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Evolutionary Dynamics of Cooperation in Multiplayer Games

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Mestrado em Física
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Abstract

Cooperation is an act where individuals can contribute something, at a cost to themselves, to provide a benefit for others. We can find situations where this kind of act can arise at almost every layer of human societies and also in the animal world.

Such a widespread behavior can be studied using Game Theory, a mathematical formulation of multi-optional interactions. The theory takes its predictions from social games between rational individuals that want to maximize their profit. When applied to dilemmas of cooperation, the theory predicts the demise of those who contribute, thus contradicting extensive empirical evidence.

Evolutionary Game Theory was created to counteract this shortcoming. It drops the rationality assumption of Game Theory and instead places individuals in a dynamical context where natural selection applies. Thus, in view of this theory, the most successful individuals (who profit the most from games) are more likely to leave descendants or be imitated by others, depending on the kind of dynamics being considered. Nevertheless, this process by itself does not yet explain the emergence of cooperation and only by adding other mechanisms to the dynamics can we make this property appear.

In this thesis we present three such mechanisms all in the context of Public Goods Games. In these games, individuals in a group choose if they want to contribute to a common good that is then transformed into a benefit to be equally shared by all group members.

The first mechanism applies to infinite well-mixed population dynamics and consists of a detaching in time the impact of the game on the system. By applying a time delay to the profits, we can modify a specific public goods game in order to give cooperation a chance.

The other mechanisms are somewhat similar and apply to finite structured populations where individuals are restricted to interacting with specific opponents. They both consider that this interaction structure is shaped by the game dynamics and can evolve over time. The second and third mechanisms are thus a numerical and analytical implementation, respectively, of this co-evolutionary dynamics.

Resumo

A Cooperação é uma acção em que temos indivíduos que podem contribuir com algo para beneficiar outros, pagando os primeiros um custo. Exemplos de situações onde a cooperação pode surgir encontram-se em quase todas as camadas da sociedade: desde pessoas a terem uma conversa ou a realizar um debate político, a jogar no mercado bolsista, a caçar ou a arranjar mantimentos ou até a construir um edifício ou uma comunidade inteira. No mundo animal também pode surgir cooperação, no contexto de caçadas, protecção contra predadores ou em lideranças de grupo.

Um comportamento tão vasto pode ser estudado utilizando Teoria de Jogos, uma formulação matemática de interacções multi-estratégicas. A teoria faz previsões através da realização de jogos sociais entre indivíduos racionais que querem maximizar o seu lucro. Quando aplicada a dilemas de cooperação, a teoria prevê a extinção da cooperação, o que contradiz vastos dados empíricos.

A Teoria de Jogos Evolutiva foi criada com o intuito de corrigir essa falha. Esta teoria deixa cair o postulado da racionalidade da teoria anterior e considera então que os indivíduos estão num contexto dinâmico sendo estes afectados pela selecção natural. Portanto, de acordo com a teoria, os indivíduos mais fortes (que obtêm mais lucros dos jogos) são os que mais hipóteses têm de deixar descendentes ou de ser imitados, consoante o tipo de dinâmicas consideradas. No entanto, este processo por si só não explica ainda a emergência da cooperação. É preciso adicionar outros mecanismos para fazer aparecer esta propriedade.

Nesta tese apresentamos três destes mecanismos, todos no contexto dos Jogos de Bem Público. Nestes jogos, indivíduos juntam-se num grupo e escolhem se querem ou não contribuir para um bem público que depois é transformado e dividido igualmente por todos os membros desse grupo.

O primeiro mecanismo aplica-se a dinâmicas de populações infinitas well-mixed onde qualquer indivíduo interage com qualquer outro com a mesma probabilidade, e consiste em separar temporalmente o impacto do jogo no sistema considerado. Aplicando um atraso temporal aos lucros podemos modificar um tipo específico de jogo de bem público de modo a que a cooperação tenha uma hipótese de subsistir.

Os outros mecanismos são algo similares e aplicam-se a populações finitas e estruturadas onde os indivíduos estão restringidos a interagir apenas com determinados oponentes. Ambos consideram que esta estrutura de interacção é moldada pelo jogo e pode evoluir ao longo do tempo. O segundo e terceiro mecanismos são portanto uma implementação numérica e analítica, respectivamente, desta dinâmica co-evolutiva.

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Chapter 1

Introduction

The word ‘Cooperation’ can elicit a wide assortment of definitions. The most accessible meaning is undoubtedly in the context of human interactions. A person is said to be cooperating with another individual if he or she is helping this other person reach some goal, or attain some benefit, that may or may not be a mutual one. Of course, a cooperative act need not take place between two individuals alone, it can involve many others interacting together.

This definition of cooperation can easily be extended to animal interactions: animals can hunt, defend from prey and practice several other activities together with one or more members of their species. The cost of practicing that activity may be less than what it would be, had this animal been alone. Cooperation does not need to be a conscious act, as it can be found everywhere, from the tiniest insect to the largest mammal.

If you factor in time, then these acts of cooperation that lower costs are inexorably tied to natural selection. If an individual, whether human or animal, can achieve something more easily than others, he or she will inevitably become more fit than them. Which in turn increases his or her chances of reproducing or of being imitated.

A mathematical framework used to model scenarios involving cooperative acts is *Game Theory* [1]. It was first developed in the late 40s and it can be used to formalize, by means of ‘social games’ between individuals, the conditions defining cooperation or any other type of multi-optional interactions; it further assumes individuals to be purely rational, in the mathematical sense of maximizing the game payoff [2]. In Chapter 2 we present some of the most emblematic games involved in defining cooperation.

A few decades later, in the 1970s this theory was extended to include the effects of natural selection and became known as *Evolutionary Game Theory* [3]. This theory differed from its classic counterpart by shifting its focus away from the individual’s rationality and instead concentrating on how their actions spread and affect their surroundings.

Many studies were made on this issue, mainly in the context of pair interactions, i.e.,

on *2-person games* [4]. Theorists soon realized, however, that most games predict that no cooperation should emerge at all. Therein lay the problem, because obviously cooperation is present not only in our society but also in the animal world. In view of this difficulties many mechanisms were devised to counter the demise of cooperation [5, 6, 7, 8, 9, 10]. While they are certainly important, this kind of pair interactions do not represent the complete picture of human or animal interactions. For that we must consider multiplayer interactions which, due of their added complexity (akin to that of N -body problems in physics), have not been so widely studied yet [11, 12, 13, 14, 15, 16, 17, 18]. Starting from the second half of Chapter 2 we focus only on these *multiplayer games*, more traditionally called *N -person games*. Of this class, we shall concentrate on a simpler form, known as *Public Goods Games*.

We provide here three new mechanisms, two of them somewhat similar. When added to N -person games they shed some light on why cooperation is a viable option for some situations we shall specify. These include scenarios where the actions of a group of entities only manifest themselves in some future time and where the closest acquaintances of an individual or animal are always changing. Surely these are situations one encounters in everyday life.

More often that not our actions are detached in time from their consequences. Academic success, stock prices, credit card bills or bountiful supplies are all consequences of some past action undertaken by an individual or group of individuals. Surprisingly, for a topic of such a widespread scope, very little research was done in the context of games with time delay, and only on 2-person games [19, 20, 21]. In Chapter 4 we investigate how time delay affects multiplayer games.

A common aspect of many social species is that their members have a limited capacity of interaction, i.e., they cannot interact with every single individual in their community. This limited capacity constitutes an underlying structure of the population and it can be modeled in terms of a network. This mathematical entity is nothing more than an abstract representation of entities (humans, animals, organizations, computers, etc.) representing certain predefined relation between them.

Networks accommodate two kinds of dynamical processes: the ones that affect the properties of its constituting entities and the ones that act on the topology of the network itself. For instance, an evolutionary game of cooperation can be of the former type [22, 23, 24, 25], while growth and evolution of structures are dynamics of the latter [26, 27].

If we couple these two types together, then the dynamics of the network's constituents can affect its global topology and vice-versa. Such structures, called *adaptive networks*, are a fairly recent topic of research [28]. To our knowledge, no study has been done to date about the workings of adaptive networks in the context of N -person games. We present in Chapters 5 and 6 numerical and analytical models, respectively, on this subject.

Chapter 2

Classical Game Theory

The prototypical framework of game theory was established by von Neumann and Morgenstern in 1944 [1]. Initially developed as a mathematical approach to economic behavior, it has since greatly expanded its scope to encompass nearly every type of multi-optional interaction. The problem of cooperation can be addressed in a unified way using the tools provided by game theory.

We follow a common application of game theory where we consider two individuals that interact using some predetermined rule or strategy that may be unique to each of them — *2-person games* [29]. Their gaming strategies can be very diverse and range from being self-regarded to adaptive and contingent on that of their adversaries. The outcome of this interaction or game relies heavily on the rationality of the participants [2].

This common approach to games is concerned with the study of equilibria, i.e., the best strategy for each player to adopt. The rationality assumption where each player tries to maximize his or her payoff, leads inevitably to an equilibrium where a player's profit cannot be higher should anyone unilaterally change strategy. This concept is known as *Nash Equilibrium* and will be detailed in Section 2.1, where we also define the basic properties of cooperation dilemmas.

In view of the theory, the dilemma of cooperation can be studied through a type of game where a player can pay a certain cost to convey a benefit to the other player. Section 2.2 deals with some of the simplest 2-person games of cooperation. In Section 2.3 we generalize some of those 2-person games to include N ($N \geq 2$) participants which, as we will see, constitute examples of a small class of *N-person games* known as *Public Goods Games*. From that point onwards, this thesis will focus solely on those many player variants of social dilemmas of cooperation.

2.1 Basic Game Concepts

A participant in a game adopts a strategy which, upon interaction with other players, grants a correspondent payoff. In this work, an individual is permitted to choose a strategy from a set of only two strategies: either Cooperator (C) or Defector (D). In general, a game can have many more strategies [4]. All individuals decide simultaneously which strategy to adopt.

Central to the theory is the identification, if they exist, of the equilibria of the game, i.e., the set of strategies to take so that each player is satisfied with their payoffs. Rational players will adopt a strategy that, taking into account the possible actions of their opponents, will benefit them the most — a best-response to all other strategies (note that, in this work we do not allow mixed strategies). If all players adopt a strategy from which none can benefit further from switching, then this set of chosen strategies constitutes the so-called *Nash Equilibrium* (NE) [30].

More formally, in a N -person game, player i can choose a strategy s_i from set $S_i = \{C, D\}$, such that $\Sigma = S_1 \times S_2 \times \dots \times S_N$ is the set of possible strategies for all players — set of strategy profiles. Let $\sigma \in \Sigma$ represent a certain strategy profile and $\bar{s}_i = (s_1, s_2, \dots, s_{i-1}, s_{i+1}, \dots, s_N)$ denote the strategies chosen by all players except i , who gets a payoff $\Pi(s_i; \bar{s}_i)$ from this profile. A strategy profile $\sigma^* \in \Sigma$ is a NE if any single player cannot get a higher payoff by unilaterally changing strategy, that is:

$$\forall_i, s_i \in S_i, s_i \neq s_i^* : \Pi(s_i^*; \bar{s}_i^*) \geq \Pi(s_i; \bar{s}_i^*) \quad (2.1)$$

When the inequality holds strictly (with $>$ instead of \geq) for all i and s_i , we have a strict NE. If instead, for some player, there is equality ($=$) in the equation above, we have a weak NE.

A game can have more than one NE depending on the relative ordering of the payoffs. If players are uncertain about the other player's choices, they will opt for the strategy that provides the higher average payoff, leading to a *risk dominant* NE. Conversely, if all players could agree on the strategies that provide all of them with the highest possible payoffs, they would be in a *payoff dominant* or *Pareto efficient* NE. If all players have the same strategy at the equilibrium, it is said to be a *symmetric* NE, otherwise it is an *asymmetric* one.

2.2 Symmetric 2-Person Games

In the simplest case of two individuals, the possible payoffs they get from a one-shot interaction depend on their chosen strategies and can be summarized in a 2×2 matrix, containing all possible payoffs of the game:

$$\begin{array}{c} \mathbf{B} \\ \begin{array}{cc} C & D \\ \mathbf{A} \begin{array}{c} C \\ D \end{array} \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array} \end{array} \quad (2.2)$$

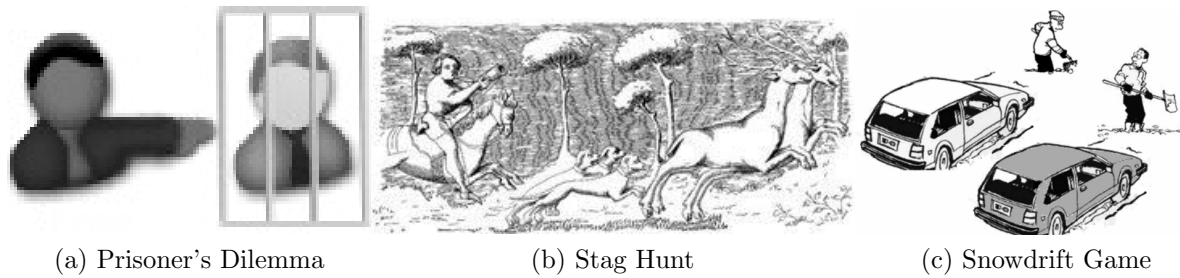


Figure 2.1: Representations of three typical 2-person games.

The entries constitute the payoffs that player A can receive. When two C 's (D 's) interact they both receive the reward R (punishment P). When a C meets a D , the first receives the sucker's payoff S , whereas the second gains the temptation to defect T and vice-versa. A game such as this one, where players A and B receive the same payoff when adopting the same strategy is called a *symmetric game*. Here we outline the most popular symmetric 2-person games of cooperation which can be characterized by such a payoff matrix.

2.2.1 Prisoner's Dilemma

The most famous dilemma of cooperation is certainly the *Prisoner's Dilemma* (PD) [31]. The original formulation, in terms of sentence years for prisoners gave the game its distinctive name. Depending on whether they tell off their partner (D) or stay quiet (C) and on the partner's action, their sentence will be different.

In this game a rational player will always defect, with no regard for the other player's intention. Using the notation of matrix (2.2), we can define this game through the following payoff relation: $T > R > P > S$. Since $\Pi(D, D) > \Pi(C, D)$ and $\Pi(C, C) < \Pi(D, C)$, the only NE for the PD is indeed (D, D) , i.e., when both players defect. It is a risk dominant equilibrium since the payoff for mutual defection is smaller than for mutual cooperation, hence the dilemma.

It is one of the toughest games for the thriving of cooperation which, paradoxically, represents many real life situations in nature and among human interactions. Areas like economics, politics, sociology and biology are therefore very keen on the study of the PD.

2.2.2 Stag Hunt

A game nearly as used as the PD is the *Stag Hunt* (SH) [32]. It can be illustrated as a hunting scenario, where two individuals can hunt either hare or stag. To catch the former, only individual effort is required (D), but the latter catch requires the collective effort of both players (C). The SH is also known as the rowing or trust game.

