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ATA DA SESSÃO DE ARGUIÇÃO DA 617ª DISSERTAÇÃO DO PROGRAMA DE PÓS-GRADUAÇÃO EM FÍSICA DEFENDIDA POR JULIUSS FRANCO PAZ VARGAS, orientado pelo professor Lucas Lages Wardil para obtenção do grau de **MESTRE EM FÍSICA**. Às 09:00 horas de quatorze de fevereiro de 2019, na sala 4129 do Departamento de Física da UFMG, reuniu-se a Comissão Examinadora, composta pelos professores **Lucas Lages Wardil** (Orientador - Departamento de Física/UFMG), **José Marcos Andrade Figueiredo** (Departamento de Física/UFMG) e **Carlos Henrique Costa Moreira** (Departamento de Matemática/UFMG) para dar cumprimento ao Artigo 37 do Regimento Geral da UFMG, submetendo o bacharel **JULIUSS FRANCO PAZ VARGAS** à arguição de seu trabalho de dissertação, que recebeu o título de **"Frequency-dependent mutation rates and the evolution of cooperation"**. Às 14:00 horas do mesmo dia o candidato fez uma exposição oral de seu trabalho durante aproximadamente 50 minutos. Após esta, os membros da comissão prosseguiram com a sua arguição e apresentaram seus pareceres individuais sobre o trabalho, concluindo pela aprovação do candidato.

Belo Horizonte, 14 de fevereiro de 2019.

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Frequency-Dependent Mutation Rates and the Evolution of Cooperation

Dissertação apresentada ao Programa de Pós-Graduação em Física do Instituto de Ciências Exatas da Universidade Federal de Minas Gerais como requisito parcial para obtenção do título de Mestre em Ciências.

Supervisor: Prof. Lucas Lages Wardil

Belo Horizonte
2019

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I am deeply thankful to my supervisor Prof. Lucas Lages Wardil. My most sincere words of thanks for his time and invaluable guidance.

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Abstract

Nesta dissertação estudamos a evolução da cooperação em populações finitas com taxas de mutação dependentes da frequência. Existem dois tipos de indivíduos: cooperadores e desertores. Os indivíduos interagem aleatoriamente, recebendo um ganho especificado pelo jogo do Dilema do Prisioneiro. O processo de Markov do nascimento-morte estudado aqui é um exemplo de um passeio aleatório com taxas de salto dependentes do sítio. Consideramos um Processo de Moran e três cenários diferentes de taxa de mutação/exploração dependentes da frequência: Agentes Mutagênicos, Exploração Conformista e Exploração Inovativa. Esta taxa de mutação/exploração denota quanto um indivíduo está aberto para mudar e experimentar novas ações diferentes ou inovadoras e explorar novas estratégias aleatoriamente. Na evolução biológica, a mutação ocorre tão raramente, mas, na evolução cultural, a exploração é um passo importante, pois os indivíduos experimentam novos comportamentos com muito mais frequência. A probabilidade de fixação de um único cooperador aparece proeminentemente nesta dissertação e sua forma é estudada na dinâmica de seleção usando a probabilidade de fixação de mutantes neutros como um ponto de referência para o estudo de seleção no Processo de Moran e nos três diferentes cenários de taxa de mutação/exploração dependentes da frequência.

Palavras-chave: Processo Estocástico, Dinâmica Evolutiva, Dilema do Prisioneiro, Probabilidade de Fixação, Coevolução Gene-Cultura.

Abstract

In this dissertation we study the evolution of cooperation in finite populations with frequency-dependent mutation rates. There are two types of individuals: cooperators and defectors. Individuals interact randomly, receiving a payoff specified by the Prisoner's Dilemma game. The birth-death Markov process studied here is an instance of a random walk with site dependent hopping rates. We consider a Moran Process and three different frequency dependent mutation/exploration rate scenarios: Mutagens, The Conformist Exploration, and The Innovative Exploration. This mutation/exploration rate denotes how much an individual is open to change and trying out new different actions or innovate and explore new strategies at random. In biological evolution, mutation occurs so rarely, but in cultural evolution, exploration is an important step since individuals try out new behaviors much more frequently. The fixation probability of a single cooperator features prominently in this dissertation and its shape is studied in selection dynamics using the fixation probability of neutral mutants as a benchmark for the study of selection in the Moran Process and in the three different frequency dependent mutation/exploration rate scenarios.

Keywords: Stochastic Process, Evolutionary Dynamics, Prisoner's Dilemma, Fixation Probability , Gene-Culture Coevolution.

Contents

1 Introduction

Evolutionary Game Theory has generated an enormous amount of interest lately [1–3]. Among the features of the Evolutionary Game Theory is that it models the animal world, it describes the science of behavior and the dynamics of the population. It is considered a dynamical version of classical game theory. It describes, mathematically, the complex phenomena: interacting agents, spatial patterns, noise, non-linearity, etc.

Most of this dissertation studies evolution under the so-called Moran Process, or variations thereof. In the Moran process, change in the composition of a finite fixed-sized population is described while two types of individuals compete. The situation of a population with N individuals is completely described by the number $i = 1, \ldots, N$ of one of the two types of individuals, so the number of the other type is $N - i$. Time is discrete: at each time step one individual is randomly selected for reproduction (by producing a copy of itself) and one individual is randomly selected to be removed from the population. In both cases the same individual can be selected.

In finite populations evolutionary dynamics manifests an equilibrium between Darwinian selection and neutral drift. For a considered term population structures were assumed to leave this equilibrium unaffected on the condition that residents and the mutants have fixed fitness values. This outcome in fact holds for a definite (large) class of population structures. Although other structures can incline the equilibrium to the extend that either selection is removed and drift rules or drift is removed and only selection is significant.

Regardless of the fact that in nature, fitness is generally affected by interactions with other individuals of the population. This is of particular interest for the evolution of cooperation. The crucial element of this evolutionary conundrum is seized by social dilemmas: cooperators afford a benefit to the group at some cost to themselves, whereas defectors achieve to exploit the group by obtaining the benefits without enduring the costs of cooperation. Hence, defectors outcompete cooperators and cooperation is annihilated due to selection. However, other processes may be in place and cooperators may have an opportunity to outcompete defectors. One example is that of punishing behavior, whereby cooperators punish defectors at a cost to themselves. If there are enough cooperators, cooperation may flourish and remain stable [4].

In this dissertation, we analyze the evolution of cooperation in the simplest scenario, where only cooperators and defectors are present in a finite well-mixed population (random interactions). We explore the effect of different functional forms of the mutation rates on the evolution of cooperation. First, we provide a brief introduction to the core ideas of evolution, followed by a comprehensive introduction to the Evolutionary Game Theory. This first introductory part was largely based on Martin Nowak's book, "Evolutionary Dynamics: Exploring the Equations of Life" [1]. Then, we present some key definitions from the theory of Markov Chains needed to define the stochastic process, the Moran process, which we use to analyze the evolution of cooperation in finite populations. In the last chapter we present the results of our explorations.

2 What Evolution is

Evolution needs populations of reproducing individuals. Evolutionary game dynamics acts on populations - neither genes, nor cells, nor individuals evolve. Selection manifests the reality that the genes or behavioral patterns of individuals with a higher fitness have a higher chance to be passed to succeeding generations by the means of biological reproduction or cultural imitation. The evolutionary process is established by:

Replication: In finite populations the transmissions of traits by the means of reproduction or imitation is generally a process involving probability. The achievement of a trait is proportional to the fitness of its carriers but a high fitness does not afford any assurance for success. With a little probability even the fittest individual of the population may not get an opportunity to pass its trait to the next generation.

Selection: Individuals with a fitness that surpasses the mean fitness in the population have a higher tendency to pass their genetic or cultural traits to progeny in succeeding generations and these traits are likely to grow in abundance. Analogously, traits that lower the fitness of an individual have little opportunities to be passed to the following generation, reduce in abundance and ultimately vanish.

Mutation: Mutations and genetic recombination in addition to impulsive alterations and mistaken imitations of behavioral patterns produce fitness differences among individuals of the population. These differences are amplified when selection acts on them over time.

2.1 Reproduction

Individuals reproduce and lead to progeny. Let us represent this process by imagining a single bacterial cell which divides by fission, so when this bacterium grows in an environment where nutrients are rich, it divides every twenty minutes. We call that time a time of one generation, upon completion of twenty minutes bacteria divide and we have two progenies, at the end of forty minutes the two progenies will themselves be ready for division, and at the end of time equal to two generations we are going to end up with four bacteria and this process will continue in the future provided the resources that are available to the bacterium are not constrained at any way.

Mathematically this process can be modeled by a difference equation (time is measured in discrete steps). Assuming that the size N_n of a cell population at time n totally defines its size at time $n + 1$, therefore the cell population is modeled by the following difference equation

$$N_{n+1} \quad = \quad 2N_n. \tag{2.1}$$

After n generations there will be 2^n cells and N_0 is the initial condition (number of cells at time 0)

$$N_n \quad = \quad N_0\, 2^n. \tag{2.2}$$

We also have another way to capture the dynamics of growth in bacteria. In order to do that we will use the tool of differential equations and say that if $N(t)$ denotes the number of bacteria at time t, then we can assume that the rate of change of $N(t)$, which is the number of bacteria at any time, is directly proportional to the size of the number of bacteria at that time and r is the rate of growth (reproductive rate). In our case the bacterium divides every twenty minutes so the rate of growth is one division every twenty minutes, that is, the rate of growth has units time inverse which is one by twenty minutes inverse. This is a differential equation formulation of modeling bacterial growth:

$$\dot{N} \quad = \quad rN. \tag{2.3}$$

And now we can simply integrate the differential equation 2.3 to obtain an analytical expression for getting an approximation of number of bacteria at time t when knowing that we are starting with a particular number of bacteria N_0 at t equal zero. Then the solution of the differential equation 2.3 is

$$N(t) \quad = \quad N_0\, e^{rt}. \tag{2.4}$$

This solution reduces to that of the difference equation in discrete time 2.2 if we settle $r = ln2$ or $e^r = 2$ and quantify the model at unit intervals of time $t = n$. By this settling, the linear discrete-time equation $N_{n+1} = 2N_n$ and the linear differential equation $\dot{N} = rN$, are directly related.

At this point a question emerges: what are the mechanisms of growth that we have not captured in these two formulations?

(i) There is no death in either of these two models.

(ii) We have unconstrained growth in our models. In real environments constraints are very likely to set in very fast and competition for resources would mean that resource availability becomes a constraint and bacterial growth slows down. So there is no concept of resource limitation in either of these two formulations and both of them allow for unconstrained growth.

Death has to be incorporated into a realistic model of growth. Assuming that d represents the death rate, we obtain the differential equation

$$\dot{N} \;=\; \text{rate of growth} - \text{death rate} \;=\; r\,N - d\,N, \tag{2.5}$$

integrating the last equation we find

$$N(t) \;=\; N_0\, e^{(r-d)\,t}. \tag{2.6}$$

We can have three scenarios associated with growth when we incorporate death into account.

a) $r > d$

In this case the exponent of equation 2.6 is positive meaning that this function grows exponentially and so the number of bacteria.

b) $r < d$

This is exactly the opposite,because the exponent associated with this function is negative and the solution is going to be of decaying nature and thus the bacterial number approaches extinction.

c) $r = d$

This is the case when the growth rate is matched by the death rate which means that the number of bacteria stays constant.

