**Modelos matemáticos para evolução
social: de cooperação à
diversidade linguística**

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**Mathematical models for social
evolution: from cooperation to
language diversity**

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Resumo

Uma das características que nos distinguem de outros seres vivos é nossa cultura. Entretanto, como comportamentos não fossilizam, é difícil reconstruir o passado para gerar *insights* sobre por que nos tornamos o que somos hoje. Juntamente com dados etnográficos e experimentais, os modelos matemáticos têm sido utilizados para abordar a questão sobre como nossos comportamentos foram moldados pela evolução.

Esta tese está dividida em duas partes. Na primeira parte, discutiremos sobre seleção multinível e sobre como o *framework* matemático chamado *Two-level Fisher Wright* (TLFW) pode nos ajudar a entender a evolução da cooperação em populações humanas. Após descrevermos o problema da cooperação através do uso de ferramentas de teoria dos jogos, revisamos algumas das teorias atuais sobre por que a cooperação evoluiu. Em seguida, empregamos o framework TLFW ao problema da emergência de altruísmo em populações de caçadores-coletores, considerando uma situação em que o conflito entre grupos direciona a seleção.

Na segunda parte, abordamos o tópico de diversidade linguística e apresentamos a importância de se estudar a competição entre línguas para ajudar a preservá-las. Traçando um paralelo entre a evolução das línguas e a evolução de normas sociais, introduzimos um modelo para analisar a persistência de dialetos, quando existe competição com uma língua padrão nacional.

Abstract

One of the features that distinguish human beings from other living species is our culture. However, since behaviors do not fossilize, it is difficult to reconstruct the past to get insights about why we are who we are. Along with ethnographic and experimental data, mathematical models have been used to address the question of how our behaviors were shaped by evolution.

This thesis is divided into two parts. In the first part, we will discuss multilevel selection and how the mathematical framework *Two-Level Fisher-Wright* (TLFW) can help us to understand the evolution of cooperation in human populations. After describing the problem of cooperation by using game theory, we review some of the present theories about why cooperation has evolved. Then, we apply the TLFW framework to the problem of the evolution of altruism in populations of hunter-gatherers, considering a situation in which group conflict drives selection.

In the second part, we discuss language diversity and present the importance of studying the competition between languages for helping to preserve them. By drawing a parallel between the evolution of language and social norms, we introduce a mathematical model to analyze the persistence of dialects competing against a national standard language.

If you never noticed, it never happened.
Haruki Murakami (1Q84)

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Chapter 1

Introduction

Although statistics has been used for some centuries to guide decisions on social problems, making mathematical models as an approach to understand social evolution is relatively new. It has joined efforts from biologists to economists and social scientists [28, 21, 11, 76], and there is no consolidated discipline that treats this approach exclusively ¹.

A badly digested doctrine of selfish genes [31] gave strength to ideas such as the character *homo economicus*, which is the basis of several mathematical models related to human behavior. As social beings, however, humans are not only motivated by individual benefits when they pursue their actions and, thus, explaining some behaviors based on the concept of the *homo economicus* has become a challenge.

The area of cultural evolution was born from this need of understanding more about social interactions and their effects at a societal level. Cultural evolution methods were derived from population biology and game theory, as its concern is to shed light on the changes which are products of the transmission of certain traits or behaviors.

In parallel, in Economics, the theory of social institutions was developed, also influenced by the ideas of evolutionary biology and game theory. An institution may be thought as the tool that governs social interactions [18]. Its evolution can trigger changes in individuals preferences and beliefs, and thus, the theory of social institutions is directly intertwined with the field of cultural evolution.

¹Recently, a review on the emergence of consensus [13] has pointed out that two articles with very similar titles, *The evolution of norms* and *The evolution of social norms*, did not share a single bibliographic entry, showing how different fields do not interact with each other in the area of social evolution.

One of the most studied problems of social evolution is the problem of the evolution of human cooperation. Cooperation can be considered the opposite behavior of selfishness, as it occurs when an individual benefits other individual without receiving any benefit from the recipient. *Hamilton's rule* [43] explains cooperation (among other phenomena) based on the relatedness between individuals.

Although Hamilton's rule is successful in explaining cooperation acts in dyadic interactions, still, this is not sufficient to understand large-scale cooperation, when individuals engage in non-dyadic interactions, as it is empirically and experimentally observed between humans. Cooperation seems to be imprinted in human behavior. And thus, studying this phenomena implies studying the process through which we came to be cooperative beings.

1.1 Motivation and Main Results

Cooperation underlies human social behavior, from the capability of joining efforts towards a common goal, to communication through the use of a language. In this thesis, we studied and created mathematical models for two different problems related to the field of evolution of cooperation: (i) evolution of altruism and (ii) language evolution.

1.1.1 Evolution of altruism

Previously, many studies have explained the evolution of altruism using several theories, from reciprocity and relatedness to multilevel selection. Fewer studies, however, have focused on the emergence of altruism, and how altruism can spread when altruists are rare in the population.

Schonmann, Caticha and Vicente [83] devised a new general framework (the two-level Fisher-Wright model) to analyze the evolution of social traits. Their model assumes a two-level selection: it considers the population is structured in groups of fixed size and that selection occurs within and between groups. Their main goal was to generalize Hamilton's rule, in order to account for the cases in which the fitness functions are non-linear, which cannot be treated by the generalized kin theory proposed by Taylor and Frank [96].

Inspired by the work of Samuel Bowles [16], we applied the two-level Fisher-Wright model to study the emergence of altruism in the presence of intergroup conflict. We extended the framework created

by Schonmann, Caticha and Vicente [83], by incorporating war as an intergroup competition stage. We also built an agent-based simulation and compared its results with the results obtained with the theoretical model.

Our results show that it is possible that the occurrence of wars had influenced the spread of altruism in the population. We found that high frequencies of wars combined with large enough war benefits provided by altruists can make altruism viable even when migration levels are high (low relatedness). The agent-based simulation results agree with the theoretical model results.

1.1.2 Language evolution

The appearance of languages has been recognized as one of the major transitions in evolution. Language influences cultural evolution and, on the other hand, language diversity is a target of cultural evolution itself.

In the last century, language diversity has been steadily decreasing all over the world. This is a worrying situation, since there is no way to predict the effects of the extinction of so many languages. In particular, one common path for language extinction is the replacement of one language by a more powerful language. This is the case when dialects disappear after the introduction of a national standard language.

We studied the competition dynamics between a local dialect and a standard language. We created a mathematical model in which we assumed individuals could choose to use the local dialect or the standard language, according to different situations, public (e.g. workplace) and private (e.g. family meetings). We considered the choice of a dialect is mainly guided by two forces: (i) attractiveness of the local/standard language; and (ii) willingness to speak the same dialect (conformity factor) inside a private group.

Our results show that conformity usually enhances the effect dictated by the difference in attractiveness between the local dialect and the standard language if conformity works favoring only those states in which all speakers use the same dialect (unanimity pressure model). However, conformity may have no effect at all if it works in proportion to the fraction among peers (peer pressure model). These findings, when confronted with data from some dialects in Japan and in China, indicate that one way to preserve local dialects is to foster public policies focused in enhancing the pride of speaking local dialects.

1.2 Thesis Structure

In this introduction, we discussed our motivations and provided a glimpse of the theory and the results we will present in the next chapters.

In chapter 2, we introduce the main mechanisms that promote the evolution and emergence of human cooperation. Part of this chapter is dedicated to multilevel selection, as this is a key concept to understand the models presented in chapter 3.

In chapter 3, we describe the core theory behind the framework Two-Level Fisher Wright (TLFW). TLFW is a general framework, which incorporates intra and intergroup selection and migration. In this chapter, we explain how this framework can model the evolution of social traits, when selection is observed at two different levels. We also describe how to calculate the conditions under which a certain social trait is viable and provide some examples of results obtained by the application of the framework to different public good games.

In chapter 4, we introduce the model we created to investigate the emergence of altruism in the presence of intergroup conflict. We show how we adapted the TLFW framework to incorporate intergroup wars and present the results we obtained with the numerical simulations and the agent-based simulation.

In chapter 5, we present our study of the survival of dialects when a more powerful language exists. We describe the motivations for creating this model and show which conditions may help a dialect to survive. A major part of this chapter is the result of a collaboration with Dr. Iwasa and Dr. Lee from Kyushu University, in Japan. Our work has been published in the journal *Bulletin of Mathematical Biology* [94].

In chapter 6, we discuss how this thesis results contribute to the field and what are some possible future directions of the studied topics.

Chapter 2

Mechanisms for the evolution of cooperation

In the first edition of *The selfish gene* [31], Dawkins assumed individuals would all be “born selfish” and, thus, they should be taught altruism. Although, along the years, his opinion has changed, this idea of a innately selfish human reflected the strength, at the time, of the *Homo Economicus* character (the "rational" agent) in economics models.

However, many daily situations and laboratory experiments show that humans do not resemble the *Homo Economicus* character when making decisions. Cooperation levels are consistently higher than what it is expected from microeconomics theory.

This revealed to be a conundrum: how could we explain the observed cooperation levels from the interaction of self-interested individuals? Much of the theory behind the evolution of cooperation was developed as a response to the stated question, and different mechanisms through which cooperation could evolve were discovered (or rediscovered). Box 1 summarizes some of that mechanisms.

Box 1: Examples of mechanisms for the evolution of cooperation.

The quest to understand human behavior regarding cooperation yielded simple rules which enabled self-regarding individuals to cooperate:

- kin relationships: sharing genes increase the likelihood of cooperation;
- reciprocity: the expectation of repeated interactions and the role of reputation inside a society can motivate behavioral changes towards more cooperative actions;
- sanctioning systems: reward or punishment, from an external authority or peers, can motivate individuals to cooperate.

As our understanding of humans as cooperative beings deepened, a myriad of psychological experiments challenged the proposed mechanisms, since humans seemed to be cooperative beyond kin relationships, the existence of sanctioning systems or the expectation of further interactions [19].

This chapter presents a concise introduction to the problems of evolution and emergence of cooperation. We describe the mechanisms of direct and indirect reciprocity and multilevel selection¹ which help explaining how cooperation has evolved.

2.1 The cooperation problem

Before delving into the ways we can solve the cooperation problem, we should define more clearly what is the cooperation problem and how game theory can help us to elucidate it.

According to Hamilton [43], we can classify different social behavior from the fitness gains/losses faced by the actor and the recipient of a given action:

	benefit to recipient	cost to recipient
benefit to actor	mutualism	selfishness
cost to actor	altruism	spite

Table 2.1: Categories of social behavior according to the interaction between actor and recipient.

In this thesis, we are mainly concerned with two concepts: *altruism* and *cooperation*. From table 2.1, altruism is the behavior in which an individual provides benefit to another individual at a cost to

¹Although sanctioning systems are very important as a mechanism for the evolution of cooperation, for conciseness, we do not discuss it in this thesis. A good review of the main theory of sanctioning systems can be found in chapter 6 of [90].

himself. On the other hand, cooperation can be defined as a behavior in which an actor provides a benefit to a recipient, including both mutualistic and altruistic behaviors.

Although simple, these definitions have caused heated discussions and more than one author has attempted to provide a unified view of cooperation and/or altruism definitions [52, 105, 53]. One point of disagreement, for example, regards the way fitness effects should be accounted, as fitness effects might vary according to the time window, the target unit (population or group) etc., and this could potentially change what one views as altruism or spite [58]. In this chapter, we use *cooperation* and *altruism* interchangeably (unless specified), since we consider altruism is a restricted version of cooperation.

2.1.1 Prisoner's Dilemma

One of the most famous games in the field of game theory and studies about the evolution of cooperation is the *Prisoner's Dilemma* (PD) game. This game was proposed by scientists at RAND corporation, an American think tank, and has received its name when a RAND consultant, Albert Tucker described it as a situation in which two suspects are taken separately to be interrogated [77]. Each one of them faces the decision of choosing to betray the partner (B), or to not betray him (N), by remaining silent, knowing that according to the chosen action, they could be in jail for a very long, long or short time, or could be set free. One important feature here is that the players could not communicate with each other, so that in order to choose the best move, one has to make assumptions about how the other player will behave. This characteristic of the game is what distinguishes non-cooperative game theory from cooperative game theory, in which players can form coalitions among them.

A short introduction to game theory concepts and formalism can be found in appendix section A.1. In the two-person PD game, there are two players, the row player (player 1) and the column player (player 2). The set of strategies S_1 , for player 1, and S_2 , for player 2, are the same, such that: $S_1 = S_2 = \{B, N\}$, in which B stands for **B**etray and N stands for **N**ot Betray. The rules in this game are as follows:

- if both players betray each other, they will only spend 1 year in prison each;
- if only one of them betrays the other, then the one who was betrayed will go to jail for 8 years while the other goes free; and

- if both of them keep silent, they go to jail for 5 years.

This situation can be described by the following payoffs matrix:

$$\begin{array}{cc} & \begin{array}{cc} N & B \end{array} \\ \begin{array}{c} N \\ B \end{array} & \begin{pmatrix} -1 & -8 \\ 0 & -5 \end{pmatrix} \end{array} \quad (2.1)$$

Note that the payoffs are only shown for one player, the row player, since the payoffs for the other player are reciprocal, i.e., the payoff for player 2 for the strategy profile (B, N) is the payoff for player 1 when the strategy profile is (N, B) .

From eq. (2.1), we see that, if player 2 betrays player 1, then, player 1 is better off by saying his partner committed the crime ($-5 > -8$). If player 2 remains silent, still, the best strategy is to betray him to go free ($0 > -1$). Since the scenario is exactly the same for player 2, we observe that if both players are willing to choose the strategy that maximizes their own payoffs, they will end up choosing B , having to stand 5 years in prison. (B, B) is called the **Nash equilibrium** of this game.

More generally, the PD game can be described by the following matrix [79, 98]:

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

in which $T > R > P > S$. The letters R , T , S and P stand, respectively, for: **R**eward, **T**emptation, **S**ucker and **P**unishment.

In eq. (2.2), two strategies are available to the players: C or D , respectively, to **C**ooperate (not betray) or to **D**efect (betray). Usually, it is also required that $2R > T + P$, so that in one round, the reward payoff is higher than the average payoff of a defection – when considering the opponent is equally likely to play C or D with the same probability. The calculus of the Nash equilibrium follows the same steps taken before so that in the general form of the PD game, we find that (D, D) is the strategy profile from which no player has incentive to deviate.

Another interesting result associated with this game is its socially optimal strategy profile. A socially optimal strategy profile is the strategy profile which yields the highest sum of payoffs, considering all players. Let's assume $2R > T + P$ in the general PD game with a payoff matrix as shown in eq. (2.2). Then, (C, C) is the socially optimal strategy profile for the PD game, since $R > P$ and $2R > T + P > T + S$. This means that the sum of the payoffs of players in the strategy profile (C, C) is higher than the payoffs of players who chose (C, D) or (D, D) , respectively. In other words, the socially best situation occurs when both players choose to cooperate in this game.

This mismatch between the socially optimal strategy profile and the Nash equilibrium is one of the reasons why the PD game has been used to tackle the problem of the evolution of cooperation. Because of this mismatch in the PD game, individuals have incentive to defect, instead of pursuing the prosocial behavior.

A second reason for using the PD game as a model game for studying cooperation is the possibility of capturing the essence of the so-called *Tragedy of the Commons* [44] through an n -person PD game (see section A.1.1): since it is always advantageous for an individual to overuse a public resource, the public resource would be depleted by its continuous overuse, affecting negatively all individuals.

2.2 Kin selection

When introducing natural selection theory, Darwin was concerned with the problem of self-sacrifice, which can be observed among bees, for example. Darwin had observed social insects in nature and had witnessed how many insects behave in a cooperative way, many times sacrificing their own reproductive chances to enhance the others' reproductive chances [33].

Although Darwin could explain this type of behavior as a consequence of the benefits it offered to kinship members, it was not until Hamilton's paper [43], in 1964, that this phenomena gained a mathematical form. Hamilton described a simple model for altruism, a special type of cooperation, in which an actor incurs a cost so that a recipient of the action can receive a benefit. This model was based on indirect fitness accounts into the actor's own fitness and the theory behind it has been called *inclusive fitness*, since it includes two types of fitness: direct and indirect fitness.

From Hamilton's model, a condition for the evolution of altruism is derived (Eq. 2.3). This condition involves the quantities r , b and c , respectively, the relatedness between actor and recipient (see Box 2), the benefit for the recipient and the cost for the actor. It is important to notice that b and c

are non-negative and their values can differ from the payoffs gained through interactions among the individuals.

$$br - c > 0 \quad (2.3)$$

This simple rule helps explain many cases of altruism in nature. Since the rule discovery, empirical studies have estimated the values of b and c and many of them predicted with success which individuals were more likely to be a recipient for a cooperative action [15].

Box 2: What is r ?

In textbooks [35], relatedness is usually defined as the probability that two individuals share the same allele. However, most of the time, this definition cannot be used to interpret r in Hamilton's rule. In Hamilton's rule, r is the chance of sharing the focal allele relative to the average probability that two individuals share the same allele, which is the allele's frequency in the population. Both of these definitions are the same when allele's frequency in the population is very low [15]. Relatedness is also defined as a regression coefficient, calculated from the regression of recipients' allele frequency on the actors' allele frequency. This is the formal way of calculating the relatedness as described by the definition above. Under this definition, random individuals are those whose relatedness is zero, i.e., the ones who share genes with each other with average frequency.

2.3 Reciprocity

Many of us have heard of the idiom: “you scratch my back and I’ll scratch yours”. Its meaning is clear: “if you help me, I will help you”, the principle behind reciprocity.

Reciprocity can be distinguished into two different types: (i) direct reciprocity, and (ii) indirect reciprocity. While in direct reciprocity, individuals are directly benefited from their (past) behavior in a current game, in indirect reciprocity, the existence of a reputation system is responsible for publicizing the good behavior of a cooperator so that other individuals who never actually interacted with her may reciprocate.

2.3.1 Repeated games

When we introduced the PD game before, we treated it as a one-shot game. However, it is not uncommon to play what is called *repeated games*, in which the same individuals repeatedly play the same game.

Two distinct approaches yield the same result:

- in microeconomic theory [40], repeated games are commonly explained in terms of *discounted utility theory*, according to which the payoff for each player is the sum of payoffs over the rounds weighted by a discount factor δ , with $0 < \delta < 1$;
- in evolutionary game theory [90], on the other hand, δ is taken as the probability of playing another round of the game, so that, the probability that the game is played for exactly n rounds is $\delta^{n-1}(1 - \delta)$.

Note that when there is no uncertainty around the number of rounds, the last round of the finitely repeated PD game is equivalent to the one-shot PD game. This means that as in the one-shot PD game, we expect both players to defect, which is not socially optimal. Through backward induction, we can see that in the finitely repeated PD game, the strategy profile in which both players defect is the only subgame perfect Nash equilibrium.

In the infinitely repeated version of the PD game (or equivalently, a version in which players are not aware of when the game ends), within both approaches, the expected payoff (or the discounted utility) of one player is given by:

$$V = v_0 + \delta v_1 + \delta^2 v_2 + \dots + \delta^n v_n + \delta^{n+1} v_{n+1} + \dots \quad (2.4)$$

in which v_i is the individual's payoff at the i -th round of the game.

Differently from the finitely repeated PD game, in this version, it is possible to achieve a state in which it is advantageous for both players to cooperate. As we shall see, this is a core property of the study of reciprocity.

2.3.2 Evolving direct reciprocity

Early in 1970s, Trivers [98] proposed a model for the natural selection of what he called reciprocally altruistic behavior. He stated his motivation of studying this behavior with a simple example: if there is an individual drowning and someone not related or distantly related saves him, “[w]hy should the rescued individual bother to reciprocate? Selection would seem to favor being saved from drowning without endangering oneself by reciprocating. Why not cheat?”.

In the same paper, after his own formulation of a model for the evolution of direct reciprocity, Trivers mentioned Hamilton had another formulation, which used game theory. Here we will use the game theoretical model, modified to account for the theory of repeated games presented in section 2.3.1.

One way to achieve the socially optimum configuration in the PD game is through the introduction of a strategy named tit-for-tat (*TFT*) in which cooperation is used for as long as it takes the counterpart to defect, only cooperating again if the counterpart does so first. Note that a player that uses *TFT* can be considered to be a *reciprocator*, since his actions (with the exception of the first round) are merely a reflex of the other player’s action in the previous round.

Suppose player 2 uses *TFT* whereas player 1 can choose between three strategies: *AllC* (playing *C* in all rounds), *AllD* (playing *D* in all rounds) and *TFT*. Also, let $V(s_i|s_{-i})$ be the payoff of the player i that plays strategy s_i against the other player’s strategy, s_{-i} .

At the start of the game, player 1 faces the following expected payoffs (following eq. (2.2)):

$$\begin{aligned}
 V(AllC|TFT) &= R + \delta R + \delta^2 R + \dots + \delta^n R + \dots = \sum_{k=0}^{\infty} \delta^k R \\
 V(TFT|TFT) &= R + \delta R + \delta^2 R + \dots + \delta^n R + \dots = \sum_{k=0}^{\infty} \delta^k R \\
 V(AllD|TFT) &= T + \delta P + \delta^2 P + \dots + \delta^n P + \dots = T + \sum_{k=1}^{\infty} \delta^k P.
 \end{aligned} \tag{2.5}$$

From eq. (2.5), it is possible to see that there are only two possible outcomes:

- either both players cooperate indefinitely, if both players use strategy *TFT* or if one of them uses *AllC* and the other uses *TFT*; or
- one of them starts by cooperating but, after the defection from the *AllD* player, both of them defect indefinitely. This happens when one of the players uses *AllD* and the other uses *TFT*.

Thus, (C, C) will be achieved only if $V(AllD|TFT) < V(TFT|TFT) = V(AllC|TFT)$ or, equivalently, $T + \sum_{k=1}^{\infty} \delta^k P < \sum_{k=0}^{\infty} \delta^k R$.

This condition can be calculated explicitly in function of R , T and P :

$$\begin{aligned} V(AllD|TFT) < V(TFT|TFT) &\implies T + \sum_{k=1}^{\infty} \delta^k P < \sum_{k=0}^{\infty} \delta^k R \\ &\implies T + \delta P \sum_{k=0}^{\infty} \delta^k < \sum_{k=0}^{\infty} \delta^k R \implies T + \frac{\delta P}{1 - \delta} < \frac{R}{1 - \delta} \\ &\implies \delta > \frac{T - R}{T - P}. \end{aligned} \tag{2.6}$$

Since $P < R$ in a prisoner's dilemma game, then, $T - P > T - R \Leftrightarrow 0 < \frac{T - R}{T - P} < 1$, i.e., it is always possible to have a sufficient high δ that makes cooperation evolve when one of the players is a reciprocator (i.e. uses *TFT*). The interpretation is that it is necessary a sufficient high discount rate or a sufficient high number of rounds for cooperation to be more advantageous than defection in the infinitely repeated prisoner's dilemma when one of the players uses *TFT*.

Another way to analyze this model is to use the concept of evolutionary stable strategies (ESS), as proposed by Maynard Smith and George Price [92] in the context of computer simulations. In fact, in the previous calculation, we found the condition for $V(AllD|TFT) < V(TFT|TFT)$, i.e., the condition for *TFT* to be an ESS against *AllD* (more details about the ESS definition can be found in the appendix section A.2).

