

Cooperation and the dynamics of adverse reaction to social ties

by

Andreas Kämpgen

Submitted in partial fulfillment of
the requirements for the degree of

Bachelor of Science

at

Julius Maximilian University Würzburg



April 2009

THESIS ADVISER

Dr. Thilo Gross

Leader of the group Dynamics of Biological Networks
Max-Planck Institute for Physics of Complex Systems

Prof. Wolfgang Kinzel

Chairholder theoretical physics III
Julius Maximilian University Würzburg

Summary

In this thesis I have investigated the dynamics of a Prisoner's Dilemma game on an adaptive network, which has been recently proposed by Segbroeck et al. [1]. In this game, the authors equip individuals with the capacity to treat unfavorable interactions differently. Additionally they introduce diversity of individual behavioral classes and investigate how this diversity in individual responses to adverse social ties influences the evolution of cooperation.

In a previous publication, Pacheco et al. have studied the game by using the active linking approximation [2]. This approximation assumes topological dynamics to proceed faster than the evolution of strategies, so that strategy updates occurs under stationary, but rewired network topology. In this regime, the evolution of strategies can be mapped onto a different game in a well mixed population, where everybody interacts equally likely with everybody else. By this means Segbroeck et al. show that diversity in individual responses promotes the evolution of cooperation [1].

In order to gain more detailed insights in the dynamical interplay of state and topology I analyzed the system with a different approximation scheme: the moment closure approximation. In this approximation the system is described by a system of ordinary differential equations (ODEs), which capture the dynamics of the moments of the system. The moment equations are truncated on a certain level to obtain a closed model. My investigations revealed that moment closure approximation provides a convenient tool for the investigation of the model under consideration. By means of numerical integration we verified the emergence of long-term cooperation in consistence with the results of [1]. Moreover, we showed that investigations using moment closure approximation can give insights that are difficult or even impossible to find by means of simulations. By applying the Netwon method, we found unstable steady states with coexistent populations of cooperators and defectors. The existence of these states is remarkable as the Prisoners's Dilemma in a well-mixed population cannot support stationary coexistence, even in unstable states.

Zusammenfassung

Im Rahmen dieser Bachelor Thesis wurde die Dynamik eines Spiels des Gefangenendilemmas auf einem adaptiven Netzwerk untersucht, das unlängst von Segbroeck et al. vorgestellt wurde [1]. In diesem Spiel werden die Spieler mit der Fähigkeit ausgestattet, ungünstige Verbindungen in einer unterschiedlichen Weise zu behandeln. Des Weiteren führen die Autoren verschiedene Verhaltenstypen ein und untersuchen wie diese Vielfalt an individuellen Reaktionen gegenüber ungünstigen Beziehungen die Evolution von Kooperation beeinflusst.

In einer früheren Publikation haben Pacheco et al. das Spiel in der Näherung einer „effektiven Verlinkung“ analysiert [2]. In dieser Näherung wird angenommen, dass die topologische Dynamik schneller als die Dynamik der Strategien verläuft, so dass die Dynamik der Strategien unter einer stationären, doch neuen Netzstruktur abläuft. Unter dieser Voraussetzung kann die Dynamik der Strategien auf ein neues Spiel in einer „gut durchgemischten Bevölkerung“, in der jeder mit jedem gleich wahrscheinlich zusammenspielt, abgebildet werden. Auf diese Weise zeigen Segbroeck et al., dass die Vielfalt an individuellen Reaktionen die Evolution von Kooperation begünstigt [1].

Um einen detaillierten Einblick in das dynamische Wechselspiel von Topologie und Strategie zu gewähren, wird das Modell mit Hilfe eines anderen Näherungsverfahrens - der „Moment-Closure-Näherung“ - untersucht. In dieser Näherung kann das System mit Hilfe von gewöhnlichen Differentialgleichungen (ODEs) beschrieben werden, welche die Dynamik von den Momenten des Systems erfassen. Die Gleichungen der Momente werden auf einer bestimmten Ebene genähert, um ein geschlossenes System zu erhalten.

Meine Untersuchungen haben gezeigt, dass die „Moment-Closure-Näherung“ ein geeignetes Instrument für die Untersuchung des vorliegenden Modells darstellt. In Konsistenz zu den Ergebnissen von Segbroeck et al. konnte die Entstehung anhaltender Kooperation anhand numerischer Integrationen nachgewiesen werden. Darüber hinaus können Untersuchungen unter Zuhilfenahme der „Moment-Closure-Näherung“ Einblicke gewähren, die nur schwer oder gar nicht zugänglich für Simulationen des Modells sind. Desweiteren konnten mit Hilfe des Newton-Verfahrens instabile stationäre Zustände mit koexistierenden Populationen von Kooperatoren und Defektoren gefunden werden. Die Anwesenheit dieser, wenn auch instabilen Zustände ist bemerkenswert da das Gefangenendilemma in einer „gut durchgemischten Bevölkerung“ keine stationären Koexistenzen unterstützt.

Contents

Summary	i
Zusammenfassung	ii
1 Introduction	1
2 Basics	4
2.1 Adaptive networks	4
2.2 Prisoner's Dilemma	4
3 Model	6
4 Moment closure	9
5 Dynamics	13
6 Summary and perspectives	18
A Appendix	20
Declaration of authorship	21
List of figures	22
Bibliography	22

1. Introduction

Cooperation is ubiquitous in nature. Cells cooperate in multicellular organisms [3]. Genes and chromosomes cooperate in genomes and eukaryotic cells [4]. On higher levels individuals cooperate to build complex life forms. There are many animals engaged in interspecific and intraspecific collaborative interactions. For instance vervet monkeys utter alarm calls to warn their fellows against predators. Widely known are so-called ‘cleaner fish’, which wait in ‘cleaning stations’ for bigger and even predatory fishes to clean their mouths from leftovers for the mutual benefit [5]. Most notably, however, is cooperation between humans. Human relations are based on cooperation from families to cities to today’s nation-states and transnational alliances. Thus cooperative interactions are observed on all levels of biological organizations.

