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The impact of diversity in the emergence of cooperation

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there is no perfection only life
Milan Kundera

Abstract

Every living structure was produced and shaped according to the fundamental mechanisms of natural selection. However, such mechanisms do not suffice to explain the emergence of the complex reciprocal ties we find so essential in the sustainability of human society. These ties provide a clear example of the type of cooperative behavior not expected to emerge naturally through the evolutionary mechanisms of natural selection, which predict a world filled with selfish entities. How cooperation emerges is thus a major scientific challenge.

One particular suited framework, called Evolutionary Game Theory, assumes that individuals interact according to well-known social dilemmas of cooperation and evolve through natural selection. Conventionally, Evolutionary Game Theory assumes infinite well-mixed populations, resulting in a set of coupled non-linear ordinary differential equations known as replicator equations. When individuals engage in a Prisoner's Dilemma of cooperation, cooperation does not emerge.

Additional mechanisms were proposed to explain the emergence of cooperation. A key mechanism assumes finite and structured populations in which individuals interact through the links of complex networks. The most successful types of networks are heterogeneous, hence characterized by the diversity among the number of links individuals possess.

Here we investigate the emergence of cooperation when a new aspect of diversity is introduced, associated with individuals that have limited resources. Furthermore, we introduce a quantity called Gradient of Selection, which extracts the population-wide dynamics on populations structured according to different types of complex networks. We use this quantity to study the impact that different types of structures have on the effective dilemma faced by the population as a whole.

Keywords: Emergence of Cooperation; Complex Networks; Complex Systems; Evolutionary Game Theory; Evolutionary Dynamics

Resumo

A cooperação é ubíqua no espectro de comportamentos humanos. Enquanto espécie, os Humanos evoluíram num ambiente que, de alguma forma, selecionou preferencialmente indivíduos cooperativos. é razoável afirmar que a evolução nos ensinou como cooperar e através do esforço cooperativo dos nossos antepassados prosperámos atingindo o estatuto de espécie mais bem sucedida no planeta Terra. Não obstante, a cooperação está presente a todas as escalas e em estruturas vivas de todas as escalas, sendo fundamental quer para a sua diversidade quer para a sua sustentabilidade, em pé de igualdade com os restantes três mecanismos da selecção natural: Selecção; Mutação e Replicação.

De um ponto de vista evolutivo a Cooperação funciona como que uma cola, permitindo que a vida se torne sustentável a partir dos outros três mecanismos que sustentam a evolução, e que, de uma perspectiva puramente racional, apenas aparentam promover a competição entre entidades. Esses mecanismos que descrevem a selecção natural foram os mesmos que levaram Herbert Spencer a descrever a selecção Natural como a sobrevivência dos mais aptos (do inglês survival of the fittest).

Para que haja cooperação é necessário que existam pelo menos duas entidades sendo que a primeira está disposta a pagar um custo para oferecer um benefício outra. Regra geral admite-se que, no acto de cooperação, o benefício é maior do que o custo. Obviamente isto abre uma janela para que uma das entidades se tente aproveitar do gesto generoso do outro recolhendo um benefício sem pagar um custo numa reciprocação cooperativa. Note-se que entidade, neste contexto, poderá ser entendida como um indivíduo ou uma bactéria, sendo que actos de cooperação se podem manifestar em diferentes organismos.

A Cooperação pode ser vista como um comportamento que os indivíduos adquirem através de um mecanismo de evolutivo de aprendizagem social, que do ponto de vista matemático é muito similar evolução biolgica, podendo co-evoluir com esta. Desta forma, os indivíduos poderão imitar outros que considerem ter mais sucesso, sendo que este processo de imitação não está livre de erros. De acordo com Herbert Spence, seria de esperar um cenário onde os comportamentos egoístas que levam a recompensas maiores, fossem mais imitados. No entanto, os dados empíricos mostram que não é isso que se passa.

Com efeito, sem a Cooperação a vida como a conhecemos não era possível, e por essa razão é da maior importância estudar e descrever os mecanismos fundamentais que levaram sua emergência.

Uma ferramenta especialmente adequada para estudar a evolução de comportamentos numa população de indivíduos é a Teoria de Jogos Evolutiva. Esta ferramenta assume que indivíduos numa população interagem de acordo com os fundamentos da Teoria de Jogos mas evoluem de acordo com os mecanismos da selecção natural. Esta formalização dinâmica da teoria de jogos, mais elaborada, introduzida por Maynard Smith nos anos 70, permitiu que a biologia evolutiva abandonasse um dos seus paradigmas mais clássicos, característico da genética de populações: selecção constante.

Fazendo uso da Teoria de Jogos para determinar o fitness de cada indivíduo, a Teoria de Jogos Evolutiva assume um paradigma em que a selecção depende da frequência de indivíduos que adoptam um determinado comportamento/estratégia. A versatilidade desta ferramenta fez como que fosse adoptada em outras áreas científicas como ligações ténues biologia. Exemplo disto são áreas como a sociologia, filosofia, economia, matemática, física e recentemente as ciências da computação.

Ao assumirmos, através da Teoria de Jogos, que os indivíduos interagem de acordo com os dilemas sociais da cooperação, entre os quais o Dilema do Prisioneiro (o mais estudado por representar o cenário mais adverso para a cooperação), podemos estudar e analisar a emergência e sustentabilidade da cooperação numa população.

Inicialmente, os trabalhos realizados em Teoria de Jogos Evolutiva tomavam as populações como infinitas e desprovidas de estrutura, um cenário em que todos os indivíduos interagem entre si com a mesma probabilidade, de tal forma que dois indivíduos com a mesma estratégia têm o mesmo fitness. Este paradigma foi adoptado por facilitar a descrição matemática da dinâmica que ocorria nestas populações. Esta aproximação tem, seguramente, o seu maior reflexo no facto de estar na origem das equações do Replicador, o (agora) muito popular e conhecido sistema de equações diferenciais acopladas e não-lineares que descreve na totalidade a dinâmica nestas populações.

Os resultados, no entanto, não foram animadores, dado que os modelos previam o insucesso dos cooperadores quando os indivíduos interagiam de acordo com o Dilema do Prisioneiro. Mecanismos adicionais que explicassem a emergência da cooperação tornaram-se, portanto necessários. Um dos mecanismos chave para a emergência da cooperação assume que as populações são estruturadas através de uma rede complexa que emula o tipo de estrutura das interacções sociais que estabelecemos e em que vivemos. Neste tipo de populações os indivíduos interagem exclusivamente com os indivíduos a que estão directamente ligados. A introdução de estrutura social traz consigo a impossibilidade de descrever a dinâmica evolutiva de uma população através da equação do Replicador (excepto em limites e aproximações muito simples), facto este que limita bastante o tipo de ferramentas que podem ser usadas para extrair informação destes sistemas.

As redes complexas inicialmente estudadas caracterizavam-se por terem uma estrutura simples e regular, influenciadas quer pelas regularidades de estruturas moleculares encontradas em cristais e superfícies, quer pela directa analogia com estruturas espaciais. Apesar de desprovidas das propriedades fundamentais encontradas entretanto nas redes sociais reais, estas redes regulares induziam, ao contrário das populações não estruturadas, a presença de diversidade nos indivíduos já que agora dois indivíduos com a mesma estratégia poderiam exibir um fitness diferente. Em grande parte devido a este mecanismo primitivo de diversidade estas redes demonstraram resultados animadores produzindo pela primeira vez um ambiente em rede no qual a cooperação emergia mesmo no Dilema do Prisioneiro.

Talvez precipitada pelo sucesso destas estruturas, ou pelas descobertas entretanto feitas em ciências de redes complexas, a comunidade abordou de forma sistemática estruturas cada vez mais complexas e consequentemente com propriedades mais semelhantes s que se observam nas redes reais de interacções humanas. Um tipo de redes que demonstrou ser capaz de obter resultados particularmente espectaculares é caracterizada pela sua forte heterogeneidade, ou seja, pela existência de diversidade entre o número de ligações que cada indivíduo possui. Com efeito, estas redes heterogéneas demonstraram ser cruciais para a emergência da cooperação. De salientar que a introdução de mais um nível de diversidade na população (heterogeneidade), mesmo que conceptualmente simples, teve um impacto muito positivo no que concerne a emergência e sustentabilidade da cooperação. Além do mais a diversidade é uma característica presente nas estruturas sociais humanas pelo que a sua ligação emergência da cooperação é, também conceptualmente, muito interessante.

Nesta Tese introduzimos e estudamos o impacto de mais um nível de diversidade na evolução da cooperação. Até aqui todos os modelos tinham como denominador comum uma situação em que cada indivíduo possuía recursos (conceptualmente) infinitos. Desta forma podiam pagar um custo fixo em cada interacção que participavam, independentemente do número de interacções. No paradigma que introduzimos neste trabalho, consideramos que os indivíduos possuem recursos limitados e que, por isso, têm de o repartir por entre todas as interações em que participam. Este cenário origina o aparecimento de uma diversidade ao nível dos custos que cada indivíduo paga por interacção, já que indivíduos cooperadores com um número de ligações diferentes numa rede complexa participam em cada uma das suas interacções com custos diferentes. Este mecanismo, por sua vez, induz uma quebra de simetria no jogo que é jogado entre cada par de indivíduos. é simples conceber situações que corroborem este efeito. Por exemplo, o tempo que cada pessoa tem é um recurso limitado que estas têm de dividir de acordo com as pessoas com quem interagem: quanto maior for o número de pessoas com quem interagem menor é o tempo que têm para cada uma.

Finalmente nesta Tese introduzimos ainda uma quantidade denominada Gradiente de Selecção. Esta quantidade é calculada numericamente e cons-

titui uma abordagem de campo-médio ao problema da dinâmica populacional, permitindo-nos extrair informação sobre o jogo efectivo em que uma população estruturada numa rede complexa se envolve como um todo. Esta quantidade vai permitir-nos estudar o impacto que diferentes tipos de estruturas populacionais têm no jogo efectivo sentido pela população, recuperando assim alguma da informação a que deixamos de ter acesso aquando da introdução de estruturas.

Palavras Chave: Emergência da Cooperação; Redes Complexas; Sistemas Complexos; Teoria de Jogos Evolutiva; Dinâmica Evolutiva

Contributions

Bellow follows a list of the manuscripts related with the present work carried out in this thesis. They are either published or submitted to publication.

- **Flávio L. Pinheiro**, João Moreira, M.D. Santos, F.C. Santos, J.M. Pacheco
  Evolution of social diversity under the distributed prisoner's dilemma
  International Journal of Autonomous and Adaptive Communications Systems in press (2011)

- F.C. Santos, **Flávio L. Pinheiro**, T. Lenaerts, J.M. Pacheco
  Role of diversity in the evolution of cooperation
  Journal of Theoretical Biology, in press (2011)

- **Flávio L. Pinheiro**, F.C. Santos, J.M. Pacheco
  Evolutionary Dynamics of Cooperation Under the Distributed Prisoner's Dilemma
  in Proceedings of 2010 International ICST Conference on Bio-Inspired Models of Network, Information and Computing Systems (BIONETICS 2010), LNICST, Springer

- J.M. Pacheco, **Flávio L. Pinheiro**, F.C. Santos
  Population structure induces a symmetry breaking favoring the emergence of cooperation
  PLoS Computational Biology, 5(12): e1000596 (2009)

Flávio L. Pinheiro

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Chapter 1

Introduction

Cooperation is ubiquitous within the spectrum of human behaviors. We, as a species, evolved in an environment that selected preferentially cooperative individuals. It is reasonable to say that evolution ”taught us” how to cooperate and through the cooperative commitment of our ancestors we thrived to become the most successful life-form on Earth. In fact cooperation is present in living structures of all scales and at all scales being as fundamental for their diversity and sustainability as were any of the other three main mechanisms of natural selection: Selection, Mutation and Replication [1].

From an evolutionary point of view Cooperation works like a glue, making life sustainable out of the other three greedy and selfish mechanisms that support evolution, which, from a rational understating, seem exclusively designed to promote competition between life entities. These were the three mechanisms that ultimately lead *Herbert Spencer* to describe Natural Selection as the ’*survival of the fittest*’ [2, 3].

Cooperation is learned by individuals, that acquire such trait, by means of an evolutionary process very similar to the biological one. In this process of ”social learning”, that may co-evolve with natural selection, individuals imitate the traits of others they consider to have more success. They may also make errors and acquire the wrong traits but thats all part of the process. However, according with the words of *Herbert Spencer*, we would expect a scenario where selfish behavior leads to higher profits, being imitated more often. This is not necessarily the case.

Without cooperation life as we know would not be feasible. For that reason it is of uttermost importance to describe, as a mean to better understand it, the fundamental mechanisms underlying the *emergence of Cooperation*. Understanding these mechanisms has relevance for fields other than biology: anthropology, economics, mathematics, political science, primatology, and psychology are adopting the evolutionary approach and developing analogies based on it. Similarly, biologists use elements of economic game theory and analyze cooperation in *evolutionary games*. This is the main topic of this Thesis.

When dealing with an interaction between two individuals involving some kind of contribution to arrive to a common goal we take as cooperators those who are willing to pay a cost (c) to provide a benefit ($b > c$) to the other. Obviously this opens a window for exploitation, as any fully rational individual would try to maximize her gain collecting the benefit without paying any cost c. We refer to such selfish individuals as defectors. If we take a rationality assumption to every individual then we would expect to find a world full with individuals where no one pays any costs, but where no one receives any benefits either. We say that individuals face a social dilemma when they are led to a mutual behavioral which does not maximize the group payoff, based on criteria of maximization of their individual payoff.

This was exactly what Game Theory predicted in the late 1940s [4] when it was developed with the rather humble goal of modeling human behavior. Under this unified framework of abstract models and metaphors scientists explored this type of problems, the fundamental concepts of the theory are discussed in chapter 2.

Under this framework we assume that individuals must opt to play one from a set of strategies with the sole knowledge of the outcomes from all possible combinations of strategies. If we take that our opponents behave rationally and choose the strategy that optimizes their individual gains then we can hope to find an optimum strategy for ourselves and draw conclusions from it.

Game theory synthesized the number of social dilemmas of two person symmetric games into three types: Stag Hunt [5], Snowdrift Game [6] and the infamous Prisoner's Dilemma [7]. The last it is also the most studied in cooperation problems, as is assumed to be the one that models most faithful the majority of human interactions while being also the one under which game theoretical models predict less success levels of cooperation. This made of the Prisoner's Dilemma the main focus of attention.

However in the late 1970s a more auspicious framework took its first steps when *Maynard Smith* [8, 9] envisioned how evolutionary biology could make use of game theory to break one of its long standing paradigms: constant selection. Using Game Theory to compute the fitnesses of individuals in a population, thus frequency dependent, while having strategies evolving according to the same canonic rules (selection, mutation and replication) he created a framework which introduces a new dynamical dimension to game theory making it suitable to study how traits evolve in populations.

This new framework quickly attracted the attention of researchers from several fields with few or no connections to biology. This was the case of sociology, mathematics, physics, philosophy and lately of computer science. The ability to model how behaviors evolve and spread on populations by modeling how individuals behavior became amazingly simple and powerful.

During the early 1980s the scientific community saw by means of peer-reviewed publications the impact that this new framework could have in tackling the problem of cooperation. Names such as *W. Hamilton* [10], *G. Hardin* [11, 12], *R. Harding* [13], *P. D. Taylor* [14] and *R. Axelrod*[15] where crucial in pave the way so that the interdisciplinarity of this field could condense into a cooperative effort to find the real mechanisms behind the emergence of cooperation. It was not however until the late 80s and the majority of the 90s that a more comprehensive mathematical description on the dynamical behavior of such systems started to emerge with significant contributions from *K. Sigmund* [16, 17], *J. Hofbauer* [16, 18], *Herbert Gintis* [19, 20, 21] and *Martin Nowak* [22, 17]. This framework came to be known as Evolutionary Game Theory and it evolved to become one of the leading paradigms in evolutionary and population dynamics studies.

In this more elaborated framework things initially were, ironically, kept simple and populations considered as infinite and well-mixed. This provided a safe heaven under which theories and models could be drawn. An introduction to the fundamentals of Evolutionary Game Theory is going to be the main topic of discussion in chapter 3.

With complete disregard by this achievements, cooperation was still a mirage on populations whose interactions were ruled by the Prisoner's Dilemma. During this same period some exploratory results on structured populations challenged the concepts of conventional Evolutionary Game Theory. Instead of structureless populations, individuals started having a well-defined list of partners with whom they interacted. This can be obviously conceptualized through a network of social ties.

Initially these networks took the shape of lattices, simple and regular structures which sometimes resemble the kind of structures physicists faced when describing the molecular structure of crystals and surfaces. However, with a complete absence of diversity these networks only aimed at modeling a population of individuals that resembled, perhaps, a population line up in an ordered military-like parade with toroidal endings (for the muse of mathematicians) where each myopic individual interacted only with the four (or eight) immediate comrades. As such every individual was topologically identical to any other agent in the population.

Even under these simple structures cooperation thrived in (a very limited and narrow)window of the Prisoner's Dilemma game parameters. Perhaps this was one of the causes that motivated the scientific community to explore far more complex structures. And almost in co-evolution with a remarkable set of discoveries that were made in network-science [23, 24, 25, 26, 27, 28, 29, 30] many results emerged that made use of these more realistic and complex (social) structures [31, 32, 33, 34, 35, 36, 37, 38, 39]. These new networks were fundamentally characterized, among other properties, by their heterogeneous landscape of social interactions as different individuals were now able to sustain different numbers of social interactions. Even with this simple recipe and under the simplest concepts of diversity cooperation proved to thrive and was now able to sustain itself even under the Prisoner's Dilemma. The impact of having a population structured by means of a complex network of social ties is assessed in chapter 4.