We use the relation $R > T > P > S$ to represent the SH. Because $\Pi(D, D) > \Pi(C, D)$ and $\Pi(C, C) > \Pi(D, C)$, aside from the NE of the PD, this game has an additional

equilibrium at (C, C) , this one Pareto efficient, as it provides the highest payoff for both players.

Going back to the hunting example, the two NE indicate that, when one hunter decides to go for stag the other should follow suit, and vice-versa. Thus, the best course of action is for both players to coordinate their actions and use the same strategy. This fact actually makes the SH more suitable to study some economic or animal interactions than the PD [32] and in fact, it is also known as the assurance game or trust dilemma.

2.2.3 Snowdrift Game

The *Snowdrift Game* (SG) was originally created to describe the course of action when two drivers are caught in a blizzard and need to clear the road to go home [33]. Evidently, each driver prefers to stay in the car (D) however if no one decides to shovel the snow (C) neither can proceed.

The SG is representative of a series of games in which the maximum payoff is obtained from doing the opposite of what the other player does. The relation $T > R > S > P$ translates this idea, which favors a mixed equilibrium. Indeed, doing the same calculations as above, we find that the NE for the game are (C, D) and (D, C) , which means that two different players can coexist in a stable equilibrium. This game is also known as hawk-dove or chicken game.

2.2.4 Harmony Game

The last game prototype is known as the *Harmony Game* (HG) [34]. It is rarely mentioned because, as the name implies, it does not constitute a dilemma at all. It represents an ideal world where C 's thrive with null effort. The HG can be written as $R > T > S > P$ and as such has only one NE at (C, C) .

2.3 N -Person Public Goods Games

The generalization of the theory to games involving more than two players interacting simultaneously makes for a richer set of applications. Only within the realm of multiplayer games can we fully study the consequences of the collective action of individuals. Group meetings of various sorts, political agreements, animal group-hunting, team sports, public transportation systems and communal decisions in both humans and animals are just some possible applications of multiplayer games. Common to them is the fact that the participants interact in groups instead of in pairs.

Such a leap, from two players to many players, involves, in its simplest form, the addition of a new independent parameter, the group size of the participants in a game, thus giving rise to a class of N -person dilemmas known as *Public Goods Games* (PGG).

Given all their added complexity, in this thesis we will focus on this simple class of N -person games. In a PGG, individuals in a group choose whether or not to contribute to a common pool from which a benefit is extracted and shared by everyone [35]. Moreover, the

size of the group, N , determines the number of individuals that play together. Moreover, a group is composed of j C 's and $N - j$ D 's. When $N = 2$, we are reduced to the previous case of 2-person games.

2.3.1 N -Person Prisoners Dilemma

The N -person *Prisoners Dilemma* (NPD) [36] is a simple example of a PGG. We have a group composed of j C 's, who contribute to the group at a cost c to themselves, and $N - j$ D 's, who contribute nothing. The sum of all contributions is then enlarged, by a certain multiplication or enhancement factor F , to become the public good of the group. This quantity is then divided evenly among all members of the group, regardless of their strategy.

The payoffs that the different individuals get from their group is given by the relations below, respectively, if they are D 's or C 's:

$$\Pi_D(j) = \frac{jFc}{N} \quad (2.3)$$

$$\Pi_C(j) = \Pi_D(j) - c \quad (2.4)$$

The above relations show that this game is indeed a generalization of the PD: If we let $N = 2$, we obtain the payoff relation of the PD from Section 2.2.1.

2.3.2 N -Person Stag Hunt Game

Some PGGs do not necessarily produce a benefit. Sometimes, a minimum number of contributors are required for a benefit to be produced, e.g., in animal group-hunting or political assemblies. Only above a certain threshold can proponents get their way, whether in hunting a larger prey or approving a new law. Once this threshold is achieved the benefits received may scale with the additional number of supporters. In the earlier examples this means more meat for the hunters and ease in the approval of laws.

This kind of group interaction can be modeled as a N -person *Stag Hunt* (NSH) [15]. In this game, similarly to the SH briefly mentioned in Section 2.2.2, the maximum payoff can be obtained if all individuals in the group coordinate to play the same strategy. As in the NPD, C 's contribute to the group by paying a cost c and D 's do not contribute at all. However, in the case of the NSH, only when the number of C 's in the group, j , is larger than a threshold M ($0 \leq M \leq N$) do we apply the enhancement factor F to produce the group benefit. Otherwise no benefit is produced. So, the payoff of a D and a C in a group will be given, respectively, by:

$$\Pi_D(j) = \frac{jFc}{N} \theta(j - M) \quad (2.5)$$

$$\Pi_C(j) = \Pi_D(j) - c \quad (2.6)$$

The presence of the threshold M is translated by the Heaviside function $\theta(a)$, with $\theta(a < 0) = 0$ and $\theta(a \geq 0) = 1$. The above equations show that, in the case of $M \leq 1$, the NSH exactly reduces to the NPD.

2.3.3 *N*-Person Snowdrift Game

It was mentioned above that, in the NSH, the benefits scale with the number of C 's in a group. However there are some situations where this is not the case. For instance, in the construction of a building, there is still a minimum number of workers necessary, but the benefit is fixed. Additionally, the more workers there are, the less individual effort will be required. Put differently, the more C 's there are in a group, the better off are the D 's.

This scenario is clearly not a NSH but a generalized SG — a *N-person Snowdrift Game* (NSG) [16]. In this game, there may be also a threshold of cooperation that must be surpassed in order for a benefit b to be produced. However, now all C 's in the group share the cost c of benefit production. According to this, the different strategists get the following payoffs:

$$\Pi_D(j) = b\theta(j - M) \quad (2.7)$$

$$\Pi_C(j) = \Pi_D(j) - \frac{c}{j}\theta(j - M) - \frac{c}{M}(1 - \theta(j - M)) \quad (2.8)$$

Where c is the minimum cost necessary to produce a benefit and the threshold M must now be larger than zero, i.e., $1 \leq M \leq N$.

Chapter 3

Evolutionary Game Theory

The field of *Evolutionary Game Theory* (EGT) was first proposed in 1973 by Maynard-Smith and Price [3]. In their paper they proposed the concept of an *Evolutionarily Stable Strategy*, that is, a strategy that cannot be invaded by any alternative strategy that is initially rare. This concept will be properly analyzed in Section 3.1.

Unlike classical game theory, EGT does not rely on the rationality of individuals. Instead it considers that they belong to a population that is affected by some sort of evolutionary dynamics and then focus on the spread of game strategies in this population. The payoffs of the game now depend on the frequency of all available strategies. Strategies that are successful, are granted a higher payoff and so they will spread throughout the population. This effect can have two distinct interpretations.

The more traditional one is inspired by biology and associates the payoff of an individual with his or her reproductive fitness. Individuals pass on their behavior to their descendants, the number of which will depend on the fitness of the progenitor. In this way, successful strategies will spread in the population to the next generation.

The other interpretation applies to cultural evolution. According to this one, the strategy of the more fit individuals will have a higher probability of being imitated. In this view, strategies spread by imitation and not by reproduction.

Both these interpretations can be studied using the same framework.

3.1 Evolutionary Concepts

Analogously to the concept of NE in classical game theory, in EGT we can define an *Evolutionarily Stable Strategy* (ESS) [3]. An ESS is in essence a NE (see Section 2.1) modified for an evolutionary setting: if all players choose this strategy, then no other strategy can invade and fixate in the population. It focus on the strategies themselves

rather than the strategy profiles of players, which means only symmetric NE can be ESSes.

We exemplify the concept of an ESS for the case of *2-person games* using the payoff matrix (2.2). C (D) is an ESS if: i) $R > T$ ($T > R$); or ii) $R = T$ and $S > P$ ($R = T$ and $P > S$). The first condition states that a strict symmetric NE, is always an ESS; and the second one says that a weak symmetric NE is an ESS if and only if this strategy profile scores better against the opposite symmetric strategy set.

The notion of invasion implies that the more adopters a strategy has, the higher overall payoff they receive, i.e., the effect of a strategy becomes frequency dependent. In EGT we associate the payoffs of individuals with their *fitness*, which gauges their reproductive or social success (in accordance with the views mentioned above). It is by studying the fitness changes of the different strategies that EGT is able to predict the evolutionary outcome of a game.

3.2 Infinite Populations

In this section we study the evolution of cooperation in an infinite well-mixed population, an endless collection of individuals that can interact with every other with equal probability. The population is fractioned in x_C C 's and x_D D 's and from it we randomly sample groups of N individuals. As usual, a group is composed of j C 's and $N - j$ D 's and grants its members either $\Pi_C(j)$ or $\Pi_D(j)$ (these are specified by the game considered).

Because the population is infinite we can perform samplings with replacement, which leads to binomially distributed group compositions. We calculate the fitness of C 's and D 's, respectively f_C and f_D , by averaging the payoffs over all the possible group compositions:

$$f_C(x_C, x_D) = \sum_{j=0}^{N-1} \binom{N-1}{j} x_C^j x_D^{N-1-j} \Pi_C(j+1) \quad (3.1)$$

$$f_D(x_C, x_D) = \sum_{j=0}^{N-1} \binom{N-1}{j} x_C^j x_D^{N-1-j} \Pi_D(j) \quad (3.2)$$

In the next section we explain the most common dynamics used to calculate the fate of cooperation from these fitness values.

3.2.1 Replicator Dynamics

Evolution dictates that a strategy that performs better than average will spread in the population (at the expense of the other one, given we have only two). The simplest formulation of this statement can be formalized through the relations:

$$\dot{x}_C = x_C(f_C - \langle f \rangle) \quad (3.3)$$

$$\dot{x}_D = x_D(f_D - \langle f \rangle) \quad (3.4)$$

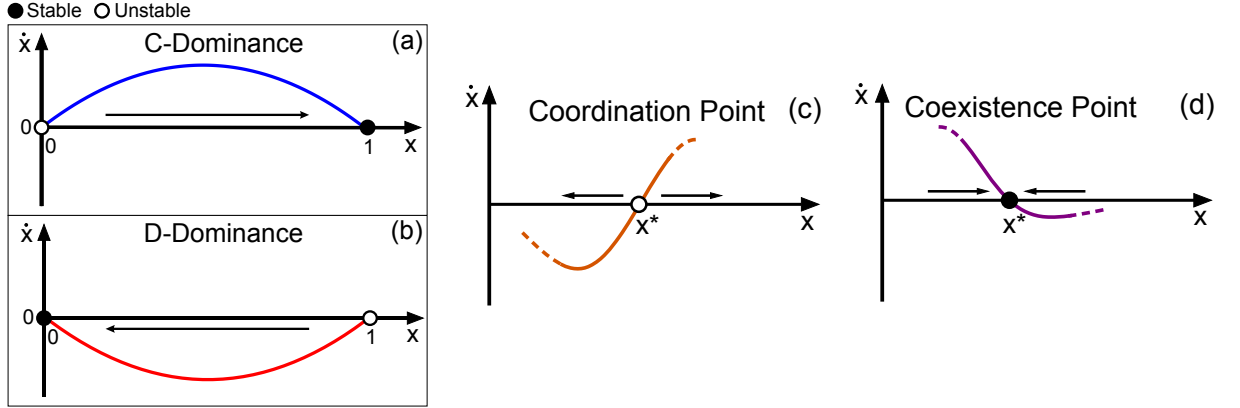


Figure 3.1: Overview of the possible replicator dynamics. (a) and (b) represent dominance scenarios, either by C 's or D 's, respectively; (c) and (d) indicate the two types of internal equilibria, respectively coordination and coexistence. The arrows indicate the direction of evolution, whether to increase or decrease the fraction of C 's.

Where $\langle f \rangle = x_C f_C + x_D f_D$ denotes the average fitness of the population (to simplify the notation, the dependence of the fitnesses on x_C and x_D was omitted). These two equations can be combined into a single differential equation if we remark that $x_D = 1 - x_C$:

$$\dot{x} = x(1-x)(f_C(x) - f_D(x)) \quad (3.5)$$

Where $x \equiv x_C$. This equation is known as the *replicator equation* and it can be used to track the evolution of C 's in an infinite well-mixed population. The previous redefinition also lets us simplify equations (3.1) and (3.2):

$$f_C(x) = \sum_{j=0}^{N-1} \binom{N-1}{j} x^j (1-x)^{N-1-j} \Pi_C(j+1) \quad (3.6)$$

$$f_D(x) = \sum_{j=0}^{N-1} \binom{N-1}{j} x^j (1-x)^{N-1-j} \Pi_D(j) \quad (3.7)$$

The replicator equation (3.5) has always two global equilibria, $x = 0$ — *full defection* or $x = 1$ — *full cooperation*. Aside from these, it can have at most $N-1$ additional internal equilibria if $f_C(x^*) - f_D(x^*) = 0$, for some $x^* \in]0, 1[$ [17]. The nature of these states can be inferred from the sign of \dot{x} near them. All the simple equilibria are summarized in Figure 3.1.

If there are no internal equilibria, then \dot{x} is either always positive or always negative, reflecting a C -dominance or D -dominance scenario, respectively. In these, regardless of the initial condition $x(0)$, selection will always favor one of the strategies and lead the population either to *full c*, if $\dot{x} > 0$ ($x = 0$ unstable and $x = 1$ stable) or *full d*, if $\dot{x} < 0$ ($x = 0$ stable and $x = 1$ unstable) (see Figures 3.1a and 3.1b). The former is typical of a HG and the latter of a PD or NPD.

The internal equilibria can be of two types and, if present, give rise to more interesting dynamics:

- If $\dot{x} < 0$ for $x < x^*$ and $\dot{x} > 0$ for $x > x^*$ the equilibrium is unstable and is called a *coordination point*: for any $x(0) < x^*$, selection will decrease x ; and for any $x(0) > x^*$, selection will instead increase x . The equilibrium coordinates the evolution of strategies (see Figure 3.1c). This situation is also known as bistability.
- If $\dot{x} > 0$ for $x < x^*$ and $\dot{x} < 0$ for $x > x^*$ the equilibrium is stable and is called a *coexistence point*: for any $x(0)$ near x^* , selection will make the population converge to the equilibrium, if no other equilibria exist in its vicinity (see Figure 3.1d). In this situation the equilibrium allows for a coexistence of the different strategies.

Not shown in Figure 3.1 is a special equilibrium that is metastable — neither stable nor unstable. It can appear, for instance, in the context of the NSG, but only for a particular combination of parameters. Any perturbation breaks this point into a coordination and a coexistence [16]. Interestingly, a metastable equilibrium also appears in Chapter 6, in the context of a special kind of NPD.

Also excluded from the analysis is the case of *neutral selection*. This happens when C 's and D 's both provide the same fitness, i.e., they are neutral. The fitness difference from the replicator equation (3.5) becomes simply $f_C(x) - f_D(x) = 0$, for all $x \in]0, 1[$ and it means that any $x(0)$ will be an equilibrium. It is a scenario that, although trivial in infinite populations, becomes an important reference point in the stochastic dynamics of finite populations as will be detailed in the next Section.