Roughly speaking cooperation means that an individual pays a cost for another individual to receive a benefit [6]. In multicellular organisms, for instance, cells give up their individual reproduction to benefit other cells [3]. In human society cooperation occurs on many different levels from simple acts like giving a stranger directions up to the payment of taxes. In contrast, defection means that an individual doesn’t cooperate [6]. Defectors reap the benefits of the cooperators investment without making any investment into cooperation themselves.

Explaining the evolutionary origin of cooperation is a persisting challenge for evolutionary biologists. Since evolution is based on competition between individuals nothing but selfish behaviour should be rewarded and promoted. At the first glance it seems that cooperative behavior should be detrimental for the reproductive fitness. One would expect that cells, for instance, would reproduce as fast as possible, rather than investing resources in the formation of multicellular organisms.

A paradigmatic model for the study of cooperation is the *Prisoner’s Dilemma* of *game theory*. Game theory is a mathematical approach to capture the strategic and economic decisions of humans in diverse situations [7]. In this context the situations are referred to as *games* [8]. In its original version the Prisoner’s Dilemma describes the following situation: Two prisoners are under suspicion of joint crime. Due to insufficient evidence for a conviction, the police offer each of both prisoners the same deal. If one testifies against the other and the other remains silent, the betrayer (acting as defector in regard to his accomplice) escapes punishment whereas the silent accomplice (acting as cooperator) receives the full ten years imprisonment. If each prisoner betrays the other, both will be sentenced to five years. In contrast, the police can sentence both prisoners to only six months imprisonment if each of them cooperates by remaining silent. It is assured that the prisoners don’t have the possibility to arrange their statements and none of

1. Introduction

them is informed about the others decision. The only rational choice in this game is to play defect, because, regardless of what the other player choses to do, a player always lowers his jail sentence by defecting. Thus each prisoner plays defect even though the individual reward would be greater if both of them cooperate.

In order to investigate the dynamics of a population of players instead of analysing the interaction between two players *evolutionary game theory* has been considered which focusses on the evolution of behavioral strategies [6]. Based on the interactions with other players individual success of strategies is measured in terms of fitness [9]. It has been shown that in any mixed population of cooperators and defectors the relative abundance of the latter type of player increases due to a higher average fitness of defectors [4]. Thus, in the Prisoner's Dilemma, natural selection favors defectors unless additional mechanism are taken into account.

The literature mainly states five mechanisms which can be accountable for the evolution of altruistic or cooperative behaviour: *kin selection*, *direct reciprocity*, *indirect reciprocity*, *network reciprocity*, and *group selection* [4]. In the following we introduce the five mechanisms briefly. The mechanism of kin selection leads to cooperation if the donor and the recipient of an cooperative act are genetic relatives. More precisely, cooperation is promoted if the degree of relationship exceeds the cost-to-benefit ratio. Cooperation, however, is also observed between unrelated individuals. The mechanism of direct reciprocity takes into account repeated encounters between the same two individuals. In games such as the *repeated Prisoner's Dilemma*, individuals cooperate in hopes of gaining a reward afterwards. This idea is seized again by the mechanism of indirect reciprocity where the decision to help is based on the reputation of the recipient. Individuals who have a good reputation due to their altruistic behaviour are more likely to receive help from other individuals. The elucidated effects so far are based on a well-mixed population, where each individual interacts equally likely with any other individual. By contrast, network reciprocity considers that some individuals interact more often than other individuals. In this case cooperators prevail by forming network cluster where they support each other. The last mechanism which promotes cooperation is group selection. Here it is taken into consideration that natural selection acts also on groups promoting rather a group of cooperators than a group of defectors. Besides the mechanisms presented in this passage, there are many other potential mechanisms for the evolution of cooperation.

One idea that has recently attracted considerable attention is to investigate the influence of individuals' behavior on the topology. An interesting possibility is offered by the paper 'Reacting differently to adverse ties promotes cooperation in social networks' presented by Segbroeck et al. [1]. The authors consider a population interacting via an adaptive network where topology and strategy dynamics co-evolve. They equip individuals with the capacity to treat unfavorable interactions differently. Additionally they introduce diversity of individual behavioral classes and investigate how this diversity in individual responses to adverse social ties influences the evolution of cooperation modeled as a 2-player Prisoner's Dilemma.

By means of the assumption that topological dynamics is much faster than the evolution

1. Introduction

of strategies the authors can carry the evolutionary dynamics to a game in a well-mixed population. In this regime, they show the evolution of cooperation in populations which exhibit such a diversity of individual behavioral classes.

In this bachelor thesis we investigate the co-evolutionary dynamics of the model using *moment closure approximation*. We start in chapter 2 with essentials of *adaptive networks* and resumes the Prisoner's Dilemma by presenting his mathematical formalization. The subsequent chapter, Chapter 3, gives a detailed view of the model under consideration. Thereafter the moment closure approximation is applied in chapter 4. In chapter 5 we present the studies of the dynamics. The final chapter 6 summarizes the results.

2. Basics

2.1. Adaptive networks

In this section we give some network notions and define *adaptive networks*. A network consists of a number of network nodes (also called vertices) and a collection of links (also called edges) that connect pairs of nodes [10]. Each node and link can be identified by an integer value $i = 1, 2, \dots, N$ and a pair of these integer values (i, j) respectively. Strictly speaking the pair (i, j) represents a connection that goes from node i to node j [11]. The topology of the network is defined by the specific pattern of connections between the nodes [12, 13]. Generally networks that exhibit nontrivial topologies are referred to as *complex networks* [14].

The nodes and links of a network can exhibit different states and represent dynamical systems [12]. Changes in the state of the network nodes are referred to as *dynamics on networks* or *state dynamics*. The *topological dynamics* or *dynamics of networks* describes changes of the topology of a network.