In 1978, a political scientist, Axelrod, used the same type of simulation for analyzing different strategies performances in prisoner's dilemma games [11]. In his setting, in each round, individuals were paired and played a PD game. Each individual played the game using one strategy, e.g. *AllC*, *AllD* etc.

The main objective of Axelrod was to compare several strategies and find the winning strategy, i.e., the one that achieved the highest average payoff. In the first tournament promoted by Axelrod, fourteen strategies were subscribed. The winner was the simple strategy tit-for-tat (suggested by Rapoport), which cooperates on the first round and then copies the behavior of the opponent for the next rounds (the same as the *TFT* strategy introduced previously). Indeed, it was a very robust strategy, since it also won the second tournament promoted by Axelrod, in which sixty strategies competed against each other.

Although *TFT* is an ESS against *AllD*, it is easy to see that it is not an unbeatable strategy in the evolutionary sense: since one cannot distinguish *AllC* and *TFT* when playing against each other, it is possible that *AllC* increases by random drift and, if it eliminates *TFT*, it would, subsequently, be invaded by *AllD*. In fact, when no mistakes are allowed, there are no evolutionary stable pure [20] or mixed strategies [34] in the repeated prisoner's dilemma game.

Only in the beginning of 1990s, Nowak and Sigmund [69] rediscovered the strategy called Simpleton (proposed by Rapoport), also known as Pavlov, and realized it could generate even higher payoffs than tit-for-tat. The Pavlov strategy uses the reasoning “win-stay, lose-shift”: if it receives a high payoff (R or T), it remains using the same behavior; however, if it receives a low payoff (P or S), it changes the behavior.

The key to the success of Pavlov strategy is the allowance of mistakes when implementing the strategies. Thus, for instance, instead of changing from C to D with probability 1 when getting the payoff S , one individual playing Pavlov will make this change with probability $1 - \epsilon$, with $0 < \epsilon < 1$. This translates into a chance of changing from C to D , even when getting R , which can be advantageous if Pavlov is playing against an *AllC* strategy (because *AllC* will not defect, by changing to D , Pavlov will retain the highest payoff, T , for all subsequent rounds).

2.3.3 Evolving indirect reciprocity

Today, especially with the aid of Internet, a considerable amount of human daily interactions occur between strangers. Direct reciprocity cannot explain cooperation in these cases, since in this type of interaction, the likelihood of further encounters with the same individual is very low.

Indirect reciprocity, on the other hand, may explain how humans sustain cooperation even in this setting: the principle is that an individual will cooperate if somebody else has cooperated with him before. One way to conceive this act is to think individuals are prone to help when they had a recent experience of being helped before. This has been termed *upstream reciprocity* (or *misguided reciprocation* [90]) and, in daily life, it can be seen, for example, in “pay it forward” campaigns², in which one customer is offered the opportunity to leave a product paid to the next customer who enters the store.

²For instance, Starbucks reported that 19,000 customers in South China bought coffee for the next customer in a *pay it forward* campaign in 2014 [1]. Although there were some breaks in the generosity chain, in which Starbucks intervened, by providing the coffee for the next customer, there seems to be a social contagion effect in place.

When the population is large, Nowak and Roch [72] showed that upstream reciprocity may foster the evolution of cooperation when combined with other mechanisms, such as direct and spatial reciprocity. This result is consistent with previous results obtained by Boyd and Richerson [23], which compared a *TFT* based on “be nice to people who are nice to others” (termed *downstream reciprocity* or *vicarious reciprocation* [90]) with a *TFT* based on “be nice if others are nice to you” (upstream reciprocity), finding that the former seemed to be more successful in promoting cooperation for groups with a larger number of players.

Hence, in the remainder of this section, we focus on *downstream reciprocity*, and introduce important results from reputation-based indirect reciprocity models. One difference from direct reciprocity models is that most models of indirect reciprocity, are built from a donor game, instead of using the traditional prisoner’s dilemma game.

In the donor game, two roles exist: donor or recipient. While as a donor, an individual is able to choose between helping the recipient (by incurring a cost $c > 0$) or not, as a recipient, an individual merely accepts being helped (receiving a benefit b) or not being helped. This game, thus, is a degenerate game, i.e., only one of the players (the donor) has a set with more than one strategy to choose from. Note that two rounds of the game with an individual placed as a donor in one round and as a recipient in another round yields the same payoffs as the original two-person prisoner’s dilemma game.

Another notion that is inexistent in direct reciprocity models is the concept of a *score* for players. This score can be binary (*good* or *bad*) or a “full score”, and intends to classify individuals according to their cooperativeness. This means individuals would be able to build a reputation by taking actions which preserve or lead to a “good” score.

The simplest model of indirect reciprocity considers an infinite population, with the same assumptions of models of direct reciprocity: probability $0 < w < 1$ of having another round; and interaction between pairs of individuals through a PD game [73]. There are two strategies in the model: *DSC* (discriminator) and *AllD*. While individuals playing *DSC* only cooperate with those who cooperated in the previous round, individuals who use *AllD* always defect. In this situation, *DSC* yields the same payoff as a *TFT* strategy, and hence is an ESS, i.e., it cannot be invaded by *AllD*.

When thinking about what determines an individual’s reputation, the following question arises: should a good player become a bad player if he refused help to a bad player? Also, it is not clear how individuals actions depend on their own reputation and on the partner’s reputation. Ohtsuki

Figure 2.1: Examples of assessment rules. In SCORING, reputations do not matter, and a donor (D) who helps a recipient (R) is always labeled *Good* (G), while donors who do not help recipients are always labeled *Bad* (B). In STANDING, the difference from the SCORING rule is that a G donor who refuses to help a B recipient is still considered to be G . In JUDGING, the difference from the STANDING rule is that helping a B recipient makes a donor to be labeled as B .

and Iwasa [74] developed a model that took into account several assessment rules (how users score other users) and action rules (how donors choose whether to help or not a recipient), and calculated the evolutionary stability of different strategies, which combined assessment rules with action rules.

In their model, they consider a binary score system, in which individuals can be labeled as *Good* (G) or *Bad* (B). All individuals are born *Good* and are assessed according to the last played game as a donor. Assessment rules determine what is the reputation of the donor according to his choice of helping or not a recipient in all possible combinations of donor-recipient reputations, G or B . Some examples of assessment rules can be seen in fig. 2.1.

By assessing other individuals, when in the role of a donor, an individual is able to choose his own actions based on the reputation of the recipient (and even looking at his own reputation). Action rules determine whether the donor will help or not help a recipient for all types of situations. The most extreme action rules are *AllC* which makes a donor help all recipients; and *AllD* which makes a donor refuses to help any recipient. Other action rules are shown in fig. 2.2.

Since both sets of rules (assessment and action) are used to compose a strategy, the total number of strategies is very large: $2^8 \times 2^4 = 2^{12} = 4096$ different strategies. Note that, while all action rules were covered by the set of *AllC*, *AllD* and the action rules in fig. 2.2, there are many more assessment rules than what was covered in fig. 2.1.

Figure 2.2: Examples of action rules. In CO, only the reputation of the recipient (R) is used to make the decision of helping (Y) or not (N) an individual: if the recipient is *Good* (G), the donor (D) helps him, otherwise, if the recipient is *Bad* (B), the donor will refuse help to him. In SELF, the decision is based solely on the reputation of the donor: a donor helps a recipient only if his own reputation is B . In AND, a donor helps a recipient only if his own reputation is B *and* if the reputation of the recipient is G . In OR, a donor helps a recipient if his own reputation is B *or* if the reputation of the recipient is G .

Iwasa and Ohtsuki investigated whether a population composed by a majority of individuals playing one strategy (for instance, CO-STANDING) could be invaded by a small number of individuals playing another strategy (e.g., AND-STANDING). They considered implementation errors and assessment errors, along with different parameter values of benefit (b) and cost (c). Since the number of strategies was very large, in order to be able to make the analytical calculations, Iwasa and Ohtsuki assumed a very large population and only compared strategies within the same assessment module. Also, they assumed a public scoring, so that any individual had the same view of reputation labels for the other individuals.

After considering all possible pairs of strategies, they reached a core with eight strategies which were robust to invasion, even considering a wide range of probability of assessment and implementation errors and values of c slightly larger than b [25]. This group of ESS strategies was called *the leading eight* (see table 2.2).

We can see that for the action modules, only CO and OR appear in the table with leading eight strategies. Note that the leading strategy number 1 is CO-STANDING, while the leading strategy number 8 is CO-JUDGING. All the other leading strategies have assessment modules which are not represented in fig. 2.1. Simple rules are prevalent, though: (i) helping a good recipient always yields a good reputation; (ii) refusing to help a good recipient always yields a bad reputation; and (iii) refusing to help a bad recipient yields a good reputation.

situation/strategy	1	2	3	4	5	6	7	8
$G \rightarrow G$	G	G	G	G	G	G	G	G
$G \rightarrow B$	G	B	G	G	B	B	G	B
$B \rightarrow G$	G	G	G	G	G	G	G	G
$B \rightarrow B$	G	G	G	B	G	B	B	B
$G \nrightarrow G$	B	B	B	B	B	B	B	B
$G \nrightarrow B$	G	G	G	G	G	G	G	G
$B \nrightarrow G$	B	B	B	B	B	B	B	B
$B \nrightarrow B$	B	B	G	G	G	G	B	B
$G \xrightarrow{?} G$	Y	Y	Y	Y	Y	Y	Y	Y
$G \xrightarrow{?} B$	N	N	N	N	N	N	N	N
$B \xrightarrow{?} G$	Y	Y	Y	Y	Y	Y	Y	Y
$B \xrightarrow{?} B$	Y	Y	N	N	N	N	N	N

Table 2.2: The leading eight strategies. For each strategy (columns numbered from 1 to 8), both assessment rules (first 8 rows) and action rules (last 4 rows) are shown. Assessment rules situations are represented showing the reputation of the donor (*Good*, G , or *Bad*, B), an arrow which may indicate whether the donor helped ($\rightarrow$) or not ($\nrightarrow$) the recipient, and the reputation of the recipient (G or B). Action rules are represented showing the reputation of the donor (G or B), an arrow $\xrightarrow{?}$ and the reputation of the recipient; possible actions are Y (to help) or N (to refuse to help).

2.4 Multilevel selection

Through the study of natural selection, we can see Darwin's principles could apply to any entity among different levels of organization in a species. Multilevel selection, also known as group(-trait) selection or population selection, refers to simultaneous selection processes that occur at different hierarchical levels, e.g. individual and group of individuals [75]. Its multiple denominations are part of its controversies among researchers in evolutionary biology field.

The general feeling about multilevel selection has changed during 20th century from acceptance to rejection and, then, a revival of the theme in recent years. While in the beginning of 20th century, Darwin's arguments about the relation between group selection and social behavior were relatively well accepted, later publications shifted the acceptance to an almost complete rejection of multilevel selection for many years [14]:

The theory of group selection has been so unpopular for the past 40 years that, until recently, it existed in the scientific limbo, somewhere between being a heretical curiosity and a useless dead end.

The past 40 years mentioned by Borello refers to the period starting in 1960s, and Wilson [106] explains the motivations behind it:

The rejection of group selection was based on three arguments. First, theoretical models indicated that D. S. Wilson and E. O. Wilson between-group selection is a weak evolutionary force compared to within-group selection. Second, the empirical evidence for group selection was speculative and could just as easily be explained in terms of within-group selection. Third, the alternative theories seemed to provide more robust explanations of altruism and cooperation without invoking group selection.

Although this idea was widespread in the community of evolutionary biologists, there was still doubt regarding the role of multilevel selection at evolutionary processes. In his review of the existing group selection models, Wade [102] first presented some inconsistencies in the terminology of multilevel selection among different researchers and, then, provided a thorough review of the compounding elements of group selection models.

A decade later, Mayo and Gilinski [61] proposed that group-level fitness could be classified in two different ways. *Group-individual fitness* refers to the average fitness of individuals in one group. On the other hand, *group-group fitness* refers to the number of groups produced, on average.

According to them, this distinction separates the models of group selection into two different types: type I models, related to group-individual fitness; and type II models, related to group-group fitness. While type I models are concerned with differences among groups due to distinct individual rates of production, type II models focus on differences among groups due to different production rates of new groups. In their paper, they provide an example that elucidates the need for these two core concepts [61]:

Suppose that the average fitness of flightless beetle individuals is k , and the average fitness of flying beetle individuals is m , where m exceeds k . Then the group-individual fitnesses of the group of flightless and the group of flying beetles are k and m , respectively, and the two groups differ in group-individual fitness. Suppose, however, that

the group of flightless beetles produces 100 distinct new groups of flightless beetles on average, and the group of flying beetles produces only 10 distinct groups of flying beetles, on average. Then the group-group fitnesses of the group of flightless and the group of flying beetles are 100 and 10, respectively, and the two groups differ in group-group fitness. While the group of flightless beetles is less fit than the group of flying beetles from the perspective of group-individual fitness, the group of flightless beetles is more fit than the group of flying beetles from the perspective of group-group fitness.

They argue that although Type I models are of interest as a way to view the evolutionary process, these models do not identify a causal group-level selection process, different from individual selection. In their opinion, only Type II models can explain differences among groups that are due to exclusively group-level events.

This distinction in multilevel selection (MLS) types was also pointed out by Damuth and Heisler [30] and Okasha [75]. However, they use a different terminology: while MLS_1 is concerned with the change in the frequencies of individuals, MLS_2 describes this change for different types of groups.

According to Okasha [75], in order to study multilevel selection, we have to define the mechanisms required by selection (character variation, fitness differences and heritability) at the multiple levels in question. He distinguishes two methods for calculating the group-level fitness: $collective\ fitness_1$, which counts the number of daughter individuals, and $collective\ fitness_2$, which counts the number of daughter groups. In models that allow different group sizes, this is an important issue, since it determines whether a group giving birth to 4 groups of 3 individuals is more successful (or not) than a group that gives birth to 3 groups of 4 individuals each.

Although there are still some disagreement around the concept of multilevel selection, the current situation is much more favorable to it, as Wilson summarizes [106]:

Today, after four decades of research, it has become clear that the 1960s consensus was in error. Group selection is theoretically plausible, there is solid empirical evidence for it, and the alternative theories have multilevel selection embedded within their own structures.

In the next paragraphs, we present the Price equation, which has been used in both kin selection and multilevel selection models. We also derive the Hamilton's rule from the Price equation, as

the derivation is helpful to understand its limitations as a rule to predict cooperation between individuals.

2.4.1 The Price equation

The Price equation has been extensively used for modeling social evolution. This equation [78] expresses the difference of the frequency of a type of particle or individual between two subsequent generations. It is simple, recursive and separates clearly the effects of inter and intragroup selection [42].

Different from other models, however, the Price equation was not developed with the intention to model one specific natural phenomenon. Hence, it does not rely on simplified assumptions about reality. It is rather built in an abstract way so that it fits several biological situations.

In the original paper [78] that derived the equation, two populations ψ_1 and ψ_2 are considered. ψ_1 is the population consisting of the parents of ψ_2 , so that ψ_2 members are offspring of ψ_1 . Population members of ψ_1 are arbitrarily labeled as 1, 2, $\dots$, N (total population size). The main objective is to track one character (e.g., gene A) frequency in these two generations. This derivation uses many symbols; these symbols and their interpretations can be seen in table 2.3.

Symbol	Meaning
N	population size of ψ_1
n_z	zygotic ploidy
g_i	dose of gene A in individual i (if $n_z = 2$, then, g_i can be 0, 1, or 2.)
p_i	frequency of gene A in individual i , $p_i = g_i/n_z$
P_1	frequency of gene A in population ψ_1
n_G	gametic ploidy
w_i	number of offspring produced (successful gametes) by individual i
g'_i	number of genes A in the set of successful gametes from individual i
p'_i	frequency of gene A in i 's set of successful gametes, $p'_i = g'_i/w_i n_G$
P_2	frequency of gene A in population ψ_2
Δp_i	difference in frequency of gene A between i and her offspring, $p'_i - p_i$

Table 2.3: Symbols used in Price equation derivation.

To find the difference in frequency of gene A between the two generations represented by population ψ_1 and ψ_2 , it is necessary to calculate P_1 and P_2 . Note that both of these quantities are just the sum of the individual frequencies of all individuals in populations ψ_1 and ψ_2 divided by the population size. In the case of ψ_1 , the calculation is straightforward, as we can see in eq. (2.7). For individuals of population ψ_2 , we calculate P_2 from the sum of total frequencies of all offspring for each individual i , which is simply $z_i p'_i$.

$$P_1 = \frac{\sum_i p_i}{N} = \bar{p} \quad (2.7)$$

$$\begin{aligned} P_2 &= \frac{\sum_i w_i p'_i}{\sum_i w_i} = \frac{\sum_i w_i p'_i}{N \sum_i (w_i/N)} \\ &= \frac{\sum_i w_i p'_i}{N \bar{w}} = \frac{\sum_i w_i (p_i + \Delta p_i)}{N \bar{w}} \\ &= \frac{\sum_i w_i p_i}{N \bar{w}} + \frac{\sum_i w_i \Delta p_i}{N \bar{w}} \\ &= \frac{(\bar{w} \bar{p} + \text{Cov}(w_i, p_i))}{\bar{w}} + \frac{\sum_i w_i \Delta p_i}{N \bar{w}} \end{aligned} \quad (2.8)$$

in which $\bar{w} = \sum_i w_i/N$ is the average number of individuals of offspring produced in the population and, in the last equality, we use the formula for the covariance between two variables $x = (x_1, \dots, x_n)$ and $y = (y_1, \dots, y_n)$, given by $\text{Cov}(x_i, y_i) = \frac{\sum_i x_i y_i}{n} - \left(\frac{\sum_i x_i}{n} \right) \left(\frac{\sum_i y_i}{n} \right)$.

Using P_1 and P_2 as obtained in eqs. (2.7) and (2.8), the Price equation is derived by calculating the quantity $\Delta P = P_2 - P_1$ in the following way:

$$\begin{aligned} \Delta P &= \left(\bar{p} + \frac{\text{Cov}(w_i, p_i)}{\bar{w}} + \frac{\sum_i w_i \Delta p_i}{N \bar{w}} \right) - \bar{p} \\ &= \frac{\text{Cov}(w_i, p_i)}{\bar{w}} + \frac{E(w_i \Delta p_i)}{\bar{w}}, \end{aligned} \quad (2.9)$$

in which we replaced $E(w_i \Delta p_i) = \frac{\sum_i w_i \Delta p_i}{N}$.

Usually, the Price equation is written in another form eq. (2.10), using a slight different notation and interpretation from what we introduced before: w represents fitness (relative or absolute, since fitness scaling does not alter the equation), z represents the character value (also called phenotype, when it is defined as a mathematical function of traits) and z_i represents the frequency of the character value in individual i .

$$\Delta \bar{z} = \frac{\text{Cov}(w_i, z_i)}{\bar{w}} + \frac{E(w_i \Delta z_i)}{\bar{w}} \quad (2.10)$$

This equation has two terms on the right side, which are, respectively, referred to be related to selection and transmission processes [36, 81]. The covariance term represents the change of the character in the population due to differential fitness and reproduction. If larger character values increase fitness, the covariance is positive and it will increase the population average character value. The remainder term in the right side encompasses the processes involved in the transmission of the character, like mutation or recombination. It represents how much the offspring resemble their parents. If offspring are exact copies of their parents, the right term is zero.

2.4.2 From Price equation to Hamilton's rule

One way to derive Hamilton's rule is to consider Price equation along with a few number of assumptions. These assumptions clarify the relationship between Hamilton's rule and linear fitness functions, which is crucial to understand the motivations of the framework we present in the next chapter. Here we follow the derivation described in [63].

Firstly, we assume individuals are perfect copies from their parents, so that the frequency of gene A does not vary across generations, i.e., $\Delta p_i = 0$. From eqs. (2.7) and (2.8), and using one of the intermediate formulas of P_2 , we can rewrite the difference $\Delta P = P_2 - P_1$ as the following equation:

$$\begin{aligned}\Delta P &= \frac{\sum_i w_i p_i}{N\bar{w}} - \frac{\sum_i p_i}{N} \\ &= \frac{E(w_i p_i)}{\bar{w}} - \frac{E(w_i) E(p_i)}{\bar{w}}.\end{aligned}\tag{2.11}$$

The version of Price equation given by eq. (2.11) can be further simplified into:

$$\bar{w}\Delta P = \text{Cov}(w_i, p_i).\tag{2.12}$$

Secondly, we should define a general equation for the fitness function w_i of individual i . We can do that by assuming **additive fitness effects**, which means gain/loss in fitness is proportional to the probability of the particular event which led to that gain/loss. Letting $b > 0$ be the gain in fitness obtained by the occurrence of an event of probability y_i ; $c > 0$ be the loss in fitness obtained by the occurrence of an event of probability h_i ; and $w_0 \geq 0$, constant, be the baseline fitness of an individual i , then, we have the following fitness function for individual i :

$$w_i = w_0 + y_i b - h_i c.\tag{2.13}$$

Since our main goal is to derive Hamilton's rule, in the next paragraphs, we restrict our analysis to the case when gene A is related to altruism. In the specific case of altruism, eq. (2.13) implicates that being helped more increases w_i linearly with a factor b and that helping the others more decreases w_i linearly with a factor $-c$.

Thirdly, since eq. (2.13) involves two more terms y_i and h_i , we should specify their general form for being able to calculate eq. (2.12) with w_i as given by eq. (2.13). This is done by assuming **additive genetics**, which implies that the behavior of an individual depends on the genotype of the actor or the recipient of altruism. This means y_i and h_i should be written as linear functions of, respectively, p_j and p_i , the frequency of gene A in the recipient of altruism j and his own frequency of gene A (when he is the actor):

$$\begin{aligned} y_i &= a + kp_j \\ h_i &= a + kp_i, \end{aligned} \tag{2.14}$$

in which a and k are parameters of the linear function and are chosen so that $0 \leq y_i \leq 1$ and $0 \leq h_i \leq 1$.

With these definitions, we can finally use w_i from eq. (2.13) and y_i and h_i from eq. (2.14) to calculate eq. (2.12):

$$\begin{aligned} \bar{w}\Delta p &= \text{Cov}(w_0 + y_i b - h_i c, p_i) \\ &= \text{Cov}[w_0 + (a + kp_j)b - (a + kp_i)c, p_i] \\ &= \text{Cov}(w_0, p_i) + \text{Cov}(ab, p_i) + \text{Cov}(bkp_j, p_i) - \text{Cov}(ac, p_i) - \text{Cov}(ckp_i, p_i). \end{aligned} \tag{2.15}$$

Many of these covariance terms disappear since one of the variables is actually a constant, e.g. $\text{Cov}(w_0, p_i)$, yielding:

$$\bar{w}\Delta p = bk\text{Cov}(p_j, p_i) - ck\text{Var}(p_i) \tag{2.16}$$

This means that the condition for the survival of the altruist gene, $\Delta p > 0$, implies:

$$b \left(\frac{\text{Cov}(p_j, p_i)}{\text{Var}(p_i)} \right) - c > 0. \tag{2.17}$$

Note that $\text{Cov}(x, y) = \text{Var}(x) \beta(y, x)$, in which $\beta(y, x)$ is the slope of the regression line of y on x , so that eq. (2.17) can be written as:

$$b\beta(p_j, p_i) - c > 0. \quad (2.18)$$

The condition for the survival of the altruist gene as written in eq. (2.18) is already close to Hamilton's rule. What remains to be done is to link the regression coefficient, $\beta(p_j, p_i)$, to relatedness, r . In order to this, we need an additional assumption: **absence of selection for altruism**, which means the allele for altruism is as likely to be selected as any other allele. This assumption provide us a way of calculating r , which can be defined as the fraction of genes IBD (identical by descent) in two individuals, i and j .

