

# A Short Introduction to Game Theory

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## 1 Introduction

This paper gives a brief overview of game theory. Therefore in the first section I want to outline what game theory generally is and where it is applied.

In the next section, I introduce some of the most important terms used in game theory, such as normal form games and Nash equilibrium as well as some of the most popular games, e.g. the *Prisoner's Dilemma* or the *Ultimatum Game*.

I then present the basic concepts of *evolutionary game theory* (EGT), a more specialized branch of game theory. We will see how EGT uses new concepts such as *evolutionary stable strategies* (ESS) and replicator dynamics, and its importance to sciences like biology and physics.

At last I present two examples, programmed in the language NetLogo, which will demonstrate the applications of EGT and the similarities to condensed matter physics.

### 1.1 Game Theory – What is it?

The concepts of game theory provide a common language to formulate, structure, analyse and eventually understand different strategical scenarios. Generally, game theory investigates conflict situations, the interaction between the agents and their decisions.

A game in the sense of game theory is given by a (mostly finite) number of players, who interact according to given rules. Those players might be individuals, groups, companies, associations and so on. Their interactions will have an impact on each of the players and on the whole group of players, i.e. they are interdependent.

To be more precise: A game is described by a set of players and their possibilities to play the game according to the rules, i.e. their set of strategies.

This description leads to a widespread definition of game theory:

The subject of game theory are situations, where the result for a player does not only depend on his own decisions, but also on the behaviour of the other players.

Game theory has its historical origin in 1928. By analysing parlour games, John von Neumann realised very quickly the practicability of his approaches for the analysis of economic problems.

In his book *Theory of Games and Economic Behavior*, which he wrote together with Oskar Morgenstern in 1944, he already applied his mathematical theory to economic applications.

The publication of this book is generally seen as the initial point of modern game theory.

### 1.2 Game Theory – Where is it applied?

As we have seen in the previous section, game theory is a branch of mathematics. Mathematics provide a common language to describe these games. We have also seen that game theory was already applied to economics by von Neumann. When there is competition for a resource to be analysed, game theory can be used either to explain existing behaviour or to improve strategies.

The first is especially applied by sciences which analyse long-term situations, like biology or sociology. In animality, for example, one can find situations, where cooperation has developed for the sake of mutual benefits.

The latter is a crucial tool in sciences like economics. Companies use game theory to improve their strategical situation in the market.

Despite the deep insights he gained from game theory's applications to economics, von Neumann was mostly interested in applying his methods to politics and warfare, perhaps descending from his favorite childhood game, *Kriegspiel*, a chess-like military simulation. He used his methods to model the Cold War interaction between the U.S. and the USSR, picturing them as two players in a zero-sum game.

He sketched out a mathematical model of the conflict from which he deduced that the Allies would win, applying some of the methods of game theory to his predictions.

There are many more applications in the sciences, which have already been mentioned, and in many more sciences like sociology, philosophy, psychology and cultural anthropology. It is not possible to list them all in this paper, more information can be obtained in the references at the end of this paper.

## 2 Definitions

I now introduce some of the basic definitions of game theory. I use a non-mathematical description as far as possible, since mathematics is not really required to understand the basic concepts of game theory.

However, a mathematical derivation is given in appendix A.1 and A.2.

### 2.1 Normal Form Games

A game in *normal form* consists of:

1. A finite number of players.
2. A strategy set assigned to each player. (e.g. in the Prisoner's Dilemma each player has the possibility to cooperate (C) and to defect (D). Thus his strategy set consists of the elements C and D.)

3. A payoff function, which assigns a certain payoff to each player depending on his strategy and the strategy of the other players (e.g. in the Prisoner's Dilemma the time each of the players has to spend in prison).

The payoff function assigns each player a certain payoff depending on his strategy and the strategy of the other players. If the number of players is limited to two and if their sets of strategies consist of only a few elements, the outcome of the payoff function can be represented in a matrix, the so-called *payoff matrix*, which shows the two players, their strategies and their payoffs.

#### Example:

Player1\Player2	L	R
U	1, 3	2, 4
D	1, 0	3, 3

In this example, player 1 (vertical) has two different strategies: Up (U) and Down (D). Player 2 (horizontal) also has two different strategies, namely Left (L) and Right (R).

The elements of the matrix are the outcomes for the two players for playing certain strategies, i.e. supposing, player 1 chooses strategy U and player 2 chooses strategy R, the outcome is (2, 4), i.e. the payoff for player 1 is 2 and for player 2 is 4.

### 2.2 Extensive Form Games

Contrary to the normal form game, the rules of an *extensive form game* are described such that the agents of the game execute their moves consecutively.

This game is represented by a game tree, where each node represents every possible stage of the game as it is played. There is a unique node called the initial

node that represents the start of the game. Any node that has only one edge connected to it is a terminal node and represents the end of the game (and also a strategy profile). Every non-terminal node belongs to a player in the sense that it represents a stage in the game in which it is that player's move. Every edge represents a possible action that can be taken by a player. Every terminal node has a payoff for every player associated with it. These are the payoffs for every player if the combination of actions required to reach that terminal node are actually played.

**Example:**

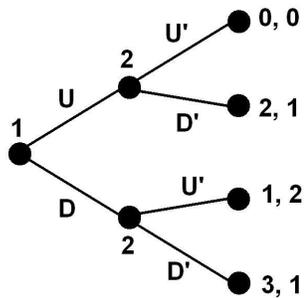


Figure 1: A game in extensive form

In figure 1 the payoff for player 1 will be 2 and for player 2 will be 1, provided that player 1 plays strategy U and player 2 plays strategy D'.