To close off the section we analyze the evolutionary dynamics of the NPD in infinite populations. We start by plugging equations 2.3 and 2.4 into the corresponding fitness expressions 3.6 and 3.7. Then we straightforwardly obtain that $f_C - f_D = c(\frac{F}{N} - 1)$ for all $x \in [0, 1]$. So, whenever $F < N$, \dot{x} is always negative which means C 's have no chance (see Figure 3.1b). The opposite happens for $F > N$, in which case D 's always lose (see Figure 3.1a).

Interestingly, this particular example shows that if conditions are adverse (low F), then it is possible to sustain cooperation if individuals organize into smaller groups. The same effect can be seen in other games like the NSH [15] and NSG [16] and will be explored further in the context of finite populations.

3.3 Finite Populations

We now turn our attention to well-mixed populations that are finite in size and therefore prone to stochastic effects. In a finite population of size Z the deterministic approach of the previous section is no longer valid (unless Z is very large) and so we must use the framework of EGT in order to study the problem of cooperation in finite populations.

A convenient way of incorporating finite population effects, while preserving the nature of the evolutionary dynamics in the limit when the population goes to infinity, is to define the dynamics by means of stochastic birth-death processes [37]. Together with other

elements of stochasticity contained in what is known as the *intensity of selection*, the evolutionary dynamics will be now determined by an interplay between selection and randomness [7].

The stochastic nature of finite populations has deep implications. For instance, in the previous section we saw that D 's always dominate in the NPD. If a finite population is playing this game then, there is a small, yet non-zero, probability that C 's can survive, as we will show in Section 3.3.1.

As the population is now finite, we can track the spread of strategies from individual to individual, but to do so we first need to define a strategy update rule for the players. Here we will use the so-called *pairwise comparison rule* [38] which provides a convenient framework to study the evolutionary game dynamics of a well-mixed finite population at all intensities of selection [39]. According to this rule, at each time step two individuals, A and B , are randomly selected from the population. The strategy of B will replace that of A with a probability given by the Fermi function:

$$p = \frac{1}{1 + e^{-\beta(f_B - f_A)}} \quad (3.8)$$

Where f_i represents the fitness that player i ($= A, B$) gets after interacting with other individuals. The quantity β (≥ 0) specifies the intensity of selection. By tuning this parameter we can regulate the stochasticity of the system and switch continuously between the two regimes mentioned above: in the limit $\beta \rightarrow 0$, the relative fitness difference does not influence selection and so evolution proceeds by neutral drift; in the opposite limit, $\beta \rightarrow \infty$, the Fermi function reduces to a step function and evolution proceeds deterministically, as the strategy of the player with the highest fitness will always replace that of the other, irregardless of the fitness difference.

The rule implies that only when the two chosen individuals have different strategies can the number of players of a given strategy change, no more than one at a time. We use this rule because, even in a N -person setting where individuals get together in groups, they usually have one individual role model that they try to imitate.

In a finite well-mixed population, under the pairwise comparison rule, an individual's fitness is again associated with the average payoff from the interactions with the other individuals.

Let k and $Z - k$ denote, respectively, the number of C 's and D 's in the population. When forming the groups, we must not let their size exceed the total population size, so $Z > N > 1$. Since Z is now finite, sampling must now be done without replacement, leading not to a binomial but to a hypergeometrical distribution of group sizes from which we derive the fitnesses of both strategies:

$$f_C(k) = \binom{Z-1}{N-1}^{-1} \sum_{j=0}^{N-1} \binom{k-1}{j} \binom{Z-k}{N-j-1} \Pi_C(j+1) \quad (3.9)$$

$$f_D(k) = \binom{Z-1}{N-1}^{-1} \sum_{j=0}^{N-1} \binom{k}{j} \binom{Z-k-1}{N-j-1} \Pi_D(j) \quad (3.10)$$

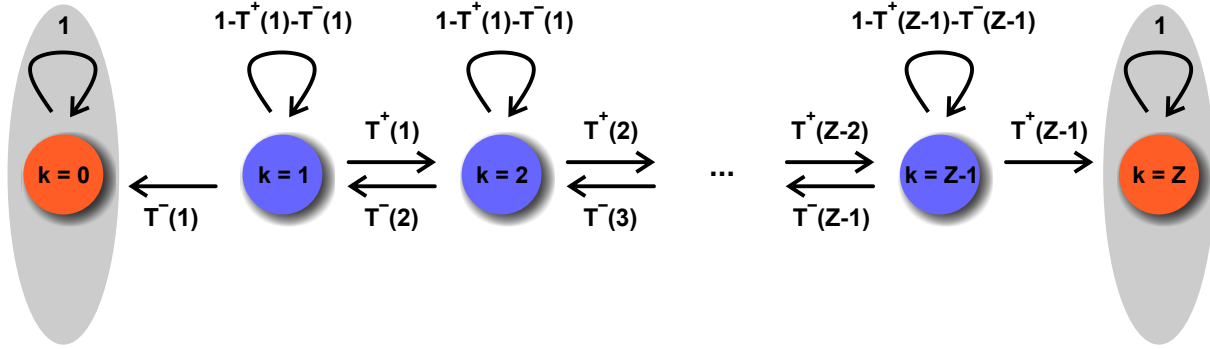


Figure 3.2: Markov chain representing the discrete stochastic process that describes the evolutionary dynamics of finite populations. Each state is defined by a different configuration of the population. The transition probabilities $T^\pm(k)$ indicate the probability of the population moving from one state to the other in one time step. The states $k = 0$ and $k = Z$ are the absorbing states of the system.

3.3.1 Transition and Fixation

The discrete process described above can be represented as a Markov chain with $Z + 1$ states, each of which represents a different configuration of the number of C 's in the population. Formally, a Markov chain is defined by its one-step transition probabilities and an initial state.

Let $T^+(k)$ be the probability of increasing the number of C 's from k to $k + 1$. Using the pairwise comparison rule, this quantity is given by:

$$T^+(k) = \frac{Z - k}{Z} \frac{k}{Z - 1} \frac{1}{1 + e^{-\beta(f_C(k) - f_D(k))}} \quad (3.11)$$

Here the first factor represents the probability of selecting a D from the population, at random and the second the probability of selecting a C from the remainder of the population, also at random. The Fermi factor tells us the probability that the chosen D will change the strategy to C .

Similarly, $T^-(k)$ is the probability to decrease the number of C 's from k to $k - 1$ which, under the pairwise comparison, is given by:

$$T^-(k) = \frac{k}{Z} \frac{Z - k}{Z - 1} \frac{1}{1 + e^{\beta(f_C(k) - f_D(k))}} \quad (3.12)$$

Analogously, the quantity $1 - T^+(k) - T^-(k)$ gives us the probability that the transition leaves the system in the same state, i.e., that the number of C 's does not change from k .

The transition matrix $\mathbf{\Lambda} = [\Lambda_{ij}]_{i,j=0,\dots,Z}$ of the Markov chain collects the transition probabilities between all possible states. It is a $(Z + 1) \times (Z + 1)$ stochastic matrix where each row sums to 1. As stated before, the pairwise comparison implies that, in each time step, the number of C 's can only change by one, at most. Consequently, $\mathbf{\Lambda}$ is a

tri-diagonal matrix:

$$\begin{aligned}\Lambda_{k,k} &= 1 - T^+(k) - T^-(k) \\ \Lambda_{k,k\pm 1} &= T^\pm(k)\end{aligned}\tag{3.13}$$

The stochastic factor in equations (3.11) and (3.12) implies that $T^\pm(k) \neq 0$ for all $k = 1, \dots, Z - 1$. Hence, the population will always reach a homogeneous state, that can be either *full d* or fully *full c*. When the system reaches this point, the extinct strategy can not return, i. e., $T^+(0) = 0$ and $T^-(Z) = 0$. In other words, the states $k = 0$ and $k = Z$ are not only homogeneous but also absorbing states of the Markov chain. The remaining $Z - 1$ states are called transient states.

Given that there are only two absorbing states, we can define the probability to reach the fully cooperative state, starting from an arbitrary number k of C' s. This is commonly referred as the *fixation probability* of k C' s and we denote it by ρ_k . The probability to reach the other absorbing state (full defection) is simply $1 - \rho_k$.

Using the transition probabilities from equations (3.11) and (3.12) and the fact that $k = 0$ and $k = Z$ are absorbing states we can write the following recursive relation for ρ_k [40]:

$$\begin{aligned}\rho_0 &= 0 \\ \rho_k &= T^-(k)\rho_{k-1} + (1 - T^+(k) - T^-(k))\rho_k + T^+(k)\rho_{k+1} \\ \rho_Z &= 1\end{aligned}\tag{3.14}$$

Together with $\mathbf{\Lambda}$ and by applying matrix notation, the above relation can be neatly written as:

$$\mathbf{\Lambda}\boldsymbol{\rho} = \boldsymbol{\rho}\tag{3.15}$$

Where $\boldsymbol{\rho}$ is a vector composed of all fixation probabilities. Interestingly, the above equation implies that the fixation probabilities are collected in the right eigenvector corresponding to the eigenvalue 1 of $\mathbf{\Lambda}$. Solving this equation yields a closed form expression for the fixation probability (see Appendix A):

$$\rho_k = \frac{1 + \sum_{i=1}^{k-1} \prod_{j=1}^i \frac{T^-(j)}{T^+(j)}}{1 + \sum_{i=1}^{Z-1} \prod_{j=1}^i \frac{T^-(j)}{T^+(j)}}\tag{3.16}$$

For the pairwise comparison the ratio of the transition probabilities will be simply $\frac{T^-(k)}{T^+(k)} = e^{-\beta(f_C(k) - f_D(k))}$.

When under neutral drift, i. e., when $\beta \rightarrow 0$, the transition probabilities are $T^\pm = \frac{1}{2}$, so their ratio is $\frac{T^-(k)}{T^+(k)} = 1$ and therefore, the fixation probability under neutral selection trivially reduces to $\rho_k^n = \frac{k}{Z}$. Since under neutral drift selection plays no part in evolution, we can take ρ_k^n as the reference value for the fixation of C' s. So, whenever $\rho_k > \rho_k^n$, selection favors the emergence of cooperation, and vice-versa for $\rho_k < \rho_k^n$. Even in a game that is completely adverse to C' s, like a NPD, there is a chance that C' s will propagate by

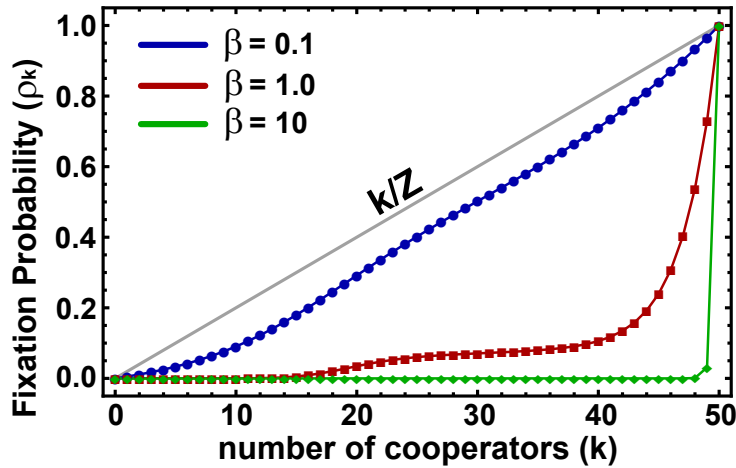


Figure 3.3: Fixation Probability $\rho(k)$ of k C' s playing a NSH in a population of size $Z = 50$ for several values of the intensity of selection β . Game parameters are $N = 10$, $F = 8$ and $M = 5$. For $\beta = 1.0$ (red line), the shape of the function indicates the presence of a coordination and a coexistence equilibria (see main text).

random drift, if their initial numbers are high enough and no other dynamical processes are taking place.

Figure 3.3 contains the fixation probabilities of C' s for a population of size $Z = 50$ playing a NSH with $N = 10$, $F = 8$, $M = 5$ and different intensities of selection (colored lines). When compared to neutral drift (gray line) it appears that selection never favors cooperation, although its chances increase alongside the stochastic effects. Despite this, for the game parameters considered, the replicator dynamics of infinite populations contains both a coordination and a coexistence equilibria, granting C' s some evolutionary edge.

In finite populations, the presence of a coordination, given its disruptive nature, should originate a step-like behavior in $\rho(k)$. By contrast, a coexistence should manifest itself through the presence of a plateau in the fixation probability and hinder the system in reaching *full c*. It will not stay in the coexistence because, according to the discrete stochastic process described above, the only absorbing states *full c* and *full d*. The system will spend many time steps near this coexistence state before eventually reaching 1. The hint of both a coordination and a coexistence in the NSH can be seen in Figure 3.3 for $\beta = 1.0$, although they seem to vanish for other intensities of selection.

The fact that ρ_k can be oblivious to internal fixed points indicates it is not a very adequate quantity to study the dynamics of finite populations. Indeed, its meaning suggests that it is appropriate mainly for dominance or pure coordination games (with only a coordination equilibrium). Even so, it is not able to really capture the dynamical process of fixation as it does not account for its time duration. For that reason, in the next section we introduce a tool that gives us the time the system spends in each state. Afterwards, in Section 3.3.3 we introduce another tool that is similar to the replicator equation as it properly captures the game dynamics of a population but which remains valid even when it is finite.

3.3.2 Mutation and Stationarity

The transition matrix $\mathbf{\Lambda}$ defined by equation (3.13) contains all possible transitions between the states of the dynamics. From it, we define the *stationary distribution*, \mathbf{h} , as the normalized left eigenvector associated with the eigenvalue 1 [41]:

$$\begin{aligned} \mathbf{h}^T \mathbf{\Lambda} &= \mathbf{h}^T \\ \sum_{i=0}^Z h_i &= 1 \end{aligned} \quad (3.17)$$

This equation can be solved to yield a closed form expression for each stationary distribution component h_k (see Appendix B):

$$h_k = \frac{\prod_{j=0}^{k-1} \frac{T^+(j)}{T^-(j+1)}}{1 + \sum_{i=1}^Z \prod_{j=0}^{i-1} \frac{T^+(j)}{T^-(j+1)}} \quad (3.18)$$

As we saw earlier in Section 3.3.1, $k = 0$ and $k = Z$ are the only absorbing states of the dynamics and therefore the population spends an arbitrarily long time in those states. In this case the stationary distribution will be just a peak at those states and zero-valued everywhere else, preventing us from seeing how the system evolves before reaching absorption. In order to ‘unmask’ the dynamics, we can add behavioral mutations to the population that prevents it from fixating in either state [18].