Within Evolutionary Game Theory, this diversity is only a first approach. In addition, diversity can also exist in connection to strategic and learning behaviors. The first is addressed in this Thesis in chapter 5, following the effects of differences in cooperative investments. This is combined with heterogeneous structures, in which some individuals may simply be chosen more frequently as role models than others, producing a significant effect in the flow of behavioral changes caused by the evolutionary dynamics. In addition, diversity in individuals' game strategy [40], imitation capacity [41, 42, 43, 44] or learning approach [45] may produce significantly different outcomes in equivalent games.

As we show in this Thesis, the combined effects resulting from heterogeneous social interactions may lead not only to a boost in the overall levels of cooperation [46, 47, 48, 35, 49, 38, 50, 39, 51] but also to a symmetry breaking of the game itself, as well as the introduction of large variance in the distribution of wealth, associated here with the ensuing accumulated game payoffs.

Approaching more realistic and consequently more complex settings has the cost that no closed-form theory is able to describe correctly the dynamics of the cooperation on a structured population. To study these systems the community had to resort on heuristic methods that only allowed to assess the overall sustainability of cooperation in a population leaving a huge gap of knowledge on the underlying mechanisms and on the overall population dynamics that was taking place. In this Thesis we propose a mean-field quantity called Gradient of Selection that is computed numerically with the intent of extracting some of this information from such systems. This quantity is described with detail in chapter 6.

At this point the reader should be wondering: how can a physicist contribute to this field? As a matter of fact physicists are quite fit to study the basic mechanisms that are described under the Evolutionary Game Theory framework [52], in particular when dealing with complex structured populations. The most important features of these networked systems is the apparent disparity between local interactions and global emergent properties. The analysis of such complex problems gave rise to the broad field of Complex Systems and can be traced back to the Ising model [53]. The application of methods developed in statistical physics of system far from equilibrium has turned out to be very fruitful [54]. Interesting parallels between non-equilibrium phase transitions and spatial evolutionary game theory have added another dimension to the concept of universality classes. Thus putting analogies aside this constitutes an excellent field for a physicist to offer a contribution.

Chapter 2

Game theory

Game theory was first introduced by *J. Von Neumann* and *O. Morgenstern* in the book *Theory of game and economical behavior* [4] back in 1944. Essentially, and as far as what concerns the work discussed in this thesis, it focuses on finding the optimal strategic behavior of rational individuals [4, 55] under a specific setting, but in general it can be seen as a theory of how to model interactions between individuals as a means to predict optimal behaviors. Game theory is thus a convenient framework, and perhaps the best suited, to model individuals strategic interactions.

In this section we overview the main concepts of classical game theory. To do so we start by briefly discussing the definition of the very celebrated *Nash Equilibria* concept (2.2) which allow us to compute the optimal strategies for rational individuals. We make use of this framework to model the three main social dilemmas for symmetric two-person interactions: Prisoner's Dilemma (2.3.1); Stag Hunt (2.3.2) and Snowdrift Game (2.3.3). Finally we introduce a space of parameters that suites our interests by allowing us to approach each of the social dilemmas with only two variables.

2.1 The costs and benefits of cooperation

Let us take a situation that is commonly known as the donation game: it is given to a pair of individuals (A and B), independently, a one shot chance to contribute a value c as a mean to provide a benefit b to the other. Thus we can define each individual that chooses to contribute to be a cooperator (C) and one that refuses to do so as a defector (D).Usually we refer to these two, clearly different, behaviors as strategies and to the two individuals taking them as the players. After each player decided upon which strategy to take, both players are awarded with the respective payoff.

We can sum up all possible outcomes in a formal form trough the following payoff matrix:

$$\begin{array}{c} \\ C \\ D \end{array}\begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} b-c & c \\ b & 0 \end{pmatrix} \end{array} \tag{2.1}$$

A payoff matrix is said to describe a symmetric game when the following interpretation is allowed: an entry of the matrix is the payoff value obtained by a row player (i) when facing a column player (j). Having access to one of such payoff matrices we can write the payoff obtained by player i simply as $\Pi_i(S_i, S_j), \forall i \neq j$, being S_k the strategy adopted by player k.

Having said this, the payoff matrix 2.1 tell us that a C always pays a cost c and provide a benefit b to the other player.

2.2 The concept of equilibrium

The question that naturally arises is: which is the best strategy to take?

In what concerns the scope of this thesis we only take the scenario where the set of strategies available for each players is restricted to pure strategies[1], in other words players can only play either C or D.

The search for a solution is strongly biased by one condition: the end goal of each player. For such reason many concepts of solution can be formulated. However when we deal with the problem of cooperation (and in game theory in general) we assume the full rationality hypothesis of both players which leads to the concept known as *Nash Equilibrium* introduced by *John Nash* in [56]. *John Nash* argues that a solution (S_i^*, S_j^*) is a *Nash Equilibrium* if it is a stable equilibria from where neither player is able to improve his payoff by changing strategy unilaterally. Following our notation we can formalize this concept as:

$$\Pi(S_i^*, S_j^*) \geq \Pi(S_i, S_j^*) \geq \Pi(S_i^*, S_j); S_{i,j}, S_{i,j}^* \in \{C, D\} \wedge S_{i,j}^* \neq S_{i,j} \tag{2.2}$$

If the inequality ($\geq$) in 2.2 holds we say we are under a weak *Nash Equilibrium*, if instead we drop the equality we say to we are under a strict *Nash Equilibrium*. In the following section, 2.3, we revise this concepts for a generalized Payoff matrix 2.4.

Additionally *John Nash* also proved that every game has at least one Nash Equilibrium.

Let us return to the donation game as an example: each player is asked to contribute an amount of 5 dollars providing 15 dollars to the other player. A player cooperates (C) if he decides to contribute; else we say he is a defector

---

[1] There is however one further interpretation of this scenario where players can opt to play a mix of the several strategies available, in other words to play a linear combination of pure strategies.

(D). The following payoff matrix portraits all possible outcomes:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} 10 & -5 \\ 15 & 0 \end{pmatrix} \end{array} \tag{2.3}$$

In this example (D, D) is the only *Nash Equilibrium*, the situation where both players defect.

We can arrive to such result by the following method: assume the opponent (j) plays C then the strategy that maximizes the payoff of i is D as $\Pi(D, C) > \Pi(C, C)$; this is also true if the opponent plays D as $\Pi(D, D) > \Pi(C, D)$. In the end i is always better off playing D; being a symmetric game this is true for both players and the equilibrium was computed. However this isn't the solution that maximizes the payoff of both players as (C, C) is higher than (D, D).

This paradoxical solution is in one hand driven by the fear of exploitation and in other by the temptation to exploit; even though mutual cooperation would be an optimum for both ($b - c > 0$) they rationally opt to not cooperate. This fact that defines a social dilemma.

Although in this example (D, D) is the only solution it is also possible to create a situation (payoff matrix) where any of the other combination of strategies ((C, D), (D, C) and (C, C)) is a solution.

2.3 General two person symmetric games

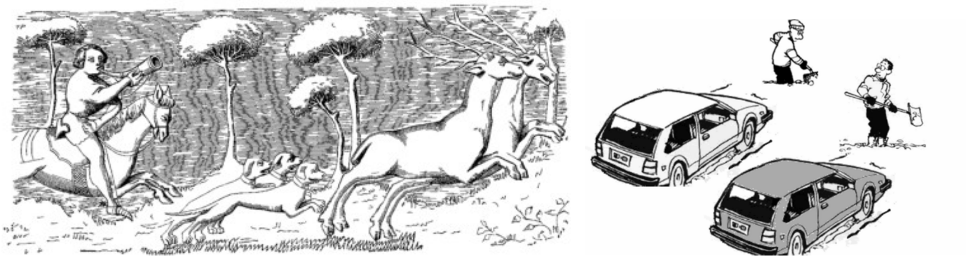
The payoff matrix introduced previously 2.1 can have a broader interpretation if we allow the four outcomes to be described by the following description:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array} \tag{2.4}$$

if both players decide to cooperate they are awarded with a Reward (R); if both decide to defect then they receive the Punishment (P); if players decide to play different strategies then the cooperator receives the Sucker's Payoff (S) for allowing a defector to profit from the Temptation (T).

Using this payoff matrix we can list a set of criteria that formalize the concept of *Nash Equilibrium*:

- C is a strict Nash equilibrium if $R \geq T$ $(\Pi(C, C) \geq \Pi(D, C))$;
- C is a Nash equilibrium if $R > T$ $(\Pi(C, C) > \Pi(D, C))$;
- D is a strict Nash equilibrium if $P \geq S$ $(\Pi(D, D) \geq \Pi(C, D))$;
- D is a Nash equilibrium if $P > S$ $(\Pi(D, D) > \Pi(C, D))$;



(a) Stag Hunt (b) Snowdrift Game

Figure 2.1: Gravures illustrating two of the three possible social dilemmas that emerge in games with two strategies. in panel (a) we depict a Stag Hunt while in panel (b) two individuals shovel snow after a Snowdrift thus depicting one possible outcome of the Snowdrift game.

these are in total accordance with what we defined previously, 2.2

When the reward for mutual cooperation is higher than the punishment, $R > P$, we are able to reproduce all three central social dilemmas of cooperation: the Prisoner's Dilemma [7]; the Stag Hunt game [5] and the Snowdrift Game [6]. Each one is defined by ordering the payoffs differently. Bellow we briefly discuss these.

2.3.1 Prisoner's Dilemma ($T > R \wedge P > S$)

The prisoner's dilemma [7] is the true social dilemma, the one where the social optimum is the opposite of the rational optimum. A classical description of the situation is as follows [7]:

> Two suspects are arrested by the police. The police does not have enough evidence for a conviction. Having separated the prisoners the police proposes a deal to each of them: to testify against the other. Each one is assured that the other would not know about the betrayal before the end of the investigation. Each prisoner must choose to betray the other or to remain silent.
>
> If one decides to defect the other by testifying while the other remains silent in a gesture of cooperation with his accomplice, then the police offers a 1-year sentence to the defector and applies the full 15-year sentence to the other. However if both decide to remain silent they are sentenced to only 5-year in jail. If both denounce each other, each receives a 10-year sentence.

What should each prisoner do? Let us start by writing the payoff matrix that describes this situation:

$$\begin{array}{c c} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} -5 & -15 \\ -1 & -10 \end{pmatrix} \end{array} \tag{2.5}$$

In this case the payoffs represent the time each prisoner will be removed from their free life. Rationally (D, D) is the only *Nash Equilibrium* according with this type of payoff matrices. Although it would be of the best interest for both prisoners that each remains in silence, obtaining a five year sentence, both are either driven by the fear of being cheated or by the temptation to get away with only a one year sentence, and defect the other in advance. The donation game, mentioned in 2.3, is thus another instance of a Prisoner's Dilemma: both players fall for the fear of being exploited and rationally opt to defect each other.

This is arguably the most difficult setting for cooperation and as consequence is the most studied.

2.3.2 Stag Hunt ($R > T \wedge P > S$)

Although the Prisoner's Dilemma has a big popularity in cooperation studies, several scholars argue that the social dilemma that best describes economical interaction between individuals in the real world is the Stag Hunt [5].

Lets take the situation presented by the French philosopher Jean Jaques Rousseau to describe this type of situations, this is illustrated in Figure 2.1a:

> Two hunters can either jointly hunt a stag (an adult deer and rather large meal) or individually hunt a rabbit (tasty, but substantially less filling). Hunting stags is quite challenging and requires mutual cooperation. If either hunts a stag alone, the chance of success is minimal. Hunting stags is most beneficial for society but requires a lot of trust among its members.

What is the best option for each hunter? With the hope of obtaining an answer to this question we start by writing down the payoff matrix that describes such situation:

$$\begin{array}{c c} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} 50 & 0 \\ 5 & 5 \end{pmatrix} \end{array} \tag{2.6}$$

the payoffs can be thought of as the amount of meat one collects if both cooperate to hunt a stag or decide to go alone for a rabbit.

Rationally both (C, C) and (D, D) are *Nash Equilibrium*, the situation where doing the same as the other player is the best strategy. Thus if

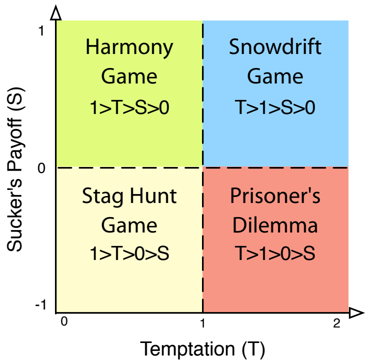


Figure 2.2: Two person games parameter space defined by the game parameters T and S, the former is usually known as the Temptation to defect while the latter is known as the Sucker's Payoff. To construct this two dimensional space we fixed the other two game parameters: the reward for mutual cooperation $R = 1$) and the punishment for mutual defection $P = 0$.

individuals cooperate and hunt a Stag they to better than cheating or being cheated, although cheat on advance is far better than being cheated, thus it is easy to conclude that the best move for both players is to coordinate their strategy.

Other names for the Stag Hunt include: *coordination game*, *assurance game* and *trust dilemma*.

2.3.3 Snowdrift Game ($T > R \wedge S > P$)

Suppose the following situation [57], depicted in Figure 2.1b:

> Two drivers on their way home are caught in a blizzard and trapped on either side of a snowdrift. Each driver has the option to get out and start shovelling or to remain in the cozy warmth of the car. If both start shovelling each has the benefit of getting home while sharing the labour costs. However, if only one shovels both drivers still get home but the lazy bum avoids the labour costs. Nevertheless and despite the shovelling, the benefit of getting home outweighs the awkward prospects of waiting for spring to melt the obstacle.

What is the best move for each of the drivers? Let us again resume the outcomes of such situation by a payoff matrix:

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} b - c/2 & b - c \\ b & 10 \end{pmatrix} \end{array} \tag{2.7}$$

we assume that the benefit of going home is b while the total labor costs of remove the snowdrift is c with $b > c > 0$.

Rationally both (C, D) and (D, C) are *Nash Equilibrium*, the situation where doing the opposite of the other player is the best strategy. In literature, depending on the source, this dilemma is also known as hawk-dove and the game of chicken.

2.4 The Parameter space

Finally, taking into account that we will study the spectrum of problems spanning the social dilemmas considered ($R > P$), it is possible to reduce the number of parameters (R, S, T and P) by normalizing the difference between $R(= 1)$ and $P(= 0)$ [34]. This allows us to define a parameter space with only two variables:

$$\begin{array}{c c} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} 1 & S \\ T & 0 \end{pmatrix} \end{array} \tag{2.8}$$

In this parameter space we are still able to define all three social dilemmas in the domain comprised by $0 < T < 2 \wedge -1 < S < 1$, see Figure 2.2. On this domain the PD is defined by $T > 1 \wedge S < 0$, the SH by $T < 1 \wedge S < 0$ while the SG is defined by $T > 1 \wedge S > 0$.

Additionally we are able to define one other game called the harmony game, $R > T \wedge S > P$, a situation where mutual cooperation is also the result of rational individual decisions, a setting with no obvious interest for the study of cooperation.

Commonly, and as it will be the case along this thesis, when using this parameter space we refer to the Temptation (T) as benefit (b) and to the Sucker's Payoff (S) as the cost (c), This has obvious influences from the formulation already discussed and formalized by the payoff matrix 2.4.

Chapter 3

Evolutionary Game Theory

In the previous chapter fundamental notions were introduced along with a simple but powerful framework: game theory. This approach allowed us to model interactions between pairs of individuals. We also made use of game theory to formalize the class of interactions that fall in what are considered to be social dilemmas ($R > S$). The rational solution for this problem, known as Nash equilibrium (NE), was also briefly introduced. However, a new dynamical dimension can be added to game theory by expanding its application to the study of the evolutionary dynamics of traits in a population. This is the main focus of this chapter.

Such approach was initially done by *Maynard Smith* and *George R. Price* when they built the foundations of what is today known as Evolutionary Game Theory (EGT), and introduced the notion of Evolutionary Stable Strategies (ESS) [8, 9] through the application of game theory in a biological context. In fact the origin of this notion is believed to be related with the unfamiliarity of both with the concept of the *NE*, see section 2.2. In EGT it is assumed a population that evolves via natural selection. In particular the fitness of each individual is associated with the payoff of the game, which, in turn, is directly translated into the reproductive success of individuals.

Before EGT models in biology took the fitness as constant for all individuals that shared the same genotype/phenotype/trait. This means a frequency independent selection, where the fitness difference between any two individuals independent of the context. We say these are populations that evolve under constant selection. EGT on the other hand is the realization that we can take the notion of genotypes/phenotypes/traits as the strategies present in game theory, in other words taking the biological fitness of an individual in the population as directly related to the game interactions Under such setting selection becomes now frequency-dependent as now fitnesses depend on the respective abundances of each strategy in the population, strategies that are more fit lead to more offspring.

Besides the obvious biological interpretation of EGT, as described above, there is a second interpretation that lays its roots on cultural evolution of social systems: successful behaviors are imitated more often than the less successful. Making use of a social learning mechanism instead of the genetic reproduction, EGT provides the perfect ground to study how a trait such as cooperation evolves and is sustained in populations.

In this chapter we start by discussing the meaning of ESS in 3.1 before an overview of the fundamental properties of EGT both in its classical point of view (section 3.2) and under an finite populations approximation (section 3.3).