**2.3 Nash Equilibrium**

In game theory, the Nash equilibrium (named after John Nash, who first described it) is a kind of solution concepts of a game involving two or more players, where no player has anything to gain by changing only his own strategy.

If each player has chosen a strategy and no player can benefit by changing his strategy while the other players keep theirs unchanged, then the current set of

strategy choices and the corresponding payoffs constitute a Nash equilibrium.

John Nash showed in 1950, that every game with a finite number of players and finite number of strategies has at least one mixed strategy Nash equilibrium.

**2.3.1 Best Response**

The best response is the strategy (or strategies) which produces the most favorable immediate outcome for the current player, taking other players' strategies as given.

With this definition, we can now determine the Nash equilibrium in a normal form game very easily by using the payoff matrix.

The formal proof that this procedure leads to the desired result is given in appendix A.2.

**2.3.2 Localizing a Nash Equilibrium in a Payoff-matrix**

Let us use the payoff matrix of the Prisoner's Dilemma, which will be introduced in 3.1, to determine the Nash equilibrium:

Player1\Player2	C	D
C	3, 3	0, 5
D	5, 0	1, 1

The procedure is the following: First we consider the options for player 1 by a given strategy of player 2, i.e. we look for the best answer to a given strategy of player 2.

If player 2 plays C, the payoff for player 1 for choosing C will be 3, for choosing D it will be 5, so we highlight his best answer, D:

	C	D
C	3, 3	0, 5
D	<b>5, 0</b>	1, 1

Now we repeat this procedure for the case,

that player 2 plays D (the best answer in this case is D, since C gains payoff 0 whereas D gains payoff 1), then we do the same for player 2 by a given strategy of player 1 and we will get:

	C	D
C	3, 3	0, <b>5</b>
D	<b>5</b> , 0	<b>1</b> , <b>1</b>

The Nash equilibrium is then determined by the matrix element, in which both players marked their best answers.

Thus, the strategies that constitute a Nash equilibrium is defection by both players, because if any player changed his strategy to C whereas the other one stays with D, he would get a less payoff.

## 2.4 Mixed Strategies

Consider the following payoff matrix, which corresponds to the game *Matching Pennies*:

Player1\Player2	Head	Tail
Head	<b>1</b> , -1	-1, <b>1</b>
Tail	-1, <b>1</b>	<b>1</b> , -1

The best responses are already marked, and it is obvious, that there is no matrix cell, in which both players marked their best response.

What do game theorists make of a game without a Nash equilibrium? The answer is that there are more ways to play the game than are represented in the matrix. Instead of simply choosing *Head* or *Tail*, a player can just flip the coin to decide what to do. This is an example of a mixed strategy, which simply means a particular way of choosing randomly among the different strategies.

The mixed strategy equilibrium of the matching pennies game is well known: each player should randomize 50-50 between the two alternatives.

Mixed strategy equilibrium points out an aspect of Nash equilibrium that is often confusing for beginners. Nash equilibrium does not require a positive reason for playing the equilibrium strategy. In matching pennies, the two players are indifferent: they have no positive reason to randomize 50-50 rather than doing something else. However, it is only an equilibrium if they both happen to randomize 50-50. The central thing to keep in mind is that Nash equilibrium does not attempt to explain why players play the way they do. It merely proposes a way of playing so that no player would have an incentive to play differently.

If, for example, player 1 chooses to play *Head* with a probability of 80 % and play *Tail* with a probability of 20 %, then player 2 will eventually anticipate the opponent's strategy. Hence he will play *Tail* everytime. This will lead to a positive payoff of  $0.8 \cdot 1 + 0.2 \cdot (-1) = 0.6$  per game for player 2, respectively a payoff of  $-0.6$  for player 1. The best payoff one can do in such a fair zero-sum game is 0, and this will be achieved by playing  $\frac{1}{2}$  Head +  $\frac{1}{2}$  Tail.

Mathematically spoken, a mixed strategy is just a linear combination of the pure strategies.

## 3 Games

Now I want to present some of the most studied games of game theory.

### 3.1 Prisoner's Dilemma (PD)

We have already used the payoff matrix of the Prisoner's Dilemma in 2.3.2 to localize the Nash equilibrium of this game, and now I want to tell the story behind this famous dilemma:

Two suspects are arrested by the police. The police have insufficient evidence for

a conviction, and, having separated both prisoners, an officer visits each of them to offer the same deal: if one testifies for the prosecution against the other and the other remains silent, the betrayer goes free and the silent accomplice receives the full 10-year sentence. If both stay silent, the police can sentence both prisoners to only six months in jail for a minor charge. If each betrays the other, each will receive a two-year sentence. Each prisoner must make the choice of whether to betray the other or to remain silent. However, neither prisoner knows for sure what choice the other prisoner will make. So the question this dilemma poses is: How will the prisoners act?

We will use the following abbreviations: To testify means to betray the other suspect and thus to defect (D), to remain silent means to cooperate (C) with the other suspect. And for the sake of clarity, we want to use positive numbers in the payoff matrix.

	C	D
C	R=3, R=3	S=0, T=5
D	T=5, S=0	P=1, P=1

- **R** is a Reward for mutual cooperation. Therefore, if both players cooperate then both receive a reward of 3 points.
- If one player defects and the other cooperates then one player receives the **T**emptation to defect payoff (5 in this case) and the other player (the cooperator) receives the **S**ucker payoff (zero in this case).
- If both players defect then they both receive the **P**unishment for mutual defection payoff (1 in this case).