It is evident that in most real world networks the dynamics of the network and the dynamics on the network are coupled. Consider for instance a simple power grid. The topology of the network is defined by the power supply lines that transmit power from plants to homes. Flow and density of load vary continuously according to energy requirements of the consumers. High loads on an electrical line can cause failures leading to the destruction of a given connection. On a longer timescale, increased energy needs require the installation of new plants or additional connections. We see that the dynamical state of the network proceeds depends on the network topology, while the evolution of the topology depends on the dynamical state of the network [12, 13]. Altogether the interdependent entities enable feedback loops that represent a key feature of *coevolutionary* or *adaptive networks*.

2.2. Prisoner's Dilemma

We introduced the 2-player Prisoner's Dilemma as a metaphor for the problems surrounding the evolution of cooperation. In this section we present the dilemma in its

2. Basics

mathematical formalization.

In the game each player makes the choice between two possible strategies C (to cooperate) and D (to defect) [15]. According to each player's strategies both players obtain certain payoffs. All possible interactions are given by the payoff matrix (note: the payoff is for the row player)

$$\begin{array}{c|cc} & C & D \\ \hline C & R & S \\ D & T & P \end{array} \quad (2.1)$$

If both players choose to cooperate (playing C), they get the reward R for mutual cooperation. If both players defect (playing D), they obtain the punishment payoff P for mutual defection. Mutual cooperation is favored ($R > P$), although rational thinking often leads to mutual defection. If one player defects and the other player cooperates, the defector obtains a payoff T (temptation to defect) which is higher than the reward R. The exploited cooperator, however, receives the sucker's payoff S, which is lower than P. In summary the parameters of the Prisoner's Dilemma obey

$$T > R > P > S. \quad (2.2)$$

According to equation (2.2) a rational player will always defect for the simple reason that he will always gain a greater payoff by playing this strategy no matter what the other player does. In the following payoff matrix (2.3) we give a numerical example by obtaining the jail terms of the original version of the Prisoner's Dilemma:

$$\begin{array}{c|cc} & C & D \\ \hline C & 6 \text{ months} & 10 \text{ years} \\ D & \text{no jail} & 5 \text{ years} \end{array} \quad (2.3)$$

This instance satisfies the equation (2.2) since shorter sentences correspond to higher payoffs.

3. Model

Let us now present the model to be discussed in detail. The network under consideration is a social network where individuals are assigned to the nodes, whose links represent the connections or interactions among individuals [2]. The number of individuals in the state i is denoted as $[i]$. The number of ij -links are denoted as $[ij]$ according to the state of the individuals which they connect. The network is considered as an graph with unweighted and undirected links. The presence of an undirected link (i, j) means that a connection exists from i to j as well as from j to i [11]. Unweighted links are not associated with a weight. In addition no multiple connections or self-connections are considered as it is often assumed in complex network literature.

The topological dynamics of this network correspond to a constant change of connections between individuals. Continuously, individuals terminate interactions and also make new relations with other individuals. The duration of an interaction between two individuals depends on the respective types or states of both individuals. The state dynamics correspond to changes of individuals' strategy due to imitation. Individuals in the population engage in a 2-person Prisoner's Dilemma, where individuals with a lower fitness copy individuals with higher fitness. The fitness strictly depends on the connections between individuals, i.e. the topology of the network. We, therefore, have a coevolution of the state dynamics and the topological dynamics (cf. Sec 2.1).

First we describe the state dynamics. Each individual adopts the strategy of cooperation or defection. Engaging in a Prisoner's Dilemma game individuals imitate other individuals with a higher fitness. In the context of evolutionary game theory we can associate the fitness of each individual with the payoff resulting from interactions with other individuals. The average fitness of each individual is given by

$$f_i = \sum_j [ij] P_{ij} (1 + \delta_{ij}) / [i] \quad (3.1)$$

where δ_{ij} is the kronecker delta and P_{ij} denotes the payoff matrix elements. To describe the game dynamics we employ the pairwise comparison rule, which describes the probability that an individual i imitates an individual j via the Fermi function

$$P_{ij \rightarrow ji} = \frac{1}{1 + e^{-\beta (f_j - f_i)}}, \quad (3.2)$$

3. Model

where the inverse temperature β controls the intensity of selection [16]. The pairwise comparison rule provides a convenient framework of state dynamics at all intensities of selection. For $\beta \rightarrow \infty$ individuals with a lower fitness deterministically are replaced by individuals with a higher fitness. However, for any finite β , the reverse process will happen with probability $1 - p$. We consider the process for weak selection $\beta \ll 1$. Since individuals are not born and do not die but only imitate each other, the total population size N is constant. The number of links, however, can change due to the fact that they are formed at certain rates and have specific lifetimes.

Saying this we get to the topological dynamics. All individuals are considered to have the same propensity \sqrt{n} to create new links such that links L_{ij} between two individuals in the state i and in the state j are equally formed at the rate n . In the Prisoner's Dilemma interactions with cooperators are the most rewarding (cf. Matrix (2.1) and Eq. (2.2)). Therefore both, cooperators and defectors, are considered to be satisfied when interacting with a cooperator [17]. On the other hand an interaction with a defector is never the best option and can be interpreted as an adverse social tie [1]. Taking this into account we confer individuals the capacity to treat favourable social ties to cooperators and adverse social ties to defectors differently. The aptness of an individual i to break connections with cooperators (C) is defined by a minimum value $\gamma_{iC} = \gamma$. By contrast, individuals which are connected to defectors (D) want to sever those interactions at higher rates γ_{iD} . Since terminations of relations usually depend on both individuals, the rate at which connections are broken is defined as $k_{ij} = \frac{1}{2}(\gamma_{ij} + \gamma_{ji})$ for each link L_{ij} , whereat we average over both individuals' rates.