We are going to add to our unconstrained equation 2.3 another factor which represents the carrying capacity K and on incorporation our equation is given by

$$\dot{N} \;=\; rN\left(1 - \frac{N}{K}\right). \tag{2.7}$$

Equation 2.7 is known as the logistic equation. The factor K represents the maximum number of individuals that can survive in a particular environment where growth stops. The behavior of 2.7 is easy to analyze. The rate of change $\dot{N}$ is zero for $N = 0$ and $N = K$. In these two cases, the density does not change. $N(t)$ increases for $0 < N < K$, and $N(t)$ decreases for $N > K$. Equation 2.7 faithfully captures the resource limitation that is taking place as bacterial numbers are increasing in time. The logistic model 2.7 makes several assumptions about the population:

- The reaction to an alteration in population density is spontaneous.
- The inherent rate of increase is lowered by a fixed quantity for every individual adjoined to those previously present.
- Crowding has an effect on all individuals and life phases of a population equitably.
- The environment is fixed; stochastic and genetic results are insignificant.

The solution of 2.7 is given by

$$N(t) = \frac{K\,N(0)\,e^{rt}}{K + N(0)\,(e^{rt} - 1)}. \tag{2.8}$$

2.2 Selection

Suppose we have different n species and they evolve. Their evolutionary success depends on its fitness and fitness basically means how many offspring they are expected to have. In this case, the simple case, fitness is constant f_i and if we look at the relative frequency of any particular species, the one with the highest fitness will dominate.

Let N_i be the number of individuals using a strategy, then the total population size is

$$N = \sum_{i=1}^{n} N_i, \tag{2.9}$$

the proportion of individuals (frequency) using a strategy is

$$x_j = \frac{N_j}{N}, \tag{2.10}$$

the rate of change of the number of individuals using a strategy $\dot{N}_j$ is given by the growth equation 2.3 and the fitness is related to the reproductive rate

$$\dot{N}_j = f_j\,N_j. \tag{2.11}$$

Rewriting equation 2.10

$$N_j = N x_j \tag{2.12}$$

Considering equation 2.9 and having in mind that $\dot{N}$ is the rate of change of total population we differentiate each side of equation 2.12 with respect to time

$$\dot{N}_j = N\,\dot{x}_j + x_j\,\dot{N} \tag{2.13}$$

Rearranging equation 2.13 and performing the required mathematical operations

$$N\,\dot{x}_j = \dot{N}_j - x_j\,\dot{N} \tag{2.14}$$

$$N\,\dot{x}_j = \dot{N}_j - x_j \sum_{i=1}^{n} \dot{N}_i \tag{2.15}$$

$$N\,\dot{x}_j = f_j\,N_j - x_j \sum_{i=1}^{n} f_i\,N_i \tag{2.16}$$

$$N\,\dot{x}_j = f_j\,N\,x_j - x_j \sum_{i=1}^{n} f_i\,N\,x_i \tag{2.17}$$

canceling N from both sides, selection can be modeled by an ordinary differential equation of the form

$$\begin{aligned} \dot{x}_j &= f_j\, x_j - x_j\, \phi(t) \;=\; x_j\,(f_j - \phi(t)) \qquad (2.18)\\ \phi(t) &= \sum_{i=1}^{n} f_i\, x_i \qquad (2.19) \end{aligned}$$

We get a selection dynamics equation 2.18 for $j = 1, 2, \ldots, n$ and equation 2.19 is the average fitness of the population.The rate of reproduction of j species for the relative frequencies is determined by the difference between the fitness and the average fitness of the population. The solution of equation 2.18 is

$$x_j(t) = \frac{x_j(0)\, e^{f_j t}}{\sum_{i=1}^{n} x_i(0)\, e^{f_i t}}; \qquad j = 1, 2, \ldots, n \qquad (2.20)$$

The adoption of normalized variables $\sum_{i=1}^{n} x_i = 1$ defines the unit simplex: $S_n^{(1)} = \{0 \le x_i \le 1\, \forall\, i = 1, 2, \ldots, n \,\wedge\, \sum_{i=1}^{n} x_i = 1\}$, as the physically available domain that achieves the conservation relation.

2.3 Mutation

The interaction of replication, mutation, and selection is the main point of Darwinian evolution, which could not be properly engage before knowledge on structures and functions of the molecules implicated in the process became accessible. Notably, the accessibility of mutants requires insight on the mechanism of mutation and the inner structure of a mutation space. Mutation can occur during reproduction and can also occur in the absence of reproduction.

Consider two types model, A and B. Assuming that u_1 represents the probability that the reproduction of A leads to B and u_2 the mutation rate from B to A, we get the mutation dynamics equations:

$$\begin{aligned} \dot{x}_{A} &= x_{A}(f_{A} - \phi) - x_{A} f_{A} u_1 + x_{B} f_{B} u_2\\ \dot{x}_{B} &= x_{B}(f_{B} - \phi) - x_{B} f_{B} u_2 + x_{A} f_{A} u_1 \end{aligned} \qquad (2.21)$$

Assume that A and B have the same fitness ($f_{A} = f_{B} = 1$) we rewrite equations 2.21 in the following way

$$\begin{aligned} \dot{x}_{A} &= x_{A}\,(1 - u_1) + x_{B}\, u_2 - \phi\, x_{A}\\ \dot{x}_{B} &= x_{A}\, u_1 + x_{B}\,(1 - u_2) - \phi\, x_{B} \end{aligned} \qquad (2.22)$$

so the average fitness is constant $\phi = 1$ and therefore $x_A + x_B = 1$, then

$$\begin{aligned} \dot{x}_A &= -x_A\, u_1 + x_B\, u_2 \\ \dot{x}_B &= x_A\, u_1 - x_B\, u_2 \end{aligned} \tag{2.23}$$

Now we want to understand the steady state of the system by making $\dot{x}_A = 0$ and $\dot{x}_B = 0$, the frequencies of A and B converge to the stable equilibrium respectively

$$\begin{aligned} x^*_A &= \frac{u_2}{u_1 + u_2} \\ x^*_B &= \frac{u_1}{u_1 + u_2} \end{aligned} \tag{2.24}$$

2.4 The Quasispecies Equation

For different n species we can model mutation as well. We denote by x_i the relative abundance (frequency) of phenotype i and have $\sum_{i=1}^{n} x_i = 1$. The fitness of phenotype i is represented by f_i, a non-negative real number relating to the rate at which the phenotype i reproduces. The average fitness of the population is represented by $\phi(t) = \sum_{i=1}^{n} f_i\, x_i(t)$. During the reproduction of an individual, mistakes can occur. The probability of replication of a variant i results in variant j is given by Q_{ij} and this mutation matrix obey $\sum_{k=1}^{n} Q_{jk} = 1$.

A common equation used to model reproduction of viruses is the quasispecies equation [5]:

$$\dot{x}_i = \sum_{j=1}^{n} Q_{ij}\, f_j\, x_j - x_i\, \phi(t) \qquad i = 1, \ldots, n \tag{2.25}$$

It describes the mutation and selection of an infinitely large population on a constant fitness landscape and the dynamics is completely determined by the mutation-selection matrix $W = [f_j\, Q_{ji}]$.

In the quasispecies model, mutation is due to the replication process (this is the situation that is suitable for viruses) and correct replication and mutations are pictured as distinct response channels of the same replication step. The number of mutations is proportional to the number of replication occurrences or descents.

In order to fulfill the terms for the suitability of the Perron-Frobenius theorem, the mutation-selection matrix W has to be a primitive matrix (a primitive matrix is a square nonnegative matrix some power which is positive). The theorem guarantees that (i) the largest eigenvalue is real, positive, and non-degenerate; and (*ii*) the largest eigenvector has only rigorously positive components.

The quasispecies model considers replication and mutation as parallel response channels of one response step, and properly, the mutation-selection matrix is a product of the mutation and the fitness matrix.

The mutation matrix Q of the quasispecies model is a stochastic matrix, $\sum_{k=1}^{n} Q_{jk} = 1$, because a replication has to be either correct or prone to error.

3 Evolutionary Games

Evolutionary game theory has been of great use for the analysis of phenomena in a wide spectrum from the dynamics of bacterial populations to the evolution of social behavior [3]. Individuals are chosen as players that engage with each other in games. Over time, games are symbolical compendia of interactions, players who choose a certain strategy either achieve better than the mean population and enlarge in frequency, or achieve worse than the mean population and reduce in frequency. Following the variation in their frequencies over time, evolutionary game theory can give perception into the ultimate outcome of the strategies in a game, for example whether they govern, cohabit or go inactive from the population.

From the perspective of the dynamics the fitness is frequency dependent. Fitness of a type i, denoted $f_i(\vec{x})$, quantifies the achievement of replication of that type. This quantity relies on the state of the entire population.

The evolution of the frequencies of strategies in a population is depicted by the replicator dynamics. In some situations, a differential equation can model the underlying dynamics on the simplex S_n.

Assume that the population is divided into n phenotypes (strategies) with frequencies x_1 to x_n. The fitness f_i of phenotype i will be a function of the conformation of the population, i. e. of the state $\vec{x} = (x_1, \ldots, x_n)$. We assume that the state $x(t)$ evolves in S_n as a differentiable function of t, if the population is very big, and if the generations combine regularly into each other,. The rate of increase $\dot{x}_i/x_i$ of phenotype i is a meter of its evolutionary success, we can denote this success as the difference between the fitness $f_i(\vec{x}) = \sum_{j=1}^{n} a_{ij}\, x_j$ of phenotype i (a_{ij} are the entries of the payoff matrix $A = [a_{ij}]$) and the average fitness $\phi(\vec{x}) = \sum_{i=1}^{n} x_i\, f_i(\vec{x})$ of the population. Therefore we get

$$\frac{\dot{x}_i}{x_i} \;=\; \text{fitness of } i - \text{average fitness}, \tag{3.1}$$

which produces the replicator equation

$$\dot{x}_i \;=\; x_i\,(\,f_i(\vec{x}) - \phi(\vec{x})\,) \qquad i = 1, \ldots, n. \tag{3.2}$$

Equation 3.2 is defined on the simplex S_n which is given by $\sum_{i=1}^{n} x_i = 1$. The simplex is invariant under 3.2: if $\vec{x} \in S_n$ then $\vec{x}\,(t) \in S_n$ for all $t \in \mathbb{R}$.

3.1 Two Player Games

Conventionally, evolutionary game theory depicts evolution in phenotype space. The distinct phenotypic characteristics are called strategies. The replicator equation is at the essence of evolutionary game dynamics.

The frequencies of the different types in the population are allowed by the replicator equation to define the fitness landscape instead of establishing the fitness of each type to be constant (constant fitness is a special case of the replicator dynamics). Consider, in an infinitely large population, two types A and B with the frequencies x and $1-x$ correspondingly. A payoff matrix expresses the interaction between the two types

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \tag{3.3}$$

In this payoff matrix it is observed that when an A individual interacts with another A individual it gets a and when interacting with a B individual it gets b. We can find the average of both strategies from this payoff matrix, $f_A(x) = a\,x_A + b\,x_B = a\,x + b\,(1-x)$ and $f_B(x) = c\,x_A + d\,x_B = c\,x + d\,(1-x)$. These average payoffs can be interpreted as fitnesses of the two strategies. According to classical selection ideas the frequency of any type increases over time if its fitness is greater than the average fitness of the population and vice versa.