As we have already seen, the logical move for both players is defection (D). The dilemma lies herein, that the best result for player 1 and player 2 as a group ( $R = 3$  for both) can't be achieved.

In defining a PD, certain conditions have to hold. The values we used above, to demonstrate the game, are not the only values that could have been used, but they do adhere to the conditions listed below.

Firstly, the order of the payoffs is important. The best a player can do is T (temptation to defect). The worst a player can do is to get the sucker payoff, S. If the two players cooperate then the reward for that mutual cooperation, R, should be better than the punishment for mutual defection, P. Therefore, the following must hold:

$$T > R > P > S.$$

In repeated interactions, another condition it is additionally required:

Players should not be allowed to get out of the dilemma by taking it in turns to exploit each other. Or, to be a little more pedantic, the players should not play the game so that they end up with half the time being exploited and the other half of the time exploiting their opponent. In other words, an even chance of being exploited or doing the exploiting is not as good an outcome as both players mutually cooperating. Therefore, the reward for mutual cooperation should be greater than the average of the payoff for the temptation and the sucker. That is, the following must hold:

$$R > (S + T)/2$$

### 3.1.1 Other Interesting Two-person Games

Depending on the order of R, T, S, and P, we can have different games. Most are

trivial, but two games stand out:

- Chicken ( $T > R > S > P$ )

	C	D
C	R=2, R=2	S=1, T=3
D	T=3, S=1	P=0, P=0

Example: Two drivers with something to prove drive at each other on a narrow road. The first to swerve loses faces among his peers (the *chicken*). If neither swerves, however, the obvious worst case will occur.

- Stag Hunt ( $R > T > P > S$ )

	C	D
C	R=3, R=3	S=0, T=2
D	T=2, S=0	P=1, P=1

Example: Two hunters can either jointly hunt a stag or individually hunt a rabbit. Hunting stags is quite challenging and requires mutual cooperation. Both need to stay in position and not be tempted by a running rabbit. Hunting stags is most beneficial for society but requires a lot of trust among its members. The dilemma exists because you are afraid of the others' defection. Thus, it is also called trust dilemma.

### 3.2 The Ultimatum Game

Imagine you and a friend of yours are walking down the street, when suddenly a stranger stops you and wants to play a game with you:

He offers you 100\$ and you have to agree on how to split this money. You, as the proposer, make an offer to your friend, the responder. If he accepts your offer, the deal goes ahead. If your friend rejects, neither player gets anything. The stranger will take back his money and the game is over.

Obviously, rational responders should accept even the smallest positive offer, since the alternative is getting nothing. Proposers, therefore, should be able to claim almost the entire sum. In a large number of human studies, however, conducted with different incentives in different countries, the majority of proposers offer 40 to 50% of the total sum, and about half of all responders reject offers below 30%

### 3.3 Public Good Game

A group of 4 people are given \$200 each to participate in a group investment project. They are told that they could keep any money they do not invest. The rules of the game are that every \$1 invested will yield \$2, but that these proceeds would be distributed to all group members. If every one invested, each would get \$400. However, if only one person invested, that "sucker" would take home a mere \$100. Thus, the assumed Nash equilibrium could be the combination of strategies, where no one invests any money. And we can show that this is indeed the Nash equilibrium.

We will not display this game in a payoff matrix, since each player has a too big set of strategies (the strategy  $s_n$  is given by the amount of money that player  $n$  wants to contribute, e.g.  $s_1 = 10$  means, that player 1 invests 10\$). Nevertheless this is a game in normal form and therefore it has a payoff function for each player. The payoff function for, let's say, player 1 is given by

$$\begin{aligned}
 P &= \frac{2 \cdot (s_1 + s_2 + s_3 + s_4)}{4} - s_1 \\
 &= \frac{2 \cdot (s_2 + s_3 + s_4)}{4} - 0,5 \cdot s_1
 \end{aligned}$$

But this means, that every investment  $s_1$  of player 1 will diminish his payoff. Therefore, a rational player will choose

the strategy  $s_n = 0$ , i.e. he will invest no money at all. But if everyone plays this strategy, no one can benefit by changing his strategy while the other players keep their strategy unchanged. And this is just the definition of the Nash equilibrium.

The dilemma lies exactly herein, since the greatest benefit for the whole group arises, if everyone contributed all of his money.

### 3.4 Rock, Paper, Scissors

The players simultaneously change their fists into any of three "objects":

- Rock: a clenched fist.
- Paper : all fingers extended, palm facing downwards, upwards, or sideways.
- Scissors: forefinger and middle finger extended and separated into a "V" shape.

The objective is to defeat the opponent by selecting a weapon which defeats their choice under the following rules:

1. Rock crushes Scissors (rock wins)
2. Scissors cut Paper (scissors win)
3. Paper covers Rock and roughness is covered (paper wins)

If players choose the same weapon, the game is a tie and is played again.

This is a classic non-transitive system which involves a community of three competing species satisfying a relationship.

Such relationships have been demonstrated in several natural systems.

## 4 Evolutionary Game Theory

Since game theory was established as a discipline for its own, it has been very successful.

However, there have been situations, which could not be properly described by the language of game theory.

Many people have attempted to use traditional game theory to analyze economic or political problems, which typically involve a large population of agents interacting. However, traditional game theory is a "static" theory, which reduces its usefulness in analyzing these very sorts of situations. EGT improves upon traditional game theory by providing a dynamics describing how the population will change over time. Therefore a new mathematical extension has been developed (mainly by John Maynard Smith in his book *Evolution and the Theory of Games*, 1982), which is called *evolutionary game theory* (EGT)

I will show in the next section, in what kinds of situations EGT might be applicable and what are the most significant differences to game theory.