According to everyday experience we further introduce differences in the aptness of breaking unwanted ties. Both, cooperators and defectors, can react in a slow or fast manner when confronted with an unfavorable connection to a defector. So, individuals are divided into different behavioral classes: slow cooperators (SC) and slow defectors (SD), whose adverse interactions to defectors have a low break-up rate $\gamma_{iD} = \gamma_s$ and fast cooperators (FC) and fast defectors (FD), whose unfavorable ties have a high break-up rate $\gamma_{iD} = \gamma_f$. We would like to remind that favourable social ties to cooperators are desired to last as long as possible and hence both cooperators and defectors will exhibit the minimum break-up rate $\gamma_{iC} = \gamma$ relating to those. An overview of the resulting break-off rates k_{ij} of links is given in the following matrix

$$\begin{array}{c}
 \text{SC} \quad \text{FC} \quad \text{SD} \quad \text{FD} \\
 \text{SC} \left(\begin{array}{cccc}
 k_{cc} & k_{cc} & k_{cs} & k_{cs} \\
 k_{cc} & k_{cc} & k_{cf} & k_{cf} \\
 k_{cs} & k_{cf} & k_{ss} & k_{sf} \\
 k_{cs} & k_{cf} & k_{sf} & k_{ff}
 \end{array} \right)
 \end{array} \tag{3.3}$$

where $k_{cc} = \gamma$, $k_{ss} = \gamma_s$, $k_{ff} = \gamma_f$, $k_{cs} = \frac{1}{2}(\gamma + \gamma_s)$, $k_{cf} = \frac{1}{2}(\gamma + \gamma_f)$ and $k_{sf} = \frac{1}{2}(\gamma_s + \gamma_f)$. For the sake of completeness, the trivial extended payoff matrix is shown in the following matrix

3. Model

$$\begin{array}{cccc} & \text{SC} & \text{FC} & \text{SD} & \text{FD} \\ \text{SC} & \left(\begin{array}{cccc} \text{R} & \text{R} & \text{S} & \text{S} \\ \text{R} & \text{R} & \text{S} & \text{S} \\ \text{T} & \text{T} & \text{P} & \text{P} \\ \text{T} & \text{T} & \text{P} & \text{P} \end{array} \right) & & & \\ \text{FC} & & & & \\ \text{SD} & & & & \\ \text{FD} & & & & \end{array} \quad (3.4)$$

In summary, it can be stated that the coupling between game strategies, behavioral classes and network dynamics will lead to a complex feedback interplay. In the following, we provide analytical insights into these co-evolutionary dynamics.

4. Moment closure

In order to study the dynamics of our model with the tools of nonlinear dynamics, we use the moment closure approximation to derive a low-dimensional emergent-level description of the system.

The system can be described by statistical quantities that are referred to as *moments* of the system. The number of individuals in the different states represent the moments of zeroth order. Henceforth, the state of slow cooperators, fast cooperators, slow defectors and fast defectors are denoted as C , \tilde{C} , D and \tilde{D} . The numbers of ij -links constitutes the first order moments of the system. Second order moments are represented by the number of connected triplets $[ABC]$ of nodes with a given sequence of states $A, B, C \in \{C, \tilde{C}, D, \tilde{D}\}$.

The dynamics of moments can be captured by a system of *ordinary differential equations* (ODEs) [18]. However, the dynamics of moments of order n depends on moments of order $n + 1$. This results in an infinite series of differential equations. Therefore we have to truncate the equations on a certain level to constitute a closed model.

We start by writing down the balance equations for the individuals and obtain one equation for each type $i = C, \tilde{C}, D, \tilde{D}$ according to

$$\frac{d}{dt}[i] = \sum_{j \neq i} (p_{ij \rightarrow ii} - p_{ij \rightarrow jj}) [ij], \quad (4.1)$$

where $p_{ij \rightarrow ii}$ denotes the probability that an individual i replaces an individual j due to selection. However, the dynamics of the individuals are entirely captured by the balance equations for $[C]$, $[\tilde{C}]$ and $[D]$ since $[\tilde{D}]$ follows from the conservation relation $[C] + [\tilde{C}] + [D] + [\tilde{D}] = N$.

As previously mentioned, the derived balance equations contain the presently unknown first order moments $[ij]$. One thinkable method to close the model is a mean-field approximation in terms of $[ij] \approx \langle k \rangle [i][j]$. Here, the quantity $\langle k \rangle$ is the *mean degree* which denotes the average number of links connected to a node [11]. However, this approximation doesn't capture the formation of new links and cutting of existing links respectively. Thus, we employ the approach of the so-called *moment expansion* and derive additional balance equations for the first order moments $[ij]$ [13].

We start by writing the equations for ii -links between individuals of the same type, that is $[CC]$, $[\tilde{C}\tilde{C}]$, $[DD]$ and $[\tilde{D}\tilde{D}]$: The maximum possible number of ii -links

4. Moment closure

is given by $[ii]_{max} = [i]([i] - 1)/2$ as no self-connections and multiple connections are considered. Thus we choose a factor $n([ii]_{max} - [ii])$ and denote the creation of new ii -links in terms of $n([ii]_{max} - [ii])$. Existing ii -links are destroyed at the break-off rate k_{ii} that is obtained from matrix (3.3). Furthermore ii -links are created if an individual i replaces an individual j due to selection, converting the respective link into an ii -link. Additional ii -links may be created due to selection if we consider connected triplets of nodes. For instance an individual i replaces an individual j that has additional connections to individuals in the state i . In this case the central individual j in the iji -triplet is replaced and two ij -links are converted into ii -links simultaneously. Equally, existing ii -links are destroyed if one individual j replaces an individual i interacting with other individuals in the state i .