3.1 Evolutionary Stable Strategy

Evolutionary Stable Strategy (ESS) is a concept introduced by *Maynard Smith* and *George R. Price* [8, 9] which tries to answer the following question: under which conditions is a population of individuals that plays strategy C resilient to a single mutant that plays D? We are able to reach an answer to this question by analyzing the relative success of each strategy according to a payoff matrix.

Take for instance the payoff matrix 2.4 and the criteria for *NE* in section 2.3. One of two conditions must be true so that C is an *Evolutionary Stable Strategy*:

$$R > T \tag{3.1a}$$

$$R = T \wedge S > P \tag{3.1b}$$

equation 3.2a is simply the definition of a strict *NE* (2.2,2.3), while 3.2b says that a strategy C is an ESS if it is a weak *NE* and strategy C is rationally better against D than mutual D.

Additionally we can add the concept of *weak ESS* if we assume that C is equally good against a D as when both players play D.

$$R > T \tag{3.2a}$$

$$R = T \wedge S \geq P \tag{3.2b}$$

These conditions describe the conditions needed so that selection in a population of C's would oppose (ESS) or be stable (weak ESS) against invasion of D's. Similar conclusions are taken if we analyze the conditions that make D an ESS.

This concept plays an important role when studying evolutionary dynamics of frequency-dependent selection, as is the case of this Thesis.

3.2 The replicator dynamics

In this section we describe the standard model of evolutionary dynamics in an infinite and well-mixed population of players, also known as the replicator dynamics [14, 16, 18, 58, 59, 60].

Assume that individuals can take one of two strategies: to cooperate (C) or to defect (D). Let us denote by x_C ($x_D = 1 - x_C$) the fraction of cooperators (defectors) in the population. Under such setting individuals interact according to a game defined by the payoff matrix 2.4. We can write the expected payoff $\pi_C(\pi_D)$ of a cooperator (defector) as:

$$\pi_C = Rx_C + Sx_D \tag{3.3a}$$

$$\pi_C = Tx_C + Px_D \tag{3.3b}$$

We assume that the payoff of an individual is associated with his fitness and this with his reproductive or social success. This makes the fitness of each individual dependent on the frequency of the different strategies present on the population (*frequency-dependent selection*).

A selection process occurs on the population where the strategies of those individuals that do better than the average spread in the population at the expense of the others.

We can write down a set of ordinary differential equations that describe such deterministic process by which the frequencies of individuals of each strategy present in the population vary over time:

$$\dot{x}_C = x_C(\pi_C - \langle \pi \rangle) \tag{3.4a}$$

$$\dot{x}_D = x_D(\pi_D - \langle \pi \rangle) \tag{3.4b}$$

where $\langle \pi \rangle$ is the average fitness of the population ($\langle \pi \rangle = \pi_C x_C + \pi_D x_D$). Equations 3.4 are known as the *replicator equations* and can be further simplified into a single ordinary differential equation (for the case of two strategies) if we take $x_D = 1 - x_C$:

$$\dot{x} = x(1 - x)(\pi_C - \pi_D) \tag{3.5}$$

where $x \equiv x_C$. The direction of selection is thus solely determined by the payoff difference $\pi_C - \pi_D$ which, if we recall the payoff matrix 2.4, can be expanded as:

$$\delta(x) = \pi_C - \pi_D = (R - T - S + P)x + (S - P) \tag{3.6}$$

When $\delta(x) > 0$ ($\delta(x) < 0$) selection favors cooperation (defection) and the value of x increases (decreases). Whenever $T = S = 0$ or $R = P = 0$ equation 3.6 resumes to either $\delta(x) = Rx + P(1-x)$ or $\delta(x) = -Tx - S(1-x)$ which can be regarded as a constant selection model, since the average payoffs for both strategies are constants and independent of frequency.

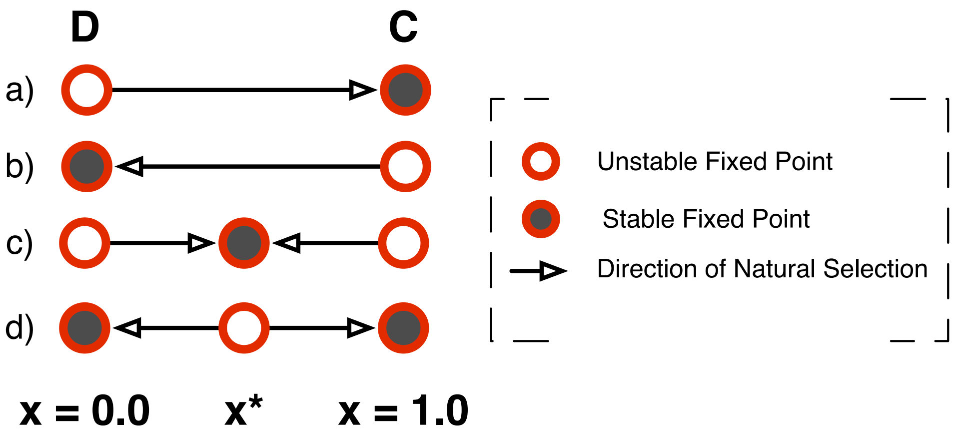


Figure 3.1: Selection dynamics of two person games that result from a frequency dependent selection in a populations composed by individuals of two strategies C and D.

Equation 3.5 has two trivial fixed points at $x^* = 0$ and $x^* = 1$, but further internal fixed points can be obtained in the domain $x^* \in]0, 1[$ depending on the existence of solutions of the form $\delta(x) = 0$

$$x^* = \frac{P - S}{(R - T - S + P)} \tag{3.7}$$

According to the dilemmas discussed previously (see prisoner's dilemma in section 2.3.1, stag hunt game in section 2.3.2 and snowdrift game in section 2.3.3) three scenarios can be observed: Dominance, Coordination (Bistability) and co-existence. There is in fact a correspondence between these solutions and the ones obtained in classical game theory: any stable fixed point of the replicator equation corresponds to a *NE* in the classical formulation. However because internal roots can also be stable we need to take into consideration the formulation of Game Theory that deals with mixed strategies for a complete correspondence, something not discussed in this Thesis.

Bellow we briefly discuss these three situations.

3.2.1 Dominance

Whenever $T > R$ and $P > S$ we obtain a negative $\delta(x)$ for all $x \in]0, 1[$. In this situation defectors are favored irrespective of the composition of the population leading to a population full of D's. The fixed point at $x^* = 0$ is stable making it the only pure strategy solution and therefore an evolutionary stable strategy. This situation corresponds to the *prisoner's dilemma* [7] we have met previously, see chapter 2.3.1.

We call such scenario D-dominance as D's dominate C's irrespective of the setting. If however $R > S$ and $S > P$ the $\delta(x)$ would be positive for all $x \in]0, 1[$ and so C's would dominate over D's (C-dominance).

The fixed points and direction of selection of $\dot{x}$ under D-dominance and C-dominance are plotted in Figure 3.1 b) and a) respectively.

3.2.2 Coordination or Bistability

Whenever $R > T$ and $P > S$ a new solution ($\delta(x) = 0$) is obtained for $x \in]0, 1[$ that is given by equation 3.7, and because $\dot{x}$ is negative for $x < x^*$ and positive for $x > x^*$ this equilibria is unstable, which makes both $x^* = 0$ and $x^* = 1$ stable equilibria. In this situation both (C, C) and (D, D) are strict *NE*.

If the initial fraction of cooperators is smaller than x_L selection drives the population to full defection, otherwise selection drives the population to full cooperation. The strategy with the largest basin of attraction is said to be risk dominant. Hence for $R + S > T + P$ cooperation is risk dominant.

The fixed points and direction of selection of $\dot{x}$ when there is an internal coordination point is depicted in Figure 3.1 d).

3.2.3 Co-existence

Whenever $T > R$ and $S < P$ a new solution ($\delta(x) = 0$) is obtained for $x \in]0, 1[$ that is given by equation 3.7, and because $\dot{x}$ is positive for $x < x^*$ and negative for $x > x^*$ this equilibria is stable, which makes both $x^* = 0$ and $x^* = 1$ unstable equilibria. Neither (C, C) and (D, D) are *NE* but a mixed strategy composed of a linear combination of both it is. This situation is sometimes referred as Hawk-Dove or polymorphic game by biologists and corresponds to the well-known *snowdrift game* [6] we have described previously, see chapter 2.3.3.

The fixed points and direction of selection of $\dot{x}$ when there is an internal co-existence point is depicted in Figure 3.1 c).

3.3 Finite populations

The replicator dynamics, as described in the previous section, was a huge success but kept two unrealistic properties: populations are neither infinite nor well-mixed. Although one can argue that for the current size of human population (≈ 7 Billion individuals) or for a culture of bacterias the infinite limit is a good approximation, or that for small groups of humans (< 100 individuals) the well-mixed hypothesis is a fairly good approach, the truth is that large populations are not well-mixed and populations may be small. In this section we aim to describe the fundamental aspects of a finite population approach with a well-mixed organization.

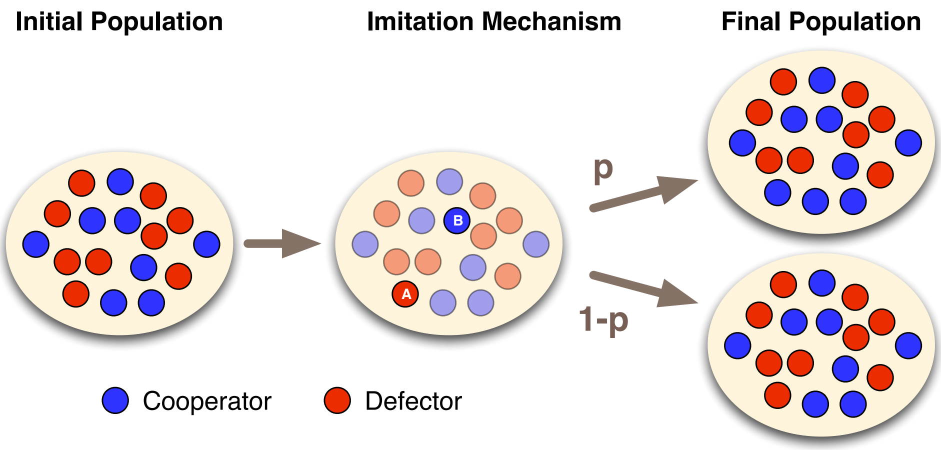


Figure 3.2: This scheme depicts the pairwise comparison rule on well-mixed and finite populations. From a unstructured population composed by individuals with one of two strategies we select two different individuals at random (A and B), with probability p A imitates the strategy of B changing the composition of the population, with probability $1-p$ the opposite happens.

By taking into account this new piece of complexity we need to take evolution out from the deterministic systems box and place it into the realm of stochastic processes. In fact selection now is composed by the sum of the deterministic natural selection process and by an amount of drift, in other words error or stochasticity. The interplay between these two ”forces” is tuned by the so called *intensity of selection.*

Suppose we have a population with a fixed number N of individuals, at a given time the population is composed by j ($\in [0, N]$) cooperators and $N-j$ defectors. For such a system to evolve we have do define an update rule; we shall adapt a rule that describes how individuals imitate the strategy of others, the *pairwise comparison rule* (in the absence of mutations) [61, 62] (see Figure 3.2). It states that: at each (discrete) time step a pair of individuals A and B are randomly chosen from the population; A imitates the strategy of B with a probability p given by the Fermi probability distribution (from statistical physics):

$$p = \frac{1}{1+e^{-\beta(\pi_B-\pi_A)}} \tag{3.8}$$

where π_A and π_B denotes the accumulated payoffs of individual A and B after interacting once with every other individual in the population. These interactions are governed by game interactions and result from the payoffs specified by a matrix of the same type as 2.4. Finally β is the intensity of selection that regulates the amount of stochasticity in the imitation process: if $\beta \to \infty$ we approach a deterministic process while for $\beta \to 0$ full stochas-

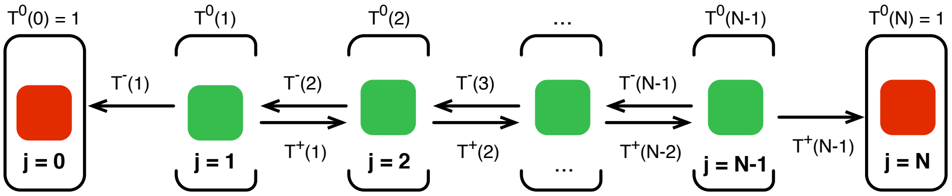


Figure 3.3: Markov chain describing the evolutionary process of two strategies that occurs in finite population. $T^0(j)$ identifies the probability that a population stays in state j while $T^{+/-}$ specify the probabilities of increasing/decreasing the number of cooperation by one. The states $j = 0$ and $j = 1$ are absorbents.

ticity is achieved as the imitation proceeds randomly. The stochastic nature of the update process and the absence of mutation makes the evolutionary dynamics in finite populations stop only when it reaches a monomorphic state, that is, when the entire population is composed only by cooperators or by defectors.

If at a specific moment we have j cooperators in the population it is possible to compute the probabilities of increasing (T^+) and of decreasing (T^-) the amount of cooperators by one element in that population.

$$T^+(j) = \frac{N-j}{N}\frac{j}{N}\frac{1}{1+e^{-\beta(\pi_D-\pi_C)}} \tag{3.9a}$$

$$T^-(j) = \frac{j}{N}\frac{N-j}{N}\frac{1}{1+e^{-\beta(\pi_C-\pi_D)}} \tag{3.9b}$$

Both the first and second terms of equations 3.9a and 3.9b have similar interpretations: $\frac{j}{N}$ ($\frac{N-j}{N}$) refers to the probability of selecting a cooperator (defector) from the entire population pool assuming a process with replacement [1]. The additional term represents the probability that a cooperator (defector) imitates the strategy of a defector (cooperator) 3.9b (3.9a) taking into account equation 3.8.

If we assume that each possible configuration of the population, defined by the number of cooperators $j \in [0, N]$, is an available state of the system then we are able to describe this system according to a finite state Markov process, Figure 3.3, as in our case the system holds no memory of its trajectory in this state space. Fundamental to such description are the probabilities of the system to jump from one state to the nearest which are defined precisely by $T^+(j)$ and $T^-(j)$, whereas the probability of the system staying in the same state is $T^0(j) = 1 - T^+(j) - T^-(j)$. Furthermore the

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[1] At the end of the day these results are similar to those obtained with the pairwise comparison rule without replacement, as long as N is not too small ($N > 10^2$)

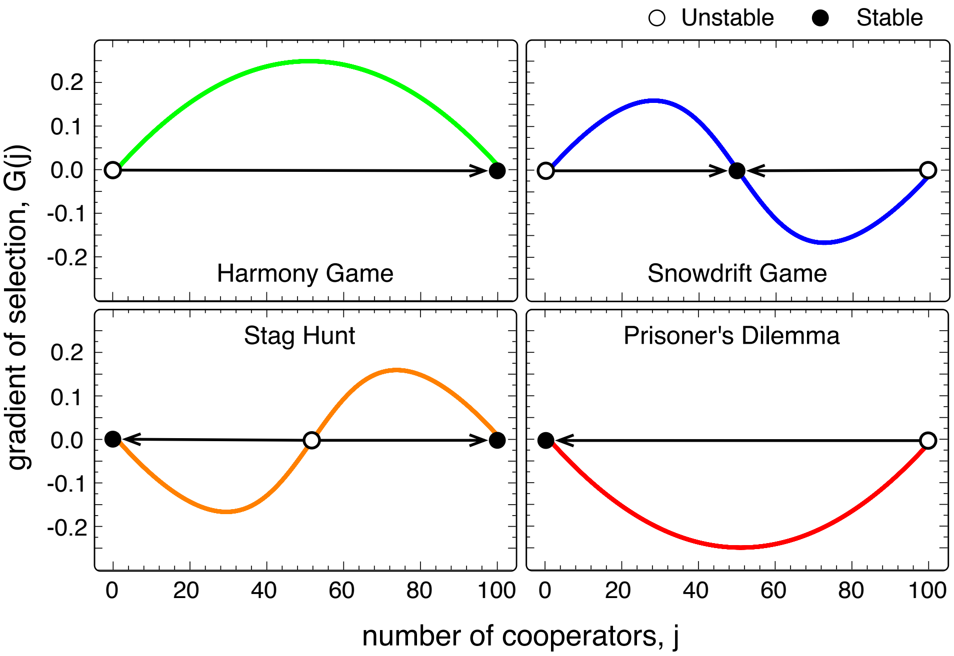


Figure 3.4: Gradient of Selection, $G(j)$ the finite populations analogous to the replicator equation computed for a population of 100 individuals under a strong selection regime, $\beta = 10.0$.

values of $T^+(j)$ and $T^-(j)$ are only zero in the configurations $j = 0$ and $j = N$. For this reason these two states are said to be absorbing states.

A new quantity called gradient of selection $G(j)$ [63, 61] can be defined as the difference $T^+(j) - T^-(j)$. From this quantity we are able to retrieve information similar to the one obtained from the right hand of the replicator equation. In the limit of large populations[2] rule this quantities turns out to be:

$$G(j) = \frac{j}{N}\frac{N-j}{N}\tanh(\frac{\beta}{2}(\pi_C - \pi_D)) \tag{3.10}$$

Consequently, under weak selection (for $\beta \ll 1$ we can linearize tanh) and large N ($x \approx \frac{j}{N}$) the replicator dynamics is recovered [61].

The sign of $G(j)$ indicates the direction of selection in the population: positive (negative) if cooperators tend to increase (decrease) [64, 65, 66].

Figure 3.4 exemplifies the shape of the $G(j)$ under the three social dilemmas plus the Harmony Game for a population of 100 individuals. Changing β accounts to change the intensity of the selection which, in this case, will correspond to increase or decrease the absolute value of $G(j)$.

