

An Application of Game Theory to Biology: Evolutionary Dynamics

by
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This thesis entitled:

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Abstract

This thesis pretends to build a bridge between Mathematics and Biology. Particularly, we are interested in setting the basics elements of Evolutionary Game Theory (EGT). EGT has proved to be a powerful tool for studying biological problems under the scope of frequency dependent selection. Economy has long benefitted from the conceptual framework of EGT. We argue that is time to Biology to reduce the gap between theoretical and practical advances. In order to achieve this goal, we present the foundations of EGT, starting with the Theory of Ordinary Differential Equations and passing through static and dynamic analysis of EGT. Finally, we briefly present the current applications of this area in Biology, emphasizing the study of the evolution of cooperation. It is important to have a solid understanding of the theory to advance the modeling or field biological work in a proper direction. We hope this work constitutes a motivation to strengthen the bonds between Mathematics and Biology in our university.

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1. Introduction

1.1 Historical Context

In 1944, von Neumann and Morgenstern's book "The Theory of Games and Economic Behaviour" (von Neumann and Morgenstern, 1944) founded a new area of work in applied mathematics: the theory of games. Its name is accurate because it studies, precisely, games with players that have to choose strategies in order to maximize their payoff. Black Jack, chess, and Rock-Scissor-Paper are such games. Obviously more complicated applications emerged, especially in economics where it became a powerful method to analyze scenarios where actors with diverging interests had to make decisions.

Traditional game theory quickly found some obstacles to have a wider use. First, it relies strongly on rationality: each of the players involved in the game is "guessing" what the others "think" in order to get the greater benefit in the game. Even for humans there is strong evidence for consistent irrational behavior (Gintis, 2008), thus it is obvious the assumption cannot be generalized to the rest of living individuals. Second, the theory dealt primarily with zero-sum games (where one player loss is gained by the other). A small subset of the games meet this requirement but most of them do not adhere to this rule.

Maynard Smith and Price (1973) revolutionized the field with a novel approach that allowed to apply game theory to biology in general. Their approach assumed that the interacting individuals have strategies, not chosen by them, but imposed by heritage (genetical or cultural). This permitted to work on biological and economic problems, where rationality is not exhibited by the players. After these studies it became clear that game theory was an innovative and indispensable framework to tackle biological problems, and in particular evolutionary ones. As a result, the field of game theory applied to evolutionary biology has grown tremendously giving birth to Evolutionary Game Theory (EGT).

EGT is a rigorous mathematical tool that allows us to study biological interactions and to model encounters between individuals with predetermined strategies. The result of these encounters determine the evolution of the population. A fundamental innovation of EGT is that the fitness (i.e: reproductive success) of the individuals is not assumed to be constant, in other words, in EGT fitness depends on frequency. A simple way to illustrate the advantages of an EGT approach is in the context of a predator-prey system. Traditionally this system has been modeled assuming a constant fitness of the players regardless of their share. Thus, in this scenario the population of preys reproduce equally under high and low levels of predators in the population. In EGT that fitness becomes a non necessarily linear function of the frequency of prey and predators, giving a more realistic approach to the biological problem.

A central point in the aforementioned studies is the concept of Nash equilibrium, introduced by John Nash (1950) in his classic paper "Equilibrium points in n-Person Games". Shortly, a game is in a Nash equilibrium if no single player can change his strategy to maximize his payoff. This idea was preserved as the Fundamental

Theorem of Game Theory. This theorem postulates that under some relaxed conditions a game always has a Nash equilibrium. This concept applies to every game, not only zero-sum games. The idea of Nash Equilibrium was refined later by Maynard Smith (1982), applied to biological contexts, and resulted in the concept of Evolutionary Stable Strategy (ESS). Briefly, an ESS is a strategy such that if it is used by the majority of the population it cannot be invaded by another strategy. (see Bulmer, 1994, for a complete discussion on how ESS and Nash equilibrium are intimate related).

The last landmark in modern EGT to be mentioned is the replicator equation introduced by Taylor and Jonker (1978). This work initiated the use of ordinary differential equations in the field and allowed to approach evolutionary change of strategies with time. Time after, many results proved the relation between the equilibria of static games and the stationary states of dynamic models.