At the moment of transition, if there is a small probability ζ that an individual changes strategy spontaneously, then $k = 0$ and $k = Z$ lose their absorbing property. With mutations, the transition probabilities are modified in the following way:

$$\tilde{T}^+(k) = \zeta \frac{Z-k}{Z} + (1-\zeta)T^+(k) \quad (3.19)$$

$$\tilde{T}^-(k) = \zeta \frac{k}{Z} + (1-\zeta)T^-(k) \quad (3.20)$$

Substituting the $T^\pm(k)$ in equation (3.18) by these modified transition probabilities we can then compute the stationary distribution which shows the temporal resilience of the internal states of the dynamics.

3.3.3 Gradient of Selection

The replicator equation is not valid for finite populations, unless they are very large, in which case it holds approximately. So, in order to properly study a finite population of any size, we need an equation that accounts for the stochastic effects inherent to this type of populations.

Inspired by their Markovian nature, we can use the balance between the transition probabilities, $T^\pm(k)$, to compute the evolutionary end state of the system, from the starting condition of k C' s. We can use either the ratio of the difference between the two

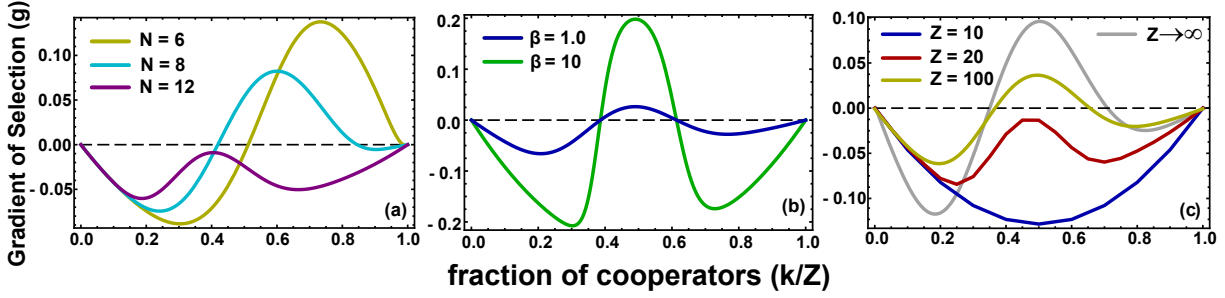


Figure 3.4: Gradient of selection for a NSH. (a) shows the effect of the group size on a game with $Z = 50$, $F = 8$, $M = 5$ and $\beta = 1$. In (b) we can see that, for $Z = 50$, $F = 8$, $N = 10$ and $M = 5$, the basins of attraction get larger alongside β . The effect of Z is illustrated in (c) where a game with $F = 8$, $N = 10$, $M = 5$ and $\beta = 1$ gets easier for C 's if they play in a large population. See main text for a more detailed explanation.

quantities. The latter was the basis of the fixation probability, as can be seen from equation (3.16). However, as was argued, ρ_k is insufficient to reveal the full dynamics of these systems. Thus, we will use the difference between the transition probabilities to build our ‘replicator-esque’ equation which, as we will see later, reduces to the usual replicator equation in the limit of large populations and small intensity of selection.

We define the *gradient of selection*, $g(k)$, as the difference between corresponding transition probabilities. Its sign indicates the influence of natural selection when the number of C 's in a population is k : whether to increase or decrease this number, until it reaches an absorbing state. Its magnitude evidences the time the system needs in order to reach the aforementioned state. The gradient of selection is then defined as:

$$g(k) \equiv T^+(k) - T^-(k) \quad (3.21)$$

We substitute equations (3.11) and (3.12) to get the explicit form of the gradient, which reads:

$$g(k) = \frac{k}{Z} \frac{Z - k}{Z - 1} \tanh \left\{ \frac{\beta}{2} [f_C(k) - f_D(k)] \right\} \quad (3.22)$$

The right-hand side of the $g(k)$ is similar to the replicator equation, in that the two homogeneous absorbing states, $k = 0$ and $k = Z$, are clearly visible. Moreover, if $g(k) = 0$ for all $k = 1, \dots, Z - 1$, then $f_C(k) - f_D(k) = 0$. This means firstly that we need simply to study the fitness difference to find the possible internal equilibrium points of the dynamics; secondly that these equilibria can be classified according to the criteria used in infinite population case (see Section 3.2.1), but considering instead the sign of g : for $g > 0$ ($g < 0$) then k will tend to increase (decrease).

The gradient only differs because of the presence of the hyperbolic tangent of the fitness difference, instead of just the fitness difference. This hyperbolic tangent stems from the pairwise comparison rule and most importantly, it implies that stochastic effects, via the presence of the intensity of selection parameter β , are really inherent to the dynamics, as was expected.

If we perform a first-order Taylor expansion of the hyperbolic tangent, for very small intensities of selection, $\beta \ll 1$, we are left with the fitness difference. If we then define the fraction of cooperators, $x = \frac{k}{Z}$, and consider a large population ($Z \rightarrow \infty$), the hypergeometrical distribution of equations (3.9) (3.10) converge to the binomial distribution of equations (3.6) and (3.7). In this limit we recover the deterministic replicator dynamics.

Figure 3.4 shows the gradient of selection of a NSH. In Figure 3.4a we see that, for $Z = 50$, $F = 8$, $M = 5$ and $\beta = 1$, by decreasing the group size and for this particular Z , we can go from a pure coordination game ($N < F$) to a dynamics with two equilibria ($M < F < N$) before finally stabilizing in a full defection game. This shows that in fact, in the finite version of the game we can have the same kind of internal dynamics as for the infinite population counterpart. Indeed, in Figure 3.4b, we have the gradient for exactly the same parameters as used in Figure 3.3, confirming our predictions about the game dynamics. More importantly, it shows that the β only affects the size of the basins of attraction, i.e., the relative speed of the dynamics, and not the location of the equilibria.

Finally, in Figure 3.4c, we get a better sense of the importance of the size of the population. Below a certain limit D 's always win but, after internal roots start to appear then C 's gain some evolutionary advantage. Furthermore, as $Z \rightarrow \infty$, those equilibria approach those of the replicator dynamics.

For a more detailed study of the NSH see [15]. Also see [16] for a similar study of the NSG. Although different in principle, they can give rise to the same type of dynamics, in the sense that one can have at most two mixed internal equilibria. Remarkably, the roots behavior for the two games is also their diverging point. While in the NSG we can have either a single metastable equilibria, the two mixed equilibria or none; in the NSH, as shown in Figure 3.4, we can have the two, a coordination equilibrium, or none.

From all the examples shown thus far, it is clear that the chances of cooperation are better in finite population models, and even in these, only for a small range of parameters. In the following chapters we present additional mechanisms that can be added to the dynamics to increase the chances of cooperation, both in infinite and finite populations.

Chapter 4

Games with Delay

Now that we have developed the essential tools for the study of the evolution of cooperation we will analyze, in this and the subsequent Chapters, different mechanisms that can facilitate the emergence of this property.

In real life there are many situations where actions have consequences that are not immediate. They only become manifest after a certain time lag. The fluctuations of the stocks market are affected by past events and decisions. The results of an exam usually only become known after some time. Animals that hunt for prey in groups must collect enough food to sustain the group until the next hunt. The harmful consequences of climate change take many years to manifest themselves. These are all scenarios of delayed returns of past actions.

Although the time delay of different actions is not necessarily the same it is certainly present. Despite this fact, the effect of such time delays has been very little investigated in the framework of EGT and even so, only in the field of the 2-person snowdrift game [19, 20, 21]. In both cases the authors concluded that the introduction of time delays does not change the position of the ESS although, for large enough values, it can be rendered unstable.

Here we consider only the NSH, defined previously in Section 2.3.2. As illustrated in Figure 3.4, this game can have two interior equilibria, a coordination (x_l) and a coexistence (x_r), depending on the relative values the game parameters. We will consider only the case when both these equilibria are present.

In Section 4.1, we apply the theory of delayed differential equations [42] to the replicator dynamics described in Section 3.2.1 and examine how it changes by the introduction of delay in the fitnesses. First we perform a stability analysis of one of the equilibria of the dynamics, in Section 4.1.1, and afterwards, in Section 4.2, we test the robustness of the system for different initial conditions and study, numerically, its behavior away from

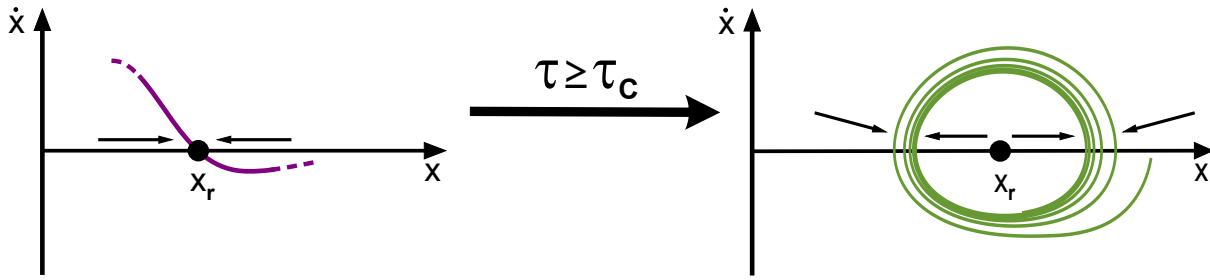


Figure 4.1: The coexistence point, x_r , of the delayed replicator equation bifurcates into a stable periodic orbit around x_r — Hopf bifurcation, above a certain critical time delay, τ_c .

the equilibria.

4.1 Delayed Replicator Dynamics

One natural implementation of delay in this type of population is in the fitness of the players. We consider that individuals replicate at a time t due to the fitness they had at time $t - \tau$, for some time delay τ ($\tau > 0$). In the simplest case, corresponding to ‘symmetric’ delay, both strategies have the same time delay. To achieve this we modify the ordinary replicator equation (3.5) to reflect this delay in the fitness:

$$\dot{x}(t) = x(t)(1 - x(t)) [f_C(x(t - \tau)) - f_D(x(t - \tau))] \quad (4.1)$$

The presence of the delay terms can affect the stability of the equilibria [42]. In fact, as we will see, the stability of x_r can be modified, but not its existence nor its position. For a certain value of τ , a Hopf bifurcation occurs: the otherwise stable coexistence point bifurcates into a stable periodic orbit around x_r .

Another change brought about by the use of delay differential equations is that we now need to choose not only an initial condition but a whole set of them, i.e., the so-called history function of the system. In effect, it is an initial condition function defined in the time interval $[-\tau, 0]$. Although this choice does not influence the stability change of x_r (or of any equilibria), it can affect the global dynamics of the system.

4.1.1 Critical Delay

To study the change in stability of x_r we can analyze the linearized version of equation (4.1) near this point. Performing a Taylor expansion of $Q(x) \equiv f_C(x) - f_D(x)$, around x_r yields:

$$Q(x) \approx Q'(x_r)(x - x_r) \quad (4.2)$$

Note that, since x_r is an interior equilibrium of the replicator equation, then $Q(x_r) = 0$. Let $y(t) \equiv x(t) - x_r$. Substituting equation (4.2) in equation (4.1) and keeping only linear

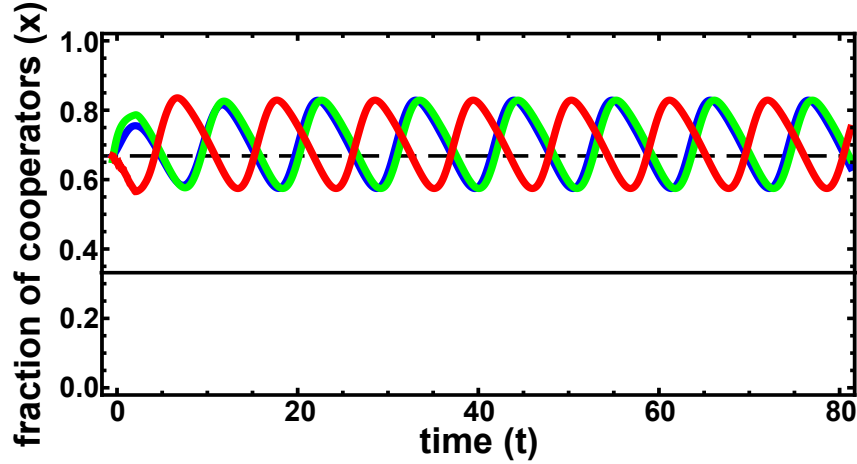


Figure 4.2: Time evolution of x for three different history functions in a delayed NSH game with $N = 20$, $M = 10$, $F = 15$ and $\tau = 2.5$ (for these parameters we have that $\tau_c \approx 1.74$). In green we used the replicator equation (3.5), in blue the function $0.05 \sin\left(\frac{t}{\tau}\right) + x_r$ and in red a completely random function just constrained to be valued x_r at $t = 0$. As we can see they all give rise to the same qualitative behavior. Also shown are the coordination (black solid line) and coexistence (black dashed line) equilibria.

terms we get a linearized delay replicator equation:

$$\dot{y}(t) = Ky(t - \tau) \quad (4.3)$$

Where $K = x_r(1 - x_r)(f'_C(x_r) - f'_D(x_r))$. According to [42], the stability of x_r is determined by the real part of the solution of the characteristic equation corresponding to equation (4.3):

$$\lambda = Ke^{-\lambda\tau} \quad (4.4)$$

The solution of this equation can be expressed using the Lambert W function¹:

$$\lambda = \frac{W(K\tau)}{\tau} \quad (4.5)$$

The system has a Hopf bifurcation when the real part of the principal branch of equation (4.5) crosses zero, for a certain value of the time delay, called the critical delay, τ_c . At this point, the stable coexistence, x_r , bifurcates into a stable periodic orbit (see Figure 4.1).

Performing the same analysis for the other equilibria, the coordination, we find no change in stability. As x_l is already unstable, the introduction of delay does not affect its properties.

¹The Lambert $W(z)$ function, also called product logarithm, is defined by the equation $z = W(z)e^{W(z)}$, for any complex number z .

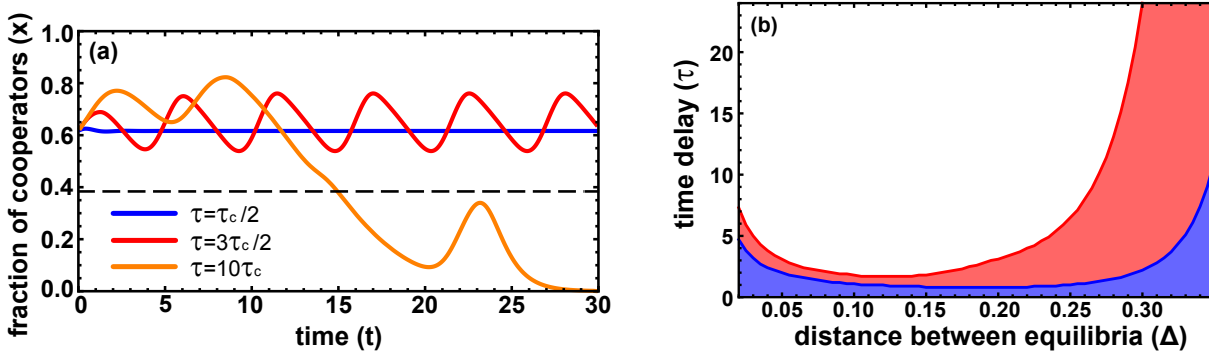


Figure 4.3: Dynamics of the delayed replicator equation. In (a) we can see the effects of increasing the time delay in a NSH game with $N = 40$, $M = 20$ and $F = 25$. We go from unperturbed dynamics (blue), to stable orbit around the coexistence (red) before finally ending up in full-defection (orange). The coordination point is represented by the black dotted line. In (b) this behavior is systematized in a bifurcation diagram parameterized by the time delay τ and the distance between the equilibria Δ . The blue and red lines represent the points above which we start to have stable orbits and full-defection scenarios, respectively.