Let $p_{j,\text{IBD}}$ be the average proportion of altruism genes relative to the number of genes which are IBD in individuals i and j . Also, let $p_{j,\overline{\text{IBD}}}$ be the the average proportion of altruism genes relative to the number of genes which are *not* IBD in individuals i and j . Then, the expected frequency of gene A for individual j given the frequency of gene A for individual i , $E(p_j|p_i)$, is given by:

$$E(p_j|p_i) = rp_{j,\text{IBD}} + (1 - r)p_{j,\overline{\text{IBD}}}. \quad (2.19)$$

Note that p_i is the frequency of gene A for individual i , which means, on average, p_i of the IBD genes of individuals i and j are altruism genes, since there is no selection for any particular gene, so that $p_{j,\text{IBD}} = p_i$. On the other hand, on average, the proportion of non-IBD genes of individuals i and j which are altruism genes, $p_{j,\overline{\text{IBD}}}$, is simply the frequency of gene A in the population, $p = \sum_i p_i / N$. Thus:

$$E(p_j|p_i) = rp_i + (1 - r)p_j. \quad (2.20)$$

Another way to calculate $E(p_j|p_i)$ is to use the coefficients α and $\beta(p_j, p_i)$ of a first order linear regression model:

$$E(p_j|p_i) = \alpha + \beta(p_j, p_i)p_i \quad (2.21)$$

In eq. (2.21), we should find the intercept α in order to calculate $E(p_j|p_i)$. This can be done by calculating least-squares estimate of the intercept of $E(p_j|p_i)$ or, in a intuitive way, we can take the expectation of both sides of eq. (2.21), so that $\alpha = E[E(p_j|p_i)] - \beta(p_j, p_i)E(p_i)$, which implies that

$\alpha = E(p_j) - \beta(p_j, p_i)E(p_i)$. Replacing α in eq. (2.21), we have:

$$E(p_j|p_i) = (1 - \beta(p_j, p_i)) E(p_i) + \beta(p_j, p_i)p_i, \quad (2.22)$$

in which we used the fact that $E(p_j) = E(p_i)$, which is valid for any i and j .

Hence, by inspection of eqs. (2.20) and (2.22), we can see that $r = \beta(p_j, p_i)$ and from eq. (2.18):

$$br - c > 0, \quad (2.23)$$

which is the usual form of Hamilton's rule.

Note that to derive the Hamilton's rule as given by eq. (2.23), we relied on four assumptions:

- individuals are perfect copies from their parents;
- w_i incorporates additive fitness effects;
- y_i and h_i incorporate additive genetics; and
- there is no selection for altruism.

These assumptions are not guaranteed to hold for all models, and this is why Hamilton's rule may not prescribe the survival of altruism in some cases, which we will see in more detail in the next chapter.

Chapter 3

Two-level Fisher-Wright model: a general framework

The two-level Fisher-Wright model is a simple, but robust framework for explaining the emergence of pro-social traits, in a two-level population structure with selection and migration. One of the most important contributions of this framework are its generality and the capability of providing an analytical condition for the viability of the analyzed pro-social trait, under weak selection. Here, we present the general framework, which will be used in the next chapter to study the spread of altruism in a situation when there are intergroup conflicts.

3.1 The model

In the two-level Fisher-Wright model (TLFW), a large number of haploid individuals are divided in g groups of fixed size n . These individuals are of two types, A or N , in which A represents the pro-social character, e.g., altruism, and N , the native (wild) type in the population (see fig. 3.1). There is no overlap of generations, reproduction is asexual and the type of an individual is determined from the type of his parent.

We can view this model as a three-stage model with an intragroup stage, an intergroup stage and a migration stage. In the intragroup stage, interactions inside the group produce payoffs which directly influence the fitness of individuals. In the intergroup stage, groups compete among each other, representing the natural process in which efficient groups are expected to grow faster and

Figure 3.1: Population structure in TLFW. Individuals are divided in a large number g of groups. Each group contains n individuals, that are classified as A or N , according to their actions in the interactions inside their groups.

split, while less efficient groups would go extinct. Finally, in the migration stage, individuals can migrate to other groups, possibly changing the distribution of labels A and N inside groups.

Before explaining how these three stages are incorporated into TLFW, we shall explain the processes underlying individual reproduction, which is tied to intragroup selection, and group reproduction, tied to intergroup selection. The individual reproduction (fig. 3.2) follows a very similar process from the original Wright-Fisher model. The offspring "choose" their parents from the parental group individuals according to the fractions of A and N , but weighted with the ratio of fitness (w_k^A or w_k^N) over the average fitness of the group ($\bar{w}_k$), in which k is the number of individuals with label A (this means the group is of type k). This modification allows the study of social evolution using this framework, by incorporating within-group social interactions that can lead to different fitness for A and N individuals.

Figure 3.2: Individual reproduction in TLFW. The fraction of individuals of a label A or N in the next generation is proportional to the fraction of individuals A or N in the current generation weighted by $w_k^A/\bar{w}_k$ or $w_k^N/\bar{w}_k$.

As mentioned previously, the fitness functions of A and N depend on the life-cycle payoffs obtained by individuals through the social interactions inside their groups. Let v_k^A and v_k^N be the payoffs for individuals labeled A and N , respectively, when inside a group of type k . Also, we assume there is

no positive payoff when there are only individuals of label N in the group, i.e., $v_0^N = 0$. Then, if δ is the parameter that controls selection strength, $\delta \in [0, 1]$, the fitness functions of A and N are given by, respectively:

$$w_k^A = 1 + \delta v_k^A \quad \text{and} \quad w_k^N = 1 + \delta v_k^N. \quad (3.1)$$

The fitness functions defined above also influence the process of group reproduction (fig. 3.3), in which groups can reproduce by competing with the other groups. Analogously to the process of individual reproduction, more successful groups produce more offspring groups, and what determines the likelihood of a group of type k outcompete other groups is its fitness, which is given by $\bar{w}_k$, the average fitness of individuals inside the group:

$$\bar{w}_k = \frac{k w_k^A + (n - k) w_k^N}{n}. \quad (3.2)$$

Figure 3.3: Group reproduction in TLFW. The average number of groups which has a parent group of type k is given by the average fitness of individuals inside this group, $\bar{w}_k$.

Two matrices are necessary to model the emergence of the social trait A : $S = (S_{kj})$, which represents the selection process and $M = (M_{jl})$, which represents the migration process. The selection process encloses the individual reproduction and the group reproduction. Each element of matrix S , S_{kj} is the expected number of groups type j among the children of a group type k and is given by:

$$S_{kj} = \bar{w}_k \Pr \left(\text{Bin} \left(n, \frac{k w_k^A}{n \bar{w}_k} \right) = j \right), \quad (3.3)$$

in which $\bar{w}_k = \frac{k w_k^A + (n - k) w_k^N}{n}$ is the average fitness of a group of type k and $\Pr(\text{Bin}(n, q) = j)$ represents the probability of j successful trials from n trials with probability q of success. Note that, in this case, q represents the probability an individual of the offspring generation has social trait A . See fig. 3.4 for an explanation about each one of the terms of this equation.

In the migration process, individuals are chosen to migrate from its group with probability $0 \leq m \leq 1$. Since the group size is fixed, this process is a permutation of the migrant individuals inside the

$$S_{kj} = \bar{w}_k \Pr \left(\text{Bin} \left(n, \frac{k w_k^A}{n \bar{w}_k} \right) = j \right)$$

↓
average number of group children of type k
probability of k individuals with social trait A give birth to j individuals with social trait A

Figure 3.4: Detailed explanation about the formalization of the selection process in the terms of matrix S from eq. (3.3).

groups to which they originally belonged. Note that, after migration, for each individual of social trait A inside a group, there are three possibilities:

- the individual was already in the group before migration;
- the individual migrated to the group and occupied the spot left by another individual of social trait A ;
- the individual migrated to the group and occupied the spot left by a wild type individual N .

Hence, each element of matrix M , M_{jl} , the expected number of groups of type j that, due to migration, become groups of type l , is given by:

$$M_{jl} = \sum_{i=0}^n \Pr(\text{Bin}(j, 1 - m + mp) = i) \Pr(\text{Bin}(n - j, mp) = l - i), \quad (3.4)$$

in which p is the fraction of individuals with social trait A in the population after selection (but before migration). See fig. 3.5 for an explanation about each one of the terms of this equation.

$$M_{jl} = \sum_{i=0}^n \underbrace{\Pr(\text{Bin}(j, 1 - m + mp) = i)}_{\text{probability of } i \text{ individuals with social trait } A \text{ remain in the group of type } j} \underbrace{\Pr(\text{Bin}(n - j, mp) = l - i)}_{\text{probability of receiving } l-i \text{ migrants with social trait } A \text{ to occupy the spots left by migrant individuals of trait } N}$$

probability of an individual not migrating from the group
probability of an individual of social trait A migrates to the group

Figure 3.5: Detailed explanation about the formalization of the migration process in the terms of matrix M from eq. (3.4).

The state of the TLFW model is given by the number of A individuals inside a group, i.e., the type of the group, at each generation. Thus, given the initial distribution of group types, $\vec{F}(t) = [F_0(t), F_1(t), \dots, F_n(t)]$ at time $t = 0$, and the transition matrices S and M , it is possible to calculate

the distribution of groups at any time $t > 0$:

$$\vec{F}(t) = \vec{F}(t-1)SM. \quad (3.5)$$

From eq. (3.5), we can calculate the total number of individuals of social trait A at any time $t > 0$:

$$F^A(t) = \sum_{k=1}^n kF_k(t), \quad (3.6)$$

in which $F_k(t)$ is the number of groups of type k at time t .

Since there is no restriction about the selection strength, δ , or about the distribution of individuals with social trait A at $t = 0$, eq. (3.5) is a general way of calculating the dynamics of the distribution of group types in a population structured in g groups with fixed size n . Box 1 provides the steps to simulate the dynamics defined by eq. (3.5) for T periods of time.

Note that to make the simulation feasible, instead of considering the absolute number of groups for each type, it is necessary to calculate the dynamics in terms of the normalized distribution of group types. In particular, $\vec{f}(t) = (f_0(t), \dots, f_n(t))$ is given by:

$$\vec{f}(t) = \left(\frac{F_0(t)}{\sum_{k=0}^n F_k(t)}, \dots, \dots, \frac{F_n(t)}{\sum_{k=0}^n F_k(t)} \right). \quad (3.7)$$

Also, it is important to note that the frequency p of social trait A in the population should be calculated after selection, so that we can use it in the calculation of the elements of matrix M , as in eq. (3.4).

Box 1: Step-by-step numerical simulation of the general TLFW.

1. Initialize the fractions of group types in the population $\vec{f}(0)$.

For t in $1, 2, \dots, T$, run steps from 2 to 4:

2. Calculate matrix S .

3. Multiply the group distribution vector $\vec{f}(t-1)$ by the selection matrix S , obtaining the distribution of groups after selection but before migration given by $\vec{f}^S(t-1) = \vec{f}(t-1)S$.

4. Calculate the fraction of individuals of social trait A in the population, given by $p = \sum_{k=0}^n k f_k^S(t-1)$, in which $f_k^S(t-1)$ is the frequency of group type k after selection.

5. Calculate matrix M using p defined in the step 4.

6. Multiply the group distribution vector $\vec{f}^S(t-1)$ by the migration matrix M , obtaining the distribution of groups after migration given by $\vec{f}(t) = \vec{f}^S(t-1)M$.

3.1.1 Evolutionary stages

The above method for calculating the evolution of social trait A in a structured population is general, since it does not rely on assumptions about the selection strength or the initial number of individuals of social trait A . However, it can be useful to divide the evolution of social trait A into different stages regarding the number of individuals of trait A in the population, namely, Very Early Stage (VES), Early Stage (ES), and Late Stage (LS), which are represented in a timeline shown in fig. 3.6.

At Very Early Stage, the mutation from N to A just occurred and there is no way of predicting the fate of that rare mutation, since there are large fluctuations of the fraction p of individuals of trait A , which can lead to extinction even when the viability condition is satisfied. At Early Stage, p is still very small and the viability condition determines whether the process will be extinct or not. If individuals of trait A survive, the distribution of group types reaches a demographic equilibrium at the so-called Stationary Early Stage, after which the fractions of group types increase. Finally, at Late Stage, the absolute number of individuals of trait A in the population is of the same order as the number of groups g .

Here we focus on approximations for Early Stage, making use of the distribution of group types at Stationary Early Stage. An analysis of the viability conditions under weak selection at Late Stage can be found in [84].

Figure 3.6: An evolutionary timeline representing the stages to which social trait A is subject, when it starts from a single mutation at VES inside a monomorphic population dominated by trait N . In ES, the fate of the mutation A is decided and A can be extinct or survive with its distribution reaching a demographic equilibrium at SES. LS occurs when the number of individuals of trait A cannot be neglected compared to the total number of groups g .

3.2 Early Stage approximations

When we are concerned only with the emergence of the social trait A , we can assume individuals A are very rare in the population. This assumption is used in the migration stage, in which we assume the probability that a group of type $k > 0$ (i.e. with one or more individuals of type A) receives another individual of trait A through migration is so small that it can be neglected. Hence, it is possible to build a simplified version of this process (see fig. 3.7).

Figure 3.7: Simplified migration process when individuals A are very rare in the population. We assume that, in the migration process, it is very unlikely that a group of type $k > 0$ receives a migrant individual of trait A .

With this simplification, matrix M can be decomposed as the sum of two other matrices, M^A and M^B , as shown in eq. (3.8). Matrix M^A represents the process of individual migrations with rate m , which implies that altruists stay in their original group with probability $1 - m$ (eq. (3.9)). On the other hand, matrix M^B describes the assignment of migrant altruists to new groups, with the restriction that, due to the small frequency of altruists in the population, migrants would only go

to groups in which there were no individuals of social trait A (eq. (3.10)).

$$M = M^A + M^B \quad (3.8)$$

$$M_{jl}^A = \Pr(\text{Bin}(j, 1 - m) = l) \quad (3.9)$$

$$M_{jl}^B = \begin{cases} = mj, & \text{if } l = 1 \\ = 0, & \text{if } l \neq 1 \end{cases} \quad (3.10)$$

Let $R = SM$, then, the element R_{kl} corresponding to the k -th row and the l -th column of matrix R is the average number of groups with type k that become groups of type l due to combined effects of selection and migration. R_{kl} can be calculated from eqs. (3.3) and (3.8) and it is given by:

$$\begin{aligned} R_{kl} &= \sum_{j=0}^n S_{kj} M_{jl} \\ &= \begin{cases} \sum_{j=0}^n \bar{w}_k \Pr\left(\text{Bin}\left(n, \frac{k w_k^A}{n \bar{w}_k}\right) = j\right) [\Pr(\text{Bin}(j, 1 - m) = 1) + mj], & \text{if } l = 1 \\ \sum_{j=0}^n \bar{w}_k \Pr\left(\text{Bin}\left(n, \frac{k w_k^A}{n \bar{w}_k}\right) = j\right) \Pr(\text{Bin}(j, 1 - m) = l), & \text{if } l \neq 1. \end{cases} \end{aligned} \quad (3.11)$$

Since all summation terms are non-negative, $R_{kl} \geq 0$, $\forall (k, l) \in [0, n] \times [0, n]$, with $[0, n] \subset \mathbb{N}$. This means $R_{kl} = 0$ can only be zero if all summation terms are zero, which happens only when $k = 0$ and $l > 0$. Thus, $k = 0$ is an absorbing state: when there are no individuals with social trait A in the group, there are no offspring with trait A and the possibility an individual with trait A comes to the group due to migration is negligible, because we are assuming individuals with trait N are predominant in the population.

From eq. (3.5), we can see the relation between the current distribution of group types and matrix $R = SM$. Let $\vec{f}_*(t) = (f_1(t), \dots, f_n(t))$ be the normalized distribution of group types at time t . Note that $\vec{f}_*(t)$ is different from $\vec{f}(t)$ by one dimension: it does not have the first dimension of $\vec{f}(t)$, given by $f_0(t)$. Despite this difference, by calculating $\vec{f}_*(t)$ we can fully determine the distribution of group types, since $\sum_{k=0}^n f_k(t) = 1$ and, thus, $f_0(t) = 1 - \sum_{k=1}^n f_k(t)$. Then, we can write the dynamics for $\vec{f}_*(t)$ as:

$$\vec{f}_*(t) = \vec{f}_*(t-1) R_*, \quad (3.12)$$

in which R_* is a reduced matrix with size $n \times n$, and is obtained by removing the first line, $(R_{0j})_{j \in \{0, 1, \dots, n\}}$, and the first column, $(R_{i0})_{i \in \{0, 1, \dots, n\}}$ of matrix $R = SM$.

Because R_* does not contain the first row and first column of matrix R , all of its elements are strictly positive and, from Perron-Frobenius Theorem [64], it follows that:

- R_* has a dominant eigenvalue ρ , which is real, positive and larger in absolute value than all other eigenvalues;
- there are two eigenvectors associated with the eigenvalue ρ : a single left eigenvector ν and a single right eigenvector ζ , with all of their entries strictly positive;
- $\lim_{k \rightarrow \infty} \frac{R_*^k}{\rho^k} = \zeta \nu'$, in which ζ and ν are normalized so that $\nu' \zeta = 1$, and ν' is the transpose of ν .

One important feature of this model is that it provides a relatively simple viability condition (Theorem 3.1) for the emergence of the cooperative trait.

Theorem 3.1. *Let R_* , the reduced matrix of matrix $R = SM$, with size $n \times n$, obtained by removing the first line, $(R_{0j})_{j \in \{0,1,\dots,n\}}$, and the first column, $(R_{i0})_{i \in \{0,1,\dots,n\}}$ of matrix R . The condition for the viability of the social trait A is given by:*

$$\rho(m) > 1 \tag{3.13}$$

in which ρ is the dominant eigenvalue of matrix R_* and m is the migration rate.

Furthermore, for $t \gg 1$, $f(t) = C \rho^t \nu$, in which C is a constant and ν is the left eigenvector associated with the dominant eigenvalue ρ of matrix R_* .

The proof of this theorem can be found in [101] and follows from the application of Theorem 7.1, Chapter II, of Harris [45], on the condition for the survival of a multitype branching process (MBP). Viewed as a MBP, R_* is the first moment of the MBP, whose types are the types of groups (from 1 to n). Harris theorem states that if the dominant eigenvalue of matrix R_* is larger than one, then, there is positive probability that the types will survive. The existence of the dominant eigenvalue is guaranteed by the Perron-Frobenius Theorem [64], for nonnegative matrices.

Another interpretation of the viability condition

We can also write the viability condition $\rho > 1$ in terms of the fraction of individuals with social trait A in the population, given by $p(t) = \sum_{k=0}^n k f_k(t)$. From the replicator dynamics for viability

selection, we can write the condition of viability as:

$$\bar{W}\Delta p = p(W^A - \bar{W}) > 0, \quad (3.14)$$

in which $\bar{W} = pW^A + (1-p)W^N$ is the average fitness over all group types and W^A (W^N) is the average fitness of an individual of social trait A (trait N).

Since we are assuming $p \ll 1$, $\bar{W} = 1$, i.e., on average, we expect to find groups composed only by individuals of wild type N . On the other hand, the probability of a random individual of trait A is in a group of type k is given by $kf_k / (\sum_{k=1}^n kf_k)$, so that the average fitness of individuals of trait A is given by $W^A = 1 + \frac{\delta \sum_{k=1}^n kf_k v_k^A}{\sum_{k=1}^n kf_k}$. Replacing these values in both sides of the equality in eq. (3.14) produces an approximated expression for Δp :

$$\Delta p = \delta p \frac{\sum_{k=1}^n k \nu_k v_k^A}{\sum_{k=1}^n k \nu_k}, \quad (3.15)$$

in which we wrote f_k as ν_k , since $f(t)$ is driven towards multiples of ν . Hence, the viability condition is given by $\Delta p > 0$ is equivalent to $\rho > 1$, when we assume a stationary regime, with $t \gg 1$ and $p \ll 1$.

3.2.1 Limit of weak selection

If $\delta = 0$ and individuals of social trait A are rare in the population, $v_k^A = v_k^N$ and, thus, $p(t) = \sum_{k=0}^n kf_k(t)$ is constant. Since, from theorem 3.1, for large t , $f(t) = C\rho^t\nu$, this means that $\rho^0 = 1$. Also, when $\delta = 0$, we denote matrix R_* and the left eigenvector ν as, respectively, R_*^0 and ν^0 .

We can think of weak selection, $\delta \rightarrow 0$, as a perturbation of the case $\delta = 0$. Because of the continuity of eigenvalues and eigenvectors, if $\delta \rightarrow 0$, then, $\rho \rightarrow 1$ and $\nu \rightarrow \nu^0$. Since ν^0 does not depend on the payoff v_k^A and v_k^N , we can expect the influence of v_k^A and v_k^N in ν vanishes as δ approaches zero.

Due to this separation of time scales, assuming weak selection, it is possible to write the viability condition $\Delta p > 0$ (according to eq. (3.15)) as:

$$\sum_{k=1}^n \pi_k v_k^A > 0, \quad (3.16)$$

in which π_k can be interpreted as the probability of an individual of social trait A belongs to a group of type k and is given by $\pi_k = \frac{k\nu_k^0}{\sum_{j=1}^n j\nu_j^0}$.

In Early Stage, when A individuals are very rare in the population, we can assume individuals of trait N are very likely to be in groups with only individuals of the same trait N . This also means it is almost certain that if you consider a focal individual of trait A , all individuals of trait A inside his group are related to him, i.e., are IBD (identical by descent). Hence, letting K be the random variable of the number of IBD individuals inside a group, we can write distribution π in the following way:

$$\pi_k = \Pr(K = k|A), \quad (3.17)$$

in which A indicates we are considering a focal individual of trait A and $k \in \{1, 2, \dots, n\}$.

Note that this equation is only valid in the stationary early stage, when the distribution of group types is already at demographic equilibrium ν^0 . We should, then, calculate the demographic equilibrium of distribution π , for $\delta = 0$.

First, let us define how we calculate the number of individuals inside a group who are IBD to a certain focal individual, member of that group. Note that an individual is IBD to another if they share the same parent or if their parents are IBD, and provided that none of them are migrants. Thus, we can express the current number of individuals of trait A who are IBD in the group of the focal individual of trait A in the current generation u , K_u in terms of the number of individuals of trait A in the previous generation $u - 1$, K_{u-1} (see fig. 3.8).

Note that the assumption $\delta = 0$ is used to calculate the probability of an individual being of social trait A . If $\delta = 0$, evolution occurs as a consequence of *random genetic drift* and can be modeled as a Wright-Fisher process. In the Wright-Fisher model, reproduction is a gene-pool process, i.e., the offspring are metaforically put into a pool, and choose a parent A according to its fraction in the population (which is the equivalent to the group the focal individual in TLFW). This is the same as a sampling with replacement, therefore, the number of A s after reproduction has a Binomial distribution with size n and probability $p = K_{u-1}/n$, in which K_{u-1} is the number of A s before reproduction (in the previous generation $u - 1$).