Consider the replicator equation when there are only two types, in the population, A and B with the following dynamics equations

$$\begin{aligned} \dot{x}_A &= x_A\,[f_A(\vec{x}) - \phi(\vec{x})] \\ \dot{x}_B &= x_B\,[f_B(\vec{x}) - \phi(\vec{x})] \end{aligned} \tag{3.4}$$

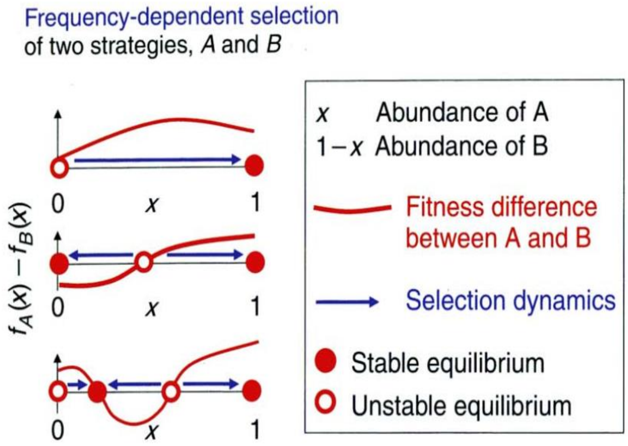
Where $\vec{x} = (x_A, x_B)$ defines the composition of the population with x_A the frequency of A and x_B the frequency of B. The average fitness is given by $\phi(\vec{x}) = x_A f_A(\vec{x}) + x_B f_B(\vec{x})$. Since $x_B = 1 - x_A$, it is enough to consider x_A , which we denote by x thus $x_B = 1 - x$, and hence

$$\dot{x} = x\,(1-x)\,[f_A(x) - f_B(x)]. \tag{3.5}$$

Analyzing for steady state equation 3.5, the equilibria are reached when $x = 0$, $x = 1$, and all values $x \in (0,1)$ leading to $f_A(x) = f_B(x)$. The equilibrium $x = 0$ leads to stability if $f_A(0) < f_B(0)$ and the equilibrium $x = 1$ is stable if $f_A(1) > f_B(1)$. An interior equilibrium, x^*, is considered stable if the derivatives of the fitnesses f_A and f_B fulfill $f'_A(x^*) < f'_B(x^*)$. Inside the interval $[0,1]$ there can be various stable and unstable equilibria. Figure 1 shows a graphical description.

These approaches can be properly expressed in the form of a differential equation which follows the variation in x over time. Substituting the linear fitness functions into

Figure 1 – Frequency-Dependent Selection (Figure from Nowak, 2006: Figure 4.2)



equation 3.5 gives

$$\dot{x} \quad = \quad x\,(1-x)\,[\,(a-b-c+d)\,x+b-d\,]. \tag{3.6}$$

Hence, through the fitness of the strategies the evolutionary game is introduced in the dynamics. Analyzing for steady state there are three possible solutions to this equation, strategy A goes extinct, $x = 0$ (we affirm that B dominates A if $a \leq c$ and $b \leq d$, where in any case one inequality must be strict), or the whole population consists of A players, $x = 1$ (we affirm that A dominates B if $a \geq c$ and $b \geq d$, where in any case one inequality must be strict), and lastly when the two strategies have equal fitness, $f_A = f_B$ which is when

$$x^* \quad = \quad \frac{d-b}{a-b-c+d}. \tag{3.7}$$

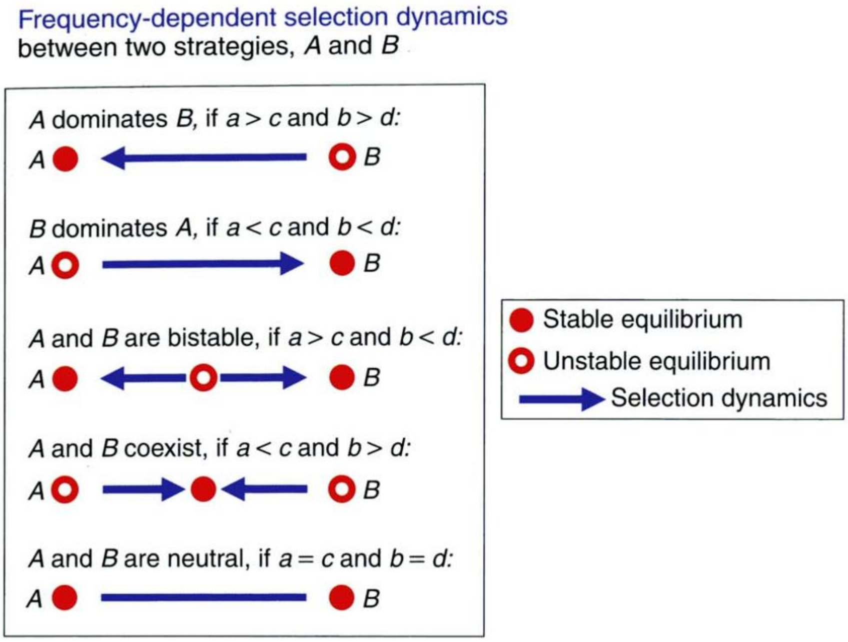
We state that A and B are bistable if $a > c$ and $b < d$. In the interval $[0, 1]$ an unstable equilibrium exists given by equation 3.7. The system will approach all-B if the initial condition, $x(0)$, is such that $x(0) < x^*$. Conversely, the system will approach all-A if $x(0) > x^*$.

We state that A and B stably coexist if $a < c$ and $b > d$. A population of A and B individuals will approach the interior, stable equilibrium given by equation 3.7.

We state that A and B are neutral if $a = c$ and $b = d$. The composition of the population will not be changed by selection. For selection dynamics any combination of A and B is an equilibrium.

See Figure 2 for a summary of the possible dynamics.

Figure 2 – Frequency-Dependent Selection Dynamics (Figure from Nowak, 2006: Figure 4.4)



3.2 The Nash Equilibrium

In modeling trouble situations among rational individuals, (if an individual holds consistent beliefs, is logically omniscient, knows the payoff matrix, and always chooses an action that maximizes the payoff that expects on the basis of beliefs, then the individual is considered rational), noncooperative game theory has become a pattern tool . Such a model details the group of strategies of every individual or player and the payoff to every player for any the strategy portrait, the register of strategies adopted by the players. The notion of Nash equilibrium (NE) is the key element in prognosticating the result of a game. Given the strategies played by the other players, in a Nash equilibrium each player's strategy maximizes his avail . In many scenarios it seems that the Nash equilibrium is not unique. The essential theoretical significance of Nash equilibrium rests on the certitude that if a game has a uniquely rational solution, then it is going to be a Nash equilibrium.

A Nash equilibrium is an aftermath in which the players' strategies are best replies to themselves. A Nash equilibrium possesses strategic stability, because none player could obtain a better payoff by adopting differently, given the coplayer's preference, and the players, therefore, have no reason to regret their own preferences when the result is exposed.

Consider the case of two players. Suppose that the game is defined by the payoff matrix between two strategies, A and B,

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \tag{3.8}$$

There are four different combination of strategies that the two players can adopt: (A, A), (B, B), (A, B), (B, A), where the first entry stands for the strategy adopted by the first player and the second entry the strategy adopted by the second player. Depending on the parameters, there can be four different Nash equilibria:

(i) (A, A) is a unique Nash equilibrium if $a \geq c$ and $b > d$.

(ii) (B, B) is a unique Nash equilibrium if $d \geq b$ and $c > a$.

(iii) (A, A) and (B, B) are both Nash equilibria if $a \geq c$ and $d > b$.

(iv) (A, B) and (B, A) are both Nash equilibria if $c \geq a$ and $b > d$.

For example, if $a \geq c$ and $b > d$, it means that no matter what the opponent does, it is always better to adopt A. Therefore, both adopt A and the outcome (A, A) is a unique Nash equilibrium. The stronger concept of strict Nash equilibrium can be defined by the same condition, except that "$\geq$" must be replaced by "$>$".

Observe that there is a distinction between the classical Game Theory and Evolutionary Game Theory. The classical Game Theory studies the Nash equilibria of the single encounters, where rational players are implicated in a game and each of them has to choose among different strategies in an effort to maximize a payoff, which rests on the strategies of all players. The composition of ideas from classical game theory and evolutionary theory resulted in Evolutionary game theory. More exactly, the Evolutionary Game Theory analyzes the evolution of the affluence of strategies in a population where strategies that provide higher payoff extend at higher rates and the payoff of a player relies on the strategies of the rest of the players and, therefore, on the rate of occurrence of each strategy inside the whole population.

3.3 Evolutionarily Stable Strategies

A strategy is evolutionarily stable if, at any time all members of the population implement it, under natural selection no discrepant behavior could overrun the population . The game between A and B is given by the general payoff matrix 3.3, and the fitnesses are given respectively by

$$\begin{aligned} f_A &= a\,x_A + b\,x_B \\ f_B &= c\,x_A + d\,x_B \end{aligned} \tag{3.9}$$

Assume a population in which the most of the players (fraction $1-\varepsilon$) plays strategy A and a few, ε plays mutant strategy B. A is an Evolutionarily Stable Strategy (ESS) if and only if it achieves strictly better than the mutant strategy B in opposition to the composed population. For such population the fitness of A is greater than the fitness of B,

$$a\,(1-\varepsilon) + b\,\varepsilon > c\,(1-\varepsilon) + d\,\varepsilon \tag{3.10}$$

This can be rewritten as

$$(1-\varepsilon)(a-c) + \varepsilon\,(b-d) > 0 \tag{3.11}$$

Thus, we have two conditions for evolutionarily stability

(i) NE condition:
$a > c$.

(ii) Stability condition:
if $\quad a = c, \quad$ then $\quad b > d$.

Condition (i) assumes that A is a NE which is not satisfactory for non-invasibility: there might be another option best reply B. On this case, condition (ii) says that A performs better against B than B itself. Then we can affirm that:

— Strict NE are ESS (symmetric games).

— All ESS are NE (but not necessarily strict NE).

— A game with two pure strategies always has an ESS.

3.4 Examples

There are four types of Nash equilibria in a symmetric two-person game. Cooperative interactions can have different payoff structures, yielding different rational solutions [6]. Players either cooperate (C) or defect (D) and receive payoffs that are known as Temptation

(T), Reward (R), Punishment (P), and Sucker (S). The general form of the payoff matrix is

$$\begin{array}{c|cc} & C & D \\ \hline C & R & S \\ D & T & P \end{array} \tag{3.12}$$

3.4.1 Prisoner's Dilemma

In the Prisoner's Dilemma game [1,3,7], without realizing the other player's choice, two players simultaneously adopt to cooperate (C) or to defect (D). If they both adopt to cooperate they divide up the highest total payoff and get R points each, although there is an inclination to defect due to the fact that defection scores $T > R$ contrary to a cooperating opponent who in that case obtains the lowest score S. If both adopt to defect they divide up the lowest total payoff and get P points each. If $T > R > P > S$ and $2R > T + S$ (see payoff matrix 3.12), a dilemma arises, since, in an isolated game, rational players adopt to defect and then divide up the lowest total payoff. Thus, adopting the same strategy of the opponent, the unique Nash equilibrium is (D, D).

3.4.2 Snow-Drift Game

The scenario of the Snow-Drift game involves two drivers who are trapped on either side of a snowdrift [1]. Each has two options: to get out and start shoveling snow (C) or to stay in the comfortable warmth of the car (D). If both stay in the car, they drop the benefit of coming back home. If the other driver resolves to start shoveling, it is more beneficial to remain in the car. If both resolve to start shoveling, the labor costs are reduced and both come back home earlier. This results in the following payoffs: $R = b - \frac{c}{2}$, $S = b - c$, $T = b$, and $P = 0$. The payoff matrix is

$$\begin{array}{c|cc} & C & D \\ \hline C & b - \frac{c}{2} & b - c \\ D & b & 0 \end{array} \tag{3.13}$$

For $b > c$, the Nash equilibrium is to adopt the opposite strategy, that is both (C, D) and (D, C) are Nash equilibria. If $b < c$, then this game approaches the Prisoner's Dilemma game.

3.4.3 Stag-Hunt

In the Stag-Hunt game is described a scenario in which two individuals go out on a hunt [3], there are two strategies: to hunt a stag (C) or to hunt a hare (D). The two players must combine actions to hunt the stag, which provides a more beneficial payoff in terms of calories. Although, if one of the players resolves to give up the combination of actions and decided to hunt a hare, which is effortless to catch, the defector will obtain a poorer, certain reward, and the other player will obtain nothing. If we put in terms of the payoff matrix 3.12 the payoff distribution $R > T > P > S$ defines a Stag-Hunt game. The Nash equilibrium is to adopt the same strategy of the opponent, that is, both (C, C) and (D, D) are Nash equilibria.