4.2 General Effects of Delay

The previous analytical analysis only refers to when the system is near or at the equilibria. To see how the delay affects the general dynamics we have to resort to numerical calculations. Not only that, but we also have to take into consideration the effect of the history function.

To see if the system is robust we compare the results obtained from different history functions. In Figure 4.2 we have the time evolution of x for three different history functions defined in the interval $[-\tau, 0]$ and constructed from: i) the ordinary replicator equation (3.5) (green line); ii) a small sinusoidal perturbation around the coexistence of type $\Omega \sin\left(\frac{ft}{\tau}\right) + x_r$ with $\Omega = 0.05$ and $f = 1$ (blue line); iii) a random function constrained to the value $x(0) = x_r$ (red line). Also indicated in the Figure are the positions of x_l (black solid line) and x_r (black dashed line). These results were obtained from a numerical integration of equation (4.1). While they seem to show some robustness, it is worth mentioning that a history function with a strong bias towards one of the strategies can easily force the system to converge to their favored equilibria, regardless of the state of the system at $t = 0$.

If we settle for a history function against which the dynamics is robust, say a sinusoidal perturbation near x_r , we can see exactly the effect of the time delay. As we can see in Figure 4.3a, for small values of τ (blue line) the dynamics remains largely unaffected and the system quickly converges to the coexistence. As we increase it, we eventually reach τ_c and the stable point bifurcates into a stable periodic orbit — Hopf bifurcation (red line). After this point, if we keep increasing τ we see that the amplitude of the orbit also

increases, until eventually it crosses the unstable equilibrium, x_l , (black dotted line) at which point the evolution will tend to the global equilibrium $x = 0$ (orange line).

We can study the dynamics not from the perspective of the game, but from the relative location of the equilibria themselves. It is simply a matter of finding the triplet (N, M, F) that gives the desired positions of x_l and x_r . This approach allows us to neatly summarize our findings in the bifurcation diagram of Figure 4.3b, parametrized by the delay τ and the distance between the equilibria $\Delta \equiv x_r - x_l$. To construct it, we set $x_r = 0.75$ and then increased Δ from 0.02 to 0.35, in steps of 0.01. To get a steady increase, we allowed for the parameters to vary continuously.

In the Figure, the blue line represents the τ_c for a given Δ and is calculated from equation (4.5). In the region below (light blue) the dynamics remains unaffected by the introduction of a time delay and in the light red one we have stable orbits that increase in amplitude with the increase of τ , until it reaches the red line. Above this point, which can only be found through a numerical computation, evolution always drives the system to *full defection*.

Chapter 5

Games with Dynamical Interaction Structure

Up to now, we focused only on well-mixed populations, both infinite and finite. This assumption means that every individual is equally likely to interact with everyone else in the population. In reality this is an unrealistic assumption, unless one is dealing with small populations that inhabit a small area, e.g. a village, where all individuals know and interact with each other very often. In general there is some sort of structure underlying a population that constrains the interactions of its constituting individuals.

Thus far, most studies of structured populations consider them to be static, i.e., individuals have a set of interacting partners that is fixed at the start and remains immutable throughout time [14, 22, 23, 24, 25, 43].

This approach provides many useful insights that may extend to more general situations. However it is still somewhat limited as real world networks are seldom static [44]. It does not apply to entities that are continuously evolving in time, such as friendship networks, where one's behavior can affect not only the behavior of his or her peers but also the chances of them meeting. Therefore, in order to study how these kind of scenarios arise and evolve over time, a new methodology is required.

Throughout the rest of this work we go beyond those studies. We center our focus on finite populations with an adaptive structure, where individuals can dynamically change their social ties, and study how the introduction of structure affects the evolutionary outcome of the game dynamics and also how this same dynamics can alter the structural layout of the population. Based on existent frameworks for 2-person games [8, 45], we create two different models for N -person games on populations with dynamical structure, a computational and an analytical one. The former will be the focus of this Chapter while the latter will be dealt in the last Chapter.

In Section 5.1 we introduce the concept of structured populations, one that uses a net-

work as a proxy to structure. Given our use of an adaptive structure for the populations, we must consider two dynamic processes occurring simultaneously. The implications of this co-evolution will be detailed in the following section. Next, in Section 5.3 we create and discuss the results of a minimal computational model of a NPD on a population of individuals that can swap friends.

5.1 Structured Populations

To try to capture the structure of a population we use a network or graph. A network is composed of nodes and edges or links that connect the nodes. The collection of links belonging to a node constitute its degree or connectivity and the set of nodes attached to the other end of those links form that link's neighborhood. Two nodes connected by a single link are said to be first neighbors, two nodes separated by two links (they share another node) are said to be second neighbors, and so on.

There are many kinds of networks with many different properties [46]. In this work we consider only undirected networks, where the links have no orientation. This means that when two first neighbors interact, their link does not impose a direction on this interaction. Those links are also considered to be unweighted, which means they all have the same properties. Regarding the connectivity of the nodes, a network can be either homogeneous, where every node has the same connectivity, or heterogeneous, where different nodes can have different connectivities. In this work, as we will use networks that are adaptive, i.e., changeable, we will encounter both types of networks.

In a networked context, the players' neighborhoods constitutes their local universe of possible interacting partners in social dilemmas of cooperation. Whenever individuals engage in games, whether 2-person or N -person, they will necessarily pick their interacting partners from their local neighborhood. Consequently, two individuals adopting the same game strategy can acquire a different fitness. If the network is heterogeneous then this effect is immediate: individuals with a higher degree will interact more often than those with a smaller one, so they have to opportunity to accumulate a higher payoff and thus get a higher fitness.

There is however, another reason for this fitness diversity, that also applies to homogeneous networks which is that the average strategy of a node's neighbors may be different from the global average of the population. This difference arises naturally in this context, as the players' neighborhood, besides from defining their possible interacting partners, also defines who they can imitate or be imitated by. This means that successful C 's (D 's) will breed C 's (D 's) around them.

Structured populations can accommodate another layer of diversity, at the level of the payoffs. On the one hand, individual contributions of C 's can be proportional to the number of links they have. This is the conventional setting, used mainly to represent a scenario where individuals have unlimited resources and always contribute the same amount to each game they play. On the other hand, we can consider that C 's have a certain fixed amount that can be divided among all the games they play. This contributive scheme can represent a more egalitarian society with limited resources. This becomes

particularly relevant whenever heterogeneous networks are at stake, as the game being played by each player actually becomes dependent on their social context [14, 25].

5.1.1 Topological Concepts

A network of size Z can have a maximum of $\overline{Z_E} = \frac{Z(Z-1)}{2}$ links. If the number of links present in the network is very small, i.e., $Z_E \ll \overline{Z_E}$, the network is said to be sparse. If the network has the maximum links possible, $Z_E = \overline{Z_E}$, it is called a complete or fully-connected network, with every node connected to every other one. This is actually a very useful limit as a complete network can mimic a finite well-mixed population.

The degree distribution $P(k_i)$ gives us the fraction of nodes in the network which have degree k_i . The average degree or connectivity of a network can be calculated directly from its $P(k_i)$:

$$\langle k \rangle = \sum_{k_i} k_i P(k_i) \quad (5.1)$$

Related to $P(k_i)$, the cumulative degree distribution, $H(k_i)$, gives the fraction of nodes with connectivity greater or equal to k_i :

$$H(k_i) = \sum_{j \geq k_i} P(j) \quad (5.2)$$

This last distribution can be used to track the maximum value of connectivity, k_{max} , because $H(k_i) = 0$ for $k_i > k_{max}$.

An important property of a network is its level of clustering, i.e., the probability that a node's second neighbor is also its first neighbor. We define the clustering coefficient of node i , l_i , as the ratio of the number of links between neighbors of i divided by the maximum possible number of edges between those neighbors. Following [47], the clustering coefficient of a network L is the average of all l_i :

$$L = \sum_{i=1}^Z l_i \quad (5.3)$$

In an homogeneous network, all nodes have the same degree, and so equal to the average, translating into a peak-shaped degree distribution:

$$P(k_i) = \delta_{k_i \langle k \rangle} \quad (5.4)$$

Square lattices and ring regular lattices are the simplest examples of homogeneous networks. Another one, which will be used in the model described latter in the Chapter, is the homogeneous random or random regular network. It can be constructed by rewiring one of the ends of all edges of a ring regular lattice while preserving the homogeneity of the degree distribution. It produces a network with an extremely low clustering coefficient [48].

Heterogeneous networks are a different story altogether. They may be associated either with a narrow-scale degree distribution like a Poisson distribution, which characterizes random networks [49], or with a broad-scale degree-distribution like exponential and power-law distributions, characteristic of the so-called exponential and scale-free networks [50], respectively. These last ones have received a lot of attention in the past decade as it has been shown that many empirical networks follow this pattern [27].

5.2 Coupling of Game and Network Dynamics

Having a population with an underlying structure that adapts itself according to whatever game is affecting the dynamics of individuals means having two different dynamics occurring simultaneously. These need not evolve at the same time scale and can have very different effects. They may be coupled together in a single co-evolutionary dynamics affecting both the individuals and their social ties.

We will consider, in general, different characteristic time scales for the two processes: the time scale associated with the network dynamics, τ_n , and the time scale of the strategy dynamics, τ_s . Depending on the relative values of these two quantities, the effects of evolution can be very different. To get a better grasp of the coupling between the two dynamics it is useful to define the ratio between their time scales, $W \equiv \frac{\tau_s}{\tau_n}$. From this ratio it is straightforward to identify two limiting cases, representing a complete separation of the time scales: $W \ll 1$ and $W \gg 1$.

Whenever $W \ll 1$, the game is very fast-paced when compared to the changes of the network structure, so that this latter remains essentially constant throughout evolution. Thus, in this limit, the dynamics of the system will be equivalent to that of an evolutionary game played on a static network. Whenever $W \gg 1$, the dynamics of the network is fast enough to ensure that it will reach a steady state before the next game round takes place. In this limit, the dynamics of the system can be approximated by that of a game played on a structure whose properties are given by the steady state of the network dynamics.

Nevertheless, it is unreasonable to expect people to establish firm social ties before engaging in actual social interactions. Realistic phenomena will take place for intermediate ranges of W , i.e., when the time scales are of comparable magnitude. The case study in the next section is a numerical approach to a co-evolutionary game dynamics where, based on the outcome of the game, individuals can either change their strategic behavior or their pool of possible interacting partners.

5.3 Rewiring Dynamics

Evolving networks means that individuals engage in new interactions and abandon old ones, according to their nature. Therefore it is only natural that this characteristic becomes incorporated in models of the evolution of cooperation. Having established, in the previous Sections, the basic concepts associated with a structured population, we can now empower the underlying network of individuals with adaptive properties.

Santos *et al.* created a setting to study, computationally, a finite structured population that can adapt their connections as they play their evolutionary 2-person games [45]. Individuals are placed in the nodes of a network and can decide, based solely on their self-interests which ties they want to maintain and which ones they want to abandon. If an individual is dissatisfied with a certain link then a competition ensues with the affected partner, for the right to rewire that link. Upon resolution, a rewiring of the link is attempted, to a random neighbor of the partner who lost the competition. The authors showed that cooperation blooms when individuals react swiftly to adverse social ties [45], meaning that the emergence of cooperation depends on the relative speed of the network adaptation and game evolution, i.e., on the ratio W . In the next section we extend this network rewiring framework to N -person games of cooperation, namely the NPD, but instead give individuals the freedom to rewire links to anyone in the population. Afterwards, in Section 5.3.2 we briefly explain the methods used and finally, in Section 5.3.3 we present and discuss our results.

5.3.1 A Minimal Co-Evolutionary Model

We assign Z individuals to the nodes of a homogeneous random network of the same size. A link in the network represents an interaction channel between the connected nodes. We follow the game rules defined in [14] where individuals engage in rounds of NPD, whose group size and constitution will be determined by their neighborhood and that of the node's neighbors. Individual i with connectivity k_i will engage in $k_i + 1$ NPDs, one centered on his/her neighborhood and k_i centered on the neighborhood of each of his/her neighbors. In this way, the size of the interacting groups, $N = k_i + 1$, can be different from individual to individual if we allow the network to adapt.

In this game, C 's contribute a certain fixed cost c in every game they participate in. So, player A , using strategy s_A (0 if D and 1 if C), gets from a single round of NPD centered on individual i a payoff given by:

$$\Pi_{A,i} = \frac{Fc}{k_i + 1} \sum_{j=0}^{k_i} s_j - cs_A \quad (5.5)$$

Where k_i is the connectivity of the group's focal individual and s_j is the strategy of neighbor j of i (here $j = 0$ stands for node i).

Throughout evolution individuals may decide either to alter their strategy, via a certain predefined rule, or to disconnect from an adverse neighbor, which means both the connectivities and strategies of players are allowed to change during simulations. This translates into a process of co-evolution between the game and the network dynamics that is implemented in an asynchronous fashion: In each time step of evolution only one update type is allowed, either a strategy or a network update. This is chosen according to the ratio W . If we assume, without loss of generality, $\tau_s = 1$, then a strategy update is chosen with a probability $\frac{1}{1+W}$ and a network update with a probability $\frac{W}{1+W}$.