Hence, the sequence of random variables $(K_0, K_1, K_2, \dots, K_t)$ is a Markov process and it can be described with a transition matrix Q , in which each element Q_{ij} is the probability of the transition from $K_{u-1} = i$ to $K_u = j$. Following the two possibilities for the focal individual of trait A (for

Figure 3.8: Explanation about the calculation of K_u , the number of individuals who are IBD in a group to which the chosen focal individual of trait A belongs, at current generation u , from the number of individuals of trait A in the previous generation $u-1$, K_{u-1} . The focal individual is represented by the orange dot, while her ancestral in the previous generation is the green dot. In the left, we depict the situation when the focal individual migrates to another group: since $p \ll 1$, she arrives to a group in which she is the only individual with trait A , so that $K_u = 1$. In the right, the assumption of $\delta = 0$ determines the probability K_{u-1}/n with which an individual is of trait A when he descends from a group with K_{u-1} individuals of trait A . In this case, the current generation will have K_u individuals who are IBD if their parents are among the K_{u-1} individuals of the previous generation and are not subject to migration.

simplicity, below, we refer to him as "focal individual") shown in fig. 3.8, we can separate the calculation of Q_{ij} into two cases:

1. if $j = 1$, there are two possibilities:

- the focal individual is a migrant, which occurs with probability m ; or
- the focal individual does not migrate, which occurs with probability $1 - m$, and individuals of trait A from the previous generation did not leave other offspring (except for the focal individual) who remained in the group, which occurs with probability $\Pr(\text{Bin}(n-1, (1-m)i/n) = 0)$;

2. if $j = 2, \dots, n$: this can only happen if the focal individual remains in his group (occurs with probability $1 - m$) and exactly $j - 1$ of the other individuals inside the group remained in the group and have parents who are among the i individuals of trait A in the previous generation, which occurs with probability $\Pr(\text{Bin}(n-1, (1-m)i/n) = j-1)$.

These two cases are reflected in the formula for Q_{ij} :

$$Q_{ij} = \begin{cases} m + (1 - m) \Pr(\text{Bin}(n - 1, (1 - m)i/n) = 0), & \text{if } j = 1 \\ (1 - m) \Pr(\text{Bin}(n - 1, (1 - m)i/n) = j - 1), & \text{if } j \neq 1, \end{cases} \quad (3.18)$$

in which $i \in \{1, 2, \dots, n\}$ and $j \in \{1, 2, \dots, n\}$.

Given Q , then, it is possible to calculate the demographic equilibrium $\pi = \pi^*$, with $\pi^* = (\pi_1^*, \pi_2^*, \dots, \pi_n^*)$, at SES (Stationary Early Stage) through the solution of:

$$\pi = Q\pi, \quad (3.19)$$

with $\sum_{k=1}^n \pi_k = 1$.

Viability condition based on relatedness

From eq. (3.17), we can see π_k is the probability of the number of individuals who are IBD to the focal individual of social trait A inside a group being k . However, from the explanation about how to calculate K in fig. 3.8, it is possible to see that in Early Stage, the number of individuals who are IBD to the focal individual of social trait A inside a group is exactly the number of individuals of social trait A inside that group. This means that, by abusing the notation and representing both quantities with the same random variable K , we can write π_k as the probability of K being equal to k without conditioning on the focal individual at eq. (3.17).

Previously we mentioned the notion of IBD (identical by descent), which can be defined as the genetic identity two individuals from the same generation t share due to a coalescent event at some past generation $t - i$, with $i > 0$, before a migration event in one of the two lineages. This means those two individuals share a common ancestral through which they became part of their group. Thus, in ES (when $p \ll 1$, i.e., A is a rare phenotype in the population), if D is a binary random variable which determines whether, given a focal individual of trait A , a co-focal individual is IBD to him ($D = 1$) or not ($D = 0$), then, relatedness can be defined as:

$$r_t = P_t(D = 1|A), \quad (3.20)$$

in which the subscript t makes the time dependence explicit.

By assuming weak selection, $\delta \rightarrow 0$, however, we can assume there is a separation of time scales, so that a demographic equilibrium is achieved through the process of genetic drift (when $\delta = 0$ and $v_k^A = v_k^N$) and, then, selection starts to affect this distribution at a rate of order δ . This implies that $r_t = r$, i.e., relatedness is independent of time.

In TLFW, we can then calculate r , by calculating the probability $P(D = 1|A)$. As explained before, under weak selection, $w_k^A \approx w_k^N$, which means the probability of the co-focal individual having the same parent of the focal individual is $1/n$ (is independent of the fact that the focal individual is of social trait A). Conversely, the probability that they have different parents is $1 - 1/n$ and, in this case, they will only be IBD if those two parents are IBD to one another, which occurs with probability r . Additionally, in both cases, the two individuals are only IBD to each other if they are not migrants, which occurs with probability $(1 - m)^2$. Thus:

$$r = (1 - m)^2 \left[\frac{1}{n} + \left(1 - \frac{1}{n} \right) r \right] \implies r = \frac{(1 - m)^2}{n - (1 - m)^2 (n - 1)}. \quad (3.21)$$

The association of relatedness (r) to the migration rate (m) makes it possible to write the viability condition obtained for ES, $\rho > 1$ in terms of r , when selection is weak:

$$r > r_c \iff r > \frac{(1 - m_c)^2}{n - (1 - m_c)^2 (n - 1)}, \quad (3.22)$$

in which m_c is the critical migration rate for which $\rho = 1$.

3.2.2 Limit of large n and small m under weak selection

Under weak selection and in the limit of $n \rightarrow \infty$ and $m \rightarrow 0$, we can calculate the distribution π at equilibrium, showing that it is distributed as a Beta distribution with parameters $\alpha = 1$ and $\beta = 2nm$. Here we indicate how to prove this result by using the moments of π .

First, we would like to generate a recurrent expression for the l -th moment of the random variable K at equilibrium, when $\pi = \pi^*$. This can be done by following the general definition of the l -th moment of a random variable K , given by: $E(K^l) = \sum_{k=1}^n k^l \pi_k$, in which $\pi_k = P(K = k)$.

Because of the nature of the elements of matrix Q (see eq. (3.18)), instead of calculating the l -th moment for K_u , the number of individuals who are IBD to a focal individual of trait A in generation u , it is more convenient to first write an expression for $K_u - 1$.

In this way, since the first value $K_u - 1$ can take is zero, the first term of the expression can be eliminated. Then:

$$\begin{aligned} \mathbb{E} \left[(K_u - 1)^l \right] &= \sum_{j=1}^l (1-m) j^l \mathbb{P} [\text{Bin}(n-1, (1-m)K_{u-1}/n) = j] \\ &= (1-m) \mu_l^B, \end{aligned} \quad (3.23)$$

in which μ_l^B is the l -th moment of a random variable distributed as $\text{Bin}(N, p)$, given by eq. (3.25) from box 2, with parameters $N = n - 1$ and $p = (1-m) \frac{K_{u-1}}{n}$.

Box 2: Moments for the Binomial distribution

For a random variable distributed as $\text{Bin}(N, p)$, the moment-generating function is given by the following expression:

$$\mathcal{M}(t) = \sum_{k=0}^N e^t \binom{N}{k} p^k (1-p)^{N-k} = (pe^t + (1-p))^N. \quad (3.24)$$

From the moment-generating function, it is possible to calculate any moment of order l by calculating the l -th derivative of $\mathcal{M}(t)$ at $t = 0$, i.e., $\mu_l = \left. \frac{d^l \mathcal{M}(t)}{dt^l} \right|_{t=0}$.

By calculating each one of the moments, it is possible to derive a general explicit formula for the l -th moment of the Binomial distribution, μ_l^B :

$$\mu_l^B = \sum_{k=0}^N N_k S(l, k) p^k, \quad (3.25)$$

in which $N_k = \frac{N!}{k!}$ and $S(l, k)$ is the Stirling number of the second kind, which counts the number of ways one can partition l elements into k nonempty sets, and it is calculated from $S(l, k) = \frac{1}{k!} \sum_{j=0}^k \binom{k}{j} (k-j)^l$.

By replacing $s = 1 - m$ and eq. (3.25) in eq. (3.23), we obtain a formula for the l -th moment of $K_u - 1$:

$$\mathbb{E} \left[(K_u - 1)^l \right] = s \sum_{j=1}^l S(l, j) (n-1)_j s^{j+1} \frac{\mathbb{E} \left(K_{u-1}^j \right)}{n}. \quad (3.26)$$

Note that a binomial expansion of $(K_u - 1)^l$ yields $\sum_{j=0}^l \binom{l}{j} (-1)^{l-j} K_u^j$, which means the left hand side of eq. (3.26) can also be written as:

$$\mathbb{E} \left[(K_u - 1)^l \right] = \sum_{j=0}^l \binom{l}{j} (-1)^{l-j} \mathbb{E} \left(K_u^j \right). \quad (3.27)$$

Since we are interested in calculating this quantity at the demographic equilibrium, K_u and K_{u-1} have the same distribution π^* and, thus, $E[(K_u - 1)^l] = E(K_{u-1}^l) = \mu_l$. By rewriting eq. (3.26) and eq. (3.27) using μ_l and combining them, we can get an expression for μ_l in function of μ_j , $j = 1, 2, \dots, l$:

$$\begin{aligned} \sum_{j=0}^l \binom{l}{j} (-1)^{l-j} \mu_j &= s \sum_{j=1}^l S(l, j) (n-1)_j s^{j+1} \frac{\mu_j}{n} \\ \mu_l + (-1)^l + \sum_{j=1}^{l-1} \binom{l}{j} (-1)^{l-j} \mu_j &= \frac{(n-1)_l}{n^l} s^{l+1} \mu_l + s \sum_{j=1}^{l-1} S(l, j) (n-1)_j s^{j+1} \frac{\mu_j}{n}, \end{aligned} \quad (3.28)$$

in which we used $S(l, l) = 1$ and $\mu_0 = 1$.

Solving eq. (3.28) for μ_l yields:

$$\mu_l = \frac{(-1)^{l+1} + \sum_{j=1}^{l-1} \left[\binom{l}{j} (-1)^{l-j+1} \mu_j + S(l, j) (n-1)_j s^{j+1} \frac{\mu_j}{n} \right]}{1 - \frac{(n-1)_l s^{l+1}}{n^l}}. \quad (3.29)$$

With eq. (3.29), we can calculate moments of any order by calculating each one of the lower order moments. For instance, the calculation of the first moment ($l = 1$) is straightforward and gives us:

$$\mu_1 = \frac{n}{n - (n-1)(1-m)^2}. \quad (3.30)$$

Theorem 3.2 enunciates formally the result previously mentioned about the distribution π^* .

Theorem 3.2. *Let X be the frequency of altruists of a group, given by K/n . If $\delta \rightarrow 0$, $m \rightarrow 0$ and $n \rightarrow \infty$, then, the distribution of X follows a Beta distribution, with parameters $\alpha = 1$ and $\beta = 2nm$, $\text{Beta}(1, 2nm)$:*

$$P(X = x) = 2nm(1-x)^{2nm-1} \quad (3.31)$$

This result can be proved by showing that the moments of K/n converge to the moments of a Beta distribution with parameters $\alpha = 1$ and $\beta = 2mn$, when $n \rightarrow \infty$ and $m \rightarrow 0$:

$$\lim_{\substack{n \rightarrow \infty \\ m \rightarrow 0}} \frac{\mu_l}{n^l} = \frac{l!}{\prod_{j=1}^l (2mn + j)} \quad (3.32)$$

Equation (3.32) can be proven by induction on l using the formula for the l -th moment, given by eq. (3.29). A full proof can be found in [85, 101].

3.3 Examples of applications

In this section, we consider the case in which the social trait A represents altruism. In order to model the evolution of altruism under the TLFW framework, we will assume individuals interact inside the group as in a public goods game (see appendix section A.1.1 for more details about it). Here we focus on three different public goods games: OOPG (Others-Only Public Goods Game), IPG (Iterated Public Goods Game) and THR (Threshold Public Goods Game).

Before showing the results of the application of the TLFW into the different payoff functions, we write the equations for the payoffs of A , v_k^A , and N , v_k^N , for every one of the games OOPG, IPG and THR. For OOPG, payoffs for A and N inside a group with size n with k altruists are given by:

$$\begin{aligned} v_k^A &= b(k-1)/(n-1) \\ v_k^N &= bk/(n-1), \end{aligned} \tag{3.33}$$

in which $b > 0$ and $c > 0$.

For IPG, payoffs for A and N inside a group with size n with k altruists are given by:

$$v_k^A = \begin{cases} -c + \frac{b(k-1)}{n-1}, & \text{if } k \leq \theta, \\ T \left(-c + \frac{b(k-1)}{n-1} \right), & \text{if } k > \theta, \end{cases} \tag{3.34}$$

$$v_k^N = \begin{cases} \frac{bk}{n-1}, & \text{if } k \leq \theta, \\ T \frac{bk}{n-1}, & \text{if } k > \theta, \end{cases} \tag{3.35}$$

in which $b > 0$, $c > 0$, $\theta > 0$ and $T > 0$.

For THR, payoffs for A and N inside a group with size n with k altruists are given by:

$$v_k^A = \begin{cases} -c, & \text{if } k < \theta, \\ -c + b, & \text{if } k \geq \theta, \end{cases} \tag{3.36}$$

$$v_k^N = \begin{cases} 0, & \text{if } k < \theta, \\ b', & \text{if } k \geq \theta. \end{cases} \quad (3.37)$$

in which $b > 0$, $b' > 0$, $c > 0$ and $\theta > 0$.

In fig. 3.9, we show how these different payoffs shown above vary according to the number of altruists in the group. We can see that it is always disadvantageous to be an altruist compared to being a non-altruist. While the fitness functions for A and N are linear on k for OOPG, for IPG and THR it is easy to identify the threshold at which the collective good starts to be produced by the non-linear increase on the fitness functions evaluated around that threshold.

Figure 3.9: Fitness functions for an altruist individual (A) and a non-altruist individual (N) versus number of altruists (k) for different public goods games. At each panel, a different public goods game is considered: from left to right, respectively, OOPG (Others-Only Public Goods Game), IPG (Iterated Public Goods Game) and THR (Threshold Public Goods Game). For all public goods games, we considered $n = 20$ and $\delta = 0.1$. OOPG parameters: $b = 5$, $c = 1$; IPG parameters: $b = 5$, $c = 1$, $T = 10$, $\theta = 8$; THR parameters: $b = 10$, $b' = 10$, $c = 1$, $\theta = 4$.

In the TLFW framework, one of the stages involves group reproduction and depends on the average fitness ($\bar{w}_k$). In fig. 3.10, it is possible to see the behavior of the average fitness as the number of altruists in the group increases. For OOPG, it is very clear that larger δ makes the average fitness level increase. For IPG and THR, if the number of altruists does not reach the threshold, different levels of δ have very limited influence on $\bar{w}_k$. If the number of altruists is larger than the threshold, however, the behavior is similar to OOPG, and, the larger δ , the points are higher. While the average fitness for OOPG and IPG are increasing functions of k , for THR, the average fitness decreases as k increases, except for k around the threshold θ , as when θ is reached, the fitness functions are much larger, as seen in fig. 3.9.

Figure 3.10: Average fitness ($\bar{w}_k$) versus number of altruists (k) at three different selection strength (δ) levels for different public goods games. At each panel, a different public goods game is considered: from left to right, respectively, OOPG (Others-Only Public Goods Game), IPG (Iterated Public Goods Game) and THR (Threshold Public Goods Game). For all public goods games, we considered $n = 20$. OOPG parameters: $b = 5$, $c = 1$; IPG parameters: $b = 5$, $c = 1$, $T = 10$, $\theta = 8$; THR parameters: $b = 10$, $b' = 10$, $c = 1$, $\theta = 4$.

In fig. 3.11, following the discussion in section 3.2.1, we show how the behavior of group type distribution differ between two different selection strength (δ) levels. While, when δ is small, different payoff functions yield very similar group type distributions, when δ is sufficiently large, their distributions grow apart from each other.

We can also use the viability condition given by theorem 3.1, $\rho > 1$, to find which sets of parameters allow altruism to emerge. In fig. 3.12, we see how the dominant eigenvalue of matrix R (as given by eq. (3.11)), ρ behave for different values of migration rates (m) and for three different selection strength levels (δ). In this figure, the parameters related to the benefit, cost, threshold (for IPG and THR) and number of iterations (for IPG) are the same as the ones in fig. 3.9. As the fitness functions for A and N are lower and closer to each other when there are few altruists in the group, when the game is IPG or THR, we can see that a wider range of migration rates meet the viability criteria, compared to OOPG. We can also see the larger δ , the higher is the maximum migration rate m such $\rho > 1$, which is intuitive from fig. 3.10.

Figure 3.11: Distribution of group types (ν_k) for different public goods games and different values of selection strength (δ). OOPG represents the others-only public goods game; IPG is the iterative public goods game; and THR is the threshold public goods game. For all public goods games, we considered $n = 20$ and $m = 0.1$. OOPG parameters: $b = 5$, $c = 1$; IPG parameters: $b = 5$, $c = 1$, $T = 10$, $\theta = 8$; THR parameters: $b = 10$, $b' = 10$, $c = 1$, $\theta = 4$.

Figure 3.12: ρ against different values of migration rates (m) at three different selection strength (δ) levels for different public goods games. Dashed black line indicates the critical value above which altruism is viable. At each panel, a different public goods game is considered: from left to right, respectively, OOPG (Others-Only Public Goods Game), IPG (Iterated Public Goods Game) and THR (Threshold Public Goods Game). For all public goods games, we considered $n = 20$. OOPG parameters: $b = 5$, $c = 1$; IPG parameters: $b = 5$, $c = 1$, $T = 10$, $\theta = 8$; THR parameters: $b = 10$, $b' = 10$, $c = 1$, $\theta = 4$.

3.4 Discussion - when relatedness is not enough

As introduced before, Hamilton's rule explains how to connect relatedness (r) between individuals to certain social behaviors, for instance, altruism. In the original formulation, as seen in section 2.4.2, the use of Hamilton's rule is restricted to situations in which selection interactions are dyadic. A more general formulation, however, should allow r to include nonlinear effects on fitness as well as effects on selection of assortment. This can be done in the TLFW framework and, in this section, we explain why it can be useful to generalize Hamilton's rule in this sense.

One of the most widely used formulations is the one from Taylor and Frank, who proposed a more straightforward way to calculate the *inclusive fitness* of an actor. By assuming the fitness of a focal individual depends on two variables: his own phenotype (characterized by a continuous quantity) and his social environment (defined by the average phenotype of the neighborhood), they are able to calculate the condition in which a rare mutation of the phenotype is an ESS.

The studied phenotype may be, for example, the amount of a substance that benefits nearby individuals but is costly to produce. We will denote this quantity as y . Following the treatment of Taylor and Frank, we would like to discover the condition under which a rare mutant could invade a monomorphic population with phenotype $y = \bar{y}$. It is assumed the rare mutation has a phenotype $y = \bar{y} + \delta$, with a small $|\delta|$.

From the definition of ESS, we know that the rare mutant (m) can invade the population of wild types (W) if the mutant's average fitness (w^m) is higher than the wild type's (w^W). Thus, to find the condition for the invasion of rare mutants, we should solve the following inequation:

$$w^m - w^W > 0. \quad (3.38)$$

The key to calculate these quantities, w^m and w^W , is the fitness of the respective focal individual. For a wild-type individual, the calculation is very straightforward, as we can assume the social environment is composed of wild-type individuals. In this case, $w^W = w(y, z) = w(\bar{y}, \bar{y})$.

Now, let X be a random variable of the frequency of mutants in the social environment of a mutant. Then, the average phenotype in the social environment of a mutant is: $z = (\bar{y} + \delta)X + \bar{y}(1 - X) = \bar{y} + \delta X$. This means that if the focal individual is the rare mutant, $w^m = E[w(\bar{y} + \delta, \bar{y} + \delta X)]$, in which E represents the expectation of w relative to X . Note that X conveys the information

about the assortment of mutant types in the population, which may be due to several factors, for instance, a common descent.

In the derivation of the condition for the invasion of rare mutants, Taylor and Frank expanded the fitness function $w(\bar{y} + \delta, \bar{y} + \delta X)$ into a Taylor series up to the first order and, then, applied the chain rule to calculate the derivatives of w in relation to X in the point $y = z = \bar{y}$. Although there was no remark about it in their derivation, this step can only be made when the partial derivatives of the fitness function w exist at the analyzed point. Note that it is not strictly necessary that the function is differentiable at that point, but the function should be well approximated by a plane.

If this condition is satisfied, then:

$$w(\bar{y} + \delta, \bar{y} + \delta X) = w(\bar{y}, \bar{y}) + \left. \frac{\partial w}{\partial y} \right|_{y=z=\bar{y}} \delta + \left. \frac{\partial w}{\partial z} \right|_{y=z=\bar{y}} \delta X. \quad (3.39)$$

Thus, using eq. (3.39) to calculate eq. (3.38), we have:

$$\begin{aligned} w^m - w^W &= E \left[w(\bar{y}, \bar{y}) + \left. \frac{\partial w}{\partial y} \right|_{y=z=\bar{y}} \delta + \left. \frac{\partial w}{\partial z} \right|_{y=z=\bar{y}} \delta X \right] - w(\bar{y}, \bar{y}) \\ &= \delta \left(\left. \frac{\partial w}{\partial y} \right|_{y=z=\bar{y}} + \left. \frac{\partial w}{\partial z} \right|_{y=z=\bar{y}} E[X] \right) \\ &= \delta (-c + br) > 0. \end{aligned} \quad (3.40)$$

From eq. (3.40), we can see $w^m - w^W > 0$ takes the form of Hamilton's equation when we replaced the partial derivatives in y and z by $-c$ and b , respectively. Also, in the above expression, we replaced $E(X)$ by r , as it can be interpreted as the average relatedness in the social environment of a mutant individual.

3.4.1 A practical example - contingent cooperation

Several of the behaviors displayed by humans are conditioned on the behavior of their peers. A remarkable example was studied by Schelling, who realized the dynamics of a standing ovation depended not only on the quality of the presentation, but on how individuals reacted to other individuals standing around them. Analogously, contingent cooperation strategies may also be dependent on thresholds: in the iterated public goods game, a contingent strategy could be to cooperate on the first round and then only cooperate if at least θ of the other individuals cooperated.

Suppose individuals can be classified as type A or type N and are divided in groups with equal size n . Within each group, individuals interact with each other in such a way that, if there are at least θ individuals of type A (who always bear a cost $c > 0$) inside the group, then all individuals of the group will receive a benefit $b > 0$. In this situation, for a small δ , an individual of type A inside a group with k individuals of type A has fitness given by:

$$w_k^A = \begin{cases} w_0 - \delta c & \text{if } k < \theta \\ w_0 + \delta (b - c) & \text{if } k \geq \theta. \end{cases} \quad (3.41)$$

In the same group, an individual of type N has fitness:

$$w_k^N = \begin{cases} w_0 & \text{if } k < \theta \\ w_0 + \delta b & \text{if } k \geq \theta. \end{cases} \quad (3.42)$$

We would like to calculate the condition in which a rare mutant type A can invade a population in which type N individuals are common. From eq. (3.41) and eq. (3.42), we can derive the form of $w(y, z)$:

$$w(y, z) = \begin{cases} w_0 - c(y - \bar{y}) & \text{if } k < \theta \\ w_0 - c(y - \bar{y}) + b(z - \bar{y}) & \text{if } k \geq \theta. \end{cases} \quad (3.43)$$

As with the general case, we start from eq. (3.38) and should calculate $w^m = E[w(\bar{y} + \delta, \bar{y} + \delta X)]$ and $w^W = w(\bar{y}, \bar{y})$. Note that this calculation is equivalent to $w^m = E(w_k^A)$ and $w^W = E(w_k^N)$.