### 4.1 Why EGT?

Evolutionary game theory (EGT) studies equilibria of games played by a population of players, where the *fitness* of the players derives from the success each player has in playing the game. It provides tools for describing situations where a number of agents interact and where agents might change the strategy they follow at the end of any particular interaction.

So, the questions of EGT are: Which populations are stable? When do the individuals adopt other strategies? Is it possible for mutants to invade a given population?

Another very prominent application is the quest for the origins and evolution of cooperation. The effects of population structures on the performance of behavioral strategies became apparent only in recent years and marks the advent of an intriguing link between apparently unrelated disciplines. EGT in structured populations reveals critical phase transitions that fall into the universality class of directed percolation on square lattices.

Together with EGT as an extension of game theory, new concepts were developed to investigate and to describe these very problems. I will now introduce two of them, which are crucial to describe EGT, evolutionary stable strategies and the replicator dynamics. The first one is applied to study the stability of populations, the latter one investigates the adoption of strategies.

## 4.2 Evolutionary Stable Strategies

An evolutionary stable strategy (ESS) is a strategy which if adopted by a population cannot be invaded by any competing alternative strategy. The concept is an equilibrium refinement to the Nash equilibrium.

The definition of an ESS was introduced by John Maynard Smith and George R. Price in 1973 based on W.D. Hamilton's (1967) concept of an unbeatable strategy in sex ratios. The idea can be traced back to Ronald Fisher (1930) and Charles Darwin (1859).

### 4.2.1 ESS and Nash Equilibrium

A Nash equilibrium is a strategy in a game such that if all players adopt it, no player will benefit by switching to play any alternative strategy.

If a player, choosing strategy  $\mu$  in a population where all other players play

strategy  $\sigma$ , receives a payoff of  $E(\mu, \sigma)$ , then strategy  $\sigma$  is a Nash equilibrium if  $E(\sigma, \sigma) \geq E(\mu, \sigma)$ , i.e.  $\sigma$  does just as good or better playing against  $\sigma$  than any mutant with strategy  $\mu$  does playing against  $\sigma$ .

This equilibrium definition allows for the possibility that strategy  $\mu$  is a neutral alternative to  $\sigma$  (it scores equally, but not better). A Nash equilibrium is presumed to be stable even if  $\mu$  scores equally, on the assumption that players do not play  $\mu$ .

Maynard Smith and Price specify (Maynard Smith & Price, 1973; Maynard Smith 1982) two conditions for a strategy  $\sigma$  to be an ESS. Either

1.  $E(\sigma, \sigma) > E(\mu, \sigma)$ , or
2.  $E(\sigma, \sigma) = E(\mu, \sigma)$  and  $E(\sigma, \mu) > E(\mu, \mu)$

must be true for all  $\sigma \neq \mu$ .

In other words, what this means is that a strategy  $\sigma$  is an ESS if one of two conditions holds:

1.  $\sigma$  does better playing against  $\sigma$  than any mutant does playing against  $\sigma$ , or
2. some mutant does just as well playing against  $\sigma$  as  $\sigma$ , but  $\sigma$  does better playing against the mutant than the mutant does.

A derivation of ESS is given in appendix A.3.

### 4.2.2 The Hawk-Dove Game

As an example for ESS, we consider the Hawk-Dove Game. In this game, two individuals compete for a resource of a fixed value  $V$  (The value  $V$  of the resource corresponds to an increase in the Darwinian fitness of the individual who obtains the resource). Each individual follows exactly one of two strategies described below:

- **Hawk:** Initiate aggressive behaviour, not stopping until injured or until one's opponent backs down.
- **Dove:** Retreat immediately if one's opponent initiates aggressive behaviour.

If we assume that

1. whenever two individuals both initiate aggressive behaviour, conflict eventually results and the two individuals are equally likely to be injured,
2. the cost of the conflict reduces individual fitness by some constant value  $C$ ,
3. when a hawk meets a dove, the dove immediately retreats and the hawk obtains the resource, and
4. when two doves meet the resource is shared equally between them,

the fitness payoffs for the Hawk-Dove game can be summarized according to the following matrix:

	Hawk	Dove
Hawk	$\frac{1}{2}(V - C), \frac{1}{2}(V - C)$	$V, 0$
Dove	$0, V$	$V/2, V/2$

One can readily confirm that, for the Hawk-Dove game, the strategy Dove is not evolutionarily stable because a pure population of Doves can be invaded by a Hawk mutant. If the value  $V$  of the resource is greater than the cost  $C$  of injury (so that it is worth risking injury in order to obtain the resource), then the strategy Hawk is evolutionarily stable. In the case where the value of the resource is less than the cost of injury, there is no ESS if individuals are restricted to following pure strategies, although there is an ESS if players may use mixed strategies.

### 4.2.3 ESS of the Hawk-Dove Game

Clearly, *Dove* is no stable strategy, since  $\frac{V}{2} = E(D, D) < E(H, D) = V$ , a population of doves can be invaded by hawks. Because of  $E(H, H) = \frac{1}{2}(V - C)$  and  $E(D, H) = 0$ ,  $H$  is an ESS if  $V > C$ . But what if  $V < C$ ? Neither  $H$  nor  $D$  is an ESS.

But we could ask: What would happen to a population of individuals which are able to play mixed strategies? Maybe there exists a mixed strategy which is evolutionary stable.

