### POLITECNICO DI MILANO

Scuola di Ingegneria Industriale e dell'Informazione Corso di Laurea Magistrale in Ingegneria Informatica Dipartimento di Elettronica, Informazione e Bioingegneria



## Extreme Selection Unifies Evolutionary Game Dynamics in Finite and Infinite Populations

Relatore: Prof. Fabio DERCOLE Correlatore: Prof. Fabio FAGNANI

> Tesi di Laurea di: Cristina VICINI - Matr. 799179

Anno Accademico 2014-2015

A papà, mamma e Chiara

## Ringraziamenti

Desidero qui ringraziare tutte quelle persone che hanno contribuito, in qualche modo, alla realizzazione di questa tesi.

Innanzitutto ringrazio il Professore Fabio Dercole che mi ha costantemente guidato in questo percorso.

Vorrei ringraziare anche il Professore Fabio Fagnani per aver accettato il ruolo di co-relatore ASP.

Un immenso grazie va a mio papà Donato e mia mamma Pinuccia non solo perché mi hanno dato l'opportunità di studiare e mi hanno sempre e comunque sostenuta, ma anche perché con il loro esempio quotidiano mi hanno trasmesso la tenacia per dare sempre il meglio in ogni occasione. Un sentito grazie anche a Chiara, non potevo chiedere una sorella maggiore migliore con cui condividere le gioie e le avversità in questa famiglia.

Un ringraziamento speciale va a Guido, che ormai mi sopporta da un po' di anni ed è sempre pronto ad aiutarmi per qualsiasi cosa e in qualsiasi momento.

Grazie anche a Marco per essere sempre stato premuroso nel rispondere a svariati problemi tecnici.

Grazie alle mie due migliori amiche di sempre, Erika, che è stata così gentile e disponibile per aver svolto una revisione grammaticale e sintattica dell'elaborato e Federica, per il suo impegno nel realizzarmi un abito su misura per questo giorno importante.

# Contents

$\mathbf{A}$	bstra	$\mathbf{ct}$		xiii
Sc	omma	ario		xv
1	Intr	oducti	ion	1
<b>2</b>	Det	ermini	istic Evolutionary Game Dynamics	<b>5</b>
	2.1	The re	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5
	2.2	Select	ion scenarios	7
3	Sto	chastic	e Evolutionary Game Dynamics	9
	3.1	Stocha	astic model for finite populations	9
	3.2	Classi	fication Parameters	11
		3.2.1	Invasion Coefficient	12
		3.2.2	Fixation Probability	13
		3.2.3	Fixation Time	14
	3.3	The N	foran Process with linear fitness	15
		3.3.1	Selection Scenarios	17
		3.3.2	Large N Limit	19
4	Sto	chastic	e dynamics under arbitrary intensity of selection	23
	4.1	The N	for an process with exponential fitness	24
		4.1.1	Selection scenarios	25
		4.1.2	Large N limit	28
		4.1.3	Strong selection	36
		4.1.4	Extreme selection	40
		4.1.5	The deterministic limit	42
	4.2	The p	airwise comparison with Fermi function $\ldots \ldots \ldots \ldots \ldots$	45
		4.2.1	Selection scenarios	46
		4.2.2	Large N limit	48
		4.2.3	Strong selection	49

		4.2.4 Extreme selection	51
		4.2.5 The deterministic limit	52
<b>5</b>	Moi	nte Carlo simulations	55
	5.1	Monte Carlo methods	55
	5.2	Implementation and results	57
6	Con	clusion and future research	63
6 A	Con Cod	nclusion and future research le	63 67
6 A	Con Cod A.1	Iclusion and future research le Code for the Moran process	63 67 67
6 A	Cod A.1 A.2	and future research         le         Code for the Moran process         Code for the pairwise comparison	<ul> <li>63</li> <li>67</li> <li>67</li> <li>70</li> </ul>

# List of Figures

2.1	Summary of the four selection scenarios for a $2x2$ game	8
3.1	Graphical illustration of a one-dimensional Markov chain $\ . \ . \ .$	10
4.1	Vanishing $\mu_i$ for extreme selection and $\Delta P_i > 0$ under the Moran process with exponential fitness	40
4.2	Vanishing $\lambda_i$ for extreme selection and $\Delta P_i < 0$ under the Moran process with exponential fitness	40
4.3	Extreme selection and $\Delta P_i = 0$ under the Moran process with exponential fitness	41
4.4	Markov chain in the scenario of mutual invasion and no fixation under the Moran process with exponential fitness	41
4.5	$\dot{x}$ in the deterministic limit for the Moran process $\ldots \ldots \ldots$	45
4.6	Vanishing $\mu_i$ for extreme selection and $\Delta P_i > 0$ under the pairwise comparison with the Fermi function	51
4.7	Vanishing $\lambda_i$ for extreme selection and $\Delta P_i < 0$ under the pairwise comparison with the Fermi function	51
4.8	Extreme selection and $\Delta P_i = 0$ under the pairwise comparison with the Fermi function	52
4.9	Markov chain in the scenario of mutual invasion and no fixation	52
4 10	is the deterministic limit for the primite comparison	02 52
4.10	$x$ in the deterministic limit for the pairwise comparison $\ldots \ldots \ldots$	53
5.1	Two-dimensional analysis for the Moran process with exponential fitness	59
5.2	Two-dimensional analysis for the pairwise comparison with exponen- tial imitation probability	60
5.3	Numerical simulations for $N = 10$ under the Moran process with exponential fitness	61

5.4	Numerical simulations for $N = 100$ under the Moran process with				
	exponential fitness	61			
5.5	Numerical simulations for $N = 1000$ under the Moran process with				
	exponential fitness	62			

# List of Tables

1.1	Symbols used in this thesis	3
3.1	Graphical notation for the invasion dynamics	13
3.2	Graphical notation for the fixation probabilities	14
3.3	Graphical notation for the fixation time	15
3.4	Selection scenarios under the Moran process with linear fitness	18
3.5	Fixation probabilities and time in the $N \to \infty$ limit for different	
	scenarios	20
3.6	Selection scenarios in the $N \to \infty$ limit under the Moran process	
	with linear fitness	21
4.1	Selection scenarios under the Moran process with exponential fitness	28
4.2	Selection scenarios in the $N \to \infty$ limit under the Moran process	
	with exponential fitness	35
4.3	Selection scenarios with strong selection under the Moran process	
	with exponential fitness	39
4.4	Selection scenarios in the $s \to \infty$ limit under the Moran process with	
	exponential fitness	42
4.5	Selection scenarios under the pairwise comparison with the Fermi	
	function	47
4.6	Selection scenarios in the $N \to \infty$ limit under the pairwise compari-	
	son with the Fermi function	48
4.7	Selection scenarios with strong selection under the pairwise compari-	
	son with the Fermi function	50
4.8	Selection scenarios in the $s \to \infty$ limit under the pairwise comparison	
	and the Fermi function	52

## Abstract

We show that when selection is extreme—the fittest strategy always reproduces or is mimicked—the unequivalence between evolutionary game dynamics in finite and infinite populations resolves, in the sense that the three generic outcomes-dominance, coexistence and mutual exclusion-emerge in well-mixed populations of any size, though the outcome remains size-dependent. We consider the simplest setting of a 2-players-2-strategies symmetric game and the two most common microscopic definitions of strategy spreading— the frequency-dependent Moran process and the imitation process by pairwise comparison—both in the case in which any intensity of selection is allowed. We show that of the seven different invasion and fixation scenarios that are generically possible in finite populations fixation being more or less likely to occur and rapid compared to the neutral game—the three that are possible in large populations are the same three that occur for sufficiently strong selection: (1) invasion and quick fixation of one strategy, (2) mutual invasion and slow fixation of one strategy, (3) no invasion and no fixation. Moreover (and interestingly), in the limit of extreme selection, (2) becomes mutual invasion and no fixation, a case that is not possible for finite intensity of selection, but that better matches the deterministic case of coexistence. In the extreme selection limit, we also derive the large population deterministic limit of the two considered stochastic processes.

## Sommario

In questa tesi affrontiamo tematiche inerenti la teoria dei giochi evolutiva, dove la dinamica della variazione in abbondanza delle strategie all'interno di una popolazione è di interesse primario.

Ripercorriamo inizialmente il modello deterministico della replicator equation per popolazioni infinite e ben mescolate, per poi approfondire l'approccio stocastico in presenza di popolazioni finite. In quest'ultimo contesto consideriamo, tra i vari metodi per definire il meccanismo di diffusione delle strategie, il processo di nascita e morte di Moran e il processo di imitazione tramite confronto a due. Entrambi sono caratterizzati da un parametro che rappresenta l'intensità di selezione, ovvero quanto il successo di una strategia nel gioco sia determinante per renderla più competitiva in termini di diffusione.

Le dinamiche evolutive sono state valutate nel caso di giochi simmetrici a 2giocatori-2-strategie. L'analisi in ambito deterministico è ormai ben nota dalla letteratura e tre sono i generici scenari evolutivi: dominanza, coesistenza e mutua esclusione. In ambito stocastico, invece, la varietà di metodi per modellare la dinamica lascia ancora aperti molti spunti di studio. In questo contesto, gli scenari evolutivi sono distinti in base al fatto che in un generico gioco un singolo giocatore, con strategia diversa rispetto al resto della popolazione, possa, più o meno probabilmente e velocemente in confronto a un individuo in un gioco neutro, diffondere la propria strategia fino a uniformare l'intera popolazione. Allo stato dell'arte, è stato ampiamente studiato il processo di Moran con fitness lineare e per il quale sono stati individuati sette generici scenari di selezione, che si riducono a tre nel caso del limite di grandi popolazioni: (1) invasione e rapido subentro di una strategia (2) mutua invasione e lento subentro di una strategia (3) no invasione e no sostituzione. Tuttavia, questo modello può imporre delle restrizioni sui valori ammissibili dall'intensità di selezione.

In questo lavoro di tesi, consideriamo invece nel dettaglio gli scenari di invasione e sostituzione per altri due meccanismi di diffusione delle strategie: il processo di Moran a fitness esponenziale e il processo di imitazione con la funzione di Fermi, che permettono entrambi al parametro di selezione di assumere un valore arbitrario.

Come primo risultato, verifichiamo che i sette generici scenari di selezione identificati in letteratura sono altrettanto gli unici validi per i processi da noi considerati. In secondo luogo, confermiamo che di questi sette scenari, solo (1)-(3) sono ammissibili in grandi popolazioni. Come terzo e principale risultato di questo lavoro, presentiamo la classificazione per forte intensità di selezione, mostrando che, qualsiasi sia la taglia della popolazione, gli scenari attendibili sono ancora (1)-(3). Inoltre, al limite di selezione estrema, quando la strategia più performante si riproduce sempre o è imitata, (2) diventa mutua invasione e no sostituzione, uno scenario che è vietato per intensità di selezione finita, ma che meglio corrisponde al caso deterministico di coesistenza. La selezione estrema pertanto riunifica la dinamica stocastica con quella deterministica, mostrando tre scenari evolutivi qualitativamente assimilabili. Tuttavia, la dinamica evolutiva di un gioco in ambito stocastico rimane comunque dipendente dalla dimensione della popolazione, ovvero lo scenario ottenuto per forte selezione può cambiare al variare della taglia della popolazione. Proseguiamo l'analisi dei due processi stocastici con la derivazione, nel limite di selezione estrema, del limite deterministico per grandi popolazioni. Per concludere, discutiamo i risultati ottenuti tramite simulazioni Montecarlo su una serie di giochi estratti casualmente e valutati rispetto allo scenario di selezione. L'obiettivo è quello di identificare l'impatto che si ha con valori via via crescenti per la dimensione della popolazione e per l'intensità di selezione. Stimiamo quindi numericamente quanto grandi debbano essere questi parametri affinché i tre scenari ammessi dalle dimostrazioni teoriche siano gli unici a essere osservati, mentre gli altri diventino sempre più rari fino a scomparire.

## Chapter 1

## Introduction

In the realm of classical game theory [1, 2], a game is a formal mathematical description of a strategic situation, where two or more rational agents interact with each other. Every player faces with a set of strategies and it is able to take the optimal decision in order to get the best for himself. This mathematical theory has been widely studied and it has led to interesting developments in economics, politics and computer engineering, mostly in the field of multi-agent systems. Starting with the seventies of the last century, however, both theory and applications were considerably stimulated by problems in evolutionary biology. It turned out that the classical approach was not satisfactory and a radical shift in perspective was required. Therefore, in 1973, Maynard-Smith and Price laid the foundations of evolutionary game theory [3].

First of all, it is necessary to consider populations of agents who interact generation after generation. There is still the concept of game, but the strategy choice of a player does not rely any longer on rationality assumptions, instead it is somewhat related to the individual's genotype or behavior. Under these terms, changes in the strategy mix within the population can be explained either by natural selection, or by mechanisms of imitation and learning. Thus, evolutionary game theory studies the behavior of systems in the long term, identifying which tactics will persist in the population and which ones will be driven out. In absence of mutations, once a strategy has been eliminated, it is not re-introduced. The reproductive success of an individual, which is commonly named *fitness*, depends not only on the relative payoff associated to its strategy in comparison with the others, but also on the composition of the population (i.e. the relative abundance of each strategy, hereafter also called frequency). This feature is usually referred as frequency dependent selection [4]. At the very beginning, the theory has been developed for well-mixed infinite populations. Such systems are traditionally described through non-linear differential equations defined by the replicator equation [5–7]. Given the initial composition of the population, the evolution of the system can be predicted deterministically. Later, the lack of applicability of this model, because of the strict assumption of infinite population, has motivated the introduction of the stochastic game dynamics in finite populations. Here, the structure of the population is modelled as the state of a Markov chain and the transition probabilities define a random walk on the sites of the chain itself. This process may exhibit spite effects, such as the possibility that the stochastic evolutionary process ends up in a configuration consisting of a strategy which had not the highest performance [8].

For the aims of this thesis, only 2-players-2-strategies symmetric games have been considered. In the deterministic background, the evolutionary dynamics can show three generic outcomes: dominance, coexistence and mutual exclusion. The system reaches a stable fixed point in which the population may consist either of a single type or of a mixture of different types. Instead, in finite population, the definition of specific parameters (invasion coefficient, fixation probability and fixation time) induces a wider classification depending on whether strategy A/B invades B/A, A and B fixate or not, and fixation is fast or slow. So far, some results have been proved considering the Moran process with linear fitness [9, 10]. Seven generic scenarios are admissible and some of them do not really match any of the three deterministic outcomes. For example, in a coexistence game, where the replicator dynamics predicts a mixed stable state, fixation could ultimately occur as a stochastic outcome for finite populations and the monomorphic state is shortly reached thanks to the fact that the evolution of the process is very quick. It is therefore interesting to better analyse, both theoretically and numerically, models of stochastic evolutionary game dynamics in order to assess whether it is possible or not to unify the selection scenarios in finite and infinite populations.

The thesis is organized as follows. In Chapter 2, we review the deterministic evolutionary game dynamics with an insight into the replicator equation and its feasible selection outcomes. Next, in Chapter 3, the background theory of stochastic evolutionary game dynamics is introduced. First of all, we discuss the parameters adopted to perform the classification of a game and then we look over the main results on the Moran process with linear fitness, considering also the large N limit. In Chapter 4, we present our theoretical results. In the former part, we show that the same classification presented in Chapter 3 holds also for the Moran process with exponential fitness and for the pairwise comparison with exponential imitation probability. In the second part, we refine the classification, showing that only three classes of selection scenarios are generically possible in large populations and they can be matched with the outcomes of the deterministic dynamics. Furthermore,

as a third and original result, we prove that, in case of strong selection, three evolutionary scenarios survive and are exactly the same as in the framework of large populations. Finally, the limit of extreme selection is examined. In chapter 5, we present the results achieved with Monte Carlo simulations performed in order to evaluate the trade-off between population size and intensity of selection in ruling out some classes. At the end, in Chapter 6, we conclude with a summary of the results that have been obtained.

To finalize this chapter, the following table gives a list of the main symbols used in this thesis.

Symbol	Definition
A, B	Strategies in the population
a,b,c,d	Payoffs
$x_A, x_B$	Frequency of strategy $A$ and $B$ in the population
$f_A, f_B$	Fitness of strategy $A$ and $B$
f	Average fitness of the population
N	Population size
i	Number of individuals of type $A$
$\lambda_i$	Transition probability from state $i$ to state $i + 1$
$\mu_i$	Transition probability from state $i$ to state $i - 1$
$\beta_i$	Ratio of the transition probabilities
$P_{A,i}, P_{B,i}$	Expected payoff for players $A$ and $B$
$\beta_1, \beta_{N-1}$	Invasion coefficients in $i = 1$ and $i = N - 1$
$\rho_{AB}, \rho_{BA}$	Fixation probabilities
$t_{fix}$	Average fixation time
s	Selection strength

Table 1.1: Symbols used in this thesis

### Chapter 2

# Deterministic Evolutionary Game Dynamics

In this work, we particularly focus our attention on the evolutionary dynamics of a symmetric game with two strategies, A and B. The corresponding matrix, which easily describes the game, is

$$\begin{array}{ccc}
A & B \\
A & a & b \\
B & c & d
\end{array}$$

The matrix is simplified by writing only the payoffs of the row player, as those of the column player are obtained by exploiting the symmetry of the game.

From time to time, two individuals of the population meet randomly and play the game, using their strategies. The outcome of each encounter yields payoff values: an A player receives payoff a when playing against another A player and payoff bwhen playing against a B player; similarly, a B player would receive a reward cfrom A and a reward d from the interaction with other Bs. Payoffs a, b, c, d can assume any real value.

### 2.1 The replicator equation

In the traditional deterministic setting, the population is assumed to be infinite and well-mixed, so that an individual can interact equally likely with each other. The evolutionary dynamics points out how the abundance of strategic types changes in the population over continuous time. The most popular description of such a dynamics is based on the replicator equation [5, 7, 11, 12].

Let us assume that the population consists of n different strategies and  $x_i$  is the fraction of individuals which adopt type i. These densities are continuous variables

 $(x_i \in [0, 1])$  and  $\sum_{i=1}^n x_i = 1$ . The reproductive success of an individual is the fitness  $f_i$ and  $f = \sum_{i=1}^n f_i x_i$  is the average fitness of the entire population. The relative spread of a strategy is governed by how well this particular type is doing compared with the population average. When the fitness of a tactic is greater than the average fitness, the frequency of that tactic will increase within the population, otherwise it will decrease. The convex set on which the dynamics takes place is the simplex  $S_n$ and the replicator equation appears as follows:

$$\dot{x}_i = x_i [f_i(x) - f].$$
 (2.1)

This equation implies a non-innovative selection dynamics, because a strategy missing in the initial population remains absent and, consequently, a strategy that is extinct will never reappear. In addition, there is no random drift, this means that the rate of change for each type cannot be interfered by random events, but it only depends on the difference between the fitness of the given type and the average fitness of the whole population. The interpretation of the replicator equation in a genetic setting highlights the relationship of the reproductive rate of a heritable trait with the fitness, while in cultural settings it results from individuals imitating better performing behavior with a probability proportional to the expected increase in the payoff.