Because type N is much more frequent in the population, we can assume his neighbors will also be type N individuals, so that definitely $k < \theta$, and we have:

$$w^W = w_0. \quad (3.44)$$

On the other hand, if the focal individual is of type A , we assume there is an increased chance that there are more type A individuals inside the group and, thus, calculating w^m is not as straightforward as when the focal individual is of type N :

$$w^m = \sum_{k=0}^n k w_k^A = w_0 - \delta c + \delta b \Pr(k \geq \theta | A) \quad (3.45)$$

We can see from eq. (3.45) that the calculation requires knowledge about the cumulative distribution of variable k (given the focal individual is of type A) or, more precisely, about $\Pr(k \geq \theta|A) = 1 - \Pr(k < \theta|A)$.

Note that the random variable K that controls the number of type A individuals inside a group corresponds to nX , with X defined as in the derivation of the Hamilton's rule through the Taylor and Frank framework. However, since the other variables y , z and θ would also be scaled by a factor $1/n$, we merely replace X by K in eq. (3.39) and find the following equation:

$$w^m = w_0 + \delta [-c + bE(K)] \quad (3.46)$$

If eq. (3.46) held, considering eq. (3.45) would imply that:

$$\Pr(k \geq \theta|A) = E(K) . \quad (3.47)$$

However, this is not always true, as the value of $\Pr(k \geq \theta|A)$ depends on the distribution of k . Thus, in some cases, relatedness is not enough for predicting whether a rare mutant is capable of invading a monomorphic population composed of wild types.

Different probability distributions can have the same mean

Mathematically, it is clear that $E(K)$ is not always the same as $\Pr(k \geq \theta|A)$. However, is it biologically relevant? Here, we intend to show an example in which the mating system influences the distribution of k , so that calculating the relatedness between individuals is not enough for calculating the mean fitness of a rare mutant of type A .

Suppose n individuals are divided in m males and f females. In this model, one offspring has male i as a father and female j as a mother with probability $\mu_i \phi_j$, with $\sum_{k=1}^m \mu_k = 1$ and $\sum_{k=1}^f \phi_k = 1$. In addition to these assumptions, we shall assume the same population structure and the same payoffs as the contingent cooperation model explained previously.

The transmission of traits is vertical and individuals of type A are born if one of his parents is of type A as well. As before, we are interested in calculating $\Pr(k|A)$ inside the group of the focal

individual. This probability depends on μ_i and ϕ_i values in the following way:

$$\Pr(k|A) = \sum_{i=1}^m \frac{\mu_i}{2} \text{Bin}\left(k; n-1, \frac{\mu_i}{2}\right) + \sum_{i=1}^f \frac{\phi_i}{2} \text{Bin}\left(k; n-1, \frac{\phi_i}{2}\right), \quad (3.48)$$

in which $\text{Bin}(k; n, p)$ is the binomial probability distribution giving the probability of k successful trials in n independent Bernoulli trials, each one with probability p of success.

The reasoning behind eq. (3.48) is that the probability an individual is type A because of his father (mother) is $\mu_i/2$ ($\phi_i/2$). At the same time, because type A is rare, all type A individuals inside a group are supposed to be related, so that they have inherited type A trait from the same parent and, thus, the probability that k of the other $n-1$ individuals are of type A is given by the probability that k individuals inherit type A from father i , $\text{Bin}(k; n-1, \frac{\mu_i}{2})$, or from mother i , $\text{Bin}(k; n-1, \frac{\phi_i}{2})$, with $k \in [0, n-1]$.

Analogously, we can reach a formula for relatedness in this model. As type A is rare, we can calculate r by calculating the probability an individual is of type A given that the focal individual is of type A , $\Pr(A|A)$:

$$r = \Pr(A|A) = \sum_{i=1}^m \frac{\mu_i^2}{4} + \sum_{i=1}^f \frac{\phi_i^2}{4} \quad (3.49)$$

When considering mating systems, it is possible that one individual is more prone to mate than his/her peers. The degree of mating skew might be modeled by assuming that $\mu_i = (1-\beta)\beta^{i-1}/(1-\beta^m)$, where $0 < \beta < 1$. In the limit $\beta \rightarrow 0$, male mating is completely skewed, while in the limit $\beta \rightarrow 1$, male mating is egalitarian. Analogously, for females, $\phi_i = (1-\alpha)\alpha^{i-1}/(1-\alpha^f)$, with $0 < \alpha < 1$. Calculating the first term of eq. (3.49):

$$\begin{aligned} \sum_{i=1}^m \mu_i^2 &= \frac{(1-\beta)^2}{(1-\beta^m)^2} \sum_{i=1}^m (\beta^2)^{i-1} = \frac{(1-\beta)^2}{(1-\beta^m)^2} \frac{(1-\beta^{2m})}{(1-\beta^2)} \\ &= \frac{(1-\beta)^2}{(1-\beta^m)^2} \frac{(1-\beta^m)(1+\beta^m)}{(1-\beta)(1+\beta)} = \frac{(1-\beta)(1+\beta^m)}{(1+\beta)(1-\beta^m)}. \end{aligned} \quad (3.50)$$

Similarly, for the second term of eq. (3.49):

$$\sum_{i=1}^f \phi_i^2 = \frac{(1-\alpha)(1+\alpha^f)}{(1+\alpha)(1-\alpha^f)} \quad (3.51)$$

Replacing eqs. (3.50) and (3.51) into eq. (3.49) yields an expression for r . If n is sufficiently large (so that m and f are sufficiently large) this becomes:

$$r \approx \frac{1}{4} \left(\frac{1-\beta}{1+\beta} + \frac{1-\alpha}{1+\alpha} \right) = \frac{1}{2} \frac{(1-\alpha\beta)}{(1+\alpha)(1+\beta)} \quad (3.52)$$

In fig. 3.13, we plot eqs. (3.48) and (3.52) for a chosen set of parameters to understand the relatedness (r) behavior concerning the variation of α and β . In the left panel, we can see that different values of α and β may yield the same relatedness level. However, having the same relatedness level does not imply that the quantity $\Pr(k \geq \theta|A)$ is the same, as shown for $\theta = 9$ in the right panel of the same figure.

Figure 3.13: In the left panel, we see how different values of α and β might lead to the same relatedness values (r). In the right panel, the distribution of k is plotted for two different sets of α and β (represented by the star and the diamond markers), which lead to the same relatedness level, $r = 0.25$. The shaded areas represent $\Pr(k \geq 9|A)$. Parameters: $n = 16$, $f = 10$ and $m = 6$.

3.4.2 A general way of calculating the condition for the invasion of rare mutants

The fitness function for the previous example, shown in eq. (3.43), is a non linear function in z , as the behavior in z direction depends on the number k of individuals of type A inside the group. As explained before, Taylor and Frank's derivation of the condition for the invasion of rare mutants depends on the differentiability of the function $w(y, z)$, in both directions, at the point $y = z = \bar{y}$. It is easy to see that because of the threshold nature of eq. (3.43), $w(y, z)$ is not differentiable at this point.

For non-differentiable functions, Taylor expansion and the chain rule cannot be applied. Thus, we have to go back to the condition for the invasion of rare mutants formula:

$$w^m - w^W = \delta E \left[\frac{w(\bar{y} + \delta, \bar{y} + \delta x) - w(\bar{y}, \bar{y})}{\delta} \right] > 0, \quad (3.53)$$

in which we have multiplied and divided the argument of the expectation function by δ .

Since we are interested in the case where $|\delta| \ll 1$, calculating eq. (3.53) can be reduced to the problem of solving the following expression:

$$\lim_{\delta \rightarrow 0} \frac{w(\bar{y} + \delta, \bar{y} + \delta x) - w(\bar{y}, \bar{y})}{\delta}. \quad (3.54)$$

Note that eq. (3.54) resembles the form of a directional derivative of $w(y, z)$ in the direction of a unit vector $\vec{v}$. In this case, we would multiply the expression from eq. (3.54) by $\sqrt{1+x^2}$ and take $\vec{v}$ as the unit vector: $\vec{v} = \left(\frac{1}{\sqrt{1+x^2}}, \frac{x}{\sqrt{1+x^2}} \right)$ at the point $y = \bar{y}$; as we are treating the case in which mutants are rare, $0 < x \ll 1$, so that $\sqrt{1+x^2}$ is negligible. Also, note that we can write z in terms of y , so that $w(y, z) = w(y, yx + \bar{y}(1-x))$. Hence:

$$w^m - w^W \approx \delta E[\nu(x)], \quad (3.55)$$

where $\nu(x) = \left. \frac{dw(y, yx + \bar{y}(1-x))}{dy} \right|_{y=\bar{y}}$ and $\nu(x)$ is called *marginal fitness*.

Using eq. (3.55), we can then calculate condition for the invasion of rare mutants for the example of contingent cooperation as shown in box 3.

Box 3: Condition for the invasion of rare mutants for the contingent cooperation example

Using eq. (3.43) and the correspondence between k and x , we can calculate $\nu(k)$:

$$\nu(k) = \begin{cases} -c & \text{if } k < \theta \\ -c + bk & \text{if } k \geq \theta \end{cases} \quad (3.56)$$

Replacing eq. (3.56) into eq. (3.55), we have:

$$w^m - w^W = -c + b\Pr(k \geq \theta|A) > 0, \quad (3.57)$$

which is the same result we would get if we used eq. (3.45).

Chapter 4

Evolving altruism in the presence of intergroup conflicts

In this chapter, we study the emergence of altruism in the presence of intergroup conflicts under a weak selection regime, by using a model based on a two-level selection model. Our results show conditions for the viability of altruistic traits in the context of hunter-gatherers societies.

4.1 Related work and motivation

Archaeological and ethnographic studies [4, 50, 54, 55] provide evidence that hunter-gatherer populations might have engaged in frequent intergroup conflicts, although it is not clear at what extent hunter gatherers were violent.

Altruism can be defined as the strictest version of cooperation, when an actor incurs a cost to benefit the recipient exclusively. Several theories have been proposed to explain its evolution but, so far, there has been no definitive answer to how altruism could have emerged in human populations. Most theories involve kin selection, indirect and direct reciprocity and multilevel selection [57].

Previously, Bowles [16, 17] modeled and discussed the emergence of altruism in this scenario, by using the Price equation. The Price equation [78] is an expression for the difference of the frequency of a type of a particle or individual between two subsequent generations. It is simple, recursive and separates clearly the effects of inter and intragroup selection [42]. Recently, there has been a discussion of whether the use of Price equation for evolutionary models is correct or not. Van Veelen

et al. [100] claim that some models based on the Price equation are not dynamically sufficient, i.e., the models use equations which does not account for changes across time.

One of the most important consequences of the Price equation is the Hamilton rule, which is a condition for the proliferation of altruism. However, it is known that the simplest form of the Hamilton rule does not hold for any scenario.

As presented in the previous chapter, an alternative framework to model the evolution of altruism was introduced by Schonmann et al. [82, 83]. They consider two levels of selection with migration in a structured population (a two-level Fisher-Wright model). Their approach generates a simple rule, which predicts the conditions in which altruism can survive. This model also recovers the original rule, the Hamilton rule, for the cases in which fitness functions are linear or, equivalently, interactions are dyadic.

4.2 The model

We consider a large population with an infinitely large number of groups of fixed size n in which individuals are randomly distributed. Each individual is labeled as an altruist (A) or as a native (N , non-altruist). Since we would like to study the proliferation of altruists in the population, we classify the groups according to their number of altruists. We define that a group will be of type k if it has exactly k altruists and, consequently, $n - k$ non-altruists.

This is a three-staged model (see fig. 4.1). In the first stage, groups may engage in conflicts between each other, and this stage is called intergroup selection. Next, there is the stage of intragroup selection, in which individuals interact inside their groups, and reproduce according to their inner-group fitness. Finally, there is migration of individuals among the groups, which decreases the relatedness level of individuals in the same group.

Each generation in our model can be characterized by the product of two matrices. One of them, the matrix S , represents the intergroup and intragroup selection processes. The other matrix, M , captures the migration process. We assume the dynamics for the number of altruists eq. (4.1) is a Markov process. Thus, by providing an initial distribution of altruists among groups, we are able to track the expected frequency of altruists in the population at a given generation.

$$N(t+1) = N(t)SM \tag{4.1}$$

Figure 4.1: Model scheme. First, there is war between groups. Secondly, intragroup selection takes place and individuals reproduce. Finally, individuals are allowed to migrate to other groups.

in which $N(t) = (N_1(t), \dots, N_n(t))$ and $N_k(t)$ is the average number of groups of type k .

In the intergroup selection stage, groups can engage in conflicts between each other with probability β . The likelihood of winning a contest depends on the number of altruists and also on parameter α , the benefit of altruists in conflicts, which measures the influence of altruists in the war outcome. A scheme of the intergroup selection process is shown in fig. 4.2.

Figure 4.2: Intergroup selection in our model. Groups engage in war with probability β and can win or lose the war according to a function λ_k that depends on the number of altruists k in the group. Three outcomes are possible from this process: either the group does not fight the war and keeps its deme; or it fights the war and may go to extinction or reproduce twice, at its own deme and at the opponent deme.

We consider $\alpha \in (0, 1)$, and the more altruists one group has, the more likely it is to win the war, as shown in eq. (4.2) for the likelihood of winning the war. If the number of altruists of the focal

group is zero, then, there is equal likelihood of winning or losing the war ¹.

$$\lambda_k = \frac{1}{2} + \alpha \frac{k}{2n} \quad (4.2)$$

In this stage, a group may go extinct (size 0), if it loses the war, or survive, and be the owner of two demes (size 2), if it wins the war. If the group had not engaged in any contest, it will keep occupying its own deme (size 1). Thus, $\bar{s}$ is the average size of a group, which depends on the probability β of engaging in war and on the likelihood λ_k of winning the war:

$$\bar{s}_k = 1 - \beta + 2\beta\lambda_k \quad (4.3)$$

By the end of intergroup selection stage, the intragroup selection stage begins, in which reproduction takes place in all groups that have survived. We assume generations do not overlap. Hence, individuals die right after giving birth to their offspring. The offspring occupies the group demes (each one with capacity for n individuals).

The reproduction process occurs according to the inner-group fitness of individuals (eq. (4.4), which is the result from interactions between individuals inside their groups. We assume weak selection, so that all individuals receive an equal baseline inner-group fitness, 1, but every altruist bears a cost c , while non-altruists do not have any associated cost.

$$\begin{aligned} v^A &= 1 - c \\ v^N &= 1, \end{aligned} \quad (4.4)$$

The proportion of altruists in the child population for each deme of each group will be the average inner-group fitness of that group members and, hence, will depend on the number of altruists inside the group, k . Thus, on average, each deme will have $\bar{v}_k$ altruists:

$$\bar{v}_k = \frac{kv^A + (n-k)v^N}{n} = 1 - c \frac{k}{n}. \quad (4.5)$$

Since we assume the group size, n , remains constant, the reproduction process can be seen as a n trials sampling without replacement, as if n children were choosing their parents from the previous

¹Although there is some controversy around defining what counts as *war* in a hunter-gatherer society [50, 38, 56, 51], from this point on, we will, for the sake of simplicity, refer to wars and conflicts interchangeably.

generation. In this process, a child can choose an altruist parent with probability $p_k^A = kv^A/n\bar{v}_k$ or a non-altruist parent with probability $p_k^N = 1 - p_k^A$. Hence, a group with k altruists (among n individuals) will become a group of l altruists after the reproduction process with probability $q_{kl} = P(\text{Bin}(n, p_k^A) = l)$, with $\text{Bin}(n, p_k^A)$ representing a random variable following a Binomial distribution with parameters n and p_k^A .

The two selection processes introduced above, war and reproduction, are enclosed in the matrix $S = (S_{kl})_{k,l=0,1,\dots,n}$. Each element S_{kl} of matrix S is the average number of groups of type l created from groups of type k , and is given by eq. (4.6). From the equation, we can see that S_{kl} is the product of the average size of a group with k altruists due to intergroup selection ($\bar{s}_k$) with the probability that a group with k altruists have l altruists due to intragroup selection (q_{kl}).

$$S_{kl} = \bar{s}_k q_{kl} = \bar{s}_k P\left[\text{Bin}\left(n, \frac{kv^A}{n\bar{v}_k}\right) = l\right] \quad (4.6)$$

It is clear that, in our model, individuals' fitness are affected by both processes describe above: the war between groups and the interactions inside groups (inner-group fitness). Since fitness is defined as the number of produced offspring over the number of parents for a given individual type, we can use matrix S to calculate it. Then, after getting the average number of offspring for each type of group, we obtain the following expression for the average fitness of altruists, i.e., the expected value of w_k^A , $E[w_k^A]$:

$$E[w_k^A] = \frac{\sum_{k=0}^n \sum_{l=0}^n l S_{kl} \nu_k}{\sum_{k=0}^n k \nu_k} \quad (4.7)$$

in which ν_k corresponds to the frequency of type k in the population, $k = 1, 2, \dots, n$.

In the last stage of our model, finally, altruists and non-altruists migrate among groups at rate m , indistinctly. As we are restricting ourselves to the weak selection regime, we can consider a simplified version of this process, following Schonmann et al. [83]. This way, we can see migration as a two-stage process, as explained in section 3.2.

Thus, the matrix M can be decomposed as a sum of two other matrices, as shown in eq. (4.8). First, individuals migrate with rate m , so that altruists will stay in its original group with probability $1 - m$ (see eq. (4.9)). And, second, due to the assumption of an infinitely large numbers of groups, and a few number of altruists in the population, migrants arrive at their new groups with the

condition that only groups with non-altruists can receive migrant altruists (eq. (4.10)).

$$M = A + B \quad (4.8)$$

$$A_{k',k''} = P(\text{Bin}(k', 1 - m) = k'') \quad (4.9)$$

$$B_{k',k''} = \begin{cases} = mk', & \text{if } k'' = 1 \\ = 0, & \text{if } k'' \neq 1 \end{cases} \quad (4.10)$$

It is possible to think about this model as a multitype branching process [83], since we are counting the numbers of groups from types 1 to n . If no group survives, this means there is no altruist in the population. Hence, from the theory of multitype branching processes, we find a condition for the viability of altruism, given by:

$$\rho(m) > 1, \quad (4.11)$$

in which $\rho(m)$ is the dominant eigenvalue of matrix R , which is a reduced matrix from the product SM , without the first row and column, as explained in section 3.2.

Furthermore, the stationary distribution of altruists in the population, is given by the left eigenvector, ν , of the matrix R . The existence of a dominant eigenvalue $\rho(m)$, dependent on the migration level m , is guaranteed because matrix R has only non-negative entries, so that we can apply the Perron-Frobenius Theorem [64].

4.2.1 Deriving an analytical condition for the emergence of altruism

In our model, there was no explicit expression for the fitness functions of altruists and non-altruists, but by using the assumptions in our model, it is possible to calculate them from eq. (4.12). Fitness is defined as the number of produced offspring over the number of parents for a given individual type. In our model, we can calculate the average number of offspring for each type of group, so that we can obtain the following expression for the average fitness of altruists, i.e., the expected value of the fitness of altruists, $E[w_k^A]$:

$$E[w_k^A] = \frac{\sum_{k=0}^n \sum_{l=0}^n l S_{kl} \nu_k}{\sum_{k=0}^n k \nu_k}, \quad (4.12)$$

in which ν_k corresponds to the frequency of type k in the population, $k = 1, 2, \dots, n$.

Replacing S_{kl} from eq. (4.6), we have:

$$E[w_k^A] = \frac{\sum_{k=0}^n \nu_k \left(1 + 2\beta\alpha \frac{k}{n}\right) \sum_{l=0}^n l P(\text{Bin}(n, p_k^A) = l)}{\sum_{k=0}^n k \nu_k}, \quad (4.13)$$

in which $p_k^A = \frac{kv^A}{n\bar{v}_k} = \frac{k(1-c)}{n(1-ck/n)}$.

The internal sum is easily calculated, since:

$$\sum_{l=0}^n l P(\text{Bin}(n, p_k^A) = l) = E[\text{Bin}(n, p_k^A) = l] = np_k^A. \quad (4.14)$$

Thus, from eq. (4.13), we have the following expression for $E[w_k^A]$:

$$\begin{aligned} E[w_k^A] &= \frac{\sum_{k=0}^n \nu_k \left(1 + 2\beta\alpha \frac{k}{n}\right) n \frac{k(1-c)}{n(1-ck/n)}}{\sum_{k=0}^n k \nu_k} \\ &= \frac{\sum_{k=0}^n k \nu_k \left(1 + 2\alpha\beta \frac{k}{n}\right) \frac{(1-c)}{(1-ck/n)}}{\sum_{k=0}^n k \nu_k}. \end{aligned} \quad (4.15)$$

But, from the definition of the expectation of a function of a random variable, $E[w_k^A]$ can be written as:

$$E[w_k^A] = \frac{\sum_{k=0}^n k \nu_k w_k^A}{\sum_{k=0}^n k \nu_k}. \quad (4.16)$$

By comparing eqs. (4.15) and (4.16), we can see that the fitness of altruists is actually a simple expression, given by eq. (4.17).

$$w_k^A = \frac{(1-c)(1+2\alpha\beta k/n)}{1-ck/n} \quad (4.17)$$

We use the expressions for the fitness of altruists and non-altruists to derive an analytical expression for the viability of altruism, when altruism is rare in the population and when certain conditions for the parameters are observed.

To find the condition for the viability of altruists, we need to compare the average fitness of altruists with the average fitness of non-altruists. The only way altruists can emerge is if their average fitness is larger than the average fitness of the non-altruists, when there are no altruists. Thus, the condition for the emergence of altruism is given by:

$$E[w_k^A] > E[w_0^N] \quad (4.18)$$

and is equivalent to eq. (4.11).

The expression for the fitness of non-altruists, when there are no altruists, is straight from v^N and is given by eq. (4.19).

$$E[w_0^N] = w_0^N = 1 \quad (4.19)$$

As shown above, the expression for the fitness of altruists is given by eq. (4.17). Thus, the average fitness of altruists can be represented by eq. (4.20).

$$E[w_k^A] = (1 - c)E\left[\frac{1 + 2\alpha\beta k/n}{1 - ck/n}\right] \quad (4.20)$$

We applied a Taylor expansion to the function $\left(\frac{1 + 2\alpha\beta k/n}{1 - ck/n}\right)$ around $c = 0$. After calculating the expectation of the resulting expression, we inserted it in the eq. (4.18), obtaining a condition for the relatedness coefficient R (eq. (4.21), under the assumptions of $n \rightarrow \infty$ and $m \rightarrow 0$.

$$R > \frac{-\alpha\beta(1 - c) + \sqrt{\alpha^2\beta^2(1 - c)^2 + c + 2\alpha\beta(1 + c)c}}{c + 2\alpha\beta(1 + c)} \quad (4.21)$$

From eq. (4.16), we see that $E[w_k^A] = \sum_{k=0}^n kw_k^A$. We can approximate this sum by an integral in the interval $[0, 1]$, by doing a change of variable $x = \frac{k}{n}$, considering we have a sufficiently large n , following [24].

$$E[w_k^A] \approx \int_0^1 w_k^A \text{Beta}(x|1, 2nm) dx \quad (4.22)$$

Since all parameters are between 0 and 1, this integral can be solved in terms of hypergeometric functions ${}_2F_1$, leading to eq. (4.23).

$$E[w_k^A] = (1 - c){}_2F_1(1, 1; 2nm + 1; c) - \frac{2\alpha\beta(-2nm - 1 + 2nm{}_2F_1(1, 1, 2nm + 2))}{2nm + 1} \quad (4.23)$$

4.3 The agent-based simulation

We performed an agent-based simulation based on the description of the model. Analogously to the theoretical model presented previously, in the agent-based simulation, for each period, there are three stages: (i) the intergroup selection stage, in which there can be conflicts between groups; (ii) the intragroup selection stage, in which individuals reproduce; and (iii) the migration stage.