Consider a population consisting of a species, which is able to play a mixed strategy  $I$ , i.e. sometimes *Hawk* and sometimes *Dove* with probabilities  $p$  and  $1 - p$  respectively.

For a mixed ESS  $I$  to exist the following must hold:

$$E(D, I) = E(H, I) = E(I, I)$$

Suppose that there exists an ESS in which  $H$  and  $D$ , which are played with positive probability, have different payoffs. Then it is worthwhile for the player to increase the weight given to the strategy with the higher payoff since this will increase expected utility.

But this means that the original mixed strategy was not a best response and hence not part of an ESS, which is a contradiction. Therefore, it must be that in an ESS all strategies with positive probability yield the same payoff.

Thus:

$$\begin{aligned}
 E(H, I) &= E(D, I) \\
 \Leftrightarrow p E(H, H) + (1 - p)E(H, D) &= p E(D, H) + (1 - p)E(D, D) \\
 \Leftrightarrow \frac{p}{2}(V - C) + (1 - p)V &= (1 - p)\frac{V}{2} \\
 \Leftrightarrow p &= \frac{V}{C}
 \end{aligned}$$

Thus a mixed strategy with a probability  $V/C$  of playing *Hawk* and a probability  $1 - V/C$  of playing *Dove* is evolutionarily stable, i.e. that it can not be invaded by players playing one of the pure strategies *Hawk* or *Dove*.

### 4.3 The Replicator Dynamics

As mentioned before, the main difference of EGT to game theory is the investigation of dynamic processes. In EGT, we are interested in the dynamics of a population, i.e. how the population evolves over time.

Let us consider now a population consisting of  $n$  types, and let  $x_i(t)$  be the frequency of type  $i$ . Then the state of the population is given by the vector  $\mathbf{x}(t) = x_1(t), \dots, x_n(t)$ .

We want now to postulate a law of motion for  $\mathbf{x}(t)$ . If individuals meet randomly and then engage in a symmetric game with payoff matrix  $A$ , then  $(A\mathbf{x})_i$  is the expected payoff for an individual of type  $i$  and  $\mathbf{x}^T A \mathbf{x}$  is the average payoff in the population state  $\mathbf{x}$ .

The evolution of  $\mathbf{x}$  over time is described by the replicator equation:

$$\dot{x}_i = x_i[(A\mathbf{x})_i - \mathbf{x}^T A \mathbf{x}] \quad (1)$$

The replicator equation describes a selection process: more successful strategies spread in the population.

A derivation of the replicator equation is given in appendix A.4

### 4.4 ESS and Replicator Dynamics

We have seen, that  $D$  is no ESS at all and for  $V > C$ ,  $H$  is an ESS. We have also seen, that for  $V < C$  the ESS is a mixed ESS with a probability of  $V/C$  for playing  $H$  and with a probability of  $1 - V/C$  for playing  $D$ .

By setting  $\dot{x}_i = 0$ , we obtain the *evolutionary stable states* of a population.

A population is said to be in an *evolutionarily stable state* if its genetic composition is restored by selection after a disturbance, provided the disturbance is not too large.

If this equation is applied to the Hawk-Dove game, the result will be the following:

For  $V > C$ , the only evolutionary stable state is a population consisting of hawks. For  $V < C$ , a mixed population with a fraction  $V/C$  of hawks and a fraction  $1 - V/C$  of doves is evolutionary stable.

This result will be derived in appendix A.5.

At this point, one may see little difference between the two concepts of evolutionary game theory. We have confirmed that, for the Hawk-Dove game and for  $V > C$ , the strategy *Hawk* is the only ESS. Since this state is also the only stable equilibrium under the replicator dynamics, the two notions fit together quite neatly: the only stable equilibrium under the replicator dynamics occurs when everyone in the population follows the only ESS. In general, though, the relationship between ESSs and stable states of the replicator dynamics is more complex than this example suggests.

If only two pure strategies exist, then given a (possibly mixed) evolutionarily stable strategy, the corresponding state of the population is a stable state under the replicator dynamics. (If the evolutionarily stable strategy is a mixed strategy  $S$ , the corresponding state of the population is the state in which the proportion of the population following the first strategy equals the probability assigned to the first strategy by  $S$ , and the remainder follow the second strategy.)

However, this can fail to be true if more than two pure strategies exist.

The connection between ESSs and stable states under an evolutionary dynamical model is weakened further if we do not model the dynamics by the replicator dynamics.

In 5.1 we use a local interaction model in which each individual plays the Prisoner's Dilemma with his or her neighbors. Nowak and May, using a spatial model in which local interactions occur between individuals occupying neighboring nodes on a square lattice, showed that stable population states for the Prisoner's Dilemma depend upon the specific form of the payoff matrix.

## 5 Applications

### 5.1 Evolution of cooperation

As mentioned before, the evolution of cooperation is a fundamental problem in biology because unselfish, altruistic actions apparently contradict Darwinian selection.

Nevertheless, cooperation is abundant in nature ranging from microbial interactions to human behavior. In particular, cooperation has given rise to major transitions in the history of life. Game theory together with its extensions to an evolutionary context has become an invaluable tool to address the evolution of cooperation. The most prominent mechanisms of cooperation are direct and indirect reciprocity and spatial structure.

The mechanisms of reciprocity can be investigated very well with the Ultimatum game and also with the Public Good game.

But the prime example to investigate spatially structured populations is the Prisoner's Dilemma.