3.4.4 Harmony Game

Referring to payoff matrix 3.12, Harmony game could be described according to the payoff matrix distribution $R > S > P$ and $R > T > P$ [2,3,8]. This game has a unique strict Nash equilibrium both players cooperating (C, C). This game is rarely mentioned in the traditional game theory analysis because it does not constitute any conflictive social dilemma.

4 Markov Chains

The outcomes of an experiment are represented by a random variable whether these outcomes are numerical or real numbers can be assigned to them.

A random variable X is a rule (or function) that assigns a real number to every outcome of a random experiment, while a random process is a rule (or function) that assigns a time function to every outcome of a random experiment. A random variable assumes discrete or continuous values [9].

Consider the discrete points in time $\{t_k\}$ for $k = 1, 2, \ldots,$ and let X_{t_k} be the random variable that represents the state of the system at t_k. The indexed collection of random variables $\{X_{t_k}\}$ forms a stochastic process. We assume that the X_{t_k} take values in some countable set S, called the state space. The elements of S are called states. The states at time t_k characterize the (exhaustive and mutually exclusive) outcomes of the system at that time.

Definition 1. *The sample description space S of a random phenomenon is the space of descriptions of all possible outcomes of the phenomenon.*

Definition 2. *An event is a set of sample descriptions. An event E is said to occur if and only if the observed outcome of the random phenomenon has a sample description in E.*

We specify a probability function $P(\cdot)$ on the family F of random events; more precisely, one defines for each event E in F a number, denoted by $P(E)$ and called the probability of E (the probability that E will occur). $P(E)$ represents the probability that (or relative frequency with which) an observed outcome of the random phenomenon is a member of E.

4.1 Markov Chains: Discrete Parameters

4.1.1 Markov Process

A Markov process is a stochastic scheme for which the development of a future state relies on the immediately previous state and only on it and not on the past history [9, 10]. Thus if $t_0 < t_1 < \ldots < t_n \quad (n = 0, 1, 2, \ldots)$ characterizes points in time, the collection of random variables $\{X_{t_n}\}$ is a Markov process for all $x_0, \ldots, x_n \in S$ if it has the next Markovian property (memoryless property)

$$P\{X_{t_n} = x_n \mid X_{t_{n-1}} = x_{n-1}, \ldots, X_{t_0} = x_0\} = P\{X_{t_n} = X_n \mid X_{t_{n-1}} = x_{n-1}\} \tag{4.1}$$

For all values of $X_{t_0}, X_{t_1}, \ldots, X_{t_n}$.

4.1.2 Markov Chains

A Markov process whose state space is discrete is called a Markov chain . Therefore, a Markov chain is a sequence of integer random variables for which the Markov property holds [9]. We deal with a discrete-parameter Markov chain $\{X_n\,,\ n \geq 0\}$ with a discrete state space $S = \{0, 1, 2, \ldots\}$, where this collection may be finite or infinite. If $X_n = i$, then the Markov chain is said to be in state i at time n (or the nth step). A discrete-parameter Markov chain $\{X_n\,,\ n \geq 0\}$ is represented for every n by

$$P\{X_{n+1} = j \,|\, X_0 = i_0, X_1 = i_1, \ldots, X_n = i\} \;=\; P\{X_{n+1} = j \,|\, X_n = i\} \tag{4.2}$$

The conditional probabilities $P\{X_{n+1} = j \,|\, X_n = i\}$ are called one-step transition probabilities.

If, for every i and j, $P\{X_{n+1} = j \,|\, X_n = i\} = P\{X_1 = j \,|\, X_0 = i\}$, for all $n \geq 0$, then the Markov chain is said to have stationary one-step transition probabilities. Hence, the presence of stationary transition probabilities means that the transition probabilities do not change over time.

Definition 3. *A discrete-parameter Markov Chain* $\{X_n\,,\ n \geq 0\}$ *on a state space* S *is said to be homogeneous if, for all* $n \geq 0$, $k \geq 0$ *and, for all* $i, j \in S$, *we get*

$$P\{X_{n+k} = j \,|\, X_k = i\} \;=\; P\{X_n = j \,|\, X_0 = i\} \tag{4.3}$$

Example. Consider a game where a coin is tossed repeatedly and the score of the player is collected by adding two points when a head turns up and adding one point for a tail.

The state space of the process is created by all possible collected scores that can occur over the progress of the game ($S = \mathbb{N}$). For any given state we notice that the distribution of possible values of the state is dependent only on the previous state, that is, the state distribution is characterized by:

$$P\{X_n = j + 1 \,|\, X_{n-1} = j\} \;=\; \frac{1}{2}$$

$$P\{X_n = j + 2 \,|\, X_{n-1} = j\} \;=\; \frac{1}{2}$$

and so the process is a Markov process. The state space is discrete and therefore the process is a Markov chain.

Besides, the distribution of possible values of a state does not depend upon the time the observation is made, so the process is a homogeneous, discrete time, Markov chain.

4.1.3 Transition Probability Matrix

Let $\{X_n\,,\, n \geq 0\}$ be a homogeneous Markov chain with a discrete infinite state space $S = \{0, 1, 2, \ldots\}$. Then

$$p_{ij} \;=\; P\{X_{n+1} = j \,|\, X_n = i\} \qquad i \geq 0,\; j \geq 0 \tag{4.4}$$

is the one-step transition probability of going from state i at n to state j at $n+1$ in spite of the value of n. The transition probabilities of $\{X_n\,,\, n \geq 0\}$ may be more conveniently arranged in a matrix form as follows:

$$P \;=\; [\,p_{ij}\,] \;=\; \begin{bmatrix} p_{00} & p_{01} & p_{02} & \cdots \\ p_{10} & p_{11} & p_{12} & \cdots \\ p_{20} & p_{21} & p_{22} & \cdots \\ \vdots & \vdots & \vdots & \end{bmatrix} \tag{4.5}$$

where the elements must satisfy the conditions

$$p_{ij} \geq 0 \qquad \sum_{j=0}^{\infty} p_{ij} \;=\; 1 \qquad i = 0, 1, 2, \ldots \tag{4.6}$$

For the case where the state space S is finite and equal to $\{1, 2, \ldots, m\}$, P is $m \times m$ dimensional; i.e.,

$$P \;=\; [\,p_{ij}\,] \;=\; \begin{bmatrix} p_{11} & p_{12} & \cdots & p_{1m} \\ p_{21} & p_{22} & \cdots & p_{2m} \\ \vdots & \vdots & \ddots & \vdots \\ p_{m1} & p_{m2} & \cdots & p_{mm} \end{bmatrix} \tag{4.7}$$

where

$$p_{ij} \geq 0 \qquad \sum_{j=1}^{m} p_{ij} \;=\; 1 \qquad i = 1, 2, \ldots, m \tag{4.8}$$

A square matrix whose elements satisfy equations 4.6 or 4.8 is called a Markov matrix or stochastic matrix because all the transitions probabilities p_{ij} are fixed and independent of time.

4.1.4 Classification of States

State j is said to be *accessible* from state i if there exists a number $n \geq 0$ such that $p_{ij}^{(n)} > 0$, and we denote $i \to j$. Two states i and j communicate if they are accessible from one another, and we denote $i \leftrightarrow j$. A Markov chain is said to be irreducible if all states communicate with each other.

In a Markov chain, a set C of states is said to be *closed* if it is improbable to move out from any state of C to any state outside C by one-step transitions, that is

$p_{ij} = 0$ if $i \in C$ and $j \notin C$. In this case $p_{ij}^{(n)} = 0$ evidently holds for every n. A peculiar example of a closed set is a single state j with transition probability $p_{jj} = 1$, then j is called an absorbing state.

A Markov chain is *irreducible* if the set of all states forms a closed set and no other set is . If we consider only the states of a closed set C, then we have a sub-Markov chain defined on C, and this can be studied independently of the other states.

The period $d(j)$ of a state j is defined by:

$$d(j) = gcd\{n \geq 1 : p_{jj}^{(n)} > 0\} \tag{4.9}$$

where *gcd* stands for greatest common divisor. If $d(j) > 1$, then state j is called *periodic* with period $d(j)$. All states of a closed set have the same period. Therefore we can refer to the period of the closed set C. If $d(j) = 1$, then we say that the state j and the closed set C are *aperiodic* (non-periodic).

We denote the probability of the process being in a state i at step n as

$$\pi_i^{(n)} = P\{X_n = i\} \tag{4.10}$$

The initial probability distribution is given by

$$\pi_i^{(0)} = P\{X_0 = i\} \tag{4.11}$$

We have that $P^{(1)} = P = [\,p_{ij}\,]$ is the one-step transition matrix and $P^{(n)} = P^n = [p_{ij}^{(n)}]$ denotes the n-step transition matrix with $p_{ij}^{(n)} = P\{X_n = j \,|\, X_0 = i\}$.

The transient probability distribution at time $n > 0$ is defined by

$$\pi_j^{(n)} = \sum_{i \in S} \pi_i^{(0)} p_{ij}^{(n)} \quad \text{or} \quad \pi^{(n)} = \pi^{(0)} P^n \tag{4.12}$$

A distribution π is stationary if

(i) $\pi_j \geq 0 \quad \forall j \in S \quad$ and $\quad \sum_{j \in S} \pi_j = 1.$

(ii) $\pi_j = \sum_{i \in S} \pi_i \, p_{ij}, \quad \pi = \pi \, P$

Let $\{X_n,\, n \geq 0\}$ be a regular homogeneous finite-state Markov chain with transition matrix P. Suppose π^* is a limiting distribution, if $\pi^{(0)}$ is an initial probability distribution,

$$\pi^* = \lim_{n \to \infty} \pi^{(n)} = \lim_{n \to \infty} \pi^{(0)} P^n = \pi^{(0)} \lim_{n \to \infty} P^n = \pi^{(0)} P^* \tag{4.13}$$

the limit can depend on $\pi^{(0)}$ and does not need to exist.

Let $f_{ij}^{(n)} = P\{X_n = j,\, X_k \neq j,\, k = 1, \ldots, n-1 \,|\, X_0 = i\}$, with $f_{ij}^{(0)} = 0$, for $n \geq 1$ be the n-step hitting probability. The hitting probability is defined as

$$f_{ij} = \sum_{n=1}^{\infty} f_{ij}^{(n)}, \tag{4.14}$$

and a state i is called transient (or non recurrent) if $f_{ii} < 1$ and recurrent if $f_{ii} = 1$.

Denoting expectation

$$m_{ij} = \sum_{n=1}^{\infty} n\, f_{ij}^{(n)}, \tag{4.15}$$

a recurrent state i is called *positive recurrent* or recurrent non-null if $m_{ii} < \infty$ and *recurrent null* if $m_{ii} = \infty$.

Definition 4. *A discrete time Markov chain is ergodic if all its states are irreducible, aperiodic and recurrent non-null (positive recurrent).*

The fundamental theorem of Markov chains is stated [10]:

Fundamental Theorem of Markov Chains. *In an ergodic Markov chain, the limiting distribution exists, does not depend on* $\pi^{(0)}$*, and equals the unique stationary distribution.*

5 Evolutionary Games in Finite Populations

5.1 Finite Populations

We study a stochastic process for evolutionary game theory in finite populations, a Moran process which is a Markov birth-death process in four steps: for two strategies, i individuals of strategy A and $N-i$ of strategy B.

(i) An individual A could be selected for reproduction and death with probability $(i/N)^2$. The number of A stays the same.

(ii) An individual B could be selected for reproduction and death with probability $[(N-i)/N]^2$. The number of B stays the same.

(iii) An individual A could be selected for reproduction and a B individual for death with probability $i(N-i)/N^2$. For this case: $i \to i+1$ and $N-i \to N-i-1$.

(iv) An individual B could be selected for reproduction and an A individual for death with probability $i(N-i)/N^2$. For this case: $i \to i-1$ and $N-i \to N-i+1$.