This area is nowadays an evolving and exciting space for new theoretic and practical results in a multidisciplinary field that includes, at least, mathematics, biology and economy.

1.2 Motivation

This thesis was initially motivated by the following problem. Since Darwin (1859), there has been a big question for evolutionary biologists: why is there cooperation in the world? Cooperation between molecules to form cells, between cells to form tissues, between animals to form social structures. This seems unnatural if we think in terms of natural selection that is supposed to promote competition but not cooperation between the individuals, yet cooperation is commonly seen in natural environments. Common hypothesis to explain this paradox appealed to two types of arguments: kin selection (Hamilton,1964) and group selection (Wynne-Edwards,1962). More recently, advances in the field of mathematical biology have produced results that contributed tremendously to this important biological question. Those advances were mostly due to theoretical EGT.

We quickly found that in order to understand this and many other issues in applied EGT to biology, we needed to have a firm basic understanding of the core of the theory involved. This is the aim of this work: provide an introduction of EGT. As expected, it is not a complete introduction but the interested reader will find references when needed. It is, at least, a consistent and rigorous presentation of the basics.

1.3 Note to the Reader

In this document you will find an approach to EGT based on normal-form games. That is, games with a finite set of players and pure strategies. Most of the time, the games will be symmetric two player games, where two individuals with the same set of available strategies are involved. We are interested in continuous time and infinite size populations.

The above restrictions are not a big loss. We think that simplicity is here an attraction. Further models may be found in Weibull (1995), Hofbauer and Sigmund (1998) and others, but they are all based on what we included here.

We begin in chapter 2 with an introduction to ordinary differential equations (ODE). A reader with experience in this field and knowledge of the Picard-Lindelöf theorem (existence and uniqueness of the solution of an ODE), may skip this chapter. It ends with many examples looking to familiarize the unexpert reader with ODEs.

Chapter 3 begins with the description of the Prisoner's Dilemma, section 3.1, that motivates a brief digression about the differences and similitudes between traditional game theory and evolutionary game theory. Section 3.3 introduces important notation for the rest of the work. Afterward, we emphasize the Nash equilibrium and Evolutionary Stable Strategies definitions and related theorems, notably the Nash's existence theorem.

Chapter 4 starts by defining a game dynamics and its solution in 4.1. Section 4.2 is an important summary of the different equilibria possibly attained by the solution of the dynamic and the relation between them. In 4.3 we make a fundamental connection between the chapter 3 concepts and the mentioned equilibria. This is mainly by the statement and proof of the Folk Theorem of EGT. Section 4.4 constitutes an application of all the previous work: the replicator equation.

Finally, chapter 5 summarizes the document and focus on some applications to biology.

At the end of each chapter, there is a discussion section. This paragraph shortly describes the respective material and presents perspectives that may not be included in the chapter.

1.4 References and Acknowledgements

This work was realized during the first semester of 2010. In the first months, I prepared some talks about Martin Nowak's book Evolutionary Dynamics (Nowak, 2006b). The attenders of these were professors José Ricardo Arteaga, Juan Manuel Cordovez, Carlos Daniel Cadena and my friend Jilberth Sebastián González. I am very grateful to all of them for their interest and support during this process. Arteaga, mathematician, and Cadena, biologist, were both especial professors for me: passionate, rigorous and kind. Cordovez got involved later on the work and he immediately dedicated time to studying the subject and made useful suggestions. González, who I admire, helped by listening to me.

The second part of the work was the redaction of the document. Chapter 2 is based on Arnol'd's Ordinary Differential Equations (1978). This brilliant mathematician died this semester and this is my little homage. The rest of the work was mainly based on Nowak's student Joseph Armao senior thesis Evolutionary Game Dynamics, Cooperation and Costly Punishment (Armao, unpublished) and Jörgen Weibull's Evolutionary Game Theory (Weibull, 1995). I owe these authors a lot: they guided me through the discovery of EGT.

2. Ordinary Differential Equations

The theory of Ordinary Differential Equations (ODE) is one of the basic tools of mathematical science and serves us to study evolutionary processes. The evolutionary processes that we will consider are deterministic, finite dimensional, and differentiable. We are interested in applying this theory to study biological evolution. Particularly, we want to model the change over time in the distribution of behaviours (strategies that can be genetically imposed or culturally acquired) in a large population of interacting individuals (Weibull, 1995).