Considering the 2-players-2-strategies symmetric game, the replicator equation defines the evolution of the population through a system of two non-linear differential equations on the simplex  $S_2$ :

$$\begin{cases} \dot{x}_A = x_A [f_A(x) - f], \\ \dot{x}_B = x_B [f_B(x) - f], \\ x_A + x_B = 1, \end{cases}$$
(2.2)

where  $x_A$  and  $x_B$  are the fraction of strategists A and B, respectively. A common choice to settle the fitness is to take it equal to the expected payoff of the player from the game, assuming many random encounters with other individuals. For players A and B, fitness is accordingly given by:

$$f_A = ax_A + bx_B, (2.3)$$

$$f_B = cx_A + dx_B,\tag{2.4}$$

while, of course, the average fitness of the population is computed as:

$$f = f_A x_A + f_B x_B. ag{2.5}$$

The system of non-linear differential equations can be analytically solved and the location and stability of fixed points can be straightforwardly determined. The equilibrium points are either on the boundary or in the interior of  $S_2$ , which is actually a line. More specifically, they are are at:

- $x_A = 0$ ,
- $x_A = 1$ ,
- and, possibly,  $x_A = \frac{d-b}{a-b-c+d}$ .

These fixed points are stable or unstable. Given a small perturbation, if it is close to a stable equilibrium, the system returns back to the equilibrium and, on the contrary, if it is near an unstable equilibrium, the system runs away in the direction of the perturbation itself.

### 2.2 Selection scenarios

A selection scenario is an evolutionary outcome of the game and it defines the behavior of the system in the long term. There are three generic outcomes, plus a non-generic result, predicted by the replicator equation for a 2x2 game [8]:

- 1. Dominance. In this scenario, one strategy is always better with respect of the other, so in the end the whole population will consist of players of just one type. If a > c and b > d, then we will observe that A dominates B, A is an evolutionary stable strategy and  $x_A = 1$  is a stable fixed point, while  $x_A = 0$  is unstable. Conversely, if a < c and b < d, we will have the symmetric scenario with the dominance of B.
- 2. Coexistence. Strategies A and B coexist in the stable interior equilibrium at  $x_A = \frac{d-b}{a-b-c+d}$ . The system will converge to this point independently of the original distribution, as long as the population is not made of all As or all Bs. This happens when a < c and b > d. The fixed points at the boundaries are unstable.
- 3. Mutual exclusion. Strategies A and B are bistable. The interior equilibrium point is unstable, while the two monomorphic points are stable and attracting.

This is the case for a > c and b < d. Depending on the initial composition of the population, except for the interior equilibrium, either A or B vanishes, while the other reaches fixation.

4. Neutrality. This is the non-generic scenario. Whenever in the payoff matrix a = c and b = d, then  $f_A = f_B$  for all frequencies. This means that each strategy fares as well as the other no matter its relative distribution in the population. There are infinite stable equilibria, as every couple  $(x_A, x_B)$  is a possible fixed point.

The following figure provides a graphical representation of the selection scenarios.



Figure 2.1: Summary of the four selection scenarios for a 2x2 game. The arrows show the direction of natural selection, black circles are stable equilibria and white circles are unstable equilibria. In the case of neutrality, the dashed line represents infinite stable fixed points.

Even if the replicator equation, as analysed in this context, does not allow to model the impact of mutations, a widespread approach in evolutionary games is to investigate the influence of a new strategy without explicitly modelling its origin. The new tactic is introduced with an initial frequency that is very small and it could be eliminated under the effect of selection, or it could invade the population. We want to stress the fact that, given the payoff matrix of a game, the selection scenario is deterministically inferred: in the presence of dominance of A, an Amutant does invade the resident population of B, but a mutant B does not invade A players (or vice versa for the symmetric situation with the dominance of B), with coexistence, A does invade B and B does invade A, and finally in the mutual exclusion scenario, no mutant can invade the local population.

### Chapter 3

# Stochastic Evolutionary Game Dynamics

Real populations are usually characterized by a finite number of individuals and infrequently occurring strategies face a significant chance of being lost, even if competitively superior. For these reasons, in the past few years, researchers have introduced stochastic evolutionary game dynamics to model also these circumstances.

Here, we consider evolutionary games under frequency dependent selection assuming a finite but constant population size. The analysis is performed over a symmetric 2-players-2-strategies game identified by the square matrix:

$$\begin{array}{ccc}
A & B \\
A & a & b \\
B & c & d
\end{array}$$

Payoffs a, b, c, d can take any real value, although, according to the microscopic mechanism of strategy spreading, there may be restrictions on these values (for example, negative payoffs could not be allowed).

### **3.1** Stochastic model for finite populations

In the stochastic setting, a possible choice is to assume a population well-mixed and composed of N individuals. Out of the total N players, *i* of them follow strategy A and the remaining N - i follow strategy B. The evolutionary process is analysed through discrete time steps and a one-dimensional Markov chain, with state space  $\{0, \ldots, N\}$ , is commonly used to characterize all the possible configurations in which the population can be found. Each state in the chain is identified by means of the number of A strategists, generically represented with *i*. It follows that 0 corresponds to the state with only B players and N with only A players. The system dynamics is stochastic and depicted as a random walk on the sites of the chain. At each time step, the number of A players can either increase by one, remain the same or fall by one. The stochastic process will sooner or later end up in one of the two pure states, all A or all B and, when such an event occurs, the population will remain in that configuration forever, because mutations are not admitted in the model. Therefore, the transition matrix of the Markov process appears like a tri-diagonal matrix. Denoting with  $P_{i,j}$  the transition probability from state i to state j, we adopt, from here and throughout the rest of the thesis, the following notation:

- 
$$P_{i,i+1} = \lambda_i$$
,  
-  $P_{i,i-1} = \mu_i$ ,  
-  $P_{i,i} = 1 - \lambda_i - \mu_i$ .

With the symbols  $\lambda$  and  $\mu$ , we easily identify the probability of a jump from one state to a neighbour in the unit time. The precise form of these transition probabilities reflects the nature of interactions in the system and the specific microscopic mechanism of strategy spreading (see [13, 14] for examples of selection dynamics in finite populations). The Markov chain with its basic quantities is represented as follows:



Figure 3.1: Graphical illustration of a one-dimensional Markov chain for a population of size N. i represents a generic state, 0 can be replaced by B and N by A to emphasize the presence of a uniform population. States 1 and N - 1 are characterized by a single mutant in a population of wild-type players and they are of interest for the analysis of the stochastic dynamics.

Computing the ratio of the hopping probabilities is a way for measuring where the system is more likely to move. For this purpose, we define:

$$\beta_i = \frac{\lambda_i}{\mu_i}.\tag{3.1}$$

This quantity describes the tendency to go from the state i to  $i \pm 1$  depending on whether  $\beta_i \ge 1$ .

To evaluate the reproductive success of a strategy, it is first necessary to take in account the expected payoff of a player in the game. Since self-interactions are excluded and the population is well-mixed (i.e. there is no explicit population structure and each individual can play with all the others), the average payoffs read as follows:

$$P_{A,i} = a \frac{(i-1)}{N-1} + b \frac{(N-i)}{N-1}, \qquad (3.2)$$

$$P_{B,i} = c \frac{i}{N-1} + d \frac{(N-i-1)}{N-1}, \qquad (3.3)$$

for players of type A and B, respectively. It is worth mentioning that the average payoffs depend on the term *i* (which is the number of players of type A in the current population). This highlights the underlying frequency dependent process. As mentioned before, the expected payoffs are key components to shape the success of the propagation of a strategy. Players with higher average payoff will reproduce (or will be imitated) with a higher probability. However, due to the occurrence of a finite number of individuals, stochastic phenomena may affect the expected evolutionary dynamics. For example, a system with a single mutant A in a resident population of (N - 1) B strategists can be characterized by  $\lambda_1 > \mu_1$ , i.e. in the first time step there are better chances to go from the state 1 to the state 2 of the Markov chain than from 1 to 0. Nonetheless, the transition from 1 to the monomorphic state 0 has a finite probability  $\mu_1$  to occur.

### **3.2** Classification Parameters

In order to compare the performance of the strategies in the long term (i.e. identify the selection scenarios) some quantities that can fully characterize the evolutionary process should be defined. In [9, 10, 15], it is mentioned that in finite population the evolutionary stability of a strategy depends on the resistance against the invasion of rare mutations, the probability that a single mutant can overtake the resident population and the timescale of the evolutionary dynamics. Therefore, three classification parameters are properly introduced. Each value should be accordingly compared with a reference target. For the identification of these targets, looking at the population genetics surroundings, the neutral evolution is picked as the benchmark case to classify the strategy's evolutionary success in a generic game. Referring to the distinction made in section 2.2, we have remarked that the neutral game is a non-generic outcome and it satisfies the conditions a = c and b = d in the payoff matrix. However, in the stochastic setting, because of the structure of the formulas (3.2) and (3.3), the previous conditions are not sufficient to observe a

neutral evolution.

**Example 1.** Suppose N = 5 and the following payoff matrix:

$$\begin{array}{ccc}
A & B \\
A & \left( \begin{array}{cc}
10 & 2 \\
10 & 2
\end{array} \right)
\end{array}$$

Because a = c > b = d, it turns out that the expected payoff for a B player is greater than the one of an A player, so strategy B is favoured.

On the opposite, when a = c < b = d, A players will have an advantage. The requirement to meet the neutral game for finite population is instead to have a = b = c = d. Under this constraint on the payoff values,  $\beta_i = 1$  for all *i*, because  $\lambda_i = \mu_i$  regardless the composition of the population. Moreover, the system is totally symmetric as  $\lambda_i = \lambda_{N-i}$  and  $\mu_i = \mu_{N-i}$ . This property makes indifferent the distinction between a mutant A or B, as the value for the classification quantities will be equivalent.

In the following paragraphs, we review the parameters that mathematically express the classification conditions, explaining the reference values holding for the neutral case. Through the capital letters A and B we represent the absorbing states. For each parameter we establish a graphical notation, using arrows, to put next to A and B to make more intuitive the interpretation of the selection outcome. B is written before A to have right/left arrows corresponding to increasing/decreasing i.

#### 3.2.1 Invasion Coefficient

The invasion coefficient evaluates if a single mutant A, or B, has chances to invade the population, namely it has a higher fitness than the resident population. Mathematically, this corresponds to the estimation of the parameter  $\beta_i$ , for i = 1and i = N - 1. Considering the neutral game, where  $\beta_1 = 1$  and  $\beta_{N-1} = 1$ , random fluctuations determine whether the system moves left or right in the chain. Given a generic game, instead, depending on whether  $\beta$  is greater or less than 1, once can say if selection acts to increase or reduce the number of A players. In particular, if  $\beta_1 > 1$ , we can say that selection favors A invading B and, if  $\beta_1 < 1$ , we assert selection opposes A invading B. The opposite holds for the mutant B and esteeming  $\beta_{N-1}$ .

The following graphical notation indicates the preferred direction of the walk at each end of the chain, near the two absorbing states:

$\beta_1 > 1  B \rightarrow$	$\beta_{N-1} > 1 \rightarrow A$
$\beta_1 < 1  B \leftarrow$	$\beta_{N-1} < 1 \leftarrow A$

Table 3.1: Graphical notation for the invasion dynamics.

#### 3.2.2 Fixation Probability

Under stochastic dynamics, a single mutant will sooner or later take over the entire population or go extinct. For this reason, every state of the Markov chain, except 0 and N, is transient. In population genetics, the probability that a mutant overcomes the wild-type players is called fixation probability.

In order to obtain a formula for the fixation probability, the variable  $x_i$  is defined as the likelihood to end up in state i = N when starting in state i. A balance equation can be written for every intermediate state:

$$x_i = \lambda_i x_{i+1} + \mu_i x_{i-1} + (1 - \lambda_i - \mu_i) x_i.$$
(3.4)

Given  $\lambda_i$ ,  $\mu_i > 0$  and the two boundary conditions  $x_0 = 0$  and  $x_N = 1$ , the generic solution is provided by [16, 17]:

$$x_{i} = \frac{1 + \sum_{j=1}^{i-1} \prod_{k=1}^{j} \beta_{k}^{-1}}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \beta_{k}^{-1}}.$$
(3.5)

This approach is valid for all processes that evolve through a sequence of one-step passages. Anyway, it is of primary importance the measure of how likely a single mutant player can overcome the wild-type players. In the situation with a single Aplayer, the probability that he reaches fixation in a population of B is exactly  $x_1$ and we name it  $\rho_{AB}$ . It is given by:

$$\rho_{AB} = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \beta_k^{-1}}.$$
(3.6)

Conversely, the probability that a single B mutant reaches fixation in a population of A individuals is  $1 - x_{N-1}$  and we call it  $\rho_{BA}$ . The formula reads as:

$$\rho_{BA} = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=j}^{N-1} \beta_k}.$$
(3.7)

We observe that the fixation probabilities are complex formulas expressed in terms of the parameter  $\beta$  and they include information on all the transition probabilities of the Markov chain.

A neutral mutant, whether it is of type A or type B, fixates with probability equal to  $\frac{1}{N}$ . This is the reference value for the comparison, so we say that selection favors A replacing B if  $\rho_{AB} > \frac{1}{N}$  and, in contrast, selection opposes A replacing B if  $\rho_{AB} < \frac{1}{N}$ . Symmetrically, similar definitions with  $\rho_{BA}$  hold for the mutant B. Again, we introduce a graphical notation, here with double arrows, to express the fact that a mutant acting in a generic game has or not more chances of fixation with respect of a neutral mutant.

$\rho_{AB} > \frac{1}{N}  B \Rightarrow$	$\rho_{BA} > \frac{1}{N} \iff A$
$\rho_{AB} < \frac{1}{N}  B \Leftarrow$	$\rho_{BA} < \frac{1}{N} \Rightarrow A$

Table 3.2: Graphical notation for the fixation probabilities.

#### 3.2.3 Fixation Time

A single mutant can eventually overcome a resident population. Evaluating also the timescale along which the process takes place provides valuable information about the evolutionary dynamics. The conditional mean time to absorption, hereafter named average fixation time or just fixation time, is the measure of the average number of time steps until the strategy of a mutant wins over the other one and the opposite absorbing state is reached, provided that such an event occurs. This time is measured in elementary time steps and the stochastic dynamics of the system is governed by the following master equation:

$$P_i(t+1) = \lambda_{i-1}P_{i-1}(t) + \mu_{i+1}P_{i+1}(t) + (1-\lambda_i - \mu_i)P_i(t), \qquad (3.8)$$

where  $P_i(t)$  is the probability of finding the system in state *i* at time *t* [18]. Solving recursively the equation, it is possible to determine the expression for the fixation time for a single *A*, or *B*, mutant. In [10], it is shown that, when there is just one different player in a resident population, the mean time to absorption does not depend on the peculiar side the walk starts. For this reason, we can call it generically  $t_{fix}$  and it reads as:

$$t_{fix} = \sum_{n=1}^{N-1} \frac{s_{0,n-1}s_{n,N-1}}{\lambda_n q_n s_{0,N-1}},$$
(3.9)

where 
$$s_{n,m} = \sum_{k=n}^{m} q_k$$
 and  $q_k = \prod_{j=1}^{k} \beta_j^{-1}$  with  $q_0 = 1$ 

The time to reach fixation depends specifically on the microscopic mechanism of strategy spreading. According to the method adopted, also for the neutral game, different reference values subsist. Here, the target value is generically named  $t_{fix-neutral}$ . If a mutant, in a generic game, takes more time to fixate with respect to a mutant in the neutral game, fixation is said to be *slow*, otherwise it is said to be *fast*. We translate this condition in a graphical notation with a double head for the fixation arrow when fixation is fast.

$t_{fix} > t_{fix-neutral}$	$\Rightarrow$
$t_{fix} < t_{fix-neutral}$	$\Rightarrow$

Table 3.3: Graphical notation for the fixation time.

### 3.3 The Moran Process with linear fitness

The Moran process is a common model of population genetics [19]. In evolutionary game theory, it is introduced as a microscopic dynamics for the strategy spreading in finite population and the reproductive success of a strategy is commonly named fitness. The process basically consists of three events that will recur continuously at each time step:

- *selection*: an individual is randomly chosen for reproduction with a probability proportional to its fitness,
- *reproduction*: the selected individual produces one identical offspring that will mature by the next time step,
- *death*: to keep the population size constant, a player taken at random from the population of adult individuals is removed.

This stochastic one-step evolution, which overlaps the Markov chain, can be referred as a birth-death process. The classical Moran process ([19, 20]), however, corresponds to the special case where selection is constant. In evolutionary game theory, instead, it is preferable to examine models under frequency dependent selection. The simplest approach to relate fitness with the distribution of players in the population is to adopt a linear fitness. For players A and B, it is defined as follows:

$$f_{A,i} = 1 - s + sP_{A,i},\tag{3.10}$$

$$f_{B,i} = 1 - s + sP_{B,i}. (3.11)$$

The parameter *s* represents the intensity of selection, or selection strength. It measures how the resulting payoff from the game influences the overall fitness. The reproductive success appears then as a convex combination of the background fitness, which is usually set to 1, and the average payoff of the player. Here, the intensity of selection can possibly range between 0 and 1 and we can distinguish three situations:

- s = 0: neutral drift, this means that updating is mostly casual due to random fluctuations through the states of the Markov chain;
- 0 < s < 1: expected payoff and drift contribute both to the evolutionary dynamics;
- s = 1: only the expected payoff determines fitness.

In [9, 10], a thorough analysis of the selection dynamics, subordinate to the Moran process with this definition for the fitness, has been carried out. The authors considered the special case with s = 1, limiting the payoffs of the game to positive values, in order to be sure to obtain a positive fitness. We will deepen their results in the next sections. Now, we conclude this part with the specific expressions for the transition probabilities for this mechanism of strategy spreading. The probability of adding an A-offspring is:

$$\lambda_i = \frac{i f_{A,i}}{i f_{A,i} + (N-i) f_{B,i}} \frac{N-i}{N}, \qquad (3.12)$$

while the probability of adding a B-offspring is:

$$\mu_i = \frac{(N-i)f_{B,i}}{if_{A,i} + (N-i)f_{B,i}} \frac{i}{N}.$$
(3.13)

Obviously,  $1 - \lambda_i - \mu_i$  is the probability that the population configuration does not change, because the newborn replaces a player of the same type. Finally, in [10], it is easily shown that under the Moran process the fixation probability of a single neutral mutant, either of type A or B, is 1/N and its fixation time is N(N-1).

#### 3.3.1 Selection Scenarios

The parameters introduced in section 3.2 are used for assessing the behaviour of the system under a stochastic dynamics. There are ideally 32 combinations depending on whether A/B invades B/A, A and B fixate or not, and fixation is fast or slow.

In [9], three theorems exclude some arrangements. We briefly retrace them.

**Theorem 3.1.** If  $\beta_1 > 1$  and  $\beta_{N-1} > 1$ , then  $\rho_{BA} < 1/N < \rho_{AB}$ .

Literally, this means that if selection favors A invading B, but opposes B invading A, then selection must favor A replacing B and oppose B replacing A. In this scenario, A dominates B. Symmetrically, when  $\beta_1 < 1$  and  $\beta_{N-1} < 1$ , then  $\rho_{AB} < 1/N < \rho_{BA}$  and B dominates A. Regarding the graphical notation, if the single arrows of the invasion coefficients point to a certain direction (i.e.  $B \rightarrow A$ , or  $B \leftarrow A$ ), then the double arrows of the fixation probabilities must point in the same direction (meaning,  $B \rightrightarrows A$ , or  $B \leftarrow A$ ).