Summing up all possible terms, we obtain the balance equations

$$\begin{aligned} \frac{d}{dt}[ii] &= n([ii]_{max} - [ii]) - k_{ii}[ii] \\ &+ \sum_{j \neq i} (p_{ij \rightarrow ii}([ij] + [iji]) - p_{ij \rightarrow jj}[ijj]) \end{aligned} \quad (4.2)$$

that describe the dynamics of the first order moments $[CC]$, $[\tilde{C}\tilde{C}]$, $[DD]$ and $[\tilde{D}\tilde{D}]$. Following a similar line of reasoning we can derive the balance equations for ij -links that connect individuals in different states:

$$\begin{aligned} \frac{d}{dt}[ij] &= n([ij]_{max} - [ij]) - k_{ij}[ij] + \sum_{m \neq i,j} (p_{im \rightarrow ii}[imj] - p_{im \rightarrow mm}[mij]) \\ &- p_{ij \rightarrow ii}([ij] - [ijj] - [iji]) - p_{ij \rightarrow jj}([ij] - [ijj] - [jjj]) \end{aligned} \quad (4.3)$$

Here we truncate the equations by approximating the second order moments in terms of first order moments. This approximation is called *moment closure approximation* and is introduced in the following.

Our equations contain three different kinds of second order moments: ABC -triplets, ABA -triplets and ABB -triplets. Let us start by approximating $[ABC]$. Actually this kind of triplet consists of an AB -pair and a BC -pair which are connected via the B -individual. We consider the AB -pair as the first half of the ABC -triplet and calculate the expectation value of additional BC -links that are connected to the B -individual. For this purpose we are interested in the expected number of links leaving the B -individual other than the one that is already occupied in the AB -link [10]. This quantity is given through the so-called *mean excess degree*

4. Moment closure

$$\langle d \rangle = \sum_d d q(d), \quad (4.4)$$

where

$$q(d) = \frac{(d+1)}{\langle k \rangle} p(d+1) \quad (4.5)$$

denotes the so-called *excess degree distribution* [19]. It is obviously that for a node of given degree k the excess degree is $q = k - 1$ and one could suspect that $\langle d \rangle \leq \langle k \rangle$. But this appears different with respect to degree correlation [10].

Existing links, indeed, are cutted depending on the connected types of individuals. New links in the network, however, are created by choosing randomly two unconnected nodes. Our network, thus, can approximately be considered as an Erdős-Rényi random graph. It is known that in this graph with a poissonian degree distribution

$$p(k) = \exp(-\langle k \rangle) \frac{\langle k \rangle^k}{k!} \quad (4.6)$$

the excess degree distribution (4.5) satisfies $q(d) = p(d)$ and thus $\langle d \rangle = \langle k \rangle$ [19]. This matter of fact becomes more obvious on further reflection: To calculate the mean excess degree we do not choose a random node in the network but choose a random link and follow it to a connected node. Therefore we have a higher probability to arrive at a node of high degree. In Erdős-Rényi random graphs this effect perfectly compensates that the excess degree of a node is smaller by one link than the total degree of the node [18].

Now that we know the expected number of additional links connecting to the B -individual, the probability to arrive at an C -individual remains to be determined. This quantity is given by $[BC]/(\langle k \rangle [B])$. Taking into account the number of AB -links we can approximate the number of ABC -triplets in the system by

$$[ABC] = \kappa \frac{[AB][BC]}{[B]}, \quad (4.7)$$

where $\kappa = \langle d \rangle / \langle k \rangle \approx 1$ [13].

In a similar way we approximate the two remaining types of second moments $[ABA]$ and $[ABB]$:

4. Moment closure

$$[ABA] = \frac{[AB]^2}{[B]} \quad (4.8)$$

$$[ABB] = 2 \frac{[BB][AB]}{[B]} \quad (4.9)$$

In the first triplet we neglect the fact that the probability for an additional AB -link connecting to a B -individual is smaller than $[AB]/(\langle k \rangle [B])$, since one of the total number of AB -links is already used up in the ABA -triplet. This approximation yields good results if the number of AB -links is reasonably large. To approximate the ABB -triplet, we have to consider a factor of 2 because both B -individuals of a given BB -link can possibly have an AB -link.

With these definitions the balance equations (4.1), (4.2) and (4.3) constitute a closed system of differential equations and can be studied with the tools of dynamical system theory.

5. Dynamics

In this chapter we present the studies of our model. The system of ordinary differential equations can be studied by standard tools of dynamical system theory.

We choose $\gamma_s = \gamma$ and integrate numerically the system for different values of γ_f (for any further system parameter see appendix A). The following figure, Fig. 5.1, shows two time series starting from an equal fraction of types.