For a stochastic process, the variable i can only change by at most one (Figure 3).

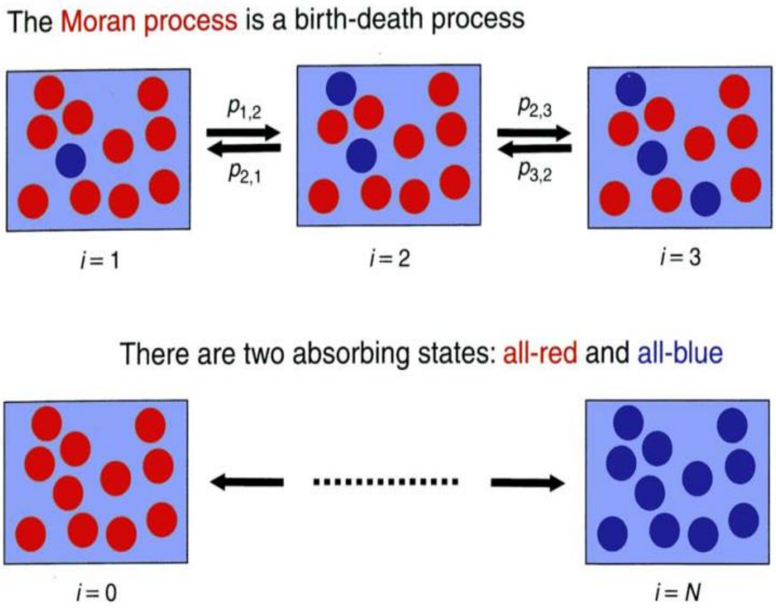
We are interested in knowing what is the probability $\mathcal{P}_i$ of ending up in a state with all $A\,(i=N)$ starting from i individuals A. For $i=1$, $\mathcal{P}_1$ is the fixation probability of A. Denote

- Transition from $i \to i+1$, $(p_{i\,,i+1})$ by the birth rate α_i.
- Transition from $i \to i-1$, $(p_{i\,,i-1})$ by the death rate β_i.
- The probability of staying in i by $p_{i\,,i} = 1-\alpha_i-\beta_i$.

$$\begin{aligned}
\mathcal{P}_0 &= 0 \\
\mathcal{P}_i &= \beta_i\,\mathcal{P}_{i-1} + (1-\alpha_i-\beta_i)\,\mathcal{P}_i + \alpha_i\,\mathcal{P}_{i+1}, \qquad i=1,\ldots,N-1 \qquad (5.1)\\
\mathcal{P}_N &= 1
\end{aligned}$$

Introducing the variables $y_i = \mathcal{P}_i - \mathcal{P}_{i-1}$ $(i=1,\ldots,N-1)$ we note that $\sum_{i=1}^{N} y_i = 1$ and $y_{i+1} = \gamma_i\, y_i$, where $\gamma_i = \beta_i \,/\, \alpha_i$, then we recover a classical result

Figure 3 – The Moran Process (Figure from Nowak, 2006: Figure 6.2)



on Markov chains:

$$\mathcal{P}_i \quad = \quad \frac{1+\sum\limits_{j=1}^{i-1}\prod\limits_{k=1}^{j}\gamma_k}{1+\sum\limits_{j=1}^{N-1}\prod\limits_{k=1}^{j}\gamma_k}. \tag{5.2}$$

The fixation probability of A is

$$\rho_A \quad = \quad \mathcal{P}_1 \; = \; \frac{1}{1+\sum\limits_{j=1}^{N-1}\prod\limits_{k=1}^{j}\gamma_k}. \tag{5.3}$$

Since $i=0$ and $i=N$ are absorbing boundary states and always absorption (all-A or all-B), the fixation probability of B is

$$\rho_B \quad = \quad 1-\mathcal{P}_{N-1} = \frac{\prod\limits_{k=1}^{N-1}\gamma_k}{1+\sum\limits_{j=1}^{N-1}\prod\limits_{k=1}^{j}\gamma_k}. \tag{5.4}$$

5.2 Random Drift with Constant Selection

Now consider the fixation in the neutral and constant fitness cases. The fixation probabilities 5.3 and 5.4, can be related with corresponding probabilities for constant selection and random drift.

If $\alpha_i = \beta_i = \gamma_i = 1$, then this is the neutral case where there is no selection but only random drift: $\rho_A = \rho_B = 1/N$. This implies the probability that an individual will produce a lineage which will take over the whole population is $1/N$.

Consider the case where A and B have constant but distinct fitnesses, $f_A = r$ for A and $f_B = 1$ for B,

$$\alpha_i = \frac{r\,i\,(N-i)}{N[N+(r-1)\,i]}$$

$$\beta_i = \frac{i\,(N-i)}{N[N+(r-1)\,i]} \tag{5.5}$$

therefore

$$\rho_A = \frac{1-r^{-1}}{1-r^{-N}}, \qquad \rho_B = \frac{1-r}{1-r^{N}} \tag{5.6}$$

We enunciate that strategy A is advantageous (selection favors the fixation of strategy A) if its fixation probability is higher than that of a neutral mutant, i. e., if $\rho_A > 1/N$.

- If $r > 1$, $\rho_A > N^{-1}$ for $N \gg 1$: selection favors the fixation of A.
- If $r < 1$, $\rho_B > N^{-1}$ for $N \gg 1$: selection favors the fixation of B.
- If $r = 1$, we go back to neutral drift.

5.3 Evolutionary Games in Finite Populations

Consider a population where the interplay between two individuals is represented by a two-person game with two accessible strategies [11]: strategy A and strategy B. Now suppose there are i individuals of strategy A and $N-i$ individuals of strategy B playing the game according to the 2×2 payoff matrix:

$$\begin{array}{c c} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \tag{5.7}$$

For each individual, there are $N-1$ other individuals. Therefore,

- the probability that a given individual A interacts with another A individual is $(i-1)/(N-1)$;
- the probability that a given individual A interacts with a B individual is $(N-i)/(N-1)$;
- the probability that a given individual B interacts with another B individual is $(N-i-1)/(N-1)$;
- the probability that a given individual B interacts with an A individual is $i/(N-1)$.

The boundary states $i=0$ and $i=N$ are absorbing. The expected payoff for A and B, respectively, are:

$$\begin{aligned} F_i &= \frac{a\,(i-1)+b\,(N-i)}{N-1} \\ G_i &= \frac{c\,i+d\,(N-i-1)}{N-1} \end{aligned} \tag{5.8}$$

Expected payoffs 5.8 are usually interpreted as fitnesses. Introducing a parameter w (selection intensity) accounting for background random drift contribution to fitness f_i for A and g_i for B

$$\begin{aligned} f_i &= 1-w+w\,F_i \\ g_i &= 1-w+w\,G_i \end{aligned} \tag{5.9}$$

Since parameter w measures the intensity of selection, it follows that, depending on the values this parameter may adopt, we have:

- $w=0$, no selection, only random drift.
- $w=1$, only selection.
- $w \ll 1$, weak selection.

Consider a Moran process with A and B individuals, and frequency dependent hopping rates:

$$\begin{aligned} \alpha_i &= \frac{i\,f_i}{i\,f_i+(N-i)\,g_i}\frac{N-i}{N} \\ \beta_i &= \frac{(N-i)\,g_i}{i\,f_i+(N-i)\,g_i}\frac{i}{N} \end{aligned} \tag{5.10}$$

Hence, noting that $\gamma_i = \beta_i/\alpha_i = g_i/f_i$, the fixation probability of A and B are respectively

$$\begin{aligned} \rho_A &= \mathcal{P}_1 = \left[1 + \sum_{j=1}^{N-1} \prod_{k=1}^{j} \frac{g_k}{f_k}\right]^{-1} \\ \rho_B &= \rho_A \prod_{k=1}^{N-1} \frac{g_k}{f_k} \end{aligned} \tag{5.11}$$

In the weak selection limit ($w \to 0$): from equations 5.9

$$\gamma_i = \frac{\beta_i}{\alpha_i} = \frac{g_i}{f_i} = \frac{1 - w\,(1 - G_i)}{1 - w\,(1 - F_i)} \tag{5.12}$$

therefore the fixation probability, ρ_A, is given by

$$\rho_A = \mathcal{P}_1 = \left[1 + \sum_{j=1}^{N-1} \prod_{i=1}^{j} \frac{1 - w\,(1 - G_i)}{1 - w\,(1 - F_i)}\right]^{-1} \tag{5.13}$$

Expression 5.12 can be approximated, up to first order; by

$$\frac{\beta_i}{\alpha_i} = 1 - w\,(F_i - G_i) \tag{5.14}$$

Now consider equations 5.8 and define the following expression

$$D_i = F_i - G_i = \frac{1}{N-1}\,[p + q\,i] \tag{5.15}$$

with $p = -a + b\,N - d\,N + d$ and $q = a - b - c + d$. Therefore up to first order in w, the fixation probability, ρ_A, in total agreement with equation 5.13, is given by

$$\rho_A = \left[1 + \sum_{k=1}^{N-1} \prod_{i=1}^{k} (1 - w\,D_i)\right]^{-1} \tag{5.16}$$

Now we will focus on the development of the following expression

$$\sum_{k=1}^{N-1} \prod_{i=1}^{k} (1 - w\,D_i) \tag{5.17}$$

For small w, expression 5.17 can be developed as follows

$$\sum_{k=1}^{N-1} \prod_{i=1}^{k} (1 - w\,D_i) = \sum_{k=1}^{N-1} 1 - w \sum_{k=1}^{N-1} \sum_{i=1}^{k} D_i \tag{5.18}$$

In a similar way, from expression 5.15

$$\sum_{k=1}^{N-1} \sum_{i=1}^{k} D_i = \frac{1}{N-1} \sum_{k=1}^{N-1} \sum_{i=1}^{k} (p + q\,i) \tag{5.19}$$

Since

$$\sum_{i=1}^{k}(p+q\,i) \quad = \quad \left(p+\frac{q}{2}\right)k+\frac{q}{2}\,k^2 \tag{5.20}$$

it follows that

$$\sum_{k=1}^{N-1}\left[\left(p+\frac{q}{2}\right)k+\frac{q}{2}\,k^2\right] \quad = \quad \frac{N}{6}\,(N-1)\,[3\,p+(N+1)\,q] \tag{5.21}$$

Substituting the values for p and q previously assigned, the expression inside the square bracket can be simplified in equation 5.21, then

$$3\,p+(N+1)\,q \quad = \quad N(a+2b-c-2d)-(2a+b+c-4d) \tag{5.22}$$

Since

$$\sum_{k=1}^{N-1}\sum_{i=1}^{k}D_i \quad = \quad \frac{N}{6}\,\left[N(a+2b-c-2d)-(2a+b+c-4d)\right] \tag{5.23}$$

therefore, it should be noticed that equation 5.18 becomes

$$\sum_{k=1}^{N-1}\prod_{i=1}^{k}(1-w\,D_i) \quad = \quad N-1-w\frac{N}{6}\,\left[N(a+2b-c-2d)-(2a+b+c-4d)\right] \tag{5.24}$$

Up to first order in w, returning to equation 5.16, we can write this equation in the form

$$\rho_{_A} \approx \frac{1}{N}\left\{1-\frac{w}{6}\,[(a+2b-c-2d)\,N-(2a+b+c-4d)]\right\}^{-1} \tag{5.25}$$

Selection favors fixation of A only if $\rho_{_A} > 1/N$, that is, only if

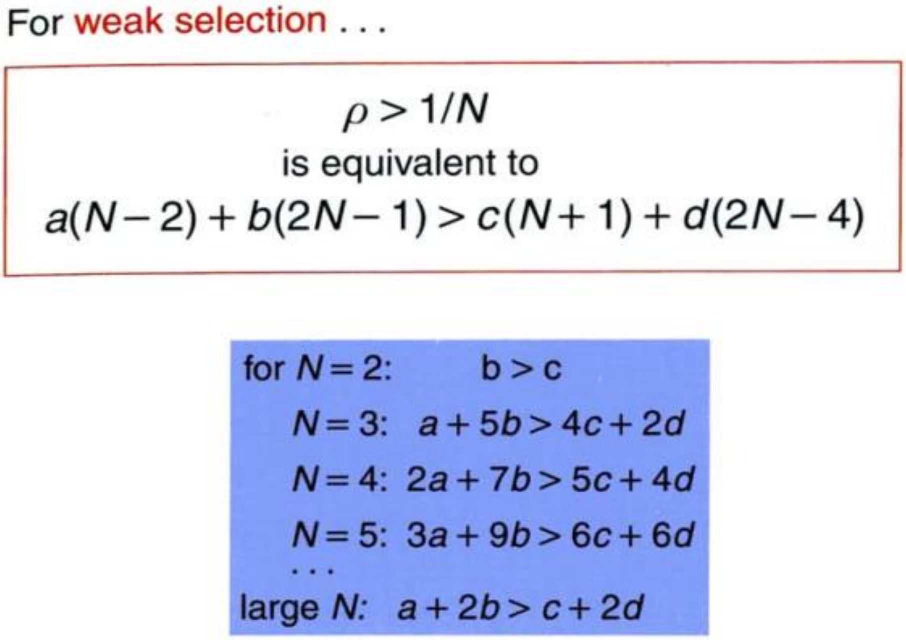
$$a\,(N-2)+b\,(2N-1) > c\,(N+1)+d\,(2N-4) \tag{5.26}$$

It must be borne in mind that for different population size, a simple condition determines whether or not selection favors the fixation of a strategy (see Figure 4).