**Theorem 3.2.** If  $\rho_{AB} < 1/N$  and  $\rho_{BA} < 1/N$ , then  $\beta_1 < 1$  and  $\beta_{N-1} > 1$ .

Under these terms, if selection opposes A replacing B and B replacing A, then selection must oppose A invading B and B invading A as well. This is the case where selection opposes changes. It cannot happen that fixation is possible but the selection does not favor the invasion. So, it is not admissible  $B \rightleftharpoons \rightleftharpoons A$ .

**Theorem 3.3.** If  $\rho_{AB} > 1/N$  and  $\rho_{BA} > 1/N$ , then  $\beta_1 > 1$  and  $\beta_{N-1} < 1$ .

The theorem states that if selection favors A and B replacing each other, then selection must favor A and B invading each other as well. This is the case where selection favors changes. Therefore, it is forbidden the scenario of mutual invasion and no fixation, represented as  $B \rightleftharpoons A$ .

In [10], two conjectures related to the fixation time are proposed for finite population. These hypothesis are based on a numerical evaluation of the equation (3.9) for numerous ( $\sim 50000$ ) random simulations of 2-players-2-strategies games and they allow to rule out some selection scenarios. According to their results:

- 1. If  $\rho_{AB} > \frac{1}{N}$  and  $\rho_{BA} > \frac{1}{N}$ , then  $t_{fix} \ge t_{fix-neutral}$ . So, if mutual invasion and mutual fixation are favored, then fixation is experienced to be slow.
- 2. If  $\beta_1 < 1$  and  $\beta_{N-1} > 1$ , then  $t_{fix} \leq t_{fix-neutral}$ . Thus, if selection opposes mutual invasion then fixation is fast, independently whether the selection favors fixation or not.

Based on the three theorems and the two conjectures, it is hence possible to reduce the casuistries for the dynamics and the speed of the evolutionary process. Only 12 qualitatively different types of game remain and the number of classes drops to 7 if symmetric situations under the interchange of A and B are grouped together. These selection scenarios actually define generic outcomes. With the exception of the neutral game, we do not consider here, and in the following, the other possible non-generic scenarios, where at least one of the five indicators ( $\beta_1$ ,  $\beta_{N-1}$ ,  $\rho_{AB}$ ,  $\rho_{BA}$ ,  $t_{fix}$ ) is equal to the corresponding reference value of the neutral game.

Below, we list the admissible selection scenarios in finite populations, for the Moran process with linear fitness.

Class	Symbol	Invasion and fixation scenario	
1.A	$B \xrightarrow{\Rightarrow} \overrightarrow{\Rightarrow} A$	Invasion and quick fixation of one strategy	
1.B	$B \overleftarrow{\leftarrow} A$		
2.A	$B \xrightarrow{\rightarrow} \leftarrow A$	Mutual invasion and slow fixation of one strategy	
2.B	$B \overleftarrow{\leftarrow} A$		
3	$B \xleftarrow{\longrightarrow} A$	No invasion and no (quick) fixation	
4.A	$B \overrightarrow{\Rightarrow} \overrightarrow{A}$	Invasion and slow fixation of one strategy	
4.B	$B \overleftarrow{=} A$		
5.A	$B \xrightarrow{\Longrightarrow} \overleftarrow{\Rightarrow} A$	Mutual invasion and quick fixation of one strategy	
5.B	$B \xrightarrow{\leftarrow} A$		
6	$B \xrightarrow{\rightarrow} \overleftarrow{\leftarrow} A$	Mutual invasion and slow fixation of both strategies	
7.A	$B \stackrel{\longleftrightarrow}{\Rightarrow\!\!\!\Rightarrow} A$	No invasion and quick fixation of one strategy	
7. <i>B</i>	$B \overleftarrow{\Leftarrow} A$		

Table 3.4: Selection scenarios under the Moran process with linear fitness.

The stochastic dynamics appears much more diversified than the deterministic one. Looking carefully at the selection scenarios in the table, however, we recover sometimes well-known outcomes. For example, it is still possible that a strategy dominates the other, even if before reaching fixation it may take more or less time. Other scenarios instead are totally new. Considering for example the case 7.A (or symmetrically the 7.B), selection does not favor the invasion of the mutant, anyway due to the fact that the process is stochastic, it turns out that it is very likely the fixation of the mutant in the population. Another unexpected result contemplates the mutual invasion but, in the end, one of the two strategies is favourite and, eventually, it will fixate. As a final remark, we point out that the selection scenario that occurs in a given game (i.e. for a given payoff matrix) typically depends on the size N of the population. In [9], some numerical examples are reported to attest the fact that the evolution in finite population is size-dependent and therefore best players will not be necessarily able to overcome the entire population. Let consider one of them.

**Example 2.** The payoff matrix of the game is:

$$\begin{array}{ccc}
A & B \\
A & \left( \begin{array}{ccc}
3.1 & 1.02 \\
3 & 1 \end{array} \right)
\end{array}$$

Because a > c and b > d, strategy A is the best reply to both A and B. In fact, the deterministic replicator dynamics predicts the dominance of the A strategy. Instead, surprisingly, in finite populations we can observe a variety of selection scenarios depending on the size N. It is shown that for  $N \leq 21$ , selection favors just the invasion and the fixation of a mutant B and the corresponding scenario is therefore  $B \Leftarrow A$ . For an intermediate range of N values, different scenarios, where selection opposes mutual invasion but can favor one of the two strategies, succeed one another. In particular, for  $21 < N \leq 30$  the scenario is  $B \Leftarrow A$ . for  $30 < N \leq 50$  it is  $B \Leftarrow A$  and finally, for  $50 < N \leq 101$  it becomes  $B \clubsuit A$ . Then, only for  $N \geq 102$ , strategy A has good chances to dominate and, indeed, the expected outcome is  $B \nRightarrow A$ .

#### 3.3.2 Large N Limit

In this section, we briefly review the results for the large N limit under the Moran process with linear fitness (for a deeper analysis see [10]). The main idea is to derive the asymptotic approximation of the basic terms in the fixation probability and fixation time formulas (3.6, 3.7, 3.9). First, let define  $q_k$ :

$$q_k = \prod_{i=1}^k \beta_i^{-1} = \exp(\sum_{i=1}^k \ln \beta_i^{-1}).$$
(3.14)

Considering a large N, the above sum can be written as an integral:

$$N \int_0^y dx \, \ln \frac{x(c-d) + d}{x(a-b) + b},\tag{3.15}$$

with  $y = \frac{k}{N}$ . The evaluation of that integral leads to the following result:

$$\tilde{q}(y) = (d/b)^y \frac{(1+y^{\frac{c-d}{d}})^{y+d/(c-d)}}{(1+y^{\frac{a-b}{b}})^{y+b/(a-b)}},$$
(3.16)

and it holds:

$$q_k = \tilde{q}(y)^N. \tag{3.17}$$

In the  $N \to \infty$  limit, it is possible to approximate  $q_k$  at the ends of the chain as it follows:

$$q_k \approx \begin{cases} (\frac{d}{b})^k & , k \ll N, \\ \tilde{q}(1)^N (\frac{a}{c})^{N-k} & , N-k \ll N. \end{cases}$$
(3.18)

In order to calculate the fixation probabilities and the fixation time when  $N \to \infty$ , only the terms around the maximum of  $\tilde{q}(y)$  are relevant. According to the relative value of the payoffs a, b, c, d, this maximum can possibly be in correspondence of:

• y = 0,

• 
$$y = 1$$
,

•  $y = y^* = \frac{d-b}{a-b-c+d}$ .

As in the replicator equation description, the relevant parameters in the large N limit behavior are a - c and b - d. In table 3.5, an exhaustive summary of the results obtained by the authors is reported.

Scenario	Symbol	Conditions	$\rho_{AB}$	$ ho_{BA}$	$t_{fix}$
		a > c, b > d:			
1.A	$B \xrightarrow{\longrightarrow} A$	$\tilde{q}(1) < 1$	$1 - \frac{d}{b}$	$\sim \tilde{q}(1)^N$	$\sim N \ln N$
		a < c, b < d:			
1.B	$B \overleftarrow{\leftarrow} A$	$\tilde{q}(1) > 1$	$\sim \tilde{q}(1)^{-N}$	$1 - \frac{a}{c}$	$\sim N \ln N$
		a < c, b > d:			
2.A	$B \xrightarrow{\Longrightarrow} A$	$q^* < \tilde{q}(1) < 1$	$1 - \frac{d}{b}$	$\sim \tilde{q}(1)^N$	$\sim (rac{\tilde{q}(1)}{q^*})^N$
2.B	$B \rightleftharpoons \overleftarrow{\leftarrow} A$	$q^* < 1 < \tilde{q}(1)$	$\sim \tilde{q}(1)^{-N}$	$1 - \frac{a}{c}$	$\sim (\frac{1}{q^*})^N$
		a > c, b < d:			
3	$B \overleftrightarrow{\Rightarrow} A$	$1 < \tilde{q}(1) < q^*$	$\sim (\frac{1}{q^*})^N$	$\sim (\frac{\tilde{q}(1)}{q^*})^N$	$\sim N \ln N$

Table 3.5: Fixation probabilities and times in the  $N \to \infty$  limit for different scenarios.  $q^*$  is the evaluation of  $\tilde{q}$  in  $y = y^*$ .

Of the seven scenarios that are generically possible in finite populations, the condition of N large excludes some of them, refining the classification to just three
outcomes. The dynamics of this stochastic process is predicted through the same assessment of the values in the payoff matrix as well as for infinite population under the replicator equation. Nevertheless, the upshot is slightly different. In fact, we can properly match the scenario 1.A and 1.B with the deterministic dominance of A or B, and the scenario 3 with the mutual exclusion. On the contrary, scenarios 2.A and 2.B predict a mutual invasion, but in the end the fixation of one of the two strategy occurs, even if this fixation is slow. This result does not well match the coexistence deterministic case, which instead expects a system with a mix of the two strategies.

According to the graphical notation, the admitted outcomes are shown in the next table:

Class	Symbol	Invasion and fixation scenario	
1.A	$B \overrightarrow{\Rightarrow} \overrightarrow{\Rightarrow} A$	Invasion and quick fixation of one strategy	
1.B	$B \overleftarrow{\leftarrow} A$		
2.A	$B \xrightarrow{\rightarrow}  A$	Mutual invasion and slow fixation of one strategy	
2.B	$B \overleftarrow{\leftarrow} A$		
3	$B \overleftarrow{\Leftarrow} A$	No invasion and no (quick) fixation	

Table 3.6: Selection scenarios in the  $N \to \infty$  limit under the Moran process with linear fitness.

# Chapter 4

# Stochastic dynamics under arbitrary intensity of selection

In order to specify how the strategies spread within a finite population, a microscopic mechanism is required. At the state of the art, two different main approaches have been defined: the fitness-based and the pairwise comparison. Often, the former method is adopted when problems in evolutionary biology are handled, while the second is more associated to phenomena of cultural evolution and imitation learning related to the propagation of behaviours and ideas. In both typologies, the relative influence of the expected payoff in determining the evolutionary success of a strategy is controlled by an external parameter, the so called intensity of selection, again denoted by s. When s = 0, the neutral evolution is recovered, even if the general condition on the payoffs in the matrix (a = b = c = d) is not satisfied.

In this chapter, we extend the theory of stochastic evolutionary game dynamics for 2-players-2-strategies games discussing our theoretical results. We present in detail two evolutionary mechanisms: the Moran process with exponential fitness and the pairwise comparison with the Fermi function. Both are structured so that the parameter s can assume any positive real value and the payoffs in the matrix have no restrictions. For each method we dedicate a specific section organized in this way: after a brief description of the process, we illustrate the selection scenarios that are generically possible. Then, we derive the behavior of the system for the large N limit. Furthermore, as a more relevant result, we establish the selection scenarios under strong and extreme selection, when the parameter s is large and tends to infinity. Finally, we conclude the analysis with the derivation of the deterministic limit under extreme selection.

### 4.1 The Moran process with exponential fitness

As introduced in section 3.3, the Moran process is structured in three phases: selection, reproduction and death. After this primary definition, a mapping from expected payoffs to fitnesses should be defined. Of course, many choices are possible and we have already explained the option with the linear fitness and the particular case of s = 1. This method has been deeply investigated also in [21] for  $s \ll 1$ , when the selection strength is very small, namely weak selection, and consequently the resulting payoff from the game provides only small perturbations on the overall fitness of a player. Anyway, this approach, although it enables an analytical description of the evolutionary process, has some weaknesses. By definition the fitness has to be positive, but if negative payoffs are present in the matrix of the game, then it becomes necessary to restrict to certain values the intensity of selection and put a maximum value  $s_{max}$ . With this limitation, it could not be possible any more to explore the case of strong selection, when fitness tends to equal the average payoff for  $s \to 1$ . This drawback can be overcome if fitness is defined as an exponential function of the payoff. This mapping is introduced in [22] and allows the selection intensity to take any positive real value. The Moran process with exponential fitness turns out to be a very general model, not only because theoretical results can be obtained for any intensity of selection, but also because payoffs have no limitations in the values they assume.

In this section, we are going to show our analytical results for this mechanism of strategy spreading. Specifically, the fitness of players A and B is defined as:

$$f_{A,i} = \exp(sP_{A,i}),\tag{4.1}$$

$$f_{B,i} = \exp(sP_{B,i}),\tag{4.2}$$

where  $P_{A,i}$  and  $P_{B,i}$  are the expected payoffs settled in (3.2), (3.3). The transition probabilities appear like:

$$\lambda_{i} = \frac{i \exp(sP_{A,i})}{i \exp(sP_{A,i}) + (N-i) \exp(sP_{B,i})} \frac{N-i}{N},$$
(4.3)

$$\mu_i = \frac{(N-i)\exp(sP_{B,i})}{i\exp(sP_{A,i}) + (N-i)\exp(sP_{B,i})}\frac{i}{N}.$$
(4.4)

The relevant parameter  $\beta_i$ , defined in formula (3.1), can be simplified as follows:

$$\beta_{i} = \frac{\exp(sP_{A,i})}{\exp(sP_{B,i})} = \exp(s(P_{A,i} - P_{B,i})) = \exp(s\Delta P_{i}),$$
(4.5)

where the difference between the average payoffs of two different players, given the configuration of the population, is shorten with  $\Delta P_i$ .

Lastly, to conclude the description of this process, we remind that for a neutral game the fixation probability of a single mutant, either of type A or B, is 1/N, while the fixation time is N(N-1).

#### 4.1.1 Selection scenarios

In order to identify the selection scenarios that are generically possible in finite populations under the Moran process with exponential fitness, we rely on the logic of the proofs of theorems 3.1, 3.2 and 3.3 in Appendix of [9].

The payoff difference  $\Delta P_i$  can be expressed in terms of  $\Delta P_1$  and  $\Delta P_{N-1}$ :

$$\Delta P_i = \frac{(N-1-i)\Delta P_1 + (i-1)\Delta P_{N-1}}{N-2},$$
(4.6)

for i = 1, ..., N - 1. Considering that the expected payoffs are linear with respect to *i* and the exponential function is an increasing function, the values of the ratio  $\beta_i$  are monotonically increasing, constant or decreasing depending on whether  $\Delta P_{N-1} \gtrless \Delta P_1$ . Thanks to the properties of the exponential function, we rewrite, for our purposes, the formulas for the fixation probabilities in this way:

$$\frac{1}{\rho_{AB}} - 1 = \sum_{i=1}^{N-1} \prod_{k=1}^{i} \beta_k^{-1} = \sum_{i=1}^{N-1} \exp(-sP_{1,i}) = s_1, \qquad (4.7)$$

$$\frac{1}{\rho_{BA}} - 1 = \sum_{i=1}^{N-1} \prod_{k=i}^{N-1} \beta_k = \sum_{i=1}^{N-1} \exp(sP_{N-i,N-1}) = s_2.$$
(4.8)

The notations  $P_{1,i}$  and  $P_{N-i,N-1}$  express the sum of the payoff differences and they can be translated in terms of the payoffs in the game matrix as follows:

$$P_{1,i} = \sum_{k=1}^{i} \Delta P_k$$

$$= \frac{i}{2(N-1)} (2(b-d)(N-1) + i(a-b-c+d) - (a-b+c-d)),$$
(4.9)

$$P_{N-i,N-1} = \sum_{k=1}^{i} \Delta P_{N-k}$$
  
=  $\frac{i}{2(N-1)} (2(a-c)(N-1) - i(a-b-c+d) - (a-b+c-d)).$   
(4.10)

It is evident that whenever  $P_{1,i}$  is positive, since it appears as an argument of the exponential function and it is multiplied by -s, it produces an addendum lower than 1 in the sum  $s_1$ ; whereas when it is negative, it produces an addendum greater than 1. The opposite for  $P_{N-i,N-1}$ , because it is multiplied by +s. Finally, given the above formulas, instead of comparing the fixation probabilities of a generic game with the benchmark 1/N, we compare  $s_1$  and  $s_2$  with N - 1.

After these preliminaries, we can now list the theorems with their proofs.

**Theorem 4.1.** If  $\beta_1 > 1$  and  $\beta_{N-1} > 1$ , then  $\rho_{BA} < 1/N < \rho_{AB}$ .

Proof.  $\beta_1 > 1$  and  $\beta_{N-1} > 1$  correspond to  $\Delta P_1 > 0$  and  $\Delta P_{N-1} > 0$ , this implies that  $\Delta P_i > 0$  for all i = 1, ..., N - 1. Therefore, the N - 1 elements in the sum  $s_1$ are lower than 1 (and positive). On the contrary, in the sum  $s_2$  they are greater than 1. That is  $s_1 < N - 1 < s_2$ , from which it follows that  $\rho_{BA} < 1/N < \rho_{AB}$ .  $\Box$ 

 $B \stackrel{\rightarrow}{\Rightarrow} \stackrel{\rightarrow}{\Rightarrow} A$  is the only option when selection favors the invasion of A but not of B.

For  $\beta_1 < 1$  and  $\beta_{N-1} < 1$  we have the symmetric version of this theorem, which implies that  $\rho_{AB} < 1/N < \rho_{BA}$ . The proof is exactly the same as above, just considering that now the elements in the sum  $s_1$  are greater than 1, while in the sum  $s_2$  are lower than 1 and thus  $s_2 < N - 1 < s_1$  allowing only  $B \rightleftharpoons \square A$ .

**Theorem 4.2.** If  $\rho_{AB} < 1/N$  and  $\rho_{BA} < 1/N$ , then  $\beta_1 < 1$  and  $\beta_{N-1} > 1$ .

*Proof.* If  $\Delta P_1 < 0$  and  $\Delta P_{N-1} > 0$ , we have to distinguish two cases according to the sign of  $P_{1,N-1}$ , which is the sum of  $\Delta P_i$  for all i.

- 1.  $P_{1,N-1} < 0 \implies \rho_{AB} < \frac{1}{N}$ , because all elements in the sum  $s_1$  are greater than 1.
- 2.  $P_{1,N-1} > 0 \implies \rho_{BA} < \frac{1}{N}$ , because all elements in the sum  $s_2$  are greater than 1.