Investigations of spatially extended systems have a long tradition in condensed matter physics. Among the most important features of spatially extended systems are the emergence of phase transi-

tions. Their analysis can be traced back to the Ising model. The application of methods developed in statistical mechanics to interactions in spatially structured populations has turned out to be very fruitful. Interesting parallels between non equilibrium phase transitions and spatial evolutionary game theory have added another dimension to the concept of universality classes.

We have already seen, that the Nash equilibrium of PD is to defect. But to overcome this dilemma, we consider spatially structured populations where individuals interact and compete only within a limited neighborhood. Such limited local interactions enable cooperators to form clusters and thus individuals along the boundary can outweigh their losses against defectors by gains from interactions within the cluster. Results for different population structures in the PD are discussed and related to condensed matter physics.

This problem has been investigated by Martin Nowak (*Nature*, **359**, pp. 826-829, 1992)

I programmed this scenario based on the investigations of Nowak. The program is written in NetLogo, the program code is given in appendix B.

### 5.2 Biodiversity

One of the central aims of ecology is to identify mechanisms that maintain biodiversity. Numerous theoretical models have shown that competing species can coexist if ecological processes such as dispersal, movement, and interaction occur over small spatial scales. In particular, this may be the case for nontransitive communities, that is, those without strict competitive hierarchies. The classic non-transitive system involves a community of three competing species satisfying a relationship similar to the children's game rock-paper-scissors,

where rock crushes scissors, scissors cuts paper, and paper covers rock. Such relationships have been demonstrated in several natural systems. Some models predict that local interaction and dispersal are sufficient to ensure coexistence of all three species in such a community, whereas diversity is lost when ecological processes occur over larger scales. Kerr et al., tested these predictions empirically using a non-transitive model community containing three populations of *Escherichia coli*. They found that diversity is rapidly lost in our experimental community when dispersal and interaction occur over relatively large spatial scales, whereas all populations coexist when ecological processes are localized.

There exist three strains of *Escherichia coli* bacteria:

- Type A releases toxic colicin and produces, for its own protection, an immunity protein.
- Type B produces the immunity protein only.
- Type C produces neither toxin nor immunity.

The production of the toxic colicin and the immunity protein causes some higher costs. Thus the strain which produces the toxin colicin is superior to the strain which has no immunity protein (A beats C).

The one with no immunity protein is superior to the strain with immunity protein, since it has lower costs to reproduce (C beats B)

The same holds for the strain with immunity protein but no production of the colicin compared to the strain which produces colicin (B beats A).

In figure 2, one can see, that on a static plate, which is an environment in which dispersal and interaction are primarily local, the three strain coexist.

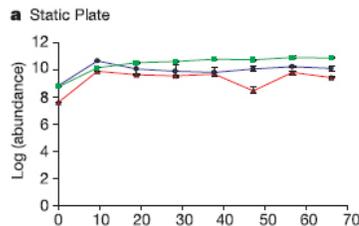


Figure 2: *Escherichia coli* on a static plate

<b>green:</b>	<b>resistant strain</b>
<b>red:</b>	<b>colicin producing strain</b>
<b>blue:</b>	<b>sensitive strain</b>

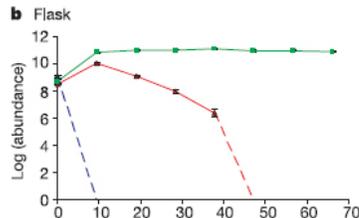


Figure 3: *Escherichia coli* in a flask

In figure 3, where the strains are held in a flask, a well-mixed environment in which dispersal and interaction are not exclusively local, only the strain, which produces the immunity protein only will survive.

## A Mathematical Derivation

### A.1 Normal form games

A game in normal form consists of:

1. A (finite) number of players  $M = \{a_1, \dots, a_n\}$
2. A strategy set  $S_i$  assigned to each player  $i \in M$ .  
The combination of all sets of strategies  $S = \prod_{i \in M} S_i$  is called strategy space.
3. A utility/payoff function  $u_i : S \mapsto \mathbb{R}$ , assigned to each player  $i \in M$ .  
 $\Rightarrow \forall s \in S : u_i(s) \in \mathbb{R}$

### A.2 Nash equilibrium and best answer

**Notations:**

1.  $s \in S = \prod_{i \in M} S_i$ ;  
 $s = (s_1, \dots, s_M)$ ;  $s_i \in S_i$
2.  $s_{-i} := (s_1, \dots, s_{i-1}, s_{i+1}, \dots, s_M)$ ;  
 $(s_i, s_{-i}) := s$ ;  $(s_{-i}, s_i) := s$
3.  $S_{-i} = \prod_{j \in M, j \neq i} S_j$ ;  
 $S_i \times S_{-i} = S$ ;  $(s_i, s_{-i}) \in S_i \times S_{-i}$

**Definition:**

A combination of strategies  $s^* \in S$  is called a Nash equilibrium iff:

$$\forall i \in M \forall s_i \in S_i : \\ u_i(s^*) = u_i(s_i^*, s_{-i}^*) \geq u_i(s_i, s_{-i}^*)$$

**Definition:**

A strategy  $\hat{s}_i \in S_i$  is called best answer to a combination of strategies  $s_{-i} \in S_{-i}$  iff:

$$\forall s_i \in S_i : u_i(\hat{s}_i, s_{-i}) \geq u_i(s_i, s_{-i}) \\ \Leftrightarrow u_i(\hat{s}_i, s_{-i}) = \max\{u_i(s_i, s_{-i}) ; s_i \in S_i\}$$

It is now easy to see, that, if every player chooses his best answer, this will

constitute a Nash equilibrium, since another strategy will not lead to an increase of the payoff, since the best answer already leads to the maximum payoff.