This chapter starts with definitions and theorems presenting the basic concepts of ODE's. Example 2.1 is a simple illustration of the use of these notions. After that, in section 2.2 we prove some support theorems with a strong geometrical component. The fundamentals of the theory of evolution are discussed in the introduced mathematical framework. Section 2.3 discusses the main result of this chapter: the proof of the existence and uniqueness of the solution of an Initial Value Problem (IVP) of first order under certain conditions. This result has strong implications in our work: it will assure us that the evolution of the biological processes we are interested in, modelled mathematically by a system of ODEs, can be followed precisely by the unique solution of an Initial Value Problem. Section 2.4 is a full set of simple examples, including some figures. The chapter ends with a discussion in section 2.5.

The presentation is strongly motivated by Arnold's (1978) book Ordinary Differential Equations by its appealing relation between geometrics and analytical facts.

2.1 Basic Concepts

Definition 2.1 A process is said to be *deterministic* if its entire future course and its entire past are uniquely determined by its state at the present instant of time. The set of the possible states of a process is called its *phase space*. A process is said to be *finite-dimensional* if its phase space is finite dimensional, i.e. the number of parameters m required to describe its state is finite. A process is said to be *differentiable* if its phase space has the structure of a differentiable manifold¹ and if its change of state with time is described by a differential function.

In our work we will consider only deterministic, finite-dimensional, and differentiable processes.

Definition 2.2 An equation that requires the determination of a function and containing one or more derivatives of the unknown function is a differential equation. The order of a differential equation is the order of the highest derivative that appears in the equation. If the unknown function depends on a single independent variable,

¹ Manifold is a geometrical object similar locally to an Euclidean space.

then only ordinary derivatives appear in the equation, and it is said to be an ordinary differential equation.

Definition 2.3 Let U be an open domain of an m -dimensional Euclidean space, and let $v : U \rightarrow R$ be a differentiable function. An Initial Value Problem (I.V.P.) of first order is a differential equation of first order with an initial condition,

$$\begin{cases} \dot{x} = v(t, x), x \in U \\ x(t_0) = x_0 \end{cases} \quad (2.1)$$

The domain U is called *phase space* and the direct product $R \times U$ the *extended phase space*. If $v = (x, t)$ does not depend explicitly on t , then the I.V.P is called *autonomous*.

Definition 2.4 A *solution* to the I.V.P. (2.1) is a differential function $\varphi : I \rightarrow U$ of the interval $I = \{t \in R \mid a < t < b\}$ ² of the real t -axis, into U , which satisfies:

$$\begin{aligned} \frac{d}{dt} \Big|_{t=\tau} \varphi(t) &= v(\varphi(t)), \forall \tau \in I \\ \varphi(t_0) &= x_0 \end{aligned}$$

Definition 2.5 When $m = 1$ in the definition 2.1, the extended phase space is the plane strip $R \times U$, the direct product of the t -axis ($t \in R$) and the x -axis ($x \in U$). A *direction field* determined by a differentiable function $v : U \rightarrow R$ is the family of the straight lines, through every point $(t, x) \in R \times U$ of the extended phase space, whose angle of inclination with respect to the positive t -axis has as tangent $v(t, x)$. An *integral curve* is a line such that at each of its points it is tangent to the direction field determined by $v(t, x)$

Example 2.1 Let us consider the following autonomous I.V.P.

