PDCAmove(b,c,v,time,N,alpha,beta,1);

figure

```

```

hold on
plot(1:time,fracCoop,'b','LineWidth',2)
plot(1:time,fracDefect,'r','LineWidth',2)
legend('cooperators','defectors ')
title(['Parameters: b = ', num2str(b), ', c = ', num2str(c) , ', v = ', ...
      num2str(v), ', \alpha = ', num2str(alpha), ', \beta = ', num2str(beta), ...
      ', Size: ', num2str(N), 'x', num2str(N)])
xlabel('Time')
ylabel('Fraction of sites occupied')
figure
plot(1:time,assort,'g','LineWidth',2);
xlabel('Time');
ylabel('Assortment');
save('temporalDynamics')

% %Assortment as a function of v
N = 100;
alpha = 0.6;
beta = 0.2;
c = 1;
b = 2;
time = 1000;
vA = 0:0.05:1;
for i = 1:length(vA)
    vA(i)
    [fracCoop fracDefect, assort] = PDCAmove(b,c,vA(i),time,N,...
        alpha,beta);
    resultC(i) = mean(fracCoop(800:1000));
    resultD(i) = mean(fracDefect(800:1000));
    resultAssortC(1,i) = mean(assort(1,800:1000));
    resultAssortC(2,i) = std(assort(1,800:1000));
    resultAssortD(1,i) = mean(assort(2,800:1000));
    resultAssortD(2,i) = std(assort(2,800:1000));
end

m = (resultAssortC(1,:) - resultC) ./ (1 - resultC);

figure
[AX H1 H2] = plotyy(vA,resultAssortC(1,:),vA,m);
set(H1,'LineStyle','none','Marker','o','LineWidth',2,'MarkerSize',8,...
    'Color','g');
set(H2,'LineStyle','none','Marker','x','LineWidth',2,'MarkerSize',8,...
    'Color','k');
set(AX(1),'YColor','g');
set(AX(2),'YColor','k');
set(get(AX(1),'Ylabel'),'String','Q_{CC}')
set(get(AX(2),'Ylabel'),'String','m')
xlabel('v')
figure
hold on
plot(vA,resultC,'ob','LineWidth',2,'MarkerSize',10)
plot(vA,resultD,'xr','LineWidth',2,'MarkerSize',10)
xlabel('v');
legend('Cooperators','Defectors')
ylabel('Fraction of sites occupied')

```

```
save('sens2V')
```