---

[2] In fact this expression is derived from the Langevin equation $\dot{x} = x(1-x)\tanh(\frac{\beta}{2}(\pi_C - \pi_D)) + \sqrt{\frac{x(1-x))}{N}}\xi$, where ξ corresponds to an uncorrelated gaussian white noise [63], for large populations the second term (drift) vanishes.

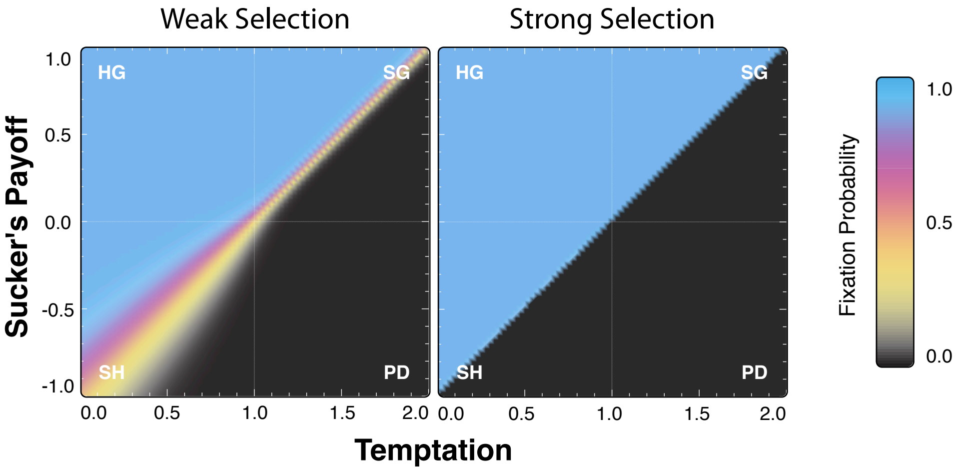


Figure 3.5: Probability of Fixation on well-mixed populations with 100 individuals under weak selection left ($\beta = 0.01$) and strong selection right ($\beta = 10.0$) regimes starting with 50 cooperators for the entire parameter space

3.4 Fixation probability

We can summarize all possible transitions between available states of the system by means of a (stochastic) matrix (sometimes called transition matrix). This matrix stores all $T^{+}(j)$, $T^{-}(j)$ and $T^{0}(j)$ that fully describe the dynamics of a given finite population. Because we are dealing with one step processes, described by the Markov chain of Figure 3.3, such matrix is by default tridiagonal, see equation 3.11.

$$M = \begin{bmatrix} T^{0}(0) & 0 & 0 & \cdots & 0 \\ T^{-}(1) & T^{0}(1) & T^{+}(1) & \ddots & \vdots \\ 0 & \ddots & \ddots & \ddots & 0 \\ \vdots & \ddots & T^{-}(N-1) & T^{0}(N-1) & T^{+}(N-1) \\ 0 & \cdots & 0 & 0 & T^{0}(N) \end{bmatrix} \tag{3.11}$$

In a population where mutations of strategies are absent $T^{0}(0)$ and $T^{0}(N)$ are 1, as these two states correspond to the global absorbing states of the population under such stochastic evolutionary process it makes sense to ask what is the probability that a system composed by $j \in]0, N[$ cooperators reaches the state where the entire population is composed by C's. We can compute this quantity if all information needed to build the transition matrix is gathered. The *fixation probability* computation resumes to the closed

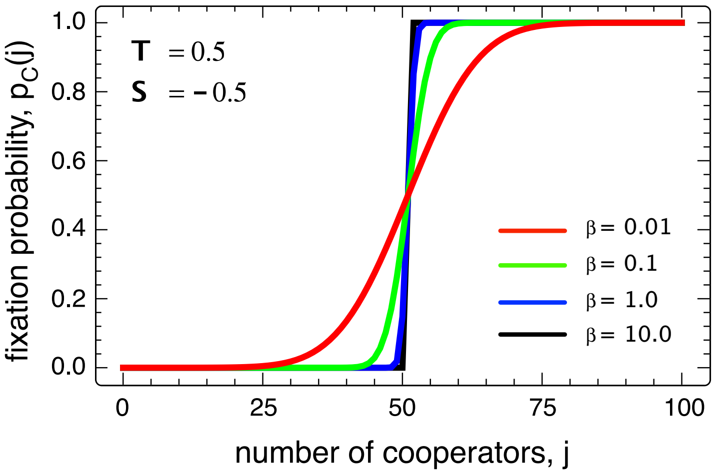


Figure 3.6: The fixation probabilty as a function of the number of cooperators for a Stag Hunt game ($T = 0.5$;$S = -0.5$) for several values of the intensity of selection (β).

form [1]:

$$\rho_C(j) = \frac{1 + \sum_{i=0}^{j-1} \Pi_{k=1}^{i} \gamma_k}{1 + \sum_{i=0}^{N-1} \Pi_{k=1}^{i} \gamma_k} \tag{3.12}$$

with $\gamma_k = \frac{T^-(k)}{T^+(k)}$.

Traulsen et. al. [61] have shown that equation 3.12 can be simplified when we are dealing with the pairwise comparison rule to

$$\rho_C(j) = \frac{\sum_{i=0}^{j-1} exp[-\beta i(i+1)u - 2\beta iv]}{\sum_{i=0}^{N-1} exp[-\beta i(i+1)u - 2\beta iv]} \tag{3.13}$$

where $2u = R - S - T + P$ and $2v = -R + SN - PN + P$.

Under neutral drift, that is when for all states $T^+ = T^-$ the fixation probability $\rho_C(j)$ is $\frac{j}{N}$. We say that selections favors C's when $\rho_C(j) > \frac{j}{N}$, while if $\rho_C(j) < \frac{j}{N}$ we say that selection favors D's.

3.5 The parameter space revisited, part i

From the previous section it is natural to wonder what is the probability that a starting fraction of cooperators fixates taking into account the several social dilemmas previously discussed? Figure 3.5 answers that question within the entire space of parameters as defined in chapter 2.4. Here we have made use of equation 3.12 for a starting condition of 50 cooperators in a population with 100 individuals under both strong ($\beta = 10.0$) and weak ($\beta = 0.01$) selection regimes to compute the respective probability of

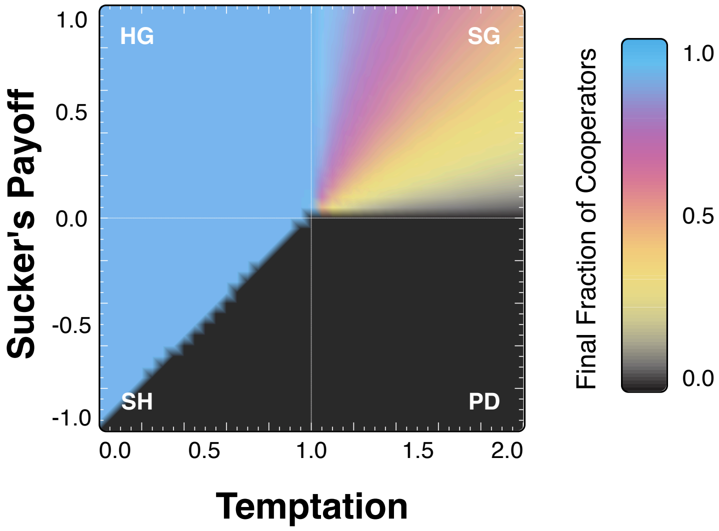


Figure 3.7: Final fraction of cooperators on well-mixed population with 1000 individuals for the entire parameter space under a strong intensity of selection regime ($\beta = 10.0$) starting with 50% of the population as cooperators..

fixation for a each pair of game parameters T and S. When $\beta = 0.0$ the probability of fixation is $1/2$ as individuals imitate others purely at random. This last scenario is the usual term of comparison to measure the success of a strategy, as referred before.

In Figure 3.5 we observe that under strong selection cooperation is favored on the Harmony Game (HG) while in the Prisoner's Dilemma (PD) the opposite happens and the population always ends in a full defection state. On the Stag Hunt (SH) and Snowdrift Game (SG) the result depends on the relative positions of the internal root of the replicator equation (see Figure 3.1), on the initial fraction of cooperators ($\frac{1}{2}$ for the scenario depicted) and on the amount of stochasticity of the imitation process.

Unfortunately, from this methodology we are only able to assess if the population either reaches or not a full cooperation state. If the game, however, leads to a stable internal fixed point, like in the case of a SG, then the population may remain there for an *arbitrary large* amount of time before reaching fixation, which under a stochastic dynamics, like this one, will always happen [67].

One way to address such problem involves taking a further step and dive into the full spirit of Monte-Carlo simulations. For that purpose we simulate the stochastic dynamics of this system numerically: we fix the population size and initial fraction of cooperators. We repeatedly employ the *pairwise comparison rule* as many times as needed until the population reaches a steady state.

In Figure 3.7 we take a look at the final fraction of cooperators after

10^6 iterations (Monte-Carlo steps) for the entire space of parameters on a population of 1000 individuals starting from 50% of cooperators. The results in Figure 3.7 depict a quite different outcome when compared with the results in Figure 3.5, in particular if we look at the SG region where we are able to recognize the existence of a co-existence (x_R) point that dominates in the population.

Chapter 4

Evolutionary dynamics on structured populations

The evolutionary problems faced by cooperators on the PD domain should be taken serious when dealing with the evolution and emergence of cooperation. Indeed, if we want to give a further step into the direction of real-world populations. These are the types of dilemmas thought to describe best most of human interactions. Hence, one may question: which mechanisms provide a sustainable ground for cooperation to thrive? As we will argue in the following chapter, diversity seems to constitute a key mechanism.

Until this point we have discussed the emergence of cooperation making use of classical game theory. In this framework the Prisoner's Dilemma (PD) (see chapter 2.3.1) provides harshest environment for cooperation. We showed how selfish individuals are favored under the PD. The populations were first taken as infinite and well-mixed (chapter 3.2), which allowed the dynamics to be described by the deterministic replicator equation. When dealing with finite populations, we had to take into account stochastic effects inherent to such systems (chapter 3.3). This rendered the problem model non-deterministic. A new description was in order formalized by means of a finite state Markov chain.

Nevertheless the problem was still unsolved and cooperation unable to take its foothold under the range of parameters that concern the PD (see chapter 2.4).

A further effort to model realistic populations may rely on adding an underlying social structure to populations. This draws obvious parallels with real-world populations as is easily evidenced by the fact that individuals do not interact with everyone else but, instead, have a well defined network of friendships as easily shown by modern *web 2.0* social networks.

A way to approach this is by modeling social structures as complex networks where individuals take the place of nodes while links between nodes represent (social) ties between individuals. In this setting individuals interactions are constrained to their nearest neighbors.

During the last fifteen years the understanding and application of complex structures to Evolutionary Game Theory (EGT) models progressed side by side with the most remarkable discoveries of network science [23, 24, 25, 26, 27, 28, 29, 30]. Research on network science was boosted by the need of a more advanced theoretical framework able to cope with the task of modeling real systems (biological, social, technological, etc) more accurately. This helped to revolutionize the way people perceive the importance of network science. In fact, structured populations seem to be part of the recipe to solve the problem of the emergence of cooperation as was shown successively during the last 10 years, with the identification of more realistic network.

The first structures to be applied to EGT were regular networks such as lattices and cycles (for instance a regular ring) [22, 39, 54]. These had a relative success by partially solving the problem of cooperation for a limited set of parameters in the PD domain. Here selection must account for the diversity of fitnesses that emerge among individuals of the same strategy, a consequence of context dependent fitnesses. However these networks are far from being realistic and present no resemblance with the real-world social networks, except, probably with modeling some form of the spatial organization.

One feature that detaches regular lattices from reality is the absence of a second type of diversity, which on the contrary, abounds in real-world social networks. This was ultimately addressed by the introduction of heterogeneous networks that provided a ground for the sustainability of cooperation [31, 32, 33, 34, 35, 36, 37, 38, 39], in a larger domain of the PD. The impact of diversity is remarkably and we depicted it in this chapter.

In the first half of this chapter we briefly discuss the principles of network science (4.1), which are useful to understand the results obtained in this Thesis. In the second half of this chapter we analyze the consequences of structural diversity in the evolutionary dynamics of cooperation.

4.1 The science of Networks: The Building Blocks

Two types of elements compose networks: nodes or vertices and links or edges, the latter connecting pairs of nodes. The complexity of a network comes from the plethora of non-trivial topologies one can build, often observed in real life systems. The properties of these building blocks (nodes and links) can be extended by assuming directed or weighted links or by assigning states to the nodes. These extensions, with exception of the last, will not be discussed here, as we limit our discussion to undirected and unweight links.

The mathematical toolbox for studying the properties of a network is graph theory. A network can be understood as a graph composed of two sets $G = \{N, L\}$ where $N = \{n_1, n_2, n_3, ..., n_{N-1}, n_N\}$ represents the set of nodes and $L = \{l_1, l_2, l_3, ..., l_{N_E-1}, l_{N_E}\}$ the set of links. The maximum number of links a graph of size N can have is $\frac{N(N-1)}{2}$. A network with that many links is called a complete network, meaning that each node is connected with every other node in the network making the structure of the topology meaningless and hence equivalent to a well-mixed population. If a network has a total number of links $L_{N_E} \ll \frac{N(N-1)}{2}$ we say the network is sparse. Most real networks fall into this category. Identifying the nodes by a positive index $i \in [1, N]$ allows defining a link by a pair of commutative indices $i, j \in [1, N]$ that represent the nodes it connects. The nodes connected by a link are said to be first neighbors or adjacent nodes. We refer to the number of links that a node has as its degree, k.

4.1.1 Degree Distribution

A network can be represented by means of a $N \times N$ square matrix, called adjacency matrix. An entry of this matrix, a_{ij}, is 1 if there is a link (l_{ij}) connecting nodes i and j, being 0 otherwise. The degree of a node can thus be computed as:

$$k_i = \sum_{j=1}^{N} a_{ij} \tag{4.1}$$

We refer to the maximum degree of the network k_{max} as the highest degree value of the set of degrees present in the graph $\{k_1, k_2, k_3, ..., k_{N-1}, k_N\}$.

We can look at this property along the entire network by defining the degree distribution $P(k)$, which stands for the frequency of individuals with degree k and that can also be taken as the probability of a node to have degree k (for very large graphs).

We can compute the first moment of this distribution to retrieve the average degree of the graph, z, that is:

$$z \equiv < k > = \sum_{k} kP(k) \tag{4.2}$$

The second moment allows to compute the variance:

$$\sigma_k^2 = \sum_{k} k^2 P(k) - (\sum_{k} kP(k))^2 = < k^2 > - < k >^2 \tag{4.3}$$

Similarly to $P(k)$ we can define the cummulative degree distribution, $D(k)$ that is the frequency of nodes with degree higher or equal to k, and can be written as:

$$D(k) = \frac{1}{N} \sum_{i=k}^{k_{max}} P(k) \tag{4.4}$$

$P(k)$ returns the frequency of a node having k first neighbors, or k nodes at the distance of one link. In principle the same can be done for nodes at higher distances resulting in degree distribution of the respective neighborhood.

4.1.2 Clustering and Distances

One quantity of interest when studying processes that occur on networks, such as information propagation, is the shortest path between every pair of nodes. If we compute all the distances between every pair of nodes we are able to retrieve not only the shortest distance but also the biggest. The latter defines the graph diameter. But it is in fact the so called average path length that is most useful, as it tell us the average distance between any pair of nodes of the network. Let us define d_{ij} as the shortest distance between the pair of nodes i and j. Thus the average path length, APL , of a graph with N nodes is given by

$$APL = \frac{1}{N(N-1)} \sum_{i,j \in N, i \neq j} d_{ij} \tag{4.5}$$

One further quantity that can be measured in graphs is the degree to which nodes tend to cluster together. A qualitative definition of clustering is that provides a measurement of the quantity of triangles present in the network. In social networks this is the same as quantifying the number of friends that have a friend in common, which in graph language is the simple triangle motif.

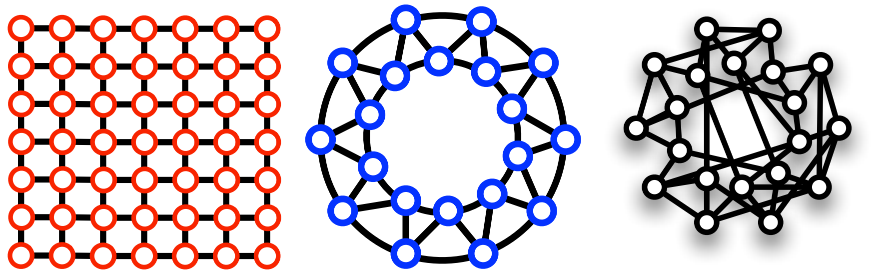
In this Thesis we always refer to the clustering coefficient C that follows the method proposed by *D.J. Watts* and *Steven Strogatz* [23] where C is the average over the cluster coefficient of each node. The cluster coefficient of a node i (c_i) is the ratio between the number triangles connected to $i(\Delta)$ and the total number of triples centered on $i(\Lambda)$:

$$c_i = \frac{\Delta_i}{\Lambda_i} = \frac{\sum_{i,l} a_{ij} a_{jl} a_{li}}{k_i(k_i-1)}, \Delta_i < \Lambda_i \tag{4.6}$$

The clustering coefficient is thus defined as

$$C = \frac{1}{N} \sum_{i=1}^{N} c_i, 0 \leq C \leq 1 \tag{4.7}$$

An example of a property characterized by C and APL is the famous *Small-world effect*, which is identified by a APL (by means of shortcuts) and a relative high value of C (strong local structure). This was first described mathematically in [23] but is also known in popular vennues by the idea as the *six degrees of separation*. There is an empirical experiment which led to the argument that every individual in the world is virtually at the distance of 6 contacts from any other individual in the world [68].