The strategy updates are regulated by the pairwise comparison rule defined in Section 3.3. In this case we first select a node A from the population, at random. Then we ran-

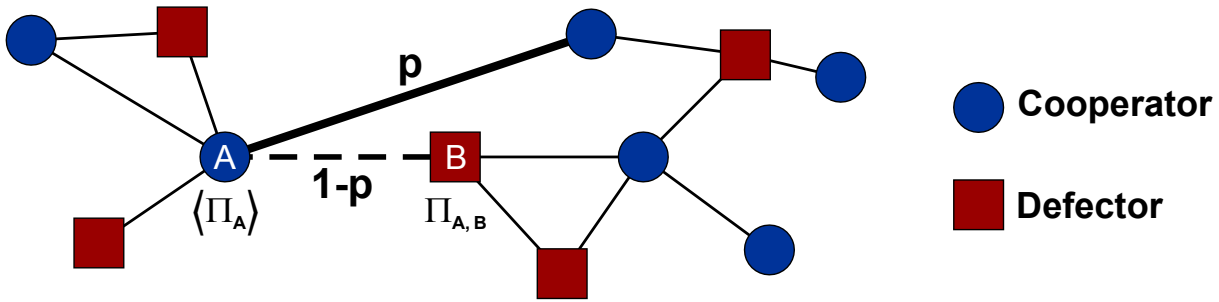


Figure 5.1: Schematic representation of the rewiring dynamics. After playing all possible NPDs, individual A gets an average payoff $\langle \Pi_A \rangle$, to which the group centered on B contributes the least, $\Pi_{A,B}$. Then, with a probability given by the Fermi rule, $p = [1 + e^{-\beta_n(\langle \Pi_A \rangle - \Pi_{A,B})}]^{-1}$, where β_n is the intensity of selection associated with the network updates, A rewires the link from B to a random individual from the population (bold line). With probability $1 - p$, A stays linked to B (dashed line).

domly select another node B among A 's first neighbors. Both these nodes will participate in all possible NPDs and the accumulated payoff from these games will constitute their fitness. Plugging these values into the Fermi function from equation (3.8), we get the probability that the strategy of B will replace that of A .

In a network update we randomly select a node A from the population. Then, after playing all the possible NPDs, the selected node compares the payoffs received from all groups centered on his/her neighbors with his/her average payoff, $\langle \Pi_A \rangle$. The link connecting A with neighbor B , center of the least favorable group will be selected for a possible rewiring. With a certain probability A rewires the link to another random individual from the whole population (see Figure 5.1). This probability is dictated by the same pairwise rule as the strategy update, albeit using the difference between the aforementioned payoffs and a specific intensity of selection, different, in general, from the previous one. We let β_s and β_n be the intensities of selection associated with the strategy and network updates, respectively.

5.3.2 Computational Methods

We start each simulation run with a homogeneous random network with Z nodes, representing the individuals, and Z_E links, delineating the social ties between individuals. All nodes have the same number of links randomly connected to other nodes at the start, but this will change in time as individuals adjust their ties. The construction algorithm for this particular type of networks is outlined in [48]. The average connectivity $\langle k \rangle = \frac{2Z_E}{Z}$ and, therefore average group size $\langle N \rangle = \langle k \rangle + 1$ are conserved since we do not create nor destroy links and we require that the network remains connected at all times. To enforce this condition we impose that nodes connected by a single link cannot lose this link.

At the end of evolution we record the final fraction of C 's as well as the maximum value of the connectivity present in the network, k_{max} , from the cumulative degree distribution

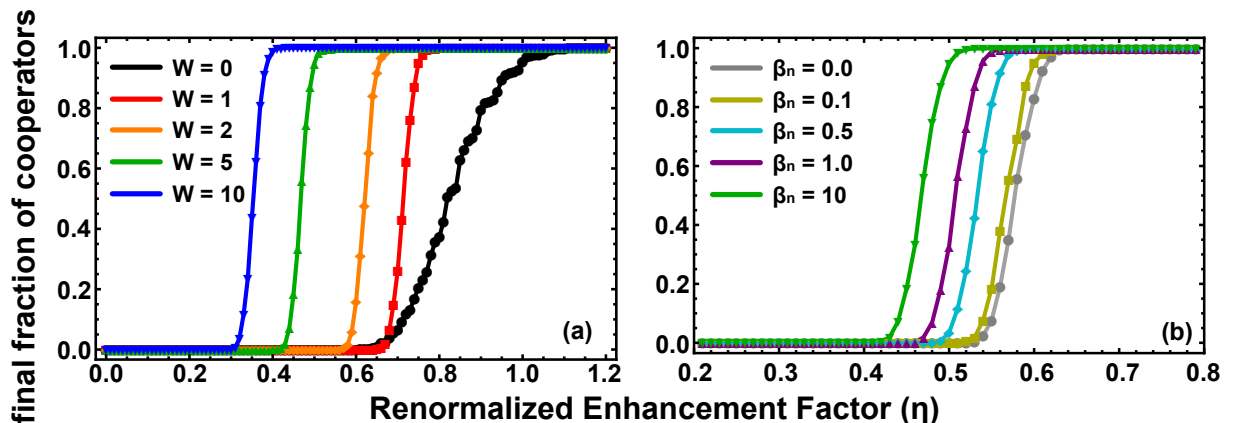


Figure 5.2: Final fraction of $C's$ as a function of the renormalized enhancement factor η . In plot (a), we observe a transition from full defection to full cooperation, that gets steeper and moves to lower η , for fixed $\beta_s = \beta_n = 10$ and increasing W . A similar effect can be observed in plot (b) where, for a fixed $W = 5$ and decreasing β_n , the transition moves to higher η . β_n has less impact on the dynamics than W .

$H(k)$ (see Section 5.1.1). This value is very useful in the sense that it provides a simple measure of the developed heterogeneity.

Our populations have $Z = 10^3$ and $\langle k \rangle = 16$. This latter value was selected because it reflects the average connectivities reported in [23] for social networks. We start by randomly selecting 50% of the nodes to become $C's$, while the remainder become $D's$. In all cases we used $c = 1$ for the cost of cooperation and $\beta_s = 10$ for the intensity of selection of the strategy updates. Each simulation runs for a maximum of 10^6 iterations and each data point in Figures of the following section results of an average over 10^3 randomly generated configurations and runs, after an initial transient period of 10^5 iterations.

5.3.3 Results and Discussion

In Figure 5.2a we have the final fraction of $C's$ as a function of the renormalized enhancement factor $\eta = \frac{F}{\langle N \rangle}$. When we have no rewiring ($W = 0$, black line) we only see a fully cooperative scenario for $\eta > 1 \iff F > \langle N \rangle$, which is the same as for an infinite or finite (with $M = 0$) well-mixed population (see Sections 3.2.1 and 3.3.3). But, as soon as we allow individuals the possibility to rewire their links ($W > 0$), the transition from *full d* to *full c* gets steeper and moves to lower values η (harder game for cooperation). This means that, if $C's$ can change their neighborhood, they will quickly exchange a bad group for a more prosperous one, thus getting a higher fitness. This in turn, makes them more likely to be imitated by the $D's$ that are also switching other groups.

In Figure 5.2b we can see a similar picture but now, instead of increasing the speed at which individuals can change friends, we fix it at $W = 5$ and decrease β_n , i.e., we introduce errors of judgment of when to disconnect from a group or not. As expected, for a certain, fixed η , by lowering β_n , we also decrease the final fraction of $C's$. However,

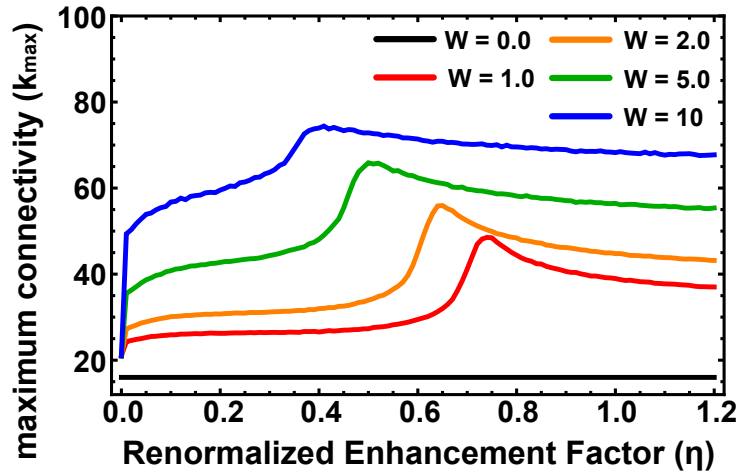


Figure 5.3: Maximum value of connectivity k_{max} as a function of the renormalized enhancement factor η . For all $W > 0$, the qualitative behavior is the same: k_{max} steadily increased until it reaches a peak and then slowly declines before stabilizing in some plateau. This peak sits at the same value of η as the transition of Figure 5.2a.

even though the steep transition in behavior is preserved, indicating that it is associated with the network itself and not the game, the extent of the impact of β_n on the dynamics of co-evolution is smaller than that of W .

In Figure 5.3 we see the reason for the steep transition. It is a plot of k_{max} at the end of evolution as a function of η and for the same parameters as Figure 5.2a. It steadily increases until it reaches a peak and afterwards slowly declines (except for $W = 10$ which constitutes a very fast game) until it reaches a sort of plateau. Most importantly is that the peak in k_{max} appears at precisely the same value of η as we reach *full c* in Figure 5.2a. This indicates that when C 's get their chance to wipe out the D 's from the population is when heterogeneity is at its maximum.

These results show that, NPD, a game that is usually dominated by D 's, can be transformed into a fully cooperative game simply by allowing individuals to not only play the game but also to actively decide whether or not they wish to stay in a given group based solely on their self-interest. Furthermore, these individuals can increase the overall levels of cooperation if they try to rewire from adverse groups more quickly, but not necessarily in a more efficient way. Finally, we obtain at the end of the game, a structure with properties much alike those of real world networks [51].

Chapter 6

Game with Dynamical Groups

In the previous Chapter we did a first study of an evolutionary game on adaptive networks. We introduced a model that gave individuals the chance to disconnect from adverse groups that did not provide a sufficient benefit. This allowed for C 's to become increasingly apt at grouping together and eliminating D 's from the population. However, this study was based on a numerical approach which can be lengthy to implement.

In this Chapter we introduce a framework called Active Linking (AL) that, unlike the one previously used in Section 5.3, allows for an analytical treatment of the dynamics of the network, at the level of its constituent links. Furthermore, in this model, which was first introduced by Pacheco *et al.* in [8], the number of links present in the network is not fixed. Individuals have an active role in the maintenance of their social ties and can decide which individual links they want to maintain.

In [8] the authors use the AL model to study finite populations playing symmetric two-player games where individuals playing different strategies have different propensity to create new links. These will have the same lifetime regardless of their type. Here we extend the original AL model to populations playing N -person PGGs, but keep the individual-based linking dynamics.

In Section 6.1 we define the rules governing the network and game dynamics. As we will show, by coupling these two dynamics together we are able to transform, at the population level, the game that is being played at the individual level. Next, in Section 6.2, we analyze, analytically, the two opposing extremes of this coupling and illustrate it with two hypothetical behavioral scenarios. Finally, in Section 6.2.3, we study the stationary distribution of the game, to see in which states the system spends most of the time.

6.1 Active Linking Dynamics

Here we detail the two dynamics that compose the AL dynamics. The structural dynamics remains largely unchanged from [8] on the basis that individuals act in groups but these change as a result of the good or bad actions of single individuals.

The game dynamics on the other hand is entirely based on PGGs.

6.1.1 Network Dynamics

We consider a finite population of C 's and D 's of constant size Z as nodes on a network. They can create new connections and destroy existing ones over time.

We assume that new links appear at a certain rate and have a lifetime that, in principle, depends on the types of the individuals they connect. Hence we need to distinguish between CC , CD and DD links. So, for each type of link we will have its own rate of creation and destruction, α_{ij} and γ_{ij} , respectively. Throughout this work we will assume, for simplicity, that the rate of link creation is the same for all types of link: $\alpha_{CC} = \alpha_{CD} = \alpha_{DD} = \alpha$.

According to this dynamics, not all links are necessarily active at the same time. If the total number of links is large, the number of links of type ij that are active at time t , $N_{ij}(t)$, can be calculated from the following differential equation:

$$\dot{N}_{ij} = \alpha [\bar{N}_{ij}(t) - N_{ij}(t)] - \gamma_{ij} N_{ij}(t) \quad (6.1)$$

Where $\bar{N}_{ij}(t)$ is the maximum possible number of ij links. This maximum will depend on the number of individuals of type i and j , $N_i(t)$ and $N_j(t)$, respectively:

$$\bar{N}_{ij}(t) = \frac{N_i(t) [N_j(t) - \delta_{ij}]}{1 + \delta_{ij}} \quad (6.2)$$

So, if at a given time t the population is composed of k cooperators, then $N_C(t) = k$ and $N_D(t) = Z - k$. With this we can rewrite equation (6.2), as:

$$\begin{aligned} \bar{N}_{CC}(t) &= \frac{1}{2}k(k-1) \\ \bar{N}_{CD}(t) &= k(Z-k) \\ \bar{N}_{DD}(t) &= \frac{1}{2}(Z-k)(Z-k-1) \end{aligned} \quad (6.3)$$

If the creation rate is much larger than the destruction rates then the resulting network will be almost static and complete (fully-connected), so that we recover the known results for well-mixed finite populations from Section 3.3.

On the other hand, if the destruction rates are larger than the creation rate, then the equilibrium network will be sparse with few links active. In all cases, at the steady state the stationary number of links of each type is given by:

$$N_{ij}^* = \phi_{ij} \bar{N}_{ij} \quad (6.4)$$

Where $\phi_{ij} = \frac{\alpha}{\alpha + \gamma_{ij}}$ represents the fraction of active ij links. Substituting equations (6.3) in equation (6.4) we can write the expressions for the number of links of each type at the steady state:

$$\begin{aligned} N_{CC}^* &= \phi_{CC} \bar{N}_{CC} = \frac{1}{2} \phi_{CC} k(k-1) \\ N_{CD}^* &= \phi_{CD} \bar{N}_{CD} = \phi_{CD} k(Z-k) \\ N_{DD}^* &= \phi_{DD} \bar{N}_{DD} = \frac{1}{2} \phi_{DD} (Z-k)(Z-k-1) \end{aligned} \quad (6.5)$$

Where ϕ_{CC} , ϕ_{CD} and ϕ_{DD} are the fractions of active CC , CD and DD links at the steady state, respectively.

6.1.2 Game Dynamics

To capture the evolution of the game strategies of a finite population we use the framework of Section 3.3. Focusing on N -person games, our case study of cooperation will be the NPD defined in Section 2.3.1. Individuals interact with $N - 1$ members of their neighborhood and get payoffs given according to equations (2.3) and (2.4), respectively, whether they are C 's or D 's.

Let us describe the dynamics of strategy evolution via a stochastic birth-death process combined with the pairwise comparison rule from equation (3.8). So, the possible strategy update probabilities will be given by equations (3.11) and (3.12) and the dynamics of the number of cooperators in the population will be governed by the gradient of selection from equation (3.22).

6.2 Time Scales Separation

As in the previous Chapter, we consider that the two dynamics co-evolving in the system will have, in general, different characteristic time scales: the time scale of the network dynamics, τ_n , and the time scale of the game dynamics, τ_s . We can obtain analytical results when both time scales are separated, i.e., in the fast strategy ($W \ll 1$) and fast linking ($W \gg 1$) limits. Both these limiting cases will be analyzed separately below.

6.2.1 Fast Strategy Limit

Whenever $W \ll 1$, the strategies of the players change very fast compared to the changes of the network structure, so the AL does not affect the strategy dynamics. Thus, in this limit, the dynamics of the system will be equivalent to that of an evolutionary game played on a static network. In the context of the fast strategy AL, our system can be conveniently represented using a complete network and we recover the results of Section 3.3.1.