In conclusion,  $\rho_{AB}$ ,  $\rho_{BA}$  cannot be both greater than 1/N. It is not admissible the case  $B \rightleftharpoons \rightleftharpoons \Huge{\leftarrow} A$ , while all other combinations of the fixation probabilities, given  $B^{\leftarrow \rightarrow}A$ , are possible. In particular  $B \rightleftharpoons \Huge{\leftarrow} A$  implies the above theorem.  $\Box$  **Theorem 4.3.** If  $\rho_{AB} > 1/N$  and  $\rho_{BA} > 1/N$ , then  $\beta_1 > 1$  and  $\beta_{N-1} < 1$ .

*Proof.* If  $\Delta P_1 > 0$  and  $\Delta P_{N-1} < 0$ , we have to distinguish again two cases according to the sign of  $P_{1,N-1}$ :

- 1.  $P_{1,N-1} < 0 \implies \rho_{BA} > \frac{1}{N}$ , because all elements in the sum  $s_2$  are lower than 1.
- 2.  $P_{1,N-1} > 0 \implies \rho_{AB} > \frac{1}{N}$ , because all elements in the sum  $s_1$  are lower than 1.

We can conclude that  $\rho_{AB}$ ,  $\rho_{BA}$  cannot be both lower than 1/N and the scenario of mutual invasion but no fixation  $(B \rightleftharpoons A)$  is forbidden. Of course, all other combinations with  $B \rightarrow \leftarrow A$  are generically possible and  $B \rightrightarrows \Leftarrow A$  implies the above theorem.

To confirm that also the two conjectures made in [10] are still valid for the Moran process with exponential fitness, we have performed similar Monte Carlo simulations (see Chapter 5 for more details). Given the combinations of invasion and fixation that are allowable by the three theorems, it turns out that:

- 1. for the scenario of mutual invasion and fixation of both strategies  $(B \rightrightarrows \Leftarrow A)$ , the fixation cannot be fast, this means that we have always observed  $t_{fix} < N(N-1)$ ;
- 2. when selection does not favor invasion  $(B \leftarrow A)$ , then the fixation is experienced to be fast  $(t_{fix} > N(N-1))$ , no matter whether the fixation is favored or not. Thus, we can possibly have  $B \Leftarrow A$ ,  $B \Rightarrow A$  or  $B \Leftarrow A$ .

Given all these results, actually, we have exactly recovered the same selection scenarios that are generically possible under the Moran process with linear fitness (as reported in table 3.4). Hence, the stochastic dynamics is still characterized by outcomes more or less in agreement with the deterministic results and outcomes totally new.

In table 4.1, the generic selection scenarios are summarised with the corresponding symbol and the description of the evolutionary dynamics.

Class	Symbol	Invasion and fixation scenario
1.A	$B \xrightarrow{\rightarrow} A$	Invasion and quick fixation of one strategy
1.B	$B \overleftarrow{\leftarrow} A$	
2.A	$B \xrightarrow{\rightarrow} \leftarrow A$	Mutual invasion and slow fixation of one strategy
2.B	$B \rightleftarrows E A$	
3	$B \overleftarrow{\Leftarrow} \overrightarrow{\Rightarrow} A$	No invasion and no (quick) fixation
4.A	$B \overrightarrow{\Rightarrow} \overrightarrow{A}$	Invasion and slow fixation of one strategy
4.B	$B \overleftarrow{\leftarrow} A$	
5.A	$B \xrightarrow{\longrightarrow} \leftarrow A$	Mutual invasion and quick fixation of one strategy
5.B	$B \xrightarrow{\leftarrow} A$	
6	$B \rightrightarrows \overleftarrow{=} A$	Mutual invasion and slow fixation of both strategies
7.A	$B \overleftrightarrow{\Rightarrow} A$	No invasion and quick fixation of one strategy
7.B	$B \xleftarrow{\leftarrow} A$	

Table 4.1: Selection scenarios under the Moran process with exponential fitness.

#### 4.1.2 Large N limit

We now propose an analysis of the large N limit for the Moran process with exponential fitness, in order to verify which selection scenarios are generically possible for  $N \to \infty$ . We follow the procedure adopted in [10] and briefly discussed in section 3.3.2.

Let us refresh how the formulas of the fixation probabilities and the fixation time look like, with a slight change in the notation for the aims of this section:

$$\rho_{AB} = \frac{1}{1 + \sum_{i=1}^{N-1} \prod_{k=1}^{j} \beta_k^{-1}} = \frac{1}{s_{0,N-1}},\tag{4.11}$$

$$\rho_{BA} = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{k=j}^{N-1} \beta_k} = \frac{1}{s_{N,0,N-1}},$$
(4.12)

$$t_{fix} = \sum_{n=1}^{N-1} \frac{s_{0,n-1}s_{n,N-1}}{\lambda_n q_n s_{0,N-1}}.$$
(4.13)

Remember that  $s_{n,m} = \sum_{k=n}^{m} q_k$ , while  $s_{N,n,m} = \sum_{k=n}^{m} q_{Nk}$ . We have to denote the basic quantities  $q_k$  and  $q_{Nk}$ . They read as:

$$q_k = \prod_{i=1}^k \beta_i^{-1} = \exp(-s\sum_{i=1}^k \Delta P_i) = \exp(-sP_{1,k}), \qquad (4.14)$$

$$q_{Nk} = \prod_{i=N-k}^{N-1} \beta_i = \exp(s \sum_{i=N-k}^{N-1} \Delta P_i) = \exp(s P_{N-k,N-1}), \quad (4.15)$$

with the boundary conditions  $q_0 = 1$  and  $q_{N0} = 1$ .

In order to analyse the behavior of the system with a large population size, we express the above sums,  $P_{1,k}$  and  $P_{N-k,N-1}$ , in terms of  $y = \frac{k}{N}$ , obtaining:

$$P_{1,k} = \frac{k}{2(N-1)} \left[ 2(b-d)(N-1) + k(a-b-c+d) - (a-b+c-d) \right]$$

$$\approx N \frac{y}{2} \left[ 2(b-d) + y(a-b-c+d) - \frac{1}{N}(a-b+c-d) \right]$$

$$\approx N \frac{y}{2} \left[ 2(b-d) + y(a-b-c+d) \right],$$
(4.16)

and

$$P_{N-k,N-1} = \frac{k}{2(N-1)} \left[ 2(a-c)(N-1) - k(a-b-c+d) - (a-b+c-d) \right]$$
  

$$\approx N \frac{y}{2} \left[ 2(a-c) - y(a-b-c+d) - \frac{1}{N}(a-b+c-d) \right]$$
  

$$\approx N \frac{y}{2} \left[ 2(a-c) - y(a-b-c+d) \right].$$
(4.17)

Given the formula of  $P_{1,k}$ , the term  $q_k$  can be straightforwardly formulated as  $q_k = \tilde{q}(y)^N$ , where  $\tilde{q}(y) = \exp(-s\left[\frac{y}{2}(2(b-d)+y(a-b-c+d)\right])$ .

As suggested in the reference paper, when  $N \to \infty$ , the relevant terms in  $q_k$  are near  $k/N \approx y_{max}$ , where  $\tilde{q}(y)$  takes its maximum at  $y_{max}$ . In particular, the value  $y_{max}$  can be at:

- y = 0,
- y = 1,

• 
$$y = y^* = \frac{d-b}{a-b-c+d}$$
,

depending on the payoff differences a - c and b - d. Therefore, we can approximate  $P_{1,k}$  and  $P_{N-k,N-1}$  as follows:

$$P_{1,k} \approx \begin{cases} (b-d) & y = 0\\ N\frac{y^*}{2}(b-d) & y = y^*\\ \frac{N}{2}(a+b-c-d) & y = 1 \end{cases}$$
(4.18)

$$P_{N-k,N-1} \approx \begin{cases} (a-c) & y=0\\ N\frac{y^*}{2} \left[2(a-c) + (b-d)\right] & y=y^*\\ \frac{N}{2}(a+b-c-d) & y=1 \end{cases}$$
(4.19)

and hence,  $\Delta P_1 \approx (b-d)$  while  $\Delta P_{N-1} \approx (a-c)$ . Finally, at the ends of the chain, the term  $q_k$  is simplified:

$$q_k \approx \begin{cases} \exp(-sk(b-d)) & k \ll N, \\ \exp(-s\frac{N}{2}(a+b-c-d))\exp(s(N-k)(a-c)) & N-k \ll N. \end{cases}$$
(4.20)

Provided all these approximations, we can now discuss the behavior of the evolutionary dynamics in the large N limit. The underlying idea, taken from the paper [10], is to use the exact expressions for the fixation probabilities and the fixation time, but to consider in the sums only those terms which mainly contribute to the final result. As we have already mentioned, these terms would be possibly at  $y = 0, y = y^*, y = 1$ .

Below, we report in details the generic cases and the evaluation of the parameters relevant for the classification.

#### - case a>c and b>d -

Invasion coefficient. Given the relative values of the payoffs in the game matrix, it follows that  $\Delta P_1 > 0$  and  $\Delta P_{N-1} > 0$ . This implies  $\beta_1 > 1$  and  $\beta_{N-1} > 1$ , meaning that selection favors only the invasion of an A mutant  $(B^{\rightarrow \rightarrow}A)$ .

Fixation probability. In this scenario, given the payoffs, all  $\Delta P_i$  are positive and as a consequence  $y_{max} = 0$ . Therefore:

$$s_{0,N-1} \approx \sum_{k=0}^{\infty} \exp(-s(b-d))^k = \frac{1}{1 - \exp(-s(b-d))},$$
 (4.21)

$$s_{N,0,N-1} \approx 1 + \exp\left(s\left((a-c)\frac{N}{2} + (b-d)\frac{N}{2}\right)\right) \to \infty.$$

$$(4.22)$$

The fixation probabilities, evaluated with respect of the benchmark value 1/N, result:

$$\rho_{AB} = \frac{1}{s_{0,N-1}} = 1 - \exp(-s(b-d)) = 1 - \frac{\exp(sd)}{\exp(sb)} > \frac{1}{N}, \quad (4.23)$$

and

$$\rho_{BA} = \frac{1}{s_{N,0,N-1}} < \frac{1}{N},\tag{4.24}$$

because  $s_{N,0,N-1}$  goes to infinity exponentially. Selection favors only the fixation of a mutant with strategy A ( $B \rightrightarrows \rightrightarrows A$ ).

Fixation time. In the  $N \to \infty$  limit, the transition probability from state *i* to state i + 1 can be expressed in terms of *y* in the following way:

$$\lambda_i = \frac{y(1-y)}{y + (1-y)\alpha(y)},$$
(4.25)

where  $\alpha(y = i/N) = f_{B,i}/f_{A,i}$ . This transition probability behaves asymptotically as:

$$\frac{1}{\lambda_i} = \begin{cases} \frac{\exp(s(d-b))}{y} & y \ll 1, \\ \frac{1}{1-y} & 1-y \ll 1. \end{cases}$$
(4.26)

In the formula of  $t_{fix}$ ,  $\lambda_i$  appears in fact in the denominator and develops singularities at y = 0 and y = 1. Let see separately the asymptotic behaviour around the two boundaries.

The ratio  $s_{0,n-1}/s_{0,N-1} \to 1$  for any finite y = n/N and hence also for y = 0. In addition, the ratio  $s_{n,N-1}/q_n$  is:

$$\frac{s_{n,N-1}}{q_n} = \sum_{k=n}^{N-1} \frac{q_k}{q_n}$$
  
=  $\exp(-s(b-d))^0 + \exp(-s(b-d))^1 + \exp(-s(b-d))^2 + \dots$   
=  $\sum_{k=0}^{\infty} \exp(-s(b-d))^k$   
=  $\frac{1}{1 - \exp(-s(b-d))}$  (4.27)

The overall contribution at y = 0 is then given by:

$$\frac{\exp(s(d-b))}{1-\exp(-s(b-d))}\sum_{n=1}^{\infty}\frac{1}{y},$$
(4.28)

the upper limit of the sum is not specified as we are considering just the terms close to the lower limit. In particular, it results:

$$\sum_{n=1}^{N} \frac{1}{y} \sim N \int_{1/N} \frac{1}{y} \, dy \sim N \ln N.$$
(4.29)

For y = 1, again  $s_{0,n-1}/s_{0,N-1} \to 1$ , while  $s_{n,N-1}/q_n$  is:

$$\frac{s_{n,N-1}}{q_n} = \sum_{k=n}^{N-1} \frac{q_k}{q_n} 
= \exp(s(a-c))^0 + \exp(s(a-c))^{-1} + \exp(s(a-c))^{-2} + \dots 
= \sum_{k=0}^{\infty} \exp(s(a-c))^{-k} 
= \frac{\exp(s(a-c))}{\exp(s(a-c)) - 1}$$
(4.30)

and the transition probability  $\lambda$  gives a contribution of  $N \ln N$ .

Taking in account all the above formulas, we derive the large N asymptotic expression for the fixation time:

$$t_{fix} \approx \left[\frac{\exp(-s(b-d))}{1-\exp(-s(b-d))} + \frac{\exp(s(a-c))}{\exp(s(a-c)) - 1}\right] N \ln N \sim N \ln N.$$
(4.31)

The fixation time is lesser than the benchmark value N(N-1), hence it is labelled as fast and in conclusion  $B \rightrightarrows A$  is the selection scenario for this case.

#### - case a<c and b<d -

Invasion coefficient. Here,  $\Delta P_1$  and  $\Delta P_{N-1}$  are both negative. As a consequence,  $\beta_1, \beta_{N-1} < 1$  and selection favors exclusively the invasion of a mutant B ( $B \leftarrow \leftarrow A$ ). Fixation probability. The value for which  $\tilde{q}(y)$  takes its maximum is at  $y_{max} = 1$ and it follows:

$$s_{0,N-1} \approx 1 + \exp\left(-s\left((a-c)\frac{N}{2} + (b-d)\frac{N}{2}\right)\right) \to \infty, \tag{4.32}$$

$$s_{N,0,N-1} \approx \sum_{k=0}^{\infty} \exp(s(a-c))^{N-k} = \frac{1}{1 - \exp(s(a-c))}.$$
 (4.33)

The fixation probabilities for this scenario result:

$$\rho_{AB} = \frac{1}{s_{0,N-1}} < \frac{1}{N},\tag{4.34}$$

and

$$\rho_{BA} = \frac{1}{s_{N,0,N-1}} = 1 - \exp(s(a-c)) = 1 - \frac{\exp(sa)}{\exp(sc)} > \frac{1}{N}, \quad (4.35)$$

allowing only the mutant B to have good chances to fixate  $(B \rightleftharpoons A)$ .

Fixation time. Following the same considerations as in the previous case, but interchanging the players A and B (switching  $a \rightleftharpoons d$  and  $b \rightleftharpoons c$  in the payoff matrix) we can easily recover the following fixation time for this scenario:

$$t_{fix} \approx \left[\frac{\exp(-s(c-a))}{1-\exp(-s(c-a))} + \frac{\exp(s(d-b))}{\exp(s(d-b)) - 1}\right] N \ln N \sim N \ln N.$$
(4.36)

The sum in the square brackets is finite and the  $t_{fix} \sim N \ln N < N(N-1)$ . The fixation time is classified as fast and we conclude that  $B \Leftarrow A$  is the selection scenario for the case a < c and b < d.

- case a<c and b>d -

Invasion coefficient. Here, we observe  $\Delta P_1 > 0$  and  $\Delta P_{N-1} < 0$ . The invasion coefficients turn out to be  $\beta_1 > 1$  and  $\beta_{N-1} < 1$ . Therefore, selection favors strategies A and B invading each other  $(B^{\rightarrow \leftarrow} A)$ .

Fixation probability. To determine the fixation probabilities, we have to differentiate two situations depending on whether  $\tilde{q}(1) \leq 1$ .

 $\tilde{q}(1) < 1$ . In this case  $P_{1,N-1} > 0$  and  $y_{max} = 0$ , then:

$$s_{0,N-1} \approx \sum_{k=0}^{\infty} \exp(-s(b-d))^k = \frac{1}{1 - \exp(-s(b-d))},$$
(4.37)

$$s_{N,0,N-1} \approx 1 + \exp\left(s\left((a-c)\frac{N}{2} + (b-d)\frac{N}{2}\right)\right) \approx \exp(sP_{1,N-1}) \to \infty.$$
(4.38)

The fixation probabilities appear as:

$$\rho_{AB} = \frac{1}{s_{0,N-1}} = 1 - \exp(-s(b-d)) = 1 - \frac{\exp(sd)}{\exp(sb)} > \frac{1}{N},$$
(4.39)

and

$$\rho_{BA} = \frac{1}{s_{N,0,N-1}} < \frac{1}{N}.$$
(4.40)

 $\tilde{q}(1) > 1$ . It this situation  $P_{1,N-1} < 0$ , while  $y_{max} = 1$ . We derive:

$$s_{0,N-1} \approx 1 + \exp\left(-s\left((a-c)\frac{N}{2} + (b-d)\frac{N}{2}\right)\right) \approx \exp(-sP_{1,N-1}) \to \infty,$$
  
(4.41)

$$s_{N,0,N-1} \approx \sum_{k=0}^{\infty} \exp(s(a-c))^{N-k} = \frac{1}{1 - \exp(s(a-c))}.$$
 (4.42)

The fixation probabilities become:

$$\rho_{AB} = \frac{1}{s_{0,N-1}} < \frac{1}{N},\tag{4.43}$$

and

$$\rho_{BA} = \frac{1}{s_{N,0,N-1}} = 1 - \exp(s(a-c)) = 1 - \frac{\exp(sa)}{\exp(sc)} > \frac{1}{N}.$$
 (4.44)

As a result, we note that even if mutual invasion is observed, according to the sign of  $\tilde{q}(1)$ , one of the two strategies is favoured for the fixation. Scenarios  $B \rightrightarrows A$  and  $B \rightrightarrows A$  are both plausible.

*Fixation time.* Also to evaluate the fixation time we make the same distinction as above. The proofs is a little bit more complex, but we can safely follow the same steps as in [10].

 $\tilde{q}(1) < 1$ . The ratio  $s_{0,n-1}/s_{0,N-1} \to 1$  as  $N \to \infty$ . The function  $P_{1,k}$  is concave and therefore  $\tilde{q}(y)$  takes its minimum at  $y = y^*$ . The quantity  $1/q_n$  in the formula of  $t_{fix}$  develops singularity exactly in  $y^*$ , while the transition probability  $\lambda_n$  is singular only in y = 0 and y = 1, where we have already seen that its contribution is of  $\sim N \ln N$ . The last term to analyse is  $s_{n,N-1}$ . It is approximated with  $\tilde{q}(1)$ , as it takes the main contribution in y = 1. Given all these asymptotic expressions, the fixation time becomes:

$$t_{fix} \sim \sum_{n=1}^{N-1} \frac{\tilde{q}(1)}{q^*}^N \sim \sqrt{N} \frac{\tilde{q}(1)}{q^*}^N.$$
(4.45)

The contribution of  $\lambda$  has been neglected as it is irrelevant with respect of the exponential growth of the  $t_{fix}$  near  $y^*$ .

 $\tilde{q}(1) > 1$ . This case is totally similar to the previous with the exception that, near  $y^*$ , the term  $s_{0,n-1} \to 1/(1 - \exp(-s(b-d)))$ , which is a constant finite number. The fixation time can be reduced as:

$$t_{fix} \sim \sqrt{N} \left(\frac{1}{q^*}\right)^N. \tag{4.46}$$

Both the  $t_{fix}$  for this scenario are exponentially large in N, which tends to infinity, and therefore the time to reach fixation is classified as slow. Graphically, we represent this condition preserving the notation  $B \rightrightarrows A$  (when  $\tilde{q}(1) < 1$ ) and  $B \rightrightarrows A$  (when  $\tilde{q}(1) > 1$ ).