(a) square lattice (b) ring regular (c) homogeneous random

Figure 4.1: Homogeneous Structures. Panel (a) shows the classical square lattice. Panel (b) shows ring regular network which is an example of a cycle graph. Panel (c) exemplifies an homogeneous random graph produced by randomizing the links on a ring regular network.

4.1.3 Homogeneous networks

Networks can be divided into two groups, if analyzed through the degree distribution: Homogeneous networks and Heterogeneous networks. All networks whose nodes share the same degree are defined as homogeneous networks. The degree distribution of these networks has a single peak for $k = z$.

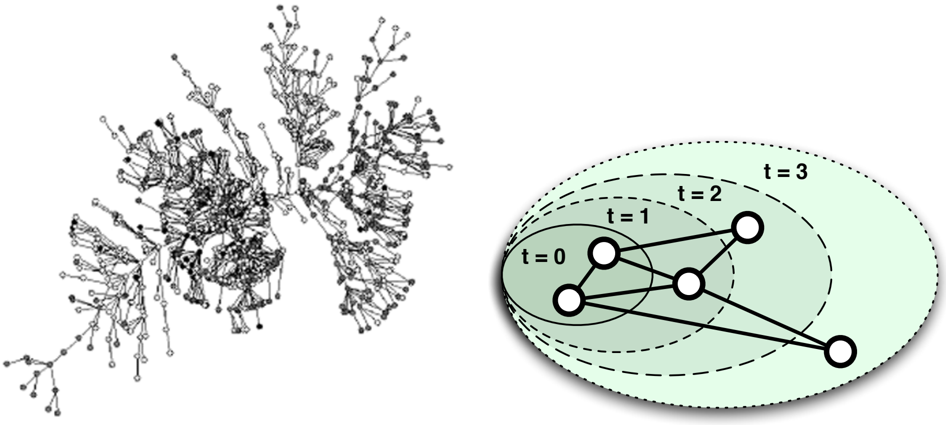
All regular networks are homogeneous and this includes all Lattices and Cycles (ring regular). These structures are usually picked by their simplicity (allowing a deeper exploration of the analytical details of models) and by the many results obtained by physicists [39].

Regular networks lack properties that are observed in real-world networks. Some of these can be emulated if we drop the regularity constraint, which can be disassembled if we allow each link of the network to see one of its ends to be rewired with probability p without changing $P(k)$. For a range of values of p we are able to reproduce the small-world effects on homogeneous networks. To networks generated this way with $p = 1$ we call homogeneous random graphs.

4.1.4 Heterogeneous networks

Heterogeneous networks are characterized by broad degree distributions in clear contrast with the single peaked $P(k)$ already mentioned for homogeneous networks. A random graph of the type studied by Erdős and Růny [69] was probably the first heterogeneous network to be intensively studied. In such graph a link between any two pair of nodes is established or absent with probability p, thus the degree distribution follows a binomial distribution, being a Poisson in the limit of a large graph. These random graphs where also explored independently by *Solomonoff* and *Rapoport* [70, 71].

Although random graphs are by now relatively easy to handle, being



(a) Scale Free structure (b) Preferential Attachment mecanhism

Figure 4.2: Scale Free Structures. Panel (a) shows a network obtained from the *New York Stock Exchange* during a 12-year trading period. Panel (b) shows the mechanism proposed to generate scale free structures: at each time step a new node is added to the network which links itself with two other nodes chosen with probability that is proportional to the number of links they already have

the mathematicians first choice, and do reproduce well the small-world APL effect, they are still far from reproducing real-world network properties such as fat tails, which are ubiquitous in real-world networks.

Graphs that have a power-law like degree distribution are commonly referred as *Scale-Free* (SF) [25]. A great deal of attention was paid to these networks during the last 10 years mainly for being able to reproduce quite well the degree distribution of networks extracted empirically [72, 27, 73]. Although this was obtained first in 1965 with by *Price* when studying the network of citations between scientific papers [74], it was not until *Barabási* and *Albert* showed that both the *WWW* and *Internet networks* had the type of same degree distribution that they become famous [25, 24]. Along with the power law degree distribution, they also discussed the two fundamental mechanisms responsible for the emergence of such shape: growth and preferential attachment [25]. The first mechanism assumes that networks grow in discrete time as new nodes are added. The second mechanism, preferential attachment, asserts that nodes with already many links will obtain new links at a higher rate than those nodes with few links. Example of preferential attachment include internet webpages, that will more likely include hyperlinks to popular webpages, (which already possess a high degree); manuscripts are more likely to cite well known works with already many citations); often the dynamics of preferential attachment is encompassed in the famous economics catchphrase *rich get richer*, which is also known in social sciences as *Matthew effect* [75]. These two mechanisms added together lead to a degree distribution exhibiting a power la behavior and the model is known today as *BA model*.

Soon after many networks extracted from real-world systems were reported to have the same power law like degree distribution [76].

Other algorithms where proposed to generate SF networks where preferential attachment remains a characteristic property [27]. SF networks presents an extreme heterogeneous setting when compared with other heterogeneous networks.

Nowadays it is thought that most real-world networks lay between the random and SF limits of heterogeneity. It is between these two limits that the so-called exponential networks fall, named for its degree distribution that decays exponentially. Empirically it was shown that power grid [26] and railway networks [77] are exponential while some "power law" networks exhibit an exponential cutoff, as is the case of movie actors [26] and some collaboration [29, 28] networks. Exponential graphs are thus of interest when studying the effect of heterogeneity as they offer a middle term between random and SF graphs. Exponential graphs can be constructed using the same growth mechanism of scale-free networks but with a random attachment instead of a preferential rule [78].

In this Thesis we make use of heterogeneous networks with three types of degree distribution: random graphs (ER) that exhibit a Poisson shaped degree distribution; exponential graphs (EXP) with a degree distribution that falls exponentially and SF graphs with power-law degree distribution. Furthermore, because some properties of SF graphs (such as degree-degree correlation and clustering coefficient) strongly depend of the algorithm we use to generated them, we make use of three different types of scale-free graphs: Barabási (SF BA) [25]; Random (SF Rnd) [79] and Minimal (SF MM) [27].

SF Barabási and Exponential graphs are constructed making use of the BA model the first using a preferential attachment assumption while the second using a random attachment rule, [25, 72], the process of the first is depicted in Figure 4.2b. To release SF BA networks from degree-degree correlations we generate SF Rnd by randomizing the links present in SF BA, this way we preserve the degree distribution. Finally we also make use of the Minimal Model [27] that generates SF graphs (SF MM) with a high value of the clustering coefficient. This provides an alternative setting to study the influence of such property in dynamical processes taking place in populations shaped by the SF paradigm. The Minimal Model algorithm assumes that we start a population with a complete graph made of 3 nodes, from this starting point we iteratively add new nodes until we reach the desired population size. At each iteration we select a link at random from the network and connected the new node to both nodes that are at the ends of the selected link.

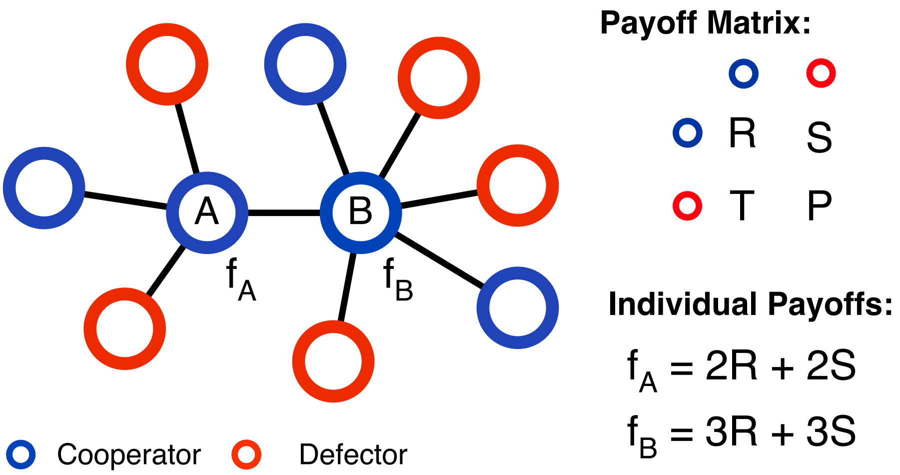


Figure 4.3: In structured populations individuals with the same strategy are able to accumulate different payoffs. Take for instance node A and B, because the composition and size of their neighborhood differs they accumulate different payoffs.

4.2 Games on graphs

While for structureless populations the direction of selection is only related with the frequency of cooperators that compose the population, on structured populations the place that each individual takes in the network is also important to determine the evolutionary outcome of cooperation. Note that a structureless population can be seen as a complete network.

An obvious consequence of this network organization in game dynamics is the appearance of many fitness values as two individuals with the same strategy may accumulate different payoffs if inserted on different contexts, see Figure 4.3. Moreover, as interaction and imitation proceed through links the payoff accumulated by an individual (related with his fitness), and imitation are limited by each individual's neighborhood.

When dealing with heterogeneous populations the number of interactions that each individual accumulates isn't necessarily the same between two individuals. This affects quantitatively the amount of payoff individuals may accumulate, in other words the imitation mechanism will depend on the pair of individuals chosen in the population were selected.

Such a complexity of the evolutionary process on structured populations makes it impossible to write down, in a closed form, an expression that fully describes the evolutionary dynamics of these populations as was done for well-mixed populations. This makes us resort almost exclusively to numerically tools to assess the impact of structure on the evolutionary outcome and establish the correlations between the present topological features and

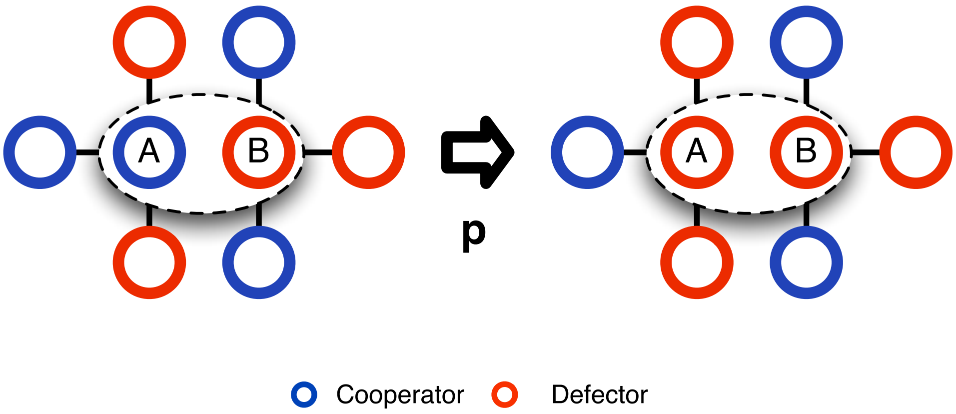


Figure 4.4: Fermi Update Rule on graphs, an individual A selects randomly one of his neighbors, B. With probability p A imitates the strategy of B changing the configuration of strategies on the network.

the evolutionary outcome.

On networks, the *pairwise update rule* must account for the fact that each individual is only able to imitate one of his nearest neighbors (the set of adjacent nodes). This can be translated in the following sequence of steps: select a random individual from the population, A, and randomly choose a neighbor of A, say B; A imitates the strategy of B with a probability p given by the Fermi probability distribution, see equation 3.8, Figure 4.4 describes this process.

This natural change in the model which arises as a result of the network organization of the population has a huge impact on the results as is unveiled in the following section.

4.3 The parameter space revisited, part ii

In this section we explore the impact that social structures have on the evolutionary outcome of cooperation by studying the final fraction of cooperators for populations of $N = 1000$ individuals and an average degree of $z = 4$. We study the final fraction of cooperators as the fraction of cooperators present in the population after 10^7 evolutionary steps. We repeated this computation for 10^4 realizations and thus show the average final fraction of cooperators. We generated 10^3 networks of each type, except for Lattices and Ring Regular, so that eventual topological singularities would be averaged pit. As an initial condition we randomly select 50% of the population to start as cooperators.

To understand the impact of structure in the evolutionary outcome it is important to have in mind the results depicted in Figure 3.7 where a similar methodology was employed for a well-mixed population with a similar size.

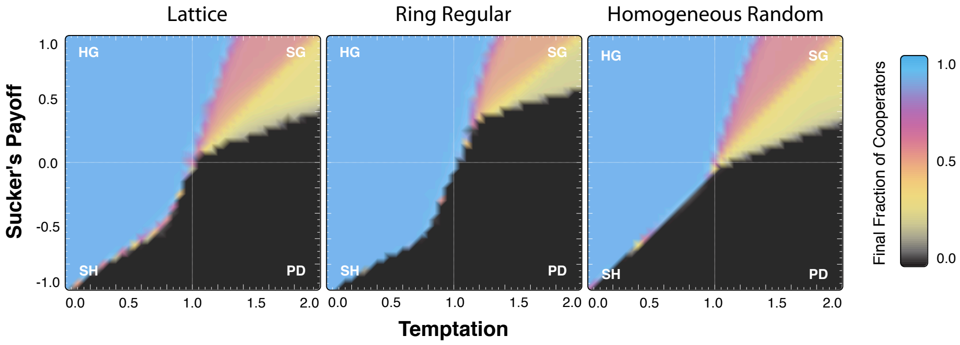


Figure 4.5: Final Fraction of Cooperators on three types of Homogeneous Populations for the entire space of parameters under a strong selection regime ($\beta = 10.0$).

Figure 4.5 depicts the evolutionary outcome on three types of homogeneous structures. The fingerprint of regularity is well detected in the results for populations organized by a regular network of social links as is the case of a Lattice and a Regular Ring shaped network. In these networks, besides the fact that every node has the same amount of connections, every node also possesses the same Cluster Coefficient. The regularity of the topological organization of these nodes allow group together, which plays an important role on homogeneous structures. These regular networks seem to have an odd impact in coordination games as is observed by the shape of the contour in Figure 4.5.

Even on a homogeneous networks note that fitness becomes context dependent.

When node equivalence is broken regarding Cluster Coefficient and topological structure, as result of randomizing the connections between all pair of nodes in the network, keeping their degree intact, we reach a structure that we call Homogeneous Random networks (Horand). These structures seem to have a limited impact in the Stag Hunt (SH) game but start to show some hope, though a limited one, under the PD game parameters. In the Snowdrift Game (SG) this structure seems to constraint the band that divides the Full C from the Full D regime, when compared with the results for fully connected populations, see Figure 3.7.

Although for these types of structures, the evolutionary outcome of a population under both the SG and SH dilemmas changes appreciably (when compared with the WM scenario 3.7), they are still unable to achieve any success for the range of parameters that comprise the PD. Moreover, with this kind of analysis it is hard to correlate any topological property with the results presented. Perhaps the greatest message is that topology and context dependent fitnesses effectively changes the evolutionary outcome for the social dilemmas depicted.

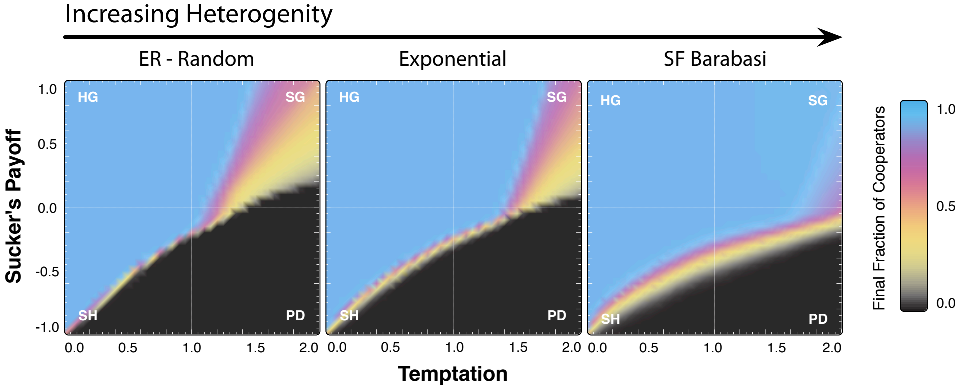


Figure 4.6: Final Fraction of Cooperators on three types of Heterogeneous Populations for the entire space of parameters under a strong selection regime ($\beta = 10.0$).

4.3.1 The Impact of Diversity

Because of the limitations of homogeneous structures referred before we naturally approach heterogeneous networks. In Figure 4.6 we assess the impact that three types of heterogeneous structures have in the evolutionary outcome of cooperation.

As we move from left to right in Figure 4.6, we increase the diversity in the interaction patterns of the population.This is measured by the corresponding the variance of the degree distributions. On heterogeneous structures such as random, exponential and Scale-free networks, different individuals will typically undergo a different number of interactions, as dictated by each individuals social context and pattern of connectivity. Given that the payoff accumulated by each individual dictates her success, diversity in social contexts will certainly have an impact on the evolution. Moreover, given that each individual context also defines the portfolio of role models an individual can chose from to revise her behavior, a heterogeneous social structure implies that some individuals may take profit from their social position to influence a larger number of members of the population than others.

These two types of diversity – in fitness and social influence – may offer some advantage to a minority of highly connected individuals (or particular strategies), irrespectively of their strategic behavior. Indeed, both Cs and Ds may benefit from interacting a large number of times, and also by influencing more individuals than others. This said, the results in Figure 4.6 may come as a surprise, as it shows that diverse environments significantly enlarge the chances of cooperation in every 2-person dilemma considered. The analysis of the role played by a minority of highly connected individuals, as often found in Scale-free networks and, to a lesser extent, in random and exponential networks, may shed a light on this result.