In the first stage, groups can engage in conflicts between each other with some fixed probability, β . This means that with probability β , one group will be paired with another, and with probability $1 - \beta$, it will not be paired with any group.

Let the focal group be a group of type k , while the non-focal group is a group of type j . The focal group will win or lose the contest, with probability λ_{kj} , which depends on the number of altruists k and j , on the group size n and on the benefits of altruists in conflicts, α . This probability is different from the one we used in the mathematical model from the main text, in the sense that now we are able to calculate it using the number of altruists in both groups involved in the contest. In the model of the main text, we used a simplified equation, which assumed the non-focal group had no altruists ($j = 0$). For the simulation, we removed this assumption and used eq. (4.24) that depends on both k and j , following Bowles [17].

$$\lambda_{kj} = \frac{e^{4\alpha\frac{k}{n}}}{e^{4\alpha\frac{k}{n}} + e^{4\alpha\frac{j}{n}}} \quad (4.24)$$

There are three possible outcomes from the intergroup selection stage: (i) the group is paired with another and it wins the contest; or (ii) the group is paired with another and it loses the contest; or (iii) the group is not paired with any group.

Next, in the intragroup selection stage, individuals reproduce according to the inner-group fitness. The inner-group fitness are the same as the ones calculated before, which are derived from a simple

function that is dependent on the type of the individual (altruist or non-altruist) and on the number of altruists inside the group of this individual.

Group reproduction follows fig. 4.2: (i) if the group has won the contest, it reproduces twice (which emulates the occupation of the loser deme); (ii) if the group has lost the contest, it becomes extinct (no reproduction); and (iii) if the group has not engaged in any contest, it reproduces repopulating its own deme. In the agent-based simulation, we still keep the assumption that generations do not overlap.

Lastly, in the migration stage, individuals migrate between groups with some fixed probability m . Group sizes remain constant, even after migration, so that individuals are selected to migrate with probability m , leaving a vacant spot inside their groups, and then, randomly distributed among all the vacant spots left by migrants. Here there is no constraint on the number of altruists of the group to which an altruist will migrate.

In summary, it is possible to see that some simplifications taken in the theoretical model were dropped in the agent-based simulation. These simplifications concerned the low frequency of altruists in the population, so that we expect the agent-based simulation yields a closer description of reality.

4.4 Results

From eq. (4.11), we calculate the critical migration rate necessary for the viability of altruism. The viability condition from eq. (4.11) will be referred as the *eigenvalue method* and it will be compared with our analytical approaches to find an expression for the viability condition. Further, we compare the results from the eigenvalue method with the results from an stochastic simulation of the model to check whether the theoretical analysis was a good approximation of the model. Finally, we show the results for sets of parameters which made sense in the context of hunter-gatherer societies.

4.4.1 Comparing results from analytical derivation

We obtained three different ways for analyzing altruism viability from our model. Although all of them are equivalent to the condition from eq. (4.18) for the spread of altruism, each one of them was built using a different method.

One of them is the *eigenvalue method* [83], described above, in which we calculate the selection and migration matrices and check if the dominant eigenvalue of the reduced matrix from the dot product of these matrices is larger than one (eq. (4.11)). The other condition is given by the eq. (4.18) and requires the calculation of the fitness functions for altruists and non-altruists. To calculate that, we assumed $m \rightarrow 0$ and $n \gg 1$ and we used two different methods: (i) a Taylor expansion around $c = 0$, which we will call *small c*, and (ii) a direct integral calculation using results from the equilibrium distribution of types in the population (*approximation*). We compare these three methods to see if they predict viability of altruism for the same set of parameters.

In fig. 4.3, we show how critical probability of war occurrence β varies in relation to α , which is the influence of altruists in the probability of winning a war, for two different values of migration rates, $m = 0.1$ and $m = 0.5$.

Figure 4.3: Critical probability of war when $c = 0.03$, $n = 26$ for different approaches of getting the viability condition.

From these results, we observe that approximation and small c curves are almost coincident for both values of m . However, the eigenvalue method curve is lower than the other curves, with a considerable difference in fig. 4.3b. This result is expected because, when deriving the analytical results, we assumed $m \rightarrow 0$ and weak selection, which in our model is translated into small values of c , α and β . This difference shows that the eigenvalue method predicts a more optimistic scenario than the analytical approximations.

4.4.2 Using realistic parameter values

In order to link our results with the context of hunter-gatherer societies, we use a range of parameters from the estimates provided by Bowles [16]. We consider the range of cost to be between 0 and

0.08 and the range of probability of conflicts to be between 0 and, approximately, 0.9. The blue area in both panels in fig. 4.4 represents these two ranges.

In this figure, the relation between the critical cost and β , the probability of engaging in war, is depicted for different levels of benefits of altruists in conflicts (α), for two different values of relatedness. In both cases, we see that if α is higher, altruism is viable for a larger set of values of c and β .

Figure 4.4: Critical cost versus probability of war for different levels of influence of altruists in the war outcome when migration is equivalent to $r = 7\%$ and $r = 15\%$ and number of individuals in the group $n = 26$. Blue area represents the set of parameters which can be considered realistic.

Although a higher relatedness helps altruism to be viable in the population, we can see that a high level of intergroup conflicts and of benefits of altruists in conflicts (α) might be able to compensate a lower relatedness, depending on the cost. In the left panel of fig. 4.4, when the relatedness is 7%, for instance, if $\beta = 0.8$ and $\alpha = 0.7$, the cost of being an altruist could be up to slightly more than 0.04.

4.4.3 Comparing simulation results with the eigenvalue method

We compared the results obtained from the eigenvalue method from the stochastic simulation of the model. As mentioned in section 4.3, the simulation description is almost identical to the mathematical model description. The only differences are that we drop the simplifications used to make the model more tractable analytically (namely, the simplification of λ_k , the probability of war, and of the migration process) and we allow for mutations to occur at a rate of 10^{-4} .

In fig. 4.5, simulation results are compared with the results obtained from the eigenvalue method for different values of c ($c = 0.03$ and $c = 0.15$) and α ($\alpha = 0.1$ and $\alpha = 0.3$). Each point corresponds

to the result of running 20 simulations, starting with no altruists in the population. We tracked the frequency of altruists in the populations and we considered that a viable set of parameters is the one in which at least one of the 20 simulations ended up with more than 90% of altruists in the population.

Figure 4.5: Comparison between simulation results and the eigenvalue method for critical migration rate (m_c) versus probability of war (β), when $n = 26$ and for two different values of α : $\alpha = 0.1$ (top figures) and $\alpha = 0.3$ (bottom figures). Simulation parameters: $N = 5000$ (number of groups), $\mu = 0.0001$ (mutation rate) and $\max_{IT} = 10000$ (maximum number of iterations).

These results show that our simulation agrees with the critical migration rate curve obtained from the eigenvalue method, our theoretical predictions from the model.

4.5 Discussion

In this chapter, we have shown that the existence of conflicts between groups could have had an important role in spreading altruism in human populations. Although in our model we did not specify the mechanism through which an altruist benefits his group in a war, it is implied that this is done through self-sacrifice: we believe altruists are more willing to risk themselves by taking an

aggressive approach towards its enemies. In this context, we might say that an altruist could have been the one who had possessed a "warrior gene".

Indeed, the association of a gene (low activity monoamine oxidase A, MAOA-L) with aggressive behavior [26, 60] has been raising attention, from both scientific community and media, to the genetical roots of human violence. This gene has been referred as the "warrior gene", because of its implications for war, and it is also present in Old World monkeys. Its survival in human genome until the present day may indicate it has undergone a positive selection event [39, 6].

Since overly aggressive behavior would be disadvantageous, it is safe to assume some mechanism promoted the balance of different variants of MAOA in the population. One study has linked altruistic punishment with warrior gene presence, by conducting behavioral experiments [62]. Further studies could cast light on the question whether warrior gene and self-sacrifice behavior are also linked.

When building this model, our goal was to investigate the viability of altruism in a setting that included conflicts between groups. We assumed the process of intergroup conflicts could be modeled analogously to group reproduction. Thus, since altruism occurs at the level of individuals and conflicts occur at the level of groups, this clearly can be characterized as a two-level selection process.

Group selection has remained a controversial theme for several decades and many authors have tried to reach a consensus by exposing weakness of one viewpoint while promoting another viewpoint [61, 65, 75, 37]. Although there has been a claim that group selection and inclusive fitness theory always yield the same results [59] and, hence, are equivalent, this is not the only opinion in the field [99, 41].

Another controversial aspect of group selection has been the formal mathematical models used to address it. Many of the models built to explain social evolution are based on the Price equation. However, usually they are not dynamically sufficient, i.e., they offer an explanation based on a static image of the analyzed process. Some researchers have tried to introduce more general frameworks [75, 83, 91, 37], covering one flaw or another pointed by their peers, including the dynamically insufficiency property mentioned above. However, none of these frameworks are widespread yet.

One of the highlights of this chapter was the derivation of a viability condition, when selection is weak, for the emergence of altruism when intergroup conflicts are frequent. This rule represents

the relation between relatedness and the parameters of our model - the influence of altruists in the war outcome, the frequency of conflicts and the migration rate among groups. Our simulation confirmed the results of the theoretical model, which supports the derived analytical conditions, under weak selection.

Chapter 5

Evolving language

In this chapter, we discuss the motivations behind the study of language evolution, and we describe the model we created to investigate the problem of the survival of a dialect, when a powerful standard language exists.

5.1 Related work and motivation

Language diversity has been declining for several decades, which is an example of a more general phenomena: the loss of cultural diversity due to globalization. According to the UNESCO Atlas of the World's Language in Danger [68], many languages are currently in danger of extinction in the world, particularly, in South America and Africa. This situation has no precedents in human history, and it is hard to understand the implications of losing thousands of languages in a short range of time. Since in many cases there are no written records of the endangered or already extinct language, there may be no possibility of recovery from this major cultural diversity loss.

Language is an example of cultural trait, so that the dynamics of language diversity is a good target for studying it by using evolutionary dynamics techniques. Szathmáry and Smith [93] identified the appearance of languages as one of the major transitions in evolution. Language provides an opportunity for cultural evolution, which is also a focus of evolutionary biology (e.g. [28] and [21]). Concerning language, Nowak and Krakauer [71] formalized the process of the emergence of a language, using a type of game known as a signaling game. This explains how words and grammar can evolve from a protolanguage of signals.

Abrams and Strogatz [2] devised a simple model for the competition of two languages. Their model consists of a single differential equation which describes the dynamics of the number of speakers of the two languages, considering there are no bilinguals in the population. They showed one of the two languages will eventually become extinct. More recent works [66, 67] have extended the framework provided by Abrams and Strogatz, by incorporating the possibility of bilinguals arising in the population. Mira et al. [67] have reached the conclusion that when the competing languages are sufficiently similar to each other, it is possible to achieve coexistence, through the emergence of a stable bilingual group of individuals.

To study the factors controlling the language diversity, we study the dynamics of dialects of a single language. We here consider the situation in which the dialect difference is not very extensive: speakers of different dialects can communicate with each other without much difficulty, although different dialects can be identified immediately from differences in accent, terminology, and expressions. For instance, this can be seen in dialect differences in contemporary Japan.

Amano et al. [5] identified the high economic growth of a region as a key driver of language extinction, by associating GDP (Gross Domestic Product) with a rapid decline of language speakers. This result could help to explain the case of dialects, in which the existence of a national standard language usually drives individuals to drop their local dialects. This severe decline of speakers may be related to the fact that individuals prefer to speak more powerful languages. The rise of a dialect as a national language has happened in history many times, exemplified by Tokyo dialect (Japanese), Paris dialect (French) and Athens dialect (Greek) [46]. The standardization process of a language may cause other dialects to be perceived as a lower-class or rural speech [47]. This endangers the survival of different dialects; in the case of Japan, it was believed that all dialects would disappear in some decades [48].

Although the standard language is adopted widely in public situations, many dialects are still used in more intimate communications, inside family or between close friends. Thus, the use of different dialects in different situations may be an important factor to maintain the dialect diversity. Sekiguchi and Nakamaru [86, 87] studied a mathematical model to explain how oblique transmission affects the inconsistency of behavior and attitude, which could be related to the use one language in public while keeping another language restrict to interactions between family and friends.

Spatial structure of the population may also act to maintain the dialect diversity. Axelrod [10] focused on the factors that promote the diversity of social behaviors, finding that when two culturally

different sites interact, stable regions of uniform cultures may appear. This is consistent with the existence of linguistic areas, when each area has speakers with slightly distinct linguistic features that may cause the edges of these linguistic areas to be completely different from each other [29]. Since language is a tool for communication between multiple people, it is quite natural to consider it would be beneficial if people adopted the same accents or expressions and, indeed, after many years of interaction, people tend to adopt the dialect of the local community to which they belong.

To build our model, we focus on the survival of a local dialect when competing against a national standard language, with the latter providing an advantage in the occupational and economic contexts. In the model, we assume that individuals may use different dialects, in response to two different situations: they may use the national language in "public situations" such as in a formal workplace, whilst they may use a local dialect "in private situations" such as in family or close friend meetings. We consider the choice of a dialect is guided by the difference in "attractiveness" of the two dialects, which reflects all the differences in the usefulness of adopting those dialects, including economic and prestige differences. In addition, we consider that the attractiveness of a dialect may change with the relative frequency of the dialect used in the local population. Specifically, we assume that each player follows a stochastic evolutionary process similar to a continuous-time Moran process, in which each player at random times adopt a dialect spoken by members of the local population with the weight of "cultural fitness" of the two dialects. The cultural fitness is the sum of "attractiveness" of the dialect and an additional term that increases with the fraction of the speakers of the dialect, in which the latter indicates conformity of the people. Analysis of the dynamics reveal that the evolutionary outcome critically depends on how conformity works: conformity enhances the effect of differential attractiveness between the local dialect and the standard language if conformity favors only those states in which all speakers use the same dialect (unanimity pressure model); but conformity has no effect at all if it works in proportion to the fraction among peers (peer pressure model).

5.2 Methods

We created a model to address the competition dynamics between a standard language (A) and a local dialect (B). We assume each individual chooses which dialect (A or B) to use in two different situations: public and private. For the sake of clarity, we will use capital letters (A and B) for A

and B dialects when used in public situations and small letters (a and b) for when they are used in private situations.

First, we analyzed the dynamics of the public and private languages, separately. We consider three factors influence the dynamics of the public and private situations: the attractiveness of A and B (π_A and π_B , and π_a and π_b , for the public and private languages, respectively) and the conformity factor (ξ). The preference for a specific language may come from several reasons. In particular, we believe the preference for the public language will be influenced by economical aspects, while the preference for the private language is being affected by the local pride of speaking one language.

The main difference between the public and private language dynamics is that, in the private language dynamics, we considered that individuals are divided in smaller groups of size n . This, in turn, affects the way conformity plays a role in the decision of individuals. We assume that while in the public language dynamics, individuals are willing to conform to a language according to the fraction of speakers of that language in the population, in the private language dynamics, individuals will try to conform according to the fraction of speakers inside the group.

We investigated the effects of conformity in the private language dynamics. We consider individuals may change their language due to conformity by observing the others: the more individuals speaking other language, the larger the effect. Consequently, the dialect with more speakers tends to be favored, disregard of how attractive it is compared to the other dialect.

5.2.1 Public language dynamics

In the public language dynamics, each speaker changes her dialect at random times, with a rate that is determined by the attractiveness of the target dialect and the conformity factor. The conformity factor indicates that the speed of this change increases with the fraction of speakers of the target dialect in the population. Thus, the rate at which a speaker of dialect A changes to a speaker of dialect B is $\pi_B + \xi z_B$, where π_B is the attractiveness of dialect B , ξ is the conformity factor, and z_B is the fraction of speakers of dialect B in the population, with $z_B = 1 - z_A$ fig. 5.1.

Figure 5.1: Schematic figure of public language dynamics. Individuals choose their languages according to their preferences and are also influenced by the number of individuals who speak each language. π_A is preference regarding speaking A, π_B for preference regarding speaking B, ξ is the conformity factor

Analogously, the rate at which a speaker of dialect B becomes a dialect A speaker is $\pi_A + \xi z_A$.

Thus, we can describe the dynamics of z_A by a single equation:

$$\begin{aligned} \frac{dz_A}{dt} &= -(\pi_B + \xi(1 - z_A))z_A + (\pi_A + \xi z_A)(1 - z_A) \\ &= \pi_A - z_A(\pi_A + \pi_B). \end{aligned} \tag{5.1}$$

Calculating the equilibrium fraction, z_A^* , is straightforward from eq. (5.1) and we can see that $z_A^* = \frac{\pi_A}{\pi_A + \pi_B}$. Furthermore, in the public language dynamics eq. (5.1), not only the fraction of A speakers, z_A , is independent of the conformity factor, ξ , but the convergence speed is also independent of ξ .

5.2.2 Private language dynamics with peer pressure model of conformity

In the private language dynamics, individuals form groups within which they interact strongly. For instance, these groups may be composed of family members or close friends. For the sake of simplicity, we here assume that all groups have the same size, n . If groups are pairs ($n = 2$), they are classified in three different types: pairs in which both individuals speak dialect A (aa), pairs in which both individuals speak dialect B (bb), and pairs that include one dialect A speaker and one dialect B speaker (ab).

In general, if each group is composed of n individuals, then, we have $n + 1$ group types in the population. Let z_m , with $m \in \{0, 1, \dots, n\}$, be the fraction of groups with exactly m A speakers and, consequently, $(n - m)$ B speakers. Also, we would like to define z_A to be the fraction of A speakers over all groups with different compositions. Thus, z_A is calculated as the weighted sum of the fractions of the different group types: $z_A = \sum_{m=1}^n \frac{m z_m}{n}$.

We assume that individuals observe their peers to make a decision about which dialect to use. In this sense, this model of introducing the conformity factor can be called *peer pressure model*. We

first analyze the cases $n = 2$ and $n = 3$, when groups are composed of pairs of individuals (three types of pairs: bb , ab , aa) or by triplets of individuals (four types of triplets: bbb , bba , baa , aaa), respectively.

Pairs

Figure 5.2 shows how the peer pressure model works when $n = 2$.

Figure 5.2: Schematic figure of peer pressure model for $n = 2$. Individuals are divided in groups of 2 individuals, who can be labeled a or b , according to the language they use in private. In the peer pressure model, the pressure to conform to one language is higher as the number of speakers of that language increases inside the group. π_a is preference regarding speaking A in private; π_b is the preference regarding speaking B in private; ξ is the conformity factor.

These dynamics between the groups with pairs are described by the following equations:

$$\begin{aligned}\frac{dz_0}{dt} &= -2\pi_a z_0 + (\pi_b + \xi) z_1 \\ \frac{dz_1}{dt} &= -(\pi_a + \pi_b + 2\xi) z_1 + 2\pi_b z_0 + 2\pi_a z_2 \\ \frac{dz_2}{dt} &= -2\pi_b z_2 + (\pi_a + \xi) z_1.\end{aligned}\tag{5.2}$$

Since $z_0 + z_1 + z_2 = 1$, we can calculate the equilibrium fractions of the pairs in the population:

$$\begin{aligned}z_0^* &= \frac{\pi_b (\pi_b + \xi)}{(\pi_a + \pi_b) (\pi_a + \pi_b + \xi)} \\ z_1^* &= \frac{2\pi_a \pi_b}{(\pi_a + \pi_b) (\pi_a + \pi_b + \xi)} \\ z_2^* &= \frac{\pi_a (\pi_a + \xi)}{(\pi_a + \pi_b) (\pi_a + \pi_b + \xi)}.\end{aligned}\tag{5.3}$$

From this, we see that the final fraction of the heterogeneous pair (ab) decreases with ξ in the population. However, by calculating $z_A^* = \frac{z_1^* + 2z_2^*}{2}$, we observe that there is no effect of ξ in the equilibrium fraction of A speakers in the population: $z_A^* = \frac{\pi_a}{\pi_a + \pi_b}$.

Triplets

The set of equations for $n = 3$ is analogous (see fig. 5.3) and we can conduct the same analysis that was done for $n = 2$.

Figure 5.3: Schematic figure of peer pressure model for $n = 3$. Individuals are divided in groups of 3 individuals, who can be labeled a or b , according to the language they use in private. In the peer pressure model, the pressure to conform to one language is higher as the number of speakers of that language increases inside the group. π_a is preference regarding speaking A in private; π_b is the preference regarding speaking B in private; ξ is the conformity factor.

The dynamics of the fractions of the triplets are given by:

$$\begin{aligned}
 \frac{dz_0}{dt} &= -3\pi_a z_0 + (\pi_b + \xi) z_1 \\
 \frac{dz_1}{dt} &= -(2\pi_a + \pi_b + 2\xi) z_1 + 3\pi_a z_0 + (2\pi_b + \xi) z_2 \\
 \frac{dz_2}{dt} &= -(\pi_a + 2\pi_b + 2\xi) z_2 + (2\pi_a + \xi) z_1 + 3\pi_b z_3 \\
 \frac{dz_3}{dt} &= -3\pi_b z_3 + (\pi_a + \xi) z_2,
 \end{aligned} \tag{5.4}$$

with $\sum_{m=0}^n z_m = 1$.

From this system of differential equations (eq. (5.4)), we can calculate the equilibrium fractions z_0^* , z_1^* , z_2^* , and z_3^* :

$$\begin{aligned}
 z_0^* &= \frac{\pi_b (\pi_b + \xi) (2\pi_b + \xi)}{(\pi_a + \pi_b) \left[2(\pi_a + \pi_b)^2 + 3\xi (\pi_a + \pi_b) + \xi^2 \right]} \\
 z_1^* &= \frac{3\pi_a \pi_b (2\pi_b + \xi)}{(\pi_a + \pi_b) \left[2(\pi_a + \pi_b)^2 + 3\xi (\pi_a + \pi_b) + \xi^2 \right]} \\
 z_2^* &= \frac{3\pi_a \pi_b (2\pi_a + \xi)}{(\pi_a + \pi_b) \left[2(\pi_a + \pi_b)^2 + 3\xi (\pi_a + \pi_b) + \xi^2 \right]} \\
 z_3^* &= \frac{\pi_a (\pi_a + \xi) (2\pi_a + \xi)}{(\pi_a + \pi_b) \left[2(\pi_a + \pi_b)^2 + 3\xi (\pi_a + \pi_b) + \xi^2 \right]}.
 \end{aligned} \tag{5.5}$$

We can see from eq. (5.5) that the final fractions of all group types have some dependence on the conformity level ξ . In fact, as observed for $n = 2$, a larger ξ changes the distribution of group types such that the fractions of homogeneous groups (aaa and bbb) increase, while the fractions of heterogeneous groups (abb and aab) decrease. However, the equilibrium fraction z_A^* of A speakers in the population depends only on the attractiveness levels of the standard language A and the

local dialect B in private, π_a and π_b :

$$\begin{aligned}
 z_A^* &= \frac{z_1^* + 2z_2^* + 3z_3^*}{3} \\
 &= \frac{3\pi_a\pi_b(2\pi_b + \xi) + 6\pi_a\pi_b(2\pi_a + \xi) + 3\pi_a(\pi_a + \xi)(2\pi_a + \xi)}{3(\pi_a + \pi_b) \left[2(\pi_a + \pi_b)^2 + 3\xi(\pi_a + \pi_b) + \xi^2 \right]} \\
 &= \frac{\pi_a \left[2(\pi_a + \pi_b)^2 + 3\xi(\pi_a + \pi_b) + \xi^2 \right]}{(\pi_a + \pi_b) \left[2(\pi_a + \pi_b)^2 + 3\xi(\pi_a + \pi_b) + \xi^2 \right]} \\
 &= \frac{\pi_a}{\pi_a + \pi_b}.
 \end{aligned} \tag{5.6}$$

Thus, the equilibrium fractions of standard language or local dialect speakers are independent of the conformity factor, ξ .