$$\begin{cases} \dot{x} = \sin x \\ x(t_0) = x_0 \end{cases} \quad (2.2)$$

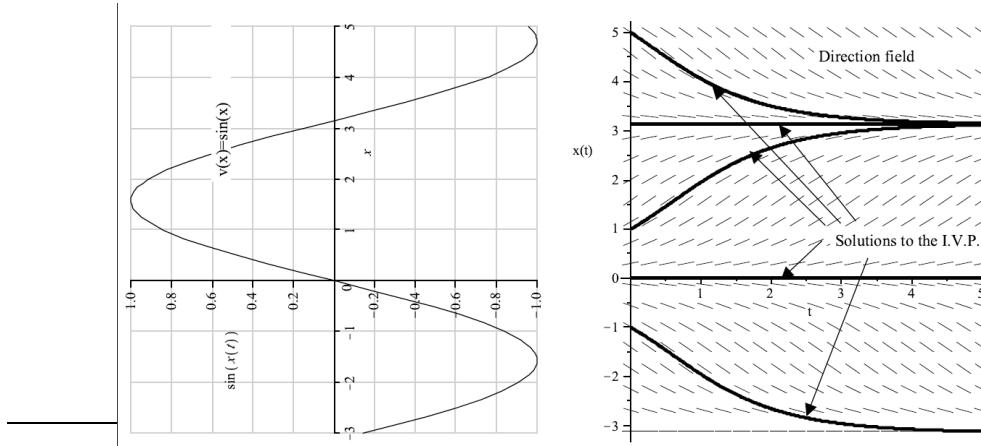


Figure-2-1: PVI $\dot{x} = \sin(x); x(0) = x_0$

² The interval I can be all R .

The phase space is R , the direction field is $v(x) = \sin(x)$. In Figure 2-1 we have two graphics: in the left, the graph of the function $v(x) = \sin(x)$ that determines the direction field and in, the right, the extended phase space showing certain solutions and the direction field. Note that the direction field coincides with the tangents at each point of the solutions. This graph was plotted using the software Maple11®

2.2 Basic Theorems

The following simple theorem proves that the problem of finding integral curves is equivalent to the problem of finding an integral. The proof is simple and elegant.

Theorem 2.1 Assume a continuous field v on a plane that maps into itself under all translations along a certain line and that does not contain directions parallel to that line. Using a convenient translation this line can always be the x-axis (see Figure 2-2). Then, finding the integral curves of this kind of field is precisely the problem of integrating a given continuous function.

Proof Note that any integral curve is the graph of a function f . The derivative of f describes the slope of this graph. Now, if we have the graph of an integral curve, by definition 2.5, in each point of the plane, its slope must be equal to the slope of the line of v , the field. But the latter is a continuous known function of the abscissa. Then we can integrate this function and obtain the integral curve searched.

We have proved that any integral curve is a primitive of an unknown function. The preceding proof permits to link in a natural way a geometrical problem to an analytical problem: the problem of finding integral curves is equivalent to the problem of solving differential equations. The formal statement is:

Theorem 2.2. A necessary and sufficient condition for f to be an integral curve, given a continuous field, is that the following holds for every t in the domain of definition of f :

$$\frac{df}{dt} = v(t, f(t)) \quad (2.3)$$

The theory of evolution presented first by Darwin (1859) resides in three fundamental blocks:

- reproduction
- selection
- mutation.

These are modern terms but the essence of Darwin's proposal remains. Darwin was strongly motivated by a lot of factors to arrive to his extraordinary theory: his voyage around the world in The Beagle, his grandfather Erasmus Darwin writings where he stated some facts about evolution, Thomas Malthus results and especially his acute sense to observe the world.

Example 2.2 Reproduction

In particular, Malthus suggested that populations should grow exponentially if the resources are unlimited. That is, if x is the size of the population, r the rate of reproduction (reproduction is exponentially distributed with mean $1/r$), t is time then the population size will change as follows:

$$\dot{x} = rx \quad (2.4)$$

It is easy to check that $x(t) = x_0 e^{rt}$ is by definition 2.4 a solution of (2.4). x_0 represents the population at the instant $t_0 = 0$.

This perturbed Darwin: given that the resources are limited it was obvious that some individuals could not survive. Which then would survive and which would die? The answer he gave later was that the fittest individuals of the population would remain. The model represented by (2.4) is an over simplification of real life, it has been improved by introducing new parameters like death rate and carrying capacity. See Nowak (2006b) for a further development.