It should be noticed that for large population size N, $\rho_{_A} > 1/N$ if $a+2\,b > c+2\,d$. How this condition can be interpreted? To illustrate, consider a game with $a > c$ and $b < d$. We have the following interpretations:

- Rational game: all-A and all-B are strict Nash Equilibrium (NE) and Evolutionarily Stable Strategy (ESS).
- Replicator Dynamics: all-A, all-B are asymptotically stable states and $x^* = \dfrac{d-b}{a-c+d-b}$ is an unstable interior rest point (NE, but not ESS).

Figure 4 – Fixation Probability for the Weak Selection Limit (Figure from Nowak, 2006: Figure 7.3)



For weak selection . . .

$$\rho > 1/N$$

is equivalent to

$$a(N-2) + b(2N-1) > c(N+1) + d(2N-4)$$

for $N = 2$: $b > c$

$N = 3$: $a + 5b > 4c + 2d$

$N = 4$: $2a + 7b > 5c + 4d$

$N = 5$: $3a + 9b > 6c + 6d$

. . .

large N: $a + 2b > c + 2d$

- In a large finite population of size N, stochastic Moran process for weak selection: the condition $a - c > 2(d - b)$ favors fixation of A leading to $x^* < 1/3$.

It must be emphasized that if the unstable rest point x^* takes place at frequency less than $1/3$, in a large yet finite population and for $w \ll 1$, selection favors the fixation of A. Hence the probability that a single A takes over the entire population of $N - 1$ individuals B is greater than $1/N$. Then if $x^* < 1/3$, it means that the attraction basin of all-B is less than $1/3$ as well.

The previous result for the weak selection limit and two strategies system 5.25 hints that the concept of evolutionary stability should be modified to account for finite size fluctuations. This leads to the concept of evolutionarily stable strategy ESS_N: A finite population of B is evolutionary stable in opposition to a second strategy A if

(i) The fitness of B is greater than that of A, i.e. $g_i > f_i$, $\forall i$. This means that selection opposes A invading B.

(ii) $\rho_A < 1/N$, hinting that selection opposes A replacing B.

These results lead to the criteria for evolutionary stability of B in a population of size N (Table 1):

Table 1 – Criteria for Evolutionary Stability of B

Deterministic ($N \to \infty$)	Stochastic (N *finite*)
$d > b$	$(d-b)\,N > 2\,d - (b+c)$
if $b = d$, then $c > a$	$c\,(N+1) + 2\,d\,(N-2) > a\,(N-2) + b\,(2\,N-1)$

Conditions for evolutionary stability depend on the population size (Table 2):

Table 2 – Conditions for Evolutionary Stability of B

B is Evolutionarily Stable Strategy (ESS_N) if	$N = 2$	$N \gg 1$ (*finite*)
Condition (1)	$c > b$	$d > b$
Condition (2)	$c > b$	$x^* = \frac{d-b}{a-c+d-b} > \frac{1}{3}$

It should be noticed that for small N, the traditional ESS conditions are neither necessary nor sufficient to assure evolutionary stability while for large N, the traditional ESS conditions are necessary but not sufficient to assure evolutionary stability.

6 Fixation Probability with Frequency Dependent Mutation/Exploration Rates

In evolutionary game theory both selection and mutation are essential to evolution [12]. Mutations possess the prospective to produce different genotypes and phenotypes while selection has an effect on those diverse phenotypes, This evolutionary process is emulated by the Moran process with mutations. Mutation is the final root of all the genetic diversity on which selection may act.

Mutations involve a high cost, however; nearly all are deleterious, diminishing the fitness of the organisms in which they take place. Therefore mutation is considered the origin of good and ill for a population.

On a population the total effect of mutation is actively dependent on the population size. Since in each generation an extensive population possesses a lot of new mutations , the probability is high that it will obtain new favorable mutations. This extensive population also possesses effective selection in opposition to the bad mutations that take place; deleterious mutations in an extensive population are maintained at a low frequency within an equilibrium between the forces of selection and those of mutation. However, a population with comparatively fewer individuals will have inferior mean fitness, not just because fewer favorable mutations emerge, but also because deleterious mutations are so prone to get at high frequencies by means of random genetic drift.

Now consider a system in which players emulate absolutely more outstanding strategies but occasionally explore randomly the accessible strategies. The main body of investigation has concentrated on how strategies propagate via genetic replication or cultural imitation, but very few consideration has received the random exploration of the obtainable set of strategies. In genetic terms, the latter correlates with mutations in the DNA, although in cultural evolution, it explains individuals testing with new performances. Habitually genetic mutations take place with very small expectations, but in behavioral tests exploration of available strategies at random is common. This phenomenon is termed "exploration dynamics" to differentiate it with the conventional center of attention to imitation.

Referring to the payoff matrix for the Prisoner's Dilemma 3.12, we consider a simplified Prisoner's Dilemma game (Donation Game) in which cooperators pay a cost $c > 0$ to generate a benefit $b > c$ to the other player [1, 3]. Defectors do not help and therefore incur no costs. Then this results in the following payoffs: $R = b - c$; $S =$

$-c$; $T = b$; $P = 0$. The payoff matrix for this simplified game is

$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array} \tag{6.1}$$

The expected payoff from the Prisoner's Dilemma interaction for C and D are respectively

$$\begin{aligned} F_i &= \frac{(i-1)\,b-(N-1)\,c}{N-1} \\ G_i &= \frac{b\,i}{N-1} \end{aligned} \tag{6.2}$$

Let the benefit $b = 1$ in equation 6.2

$$\begin{aligned} F_i &= \frac{(i-1)-(N-1)\,c}{N-1} \\ G_i &= \frac{i}{N-1} \end{aligned} \tag{6.3}$$

The fact of fixing the benefit does not involve loss of information on the properties of the payoff matrix for the donation game.

In a population of size N with i cooperators and $N-i$ defectors , the fitness of cooperators f_i and defectors g_i are given by

$$\begin{aligned} f_i &= 1-w+w\,F_i \;=\; 1-w+\frac{w}{N-1}\,[(i-1)-(N-1)\,c] \\ g_i &= 1-w+w\,G_i \;=\; 1-w+\frac{w}{N-1}\,i \end{aligned} \tag{6.4}$$

Considering the simple case of competition between two strategies C and D. We introduce frequency dependent mutation rates by modifying the discrete-time transition probabilities of equation 5.10. Denote by u_1 the mutation rate from C to D: type C mutates into type D. Conversely, denote by u_2 the mutation rate from D to C: type D mutates into type C.

For frequency dependent mutation rates in the Moran-Markov chain process, the transition probabilities of the Markov chain can then be expressed as follows

$$\begin{aligned} p_{i,i+1} &= \frac{i\,f_i\,(1-u_1)}{i\,f_i+(N-i)\,g_i}\,\frac{N-i}{N}+\frac{(N-i)\,g_i\,u_2}{i\,f_i+(N-i)\,g_i}\,\frac{N-i}{N} \\ p_{i,i-1} &= \frac{(N-i)\,g_i\,(1-u_2)}{i\,f_i+(N-i)\,g_i}\,\frac{i}{N}+\frac{i\,f_i\,u_1}{i\,f_i+(N-i)\,g_i}\,\frac{i}{N} \\ p_{i,i} &= 1-p_{i,i+1}-p_{i,i-1} \end{aligned} \tag{6.5}$$

Rearranging equations 6.5 we obtain

$$\begin{aligned} p_{i,i+1} &= \frac{1}{i\,f_i + (N-i)\,g_i}\,\frac{N-i}{N}\,\left[i\,f_i\,(1-u_1) + (N-i)\,g_i\,u_2\right] \\ p_{i,i-1} &= \frac{1}{i\,f_i + (N-i)\,g_i}\,\frac{i}{N}\,\left[i\,f_i\,u_1 + (N-i)\,g_i\,(1-u_2)\right] \\ p_{i,i} &= 1 - p_{i,i+1} - p_{i,i-1} \end{aligned} \tag{6.6}$$

Making use of the fact that $\gamma_i = p_{i,i-1}/p_{i,i+1}$, we obtain

$$\gamma_i = \frac{i}{N-i}\,\frac{i\,f_i\,u_1 + (N-i)\,g_i\,(1-u_2)}{i\,f_i\,(1-u_1) + (N-i)\,g_i\,u_2} \tag{6.7}$$

Now combining equations 6.4, 6.6 and 6.7, we can determine the fixation probability ρ_C of a single cooperator (the probability to eventually go from state 1 to state N is the fixation probability of a single cooperator, denoted by ρ_C).

$$\rho_C = \left[1 + \sum_{k=1}^{N-1}\prod_{i=1}^{k}\gamma_i\right]^{-1} \tag{6.8}$$

The most important question from an evolutionary perspective is the fixation probability of cooperation, ρ_C, which is the probability that a single cooperator out of $N-1$ defectors turns the entire population into cooperators, i. e. the probability of concurrence to complete cooperation.

The fixation probability of neutral mutants, $1/N$, can be used as a benchmark for studying selection in finite populations.

Frequency dependent mutation rates are frequently rational from a biological perspective, there are many motives to analyze randomly cooperator configurations [12]. An evolutionary process, usually transitions, transits eventually over states with many cooperators, even when initiating from a state with a single cooperator. From a mathematical point of view, it should be asked how selection acts on the fixation probability of cooperators from each possible transient state that might emerge in an evolutionary trajectory. Moreover, many mutant states could emerge in the migration process or with the appearance of environmental mutagenic agents, which, even when rare, might result in several cooperators entering the population at once.

Traditionally there are two possible interpretations for evolutionary processes. In cultural evolution, the selection process represents a situation in which successful strategies are expanded by imitation. Mutations are frequently taken as errors in the process of imitating others, or planned exploration undertaken by individuals. Mutations are typically supposed to be uniform, such that any strategy can mutate to any other with identical probability. Non-uniform mutations emerge when these probabilities are no longer the same, and from a given population not all states are accessible , or some states are easier to reach than others. It should be noticed that the outcome of evolution can completely be changed by such asymmetries .