#### - case a>c and b<d -

Invasion coefficient. According to the relative values of a and c, b and d, it follows  $\Delta P_1 < 0$  and  $\Delta P_{N-1} > 0$ . Therefore,  $\beta_1 < 0$  while  $\beta_{N-1} > 0$  and no mutant is

favored for the invasion  $(B^{\leftarrow \rightarrow}A)$ .

Fixation probability. In this framework, the main contributions to  $s_{0,N-1}$  and  $s_{N,0,N-1}$  come to the terms around  $y_{max} = y^*$ . We observe:

$$s_{0,N-1} \approx 1 + \exp(-sP_{1,k^*}) \approx \exp\left(-s\frac{N}{2}y^*(b-d)\right) \to \infty, \tag{4.47}$$

$$s_{N,0,N-1} \approx \exp(sP_{k^*,N-1}) \approx \exp\left(s\frac{N}{2}y^*(a-c)\right) \to \infty.$$
 (4.48)

The fixation probabilities result:

$$\rho_{AB} = \frac{1}{s_{0,N-1}} < \frac{1}{N},\tag{4.49}$$

and

$$\rho_{BA} = \frac{1}{s_{N,0,N-1}} < \frac{1}{N}.$$
(4.50)

According to this result, we can set the arrows in this way:  $B \rightleftharpoons A$ .

Fixation time. To derive the fixation time in this case, we significantly rely on the assumptions reported in [10] for the corresponding scenario. They remark that singularities are present at y = 0,  $y = y^*$  and y = 1. They provide arguments to assert that close to y = 0 and y = 1 the contribution is in the order of magnitude of  $\sim N \ln N$ , while in  $y = y^*$  is  $\sim N$ . The overall result leads to an asymptotic behavior of the fixation time in the order of  $\sim N \ln N$ . Hence, the evolution of the process is quick and the graphical notation becomes  $B \Leftarrow A$ .

In summary, in the  $N \to \infty$  limit, some generic selection scenarios are excluded, reducing the evolutionary dynamics to the following options:

Class	Conditions	Symbol	Invasion and fixation scenario
1.A	a > c, b > d	$B \xrightarrow{\Rightarrow} \Rightarrow A$	Invasion and quick fixation of one strategy
1.B	a < c, b < d	$B \overleftarrow{\leftarrow} A$	
2.A	a < c, b > d	$B \xrightarrow{\rightarrow} \leftarrow A$	Mutual invasion and slow fixation of one strategy
2.B	a < c, b > d	$B \overleftarrow{\leftarrow} A$	
3	a > c,  b < d	$B \overleftarrow{\Leftarrow} \overrightarrow{\Rightarrow} A$	No invasion and no (quick) fixation

Table 4.2: Selection scenarios in the  $N \to \infty$  limit under the Moran process with exponential fitness.

This result is totally in agreement with the table 3.6 inherent the Moran process with linear fitness, proving that also with the exponential fitness the evaluation of the payoff difference a - c and b - d is sufficient to deduce the qualitative behavior of the system in the long term when  $N \to \infty$ .

In conclusion, comparing this stochastic framework with large N and the deterministic outcome contemplated by the replicator equation, we can point out similarities and differences. For example, the scenarios 1.A and 1.B properly reflect the dominance of a strategy. Scenarios 2.A and 2.B may be partially matched with the coexistence case. Here, in fact it is certain that the system will fixate in a state, even if the absorbing time is exponentially large with N. Finally, scenario 3 recalls the mutual exclusion outcome. In the deterministic dynamics it is impossible to move from the neighbourhood of an absorbing state to the other one, because of the repulsive unstable fix point in the middle. In the same way, the stochastic dynamics predicts that the fixation probability of a mutant is exponentially small. However, interestingly, due to the intrinsic stochasticity of the process, it is possible for a mutant to reach its corresponding pure state and when such an event occurs, the fixation is experienced to be fast.

#### 4.1.3 Strong selection

In this section, we are going to present the main result of this thesis. The specific choice of the mapping from payoff to fitness allows a strong selection analysis of the process (i.e. when the intensity of selection is large but still finite). The basic intuition, which underlines the following considerations, is founded on the fact that, given a large s in the formula (4.5), if the payoff difference  $\Delta P_i$  is negative then  $\beta_i \rightarrow 0$  and a B player is almost certainly selected for the reproduction, while, on the opposite, if  $\Delta P_i$  is positive then  $\beta_i \rightarrow \infty$  and an A player almost surely reproduces. Considering the expressions in (4.7) for the fixation probabilities and the formulas (4.14), (4.15) of the basic quantities for the computation of the fixation time, we can derive the behaviour of the aforementioned classification parameters. Four generic scenarios are discriminated, according to the relative value of the invasion coefficients  $\beta_1$  and  $\beta_{N-1}$ .

- case  $\beta_1 > 1$  and  $\beta_{N-1} > 1$   $(B \rightarrow A)$  -

Fixation probability. In this case  $\Delta P_i > 0$  for all *i*. For this reason  $s_1 \to 0$ , whereas  $s_2 \to \infty$ . The fixation probabilities turn out to  $\rho_{AB} \to 1$ ,  $\rho_{BA} \to 0$ . It is almost certain that a mutant *A* will fixate. We graphically represent this as  $B \rightrightarrows \rightrightarrows A$ . Fixation time. Regarding the components in the formula of the fixation time, for large *s* we observe that  $s_{0,n-1}$ ,  $s_{0,N-1} \to 1$ , while  $s_{n,N-1} \approx q_n$ . The only relevant variable remains  $\lambda_n$ . However, since  $f_{A,n} \gg f_{B,n}$ , this transition probability can be approximated as (N-n)/N. In the end, it results:

$$t_{fix} = \sum_{n=1}^{N-1} \frac{1}{\lambda_n}$$
  
=  $N \sum_{n=1}^{N-1} \frac{1}{N-n}$   
=  $N \sum_{n=1}^{N-1} \frac{1}{n} < N(N-1)$  (4.51)

The above relation holds for N > 2 and we can conclude that in this scenario the fixation is fast and we represent it through  $B \xrightarrow{\rightarrow} A$ .

- case  $\beta_1 < 1$  and  $\beta_{N-1} < 1$  ( $B^{\leftarrow} \leftarrow A$ ) -

Fixation probability. Here, we observe  $\Delta P_i < 0$  for all *i*. It follows that  $s_1 \to \infty$ , while  $s_2 \to 0$ . For this reason, the fixation probabilities tend to  $\rho_{AB} \to 0$ ,  $\rho_{BA} \to 1$ . A mutant *B* will fixate almost surely and the corresponding notation is  $B \rightleftharpoons \square A$ . Fixation time. In order to examine the fixation time in this scenario, we can rewrite the formula (3.9) obtaining a sort of a dual formula:

$$t_{fix} = \sum_{n=1}^{N-1} \frac{s_{N,0,n-1}s_{N,n,N-1}}{\mu_{N-n}q_{Nn}s_{N,0,N-1}},$$
(4.52)

where  $s_{N,n,m} = \sum_{k=n}^{m} q_{Nk}$  and  $q_{Nk} = \prod_{j=N-k}^{N-1} \beta_j$  with  $q_{N0} = 1$ . It follows that  $s_{N,0,n-1}$ ,  $s_{N,0,N-1} \to 1$ , while  $s_{N,n,N-1} \approx q_{Nn}$ . The transition probability  $\mu$  is approximated with n/N, because  $f_{B,n} \gg f_{A,n}$ , and it is the only component relevant for the computation of the fixation time which turns out to be:

$$t_{fix} = \sum_{n=1}^{N-1} \frac{1}{\mu_{N-n}}$$
  
=  $N \sum_{n=1}^{N-1} \frac{1}{N-n}$   
=  $N \sum_{n=1}^{N-1} \frac{1}{n} < N(N-1)$  (4.53)

Hence, when the mutant B is favored for the invasion and the fixation, the time process is fast and the corresponding notation is  $B \Leftarrow A$ . It holds for N > 2.

- case  $\beta_1 > 1$  and  $\beta_{N-1} < 1$   $(B \to A)$  -Fixation probability. In this context, there exists an  $i^*$  for which  $\Delta P_{i < i^*} > 0$  and  $\Delta P_{i \ge i^*} < 0$ . As a consequence, the sum of the overall  $\Delta P_i$ , represented as  $P_{1,N-1}$ , can be potentially greater or lower than zero. We have to consider separately these cases.

- 1.  $P_{1,N-1} > 0$ : this implies  $s_1 \to 0$  and  $s_2 \to \infty$ . It follows  $\rho_{AB} \to 1$  and  $\rho_{BA} \to 0$ . The scenario is  $B \rightrightarrows A$ .
- 2.  $P_{1,N-1} < 0$ : this implies  $s_1 \to \infty$  and  $s_2 \to 0$ . It follows  $\rho_{AB} \to 0$  and  $\rho_{BA} \to 1$ . The scenario is  $B \rightleftharpoons \triangleq A$ .

*Fixation time.* Also for the fixation time, it is necessary to analyse case by case what happens.

1.  $P_{1,N-1} > 0$ . Here,  $s_{0,n-1}$ ,  $s_{0,N-1} \rightarrow 1$ . For the other two components we have to made a distinction, because they behave differently in accordance to the sign of  $\Delta P_i$ . In particular, we denote with  $n^*$  the first index for which the payoff difference becomes negative and with  $k^*$  the index which satisfies the condition  $P_{1,k^*} > P_{1,N-1}$ ,  $P_{1,k^*-1} < P_{1,N-1}$ . We derive:

$$s_{n,N-1} \approx \begin{cases} q_n & n < k^* \\ q_{N-1} & n \ge k^* \end{cases}$$
 (4.54)

$$\lambda_n \approx \begin{cases} \frac{N-n}{N} & n < n^* \\ \frac{n}{N} \exp(s\Delta P_n) & n \ge n^* \end{cases}$$
(4.55)

The formula of the fixation time can be split with respect of  $k^*$  and  $n^*$ :

$$t_{fix} = N \sum_{n=1}^{k^*-1} \frac{1}{N-n} + N \sum_{n=k^*}^{n^*-1} \frac{\overbrace{q_{N-1}/q_n}^{\to\infty}}{N-n} + N \sum_{n=n^*}^{N-1} \underbrace{\underbrace{\frac{e^{-\infty}}{q_{N-1}/q_n}}_{\to 0}}_{\to 0} \frac{1}{n}.$$
 (4.56)

The last two addenda tend exponentially to infinity and it results  $t_{fix} > N(N-1)$ . The fixation is therefore slow and the corresponding scenario is  $B \stackrel{\sim}{\Rightarrow} \stackrel{\leftarrow}{\Rightarrow} A$ .

2.  $P_{1,N-1} < 0$ . As previously done, also in this situation it is better to adopt the dual formula for the fixation time. Hence, the analysis is totally symmetric to the above case and it confirms that also in this scenario the fixation is slow, then the notation remains  $B \rightleftharpoons \Subset A$ .

- case  $\beta_1 < 1$  and  $\beta_{N-1} > 1 (B^{\leftarrow \rightarrow}A)$  -

Fixation probability. Here, we can identify an  $i^*$  for which  $\Delta P_{i < i^*} < 0$  and  $\Delta P_{i \ge i^*} > 0$ . Anyway, in this case we do not have to discriminate the sign of  $P_{1,N-1}$ , as the first element in  $s_1$  and  $s_2$  (determined respectively by  $(-s\Delta P_1)$  and  $(s\Delta P_{N-1})$ ) tends to infinity. So, both  $s_1, s_2 \to \infty$ . This implies  $\rho_{AB} = 0$  and  $\rho_{BA} = 0$  and  $B \Leftarrow A$  is the only admissible scenario, while the cases with no invasion, but the fixation of one strategy over the other are not possible any more.

Fixation time. The terms in the formula of the fixation time behave differently depending on whether  $\Delta P_i \geq 0$ . Until  $\Delta P_i < 0$ , we have  $s_{0,n-1} \approx q_{n-1} = \frac{\lambda_n}{\mu_n} q_n \approx \frac{N}{n} \lambda_n q_n$  and  $s_{n,N-1} \approx s_{0,N-1}$ . As soon as  $\Delta P_i > 0$ , we observe instead  $s_{0,n-1} \approx q_{n^*-1}$ ,  $s_{n,N-1} \approx q_n$ ,  $s_{o,N-1} \approx q_{n^*-1}$  and  $\lambda_n = \frac{N-n}{N}$ . The formula is therefore split in two and the index  $n^*$  corresponds to the moment when we observe the inversion in the sign of the payoff difference. Given all the approximations above, the fixation time is reduced as follows:

$$t_{fix} = N \sum_{n=1}^{n^*-1} \frac{1}{n} + N \sum_{n=n^*}^{N-1} \frac{1}{N-n} < N(N-1).$$
(4.57)

It holds for N > 3 and states that fixation is fast. The final scenario is  $B \Leftarrow \Rightarrow A$ .

Grouping together all these results, we obtain the following table for the generic selection scenarios:

Class	Conditions	Symbol	Invasion and fixation scenario
1.A	$\beta_1 > 0,  \beta_{N-1} > 0$	$B \xrightarrow{\rightarrow} \xrightarrow{\rightarrow} A$	Invasion and quick fixation of one strategy
1.B	$\beta_1 < 0,  \beta_{N-1} < 0$	$B \xleftarrow{\leftarrow} A$	
2.A	$\beta_1 > 0,  \beta_{N-1} < 0$	$B {\stackrel{\rightarrow}{\Rightarrow} \stackrel{\leftarrow}{\Rightarrow}} A$	Mutual invasion, slow fixation of one strategy
2.B	$\beta_1 > 0,  \beta_{N-1} < 0$	$B \rightleftharpoons \overleftarrow{\leftarrow} A$	
3	$\beta_1 < 0,  \beta_{N-1} > 0$	$B \overleftarrow{\Leftarrow} \overrightarrow{\Rightarrow} A$	No invasion and no (quick) fixation

Table 4.3: Selection scenarios with strong selection under the Moran process with exponential fitness.

This is a significant result, as we have recovered the same three generic outcomes admissible in the large N limit (see table 4.2), without imposing specific conditions on the value of N. This means that even with a small and finite value for the population size, the strong selection is able to reunify the stochastic dynamics with the deterministic evolution. However, unlike the framework with large N, where the selection scenarios are listed according to the relative value of the payoffs, as it happens with the classification under the replicator equation, with the strong selection we can discriminate the outcome according to the invasion coefficients. Moreover, given a generic game and the strong selection, different population sizes may induce a different expected evolutionary scenario, as the invasion coefficients, which allow to discriminate the outcome, depend both on the payoffs a,b,c,d and on N.

#### 4.1.4 Extreme selection

In the limit of  $s \to \infty$  (i.e. for extreme selection), the fittest individual is always selected for reproduction. Therefore, according to the sign of the payoff difference, either  $\lambda$  or  $\mu$  is 0. The transition probabilities can be approximated as follows:

$$\lambda_{i} = \frac{if_{A,i}}{if_{A,i} + (N-i)f_{B,i}} \frac{N-i}{N} \approx \begin{cases} \frac{N-i}{N} & \Delta P_{i} > 0\\ \frac{i}{i + (N-i)\exp(-s\Delta P_{i})} \frac{N-i}{i} \to 0 & \Delta P_{i} < 0 \end{cases}$$
(4.58)

$$\mu_i = \frac{(N-i)f_{B,i}}{if_{A,i} + (N-i)f_{B,i}} \frac{i}{N} \approx \begin{cases} \frac{N-i}{i\exp(s\Delta P_i) + (N-i)}\frac{i}{N} \to 0 & \Delta P_i > 0\\ \frac{i}{N} & \Delta P_i < 0 \end{cases}$$
(4.59)

In the following figures we analyse in more details what happens in the Markov chain with respect to the sign of  $\Delta P_i$ .

$$1 - \lambda_i = \frac{i}{N}$$

$$i - 1$$

$$\lambda_i = \frac{N - i}{N}$$

$$i + 1$$

Figure 4.1: Vanishing  $\mu_i$  for extreme selection and  $\Delta P_i > 0$  under the Moran process with exponential fitness.



Figure 4.2: Vanishing  $\lambda_i$  for extreme selection and  $\Delta P_i < 0$  under the Moran process with exponential fitness.



Figure 4.3: Extreme selection and  $\Delta P_i = 0$  under the Moran process with exponential fitness.

For  $s \to \infty$ , the direction of the process becomes deterministic and thus the fixation probabilities will be exactly either 0 or 1. However, the process is only semi-deterministic as the fixation time remains stochastic. In fact, due to the random death and consequently the non vanishing  $(1 - \lambda_i - \mu_i)$  probabilities, the system can remain longer or shorter in a particular state. In [23], a variation of the Moran process, where the player's death is not random but it is proportional to the inverse of its fitness, leads to a fully deterministic behaviour for extreme selection.

To conclude, it is worth noting that, whereas scenarios 1.A, 1.B and 3 are still valid with the extreme selection, we lose scenarios 2.A and 2.B from the table 4.3 concerning the strong selection framework. In fact, given these implications:

 $- \Delta P_1 > 0 \implies \mu_1 = 0,$ 

$$-\Delta P_{N-1} < 0 \implies \lambda_{N-1} = 0,$$

we set  $\rho_{AB} = \rho_{BA} = 0$ , since it is not possible to reach an absorbing state. The Markov chain appears as:



Figure 4.4: Markov chain in the scenario of mutual invasion and no fixation under the Moran process with exponential fitness.

The formulas for the fixation probabilities (3.6) and (3.7) are derived assuming  $\lambda_i$ ,  $\mu_i > 0$  for all *i* in the balance equations. For any finite and arbitrarily strong selection strength, this is true, but it fails at the limit  $s \to \infty$ . Hence, we observe that the scenario of "mutual invasion and slow fixation" becomes "mutual invasion"

and no fixation" at extreme selection. We have to stress that this scenario is forbidden by the theorem 4.3, but it turns out to be allowed with extreme selection. This result better matches the deterministic case of coexistence, where the two strategies invade each other and in the long term they coexist with a certain distribution in the population.

The following table summarises the evolutionary dynamics with extreme selection:

Class	Symbol	Invasion and fixation scenario
1.A	$B \xrightarrow{\rightarrow} A$	Invasion and quick fixation of one strategy
1.B	$B \overleftarrow{\leftarrow} A$	
2	$B \stackrel{\rightarrow}{\Leftarrow} \stackrel{\leftarrow}{\Rightarrow} A$	Mutual invasion and no fixation
3	$B \xleftarrow{\rightarrow}{\leftrightarrow} A$	No invasion and no (quick) fixation

Table 4.4: Selection scenarios in the  $s \to \infty$  limit under the Moran process with exponential fitness.

#### 4.1.5 The deterministic limit

In this last section, we want to discuss how the deterministic replicator dynamics and the stochastic evolutionary game dynamics for the Moran process with exponential fitness are related to each other. In order to perform this task, we follow the arguments suggested in [24].