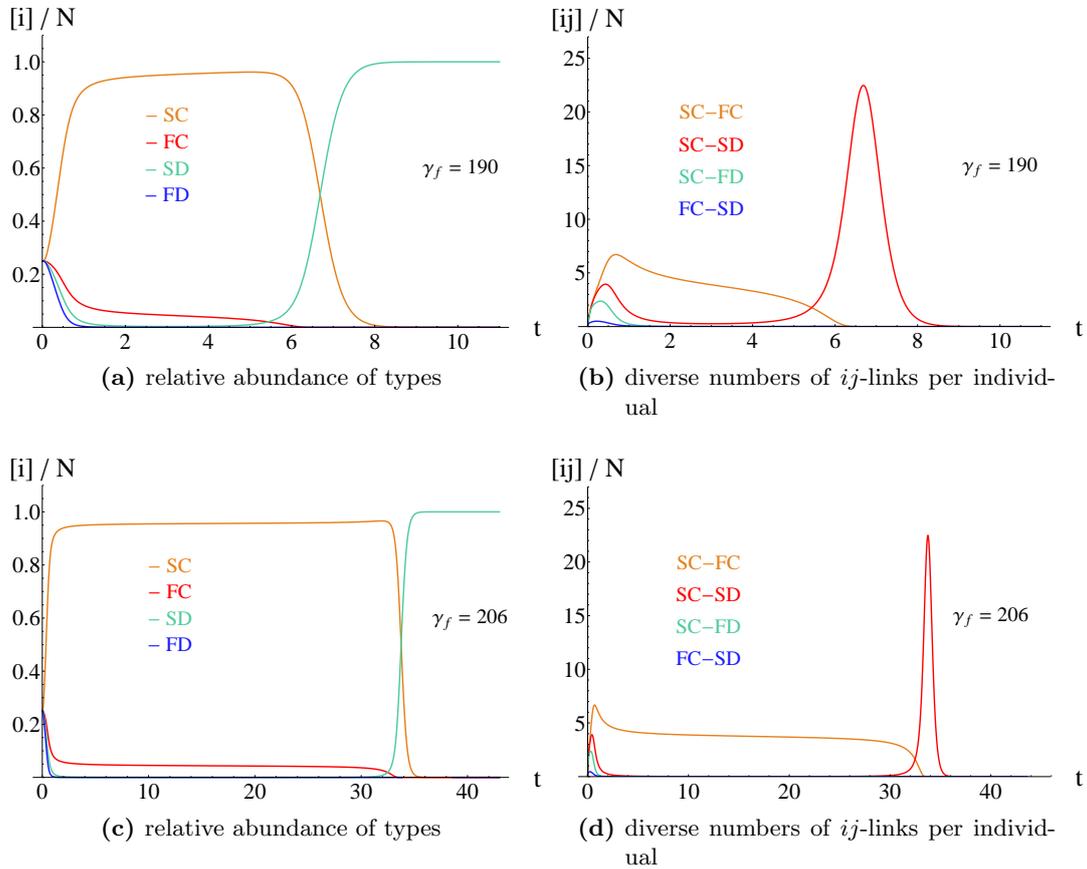


Figure 5.1.: relative abundance of types and diverse numbers of ij -links for different values of γ_f

In the first panel, Fig. 5.1a, we see that the relative abundance of slow cooperators

5. Dynamics

initially increases very quickly: slow cooperators equally establish connections to all types of individuals within population, whereas fast cooperators avoid interactions with both slow and fast defectors. Additionally, fast defectors avoid interactions to both slow defectors and among themselves. So, slow cooperators take the lead by establishing many relations (see Fig. 5.1b). Due to a resulting higher fitness, the population evolves into a cooperative state.

Defectors, however, don't become extinct. After a certain amount of time, slow defectors do invade the population due to the higher payoff that they receive from each individual interaction. They quickly take over the entire population. For higher γ_f , the takeover occurs later in time (see Fig. 5.1c).

At a certain value of γ_f the time for defectors to invade becomes infinitely long. The corresponding time series is shown in figure 5.2.

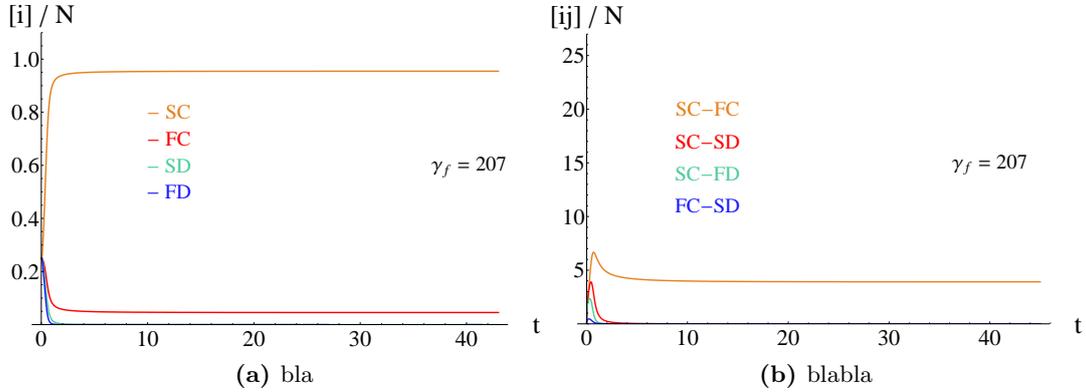


Figure 5.2.: relative abundance of types and diverse numbers of ij -links for $\gamma_f = 207$

In consistence with the results of [1], our data verify that giving individuals control over the number and nature of their social ties can lead to the emergence of long-term cooperation. Most importantly, we show that moment closure approximation provides a convenient tool for the investigation of the model.

In large parameter ranges the system approaches alternative final states characterized by full cooperation or full defection respectively. Which state is approached in a given simulation depends on the initial conditions of the system. In our system, an unstable steady state is located at the boundary of the two basins of attraction. This state can be computed by Newton's method.

As γ_f approaches $\gamma_{f,critical}$, we find coexistence of \tilde{C} -individuals and D -individuals, when C -individuals and \tilde{D} -individuals are extinct. The following figure, Fig. 5.3, shows the relative abundance of types within population. The number of links per individual are shown in Fig. 5.4. The existence of these states is remarkable as the Prisoner's Dilemma in a well-mixed population cannot support stationary coexistence, even in unstable states.

5. Dynamics

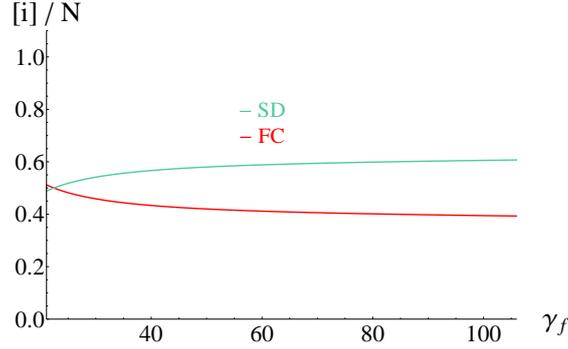


Figure 5.3.: Coexisting subpopulations of \tilde{C} -individuals and D -individuals: relative abundance of $[\tilde{C}]$ and $[D]$

At higher values of γ_f we see that the unstable steady states exhibit a higher relative abundance of D -individuals. This can be explained as the fitness of \tilde{C} -individuals is mainly determined by interactions among themselves. Unfavorable interactions with D -individuals are less profitable. In contrast, D -individuals live on the more rewarding interactions with \tilde{C} -individuals. At higher values of γ_f \tilde{C} -individuals sever their unfavorable ties more quickly. The corresponding fall of $\tilde{C}D$ -interactions (see Fig. 5.4) is more disadvantageous for \tilde{D} -individuals than for \tilde{C} -individuals. As the average fitness of both populations in the stationary state has to equal the advantage that the cooperators gain by faster rewiring has to be compensated by a disadvantage to maintain stationarity. For this reason the stationary state moves towards a higher abundance of D -individuals. The corresponding increase of DD -interactions and decrease of $\tilde{C}\tilde{C}$ -interactions compensate for the advantage of cooperators (see Fig. 5.4).