### A.3 Evolutionary stable strategies (ESS)

In order for a strategy to be evolutionarily stable, it must have the property that if almost every member of the population follows it, no mutant (that is, an individual who adopts a novel strategy) can successfully invade. This idea can be given a precise characterization as follows: Let  $E(s_1, s_2)$  denote the payoff (measured in Darwinian fitness) for an individual following strategy  $s_1$  against an opponent following strategy  $s_2$ , and let  $W(s)$  denote the total fitness of an individual following strategy  $s$ ; furthermore, suppose that each individual in the population has an initial fitness of  $W_0$ .

We consider now a population consisting mainly of individuals following strategy  $\sigma$  which shall be an ESS with a small frequency  $p$  of some mutants playing  $\mu$ . Then if each individual engages in one contest

$$W(\sigma) = W_0 + (1 - p)E(\sigma, \sigma) + pE(\sigma, \mu), \\ W(\mu) = W_0 + (1 - p)E(\mu, \sigma) + pE(\mu, \mu).$$

Since  $\sigma$  is evolutionarily stable, the fitness of an individual following  $\sigma$  must be greater than the fitness of an individual following  $\mu$  (otherwise the mutant following  $\mu$  would be able to invade), and so  $W(\sigma) > W(\mu)$ . Now, as  $p$  is very close to 0, this requires either that

$$E(\sigma, \sigma) > E(\mu, \sigma)$$

or that

$$E(\sigma, \sigma) = E(\mu, \sigma) \quad \text{and} \\ E(\sigma, \mu) > E(\mu, \mu).$$

### A.4 Replicator equation

The fitness of a population is given by  $(A\mathbf{x})_i$  and the total fitness of the entire population is given by  $\mathbf{x}^T A\mathbf{x}$ . Thus, the relative fitness of a population is given by

$$\frac{(A\mathbf{x})_i}{\mathbf{x}^T A\mathbf{x}}$$

Let us assume that the proportion of the population following the strategies in the next generation is related to the proportion of the population following the strategies current generation according to the rule:

$$x_i(t + \Delta t) = x_i(t) \frac{(A\mathbf{x})_i}{\mathbf{x}^T A\mathbf{x}} \Delta t$$

for  $\mathbf{x}^T A\mathbf{x} \neq 0$ . Thus

$$x_i(t + \Delta t) - x_i(t) = x_i(t) \frac{(A\mathbf{x})_i - \mathbf{x}^T A\mathbf{x}}{\mathbf{x}^T A\mathbf{x}} \Delta t$$

This yields the differential equation for  $\Delta t \rightarrow 0$ :

$$\dot{x}_i = \frac{x_i[(A\mathbf{x})_i - \mathbf{x}^T A\mathbf{x}]}{\mathbf{x}^T A\mathbf{x}} \quad (2)$$

for  $i = 1, \dots, n$  with  $\dot{x}_i$  denoting the derivative of  $x_i$  after time.

The simplified equation

$$\dot{x}_i = x_i[(A\mathbf{x})_i - \mathbf{x}^T A\mathbf{x}] \quad (3)$$

has the same trajectories than (2), since every solution  $\mathbf{x}(t)$  of (2) delivers according to the time transformation

$$t(s) = \int_{s_0}^s \mathbf{x}(t)^T A\mathbf{x}(t) dt$$

a solution  $\mathbf{y}(s) := \mathbf{x}(t(s))$  of (3).

Equation (3) is called the *replicator equation*.

### A.5 Evolutionary stable state of the Hawk-Dove game

We want to show, that the replicator dynamics and ESS yield to the same result

for the Hawk-Dove game.

The replicator equation is given by

$$\dot{x}_i = x_i[(A\mathbf{x})_i - \mathbf{x}^T A\mathbf{x}]$$

Let us denote the population of hawks  $x_1$  with  $p$ , thus the population of doves  $x_2$  will be denoted with  $1 - p$ . The first term  $A\mathbf{x}$  gives

$$\begin{pmatrix} \frac{p}{2}(V - C) + V(1 - p) \\ \frac{V}{2}(1 - p) \end{pmatrix}$$

Since *Hawk* is denoted with  $x_1$ , we will use the first component of the vector  $A\mathbf{x}$ .

The second term  $\mathbf{x}^T A\mathbf{x}$  delivers

$$\frac{p^2}{2}(V - C) + pV(1 - p) + \frac{V}{2}(1 - p)^2$$

Thus:

$$\begin{aligned} \dot{p} &= p \left[ \frac{p}{2}(V - C) + V(1 - p) - \frac{p^2}{2}(V - C) - pV(1 - p) - \frac{V}{2}(1 - p)^2 \right] \\ &= p \left[ \frac{C}{2} p^2 - \frac{1}{2}(V + C)p + \frac{V}{2} \right] \\ &= p \left[ p^2 - \frac{V+C}{C} p + \frac{V}{C} \right] \end{aligned}$$

In order to be a population evolutionary stable we set the changes of the population per time to zero, so that there is no change in time. This gives:

$$\begin{aligned} \dot{p} &= 0 \\ \Rightarrow p \left[ p^2 - \frac{V+C}{C} p + \frac{V}{C} \right] &= 0 \end{aligned}$$

This is certainly true for  $p = 0$ . This is the trivial solution. Two other solutions can be obtained by evaluating the term in the brackets:

$$p^2 - \frac{V+C}{C} p + \frac{V}{C} = 0$$

This gives

$$\begin{aligned} p_{1/2} &= \frac{V+C}{2C} \pm \sqrt{\frac{V^2+2VC+C^2}{4C^2} - \frac{V}{C}} \\ &= \frac{V+C}{2C} \pm \sqrt{\frac{V^2-2VC+C^2}{4C^2}} \\ &= \frac{V+C}{2C} \pm \frac{V-C}{2C} \end{aligned}$$

Thus:

$$p_1 = 1, \quad p_2 = \frac{V}{C}$$

$p_1 = 1$  is another trivial solution, thus the only relevant result is  $p_2 = \frac{V}{C}$ .