At a first glance, under the PD game, Ds would profit from being in pivotal positions of the network, in particular when surrounded by a significant number of Cs. By exploiting a large number of Cs, their choices will be most likely imitated by their cooperative neighbors. However, in doing so, the central defector will see his fitness reduced, as defectors success is contingent on the number of Cs in the neighborhood. Few generations will be sufficient to make defectors vulnerable to the increasing influence of nearby Cs who maintained their Cooperative trait. Scale-free networks provide ideal conditions for the existence of such cooperators. The existence of interconnected hubs with a broad range of connectivities creates star-like structures of different sizes, in which Cs may play a central role while managing to resist the invasion of Ds, by profiting from a large number of mutual cooperative exchanges. Whenever this happens, these cooperative leading fellows (at their own scale) do profit from their locally cooperative environment to become role models, even to those Ds who eventually end up as victims of their own success [48, 80, 35].

In the appendix we make use of the same methodology to assess the impact of two further Scale-Free structures (Scale-free Random and Scale-free Minimal-Model) while repeating the computations for a scenario where the evolutionary dynamics is under weak selection.

Chapter 5

Context dependent investments and symmetry breaking of the Prisoner's dilemma

In the previous chapter we have witnessed the impact of introducing two different layers of diversity into the population dynamics: diversity in fitnesses and in the role individuals play in populations. The impact of both as depicted in Figure 4.6 allows us to conclude that context diversity provides a sustainable ground for cooperation to thrive under the PD.

The structures that had more impact are characterized by a strong accentuated heterogeneity in the nodes degree, putting evidence the importance of having individuals that act as role models on a population were traits evolve through a mechanism of imitation.

In this chapter we grasp yet into another layer of diversity as we approach a situation where the amount that each individual contributes may not be the same, in particular when we consider a scenario of limited resources.

5.1 The distributed prisoner's dilemma

Quite often we are confronted with situations in which the act of giving is more important than the amount given. Take for instance a charity event. Some celebrities are usually invited to participate. Their appearance is given maximal audience, and shown contributing a large amount of money. With their media coverage, which is impressive to many, promoters hope to induce a large number of (much smaller) contributions from anonymous (non-celebrities, the overwhelming majority) charity participants, who feel compelled to contribute given the fact that their role model (the celebrity) contributed. Clearly the majority imitates the act of giving and not the

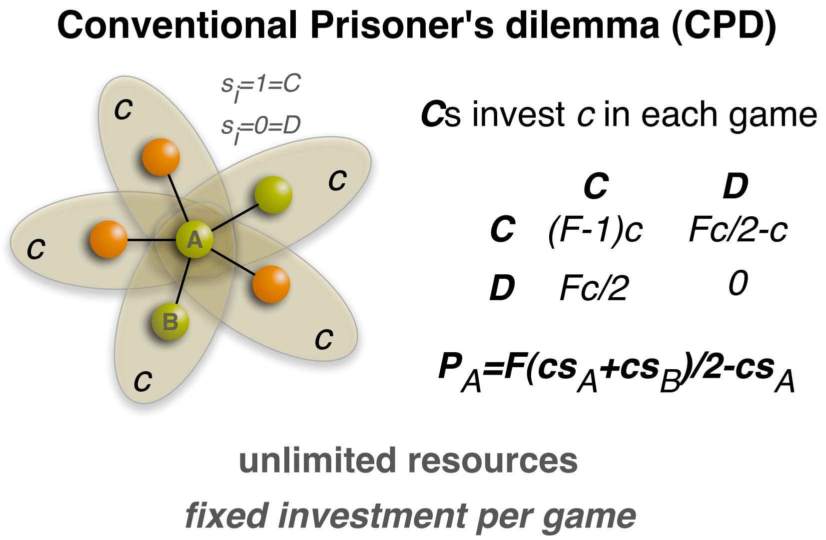


Figure 5.1: In this Figure we represent the contribute scheme of the Conventional Prisoner's Dilemma, which is similar to a setting where individuals have unlimited resources to invest on their interactions. Under this assumption a cooperator **A** invests the same cost c per interaction, which let us resume all the possible outcomes by a payoff matrix, or alternatively by the expression P_A

amount given.

Many other examples from real life could be provided along similar lines, from trivia, to fads, to stock markets, to Humanitarian causes up to the salvation of planet Earth [81, 82]. Many of these situations provide examples of public goods games (PGG) [83] which are often hard to dissociate from reputation building, social norms and moral principles [17, 84, 85, 86, 87].

The simplest PGG involves only two individuals. Both have the opportunity to contribute a cost c to a common pool. A Cooperator (C) is one who contributes; otherwise he is a Defector (D).The total amount contributed is multiplied by an enhancement factor F and equally shared among the two participants. Hence, player i $(i = 1, 2)$ using strategy s_i ($s_i = 1$ if C, 0 if D) gets a payoff $P_i = Fc(s_1 + s_2)/2 - cs_i$ from this game, leading to the following payoff matrix:

$$\begin{array}{c c} & \begin{array}{cc} C & \quad D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} (F-1)c & Fc/2-c \\ Fc/2 & 0 \end{pmatrix} \end{array} \tag{5.1}$$

This payoff matrix is in all similar to those we have made use previously, in particular along chapter 2, but now we have written each outcome from the usual PGG point of view. For $F \leq 1$ Ds dominate unconditionally. For

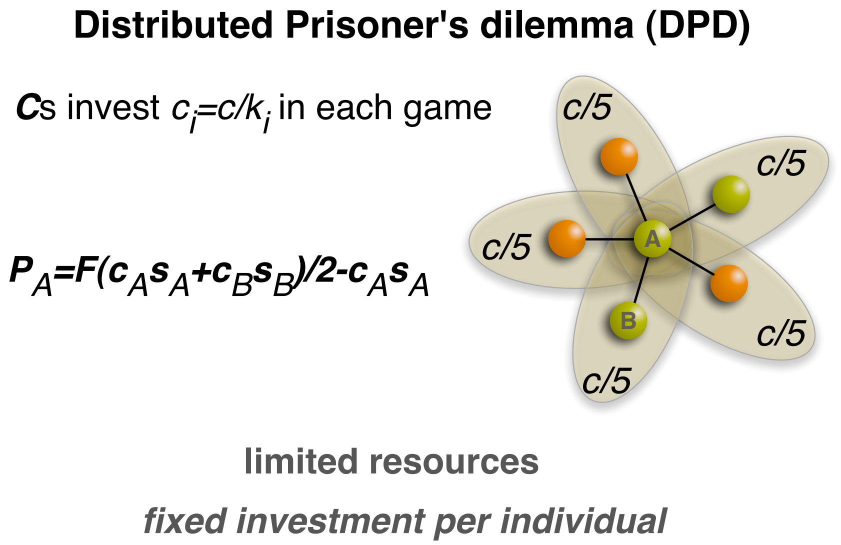


Figure 5.2: In this Figure we represent the contribute scheme of the Distributed Prisoner's Dilemma, which is similar to a setting where individuals have limited resources to invest on their interactions. Under this assumption the cooperator divides an amount c per all interactions where he participates, this makes impossible to write the possible outcomes on a payoff matrix. Ultimately this leads to a break of symmetry of the game, as two individuals may invest different amounts in the same game, which is made clear by the context dependent of the contributions of each individual in the expression of P_A.

$F = 2$ no strategy is favored in well mixed populations (neutral drift); yet, for $F > 2$, it is better to play C despite the fact that, in a mixed pair, a D collects a higher payoff than a C. For $1 < F < 2$ the game falls into the popular symmetric one-shot two-person prisoner's dilemma [7], which has been widely investigated [18, 1, 22, 3, 88, 60, 47, 34, 48, 35, 38, 80, 39, 89, 90, 36, 33, 37, 91, 92, 93, 94]. We will refer to this contributive scheme as the Conventional Prisoner's Dilemma (CPD).

In the social dilemma with the payoff matrix given by equation (5.1), every C pays a fixed cost c per game, providing the corresponding same benefit to the partner. However, if what matters is the act of giving and not the amount given, then there is no reason to assume that everybody contributes the same cost c to each game. Depending on the amount associated with each individual contribution, the overall result of the evolutionary dynamics may change. The two person game introduced above provides not only the ideal ground to introduce such a diversity of contributions, but also an intuitive coupling between game dynamics and social structure: The first (second) individual contributes a cost c_1 (c_2) if playing C and nothing otherwise. Hence, player i ($i = 1, 2$) now gets the following payoff from this game:

$$P_i = F(c_1 s_1 + c_2 s_2)/2 - c_i s_i \tag{5.2}$$

reflecting the symmetry breaking induced by possibly different contributions from different cooperating individuals, we call to this scheme of contributions the Distributed Prisoner's Dilemma (DPD).This poses a natural question: Who will acquire an evolutionary edge under these conditions?

Often the amount that each individual contributes is correlated with the social context he is actually embedded in [80, 43]. Modern communities are grounded in complex social networks of investment and cooperation, in which some individuals play radically different roles and interact more and more often than others. As discussed in chapter 4 empirical studies have demonstrated that social networks share both small-world properties and heterogeneous degree distribution [72, 95, 96]. In such heterogeneous communities, where different individuals may be embedded in very different social environments, it is hard to imagine that every C will always provide the same amount in every game interaction, hence reducing the problem to the standard two-person prisoner's dilemma studied so far. In the context of N-person games played in prototypical social networks, it has been found that the diversity of contributions greatly favors cooperation. However, and similar to the relation between two-body and many-body interactions in the Physical Sciences, N-person public goods games have an intrinsic complexity which cannot be anticipated from two-person games. As such it is not clear in which way heterogeneous networks, which naturally induce the symmetry breaking alluded to before, enhance or inhibit the evolution of cooperation.

5.2 Discussion and Results

Figure 5.3 shows the final fraction of cooperators, corresponding to the average, over 10^3 runs and networks[1], of the value obtained for this fraction, in each run, after 10^5 generations. This is done for each point (F and degree) and for the three different population structures.

Figure 5.3A shows the outcome of evolving the conventional 2-person PD ($1 < F < 2$), in which case each player contributes a fixed amount c to each game he participates. The existence of a minority of highly connected individuals in SF networks (line and filled circles) allows the population to preserve high cooperative standards, while on homogeneous networks (line

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[1] Three types of networks were explored in this work: Ring Regular (REG); Exponential (EXP) and Scale-free Barabsi (SF). The first type presents an example of a homogeneous structure, the scale-free is an extremely heterogeneous network while the Exponential network provides a middle term between these two types of networks. For more details on the properties of these networks see chapter 4

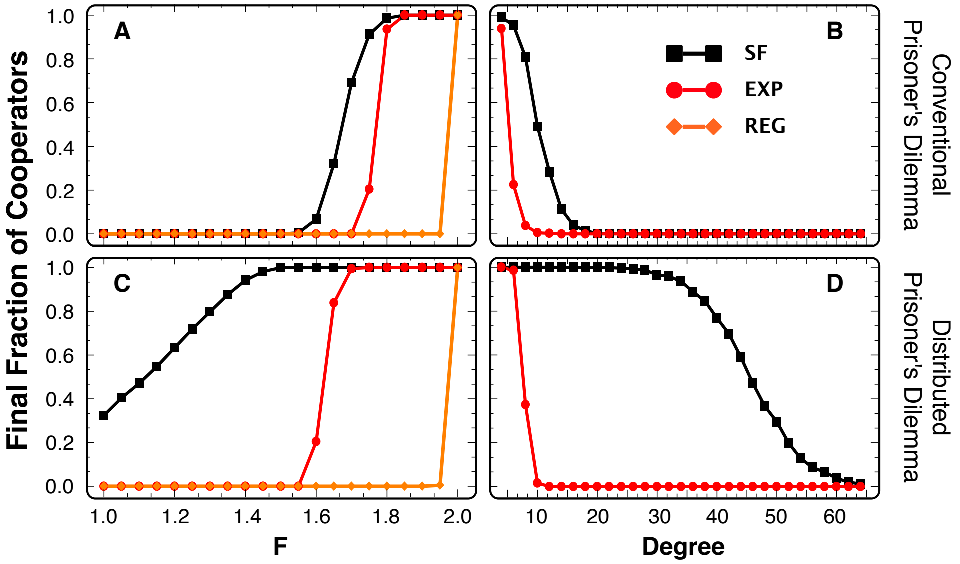
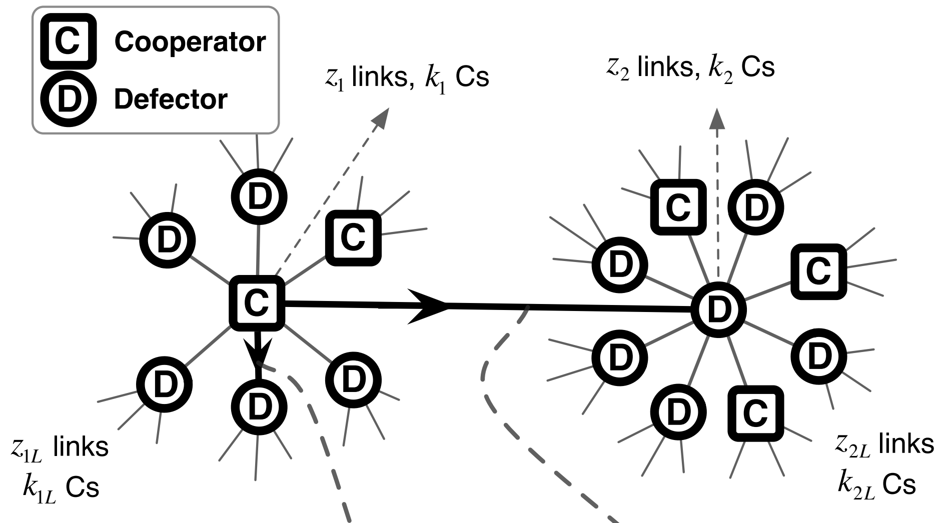


Figure 5.3: Final fraction of cooperators as a function of i) the enhancement factor F (panels A and C) and ii) the degree for the EXP and SF networks with $F = 1.8$ (panels B and D). Panel A: Under CPD Cooperation is able to dominate on SF networks (black squares), unlike what happens on REG structures (orange circles). On exponential networks, intermediate levels of cooperation emerge, as a result of the heterogeneity of such topologies (empty diamonds). Panel C: Under DPD the advantage of Cs is dramatically enhanced when the same cost is evenly shared among each neighbor. As expected, abandoning the well-mixed regime leads to a break-up of neutrality for $F = 2$. Panels B and D : Cooperation is able to dominate on sparse networks. Yet only under DPD, combined with high levels of heterogeneity attained on Scale-free networks, one observes the maintenance of cooperative behavior in highly connected populations. The results were obtained for networks of 10^3 nodes and variable average degree ($z = 4$ in panels A and C) starting with 50% of Cs randomly distributed in the population.

and empty diamonds), Ds dominate for the entire range of parameters, as a result of the pairwise comparison rule adopted. Heterogeneous networks thus pave the way for the emergence of cooperation. Highly connected individuals (i.e. hubs) work as catalysers of cooperative behavior, as their large number of interactions allows them to accumulate a high fitness. This, in turn, leads them to act as role models for a large number of social ties. To the extent that hubs are Cs, they influence the vast majority of the population to follow their behavior. Clearly, this feature has a stronger impact on SF networks than on EXP networks, the difference between these two types of networks stemming from the presence or absence, respectively, of the



$0 \le \eta = \frac{2}{F} - 1 \le 1$

	leaves (hub-neighbors)	hub
CPD	a) $\frac{k_1}{z_1} > \eta + \frac{k_{1L}}{z_1}$	b) $\frac{k_1}{z_1} > \eta + \frac{k_2}{z_1}$
DPD	c) $\frac{k_1}{z_{1L}} > \eta + \frac{1}{z_1} + \frac{k_{1L} - 1}{z_0}$	d) $\frac{k_1}{z_{1L}} > \eta + \frac{1}{z_1} + \frac{k_2 - 1}{z_{2L}}$

Figure 5.4: From the definitions of the parameters in the figure one obtains that DPD leads systematically to less stringent conditions for invasion of the C (squares) occupying the left hub, explaining the increased success of Cs under DPD. On general heterogeneous populations with average connectivity z_0, conditions *a)* and *b)*, as well as *c)* and *d)*, show that it is easier to invade a D (circles) on a leaf than in the center of another hub. This invasion creates a positive feedback resulting from cooperative leaves surrounding the left hub (k_1 - k_2 increases) allowing a subsequent invasion of the right hub.

preferential attachment mechanism (see chapter 4).

The results in Figure 5.3A and 5.3B are based on a CPD assumption thus following in close the results already discussed in chapter 4, while Figure 5.3C and 5.3D considers the DPD dilemma. While on homogeneous networks the fate of cooperation is the same as before - it amounts to rescaling the intensity of selection - heterogeneity in the amount contributed by each individual to each game creates a remarkable boost in the final number of Cs for the entire range of F, which increases with increasing heterogeneity of the underlying network. Comparison with the results of Figure 5.3A shows that under DPD preferential attachment plays a prominent role, since it constitutes the network wiring mechanism distinguishing EXP networks from SF networks. Changing from CPD to DPD induces moderate boosts in the equilibrium fraction of Cs on EXP networks, but a spectacular boost of cooperation on SF networks: Hubs become extremely influential under the DPD.