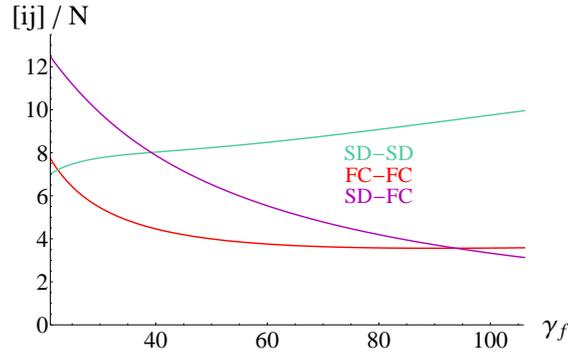


Figure 5.4.: Coexistent subpopulations of \tilde{C} -individuals and D -individuals: number of interactions $[\tilde{C}\tilde{C}]$, $[\tilde{C}D]$, and $[DD]$ per individual

5. Dynamics

We can confirm the result in the limit in which topological dynamics is much faster than state dynamics, so that state dynamics occurs under stationary, but rewired network topology [1]. The active linking dynamics (cf. Eq. (4.2) and Eq. (4.3)) are governed by

$$\frac{d}{dt}[\text{ij}] = n([\text{ij}]_{\max} - [\text{ij}]) - k_{\text{ij}}[\text{ij}]. \quad (5.1)$$

These equations lead to an equilibrium distribution of links given by $[\text{ij}]^* = \phi_{\text{ij}}[\text{ij}]_{\max}$, where $\phi_{\text{ij}} = n(n + k_{\text{ij}})^{-1}$ denotes the fraction of active links [2]. With the aid of this quantity, the state dynamics can be mapped onto a different game in a well mixed population with the same composition of cooperators and defectors. Thus, the game is characterized by the rescaled payoff matrix

$$\begin{array}{c} \text{SC} \quad \text{FC} \quad \text{SD} \quad \text{FD} \\ \text{SC} \begin{pmatrix} \text{R} \phi_{\text{cc}} & \text{R} \phi_{\text{cc}} & \text{S} \phi_{\text{cs}} & \text{S} \phi_{\text{cs}} \\ \text{R} \phi_{\text{cc}} & \color{red}{\text{R} \phi_{\text{cc}}} & \color{red}{\text{S} \phi_{\text{cf}}} & \text{S} \phi_{\text{cf}} \\ \text{T} \phi_{\text{cs}} & \color{red}{\text{T} \phi_{\text{cf}}} & \color{red}{\text{P} \phi_{\text{ss}}} & \text{P} \phi_{\text{sf}} \\ \text{T} \phi_{\text{cs}} & \text{T} \phi_{\text{cf}} & \text{P} \phi_{\text{sf}} & \text{P} \phi_{\text{ff}} \end{pmatrix} \end{array} \quad (5.2)$$

In the particular case of coexistent \tilde{C} -individuals and D -individuals, we are interested in the middle part (distinguished by red face) of matrix (5.2). For $\gamma_f = \gamma$ we obtain the following matrix

$$\begin{array}{c} \text{FC} \quad \text{SD} \\ \text{FC} \begin{pmatrix} 1 & 0.45 \\ 1.05 & 0.5 \end{pmatrix}, \end{array} \quad (5.3)$$

in which the elements are scaled to the first matrix element $R\phi_{\text{cc}}$ which is independent of γ_f . According to our model, the payoffs correspond to the Prisoner's Dilemma. For increasing γ_f , however, the payoffs for unilateral defection and unilateral cooperation decrease due to the mapping. For $\gamma_f = 17.5$ we obtain the matrix

$$\begin{array}{c} \text{FC} \quad \text{SD} \\ \text{FC} \begin{pmatrix} 1 & 0.21 \\ 0.49 & 0.5 \end{pmatrix}, \end{array} \quad (5.4)$$

5. Dynamics

which corresponds to a coordination game, in which choosing the same strategy is rewarded [2]. It is well known that unstable steady states can occur in this type of game [2]. This corresponds to our result since unstable steady states aren't observed below $\gamma_f = 17.5$. Our result, however, takes the co-evolutionary dynamics of state and topology into account and reveals a minimal $\gamma_{f_{critical}}$ from which on coexisting states occur. In aggregate our results show that investigations using moment closure approximation can give insights that, for instance, are difficult or even impossible to find by means of simulations.

6. Summary and perspectives

In this thesis I have investigated the dynamics of a Prisoner's Dilemma game on an adaptive network, which has been recently proposed by Segbroeck et al. [1]. In this game, the authors equip individuals with the capacity to treat unfavorable interactions differently. Additionally they introduce diversity of individual behavioral classes and investigate how this diversity in individual responses to adverse social ties influences the evolution of cooperation.

In a previous publication, Pacheco et al. have studied the game by using the active linking approximation [2]. This approximation assumes topological dynamics to proceed faster than the evolution of strategies, so that strategy updates occurs under stationary, but rewired network topology. In this regime, the evolution of strategies can be mapped onto a different game in a well mixed population, where everybody interacts equally likely with everybody else. By this means Segbroeck et al. show that diversity in individual responses promotes the evolution of cooperation [1].