General group size

This independence of ξ on the fraction z_A is also observed for other values of n . One simple way to see this result holds is to observe that, in equilibrium, the mean transition frequency from A to B is the same as the mean transition frequency from B to A . The mean conformity effect depends on which group type an individual is part of. Suppose an individual that speaks A is in the group type m , with m A speakers. This means that the conformity effect for this individual to change from A to B is given by $\xi(n-m)/(n-1)$. By contrast, the conformity effect for an individual that speaks B to become an A speaker in this same group would be given by $\xi m/(n-1)$.

More formally, we can generalize the differential equations for any $n \geq 2$, as shown below:

$$\frac{dz_0}{dt} = -n\pi_a z_0 + (\pi_b + \xi) z_1 \tag{5.7a}$$

$$\begin{aligned}
 \frac{dz_j}{dt} &= - \left[(n-j)\pi_a + j\pi_b + \frac{2j(n-j)\xi}{n-1} \right] z_j \\
 &\quad + (n-j+1) \left(\pi_a + \frac{(j-1)\xi}{n-1} \right) z_{j-1} \\
 &\quad + (j+1) \left(\pi_b + \frac{(n-j-1)\xi}{n-1} \right) z_{j+1}
 \end{aligned} \tag{5.7b}$$

$$\frac{dz_n}{dt} = -n\pi_b z_n + (\pi_a + \xi) z_{n-1} \tag{5.7c}$$

with $j = 1, 2, \dots, n-1$.

Thus, we can calculate dz_A/dt by using the definition of z_A , given by $z_A = \frac{1}{n} \sum_{j=1}^n j z_j$:

$$\frac{dz_A}{dt} = \frac{d}{dt} \left(\frac{1}{n} \sum_{j=1}^n j z_j \right) = \frac{1}{n} \sum_{j=1}^n j \frac{dz_j}{dt} \quad (5.8)$$

Replacing the terms from eqs. (5.7b) and (5.7c), we get the following equation:

$$\begin{aligned} \frac{dz_A}{dt} &= \frac{-1}{n} \sum_{j=1}^{n-1} j \left[(n-j) \pi_a + j \pi_b + \frac{2(n-j) j \xi}{n-1} \right] z_j \\ &\quad + \frac{1}{n} \sum_{j=1}^{n-1} j (n-j+1) \left(\pi_a + \frac{(j-1) \xi}{n-1} \right) z_{j-1} \\ &\quad + \frac{1}{n} \sum_{j=1}^{n-1} j (j+1) \left(\pi_b + \frac{(n-j-1) \xi}{n-1} \right) z_{j+1} \\ &\quad - n \pi_b z_n + (\pi_a + \xi) z_{n-1} \end{aligned} \quad (5.9)$$

We can make a simple variable change in the last two summation terms so that they are also written in function of z_j . This change yields:

$$\begin{aligned} \frac{dz_A}{dt} &= \frac{-1}{n} \sum_{j=1}^{n-1} j \left[(n-j) \pi_a + j \pi_b + \frac{2(n-j) j \xi}{n-1} \right] z_j \\ &\quad + \frac{1}{n} \sum_{j=0}^{n-2} (j+1) (n-j) \left(\pi_a + \frac{j \xi}{n-1} \right) z_j \\ &\quad + \frac{1}{n} \sum_{j=2}^n (j-1) j \left(\pi_b + \frac{(n-j) \xi}{n-1} \right) z_j \\ &\quad - n \pi_b z_n + (\pi_a + \xi) z_{n-1} \end{aligned} \quad (5.10)$$

Thus, we have some expression which can be written as:

$$\frac{dz_A}{dt} = \sum_{j=2}^{n-2} a_j z_j + C \quad (5.11)$$

The coefficients a_j for z_j , for $j = 2, 3, \dots, n-2$ can be calculated from eq. (5.10):

$$\begin{aligned} n a_j &= -j (n-j) \pi_a - j^2 \pi_b - \frac{2(n-j) j^2 \xi}{n-1} + (n-j) (j+1) \pi_a \\ &\quad + \frac{(n-j) j (j+1) \xi}{n-1} + (j-1) j \pi_b + \frac{(n-j) j (j-1) \xi}{n-1} \end{aligned} \quad (5.12)$$

Hence, after some algebraic manipulations, we can find that the expression for a_j is given by:

$$a_j = \frac{1}{n} [(n-j) \pi_a - j \pi_b] \quad (5.13)$$

The independent term C is formed from the terms outside the summation term (for $j = 2, 3, \dots, n-2$), cf. eq. (5.11), and can be written as:

$$\begin{aligned} nC = & -[(n-1) \pi_a + \pi_b + 2\xi] z_1 - (n-1) [\pi_a + (n-1) \pi_b + 2\xi] z_{n-1} \\ & + n\pi_a z_0 + 2[(n-1) \pi_a + \xi] z_1 + (n-2)(n-1) \left(\pi_b + \frac{\xi}{n-1} \right) z_{n-1} \\ & + (n-1) n\pi_b z_n - n^2 \pi_b z_n + n(\pi_a + \xi) z_{n-1} \end{aligned} \quad (5.14)$$

Since $z_0 = 1 - \sum_{j=1}^n z_j$, we can group the terms for each z_i , getting the following expression for C :

$$C = \pi_a - (\pi_a + \pi_b) [z_1 + (n-1) z_{n-1} + n z_n] - \pi_a \sum_{j=2}^{n-2} z_j \quad (5.15)$$

By replacing eqs. (5.13) and (5.15) into eq. (5.11), we get:

$$\frac{dz_A}{dt} = - \sum_{j=1}^n \frac{j(\pi_a + \pi_b) z_j}{n} + \pi_a \quad (5.16)$$

Finally, using the definition for z_A , the final expression for dz_A/dt can be written as:

$$\frac{dz_A}{dt} = -(\pi_a + \pi_b) z_A + \pi_a \quad (5.17)$$

From eq. (5.17), we can conclude that for any $n \geq 2$, there is no dependence on ξ in both the equilibrium point and the dynamics of z_A , the average fraction of A speakers in a population divided in groups of n individuals.

5.2.3 Private language dynamics with an alternative model of conformity - the unanimity pressure model

In the former model, we assumed that individuals would change their dialect due to conformity pressure if there is at least one individual speaking another dialect in the group. Human psychology, however, seems to work in another way. One famous study by Asch [8] reported that individuals tend to conform to the others more frequently if nobody else agrees with them.

Following Asch's experimental result, in this alternative model, conformity influences only the transitions to the extreme states (e.g. aab to aaa , or abb to bbb), and we call it the *unanimity pressure model*, described in fig. 5.4 for $n = 3$. When the group size is two, both approaches yield the same set of equations, thus, here we treat the case in which $n = 3$.

Figure 5.4: Schematic figure of unanimity pressure model. Individuals are divided in groups of 3 individuals, who can be labeled a or b , according to the language they use in private. In the unanimity pressure model, there is pressure to conform to one language only if all the other individuals speak that language inside the group. π_a is preference regarding speaking A in private; π_b is the preference regarding speaking B in private; ξ is the conformity factor.

In the unanimity pressure model, the dynamics of the fractions of the triplets are given by:

$$\begin{aligned}
 \frac{dz_0}{dt} &= -3\pi_a z_0 + (\pi_b + \xi) z_1 \\
 \frac{dz_1}{dt} &= -(2\pi_a + \pi_b + \xi) z_1 + 3\pi_a z_0 + 2\pi_b z_2 \\
 \frac{dz_2}{dt} &= -(\pi_a + 2\pi_b + \xi) z_2 + 2\pi_a z_1 + 3\pi_b z_3 \\
 \frac{dz_3}{dt} &= -3\pi_b z_3 + (\pi_a + \xi) z_2.
 \end{aligned} \tag{5.18}$$

Using the assumption that $z_0 + z_1 + z_2 + z_3 = 1$, we can find the equilibrium points, which are given by:

$$\begin{aligned}
 z_0^* &= \frac{\pi_b^2 (\pi_b + \xi)}{(\pi_a + \pi_b)^3 + \xi (\pi_a^2 + \pi_b^2)} \\
 z_1^* &= \frac{3\pi_a \pi_b^2}{(\pi_a + \pi_b)^3 + \xi (\pi_a^2 + \pi_b^2)} \\
 z_2^* &= \frac{3\pi_a^2 \pi_b}{(\pi_a + \pi_b)^3 + \xi (\pi_a^2 + \pi_b^2)} \\
 z_3^* &= \frac{\pi_a^2 (\pi_a + \xi)}{(\pi_a + \pi_b)^3 + \xi (\pi_a^2 + \pi_b^2)}.
 \end{aligned} \tag{5.19}$$

Hence, since $z_A = (z_1 + 2z_2 + 3z_3) / 3$, the equilibrium point of the fraction of A speakers in the population, z_A^* is given by:

$$z_A^* = \frac{\pi_a \left[(\pi_a + \pi_b)^2 + \pi_a \xi \right]}{(\pi_a + \pi_b)^3 + \xi (\pi_a^2 + \pi_b^2)}. \quad (5.20)$$

From the derivative of z_A^* in relation to ξ (eq. (5.21)), we can see that $(\pi_a - \pi_b)$ determines if an increase in ξ will increase or decrease the fraction z_A :

$$\frac{\partial z_A^*}{\partial \xi} = \frac{\pi_a \pi_b (\pi_a - \pi_b) (\pi_a + \pi_b)^2}{\left[(\pi_a + \pi_b)^3 + \xi (\pi_a^2 + \pi_b^2) \right]^2}. \quad (5.21)$$

Thus, a stronger conformity enhances the fraction of the most attractive language.

5.3 Combining the public and private language dynamics

Combining the public and private language dynamics can be done in several ways. Here, we use a strong assumption to make the analysis feasible: we assume that the cost of using two different dialects is infinitely large. This implies that no individual would be willing to speak one dialect in public while speaking another dialect in private, so that there are no mixed individuals (Aa , Ab , Ba or Bb) in the population. Thus, as in the private language dynamics, we have four types of groups in the population, BBB (composed of three individuals Bb), BBA (composed of two individuals Bb and one individual Aa), BAA , AAA .

We are also assuming that there is a parameter λ_{pub} which determines how much the public interactions influence on the choice of the dialect. Analogously, λ_{priv} measures the influence of private interactions on the choice of a dialect, and $\lambda_{priv} = 1 - \lambda_{pub}$, with $\lambda_{pub} \in [0, 1]$. When $\lambda_{pub} = 1$, private interactions are not taken into account and we have a model that represents an only public language dynamics. Conversely, if $\lambda_{priv} = 1$, we have a model that corresponds exactly to the private language dynamics, studied in the previous section.

5.3.1 Combined language dynamics with peer pressure model of conformity

Again, let z_i be the fraction of the group types that have i A speakers in the group. In fig. 5.5, we can see a scheme of how are the transition rates between different z_i , for $i = 0, 1, 2, 3$.

This implies that, for $n = 3$, we have the following set of equations:

$$\begin{aligned}
\frac{dz_0}{dt} &= -3[\lambda_{pub}(\pi_A + \xi z_A) + \lambda_{priv}\pi_a]z_0 + [\lambda_{pub}(\pi_B + \xi(1 - z_A)) + \lambda_{priv}(\pi_b + \xi)]z_1 \\
\frac{dz_1}{dt} &= -[\lambda_{pub}(2\pi_A + \pi_B + \xi(1 + z_A)) + \lambda_{priv}(2\pi_a + \pi_b + 2\xi)]z_1 \\
&\quad + 3[\lambda_{pub}(\pi_A + \xi z_A) + \lambda_{priv}\pi_a]z_0 + 2\left[\lambda_{pub}(\pi_B + \xi(1 - z_A)) + \lambda_{priv}\left(\pi_b + \frac{1}{2}\xi\right)\right]z_2 \\
\frac{dz_2}{dt} &= -[\lambda_{pub}(\pi_A + 2\pi_B + \xi(2 - z_A)) + \lambda_{priv}(\pi_a + 2\pi_b + 2\xi)]z_2 \\
&\quad + 2\left[\lambda_{pub}(\pi_A + \xi z_A) + \lambda_{priv}\left(\pi_a + \frac{1}{2}\xi\right)\right]z_1 + 3[\lambda_{pub}(\pi_B + \xi(1 - z_A)) + \lambda_{priv}\pi_b]z_3 \\
\frac{dz_3}{dt} &= -3[\lambda_{pub}(\pi_B + \xi(1 - z_A)) + \lambda_{priv}\pi_b]z_3 + [\lambda_{pub}(\pi_A + \xi z_A) + \lambda_{priv}(\pi_a + \xi)]z_2,
\end{aligned} \tag{5.22}$$

with $\sum_{m=0}^n z_m = 1$.

Figure 5.5: Schematic figure of the combined dynamics for the peer pressure model. Individuals choose their languages influenced by preferences in both public and private situations and receive pressure to conform in private according to the peer pressure model. λ_{pub} (λ_{priv}) is the weight of public (private) interactions; π_A (π_a) is preference regarding speaking A in public (in private); π_B (π_b) is the preference regarding speaking B in public (in private); ξ is the conformity factor.

By using the previous results of the public situation model and the private situation with the peer pressure model and considering $\lambda_{priv} = 1 - \lambda_{pub}$, we can calculate the equilibrium fraction of z_A :

$$z_A^* = \frac{\lambda_{pub}(\pi_A - \pi_a) + \pi_a}{\lambda_{pub}(\pi_A - \pi_a + \pi_B - \pi_b) + \pi_a + \pi_b}. \tag{5.23}$$

5.3.2 Combined language dynamics with unanimity pressure model of conformity

In the unanimity pressure model, the transition rates between the states are different in the private component, as shown in fig. 5.6, depicting the case in which $n = 3$.

Figure 5.6: Schematic figure of the combined dynamics for the unanimity pressure model. Individuals choose their languages influenced by preferences in both public and private situations and receive pressure to conform in private according to the unanimity pressure model. λ_{pub} (λ_{priv}) is the weight of public (private) interactions; π_A (π_a) is preference regarding speaking A in public (in private); π_B (π_b) is the preference regarding speaking B in public (in private); ξ is the conformity factor.

From these transition rates, we can write the following equations:

$$\begin{aligned}
\frac{dz_0}{dt} &= -3 [\lambda_{pub} (\pi_A + \xi z_A) + \lambda_{priv} \pi_a] z_0 + [\lambda_{pub} (\pi_B + \xi (1 - z_A)) + \lambda_{priv} (\pi_b + \xi)] z_1 \\
\frac{dz_1}{dt} &= - [\lambda_{pub} (2\pi_A + \pi_B + \xi (1 + z_A)) + \lambda_{priv} (2\pi_a + \pi_b + \xi)] z_1 \\
&\quad + 3 [\lambda_{pub} (\pi_A + \xi z_A) + \lambda_{priv} \pi_a] z_0 + 2 [\lambda_{pub} (\pi_B + \xi (1 - z_A)) + \lambda_{priv} \pi_b] z_2 \\
\frac{dz_2}{dt} &= - [\lambda_{pub} (\pi_A + 2\pi_B + \xi (2 - z_A)) + \lambda_{priv} (\pi_a + 2\pi_b + \xi)] z_2 \\
&\quad + 2 [\lambda_{pub} (\pi_A + \xi z_A) + \lambda_{priv} \pi_a] z_1 + 3 [\lambda_{pub} (\pi_B + \xi (1 - z_A)) + \lambda_{priv} \pi_b] z_3 \\
\frac{dz_3}{dt} &= -3 [\lambda_{pub} (\pi_B + \xi (1 - z_A)) + \lambda_{priv} \pi_b] z_3 + [\lambda_{pub} (\pi_A + \xi z_A) + \lambda_{priv} (\pi_a + \xi)] z_2,
\end{aligned} \tag{5.24}$$

with $\sum_{m=0}^n z_m = 1$.

Since it is not feasible to get analytical results for the stable fractions of z_i , $i = 0, 1, 2, 3$, we analyze these equations through numerical simulations as shown in the next section.

5.4 Results

In this section, we show the results of our numerical analyses obtained from the equations of our models. We divided this section in two parts. In the first part, we explain the results related to the peer pressure model. In the second part, we explain the results related to the unanimity pressure model.

5.4.1 Peer pressure model

In fig. 5.7, we see how the distribution varies according to the conformity factor ξ for the private language dynamics in the peer pressure model. We can see that in the left panel (fig. 5.7a), when $\xi = 1$, the distribution is slightly right skewed, since $\pi_b > \pi_a$. However, when the conformity factor is larger, $\xi = 100$, in the right panel (fig. 5.7b), we see that the intermediate heterogeneous group fractions are reduced to almost zero and the groups are distributed in groups of types *aaa* and *bbb*. There are more groups of types *bbb*, since $\pi_b > \pi_a$, and as the difference between π_a and π_b gets larger, the distribution is more skewed for small ξ and the difference between the levels of z_0 and z_3 becomes more pronounced.

Figure 5.7: Equilibrium distribution of group types fractions in equilibrium for the peer pressure model with $n = 3$ for different conformity levels (ξ). z_i corresponds to the fraction of the group type with i A speakers. The dashed pink line represents the equilibrium fraction of A speakers in the population, z_A . Private language dynamics with parameters: $\pi_a = 0.5$, $\pi_b = 0.6$.

The pink line in both panels in fig. 5.7 is the average value, i.e., the average number of A speakers in the population, z_A . This line is exactly at the same height in both panels, since the final fraction of z_A is independent of ξ , as proven in eq. (5.6).

The independence on the conformity factor can also be observed in fig. 5.8. In this figure, we plotted the curves for the final fraction of A speakers in function of π_a , the attractiveness of language A , for two different ξ values. We can see that both curves coincide.

Figure 5.8: Final fraction of A speakers over π_a values for the peer pressure model for fixed π_b . The red line (with 20% of transparency) corresponds to the case in which $\xi = 1$, while the blue line (with 20% of transparency) depicts the situation when $\xi = 100$. Private language dynamics with fixed parameter: $\pi_b = 0.6$.

Using the combined dynamics with the peer pressure model, we compared the trajectories of z_A for different values of λ_{pub} , considering a strong difference in attractiveness in the public situation ($\pi_A = 0.8$ and $\pi_B = 0.3$) and a slight difference in attractiveness in the private situation ($\pi_a = 0.5$ and $\pi_b = 0.6$). We can see from fig. 5.9 how larger values of λ_{pub} increase the final fraction of z_A . This happens for two reasons: (i) the final fraction is independent of ξ ; and (ii) in public situations the standard language A is more attractive than the local dialect B , i.e., $\pi_A > \pi_B$.

Figure 5.9: Trajectories of z_A for different values of λ_{pub} using the peer pressure model. Parameters: $\pi_A = 0.8$, $\pi_B = 0.3$, $\pi_a = 0.5$, $\pi_b = 0.6$, $\xi = 1$.

As previously mentioned, when $\lambda_{pub} = 0$ (red curve in fig. 5.9), the pure private language dynamics is recovered. In contrast to the results with higher levels of λ_{pub} , in the pure private language

dynamics, we observe that, in the equilibrium, the majority of the individuals are B speakers, since public situations do not influence on the choice of the dialect and $\pi_a < \pi_b$ for private situations.

Using the formula given by 5.23, we can calculate the critical λ_{pub} needed in order to have $z_A^* = 0.5$. In fig. 5.10, we show how this critical λ_{pub} changes for different values of π_a when $\pi_b \in \{0.3, 0.5, 0.7\}$. As expected, we can see that as π_a increases, and π_b decreases, $z_A > z_B$ is attained even for low values of λ_{pub} . By contrast, if π_b is larger, then, even with $\lambda_{pub} > 0.5$, it might be possible to get the majority of individuals to speak the dialect B , as long as π_a is sufficiently small.

Figure 5.10: Critical values of λ_{pub} such that the final fraction of z_A is larger or less than 0.5 for different levels of π_b using the peer pressure model. Parameters: $\pi_A = 0.8$, $\pi_B = 0.3$, $\xi = 1$.

5.4.2 Unanimity pressure model

In the unanimity pressure model, there is no conformity effects in the transition rates between heterogeneous groups and we found that ξ influences both the final fractions of the group types and the final average fraction of the group types, z_A . In fig. 5.11, we compare the distribution of group types for the private language dynamics with the unanimity pressure model. The left panel (fig. 5.11a) shows the case in which $\xi = 1$ and the right panel (fig. 5.11b) shows the case in which $\xi = 100$. We can see that when ξ is low, the distribution is skewed towards the group types with more B speakers (since $\pi_b > \pi_a$). On the other hand, when ξ is large, it makes the distribution to be concentrated mostly in the extremes, $aaa(z_3)$ and $bbb(z_0)$. A larger ξ also enhances the effect dictated by π_a and π_b , yielding a lower fraction of z_A (pink line).

Figure 5.11: Equilibrium distribution of group types fractions in equilibrium for the unanimity pressure model with $n = 3$ for different conformity levels (ξ). z_i corresponds to the fraction of the group type with i A speakers. The dashed pink line represents the equilibrium fraction of A speakers in the population, z_A . Private language dynamics with parameters: $\pi_a = 0.5$, $\pi_b = 0.6$.

Figure 5.12: Final fraction of A speakers over π_a values for the unanimity pressure model for fixed π_b . The red line (with 20% of transparency) corresponds to the case in which $\xi = 1$, while the blue line (with 20% of transparency) depicts the situation when $\xi = 10$. Private language dynamics with fixed parameter: $\pi_b = 0.6$.

We can observe more closely the effects of ξ in fig. 5.12. Here, we plotted the final fraction of A speakers, z_A^* , in function of π_a , for a fixed π_b and two different conformity factor values. We see that

when ξ is larger, z_A^* is smaller for $\pi_a < \pi_b$ and is larger for $\pi_a > \pi_b$, which shows the relationship of z_A^* and ξ , as predicted by eq. (5.21).

Besides influencing in the equilibrium fractions of the group types and in the average equilibrium fraction of A speakers, in the unanimity pressure model, different from the peer pressure model, ξ affects the speed of convergence of z_A towards the equilibrium. In fig. 5.13, we compare the private language dynamics with the unanimity pressure model for two different initial conditions at two different levels of the conformity factor ξ . We can see that in spite of different initial conditions, the dynamics of z_A is led to a single equilibrium, for both low and high ξ values. As seen in the previous graph, the final fraction of z_A is dependent on ξ , with a larger ξ leading to a lower z_A^* . It is also clear that the convergence towards the equilibrium is much slower for higher ξ levels, and this phenomena is caused by the time taken for shifting the group distribution to the extremes, which happens when ξ is larger.