As we have seen in section 3.2.3, the stochastic process can be formulated in terms of the Master equation in formula (3.8). We now consider it in this form:

$$P_i(\tau+1) - P_i(\tau) = P_{i-1}(\tau)\lambda_{i-1} - P_i(\tau)\mu_i + P_{i+1}(\tau)\mu_{i+1} - P_i(\tau)\lambda_i, \qquad (4.60)$$

where  $P_i(\tau)$  denotes the probability that the system is in state *i* at time  $\tau$ . At this point, introducing the notation x = i/N and  $t = \tau/N$ , defining the probability density  $\rho(x,t) = NP_i(\tau)$  and replacing  $\lambda_i$  and  $\mu_i$  with  $\lambda(x)$  and  $\mu(x)$ , the Master equation can be opportunely rewritten as follows:

$$\rho(x,t+\frac{1}{N}) - \rho(x,t) = \rho(x-\frac{1}{N},t)\lambda(x-\frac{1}{N}) + \rho(x+\frac{1}{N},t)\mu(x+\frac{1}{N}) - \rho(x,t)\mu(x) - \rho(x,t)\lambda(x).$$
(4.61)

For  $N \gg 1$ , the left-hand side of the above equation becomes  $\frac{\partial}{\partial t}\rho(x,t)$ , whereas the

right-hand side can be Taylor expanded at (x, t) up to second order obtaining:

$$\frac{\partial}{\partial t}\rho(x,t) = -\frac{\partial}{\partial x}\left[a(x)\rho(x,t)\right] + \frac{1}{2}\frac{\partial^2}{\partial x^2}\left[b^2(x)\rho(x,t)\right],\qquad(4.62)$$

that is equivalent to the following stochastic differential equation:

$$\dot{x} = a(x) + b(x)\xi, \qquad (4.63)$$

where  $a(x) = \lambda(x) - \mu(x)$ ,  $b(x) = \sqrt{(1/N) [\lambda(x) + \mu(x)]}$  and  $\xi$  is an uncorrelated Gaussian noise. The selection term is represented by a(x), while  $b(x)\xi$  is the diffusion term taking stochasticity into account. Both terms depend on the composition of the population and on the game payoffs. Moreover, b(0) = b(1) = 0 for any N and b(x) = 0 for any x in (0, 1) in the limit of  $N \to \infty$ . Thus, in this limit, we obtain the deterministic differential equation:

$$\dot{x} = a(x) = \lambda(x) - \mu(x). \tag{4.64}$$

We can now examine the previous formula considering the specific transition probabilities holding for the Moran process with exponential fitness. For this aim, we suitably rewrite the formula of  $\lambda$  and  $\mu$ , which are expressed in terms of *i*, in order to obtain something in terms of *x*.

$$\lambda_{i} = \frac{if_{A,i}}{if_{A,i} + (N-i)f_{B,i}} \frac{N-i}{N} = \frac{if_{A,i}}{\frac{if_{A,i} + (N-i)f_{B,i}}{N}} \frac{N-i}{N^{2}}$$

$$= \frac{f_{A,i}}{f} \frac{i}{N} \frac{N-i}{N},$$
(4.65)

where f is the average fitness in the population. Remembering that x = i/N and in the limit  $N \to \infty$ , it follows:

$$\lambda(x) = \frac{f_{A,x}}{f_x} x(1-x),$$
(4.66)

with  $f_x = x f_{A,x} + (1-x) f_{B,x}$ . Similarly, for  $\mu$  we have:

$$\mu_{i} = \frac{(N-i)f_{B,i}}{if_{A,i} + (N-i)f_{B,i}} \frac{i}{N} = \frac{(N-i)f_{B,i}}{\frac{if_{A,i} + (N-i)f_{B,i}}{N}} \frac{i}{N^{2}}$$

$$= \frac{f_{B,i}}{f} \frac{N-i}{N} \frac{i}{N},$$
(4.67)

and thus:

$$\mu(x) = \frac{f_{B,x}}{f_x} (1-x)x. \tag{4.68}$$

Replacing formula (4.66) and (4.68) in (4.64), we derive the deterministic limit for the Moran process with exponential fitness and finite selection strength:

$$\dot{x} = x(1-x)\frac{f_{A,x} - f_{B,x}}{f_x}.$$
(4.69)

Through some maths, we can also recover the differential equations specifically for players A and B:

$$\dot{x}_A = x_A \frac{f_{A,x} - f_x}{f_x},$$
(4.70)

$$\dot{x}_B = x_B \frac{f_{B,x} - f_x}{f_x},$$
(4.71)

These results are valid for any finite s. If we assume the extreme selection framework where  $s \to \infty$ , the average fitness  $f_x$  can be reduced as follows:

$$f_x = \begin{cases} x f_{A,x} & f_{A,x} > f_{B,x} \\ (1-x) f_{B,x} & f_{A,x} < f_{B,x} \end{cases}$$
(4.72)

Consequently, the differential equation becomes:

$$\dot{x} = \begin{cases} 1 - x & f_{A,x} > f_{B,x} \\ -x & f_{A,x} < f_{B,x} \end{cases}$$
(4.73)

We graphically represent now in figure 4.5 the trend of  $\dot{x}$  considering the different selection scenarios.

Graph (1) refers to the A-dominance scenario. When few A players are present in the population, the system quickly moves away from the pure B state, whereas it gradually slows down while approaching the pure A state (the convergence to the pure A state is asymptotic). In graph (2), the coexistence scenario is represented. When few mutants, either of type A or B, are present in the population, the system converges in finite time toward the mixed state. Finally, in graph (3), with the mutual exclusion scenario the system moves away from the interior mixed point, converging asymptotically in one of the two pure states, depending on the initial condition.



Figure 4.5:  $\dot{x}$  in the deterministic limit for the Moran process.

### 4.2 The pairwise comparison with Fermi function

In pairwise comparison processes, a pair of individuals is sampled at random at each time step and subsequently one of these individuals may adopt the strategy of the other. More precisely, one player is selected as a focal and evaluates its success comparing its own payoff with the one of the other player, which acts as a role model. The focal then adopts the strategy of the role with a probability that increase with the payoff difference. One common choice for this imitation probability, in order to allow any intensity of selection, is the Fermi function from statistical physics [25, 26]. Naturally, this probability is rearranged to become a function on the payoff difference between the role and the focal [27]. It takes the following form:

$$p_i = \frac{1}{1 + \exp(-s(P_{role,i} - P_{focal,i})))}.$$
(4.74)

If the role player has a higher payoff, the focal one moves to its strategy with probability  $p_i > 1/2$ . Otherwise, it switches with  $p_i < 1/2$ . In general, the more a player fares better in the population, the more is likely to be imitated. It is obvious that the composition of the population can change only if the focal and the role are selected of the opposite type. The shape of the probability p is controlled by the parameter s. From a physical point of view, s is interpreted as in inverse temperature, while in evolutionary game theory, it represents the balance between selection and random fluctuations in finite populations. Since the selection strength is an argument of the exponential function in the formula, it is possible to analyse evolutionary game dynamics at all intensities of selection (from neutral selection when s = 0, up to the extreme limit when  $s \to \infty$ ) and for any game matrix.

At the state of the art, some results have been reported for the weak selection framework, when  $s \ll 1$ . In [28], for example, the imitation probability is reduced to a linear function in the payoff difference and analytical results are derived for the fixation probabilities. Here, for the specific case of a 2-players-2-strategies game, the transition probabilities are:

$$\lambda_i = \frac{1}{1 + \exp(-s(P_{A,i} - P_{B,i}))} \frac{i}{N} \frac{N - i}{N}, \qquad (4.75)$$

$$\mu_i = \frac{1}{1 + \exp(-s(P_{B,i} - P_{A,i}))} \frac{N - i}{N} \frac{i}{N}.$$
(4.76)

In the case of  $\lambda$ , the role is the *A* player and it could be imitated by the focal *B*, increasing in this way the number of the *A*-strategists. In  $\mu$  we observe respectively the opposite. Expected payoffs are the same as defined in (3.2) and (3.3). The fundamental quantity  $\beta_i$  appears like:

$$\beta_i = \frac{1 + \exp(-s(P_{B,i} - P_{A,i}))}{1 + \exp(-s(P_{A,i} - P_{B,i}))} = \exp(s\Delta P_i).$$
(4.77)

We mention here the exact correspondence of this final formula to compute  $\beta$  with the formula (4.5), a remarkable result that will be deeply discussed in the following section.

In conclusion, under this pairwise comparison process, when we get the condition of the neutral game, no strategy has an advantage over the other in any state of the population and  $p_i = 1/2$  for all *i*. As mentioned in [21], the probability of fixation of a neutral mutant is 1/N, while the time to reach fixation is 2N(N-1).

#### 4.2.1 Selection scenarios

We want now to derive the selection scenarios for this process. As usual, classification depends on the evaluation of the invasion coefficient, the fixation probability and the fixation time with respect to the reference values of the neutral game. First of all, we have to check whether the three theorems (4.1, 4.2, 4.3) are still valid. Observing that the ratio between the transition probabilities in formula (4.77) reads exactly the same as (4.5), we conclude that  $\beta_i$  for the pairwise comparison and the Fermi function is identical to  $\beta_i$  for the Moran process and the exponential fitness, for all *i*. Since all the proofs in section 4.1.1 are based on considerations on  $\Delta P_i$ , which is obviously the same because the average payoffs are defined both through the same formulas, and on  $\beta_i$ , which turns out to be identical as just shown, it follows that even in this pairwise comparison process the theorems are confirmed. This is an amazing result, because despite the fact that the two microscopic processes of strategy spreading are totally different (i.e. the transition probabilities are different), the macroscopic properties of invasion and fixation in the evolutionary dynamics are the same. Considering the two classes of stochastic evolutionary dynamics, the birth-death processes and the imitation learning, it is worth noting that the couple Moran process with exponential fitness and pairwise comparison with the Fermi function is the unique pair leading to identical outcomes in the fixation probabilities for arbitrary games and for any intensity of selection, as pointed out in [29] through a formal proof.

Regarding the validity of the two conjectures, which impose constraints on the match of some combinations of invasion and fixation with the fixation time, we have performed Monte Carlo experiments checking that some selection scenarios, contemplated by the theorems, appear only to be fast or slow. Again, as widely shown in Chapter 5, the admissible configurations are the same as in the Moran process. For convenience, we present once again the summary table of the generic selection scenarios.

Class	Symbol	Invasion and fixation scenario
1.A	$B \xrightarrow{\Rightarrow} \overrightarrow{\Rightarrow} A$	Invasion and quick fixation of one strategy
1.B	$B \overleftarrow{\leftarrow} A$	
2.A	$B \stackrel{\longrightarrow}{\Rightarrow} \stackrel{\leftarrow}{\Rightarrow} A$	Mutual invasion and slow fixation of one strategy
2.B	$B \overleftarrow{\leftarrow} A$	
3	$B \xleftarrow{\longrightarrow} A$	No invasion and no (quick) fixation
4.A	$B \overrightarrow{\Rightarrow} \overrightarrow{A}$	Invasion and slow fixation of one strategy
4.B	$B \not \equiv \not \equiv A$	
5.A	$B \xrightarrow{\Longrightarrow}  A$	Mutual invasion and quick fixation of one strategy
5.B	$B \overleftarrow{\Leftarrow} A$	
6	$B \xrightarrow{\rightarrow} \overleftarrow{\leftarrow} A$	Mutual invasion and slow fixation of both strategies
7.A	$B \stackrel{\longleftarrow}{\Rightarrow} A$	No invasion and quick fixation of one strategy
7.B	$B \underset{\notin}{\overleftarrow{\leftarrow}} A$	

Table 4.5: Selection scenarios under the pairwise comparison with the Fermi function.

#### 4.2.2 Large N limit

The analysis of the large N limit in the case of the pairwise comparison with the Fermi function can be performed following the same arguments proposed in section 4.1.2 for the Moran process with exponential fitness, as all the approximations still persist. We only have to check if the transition probability  $\lambda$  behaves asymptotically in the same way when  $N \to \infty$ . Given y = i/N, we can write  $\lambda_i$  in terms of y:

$$\lambda_i = p_i(y)y(1-y). \tag{4.78}$$

Specifically, the imitation probability  $p_i(y)$  appears as:

$$p_i(y) = \frac{1}{1 + \exp(-s((a-c)y + (b-d)(1-y)))}.$$
(4.79)

The transition probability  $\lambda$  is at the denominator of the formula of the fixation time, therefore it develops singularities at y = 0 and y = 1, exactly as in the case of the Moran process. Hence, we can conclude that the asymptotic behavior of the fixation time satisfies the same properties and we recover the same selection scenarios. However, since:

$$\frac{1}{\lambda_i} = \begin{cases} \frac{1 + \exp(-s(b-d))}{y} & y \ll 1, \\ \frac{1 + \exp(-s(a-c))}{1-y} & 1 - y \ll 1, \end{cases}$$
(4.80)

the multiplicative coefficients of the fixation time will be pretty different. As we are considering the large N limit, what really matters for the classification is only the order of magnitude and therefore we can safely neglect them. The selection scenarios are listed in the following table:

Class	Conditions	Symbol	Invasion and fixation scenario
1.A	a > c, b > d	$B \xrightarrow{\rightarrow} A$	Invasion and quick fixation of one strategy
1.B	a < c, b < d	$B \overleftarrow{\leftarrow} A$	
2.A	a < c, b > d	$B \xrightarrow{\Longrightarrow} A$	Mutual invasion and slow fixation of one strategy
2.B	a < c, b > d	$B \rightleftarrows E A$	
3	a > c,  b < d	$B \overleftarrow{\Leftarrow} A$	No invasion and no (quick) fixation

Table 4.6: Selection scenarios in the  $N \to \infty$  limit under pairwise comparison with the Fermi function.

#### 4.2.3 Strong selection

We discuss now the strong selection surrounding for the pairwise comparison. As we have already reported, for this process the analytical expressions for the invasion coefficients and the fixation probabilities are totally identical to the ones of the Moran process with exponential fitness. For this reason, to study how the selection scenarios appear given a large s, we have to consider just the fixation time. The variables  $s_{0,n-1}$ ,  $s_{n,N-1}$ ,  $s_{0,N-1}$  and  $q_n$  behave in the same way, because their main component is the quantity  $\beta$ . Therefore, the analysis can be widely reduced, as we have only to verify if the definition of the transition probability  $\lambda$  (or  $\mu$  in the dual formula (4.52)) under the pairwise comparison process involves a different classification. Again four cases are distinguished, suggesting in the parenthesis the partial graphical notation of the scenario that we can already infer.

- case  $\beta_1 > 1$  and  $\beta_{N-1} > 1$  ( $B \rightrightarrows A$ , or  $B \rightrightarrows A$ ) -Fixation time. The transition probability  $\lambda_n \to \frac{n(N-n)}{N^2}$ . Then:

$$t_{fix} = \sum_{n=1}^{N-1} \frac{1}{\lambda_n} = N^2 \sum_{n=1}^{N-1} \frac{1}{n(N-n)} < 2N(N-1)$$
(4.81)

The expression holds for N > 2 and the fixation is therefore fast. The scenario is  $B \xrightarrow{\longrightarrow} A$ .

- case  $\beta_1 < 1$  and  $\beta_{N-1} < 1$  ( $B \Leftarrow A$ , or  $B \Leftarrow A$ ) -

Fixation time. By symmetry and using the dual formula of the fixation time, it turns out that the fixation time is lower than the benchmark value 2N(N-1). Hence, also when we observe that selection favors the mutant B, the time scale of the process is fast and the notation becomes  $B \overleftarrow{\Leftarrow} \overleftarrow{\Leftarrow} A$ .

- case  $\beta_1 > 1$  and  $\beta_{N-1} < 1$   $(B \rightrightarrows A \text{ or } B \rightleftarrows A)$  -

Fixation time. This case have to be analysed considering that there exists  $k^*$  for which  $P_{1,k^*} > P_{1,N-1}$ ,  $P_{1,k^*-1} < P_{1,N-1}$  and the index  $n^*$  for which the payoff difference changes sign. Again, we observe the following approximations:

$$s_{n,N-1} \approx \begin{cases} q_n & n < k^* \\ q_{N-1} & n \ge k^* \end{cases}$$

$$(4.82)$$

$$\lambda_n \approx \begin{cases} \frac{n(N-n)}{N^2} & n < n^* \\ \frac{n(N-n)}{N^2} \frac{1}{1 + \exp(-s\Delta P_n)} & n \ge n^* \end{cases}$$
(4.83)

We should also separate the scenarios according to  $P_{1,N-1} \ge 0$ .

1.  $P_{1,N-1} > 0$ : under these conditions the fixation time results:

$$t_{fix} = N^2 \sum_{n=1}^{k^*-1} \frac{1}{n(N-n)} + N^2 \sum_{n=k^*}^{n^*-1} \frac{\overbrace{q_{N-1}/q_n}^{\to\infty}}{n(N-n)} + N^2 \sum_{n=n^*}^{N-1} \frac{\overbrace{q_{N-1}/q_n}^{\to\infty}}{n(N-n)} (1 + \exp(-s\Delta P_n))$$
(4.84)

The fixation is slow and the scenario remains  $B \rightrightarrows A$ .

- 2.  $P_{1,N-1} < 0$ : This is the case where the dual formula of the fixation time fits better, because the analysis is straightforward as above with the corresponding dual variables. It turns out that the fixation time is lower than 2N(N-1), so the fixation process is slow and  $B \rightleftharpoons \sqsubseteq A$  is the outcome.
- case  $\beta_1 < 1$  and  $\beta_{N-1} > 1$   $(B \Leftarrow A, \text{ or } B \Leftarrow A)$  -

Fixation time. We can easily approximate almost all the variables in the formula and the only relevant component remains the transition probability  $\lambda$ . Hence the time read as:

$$t_{fix} = N^2 \sum_{n=1}^{n^*-1} \frac{1}{n(N-n)} + N^2 \sum_{n=n^*}^{N-1} \frac{1}{n(N-n)} < 2N(N-1).$$
(4.85)

It holds for N > 2 and it assert that the fixation is fast. We represent it as  $B \Leftarrow A$ .

Given all these results, we have actually shown that also for the pairwise comparison with the Fermi function the strong selection reduces the admissible selection scenarios in the same way as the Moran process with the exponential fitness. The fact that the transition probabilities are totally different does not influence the time scale of the evolutionary process with a large intensity of selection. Below, we summarise the outcomes.

Class	Conditions	Symbol	Invasion and fixation scenario
1.A	$\beta_1 > 0, \ \beta_{N-1} > 0$	$B \xrightarrow{\Rightarrow} \Rightarrow A$	Invasion and quick fixation of one strategy
1.B	$\beta_1 < 0, \ \beta_{N-1} < 0$	$B \xleftarrow{\leftarrow} A$	
2.A	$\beta_1 > 0, \ \beta_{N-1} < 0$	$B \xrightarrow{\rightarrow}  A$	Mutual invasion, slow fixation of one strategy
2.B	$\beta_1 > 0, \ \beta_{N-1} < 0$	$B \overleftarrow{\leftarrow} A$	
3	$\beta_1 < 0, \ \beta_{N-1} > 0$	$B \xleftarrow{\rightarrow}{\leftarrow} A$	No invasion and no (quick) fixation

Table 4.7: Selection scenarios with strong selection under the pairwise comparison with the Fermi function.