In order to gain more detailed insights in the dynamical interplay of state and topology I analyzed the system with a different approximation scheme: the moment closure approximation. In this approximation the system is described by a system of ordinary differential equations (ODEs), which capture the dynamics of the moments of the system. The moment equations are truncated on a certain level to obtain a closed model. My investigations revealed that moment closure approximation provides a convenient tool for the investigation of the model under consideration. By means of numerical integration we verified the emergence of long-term cooperation in consistence with the results of [1]. Moreover, we showed that investigations using moment closure approximation can give insights that are difficult or even impossible to find by means of simulations. By applying the Netwon method, we found unstable steady states with coexistent populations of cooperators and defectors. The existence of these states is remarkable as the Prisoners's Dilemma in a well-mixed population cannot support stationary coexistence, even in unstable states.

Future investigations should focus on detailed bifurcation analysis to elucidate the transition of steady states from one type of dynamical behavior to another one. Further, detailed-level simulations of the full model could be compared with the analytical results.

Already the present results show that the interplay between individual behavior and social structure can be important for the evolution of cooperation. The introduced diversity in individual responses, however, doesn't constitute a completely new mechanism. In fact, defectors are recognized as such and receive a 'topological punishment' due to

6. *Summary and perspectives*

the cutting of connections. So, the mechanism under consideration can be associated with spatial effects, i.e network reciprocity. Our model, however, shows that previously studied mechanisms can be shaped in new forms due to the interplay of topological dynamics and state dynamics.

In the context of the physics of adaptive networks simple game theoretical models provide important examples. This class of systems has recently come into focus. In conclusion, this thesis has showed that the example of an adaptive system under consideration can be understood by means of moment closure approximation.

A. Appendix

The system parameter are chosen as follows:

$T = 2.1$, $R = 2$, $P = 1$, $S = 0.9$, $n = 0.5$, $\gamma = 5$, $\gamma_s = 5$, $\beta = 0.01$, $N = 1000$;

Note: The system doesn't exhibit a constant mean degree since the number of links change due to formation and cutting. The resulting number of links will be normalized to the total population size N , which is maintained as system parameter.

Declaration of authorship

I certify that the work here is, to the best of my knowledge and belief, original and the result of my own investigations, except as acknowledged, and has not been submitted for a degree at this or any other University.

Date, place, signature

List of Figures

5.1	relative abundance of types and diverse numbers of ij -links for different values of γ_f	13
5.2	relative abundance of types and diverse numbers of ij -links for $\gamma_f = 207$.	14
5.3	Coexisting subpopulations of \tilde{C} -individuals and D -individuals: relative abundance of $[\tilde{C}]$ and $[D]$	15
5.4	Coexistent subpopulations of \tilde{C} -individuals and D -individuals: number of interactions $[\tilde{C}\tilde{C}]$, $[\tilde{C}D]$, and $[DD]$ per individual	15

Bibliography

- [1] S. Van Segbroeck, F. C. Santos, T. Lenaerts, and J. M. Pacheco. Reacting differently to adverse ties promotes cooperation in social networks. *Physical Review Letters*, 102(5):058105, 2009.
- [2] J. M. Pacheco, A. Traulsen, and M. A. Nowak. Coevolution of strategy and structure in complex networks with dynamical linking. *Physical Review Letters*, 97(25):258103, 2006.
- [3] R. E. Michod and D. Roze. Cooperation and conflict in the evolution of multicellularity. *Heredity*, 86:1–7, 01 2001.
- [4] M. A. Nowak. Five Rules for the Evolution of Cooperation. *Science*, 314(5805):1560–1563, 2006.
- [5] C. Arnal, O. Verneau, and Y. Desdevises. Phylogenetic relationships and evolution of cleaning behaviour in the family labridae: importance of body colour pattern. *Journal of Evolutionary Biology*, 19(3):755–763, 2006.
- [6] M. A. Nowak, A. Sasaki, C. Taylor, and D. Fudenberg. Emergence of cooperation and evolutionary stability in finite populations. *Nature*, 428(3):646–650, 2004.
- [7] H. Ohtsuki and M. A. Nowak. Evolutionary games on cycles. *Proceedings of the Royal Society B: Biological Sciences*, 273(1598):2249–2256, 2006.
- [8] J. Nash. Two-person cooperative games. *The Econometric Society*, 21(1):128–140, 1953.
- [9] A. Traulsen, C. Hauert, H. De Silva, M. A. Nowak, and K. Sigmund. Exploration dynamics in evolutionary games. *Proceedings of the National Academy of Sciences*, 106(3):709–712, 2009.
- [10] M. E. J. Newman. The structure and function of complex networks. *SIAM Review*, 45:167, 2003.

Bibliography

- [11] L. da F. Costa, F. A. Rodrigues, G. Travieso, and P. R. V. Boas. Characterization of complex networks: A survey of measurements. *Advances In Physics*, 56:167, 2007.
- [12] T. Gross and B. Blasius. Adaptive coevolutionary networks: A review. *Journal of the royal society-interface*, 5:259, 2008.
- [13] T. Gross. The interplay of network state and topology in epidemic dynamics. In *Handbook of Biological Networks*. World Scientific, Singapore, 2009.
- [14] R. Albert and Albert-Laszlo Barabasi. Statistical mechanics of complex networks. *Reviews of Modern Physics*, 74:47, 2002.
- [15] K. Sigmund and M. A. Nowak. Evolutionary game theory. *Current Biology*, 9(14):R503–R505, 1999.
- [16] A. Traulsen, M. A. Nowak, and J. M. Pacheco. Stochastic dynamics of invasion and fixation. *Physical Review E*, 74:011909, 2006.
- [17] F. C. Santos, J. M. Pacheco, and T. Lenaerts. Cooperation prevails when individuals adjust their social ties. *PLoS Comput Biol*, 2:e140, 10 2006.
- [18] L. Do and T. Gross. Contact processes on adaptive networks. In *Adaptive Networks: Theory, Models and Applications*. Springer Verlag, Heidelberg, 2009.
- [19] J. Reichardt. Introduction to the physics of complex networks. Institute for Theoretical Physics, University of Würzburg, lecture notes, 2009.