What is more, the game being played remains unaffected throughout evolution and the network dynamics only becomes relevant when the system reaches an equilibrium state of the strategies. Letting the topology change also allows to escape these states.

6.2.2 Fast Linking Limit

Whenever $W \gg 1$, the network dynamics is fast enough to ensure that the network will reach a steady state before the next strategy update takes place. As different types of links can have different destruction rates γ_{ij} , then C 's and D 's will have different connectivity values. At the steady state we can compute the average connectivity of the different strategies:

$$\langle k_C \rangle = \frac{N_{CD}^* + 2N_{CC}^*}{k} \quad (6.6)$$

$$\langle k_D \rangle = \frac{N_{CD}^* + 2N_{DD}^*}{Z - k} \quad (6.7)$$

Substituting equations (6.5) in equations (6.6) and (6.7) we can express $\langle k_C \rangle$ and $\langle k_D \rangle$ as a function of the fraction of active links:

$$\langle k_C \rangle = \phi_{CD}(Z - k) + \phi_{CC}(k - 1) \quad (6.8)$$

$$\langle k_D \rangle = \phi_{CD}k + \phi_{DD}(Z - k - 1) \quad (6.9)$$

The patent difference between the average connectivities of C 's and D 's, implies that the average group will have different compositions whether the focus individual is a C or a D . In a finite population of size Z with a total of k C 's we can use a hypergeometric sampling to calculate the probability of having j cooperators in a group of size N , centered on a C or a D , respectively:

$$G_C(k, j) = \binom{\langle k_C \rangle}{N-1}^{-1} \binom{2N_{CC}^*/k}{j} \binom{N_{CD}^*/k}{N-j-1} \quad (6.10)$$

$$G_D(k, j) = \binom{\langle k_D \rangle}{N-1}^{-1} \binom{N_{CD}^*/(Z-k)}{j} \binom{2N_{DD}^*/(Z-k)}{N-j-1} \quad (6.11)$$

Using equations (6.10) and (6.11) we can now determine the fitness of C 's and D 's by simply averaging the payoffs that both strategies get from the NPD (see equations (2.3) and (2.4)) over all possible group sizes:

$$f_C(k) = \sum_{j=0}^{N-1} G_C(k, j) \Pi_C(j+1) \quad (6.12)$$

$$f_D(k) = \sum_{j=0}^{N-1} G_D(k, j) \Pi_D(j) \quad (6.13)$$

Plugging these fitness values in equations (3.11) and (3.12) we find the $T^\pm(k)$. We can then compute the $g(k)$ and analyze the evolutionary dynamics of C 's and D 's. In particular, we can study the internal roots of the gradient and from there infer the equilibrium state of the population. This is equivalent to evaluating the roots of the gradient and their stability. Let $\Gamma(k) \equiv f_C(k) - f_D(k)$; after some manipulation (see Appendix C) we obtain:

$$\Gamma(k) = \frac{Fc}{N} \left(\frac{N\phi_{CC}(k-1) + \phi_{CD}(Z-k)}{\phi_{CC}(k-1) + \phi_{CD}(Z-k)} - \frac{(N-1)\phi_{CD}k}{\phi_{CD}k + \phi_{DD}(Z-k-1)} \right) - c \quad (6.14)$$

This equation is, at most, a second order polynomial on k , so that $g(k)$ has between zero and two internal equilibria, besides the other two global ones, at $k = 0$ and $k = Z$ (see equation (3.22)). More importantly, with equation (6.14) we can determine the stability of the gradient's roots simply by figuring out the signs of $\Gamma(1)$ and $\Gamma(Z-1)$:

$$\Gamma(1) = \frac{Fc}{N} \left(1 + \frac{1-N}{1+(Z-2)/\mu} \right) - c \quad (6.15)$$

$$\Gamma(Z-1) = \frac{Fc}{N} \left(1 + \frac{1-N}{1+(Z-2)/\nu} \right) - c \quad (6.16)$$

Where $\mu = \phi_{CD}/\phi_{DD}$ and $\nu = \phi_{CD}/\phi_{CC}$. Remembering that $Z > N > 1$, we immediately get, for all $\mu, \nu \neq 0$:

$$\frac{1-N}{1+(Z-2)/\mu} < 0 \quad (6.17)$$

$$\frac{1-N}{1+(Z-2)/\nu} < 0 \quad (6.18)$$

For $F < N$, it is easy to see from equations (6.17) and (6.18) that $\Gamma(1) < 0$ and $\Gamma(Z-1) < 0$, for all $\mu, \nu \neq 0$. This means firstly that the gradient's global equilibria, $k = 0$ and $k = Z$ are, respectively, stable and unstable; and secondly, that it can also have either two mixed internal equilibria (the 'left one' unstable and the 'right one' stable) or a single metastable internal equilibria. In other words we can either have an effective full defection game, in which case the game remains unchanged from the usual finite population version of the NPD; or an effective NSG (see Section 3.3.3), with a gradient having both a coordination (k_u) and coexistence (k_s) equilibria, with $k_u \leq k_s$. To sum up, as long as $F < N$, a single C is always disadvantageous and a single D is always advantageous.

For $F > N$, the situation will be reversed although in a not so straightforward fashion. This can be seen if we write the conditions for $\Gamma(1) > 0$ and $\Gamma(Z-1) > 0$ as:

$$\frac{F}{N} > \frac{1 + \mu/(Z-2)}{1 - \mu(N-2)/(Z-2)} \quad (6.19)$$

$$\frac{F}{N} > \frac{1 + \nu/(Z-2)}{1 - \nu(N-2)/(Z-2)} \quad (6.20)$$

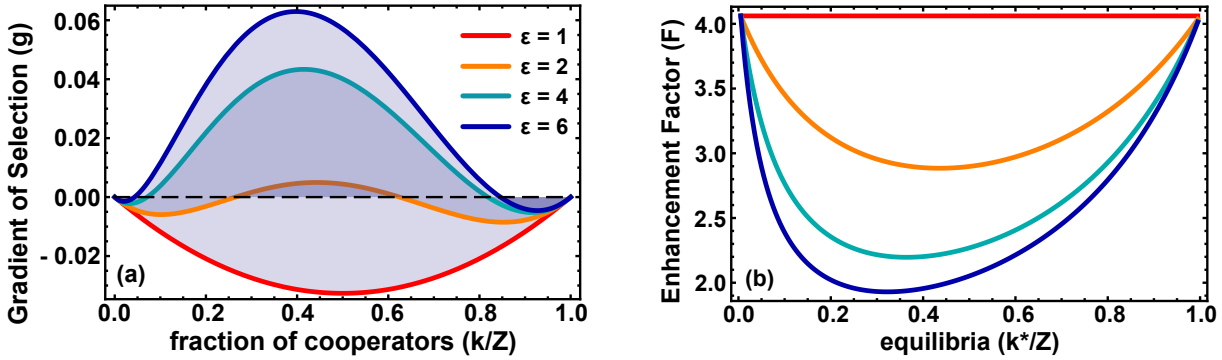


Figure 6.1: Dynamics of a NPD in a Free Choice World. In (a) the gradient of a selection for $Z = 200$, $N = 4$, $F = 3$, $\beta = 1$, $\alpha = 0.04$ and $\gamma = 0.1$. Increasing ε effectively transforms the game, at the population level, from a NPD into a NSG. In (b) the gradient's internal roots, k^* , as a function of F . Above a certain critical value, two internal roots appear that move to the absorbing states as ε gets larger.

These equations show that, for a given μ and ν , there is a critical value of the multiplication factor, F_c , above which we get the (gradient-wise) reverse of the previous case, i.e., either a HG or a *reversed N-person snow-drift game* — with $k_s \leq k_u$. Moreover, F_c converges to N with the increase in population size, Z . To sum up, as long as $F > F_c$, a single C is always advantageous and a single D is always disadvantageous and also $F_c \xrightarrow{Z \rightarrow 1} N$.

Let us illustrate these findings with two example situations dubbed Free Choice World and Bound Choice World, based on two distinct orderings of the different death rates γ_{ij} .

6.2.2.1 Free Choice World

The Free Choice World (FCW) is a scenario where the lifetime of a social link depends only on whether it represents a mutually beneficial relation or not. Put differently, if at least one of the linked players is a D , then it will negatively affect the duration of said link. Obviously the FCW is a very naive world, which oversimplifies the network dynamics. Even so, many of its results remain valid for general scenarios.

The FCW translates into:

$$\begin{aligned} \gamma_{DD} = \gamma_{CD} &> \gamma_{CC} \\ \Leftrightarrow \gamma_{DD} = \gamma_{CD} &= \varepsilon \gamma_{CC} \end{aligned} \quad (6.21)$$

Where $\varepsilon \geq 1$ is a measure of a player's reaction to an adverse partner, i.e., it represents how fast a link involving a D is destroyed.

In Figure 6.1a we can see the gradient of selection of a population of size $Z = 200$ playing a NPD with $F < N$ in a FCW. For $\varepsilon = 1$, meaning that all links have the same lifetime, the game remains unaffected by the linking dynamics. The picture changes for $\varepsilon \geq 2$, where two mixed internal roots, k_u and k_s , begin to appear.

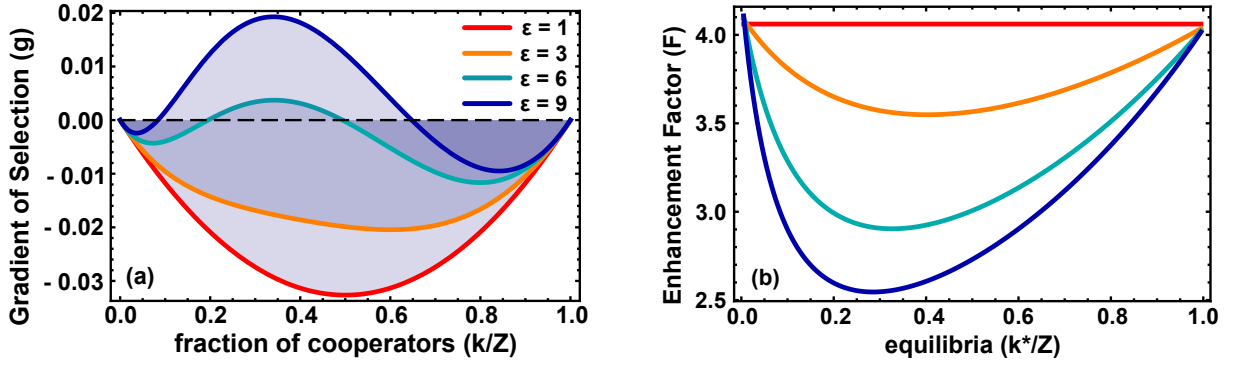


Figure 6.2: Dynamics of a NPD in a Bound Choice World. In (a) the gradient of a selection for $Z = 200$, $N = 4$, $F = 3$, $\beta = 1$, $\alpha = 0.04$ and $\gamma = 0.1$. we observe the same qualitative behavior as in Figure 6.1a. In (b) the gradient's internal roots, k^* , as a function of F . Again we see that, above a certain critical value of F the dynamics changes, from a NPD to a NSG.

The dependence of the gradient's roots on the game parameters can be seen from Figure 6.1b. For each value of F , one defines a horizontal line that, at the intersection with each curve (one curve for a given, fixed ε), gives us the position of the equilibria, k^* . Figure 6.1b also shows that, as expected, only two types of dynamics scenarios (effective games) can appear: for large values of F we have the two mixed internal fixed points characteristic of the NSG; while, for low values of F , we get the distinctive defection dominance scenario of the NPD.

Curiously, for a fixed F , with increasing ε and therefore increasing destruction rates of adverse links, we observe not only a decrease in k_u , i.e., the critical number of C 's necessary to overcome the coordination barrier and reach a cooperative basin of attraction, but also an increase in k_s , i.e., the stable number of C 's of this basin.

6.2.2.2 Bound Choice World

The Bound Choice World (BCW) is a scenario where the lifetime of a social link depends on the actions of both players. In the BCW a link involving two D 's will be more feeble than a link between a C and a D , which in turn is more feeble than a link between two C 's. These relations translate into:

$$\begin{aligned} & \gamma_{DD} > \gamma_{CD} > \gamma_{CC} \\ \Leftrightarrow & \begin{cases} \gamma_{DD} = \varepsilon \gamma_{CC} \\ \gamma_{CD} = \frac{\gamma_{CC} + \gamma_{DD}}{2} \end{cases} \end{aligned} \quad (6.22)$$

In Figures 6.2a and 6.2b we have the gradient of selection and its roots, respectively, for a NPD being played on a BCW. As we can see, while this scenario is not as simplistic as the FCW, they both produce qualitatively the same results. Moreover, in this scenario individuals need to be more proficient at assessing bad links (higher ε) in order to reach

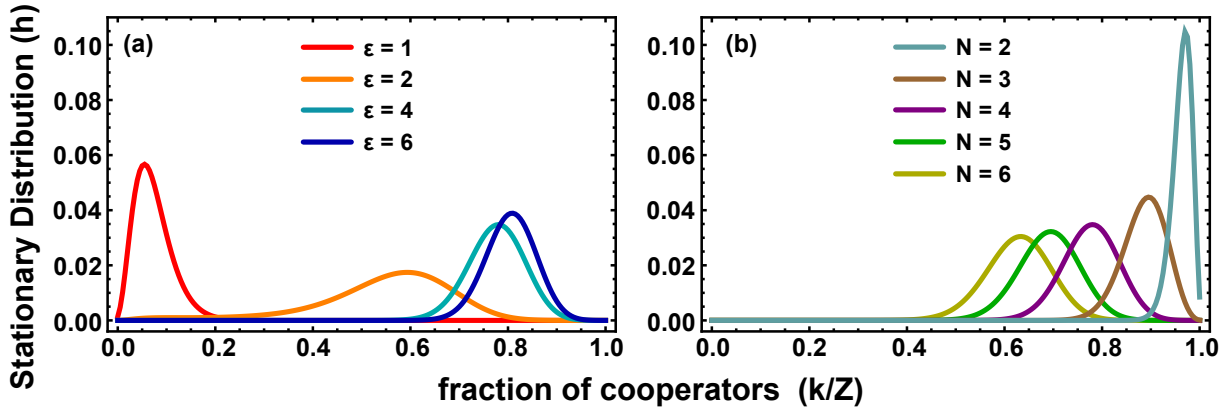


Figure 6.3: Stationary distribution of cooperators in a FCW. In (a) we used the same game parameters as in Figure 6.1a and with a mutation probability of $\zeta = 0.01$. The more proficient individuals are at assessing adverse ties (higher ε), the easier it is for C 's to overcome the coordination barrier. In (b) we observe the same picture when we fix $\varepsilon = 4$ and vary the N . The lower the N the higher the k_s and therefore the more time the system spends near that equilibrium.

the same level of cooperation as in the FCW. This is justifiable on the account that D 's now have a say in the duration of the link, as they rather keep a link with a C than one with a D .