## B Pogram Code

### B.1 Spatial PD

```

globals [movie_on?]
patches-own [num_D z z_prev score d score_h neighbor_h]

to setup
  ca
  ;1/3 will be defectors (z=1, red); 2/3 cooperators (z=0; blue)
  ask patches [ifelse ((random 3) < 1) [set pcolor red set z 1][set pcolor blue set z 0]]
  ;d=delta*(2.0*(random(1.0)-1.0))
  ask patches [set d delta * (2.0 * (random-float 1.0) - 1.0)]
  set movie_on? false
end

to single-D
  ca
  ask patches [set pcolor blue set z 0]
  ask patches [set d delta * (2.0 * (random-float 1.0) - 1.0)]
  ask patch 0 0 [set pcolor red set z 1]
  set movie_on? false
end

to go
  play-game
  update
  if (movie_on?) [movie-grab-view]
end

to play-game
  ask patches [set z_prev z]
  ask patches
  [
    ; num_D = number of neighbors that are defectors
    set num_D nsum z
    ifelse z = 1
    [
      ; if patch is defector: score is T times number of cooperators (8-num_D)
      set score (T * (8 - num_D)) + (P * (num_D + 1))
    ]
    [
      ; if patch is cooperator: score is 1=R times number of cooperators (+1=itself)
      set score (R * (9 - num_D)) + (S * num_D)
    ]
  ]
end

to update
  ; find the neighbor with the highest payoff
  ask patches
  [
    ; neighbor_h = the neighbor with the highest score
    set neighbor_h max-one-of neighbors [score]
    ; score_h = highest score
    set score_h score-of neighbor_h

    ifelse (score_h >= score + d)
    [
      ; if highest score > own score (+d)
      ifelse z_prev = 1
      [
        ; if this patch is defector:
        ; if neighbor with highest score is cooperator: set patch to cooperator (z=0, green)
        ; else: stay defector
        ifelse (z_prev-of neighbor_h) = 0 [set pcolor green set z 0][set pcolor red]
      ]
    ]
  ]

```

```
    ]
  [
    ; if this patch is cooperator:
    ; if neighbor with highest score is defector: set patch to defector (z=1, yellow)
    ; else: stay cooperator
    ifelse (z_prev-of neighbor_h) = 1 [set pcolor yellow set z 1][set pcolor blue]
  ]
  set d delta * (2.0 * (random-float 1.0) - 1.0)
]
[
  ; if own score is the highest:
  ; if cooperator: set color blue, otherwise red
  ifelse z = 0 [set pcolor blue][set pcolor red]
]
]
end

to perturb

  if mouse-down?
  [
    ask patch-at mouse-xcor mouse-ycor [set z 1 - z ifelse z = 0 [set pcolor blue][set pcolor red]]
    ;need to wait for a while; otherwise the procedure is run a few times after a mouse click
    wait 0.5
  ]
end

to movie_start
  movie-start "out.mov"
  set movie_on? true
end

to movie_stop
  movie-close
  set movie_on? false
end
```

## B.2 Hawk-Dove game

```

breed [hawks hawk]
breed [doves dove]
globals [deltaD deltaH p total counter decrement reproduce_limit]
turtles-own [energy]

to setup
  ca
  set-default-shape hawks "hawk"
  set-default-shape doves "butterfly"

  createH n_hawks
  createD n_doves

  ask turtles [set energy random-float 10.0]

  set reproduce_limit 11.0
  set decrement 0.05
end

to go
  ask turtles
  [
    move
    fight
    reproduce
  ]

  while [count turtles > 600]
    [ask one-of turtles[die]]

  do-plot
end

to createH [num_hawks]
  create-custom-hawks num_hawks
  [
    set color red
    set size 1.0
    setxy random-xcor random-ycor
  ]
end

to createD [num_doves]
  create-custom-doves num_doves
  [
    set color white
    set size 1.0
    setxy random-xcor random-ycor
  ]
end

to fight
  ifelse (is-hawk? self)
  [
    if ((count other-hawks-here = 1) and (count other-doves-here = 0))
      [set energy (energy + 0.5 * (V - C))]
    if ((count other-hawks-here = 0) and (count other-doves-here = 1))
      [set energy (energy + V)]
  ]
  [
    if ((count other-hawks-here = 0) and (count other-doves-here = 1))

```

```
    [set energy (energy + V / 2)]
  ]
  ;set pcolor-of patch-here black

end

to move      ;; turtle procedure
  rt random-float 50 - random-float 50
  fd 1
  set energy (energy - decrement)
end

to reproduce
  if energy > reproduce_limit
  [
    set energy (energy / 2)
    hatch 1 [rt random 360 fd 1]
  ]
  if energy < 0
  [die]

end

to do-plot
  set-current-plot "ratio"
  set-current-plot-pen "ratio"
  if any? turtles
  [plot count hawks / count turtles]
  ;
end
```

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