#### 4.2.4 Extreme selection

For extreme selection,  $s \to \infty$ , the probability  $p_i$  becomes a step function:

$$p_{i} = \frac{1}{1 + \exp(-s(P_{role,i} - P_{focal,i}))} = \begin{cases} 1 & P_{role,i} > P_{focal,i} \\ \frac{1}{2} & P_{role,i} = P_{focal,i} \\ 0 & P_{role,i} < P_{focal,i} \end{cases}$$
(4.86)

Only the sign of the difference between the payoff of the role player and the focal player is important. Thus, if the role player fares better in the population, it will be always imitated, no matter how better its strategy is, as even a small difference in the payoffs implies a change in the tactic of the focal. Therefore, in the Markov chain we can observe vanishing transition probabilities according to the sign of  $\Delta P_i = P_{role,i} - P_{focal,i}$ .



Figure 4.6: Vanishing  $\mu_i$  for extreme selection and  $\Delta P_i > 0$  under the pairwise comparison and the Fermi function.



Figure 4.7: Vanishing  $\lambda_i$  for extreme selection and  $\Delta P_i < 0$  under the pairwise comparison and the Fermi function.

With an extreme imitation dynamics, the evolution reduces to a semi-deterministic process, because the direction is deterministically inferred while the speed of the process remains stochastic. In fact, the probability that the focal and the role have the same strategy is not zero and thus the process may arbitrarily stay in the same state for many time steps.

Finally, also in this context we notice that the two symmetric selection scenarios of "mutual invasion and slow fixation of one strategy" disappear. It turns out that



Figure 4.8: Extreme selection and  $\Delta P_i = 0$  under the pairwise comparison and the Fermi function.

when  $\Delta P_1 > 0$  and  $\Delta P_{N-1} < 0$ , then  $\rho_{AB} = \rho_{BA} = 0$ , because of the vanishing  $\mu_1$  and  $\lambda_{N-1}$ . The Markov chain is the following:



Figure 4.9: Markov chain in the scenario of mutual invasion and no fixation under the pairwise comparison with the Fermi function.

The table with the selection scenarios is therefore rewritten:

Class	Symbol	Invasion and fixation scenario
1.A	$B \xrightarrow{\rightarrow} A$	Invasion and quick fixation of one strategy
1.B	$B \overleftarrow{\leftarrow} A$	
2	$B \rightleftharpoons \overleftarrow{\leftarrow} A$	Mutual invasion and no fixation
3	$B \xleftarrow{\rightarrow}{\leftarrow} A$	No invasion and no (quick) fixation

Table 4.8: Selection scenarios in the  $s \to \infty$  limit under the pairwise comparison and the Fermi function.

#### 4.2.5 The deterministic limit

To conclude this chapter, we report our last result. Also for the pairwise comparison it is possible to explore mathematically the transition from the stochastic description of the evolutionary process in finite population towards the deterministic theory of the replicator equation. We can start directly from the equation (4.64), as the background theory has been already widely presented in the corresponding section.

In the limit of  $N \to \infty$  the transition probabilities and the expected payoffs of formulas (3.2) and (3.3) are rewritten in terms of x = i/N. They read as:

$$\lambda(x) = \frac{1}{1 + \exp(-s(P_{A,x} - P_{B,x}))} x(1 - x), \tag{4.87}$$

$$\mu(x) = \frac{1}{1 + \exp(-s(P_{B,x} - P_{A,x}))} (1 - x)x, \qquad (4.88)$$

In order to get the rate of change of the variable x, we have to perform the subtraction between  $\lambda(x)$  and  $\mu(x)$ . Through some maths we obtain:

$$\dot{x} = \lambda(x) - \mu(x) = \frac{1 - \exp(-s(P_{A,x} - P_{B,x}))}{1 + \exp(-s(P_{A,x} - P_{B,x}))} x(1 - x)$$
(4.89)

In the limit of extreme selection, the multiplicative term can be reduced as follows:

$$\frac{1 - \exp(-s(P_{A,x} - P_{B,x}))}{1 + \exp(-s(P_{A,x} - P_{B,x}))} = \begin{cases} 1 & P_{A,x} > P_{B,x} \\ -1 & P_{A,x} < P_{B,x} \end{cases}$$
(4.90)

The differential equation that governs the evolutionary dynamics becomes:

$$\dot{x} = \begin{cases} x(1-x) & P_{A,x} > P_{B,x} \\ -x(1-x) & P_{A,x} < P_{B,x} \end{cases}$$
(4.91)

We can now represent graphically the trend of  $\dot{x}$  in the different selection scenarios.



Figure 4.10:  $\dot{x}$  in the deterministic limit for the pairwise comparison. Case (1) refers to the dominance of strategy A, case (2) represents the coexistence scenario and finally case (3) shows the mutual exclusion.

# Chapter 5

# Monte Carlo simulations

This chapter is structured in two parts: in the former, we briefly report some theoretical hints on Monte Carlo methods, while in the latter we show our experimental activities. We perform Monte Carlo simulations of random games from the point of view of the expected selection scenario identified by means of the evaluation of the classification parameters. First of all, we want to verify that the corresponding selection outcome belongs to one of the seven scenarios eligible for finite populations under the Moran process with exponential fitness and the pairwise comparison with exponential imitation probability. Moreover, we want to numerically estimate how large the parameters of the population size and the intensity of selection should be in order that the three scenarios allowed by the theoretical proofs for N and s large are the only ones to be observed, while all the others become increasingly rare and eventually disappear.

### 5.1 Monte Carlo methods

Monte Carlo methods represent a significant class of computational algorithms that can be adopted to obtain numerical results for problems in many application fields. In [30], a distinction between a simulation, a Monte Carlo method and a Monte Carlo simulation is proposed. A simulation is a fictitious representation of reality, a Monte Carlo method is a technique that can be used to solve a mathematical or statistical problem, and finally a Monte Carlo simulation uses repeated sampling to determine the properties or the behavior of phenomena and systems. For our purposes, we discuss more in detail the Monte Carlo simulations. Typically, the general pattern to describe such simulations is arranged in the following steps:

a. Definition of the domain of possible inputs.

- b. Random generation of inputs from a given probability distribution over the domain. Each set of samples defines an iteration of the Monte Carlo simulation and usually this step is performed hundreds or thousands of times.
- c. According of the specific problem, a computation on every set of inputs is performed and properly recorded.
- d. Results are then aggregated to statistically infer properties on the system taken in consideration.

Monte Carlo simulations not only supply a comprehensive view of what may happen, but also how likely it is to happen, providing in this way a probability distribution of possible outcomes.

We report now a theorem proposed in [31] and here revisited for our purposes:

**Theorem 5.1.** Given a violation parameter  $0 < \alpha < 1$  and a confidence parameter  $0 < \beta < 1$ , performing N simulations (i.e. extracting N set of samples), if

$$N \ge \frac{2}{\alpha} \left( \ln \frac{1}{\beta} + 1 \right),\tag{5.1}$$

then with probability no smaller than  $1 - \beta$ , a selection scenario, which should not be present, exists in the set of all possible 2-players-2-strategies games, with population size and selection strength fixed, at most in an  $\alpha$ -fraction.

Therefore, this is the theoretical background of Monte Carlo simulations on which we found our numerical results in order:

- 1. to support the two conjectures that exclude some combinations of invasion and fixation probability with a certain fixation time,
- 2. to assess the order of magnitude of the population size and the intensity of selection which allows to rule out some selection outcomes reducing to three the only admissible scenarios.

As far as concerns the results of the theorems in the section 4.1.1 and 4.2.1, respectively for the Moran process with exponential fitness and the pairwise comparison with the Fermi function, we know that some selection scenarios are forbidden. Then, we expect that such outcomes will never occur in the simulations, because mathematical proofs already exclude them.
#### 5.2 Implementation and results

The code has been completely implemented in MATLAB. In the following, we just point out the basic structure of the main variables (for a deeper analysis, part of the code is reported in Appendix A).

Sampling of random games. As both the Moran process with exponential fitness and the pairwise comparison with the Fermi function are characterized by the main quantity  $\beta_i$  and this quantity depends on the payoff difference, it follows that the two processes are invariant to adding a constant to all entries of the payoff matrix. For this reason, the variables a, b, c and d, which define the game matrix, have been extracted randomly with a uniform distribution in [0, 1], without loss of generality. We have performed 10000 random sampling of games and this corresponds more or less to set  $\alpha = \beta = 0.001$ . To completely identify a game in the set of all possible games, we have also to establish the population size and the selection strength. For this aim, we have not sampled random values, but we have used deterministic, pseudo-random sequences. Hence, each game matrix has been evaluated on a fixed grid of (Sv, Nv) values, where the variable Sv identifies 61 values for the selection strength, while Nv identifies 45 values for the population size.

The next step consists in the computation of the classification parameters. We briefly discuss each one.

Invasion coefficient. Formulas (4.9) and (4.10) have been easily implemented defining a row vector containing the sums of the payoff differences for different indices. In particular, variables Deltap1 and DeltapN1 represent respectively  $\Delta P_1$  and  $\Delta P_{N-1}$ . Evaluating these variables with respect to 0 corresponds exactly to evaluate the invasion coefficients  $\beta_1$  and  $\beta_{N-1}$  with respect to 1.

Fixation probability. Numerical implementations of the fixation probabilities are more difficult to obtain, due to the sum of products. Instead of computing exactly  $\rho_{AB}$  and  $\rho_{BA}$ , we use formulas (4.7), (4.8) which define  $s_1$  and  $s_2$ . In the code, they respectively correspond to sumAB and sumBA and have to be compared with N - 1.

Until here, the implementation is totally identical for the two evolutionary processes, since the above classification parameters turn out to be the same, as we have seen from the theory in section 4.2.1. On the contrary, for the computation of the last indicator, the  $t_{fix}$ , it is also necessary to settle the transition probability  $\lambda$ (or  $\mu$  in the case the dual formula (4.52) is adopted). Since the definition of these variables is different according to the microscopic method of strategy spreading, we will distinguish the two situations. Anyway, in both cases, the transition probabilities have not been divided by N, in order to avoid too small numbers when large population size or selection strength are analysed. As a consequence, the fixation time has to be compared only with N - 1, in the case of the Moran process, and with 2(N - 1), in the case of the pairwise comparison.

**Fixation time.** The most argue part refers the implementation of the fixation time. With the more straightforward translation of the formula into the code, whenever the intensity of selection or the population size becomes larger, we fare problems of obtaining NaN in the overall result. This is due to the fact that the single components in the formula may tend to 0 or Inf and subsequently indeterminate forms may arise. It follows that we cannot discriminate the resulting time. For this reason, in order to get always a finite results (or at least Inf that can be interpreted as a very long fixation time which allows us to classify the process as slow), we turn to the theory of large s in sections 4.1.3 and 4.2.3, considering which terms develop singularities and which ones tend to infinity. According to the theoretical analysis, we have to discriminate four cases, depending on the relative values of the invasion coefficients. Therefore, in the code, the variable ftimeadj is computed differently in accordance with the corresponding case. The underlying idea is to rearranged the terms in order to manage the eventual indeterminate forms. Note that in the case of the *B*-dominance or in the mutual exclusion scenario when  $P_{1,N-1} < 0$ , we use the dual formula for the computation of the fixation time.

Once all the indicators have been obtained and compared with the reference values, it is hence possible to associate to a game the corresponding expected selection scenario.

We can now show the results achieved.

First of all, we have to say that the evaluation of the classification parameters has always led to one of the seven generic selection scenario. In the figures 5.1 and 5.2, for each pair of values (s, N) for the selection strength and the population size, a shade in greyscale represents the frequency of the sampled games which have an expected selection scenario of type (4), (5), (6) or (7) (look at table 4.1 for the description of the scenarios with the numbering). These outcomes are exactly those that should disappear when s and N become larger. The more the color is dark, the higher frequency of these four scenarios is found. We can then notice that for low values of s and N, it is very likely to find a game in (4)-(7). However, we do not observe totally black points, because, of course, a percentage of the games actually falls in the classification (1)-(3).

Secondly, we can assert that the two conjectures proposed in [10] are still valid, as in these simulations we have never observed some combinations of the fixation time for some scenarios allowed by the theorems. In particular, the scenario



Figure 5.1: Two-dimensional analysis for the Moran process with exponential fitness.

which predicts mutual invasion and the fixation of both strategies has been always characterized by a slow fixation time and thus we can exclude its counterpart with the fast time process. Instead, whenever the variables Deltap1 and DeltapN1 predict mutual exclusion, the corresponding fixation time turns out to be always fast, i.e. we have never observed scenarios of mutual exclusion with slow fixation time whatever the fixation probabilities are. Considering these results, we attest that the two conjectures are still valid for the Moran process with exponential fitness and the pairwise comparison with exponential imitation probability.

Figures inherent the two-dimensional analysis well show that increasing the parameter s or N, the percentage of the games with selection scenario in (4)-(7) dramatically decreases. When both are large enough, it is very likely to observe just scenarios in (1)-(3) and the image appears almost totally white. We can also numerically estimate how large these parameters should be: the three contour lines, from left to right, correspond respectively to frequencies 0.1, 0.01 and 0.001, which mean only 10%, 1% and 0.1% of games with expected selection scenario in (4)-(7). In the case of the Moran process with exponential fitness, when the intensity of selection is greater than about  $10^3$ , we can approximately identify the strong



Figure 5.2: Two-dimensional analysis for the pairwise comparison with exponential imitation probability.

selection framework, while when the population has more than  $10^4$  individuals this corresponds to large N limit. The overall result is in accordance with the theoretical proofs, which state that with large population size or strong selection only (1)-(3) are the admissible outcomes and now we have also seen, numerically speaking, the order of magnitude of this term *large* for N and for s. In the case of the pairwise comparison, the figure appears more or less the same as the one of the Moran process. However, looking carefully at the contour lines, we can state that a bigger value for the intensity of selection or the population size is required to reduce the frequency of scenarios (4)-(7).

In the last set of figures, we show for a fixed population size how the frequency of the selection scenarios changes. Each generic evolutionary outcomes is represented through a color and we observe that with increasing selection strength only three colors, which correspond exactly to scenarios (1)-(3), remains. Moreover, we note a sort of trade-off between the population size and the intensity of selection, as increasing N, a lower value of s is sufficient to rule out the scenarios (4)-(7).

The following figures are related to the Moran process with exponential fitness and similar images apply also for the pairwise comparison.



Figure 5.3: Numerical simulations for N = 10 under the Moran process.



Figure 5.4: Numerical simulations for N = 100 under the Moran process.



Figure 5.5: Numerical simulations for N = 1000 under the Moran process.

### Chapter 6

## Conclusion and future research

Among the vastness of theoretical models of evolutionary games proposed in the last years, in this thesis we have considered a very specific framework: a 2-players-2-strategies symmetric game in a well-mixed population. The results concern a quantitative and qualitative description of the evolutionary dynamics for two different recently introduced mechanisms of strategy spreading under frequency dependent selection: the Moran process with exponential fitness and the pairwise comparison with the Fermi function. The former belongs to the class of birth-death processes, whereas the latter regards the imitation learning evolution. In both methods, selection is parametrized by a quantity called intensity of selection.

As a first result, we have ascertained that the generic selection scenarios established in the literature for the Moran process with linear fitness are also the only ones admissible in the aforementioned processes.

After, through an approximation in the limit of large populations, we have recovered the connection with the traditional description of the evolutionary dynamics defined by the replicator equation. As previously shown in other surveys for the case of the linear fitness, also in this context the selection scenarios can be discriminated just by the relative magnitude of the entries in each column of the payoff matrix of the game.

The main result of this thesis, however, is the characterization of the evolutionary outcomes under strong selection. We have proved that when the intensity of selection is large, but still finite, some generic scenarios are excluded from the classification and the remaining are the same as for the large N limit, then they can be matched with the three generic outcomes known from the replicator equation. However, the evolutionary dynamics of a given game with strong selection remains dependent on the population size, i.e. the expected scenario can possibly change varying the number of individuals. Finally, exploring the extreme selection limit, we have refined the classification obtaining a result that better matches the deterministic description of the evolutionary outcomes.

To sum up all these results, we have challenged some of the key theoretical issues frequently discussed while modelling stochastic dynamics and comparing it with the deterministic background.

Regarding the experimental activities, by means of Monte Carlo simulations, we have also performed a numerical analysis to esteem how large should be the population size or the selection strength in order to observe the only three generic selection scenarios expected by the theoretical proofs. The results obtained from this analysis may be particularly useful at the time when real systems are modelled and these parameters have to be set. Having a rough idea of which scenarios might arise is an important starting point.

In the end, we can point out suggestions for future developments of this work.

- We have not deeply explored the non-generic selection scenarios, when at least one of the five indicators for the classification is exactly equal to the corresponding benchmark of the neutral game. A possible extension to this work would be to better investigate also the behavior of the system in these cases.
- We have admitted the presence of only two different strategies. In real systems however, many more strategies are conceivable. At the state of the art, for games with more than two strategies it has been shown that the dynamics becomes much more complex in the deterministic model [32]. In the stochastic setting, numerical examples through individual-based simulations have been analysed rather than theoretical models, due to the tricky mathematical description. However, it would be worthwhile to find conditions on the payoffs in the game matrix also for a generic game with n strategies.
- Another restriction of the models we have studied is that they do not allow the possibility to exit from an absorbing state once it has been reached. To better describe genetic mutations, or exploration dynamics, it is possible to introduce a variable which describes this phenomenon. At the start of the art, some models with the mutation rate have been proposed, for example in [33] an analysis under the Moran process with linear fitness and the strong selection, when fitness equals the expected payoff, has been performed. It is worth checking whether and how the dynamics changes with the two evolutionary processes we have considered.

- Finally, as last point, we have assumed a well-mixed population where players interact through random encounters. This is unrealistic in many contexts, as a player usually has the opportunity to interact only with its neighbours. Overlapping a structure, as a graph or a grid for example, on the population allows to deal with this feature. According to the system under examination, one can hence identify the better shape. Expected payoffs for the players would be possibly different and also the formulas for the transition probabilities in the Moran process or in the pairwise comparison can change if constraints on the population shape are imposed. This suggests that the analysis of the selection scenarios may differ too.

## Appendix A

### Code

In this appendix, the relevant part of the Matlab code for computing the classification parameters of a game is reported. All the necessary values are properly saved in a specific file .txt which is subsequently read by another MATLAB script (here not listed) to effectively perform the classification. In that script, a mere comparison between the computed variables and the benchmark values is then performed and it allows to discriminate between the selection scenarios. In the following, we report both the code for the Moran process and the pairwise comparison. Note that they are almost the same with the exception of the definition of the transition probabilities which are different for the two processes.