6.1 The Moran Process

Evolutionary game dynamics is responsible for the study of evolution of phenotypes. It regularly explores the natural event of a population of strategies playing a game, liable to selection and mutation. In this configuration the Moran process is one of the most studied formalisms which assumes a constant finite population size [1]: At every time step one strategy is selected for birth in proportion to its performance in the present population . A replication of this strategy is added to the population after removing a random strategy, selected for death, from the population. In the long run the outcome of selection and mutation can be estimated by inspecting the population mean composition.

Note that as a birth-death process, the Moran process, can be contemplated as a finite Markov chain, a random process picturing a system undertaking transitions among a finite number of possible states. It should be observed that in a Markov chain, the occurrence of a future state depends on the immediately preceding state an only on it.

Since there are no mutations, two absorbing states, state 0 and state N, exist in this Markov chain. A state is calling absorbing, if the system can not leave this state once reaches it.

In accordance with the above description the Moran process can be modeled assuming that the probabilities of mutation are given by

$$\begin{aligned} u_1 &= 0 \\ u_2 &= 0 \end{aligned} \tag{6.9}$$

which clearly point out the absence of mutation processes.

6.2 Frequency Dependent Mutation/Exploration Rates

In this section we implement frequency dependent mutation/exploration models in the evolutionary game theoretic framework.

The Moran process can also be interpreted as a social process. Instead of biological reproduction, the birth and death process represents the spread of strategies due to, for example, imitation of successful strategies [13]. In this cultural context, the mutation can be interpreted as random exploration [12]. Instead of imitating, the individuals want to explore randomly the available strategies.

In the following, a description is given of the models to be studied, which are characterized by the existence of frequency dependent mutation/exploration rates.

Mutagens These mutagenic agents can be defined as chemical compounds or types of radiation (x-rays, γ-rays, β-rays, α-rays, cosmic rays or UV) that generate irreparable or inheritable alterations (mutations) in the cellular genetic information, deoxyribonucleic acid (DNA) [14, 15]. Mutagenic injuries continue when they avoid exposure by defensive cellular DNA restoration mechanisms, when mistakes occur in the restoration process, or when restoration mechanisms are affected by widespread injury. These alterations become fixed in the genetic material and are inherited by all daughter cells in the posterior cellular reproduction. In such a way, mutagenesis gets to be a cumulative process, which extends throughout the lifetime of an organism.

Therefore, a mutagen is a natural or human-made agent that can alter the structure or sequence of the genetic material and induce mutation.

In spite of the fact that several dietary and environmental factors have been categorized as mutagens, cells are frequently subjected to a blast of spontaneous DNA injury. In essence, through food and water notable exposure to mutagenic composites can take place, and also through environmental and occupational causes [16]. Most natural components of food are mutagenic and are generated by plants as protection agents. Clearly, during food manufacturing or filtering from packing materials, supplemental food-related mutagens can be existent as remainders of composites utilized to carry out such processes. During food cooking and preparation mutagenic composites can also emerge . The activity of mutagens can be modulated by many compounds contained also in foods. Mutagens present in food can be cataloged into three groups: naturally arising compounds, those formed by cooking or processing, and supplements and toxins, including pesticides.

Since food and drinking water are major sources of human exposure to mutagens, the water can be defined as the first archaic mutagen of evolution, the adopter of nucleic acids.

We propose a model which represents the characteristics of a mutagenic agent. Suppose that mutagens are produced as a consequence of the behavior of defectors – individuals who do not care spending resources in protecting environment. Suppose also that the mutation is deleterious in the sense that it disables the cooperative phenotype, and hence there is only mutation of cooperators changing into defectors. Based on the previous description mutagens can be modeled assuming that the mutation/exploration rates are given by

$$\begin{aligned} u_1 &= u_0 \frac{N-i}{N}, \qquad u_0 = 10^{-1} \\ u_2 &= 0 \end{aligned} \tag{6.10}$$

Keep in mind that i is the number of cooperators and $N - i$ is the number of defectors in a population of size N .

Conformist Exploration Different from other animal species, among human societies most of the variation is cultural. Since genetically identical people living in identical ambients expose surprisingly distinct patrons of behavior, they keep different, culturally obtained convictions and virtues. It is worth noting that this cultural transmission is based in complex, inferred psychological procedures that have probably been shaped by natural selection.

Conformist exploration can be cataloged as a gene-culture coevolutionary theory, which, is a branch of theoretical population genetics and apart from modeling the differential transmission of genes from one generation to the next, includes cultural traits in the analysis.

The two transmission structures cannot be considered separately, both inasmuch as what an individual assimilates may depend on its genotype, and also due to the selection acting on the genetic structure which may be created or altered by the propagation of a cultural trait.

The nature of these evolved psychological procedures must be clearly understood because these procedures decide which beliefs and values propagate and remain in human societies. Boyd and Richerson [17] exposed that a propensity to obtain the typical behavior presented in a society was adaptable in an elementary pattern of evolution in an environment that varies spatially, due to such a propensity which expands the probability of obtaining adaptable beliefs and values.

It is assumed that the Social learning skills of our species, according to the evolutionary approaches of culture, are genetically evolved cognitive adaptations to survive in environments in which acquiring information individually is costly. On this basis, a remarkable amount of theoretical research has explored the terms under which natural selection will favor different learning strategies [17, 18]. The basic assumption of the proposed model is that it provides predictions about when individuals, both human and non-human, must trust their individual or asocial experience and when they must implement one or more social learning strategies, such as conformist transmission (a propensity to copy excessively the majority or plurality) [19]. Conformist transmission implies that individuals possess a propensity to preferentially adopt the cultural traits that are most frequent in the population [20].

According to the previous description the conformist exploration can be modeled assuming that the mutation/exploration rates are given in the following way

$$\begin{aligned} u_1 &= u_0 \frac{N-i}{N}, \qquad u_0 = 10^{-1} \\ u_2 &= u_0 \frac{i}{N} \end{aligned} \tag{6.11}$$

Note that i is the number of cooperators and $N - i$ is the number of defectors in a population of size N.

Innovative Exploration An innovation is defined as “an idea, practice, or object that is perceived as new by an individual or other unit of adoption” (Rogers [21]) .

Everett Rogers’s theory of innovation diffusion [21] is presented as a fundamental understanding of adoption theories used in a broad domain of comprehension the prediction of change that begins with his work in 1962 *The Diffusion of Innovations* as the most influential and debatable production in this area. Diffusion consists of three main stages: **adoption** (the resolution to commit to a project or innovation); **implementation** (actually accomplishing the program); and **institutionalization** (integration and sustainability of the long-term program, through policies and practices).

The Diffusion of Innovations model recognizes five categories of participants that are characterized by their respective rates of adoption of innovative ideas or programs [21]: innovators (2.5 %), early adopters (13.5 %), early majority (34 %), late majority (34 %), and laggards (16 %).

Diffusion of Innovations theory also considers how some perceived characteristics of an innovation can affect the ease with which it will be adopted [22]. Those characteristics are:

Relative Advantage: The degree to which innovation is considered better than previously available ideas or programs.

Compatibility: The degree to which innovation is coherent with the values, experiences, and needs of potential adopters.

Complexity: How difficult it is to understand innovation or how complex it is to use it.

Trialability: The degree to which innovation can be experimented in a limited way without a large investment.

Observability: The degree to which the effects of an innovation are perceptible to others.

Here we consider a population that is composed only of innovators – those who are eager to adopt novelties. For the modeling of the innovative exploration we assume that the mutation/exploration rates are given by

$$
\begin{aligned}
u_1 &= \begin{cases} u_0 \, \dfrac{i}{N} & \text{if} \quad 0 \le i \le N-1 \qquad u_0 = 10^{-1} \\[2ex] 0 & \text{if} \quad i = N \end{cases} \\[3ex]
u_2 &= \begin{cases} u_0 \, \dfrac{N-i}{N} & \text{if} \quad 1 \le i \le N \qquad u_0 = 10^{-1} \\[2ex] 0 & \text{if} \quad i = 0 \end{cases}
\end{aligned}
\tag{6.12}
$$

Note that i is the number of cooperators and $N-i$ is the number of defectors in a population of size N.

Cultural innovations are not exactly mutations, since it is often a directed innovation (innovation with a purpose) and not a random error [23].

6.3 Results and Discussion

We can replace the transitions rates $p_{i,\,i+1}$ in equations 6.6 with the birth rate b_i and $p_{i,\,i-1}$ with the death rate d_i, so that we have

$$
\begin{aligned}
b_i &= p_{i\,,i+1} = \frac{1}{i\, f_i + (N-i)\, g_i} \, \frac{N-i}{N} \, \left[i\, f_i \, (1-u_1) + (N-i)\, g_i \, u_2 \right] \\[2ex]
d_i &= p_{i\,,i-1} = \frac{1}{i\, f_i + (N-i)\, g_i} \, \frac{i}{N} \, \left[i\, f_i \, u_1 + (N-i)\, g_i \, (1-u_2) \right]
\end{aligned}
\tag{6.13}
$$

The rates b_0 and d_N determine the type of boundary. If $b_0 = d_N = 0$ then the states 0 and N are absorbing, otherwise they are reflecting.

We find the boundaries b_0 and d_N for equations 6.13 obtaining the following results

$$
\begin{aligned}
b_0 &= u_2 \qquad (i = 0) \\[2ex]
d_N &= u_1 \qquad (i = N)
\end{aligned}
\tag{6.14}
$$

It should be evident that in equations 6.9 for the Moran Process we have absorbing boundaries.

Now we focus our attention on the models with frequency dependent mutation/exploration rates. Equations 6.10 similarly determine that for mutagens we have also absorbing boundaries. Equations 6.11 state that for the conformist exploration we obtain absorbing boundaries. For the innovative exploration, equations 6.12 determine that we have absorbing boundaries.

Fixation, which is frequently a result of the annihilation of one or more types of individuals inside a population, is a main aspect of biological systems, especially in the area of population genetics from which the term originated. Many systems exhibit fixation (or extinction), such as the perishing of a disease, the diffusion of an opinion, or the spread of mutated cells through a tissue. We have obtained a greater understanding of fixation because of the analytical characterization of the evolutionary dynamics observed in stochastic processes,

A key decisive factor of the dynamics is given by the probability of fixation of a single cooperator: if a mutation leads to a new strategy, what are the chances of this individual taking over the entire population?

Having in mind the foregoing question, we have introduced frequency dependent mutation/exploration rates in the birth-death transition probabilities, and after having done this, shapes of the fixation probability of a single cooperator, ρ_C, were obtained as a function of three different parameters: the cost (c), the selection intensity (w), and the population size (N). Analysis of these shapes must be performed for the Moran process and for the three different frequency dependent mutation/exploration rate scenarios: Mutagens, Conformist Exploration, and Innovative Exploration. We use the fixation probability of neutral drift, $1/N$, as a benchmark for studying the fixation probability driven by mutant/exploration rates.