We have considered two hypothetical scenarios that, despite being different, give rise to essentially the same dilemmas. They have in common the relative ordering of the destruction rates: $\gamma_{DD} \geq \gamma_{CD} > \gamma_{CC}$. This relation suggests that to sustain cooperative action in a population one needs to allow individuals to remake their social neighborhood, by getting out of adverse relations and keeping the favorable ones, regardless of the speed at which they do it.

From now on we will consider only the FCW as an example situation for the AL.

6.2.3 Stationary Distribution of Cooperators

The gradients shown in Figures 6.1a and 6.2a provide the global picture of the dynamics but they can be complemented by the stationary distribution that tells us how stable in time is a given composition of the population (see Section 3.3.2). If we now assume that the stochasticity of the population includes some sort of behavioral mutation, ζ , we can use the modified transition probabilities $\tilde{T}^\pm(k)$ from equations (3.19) and (3.20) and compute the stationary distribution.

Figure 6.3a shows that distribution for the FCW with the same parameters as in Figure 6.1a with an added $\zeta = 0.01$. As expected, for $\varepsilon = 1$, the population spends most of the time near the $k = 0$ state, as we have a *full d* game. But, as we go from the NPD to the NSG ε , we see only a peak near the coexistence equilibrium, where an additional one would be expected, before the coordination. For higher ε we observe larger numbers

of $C's$.

Interestingly, the Figure shows that, regardless of the initial condition, the population is able to tunnel through the coordination barrier and spend most of its time at or around k_s . This fact is simply a consequence of the stochastic effects (mutations included) and of the presence of a stable internal equilibrium.

In Figure 6.3b we can see the effect of N on the stationary distributions. Using the same parameters as in the other distribution but setting $\varepsilon = 4$ we vary the group size. For all the values used in this Figure we always get mixed internal equilibria that move closer to the monomorphic states as N gets lower. Qualitatively the picture is very similar, in the sense that, as long as we include mutations the population is blind to the coordination and quickly converges to the coexistence.

Chapter 7

Final Remarks

In this work we used the framework of EGT to study the evolution of cooperation in the context of N -person PGGs. Following a brief introduction on the basic formulation of social dilemmas of cooperation, both 2-person and N -person, we described the tools necessary for this analysis. After that we presented three models that added a mechanism each to facilitate the emergence of the property in question.

In infinite, well-mixed populations we use the *replicator equation* to compute the time evolution of the fraction of cooperators, x . This equation accounts for the variations of fitness of both strategies as x evolves, which are dictated by the rules of game being played (in the form of the payoffs). The evolutionary dynamics show that, at equilibrium we can have either a stable coexistence of a mix of C 's and D or a complete dominance of only one of the strategies.

Finite, well-mixed populations, with their inherent stochastic effects, make for a more interesting case study. The dynamics is no longer deterministic and can be modeled (in our case of just two game strategies) as a one dimensional Markov chain. In the absence of mutations, only the fully cooperative and fully defective states are absorbing, in which case a stable coexistence is not possible.

To study these populations one can use the *fixation probability* of k individuals that tells us how likely the system converges to *full cooperation*, for a given starting condition. However, in the presence of stochastic effects, the fixation probability cannot extract the complete dynamical picture. Another tool we can use is the *stationary distribution* of C 's, a probability distribution of the time spent in each state. This is particularly relevant in the presence of behavioral mutations, i.e., individuals spontaneously changing their strategy. A third quantity that describes the game dynamics of a finite population is the *gradient of selection*. An analog of the replicator equation, that naturally incorporates the stochastic effects of the system, without them masking the dynamics.

The first model of this work applies to infinite populations and is based on a modified

replicator equation that uses the fitness from past actions of players. It is a so-called *delayed replicator equation*. This rather small modification can have a profound impact on the dynamics of the game. For a large enough delay, we get a Hopf bifurcation with the stable internal root of the NSH bifurcating into a stable periodic orbit. What is more, for an even larger delay, the dynamics is forcibly driven to full defection, at least for a reasonable set of history functions. In principle it would be possible to construct a history function with which the system can converge to any stable equilibrium, but it would still be unable to change the nature of any of the equilibria.

These results imply that one must be careful when investing in the stock market, stockpiling something for future use or deciding when to act against climate change. If the wait for the reward is too long, then that might not come in the form one originally expected, at least in large populations.

A more detailed look at populations show the existence of an underlying structure that guides the actions of its members. This can be captured in a network of social interactions that can serve as the playground for games of cooperation. Taking a clue from real networks we assumed that its structure co-evolves with the game dynamics of the constituent nodes, thus forming an adaptive network. Such a framework spawned the other two models presented here.

The computational rewiring model had the nodes of a network playing a NPD and simultaneously changing from adverse to advantageous groups based on their self-interests. By explicitly introducing the time scales of these two processes, strategy and linking dynamics, we could regulate their coupling (W). We showed that an increased proficiency at changing groups translated into higher observed levels of cooperation, when compared to those of the usual NPD. More importantly, we saw that a swifter link-assessing population had an underlying structure that is very heterogeneous at their peak efficiency.

The analytical AL model, starting from a mean-field description of a network, lets individuals play a NPD and assess the duration of each individual link. Unlike the previous model however, the analytical treatment of the AL is only valid for extreme couplings of the two time scales. In the fast strategy limit it reproduces known results from finite well-mixed populations; but in the fast linking limit it shows that, because the social ties are extremely volatile, the game at a population level differs from the one at individual level. In a population where structure changes at a very quick pace and individuals play a NPD (a usually fully defective game), the results is an overall NSG, a mixed equilibria game.

These last two models indicate that the reason that we have a somewhat cooperative society, composed of many self-regarding and selfish individuals, results perhaps from the fact that some human relations are very short-lived. This allows for a very heterogeneously structured population, very much alike an actual social network.

All in all, these three models show the advantages of using the framework of EGT to study social dilemmas. By stripping interactions down to the essential components, EGT is able to extract a clear explanation for the phenomena of cooperation that seems well in accord with empirical knowledge. Furthermore, the switch to group-based games is essential if we are to accurately analyze all the myriad of human and animal interactions.

Appendices

Appendix A

Fixation Probability ρ_k

In this Appendix we deduce the closed form expression for the fixation probability (equation (3.16)), from section 3.3.1. Refer to equations (3.11), (3.12) and (3.14) and accompanying explanation for all necessary clarification, if any.

Let us first introduce the auxiliary variables:

$$\omega_k \equiv \rho_k - \rho_{k-1} \tag{A.1}$$

$$R_k \equiv \frac{T^-(k)}{T^+(k)} \tag{A.2}$$

Where $k = 1, \dots, Z$. From (A.1) we note that:

$$\begin{aligned} \sum_{i=1}^k \omega_i &= \rho_1 - \rho_0 + \rho_2 - \rho_1 + \dots + \rho_k - \rho_{k-1} \\ &= \rho_k - \rho_0 \\ &= \rho_k \end{aligned} \tag{A.3}$$

And, by analogy:

$$\begin{aligned} \sum_{i=1}^Z \omega_i &= \rho_1 - \rho_0 + \rho_2 - \rho_1 + \dots + \rho_Z - \rho_{Z-1} \\ &= \rho_Z - \rho_0 \\ &= 1 \end{aligned} \tag{A.4}$$

From equations (3.14) we find that $\omega_{k+1} = R_k \omega_k$. Therefore, we have $\omega_1 = \rho_1$, $\omega_2 = R_1 \omega_1 = R_1 \rho_1$, $\omega_3 = R_2 \omega_2 = R_2 R_1 \rho_1$ and, in general:

$$\omega_k = \left(\prod_{j=1}^{k-1} R_j \right) \rho_1 \tag{A.5}$$

Substituting in equation (A.4) we get:

$$\begin{aligned}
& \sum_{i=1}^Z \omega_i = 1 \\
& \Leftrightarrow \omega_1 + \sum_{i=1}^{Z-1} r_{i+1} = 1 \\
& \Leftrightarrow \rho_1 \left(1 + \sum_{i=1}^{Z-1} \prod_{j=1}^i R_j \right) = 1 \\
& \Leftrightarrow \rho_1 = \frac{1}{1 + \sum_{i=1}^{Z-1} \prod_{j=1}^i R_j} \tag{A.6}
\end{aligned}$$

On the other hand, if we substitute equation (A.5) in equation (A.3) we will get:

$$\rho_k = \rho_1 \left(1 + \sum_{i=1}^{k-1} \prod_{j=1}^i R_j \right) \tag{A.7}$$

Finally, we obtain the closed form of the fixation probability:

$$\rho_k = \frac{1 + \sum_{i=1}^{k-1} \prod_{j=1}^i R_j}{1 + \sum_{i=1}^{Z-1} \prod_{j=1}^i R_j} \tag{A.8}$$

Appendix B

Stationary Distribution h_k

Here we deduce the closed form expression for the stationary distribution (equation (3.18)), from section 3.3.2. Refer to equations (3.11), (3.12) and (3.13) and accompanying explanation for all necessary clarification, if any.

For latter convenience we recall here the definition of the stationary distribution \mathbf{h} , as the left eigenvector associated with the eigenvalue 1 of $\mathbf{\Lambda}$:

$$\mathbf{h}^T \mathbf{\Lambda} = \mathbf{h}^T \tag{B.1}$$

$$\sum_{i=0}^Z h_i = 1 \tag{B.2}$$

If we write equation (B.1) explicitly for each component we get the following recursive relation:

$$h_0 = h_0 (1 - T^+(0)) + h_1 T^-(1) \tag{B.3}$$

\vdots

$$h_k = h_{k-1} T^+(k-1) + h_k (1 - T^+(k) - T^-(k)) + h_{k+1} T^-(k+1) \tag{B.4}$$

\vdots

$$h_Z = h_{Z-1} T^+(Z-1) + h_Z (1 - T^-(Z)) \tag{B.5}$$

From (B.3) we get $h_1 = h_0 \frac{T^+(0)}{T^-(1)}$ and analogously $h_2 = h_1 \frac{T^+(1)}{T^-(2)} = h_0 \frac{T^+(1) T^+(0)}{T^-(2) T^-(1)}$. In general we have that:

$$h_k = h_0 \frac{T^+(k-1) T^+(k-2) \cdots T^+(0)}{T^-(k) T^-(k-1) \cdots T^-(1)} = h_0 \prod_{j=0}^{k-1} \frac{T^+(j)}{T^-(j+1)} \tag{B.6}$$

From equation (B.2) we obtain:

$$\begin{aligned}
 1 &= \sum_{i=0}^Z h_i \\
 1 &= h_0 \left(1 + \sum_{i=1}^Z \prod_{j=0}^{i-1} \frac{T^+(j)}{T^-(j+1)} \right) \\
 \Leftrightarrow h_0 &= \frac{1}{1 + \sum_{i=1}^Z \prod_{j=0}^{i-1} \frac{T^+(j)}{T^-(j+1)}} \tag{B.7}
 \end{aligned}$$

Substituting (B.7) in (B.6) we finally obtain the closed form expression for the components of the stationary distribution:

$$h_k = \frac{\prod_{j=0}^{k-1} \frac{T^+(j)}{T^-(j+1)}}{1 + \sum_{i=1}^Z \prod_{j=0}^{i-1} \frac{T^+(j)}{T^-(j+1)}} \tag{B.8}$$

Appendix C

Fitness Difference $\Gamma(k)$

In this Appendix we try to simplify the fitness difference $\Gamma(k)$ from Chapter 6 valid in the limit of fast linking dynamics. If needed, refer to section 6.2.2 for the explanation of expressions used there first.

Before beginning we deduce the expected value of a hypergeometric distribution as it will be useful for what follows. First we remark that:

$$E(J) = \binom{B}{N}^{-1} \sum_{j=0}^N j \binom{A}{j} \binom{B-A}{N-j} = \binom{B}{N}^{-1} \sum_{j=1}^N j \binom{A}{j} \binom{B-A}{N-j} \quad (\text{C.1})$$

Since for $j = 0$ the summation is 0. We also like to recall the following combinatorial identities:

$$j \binom{A}{j} = A \binom{A-1}{j-1} \quad (\text{C.2})$$

$$\binom{B}{N} = \frac{B}{N} \binom{B-1}{N-1} \quad (\text{C.3})$$

Using equations (C.2) and (C.3) in (C.1) we then obtain:

$$E(J) = \frac{NA}{B} \binom{B-1}{N-1}^{-1} \sum_{j=1}^N \binom{A-1}{j-1} \binom{B-A}{N-j} = \frac{NA}{B} \quad (\text{C.4})$$

Where we have simply used the fact that the distribution is normalized.

Now, if we substitute equations (2.3), (2.4), (6.10) and (6.11) into their respective

positions in equations (6.12) and (6.13), we get:

$$f_C(k) = \binom{\langle k_C \rangle}{N-1}^{-1} \sum_{j=0}^{N-1} \binom{2N_{CC}^*/k}{j} \binom{N_{CD}^*/k}{N-j-1} \left(\frac{(j+1)Fc}{N} - c \right) \quad (\text{C.5})$$

$$f_D(k) = \binom{\langle k_D \rangle}{N-1}^{-1} \sum_{j=0}^{N-1} \binom{N_{CD}^*/(Z-k)}{j} \binom{2N_{DD}^*/(Z-k)}{N-j-1} \frac{jFc}{N} \quad (\text{C.6})$$

Using the property (C.4), the above equations greatly simplify to:

$$f_C(k) = \left(\frac{2(N-1)N_{CC}^*}{k\langle k_C \rangle} + 1 \right) \frac{Fc}{N} - c \quad (\text{C.7})$$

$$f_D(k) = \frac{(N-1)N_{CD}^*}{(Z-k)\langle k_D \rangle} \frac{Fc}{N} \quad (\text{C.8})$$

If we now rewire it in terms of fraction of active links at the steady state, ϕ_{ij} , we get (see equations (6.5), (6.8) and (6.9)):

$$f_C(k) = \frac{N\phi_{CC}(k-1) + \phi_{CD}(Z-k)}{\phi_{CC}(k-1) + \phi_{CD}(Z-k)} \frac{Fc}{N} - c \quad (\text{C.9})$$

$$f_D(k) = \frac{(N-1)\phi_{CD}k}{\phi_{CD}k + \phi_{DD}(Z-k-1)} \frac{Fc}{N} \quad (\text{C.10})$$

Subtracting the two equation we then get the final expression for the fitness difference, $\Gamma(k)$:

$$\Gamma(k) = \frac{Fc}{N} \left(\frac{N\phi_{CC}(k-1) + \phi_{CD}(Z-k)}{\phi_{CC}(k-1) + \phi_{CD}(Z-k)} - \frac{(N-1)\phi_{CD}k}{\phi_{CD}k + \phi_{DD}(Z-k-1)} \right) - c \quad (\text{C.11})$$

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