#### A.1 Code for the Moran process

```
1 777777777777777777777777777777
2 % Parameters %
4
  ngames = 10000;
5
6
  % Selection
7
   s10min = -2;
8
9
    s10max = 4;
    sv = logspace(s10min, s10max, 61);
10
11
12 % Population
    Nv = [4, 5, 6, 8, floor(logspace(1, 5, 41))];
13
14
16 % Code %
17 7777777777777777777777777
18
19 % open file
    fd=fopen('data.txt','wt');
20
```

```
^{21}
22
       for game = 1:ngames
23
      % game sample
24
         {\tt a}\ =\ {\tt rand}\,;
25
26
         b = rand;
         c = rand;
27
         d = rand;
^{28}
29
      % Population loop
30
          for N = Nv
31
         N1 = N-1;
32
33
34
      % Delta p_{1,k}, Delta p_{k,N-1}
         \texttt{Deltap1k} \ = \ (1:\texttt{N1}) \ / 2 \ / \ \texttt{N1} \ . \ * \ (2 \ * \ (b-d) \ * \ \texttt{N1} \ + \ (1:\texttt{N1}) \ * \ (a-b-c+d) \ - \ (a-b+c-d)) \ ;
35
          \texttt{DeltapNkN1} = (1:\texttt{N1})/2/\texttt{N1}.*(2*(\texttt{a-c})*\texttt{N1} - (1:\texttt{N1})*(\texttt{a-b-c+d}) - (\texttt{a-b+c-d}));
36
37
          Deltap1 = Deltap1k(1);
38
          DeltapN1 = DeltapNkN1(1);
39
      % print game
40
          fprintf(fd, '%e %e %e %e %d %e %e ',a,b,c,d,N,Deltap1,DeltapN1);
41
42
      % Selection loop
43
44
          for s = sv
45
         % exp of Delta p_{1,k}, Delta p_{k,N-1} / N1
46
47
            eDeltap1k = exp(-s*Deltap1k);
            eDeltapNkN1 = exp(s*DeltapNkN1);
48
49
         % fixation probabilities (sumAB, sumBA to be compared with N1)
50
            sumAB = sum(eDeltap1k);
51
            sumBA = sum(eDeltapNkN1);
52
53
         % fitnesses and transition probabilities
54
            Deltaf = \exp(s * (a * (0:N1-1)+b*(N1:-1:1) - c*(1:N1) - d*(N1-1:-1:0)) / N1);
55
            \texttt{lambda} = (1:\texttt{N1})./((1:\texttt{N1})+(\texttt{N1}:-1:1).*\texttt{Deltaf}.^{(-1)}).*(\texttt{N1}:-1:1); \%/N; \text{ not } \leftrightarrow
56
                 divided by N to avoid too small numbers
            \mathtt{mu} = (\mathtt{N1:-1:1}) . / ((1:\mathtt{N1}) . * \mathtt{Deltaf} + (\mathtt{N1:-1:1})) . * (1:\mathtt{N1}); \%/\mathrm{N}; same as for \leftrightarrow
57
                 lambda
58
            mu=flip(mu);
59
         \% fixation time (ftimeadj to be compared with N1)
60
            cumeDeltap1k = [0 \ cumsum(eDeltap1k(1:N1-1))];
61
62
            cumeDeltapNkN1 = [0 \ cumsum(eDeltapNkN1(1:N1-1))];
63
         % case-specific computation
64
            switch num2str(([Deltap1,DeltapN1]>0) - ([Deltap1,DeltapN1]<0), '%2d')
65
66
               case { '1 1', '1 0', '0 1', '0 0' } % A-DOMINANCE
67
               \texttt{ftimeadj} = (1 + \texttt{cumeDeltap1k(N1)}) / (\texttt{lambda(N1)*(1 + \texttt{sumAB})});
68
               for i = 1:N1-1
69
                 ftimeadj = ftimeadj + \leftrightarrow
70
                       (1+cumeDeltap1k(i))*(1+sum(exp(-s*(Deltap1k(i+1:N1) ...))))
71
                       -Deltap1k(i))))/(lambda(i)*(1+sumAB));
72
               end
73
               case { '-1-1 ', '-1 0 ', '0-1 '} % B-DOMINANCE
74
```

```
75
               \texttt{ftimeadj} = (1 + \texttt{cumeDeltapNkN1(N1))} / (\texttt{mu(N1)} * (1 + \texttt{sumBA}));
               for i = 1:N1-1
76
77
                  ftimeadj = ftimeadj + \leftrightarrow
                       (1+cumeDeltapNkN1(i))*(1+sum(exp(s*(DeltapNkN1(i+1:N1))...)))
                       -DeltapNkN1(i)))))/(mu(i)*(1+sumBA));
78
               end
79
80
               case { '-1 1 '} % MUTUAL EXCLUSION
81
               Deltap = (a-b-c+d)/N1;
82
               is = ceil(-Deltap1/Deltap);
83
               s1N1 = sum(exp(-s*(Deltap1k(1:N1)-Deltap1k(is))));
84
               \texttt{ftimeadj} = \texttt{s1N1} / (\texttt{mu(N1)} * (\texttt{exp}(\texttt{s*Deltap1k}(\texttt{is})) + \texttt{s1N1}));
85
               for i = 2:N1
86
                  if i <= is
87
                    \texttt{ftimeadj} = \texttt{ftimeadj} + \hookleftarrow
88
                          (\exp(s*Deltap1k(i-1))+sum(\exp(-s*(Deltap1k(1:i-2))))
89
                          -Deltap1k(i-1)))+1*sum(exp(-s*(Deltap1k(i:N1) ...))
90
                          -Deltap1k(is))))/(mu(N-i)*(exp(s*Deltap1k(is))+s1N1));
                  else
91
                    ftimeadj = ftimeadj + \leftrightarrow
92
                          (\exp(s*Deltap1k(is))+sum(\exp(-s*(Deltap1k(1:i-1))))
                          \texttt{-Deltap1k(is))))*(1+sum(exp(-s*(\texttt{Deltap1k(i+1:N1)} \ldots
93
                          -Deltap1k(i)))))/(lambda(i)*(exp(s*Deltap1k(is))+s1N1));
94
95
                 end
               end
96
97
               case { '1-1 '} % COEXISTENCE
98
               if Deltap1k(N1) >= 0
99
                  \texttt{ftimeadj} = (1 + \texttt{cumeDeltap1k(N1)}) / (\texttt{lambda(N1)*(1 + \texttt{sumAB})});
100
                  for i = 1:N1-1
101
                    ftimeadj = ftimeadj + \leftrightarrow
102
                         (1+cumeDeltap1k(i))*(1+sum(exp(-s*(Deltap1k(i+1:N1))...)))
103
                          -Deltap1k(i))))/(lambda(i)*(1+sumAB));
                 end
104
               else
105
                 \texttt{ftimeadj} = (1 + \texttt{cumeDeltapNkN1(N1))} / (\texttt{mu(N1)*(1 + \texttt{sumBA}));}
106
                  for i = 1:N1-1
107
108
                    \texttt{ftimeadj} = \texttt{ftimeadj} + \hookleftarrow
                          (1+cumeDeltapNkN1(i))*(1+sum(exp(s*(DeltapNkN1(i+1:N1) ...))))
109
                          -DeltapNkN1(i)))))/(mu(i)*(1+sumBA));
110
                 end
               end
111
112
113
            {\bf end}
114
115
       % print results
116
          fprintf(fd, '%e %e %e ', sumAB, sumBA, ftimeadj);
117
    % end selection loop
118
119
          end
120
    % end population loop
121
          end
122
123
124 % end game loop
125
      end
```

#### A.2 Code for the pairwise comparison

```
2 %
        Parameters
                           %
3 777777777777777777777777777
4
   ngames = 10000;
\mathbf{5}
6
7 % Selection
      s10min = -2;
8
      s10max = 4;
9
      sv = logspace(s10min, s10max, 61);
10
11
12 % Population
      Nv = [4, 5, 6, 8, floor(logspace(1, 5, 41))];
13
14
16 %
              Code
                            %
17 9878787878787878787878787878787878
18
  % open file
19
      fd=fopen('data.txt','wt');
20
21
22
      for game = 1: ngames
23
     % game sample
24
25
        a = rand;
26
        b = rand;
27
        c = rand;
28
        d = rand;
29
     % Population loop
30
        for N = Nv
^{31}
        N1 = N-1;
32
33
     \% Delta p_{1,k}, Delta p_{k,N-1}
34
         \texttt{Deltap1k} = (1:\texttt{N1})/2/\texttt{N1}.*(2*(\texttt{b-d})*\texttt{N1} + (1:\texttt{N1})*(\texttt{a-b-c+d}) - (\texttt{a-b+c-d}));
35
        \texttt{DeltapNkN1} \ = \ (1:\texttt{N1}) \ / \ 2 \ / \ \texttt{N1} \ . \ * \ (2 \ * \ (\texttt{a-c}) \ * \ \texttt{N1} \ - \ (1:\texttt{N1}) \ * \ (\texttt{a-b-c+d}) \ - \ (\texttt{a-b+c-d}) \ ) \ ;
36
37
        Deltap1 = Deltap1k(1);
        DeltapN1 = DeltapNkN1(1);
38
39
      % print game
40
         fprintf(fd, '%e %e %e %e %d %e %e ',a,b,c,d,N,Deltap1,DeltapN1);
41
42
      % Selection loop
43
         for s = sv
44
45
        % exp of Delta p_{1,k}, Delta p_{k,N-1} / N1
46
           eDeltap1k = exp(-s*Deltap1k);
47
           eDeltapNkN1 = exp(s*DeltapNkN1);
48
49
        % fixation probabilities (sumAB, sumBA to be compared with N1)
50
           sumAB = sum(eDeltap1k);
51
           sumBA = sum(eDeltapNkN1);
52
53
```

```
54
          % fitnesses and transition probabilities
             \texttt{Deltaf} = \exp(\texttt{s} * (\texttt{a} * (0:\texttt{N1}-1) + \texttt{b} * (\texttt{N1}:-1:1) - \texttt{c} * (1:\texttt{N1}) - \texttt{d} * (\texttt{N1}-1:-1:0)) / \texttt{N1});
55
56
             pBA = 1./(1 + Deltaf.^{(-1)});
             pAB = 1./(1 + Deltaf);
57
             lambda = pBA.*(1:N1).*(N1:-1:1)./N;
 58
             mu = pAB.*(1:N1).*(N1:-1:1)./N;
 59
             mu=flip(mu);
 60
 61
          % fixation time (ftimeadj to be compared with 2*N1)
 62
             cumeDeltap1k = [0 \ cumsum(eDeltap1k(1:N1-1))];
 63
             cumeDeltapNkN1 = [0 \ cumsum(eDeltapNkN1(1:N1-1))];
 64
 65
          \% case-specific computation
 66
             switch num2str(([Deltap1,DeltapN1]>0) - ([Deltap1,DeltapN1]<0), '%2d')
 67
 68
                case { '1 1', '1 0', '0 1', '0 0' } % A-DOMINANCE
 69
 70
                \texttt{ftimeadj} = (1 + \texttt{cumeDeltap1k(N1)}) / (\texttt{lambda(N1)} * (1 + \texttt{sumAB}));
                for i = 1:N1-1
 71
                  ftimeadj = ftimeadj + \leftrightarrow
 72
                       (1+cumeDeltap1k(i))*(1+sum(exp(-s*(Deltap1k(i+1:N1) ...))))
 73
                        -Deltap1k(i))))/(lambda(i)*(1+sumAB));
 74
                end
 75
                case { '-1-1 ', '-1 0 ', '0-1 '} % B-DOMINANCE
 76
                \texttt{ftimeadj} = (1 + \texttt{cumeDeltapNkN1(N1))} / (\texttt{mu(N1)} * (1 + \texttt{sumBA}));
 77
                for i = 1:N1-1
 78
                  \texttt{ftimeadj} = \texttt{ftimeadj} + \Leftarrow
 79
                       (1+cumeDeltapNkN1(i))*(1+sum(exp(s*(DeltapNkN1(i+1:N1) ...))))
                        -DeltapNkN1(i)))))/(mu(i)*(1+sumBA));
 80
                end
 81
 82
                case { '-1 1 '} % MUTUAL EXCLUSION
 83
                Deltap = (a-b-c+d)/N1;
 84
                is = ceil(-Deltap1/Deltap);
 85
                s1N1 = sum(exp(-s*(Deltap1k(1:N1)-Deltap1k(is))));
 86
                \texttt{ftimeadj} = \texttt{s1N1} / (\texttt{mu(N1)} * (\texttt{exp(s*Deltap1k(is))} + \texttt{s1N1}));
 87
                for i = 2:N1
 88
                  if i <= is
 89
 90
                     \texttt{ftimeadj} = \texttt{ftimeadj} + \Leftarrow
                          (\exp(s*Deltap1k(i-1))+sum(\exp(-s*(Deltap1k(1:i-2))))
                           -Deltap1k(i-1)))+1)*sum(exp(-s*(Deltap1k(i:N1) ...))
 91
                          \texttt{-Deltap1k(is)))} / (\texttt{mu(N-i)} * ( \underbrace{\exp(\texttt{s} \times \texttt{Deltap1k(is)}) + \texttt{s1N1}));
 92
                  else
 93
                     \texttt{ftimeadj} = \texttt{ftimeadj} + \hookleftarrow
 94
                          (\exp(s*Deltap1k(is))+sum(\exp(-s*(Deltap1k(1:i-1))))
                           -Deltap1k(is)))) *(1+sum(exp(-s*(Deltap1k(i+1:N1)))))
 95
                           -Deltap1k(i))))/(lambda(i)*(\exp(s*Deltap1k(is))+s1N1));
96
 97
                  end
                end
 98
 99
                case { '1-1 '} % COEXISTENCE
100
                if Deltap1k(N1) >= 0
101
                  \texttt{ftimeadj} = (1 + \texttt{cumeDeltap1k(N1)}) / (\texttt{lambda(N1)*(1 + \texttt{sumAB})});
102
103
                  for i = 1: N1-1
104
                     ftimeadj = ftimeadj + \leftrightarrow
                          (1+cumeDeltap1k(i))*(1+sum(exp(-s*(Deltap1k(i+1:N1))...)))
                          -Deltap1k(i)))))/(lambda(i)*(1+sumAB));
105
```

```
106
                   {\bf end}
107
                else
108
                   \texttt{ftimeadj} \; = \; (1 + \texttt{cumeDeltapNkN1(N1))} / (\texttt{mu(N1)*}(1 + \texttt{sumBA})) \; ;
                   for i = 1:N1-1
109
                     \texttt{ftimeadj} \ = \ \texttt{ftimeadj} \ + \ \hookleftarrow
110
                           (1+cumeDeltapNkN1(i))*(1+sum(exp(s*(DeltapNkN1(i+1:N1) ...))))
                           -DeltapNkN1(i)))))/(mu(i)*(1+sumBA));
111
112
                   {\bf end}
                end
113
114
115
             {\bf end}
116
117
       % print results
118
           fprintf(fd, '\%e \%e \%e ', sumAB, sumBA, ftimeadj);
119
120 % end selection loop
121
          end
122
123 % end population loop
124
          end
125
126 % end game loop
     end
127
```

# Bibliography

- J von Neumann and O Morgenstern. Theory of Games and Economic Behavior. Princeton University Press, 1944.
- John Nash. Non-cooperative games. Annals of mathematics, pages 286–295, 1951.
- [3] J Maynard Smith and GR Price. The logic of animal conflict. Nature, 246:15, 1973.
- [4] Martin A Nowak. *Evolutionary dynamics*. Harvard University Press, 2006.
- [5] Peter D Taylor and Leo B Jonker. Evolutionary stable strategies and game dynamics. *Mathematical biosciences*, 40(1):145–156, 1978.
- [6] John Maynard Smith. *Evolution and the Theory of Games*. Cambridge university press, 1982.
- [7] Josef Hofbauer and Karl Sigmund. Evolutionary games and population dynamics. Cambridge University Press, 1998.
- [8] Martin A Nowak and Karl Sigmund. Evolutionary dynamics of biological games. science, 303(5659):793-799, 2004.
- [9] Christine Taylor, Drew Fudenberg, Akira Sasaki, and Martin A. Nowak. Evolutionary game dynamics in finite populations. *Bulletin of mathematical biology*, 66(6):1621–1644, 2004.
- [10] Tibor Antal and Istvan Scheuring. Fixation of strategies for an evolutionary game in finite populations. *Bulletin of mathematical biology*, 68(8):1923–1944, 2006.
- [11] Josef Hofbauer, Peter Schuster, and Karl Sigmund. A note on evolutionary stable strategies and game dynamics. *Journal of Theoretical Biology*, 81(3):609– 612, 1979.

- [12] Josef Hofbauer and Karl Sigmund. Evolutionary game dynamics. Bulletin of the American Mathematical Society, 40(4):479–519, 2003.
- [13] Arne Traulsen and Christoph Hauert. Stochastic evolutionary game dynamics. *Reviews of nonlinear dynamics and complexity*, 2:25–61, 2009.
- [14] Philipp M Altrock, Chaitanya S Gokhale, and Arne Traulsen. Stochastic slowdown in evolutionary processes. *Physical Review E*, 82(1):011925, 2010.
- [15] Martin A Nowak, Akira Sasaki, Christine Taylor, and Drew Fudenberg. Emergence of cooperation and evolutionary stability in finite populations. *Nature*, 428(6983):646–650, 2004.
- [16] Howard E Taylor and Samuel Karlin. A first course in stochastic processes. Elsevier Science & Technology., 1975.
- [17] Nicolaas Godfried Van Kampen. Stochastic processes in physics and chemistry, volume 1. Elsevier, 1992.
- [18] Narendra S Goel and Nira Richter-Dyn. Stochastic models in biology. Elsevier, 1974.
- [19] Patrick Alfred Pierce Moran et al. The statistical processes of evolutionary theory. The statistical processes of evolutionary theory., 1962.
- [20] Warren J Ewens. Mathematical Population Genetics. Springer, 1979.
- [21] Philipp M Altrock and Arne Traulsen. Fixation times in evolutionary games under weak selection. New Journal of Physics, 11(1):013012, 2009.
- [22] Arne Traulsen, Noam Shoresh, and Martin A. Nowak. Analytical results for individual and group selection of any intensity. *Bulletin of mathematical biology*, 70(5):1410–1424, 2008.
- [23] Philipp M. Altrock and Arne Traulsen. Deterministic evolutionary game dynamics in finite populations. *Physical Review E*, 80(1):011909, 2009.
- [24] Arne Traulsen, Jens Christian Claussen, and Christoph Hauert. Coevolutionary dynamics: from finite to infinite populations. *Physical review letters*, 95(23):238701, 2005.
- [25] Christoph Hauert and György Szabó. Game theory and physics. American Journal of Physics, 73(5):405–414, 2005.

- [26] Lawrence E Blume. The statistical mechanics of strategic interaction. Games and economic behavior, 5(3):387–424, 1993.
- [27] Arne Traulsen, Jorge M. Pacheco, and Martin A. Nowak. Pairwise comparison and selection temperature in evolutionary game dynamics. *Journal of theoretical biology*, 246(3):522–529, 2007.
- [28] Arne Traulsen, Martin A Nowak, and Jorge M Pacheco. Stochastic dynamics of invasion and fixation. *Physical Review E*, 74:011909, 2006.
- [29] Bin Wu, Benedikt Bauer, Tobias Galla, and Arne Traulsen. Fitness-based models and pairwise comparison models of evolutionary games are typically differenteven in unstructured populations. New Journal of Physics, 17(2):023043, 2015.
- [30] Shlomo S Sawilowsky and Gail C Fahoome. Statistics via monte carlo simulation with fortran. *Rochester Hills, MI, JMASM*, 2003.
- [31] Marco C Campi, Simone Garatti, and Maria Prandini. The scenario approach for systems and control design. Annual Reviews in Control, 33(2):149–157, 2009.
- [32] Brian Skyrms. Chaos in game dynamics. Journal of Logic, Language and Information, 1(2):111–130, 1992.
- [33] Drew Fudenberg, Martin A. Nowak, Christine Taylor, and Lorens A. Imhof. Evolutionary game dynamics in finite populations with strong selection and weak mutation. *Theoretical population biology*, 70(3):352–363, 2006.