Figure 5.13: Fractions of A speakers over time for different initial conditions and different ξ for the unanimity pressure model. The red lines represent the trajectories when the population is initially composed only by group types with only A speakers. The blue lines represent the opposite situation, in which the population is initially composed of group types with only B speakers. Solid lines and dashed lines correspond to the dynamics with $\xi = 1$ and $\xi = 100$, respectively. Private language dynamics with parameters: $\pi_a = 0.5$, $\pi_b = 0.6$.

We can also see this difference in the convergence rates for different ξ for different values of λ_{pub} in fig. 5.14. When ξ is low (top panel, fig. 5.14a), the graph is similar to the one for the peer pressure model, and as λ_{pub} increases, the average fraction of A speakers increase as well, since $\pi_A > \pi_B$. An interesting phenomenon is observed in the bottom panel (fig. 5.14b). Larger values

of ξ allow intermediate values of λ_{pub} (between private and public language dynamics) to increase the final fraction z_A up to higher levels than what is observed in the only public language dynamics ($\lambda_{pub} = 0$).

Figure 5.14: Trajectories of z_A for different values of λ_{pub} using the unanimity pressure model. Parameters: $\pi_A = 0.8$, $\pi_B = 0.3$, $\pi_a = 0.5$, $\pi_b = 0.6$

In fig. 5.15, we show how the fractions z_0 , z_1 , z_2 and z_3 are changing at each time step for different values of λ_{pub} . Here, again, we are comparing two scenarios: one with $\xi = 1$ (top panel, fig. 5.15a) and one with $\xi = 10$ (bottom panel, 5.15b). We see that convergence time is longer when ξ is large, because in this case, there is a flow from groups of type *bbb* to *abb*, and then, to *aab*, and finally to *aaa*. Interestingly, the way the curves are ordered also changes according to ξ . When ξ is low, z_0^* and z_1^* are higher the lower the value of λ_{pub} . The opposite situation occurs for z_2^* and z_3^* , which are higher the larger λ_{pub} is, reflecting the conflict of the attractiveness in public and in private. On the other hand, when $\xi = 10$, there is no such pattern, and we see that for intermediate values of λ_{pub} , the final fractions z_0^* , z_1^* and z_2^* are considerably lower than in the case of $\xi = 1$.

Figure 5.15: Trajectories of z_0 , z_1 , z_2 and z_3 for different values of λ_{pub} using the unanimity pressure model. Parameters: $\pi_A = 0.8$, $\pi_B = 0.3$, $\pi_a = 0.5$, $\pi_b = 0.6$

When ξ is high, different combinations of λ_{pub} and attractiveness of A and B in public and private situations sometimes make the dynamics dependent on the initial condition. One such example is shown in fig. 5.16. For $\xi = 1$ (solid lines), both initial conditions lead to the same final fraction. However, when $\xi = 10$ (dashed lines), we see that low initial z_A produces a low final z_A level and that a high initial z_A produces a high final z_A level.

Figure 5.16: Fractions of A speakers over time for different initial conditions and different ξ for the unanimity pressure model when $\lambda_{pub} = 0.4$ and $\lambda_{priv} = 0.6$. The red lines represent the trajectories when the population is initially composed only by group types with only A speakers. The blue lines represent the opposite situation, in which the population is initially composed of group types with only B speakers. Solid lines and dashed lines correspond to the dynamics with $\xi = 1$ and $\xi = 10$, respectively. Other parameters: $\pi_A = 0.6$, $\pi_B = 0.5$, $\pi_a = 0.2$, $\pi_b = 0.2$.

We compared how this initial condition dependence affects the equilibrium and the result is shown in fig. 5.17. In these figures, the blue points are stable equilibria and the red crosses are the unstable or approximate saddle points, for six different values of λ_{pub} . For intermediate values of λ_{pub} , we see that for values of π_A , in a range close to π_B , there are two stable points. As λ_{pub} decreases or increases, this region with two stable points decreases, so that in the extremes there is only a single equilibrium for any π_A value.

5.5 Discussion

In this chapter, we studied the competition dynamics between a local dialect and a standard language. We created a mathematical model to understand how dialect adoption changes when individuals are allowed to choose dialects for two different situations, public and private. Our results showed that for the case in which the two processes (public and private) are completely separated, what determines if a dialect or a standard language will prevail in each situation is how much

Figure 5.17: Equilibrium points z_A in function of π_A for different λ_{pub} . Blue points represent the stable equilibrium points, while red crosses represent unstable equilibrium points or approximate saddle points. Parameters: $\pi_B = 0.3$, $\pi_a = 0.5$, $\pi_b = 0.6$, $\xi = 10$

individuals are attracted to the dialect or to the standard language. However, conformity may play a role in the private situation, if individuals actions are ruled by the unanimity pressure model, in which individuals are willing to conform only if all the other individuals in the group speak another dialect. In this case, conformity affects both the convergence time and the equilibrium fraction of speakers of each dialect, but only enhances the effect dictated by the attractiveness parameters for the local dialect and the standard language.

We also studied the other extreme case in which the public and private language dynamics are coupled - when no individuals who speak different dialects in public and private are allowed in the population. In this case, for the unanimity pressure model, we found that depending on how much

influence is placed in public/private situations, when conformity is high, some sets of parameters may lead to dynamics that depend on the initial conditions. In particular, it is possible that a local dialect prevail over the standard language, even if more importance is placed on the public situations and if there is higher attractiveness for the standard language in public ($\pi_A > \pi_B$). This occurs when, initially, the majority of speakers use the local dialect in public and the attractiveness for the local dialect, in private, is not lower than the one for the standard language.

One interesting result from our models was that conformity level only affects the stable fractions of dialect speakers in the unanimity pressure setting. In fact, there has been some studies on conformity that supports the unanimity pressure over our peer pressure setting. Asch [8, 9] conducted several experiments to test how individuals conform their opinion to the others' opinions. He designed a simple experiment that consisted of asking individuals to choose among three lines with different sizes which one corresponded to the line shown separately. The three lines were clearly different from one another and it was easy for anyone to spot the correct answer. However, few individuals would always sustain the correct answer when confronted with a majority carrying a different opinion. Testing with the size of majority revealed that: (i) the size of majority only affects the conformity levels until a certain threshold; (ii) having a partner to agree with you (breaking the unanimity) makes individuals more prone to sustain their original opinion. These results could indicate that unanimity pressure is strongly felt by individuals inside a group. It also suggests a more realistic peer pressure setting would be to make individuals more prone to conform only when they are against the majority inside a group.

In China and in Japan, there has been a change in the use of dialects, since the introduction of policies to spread a standard language, around the end of 19th century in Japan [88] and the beginning of 20th century, in China [12]. Although in Japanese language, there exists a subtle difference between what was enforced as the standard language and the common language used nowadays [88], we here consider them to be the same.

Some researchers have focused in tracing the use of different dialects across time. For instance, in the case of Chongqing dialect (China), although its use has declined along the years, it has been kept as the primary language for communication within family and friends [95]. In Japan, one study [47] asked individuals to report their use of the local dialect versus the standard language in different situations, that could be divided into public and private categories. In the results, there

was a common pattern of using frequently the local dialect in private interactions while rarely using it in public interactions.

However, Kansai dialect (from Osaka region) is a singular case: many individuals stated that they used the local dialect frequently even for some situations considered to be public. One possibility for the reason why Kansai dialect is so different from the other dialects could be related to a higher cost associated with the use of different ways of speaking in public and private. This would make the language dynamics more similar to our coupled dynamics, in which individuals always use only one of the languages to communicate.

Also, another Japanese survey [3] asked individuals to report their preferences regarding their dialect and whether they use the dialect in private but the standard language in public. In general, most individuals reported that they do not use the dialect in public and revealed preference toward the local dialect. These results indicate that the attachment to the local dialect is higher for private interactions than for public interactions, in which the standard language dominates.

In this survey, Okinawan dialect stands out, as more than 90% of individuals answered that they liked their dialect. It is interesting to observe that these individuals also like the standard language as well and more than 80% of them said they separate the use of local dialect and standard language or do not use the local dialect at all. One possibility is that this reflect some negative feeling about the use their dialect in public. In fact, the number of Okinawan people who liked their dialect was lower before, but NHK surveys show that since 1978, probably due to campaigns promoting Okinawan dialect, this number has been steadily increasing while the number of people that reported using the local dialect with family and friends has been increasing [3].

This case, in combination with our model results, suggests that if we want one local dialect to persist in the presence of a national standard language, one way to do it is to enforce public policies that promote the local dialect pride, so that we can increase the preference of individuals toward their local dialect.

Chapter 6

Conclusions and perspectives

In this thesis, we studied two social evolution problems: the emergence of altruism when there are intergroup wars, and the persistence of local dialects in the presence of a national standard language. Both problems are inherent of human nature and can be seen as part of the areas of evolution of cooperation and cultural evolution.

In the first problem we tackled the question of emergence. We were concerned with the question of how could altruism emerge in a hunter-gatherers society when there were likely frequent intergroup wars. To investigate that question, we created a mathematical model based on the framework *Two-Level Fisher Wright* under the assumption of weak selection. We created a mathematical model and performed numerical simulations along with an agent-based simulation that confirmed that intergroup wars have possibly played a role in the emergence of human altruism.

While the proposed model is general in its structure, some assumptions could be changed in order to analyze other aspects of the problem. One example is the assumption that β is constant. It would be interesting to analyze what happens when β changes as a function of time, since groups may not always be at war with each other. Another direction could be to incorporate a selection strength parameter explicitly into the model. This could be done by redefining the fitness functions similarly to what was done in chapter 3.

In the second problem, we modeled a different part of evolution, and focused on the persistence of a language. In this case, we were interested not only in finding an explanation to what happens in some local communities which preserve their local dialects, despite having a national language reinforced by a central authority, but also we expected our model could indicate ways to increase

the chances of survival of that local dialects. Our results suggest that if we want one local dialect to persist in the presence of a national standard language, one way to do it is to enforce public policies that promote the local dialect pride, so that we can increase the preference of individuals toward their local dialect.

We can see two interesting further directions for this model. One of them concerns relaxing the assumption of extremely high or low cost of using two languages, so that we can calculate how the dynamics changes when the cost is at an intermediate value and allows individuals to use separate languages at different types of interaction. Another direction would be to think of how to accommodate variations in dialect preference levels along time, since environmental and cultural changes, that could arise either naturally or motivated by public policies, might have some impact in the way dialects are perceived by individuals.

Appendices

Appendix A

Short introduction to evolutionary game theory

The development of the field of Game Theory is usually attributed to von Neumann and Morgenstern, although Borel had also delineated some of the ideas of this theory in early 1920s [104]. Game theory has been used primarily in Economics, and is divided into two subdisciplines: cooperative game theory and non-cooperative game theory. Evolutionary game theory has been developed from the non-cooperative game theory, thus, we will focus on explaining the basic notions of non-cooperative games before introducing the concepts and equations behind evolutionary game theory. The following paragraphs are based on basic concepts of game theory and evolutionary game theory found in [40, 90, 103, 70].

A.1 Basic notions of game theory

In this section, we provide basic notions of game theory, both formally and informally. First, we start from the definition of a game and the different types of strategies a player may adopt. Then, we explain how to analyze a game using the concept of Nash Equilibrium.

In non-cooperative game theory, in order to describe a game, we need three elements: the number of players, possible actions (strategies) for each player and payoffs, which can vary according to what actions were played and who played them. Many daily situations can be modeled as games; common examples include: matching pennies, rock-paper-scissors etc. The key part of a game is

the interaction among players. Thus, not every situation can be modeled as a game. For instance, peg solitaire is not a game in the sense of game theory.

More formally, we define a game as the set (N, S, V) , in which, N is the number of players; S is the space of strategies in the game, $S = \times_{i \in I} S_i$, where $I = \{1, 2, \dots, N\}$ and S_i is the set of k_i strategies of player i ; and V is the matrix containing the payoff values for each interaction. The vector $(s_1, s_2, \dots, s_N)$, which consists of all strategies $s_i \in S_i$ played, for each player $i = 1, 2, \dots, N$, is called a strategy profile. Payoffs matrix V is built by applying a payoffs function $f : (s_1, s_2, \dots, s_N) \rightarrow \mathbb{R}^N$. A simplified template of a game is shown in fig. A.1.

Figure A.1: Necessary elements of a game: a set of strategies, number of players and a payoff function f . For illustrative purposes, here we limit $N = 3$ players, we consider all the players have the same set of strategies and we show a map for only one strategy profile.

Note that when players deterministically choose which strategy to use, we say they are using *pure strategies*. It also would be possible for a player to randomize their strategies. In this case, players choose their strategies according to a probability distribution, leading to an infinite number of combinations. This probability distribution is what is commonly referred as a *mixed strategy*.

Definition A.1. Mixed strategy. Suppose a player i has k_i strategies: $s_1, s_2, \dots, s_{k_i}$, for $s_i \in S$. A mixed strategy is a strategy in which the player i chooses the pure strategy s_{ij} with probability p_{ij} , for $j = 1, 2, \dots, k_i$. Hence, it is a probability distribution over the set of pure strategies, with the following form:

$$\sigma_i = (p_{i1}, p_{i2}, \dots, p_{ik_i})$$

in which $\sum_{j=1}^{k_i} p_{ij} = 1$.

If $p_{ij} = 0$ for a particular j , and $p_{im} = 0$ for every $m \neq j$, then σ_i is a pure strategy. If $p_{ij} > 0, \forall j$, then all strategies are used and σ_i is said to be a completely mixed strategy.

A core concept in game theory is the Nash equilibrium. Informally, a Nash equilibrium is defined as the action from which the players do not have incentive to deviate. This means that if no other information is given, they will stick to the chosen strategy, because individually changing the strategy is not advantageous.

More formally, to define Nash equilibrium, we shall use the concept of **best response**. A best response is defined in relation to a strategy profile $y \in \Theta$. It is the strategy such that no other strategy can give a strictly higher payoff.

Definition A.2. Best response. Let $\pi_i : S \rightarrow \mathbb{R}$ be the payoff function for player i , and let y_{-i} represents the strategy profile of the players other than i . A best response correspondence is given by:

$$\tilde{\beta}_i(y) = \{x_i \in \Delta_i : \pi(x_i, y_{-i}) \geq \pi(z_i, y_{-i}) \quad \forall z_i \in \Delta_i\}. \quad (\text{A.1})$$

The combined best response correspondence is just the cartesian product of all players' correspondences: $\tilde{\beta}(y) = \times_{i \in I} \tilde{\beta}_i(y) \subset \Theta$. From this, the definition of Nash equilibrium follows:

Definition A.3. Nash equilibrium. A strategy profile $\sigma \in \Theta$ is a Nash equilibrium if $\sigma \in \tilde{\beta}(\sigma)$, i.e., σ is a Nash equilibrium if it is a best response to itself.

A.1.1 Public good games

Public goods are ubiquitous in human societies. However, their existence is subject to a problem called the *Tragedy of the Commons* [44]: it is always advantageous to overuse a public resource, hence the public resource may be depleted because of the continuous overuse.

The games classified as public goods games model the interaction of the individuals that share a common resource. In the classical public goods game, n individuals contribute to a common resources pool. They can either cooperate (C), by contributing to the pool a fixed value c , or defect (D), by not contributing. The sum of the individual contributions is then multiplied by a factor $\alpha > 0$ and divided among all individuals in the population. Hence, defectors are free-riders: they get the benefit without cost.

This basic public goods game can be divided into two types, according to how the contribution share is calculated: self-return public goods game (SRPG) or others-only public goods game (OOPG) [90].

Let n be the number of individuals in the population and k be the number of cooperators. In SRPG, only cooperators pay a cost c , but all individuals (C or D) receive an equal share of the total amount (bk/n). In OOPG, the cooperator does not receive her own share, receiving $b(k-1)/(n-1)$, and pays the same cost c . On the other hand, a defector receives payoff $bk/(n-1)$. In both cases, b is the marginal benefit of the game, which is the product of the multiplier α with the cost c , i.e., $b = \alpha c > 0$. These payoffs are represented in table A.1.

Game	v_k^C	v_k^D	Parameters
SRPG	$bk/n - c$	bk/n	$b > 0, c > 0$
OOPG	$b(k-1)/(n-1) - c$	$bk/(n-1)$	$b > 0, c > 0$

Table A.1: Summary table with the payoffs for SRPG and OOPG.

Note that if we denote the benefit in OOPG as B and the benefit in SRPG as b , we can find a relation between them. Given that the cost c is the same for both games, we can see that $B = \frac{(n-1)b}{n}$. Thus, results obtained for OOPG (or conversely, SRPG) can be easily extended to the other public goods game.

In both games, if the population is very large, since the payoff of a defector is always greater than the one of a cooperator, cooperation never wins. One way to make cooperation feasible is to incorporate repeated interactions between the players into the game. There are many ways to do that, including the addition of a punisher type of player who can punish those who free ride, for example. Another simple model has become known as Iterated Public Goods Game (IPG) and is based on the mechanism of reciprocity [49, 22].

IPG can be considered one possible generalization (in the number of players) of TFT (tit-for-tat game), presented in section 2.3.2 of the main text. In the two-players version of TFT, individuals play cooperate in the current round if the other player cooperated in the previous round of the game. In the first round, it is common to assume individuals always cooperate. For the n -players version, we keep the same assumption of cooperativeness in the first round. Then, individuals can be conditional cooperators (C) or defectors (D). Conditional cooperators will cooperate in other rounds by looking at the immediate previous round cooperation level: if the number of cooperators k was larger than a threshold $\theta \geq 0$, then individuals cooperate by paying a cost c and receive a benefit $b(k-1)/(n-1)$. Defectors, on the other hand, always receive a benefit $bk/(n-1)$, without paying any cost.

Note that, as in the two-players version of TFT, the number of rounds is not fixed: at any period, the probability of having a further round is given by $0 < \omega < 1$. This means, on average, any game will have T rounds, with $T = 1/(1 - \omega)$. Also, note that future cooperation depends on the initial number of cooperators in the first round. If, in the first round, $k \leq \theta$, benefit is only produced in that first round. On the other hand, if $k > \theta$ in the first round, then, the expected payoff of a cooperator will be the average number of rounds T multiplied to the net benefit $(-c + b(k - 1)/(n - 1))$ at a single round. Analogously, for a defector, the expected payoff would be $Tbk/(n - 1)$.

Hence, the payoffs for C and D in IPG are given by:

$$v_k^C = \begin{cases} -c + \frac{b(k-1)}{n-1}, & \text{if } k \leq \theta, \\ T \left(-c + \frac{b(k-1)}{n-1} \right), & \text{if } k > \theta, \end{cases} \quad (\text{A.2})$$

$$v_k^D = \begin{cases} \frac{bk}{n-1}, & \text{if } k \leq \theta, \\ T \frac{bk}{n-1}, & \text{if } k > \theta. \end{cases} \quad (\text{A.3})$$

In [49, 22], it was found that cooperators could coexist with defectors if certain conditions are met, for instance, a sufficient large number of cooperators. In particular, [22] investigated the relation between group size and reciprocal cooperation and found that under random formation of groups, the set of conditions which make cooperation attainable in sizable groups is very restricted, which implied further explanations would be necessary to explain cooperation as seen among humans.

Another common public goods game is called *Volunteer's Dilemma* (VD)[32]. This is a modified n-person Prisoner's Dilemma (NPD) in which individuals who are suspects of committing a crime are offered two options: cooperate by volunteering to confess or defect by remaining silent. If none of them volunteers, all of them goes to jail for ten years; if at least one of them volunteers and confess the crime, those who volunteered go to jail for one year, while the others who defected are released with no jail time.

This game has also been called Threshold Public Goods Game (TPG or THR) (e.g. in [27]) or Step-Level Public Goods Game (e.g. in [80]) because of the nature of the payoff functions. In the main text, we adopted the name Threshold Public Goods Game (THR) to refer to this game.

In the general case of VD, we consider benefit is produced whenever the number k of volunteers is at least θ ; for instance, in the above example of the prisoners, $\theta = 1$. Cooperators receive benefit

$b > 0$ (if $k \geq \theta$) and are inflicted a cost $c > 0$ while defectors receive a benefit $b' > 0$ (if $k \geq \theta$), which may be different from the benefit received by cooperators (as, for instance, in the case of VD as described by [32]). The payoffs for C and D , v_k^C and v_k^D , depend on the number k of volunteering individuals and are given by:

$$v_k^C = \begin{cases} -c, & \text{if } k < \theta, \\ -c + b, & \text{if } k \geq \theta, \end{cases} \quad (\text{A.4})$$

$$v_k^D = \begin{cases} 0, & \text{if } k < \theta, \\ b', & \text{if } k \geq \theta. \end{cases} \quad (\text{A.5})$$

An interesting result about VD and public goods game, in general, can be found in [7], which showed VDs, in contrast to the original version of NPD, can lead to equilibrium frequencies in which both C and D coexist. This result is particularly important, since it proved that it is possible to achieve cooperation even in the absence of repeated interactions and regardless of the relatedness level among individuals.

A.2 Basic notions of evolutionary game theory

Evolutionary game theory started from the work of Maynard Smith and George R. Price [92], who published, in 1973, a paper about animal conflict strategies. Inspired by the (unpublished) paper of Price on the advantage of the retaliation strategy in intraspecific conflicts [89], Smith was responsible for the development of the concept of Evolutionary Stable Strategies. According to them, an *evolutionary stable strategy* (ESS) “is a strategy such that, if most of the members of a population adopt it, there is no ‘mutant’ strategy that would give higher reproductive fitness” [92].

While non-cooperative game theory is focused on games at individuals level, evolutionary game theory is concerned with games at population level, so that now strategy profiles $x = (x_1, x_2, \dots, x_n)$ identify the fraction x_i of the population which play each pure-strategy. Furthermore, calculating the payoffs for evolutionary games means averaging the payoffs over all individuals inside the population, i.e., calculating expected payoffs.

Definition A.4. Let $E_x[y]$ be the expected payoff from playing y against x . A strategy a is an ESS if:

$$E_a[a] > E_a[b], \quad \forall b \neq a \quad (\text{A.6})$$

If, however, $E_a[a] = E_a[c]$, for some c , then, a is an ESS if:

$$E_c[a] > E_c[c], \quad (\text{A.7})$$

The ESS is a refinement of a Nash equilibrium, in the sense that it is a strict Nash equilibrium. While the payoff obtained by a Nash equilibrium strategy profile should only be higher or equal to the payoff calculated for other strategy profiles, in the case of an ESS, the relation is strict: the payoff should be higher than all other payoffs.

Peter Taylor and Leo Jonker [97] were the ones responsible for linking a dynamics to the concept of ESS. They proposed a differential equation that allows us to follow the evolution of strategies frequencies in a population. This equation is called *replicator equation*.

Taylor and Jonker assumed a game in which n pure strategies, $s_1, s_2, \dots, s_n$, are available for the individuals of a population. At each period t , the state of the population is given by a vector $(x_1, x_2, \dots, x_n)$, in which each coordinate x_i is the frequency of individuals playing the pure strategy s_i . Also, let f_i be the expected payoff from playing s_i and suppose it represents the incremental effect on an individual's fitness. Then, the replicator equation is given by Eq. A.8.

$$\frac{dx_i}{dt} = x_i(f_i - \phi) \quad (\text{A.8})$$

in which $\phi = \sum_{i=1}^n x_i f_i$ is the average expected payoff.

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