In order to understand the mechanism underlying the population-wide boost of cooperation obtained, we consider a prototypical element of a heterogeneous network (similarly to what has been done in [80, 39, 32]) as shown in Figure 5.4, and investigate the microscopic balance determining individual change. In particular, we investigate under which conditions the central C on the left – a stereotypical hub – becomes advantageous, that is, accumulates a higher fitness than any of his neighbors (see Figure 5.4). We consider a C-hub with z_1 links (k_1 of which are Cs, left in Figure 5.4) and a D-hub with z_2 links (k_2 of which are Cs, right in Figure 5.4). We assume, for simplicity, that all neighbors of the C hub have z_{1L} links each (k_{1L} of which are Cs), whereas all neighbors of the D hub have z_{2L} links (k_{2L} of which are Cs). The remaining nodes have z_0 links, where z_0 stands, e.g., for the average connectivity of the population. We implicitly assume that the neighbors of the hubs have smaller connectivities, and consequently we call them "leaves".

The conditions are explicitly provided in Figure 5.4 for both DPD and CPD. In both paradigms, for the C-hub to invade the D-hub (or any of his D-leaf neighbors) depends crucially on the difference between the number k_1 of C-neighbors of the C-hub and the number k_2 (k_{1L}) of C-neighbors of the D-hub (D-leaf). In both DPD and CPD the invasion threshold is always smaller for leaf invasion compared to hub invasion. Furthermore, the threshold for invasion is also smaller under DPD compared to CPD. Finally, as one would expect, all thresholds coincide when networks are homogeneous, the threshold conditions making it harder for invasion to occur in these networks. As a result, on heterogeneous networks, the conditions which render a C-hub advantageous with respect to a D-hub are more stringent than those associated with invasion of a neighbor D-leaf, which leads to an invasion pattern in which leaves are invaded before hubs [48]. Furthermore, one should not overlook that successful Ds tend to place other Ds in their neighborhood [48] which acts as a negative feedback mechanism reducing their fitness in time. On the contrary, successful Cs see their fitness increase in time, as more Cs join their neighborhood, reinforcing their fitness.

The impact of the DPD paradigm, however, is most dramatic if one takes into consideration that the condition for the C-hub to become advantageous becomes less stringent the larger his connectivity. On the contrary, under the CPD paradigm, the cost of cooperation plays a major role in the overall fitness of the C-hub, which means that the larger his connectivity, the harder it will be for the C-hub to become advantageous with respect to any of his D-neighbors. Finally, the threshold conditions in Figure 5.4 also show that under DPD the range of game interaction is enlarged, as second neighbors of a hub also play a role in defining the invasion thresholds, unlike what happens under CPD. The insights provided by the prototypical configuration in Figure 5.4 become more explicit if one computes the outcome of cooperation in SF networks for social networks with different average connectivities and both contributive schemes (Figure 5.4). As the average degree (z) becomes sizable cooperation will inevitably collapse [47, 48], but while cooperation can hardly resist for $z > 10$ in the case of CPD, under DPD Cs survive for values of z roughly four times larger. This is of particular importance given that social networks often exhibit high average connectivity values ($2 \leq z \leq 100$)[72]: Cooperation prevails under a DPD contributive system, even on less sparse static network structures. For intermediate regimes of heterogeneity (EXP networks), under DPD cooperation is also sustained up to higher values of z, but to a lesser extent: Once more, the impact of large hubs resulting from the preferential attachment mechanism underlying SF networks plays an impressive role under DPD.

Chapter 6

Gradient of Selection

In this thesis we have already introduced the fundamentals for the evolutionary dynamics on infinite and finite well-mixed populations (chapter 3). In the case of an infinite and well-mixed population the dynamics is deterministic and completely described by the replicator equation, while for finite populations the inherent stochasticity required a new approach which in the limit of large population and under weak selection regimes resumes to the replicator dynamics.

In chapter 4 we have assessed the impact of complex structures in the evolutionary outcome of cooperation. The introduction of complex structures made the computation of the fitness context-dependent. As a result it become impossible to write down a closed form set of equations that fully describe the evolutionary process for such systems. In other words a complete dynamical picture of the system has been impossible to gather.

These complex network structures added two layers of diversity previously absent from the well-mixed models, in particular diversity among the fitnesses that individuals have and, for heterogeneous networks, the diversity among the number of interactions that each individual participates. This was shown to have a huge impact in the overall picture of sustainability of cooperation across the social dilemmas of cooperation: Stag Hunt (SH); Snowdrift Game (SG) and Prisoner's Dilemma (PD)

In this chapter we introduce a mean-field quantity that we call Gradient of Selection, which is computed numerically and has the purpose of extract dynamical properties that emerge in structured populations. This quantity constitutes a mean-field observable, as we extract information from every possible transitions taking place in every node of the network to draw an average picture of the dynamics of the entire population, which is network dependent but context independent.

Later we make use of this new description to assess the impact that the breaking the symmetry the evolutionary dynamics of cooperation in the

Distributed Prisoner's Dilemma, hence establishing a connection chapter 5. In this way we conclude our study on the impact of context dependent investments.

6.1 Gradient of Selection

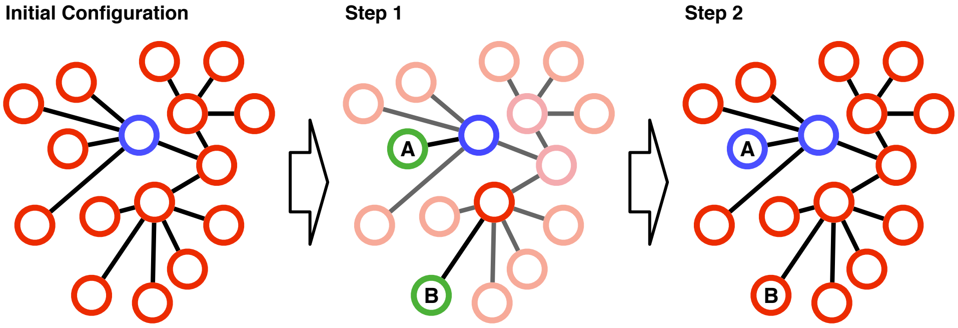


Figure 6.1: Initially we place a Cooperator at random in the population. **Step 1** We choose a Defector at random in the population A. **Step 2** if A has a Cooperator neighbor, it (not) becomes a Cooperator, if not has is the case of B, go back to **1**. These steps are repeated until the right number of Cooperators is reached.

Let us take a population with N individuals of which j are cooperators. The gradient of selection $G(j)$ returns the direction of selection and is computed by taking a mean-file approach to the problem[1] $G(j)$ is defined as follows [97]:

$$G(j) = T^{+}(j) - T^{-}(j) \tag{6.1}$$

where $T^{+}(j)$ ($T^{-}(j)$) is the probability of having one more (less) cooperator in the population. This terms have now to take into account the population structure and ar defined as:

$$T^{+/-}(j) = \frac{1}{N}\sum_{i=1}^{ADs/ACs}\frac{1}{k_i}\sum_{m=1}^{c_i/d_i}(1+\exp(-\beta(f(m)-f(i)))^{-1} \tag{6.2}$$

where ACs (ADs) identifies a sum over all cooperators (defectors) in the population, k_i is the degree of individual i, c_i (d_i) identifies a sum over all neighbors of individual i that are cooperators (defectors) and $f(i)$ is the fitness of individual i [66].

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[1] Sometimes is more convenient to express the gradient of selection after normalizing the number of cooperators by the size of the population which leads to a gradient of selection $G(x)$ where $x = \frac{j}{N}$

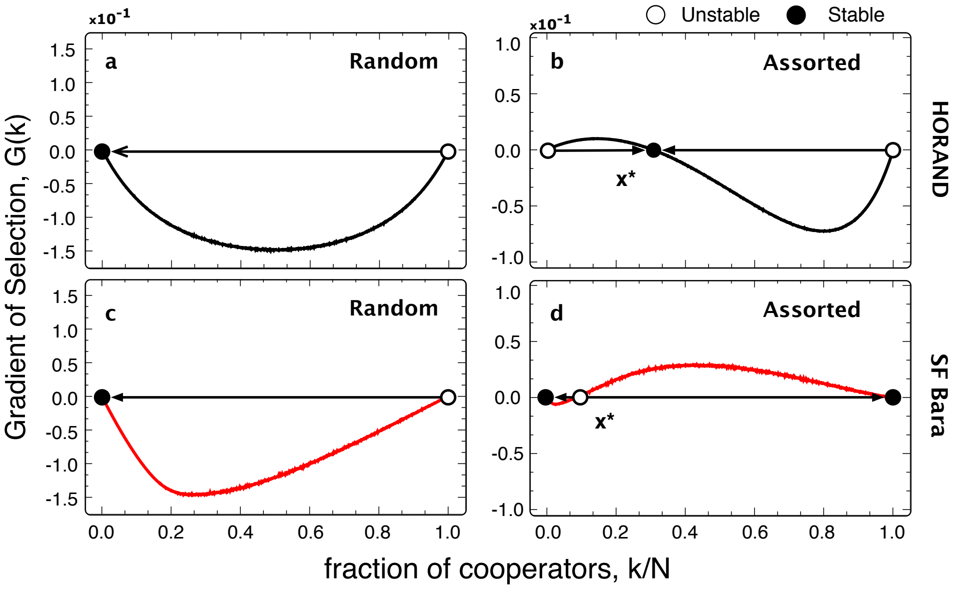

Figure 6.2: $G(j)$ for homogeneous random graphs (**HORAND** in black) and a scale-free Barabasi (**SF Bara** in red). Strategies are randomly placed in the network (Panels **a** and **c**) or "percolated" (Panels **b** and **d**) in the sense described in the main text (see also Figure 6.1). In the case of the **HORAND** the $G(j)$ where computed for $B = 1.01$ and $C = -0.01$, while for **SF Bara** we used $B = 1.25$ and $C = -0.25$. For both structures we used the same intensity of selection $\beta = 10.0$ being the population made of 1000 individuals with average degree of $z = 4$.

The gradient of selection must be computed for as many states as possible and for a large number of networks of a fixed class, thus returning a quantity that becomes context independent but network dependent.

The fact that both T^+ and T^- depend on the properties and context of each individual that makes it impossible to bring the dynamics into a closed form. For $0 < j < N$ three different results can be obtained:

$\mathbf{G(j) > 0}$ It is more likely that the number of cooperators will increase;

$\mathbf{G(j) < 0}$ It is more likely that the number of cooperators will decrease;

$\mathbf{G(j) = 0}$ The population is in a state of neutral drift and it is equally likely that the number of cooperators increase or decrease.

This tool allows us to extract overall dynamical information from a structured population. In the following sections we discuss the consequences of several types of structure in the effective game underlying the population-wide dynamics.

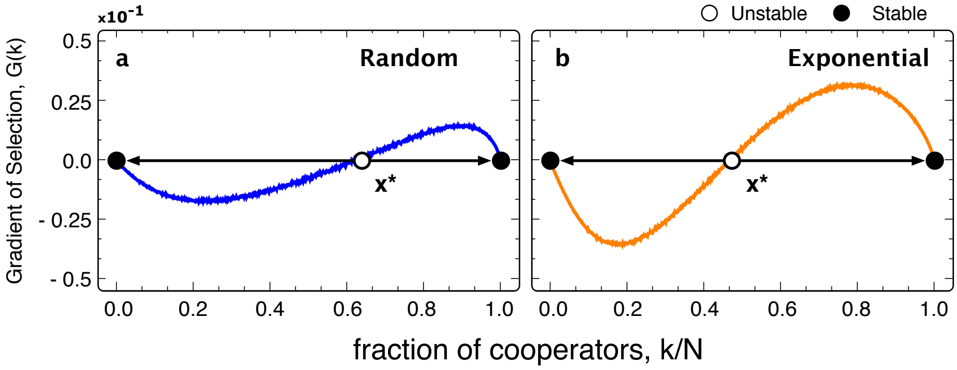

Figure 6.3: $G(j)$ for two heterogenous structures, in particular random graphs (panel **a**) and exponential graphs (panel **b**). These results are in accordance with our assumptions that heterogeneous networks change the effective dilemma faced by individuals from a Prisoner's Dilemma to a Coordination Game. The $G(j)$ was computed for populations with 1000 individuals and average degree of $z = 4$. Regarding the game parameters we used we used a benefit of 1.5 and a cost of -0.5 for the Exponential graphs, while for the random graphs we used a benefit of 1.25 and a cost of -0.25.

6.2 The impact of strategy assortment

Let us describe how to extract information by placing cooperators on a network according to a pre-defined procedure.

In most cases the number of possible arrangements of strategies (configurations) in the population is huge and the evolutionary process does not necessarily accesses configurations with an equal probability. In fact the evolutionary process proceeds by making use of a restricted set of possible states within the plethora of available states. It is important to note that what we are trying to model here is the impact of population structure on the evolutionary outcome and not to compute the average gradient over all possible strategies arrangements.

At start strategies are placed at random. This makes it easy to assess which type of social dilemma or effective game the population faces at the start of the evolutionary process.

In panels **a** and **c** of Figure 6.2 we show $G(j)$ for two types of structures (Homogeneous Random Graphs and Scale Free Barabási) with 1000 individuals for a situation where strategies are randomly assigned. It is possible to observe that $G(j)$ is negative and thus the effective dilemma played by the population is of the same type social dilemma that rules the pair interactions: the Prisoner's Dilemma.

However this picture only remains true if the evolutionary process kept assorting strategies randomly. Obviously this is not the case and after a

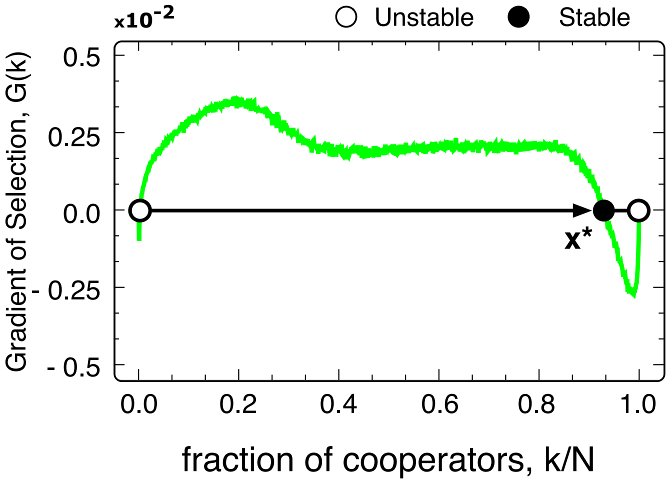

Figure 6.4: $G(j)$ computed for a population that is structured according to a lattice where individuals are linked with their 4 nearest neighbors. This result is in accordance with our assumptions that homogeneous networks change the effective dilemma faced by individuals from a Prisoner's Dilemma to a Co-existence Game. $G(j)$ was computed for populations with 1000 individuals and average degree of $z = 4$. Regarding the game parameters a benefit of 1.01 and a cost of -0.01.

few iterations the scenario becomes quite different from the original one. A simple rule encompasses the type of assortment that is promoted by the evolutionary process: cooperators (defectors) breed cooperators (defectors) [36]. This can be empirically verified if we look at the type of arrangements that are present in the population during later stages of the evolution process.

To study the impact that structures have in the evolutionary process we make use of an algorithm that assorts cooperators in a way that qualitatively follows the evolutionary rule by which strategies are assorted. This allow us to compute $G(j)$ afterwards. Conclusions on the impact of such structures are then drawn. The following algorithm describes how the placement of cooperators is done in a "percolated", or assorted way:

First Select a D, i, at random from the population;

Second Check if i has at least one cooperator in his neighborhood, if yes, i becomes a C, else nothing happens.

Repeat the last two steps until the desired fraction of cooperators in the population is achieved.

This algorithm is also summarized in Figure 6.1.

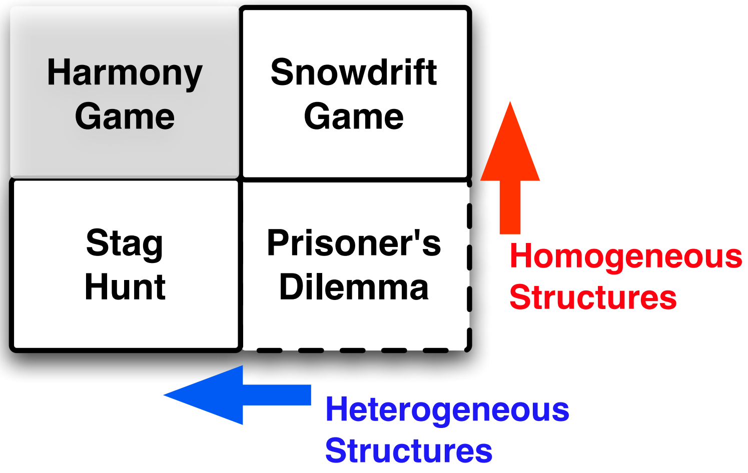

Figure 6.5: This scheme summarizes the impact that each type of structure has in the effective dilemma played by the population.

It is easy to reckon that evolution tends to assort strategies. It is difficult however to know for sure with which degree are these strategies "percolated" during the evolutionary process. For instance will the dynamics promote a single giant component or is it going to create a variety of small clusters of different strategies? For the sake of simplicity we will take strategies which grow into a single giant component.

Nevertheless if we accept that evolution naturally "percolates" strategies even when populations start from a random initial conditions then we are able, with the help of the algorithm described above, to extract which type of assortment occurs during the evolutionary process on the effective game played by the population.