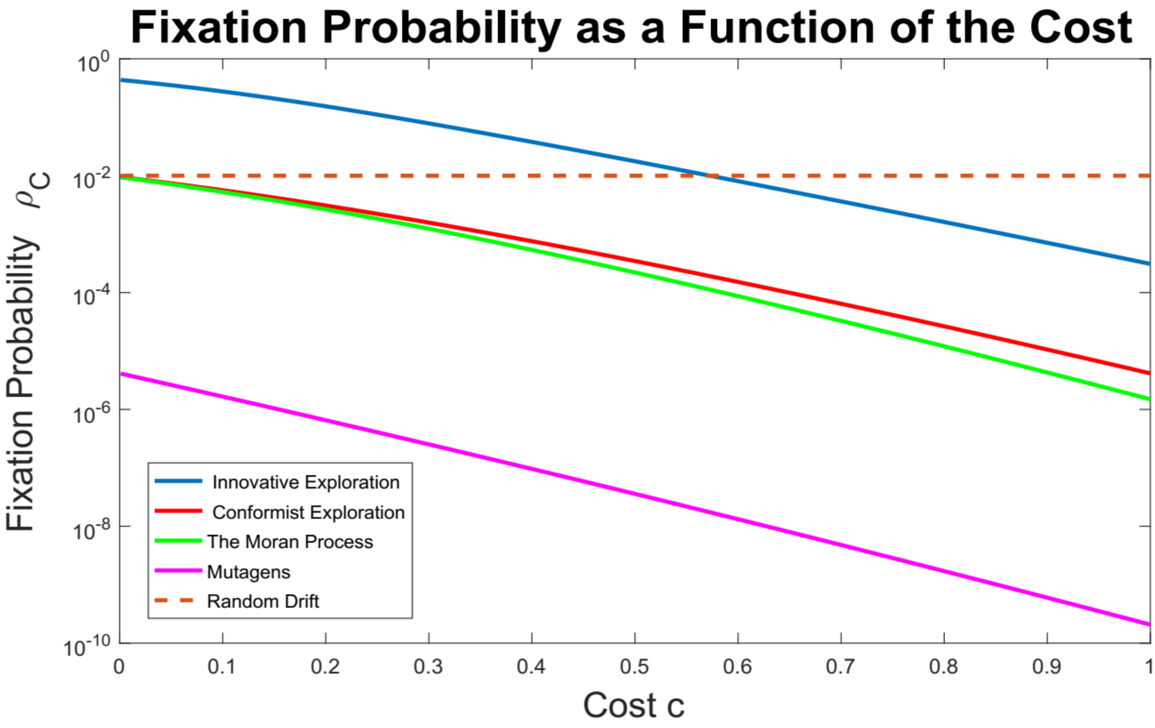
The fixation probability for an individual C player in a population of D players is represented by equation 6.8.

Replacement of D by C is favored by selection when $\rho_C > 1/N$, that is, when the fixation probability of a single cooperator is greater than the fixation probability of neutral drift which is being used as a benchmark for studying selection in finite populations.

Figure 5 illustrates the fixation probability shapes as a function of the cost, c, for the simplified Prisoner's Dilemma game (Donation Game). It should be noted that the fixation probability decreases as the cost increases for the Moran process and for the three mutant/exploration rate scenarios.

Using as a benchmark the fixation probability of neutral mutants (random drift) we can see from figure 5 that selection favors cooperation in the innovative exploration dynamics (greater than neutral), but approximately between the values 0.5 and 0.6 for the cost, selection begins to oppose it (less than neutral). While for a zero cost the conformist exploration and the Moran process behave as random drift, selection opposes mutagens . For increasing values of the cost, selection opposes the Moran process and the three types

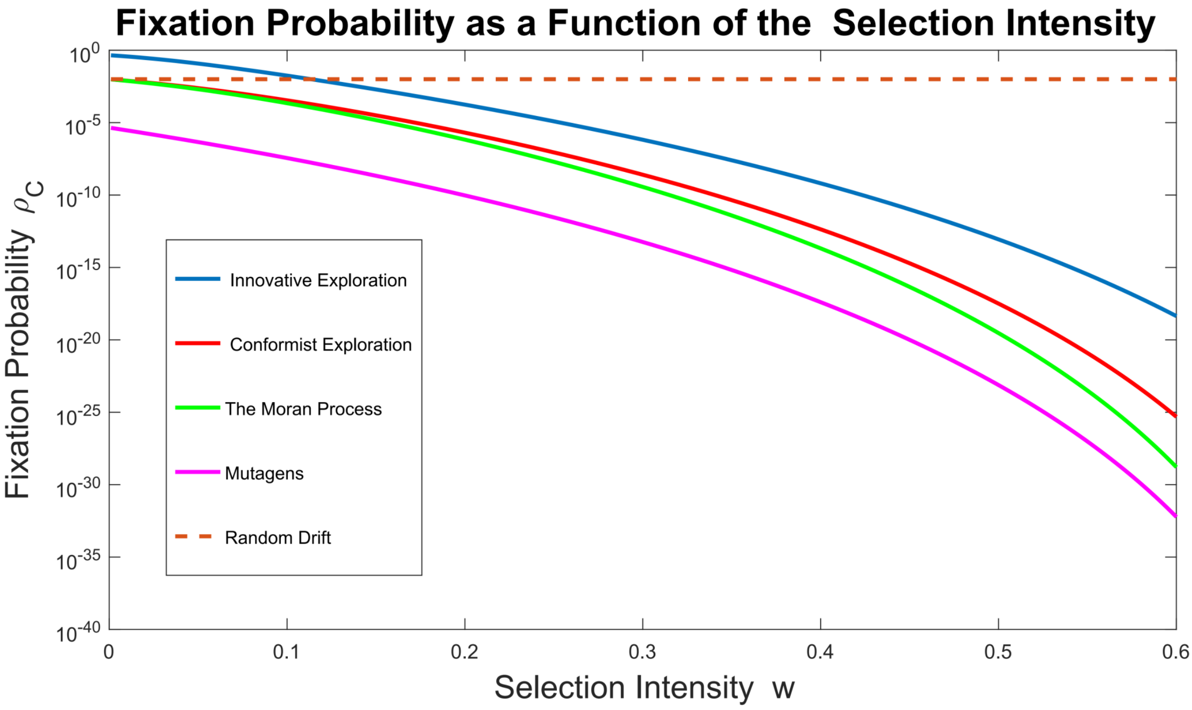
Figure 5 – Fixation Probability as a Function of the Cost (Population Size $N = 100$, Selection Intensity $w = 0.1$)



of mutation/exploration rates.

A graphic representation of the fixation probability as a function of the selection intensity, w, appears in figure 6, which shows in analogy to the previous case that the fixation probability decreases as the selection intensity gets stronger for the Moran process and for the three mutation/exploration rate scenarios.

Figure 6 – Fixation Probability as a Function of the Selection Intensity (Population Size $N = 100$, Cost $c = 0.5$)

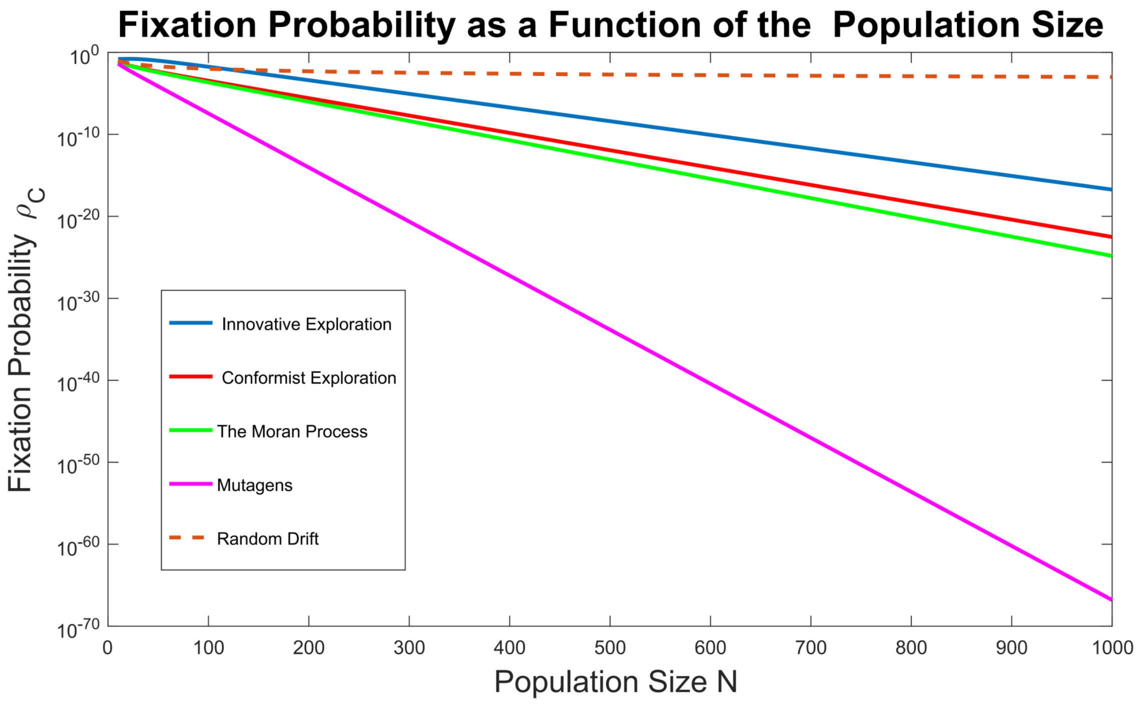


Selection favors the innovative exploration (greater than neutral), but around the value 0.1 for the intensity, we can see that selection begins to oppose it (less than neutral). It is seen that selection opposes mutagens. For a zero intensity (cooperators and defectors have the same fitness), the conformist exploration and the Moran process perform a random drift like behavior, and as the selection intensity gets stronger, selection opposes the four behaviors.

Figure 7 illustrates the possible shapes of the fixation probability as a function of the population size. Similarly as the previous cases, the fixation probability decreases with the growth of the population size for the Moran process and for the three mutation/exploration rate scenarios.

It should be noted that close to zero population, the Moran process and the three mutation/exploration rate scenarios perform a random drift like behavior, then selection favors the innovative exploration (greater than neutral) up to the value of 100

Figure 7 – Fixation Probability as a Function of the Population Size (Selection Intensity $w = 0.1$, Cost $c = 0.5$)



approximately for the population size. It may be noted that selection opposes the Moran process and the three mutation/exploration rate scenarios (less than neutral) as the population grows.

7 Conclusions

We can now see that our attention must be directed to reading, interpreting, and analyzing the results.

We have studied in particular a stochastic evolutionary $2X2$ game known as the simplified Prisoner's Dilemma , focusing our attention on the expression for the fixation probability in the presence of frequency dependent mutation/exploration rates.

The main direction of this dissertation is in the analysis and interpretation of the fixation probability of a single cooperator driven by mutation/exploration rates and how these rates influence in obtaining the several fixation probability shapes as functions of three different parameters (the cost, the selection intensity, and the population size), which are studied in selection dynamics.

In this dissertation we have applied the properties of Markov chains to the concepts of evolutionary game theory (more precisely the Moran process which is a birth-death Markov chain) with the highest objective of performing an analysis of the fixation probability shapes driven by different frequency dependent mutation/exploration rates, in such a way that we can decide whether selection favors or opposes them using as a benchmark the neutral drift fixation probability.

In addition to the Moran process, we have made use of three different models to introduce the frequency dependent mutation/exploration rates in the transition probabilities of the Markov chain: The Innovative Exploration, Mutagens, and The Conformist Exploration.

We have considered a system with mutations occurring during the dynamics. This process removes the possibility of fixation and extinction. The combination of mutation and selection can lead to non-trivial stationary states. Since we have introduced mutation by modifying the discrete-time transition probabilities of equations 5.10, the equations resulting from the modification are equations 6.13.

Note that the transition probabilities b_0 and d_N are represented by equations 6.14 and they are non-zero. Despite the fact that we have introduced frequency dependent mutations during reproduction events, the states 0 and N are absorbing for each frequency dependent mutation/exploration rate model.

We have obtained the fixation probability as a function of three different parameters: the cost c, the selection intensity w, and the population size N. Note further that these fixation probability shapes driven by frequency dependent mutation/exploration rates, decrease as any of the parameters increases for the three different models and for the

Moran process.

Figures 5, 6, and 7 illustrate the fact that selection favors, partially, the innovative exploration (greater than neutral), but it is observed that selection opposes the Moran process and the three mutation /exploration rate models as any of the parameters increases (less than neutral).

It must be emphasized that we have used the fixation probability of neutral mutants, $1/N$, as a benchmark for studying selection dynamics in finite populations.

When we state that selection favors one of the studied models (the Moran process and the three different mutation/exploration rate scenarios), we actually mean that selection favors fixation of strategy C (cooperator) and this occurs if the fixation probability of a single cooperator is greater than neutral. If selection opposes one of the models (selection opposes fixation of strategy C), then the fixation probability of a single cooperator is less than neutral.

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