In panels **b** and **d** of Figure 6.2 we show the $G(j)$ computed for the same structures but for a situation where strategies are assorted or "percolated" by means of the algorithm described above. Clearly, the effective dilemma now portraited is quite different, and it is different for the two structures. In particular we are able to observe what kind of change occurs in the effective dilemma played in two types of networks. Here we argue that the evolutionary process changes the effective game felt on a homogeneous networked population from a Prisoner's Dilemma to a Co-existence game. A corresponding transformation occurs on heterogeneous networked populations, where the effective game changes from a Prisoner's Dilemma to a Coordination game which has its parallels with the Stag Hunt dilemma. In Figures 6.3 and 6.4 we expand these results for additional heterogeneous and homogeneous structures. Remarkably the same conclusions hold for these different types of structures.

Such results can lead us to a broader conclusion: studying the evolution-

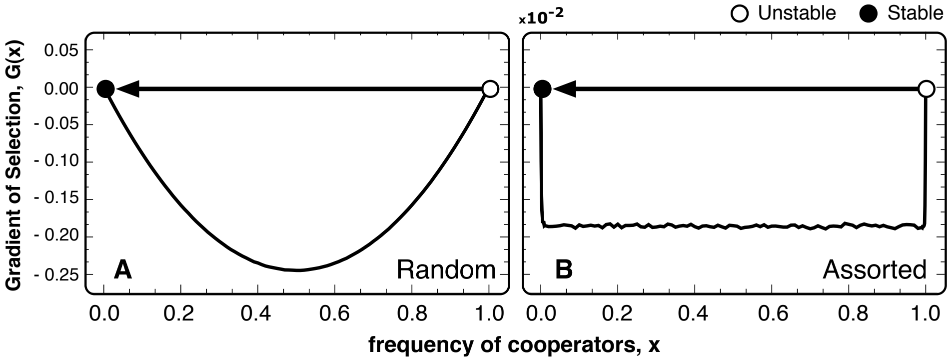

Figure 6.6: G(x) for Regular Networks and F = 1.25. Both random and assorted distributions of strategies are considered. For both distributions the G(x) is always negative, meaning, that the features of the initial prisoner's dilemma remain intact at a population-wide level.

ary outcome of a population under the PD of cooperation on networks is equivalent to study a different dilemma on a well-mixed population. Studying the PD on an homogeneous structure is similar to study a SG on a well-mixed population whereas studying the PD on Heterogeneous structures is equivalent to the SH dilemma in a well-mixed population. In this way we now know that the evolutionary process changes the effective dilemma faced by a networked population, and we can even say which type of change occurs. We consider this approach a good starting point for any study that aims to extract dynamical information from a population. Note that sometimes the initial dilemma faced by the population does not correspond exactly with the one that is modeled. But can we make use of this description to assess the impact that other subtle changes have on the evolutionary dynamics at a population-wide level?

In the following section we make use of the $G(j)$ to assess the impact that the third layer of diversity discussed in the previous chapter has on the effective game faced by the population.

6.3 The impact of breaking the game symmetry

In chapter 5 we assessed the impact of breaking the game symmetry by context dependent investments. From that analysis we found that heterogeneous networks boost cooperation (Figure 5.3). A close-up analysis of how important nodes that make up such heterogeneous networks, the hubs, interact with each other gives us a glimpse of the way in which they favor cooperation, as a result of the symmetry breaking game dynamics. The same analysis carried out on homogeneous networks is useless, however, as game

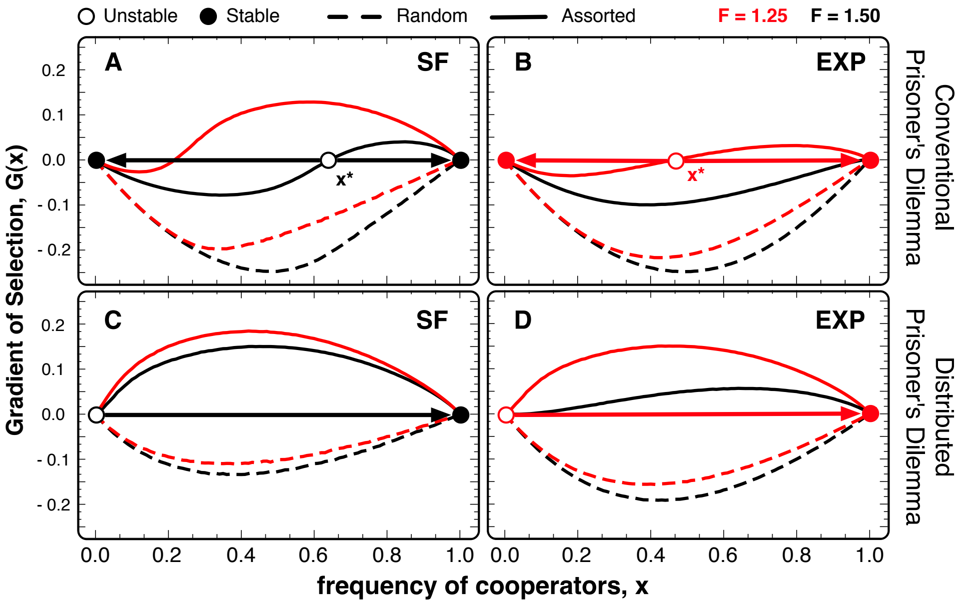

Figure 6.7: $G(x)$ for $F = 1.25$ (red lines) and $F = 1.50$ (black lines) for random (dashed lines) and assorted (solid lines) distributions of strategies for two types of heterogeneous networks (EXP and SF). Under the CPD paradigm (panels A and B) and with the appropriate value of F, heterogeneous networks lead to the appearance of an unstable fixed point x^* (open circles) characteristic of a coordination game. Under DPD (panels C and D), the change in the effective game is even more marked and in the case of SF networks the game transformation occurs between a $G(x)$ always negative (PD) to a scenario where it is positive for most values of x, characteristic of a Harmony game, where cooperators dominate unconditionally. In both panels the networks employed had 10^3 nodes and an average degree $z = 4$, and $\beta = 10.0$.

symmetry is kept intact on such networks. In order to probe deeper into the mechanism(s) underlying the prevalence of cooperators in the Distributed Prisoner's Dilemma (DPD), we will make use of the Gradient of Selection as defined in the previous chapter. In this we overlook the microscopic details of the competition and self-organization of Cs and Ds, but we gain an overview of the game dynamics in a mean-field, yet network dependent, prespective..

In Figures 6.6 and 6.7 we plot the $G(x)$ as a function of x for both random and assorted distributions of strategies accounting for two different values of F and both PD paradigms: CPD and DPD.

On homogeneous networks (Figure 6.6) Ds are always advantageous. On heterogeneous networks the initial PD (dashed lines) is effectively transformed into a different game (full lines). Figure 6.7A and 6.7B indicates that, in the case of CPD, introducing diversity in roles and positions in the social network effectively leads to a coordination game, characterized (in an infinite, well-mixed population) by a critical fraction x^* above which Cs are always advantageous ($G < 0$ for $x < x^*$ and $G > 0$ for $x > x^*$). This result provides a powerful qualitative rationale for many results obtained previously on heterogeneous networks under strong selection [47, 34, 80] in which degree heterogeneity is shown to induce cooperative behavior, inasmuch as the initial fraction of Cs is sufficient to overcome the coordination threshold. Moreover, Figure 6.7C shows that changing the contributive scheme from CPD to DPD in SF population structures acts to change a PD effectively into a Harmony game where Cs become advantageous irrespectively of the fraction of Cs ($x^* \approx 0$)

6.3.1 Conclusions

From these results we can understand in which way the results of the study of chapter 5 are obtained, providing evidence of the impact that breaking the symmetry of cooperative contributions in the global effective dilemma faced by the population.

On strongly heterogeneous networks, the results of Figure 5.3 provide an impressive account of the impact of this diversity of contributions. Our results suggest that whenever the act of cooperation is associated to the act of contributing, and not to the amount contributed, cooperation blooms insofar as the structure of the social web is heterogeneous, leading individuals to play diverse roles. The multiplicity of roles and contributions induced by the social structure effectively transforms a local cooperative dilemma into a global coordination game [5]. Moreover our results provide additional evidence that the assortation of strategies arising from the intricate nature of collective dynamics of cooperation in a complex network leads to a change in the effective game played by the population: While locally cooperation can be understood as a PD, globally it is effectively described by a coordination dilemma[5].

Chapter 7

Final Remarks

We started this thesis by introducing the fundamentals of Evolutionary Game Theory (chapters 2 and 3). This framework provided us with the tools needed to model two-person interactions for the three main social dilemmas (Stag Hunt, Prisoner's Dilemma and Snowdrift Games). A description of how the composition of an infinite and finite well-mixed population of such type of individuals changes in time was also provided. Regarding the evolutionary dynamics of cooperation we faced the problem addressed the emergence of cooperation, which under this description simply does not happen.

The impact of introducing population structure in the evolutionary outcome of cooperation was then discussed in chapter 4. The results were obtained making use of the * numerical tools used by the community. The main problems with the use of such tools were put into evidence. The impact of structures where the diversity among the fitnesses that individuals collect and on the amount of interactions that each participates was discussed.

In chapter 5 we studied a third mechanism of diversity and assessed its impact on the evolutionary outcome of the population. This third root of diversity assumes that when individuals have a limited amount of resources to invest, the symmetry of the Prisoner's Dilemma game is broken on heterogeneous populations. In other words it would be possible for two individuals to interact under the same dilemma using the same strategy (C) but contribute a different amount.

In chapter 6 we defined a quantity denominated Gradient of Selection. This mean-field quantity allowed to extract the dynamical properties from a population by looking at the pair-interaction properties of its individuals. The main properties and conclusions that we we were able to extract were discussed. The impact of structures and of diversity in the evolutionary dynamics was for the first time assessed from a dynamical point of view. Finally we made use of this new quantity to assess the impact that breaking of symmetry in the Prisoner's Dilemma introduced in the effective game faced by the population.

We have thus investigated the impact that three simple forms of diversity have in the sustainability of cooperation, even when individuals are deprived of complex enforcement mechanisms, reputation or punishment [98, 99, 100, 101, 102, 5, 103, 104, 105]. Nevertheless there are other forms of diversity that have been pointed out in recent literature and which corroborate the findings discussed in this thesis, for instance diversity on the learning rates [44, 41, 43] and diversity of signals when employing a dynamics that involves signaling between individuals [106]. All this insights correlate positively with recent experiments that aim to understand the impact of diversity and globalization [107] in human cooperation.

7.1 Comment on the methods

All results presented in this thesis were computed by the author during the time of this thesis and comprised many hours of computation in two clusters that sum up to a total of 186 cores. All numerical tools were developed in $C/C{+}{+}$ as it provided a convenient computational framework. Additionally we have also made use of $Mathematica$ 7.0 to compute some of the results in chapter 3.

Future work should comprise further development of the numerical tools used to extract the gradient of selection from structured populations and a better understanding on how strategies in the population are assorted by the evolutionary mechanism. An extension of this quantity for two player games with three strategies seems a natural step that should be achieved when the appropriate computational resources are made available.

It is of our belief that this tool can, in the near future, be used to extract information from the evolutionary dynamics itself, allowing us to peer into the impact of further dynamics that co-evolve with the imitation.

Appendix A

Notes on the evolutionary dynamics on structured populations

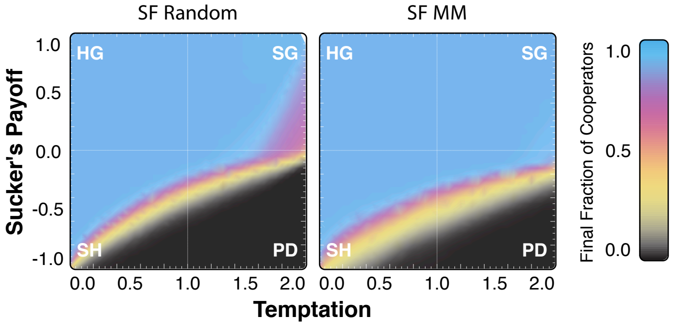

Figure A.1: Final Fraction of Cooperators for two types of SF Populations: Scale-Free Random and Scale-Free Minimal Model. The Final Fraction of Cooperators was computed for the entire space of parameters under a strong selection regime ($\beta = 10.0$).

In this appendix we deliver additional results on the impact that structured populations have on the evolutionary outcome of cooperation. The results follow the same style that was used chapter 4 to discuss and describe the impact of a group of networks under strong selection. Here we expand this group by including two extra types of heterogeneous structures: Scale-free Random and Minimal Model (see section 4.1.4). Finally we repeat the same methods to assess the impact that a weaker intensity of selection has on the evolutionary outcome on structured populations.

Similar to chapter 4, all results were obtained for at least 1000 different networks of each type (except for regular networks) with a size of 1000 and an average degree of $z = 4$. Our numerical simulations determined the fraction of cooperators of cooperators present in the population after 10^7

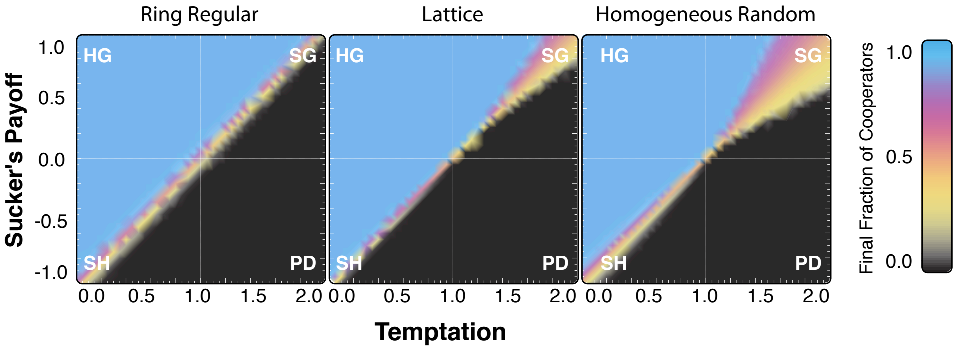

Figure A.2: Final Fraction of Cooperators for three types of Homogenous Populations: Ring Regular, Lattice and Homogeneous Random. The Final Fraction of Cooperators was computed for the entire space of parameters under a weak selection regime ($\beta = 0.1$).

evolutionary steps. We repeated this computation over 10^4 realizations and thus present the average final fraction of cooperators. As an initial condition we randomly select 50% of the population to start as cooperators.

In Figure A.1 we put into evidence the impact of a pure scale-free distribution (SF Random) characterized by the absence of any type of topological correlations, and of a scale-free distribution with a large cluster coefficient (SF MM). The Impact of the last, which adds a large cluster coefficient to the natural degree-degree correlation that emerges from any growing algorithm with preferential attachment, proves to be higher.

In Figures A.2 and A.3 we show similar results to those already discussed in Figures 4.5,4.6 and A.1 but for a weaker intensity of selection regime ($\beta = 0.1$). In general, for homogeneous networks this imply that the results approach the well-mixed scenario. On the other hand, for heterogeneous networks (and scale-free structures in particular) this seems to improve the overall sustainability of cooperation as the area of the Prisoner's Dilemma that has a final fraction of cooperators above 0 increases.

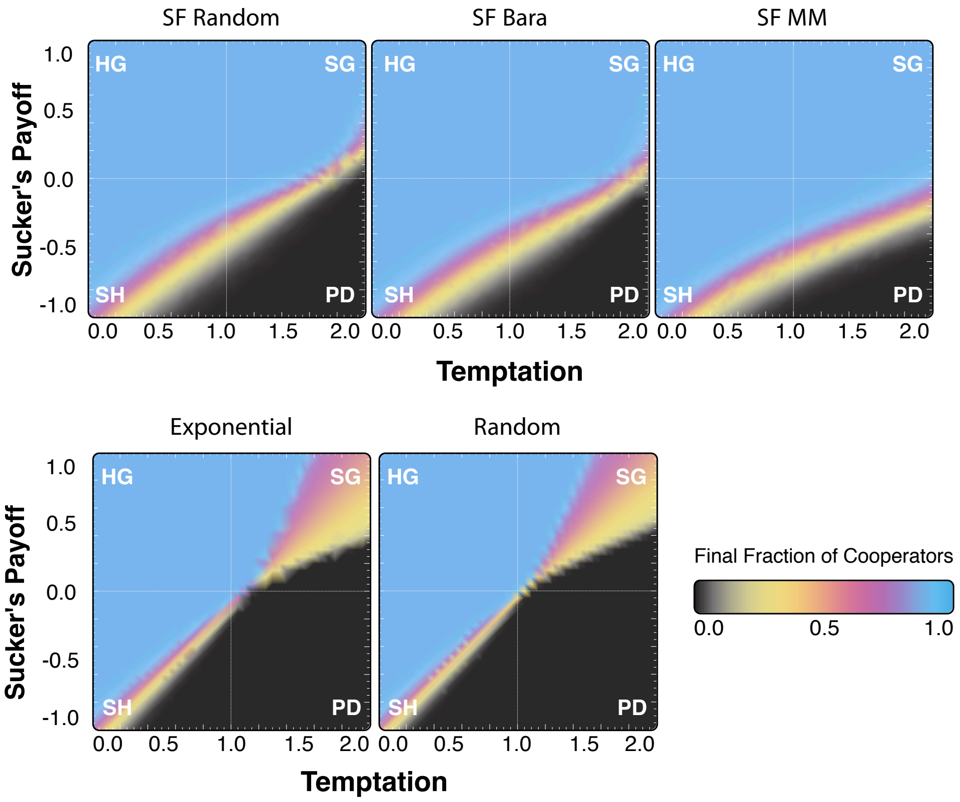

Figure A.3: Final Fraction of Cooperators for three of SF Populations: Scale-Free Random, Scale-free Barabasi and Scale-Free Minimal Model and two less extreme heterogeneous populations: Exponential and Random. The Final Fraction of Cooperators was computed for the entire space of parameters under a weak selection regime ($\beta = 0.1$).

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