Example 2.3 Selection

Now let's see how to model selection. Here we are interested in studying the change of the share of the population size of two types, x and y . These types are competing for one or many resources important for their maintenance in the ambient. The simplest case is modeled by:

$$\begin{cases} \dot{x} = ax \\ \dot{y} = by \end{cases} \quad (2.5)$$

Where a and b are the reproductive rates of x and y respectively. It is crucial to note that, at least if it's not explicitly stated, the reproductive rates are for us direct measures of fitness. The solutions of (2.5) are equivalent to the solution of (2.4), our interest here is to study the change of *proportion* of the types. For this we introduce a new function φ :

$$\varphi(t) = \frac{x(t)}{y(t)} \quad (2.6)$$

It is easy to check that

$$\dot{\varphi} = (a - b)\varphi \quad (2.7)$$

And the following is a solution of (2.7), again by definition 2.4:

$$\varphi(t) = \varphi_0 e^{(a-b)t} \quad (2.8)$$

where φ_0 represents the proportion of the types in the population at the instant $t_0 = 0$.

Note that (2.8) implies that

$$\text{if } a \geq b \text{ then } \varphi \rightarrow \infty \text{ and if } a \leq b \text{ then } \varphi \rightarrow 0 \quad (2.9)$$

Example 2.4 Mutation

During the reproduction of DNA or RNA, a constant process in every living organism, there may be errors. These are called mutations. Suppose again there are two types with respective shares x and y but we require now that $x + y = 1$, that is the population size is constant.

Note μ_1 the mutation rate of one type to an other and μ_2 , the converse. Mutation rate is the probability that the reproduction of one type ends in the other one. Then we have:

$$\begin{aligned}\dot{x} &= x(1 - \mu_1) + y\mu_2 - \phi x \\ \dot{y} &= x\mu_1 + y(1 - \mu_2) - \phi y\end{aligned}$$

Where ϕ is a parameter for maintaining the size of the population constant (interestingly, this parameter must be the average fitness of the population, see Nowak (2006)).

If we assume that both have the same fitness equal to 1, then we have $\phi = 1$. Recalling that $x + y = 1$, the system reduces to:

$$\dot{x} = \mu_2 - x(\mu_2 + \mu_1) \Rightarrow (\dot{x} = 0 \Rightarrow x' = \frac{\mu_2}{\mu_1 + \mu_2})$$

Where x' is the share of the first type at the equilibrium, that is the proportion when the population is stable.

In the absence of differences in the fitness of the types, we note that mutation leads to coexistence. The proportions are determined by the mutation rates. There may be selection for a type if the mutations rates are very different, this is an example of selection with constant fitness.

The preceding cases are quite interesting because they present the basic mathematical formulation of the essence of the theory of evolution (the mutation model is not included but it is similar) and because they show how to apply theorems 2.1, 2.2 and definition 2.4. In each case, even if not explicitly presented, we found the solution to a differential equation integrating a continuous function. Differentiating the solution we can check if it is correct.

Remark 2.1 We conclude this example with two observations:

- Equation (2.9), in its simplest form, a rigorous demonstration of the “survival of the fittest”: when the fitness of a population is superior to the fitness of the other, the former tends to outcompete the latter. Again, see Nowak (2006) for a complete presentation of improved models, especially if the total population

must have a constant size and if there can be more than two types. The extension of the model is natural.

- The model of selection presented will be useful to make a fundamental contrast with the evolutionary game theory (EGT) presented in the next chapter. Here we introduced the constants a and b as fitness measures. In EGT, the model will be analogous but fitness measures will not be constants but dependent of frequency.

In this example we showed explicitly solutions of various first order ODE's. The solution in these cases, at least, exists. Nonetheless we can't be sure if the solution exist always, and, even in these cases, it's uniqueness. We address this problem now.

Definition 2.6 Consider an autonomous I.V.P.

$$\begin{cases} \dot{x} = v(x), x \in U \\ x(t_0) = x_0 \end{cases} \quad (2.10)$$

If $v(a) = 0$, we say that a is an equilibrium position.

Theorem 2.3. The solution $x \equiv \varphi(t)$ of the IVP

$$\begin{cases} \dot{x} = v(x), x \in U \\ x(t_0) = x_0 \end{cases} \quad (2.11)$$

with no equilibrium positions is given by

$$t - t_0 = \int_{x_0}^x \frac{d\epsilon}{v(\epsilon)} \quad (2.12)$$

Conversely, $x \equiv \varphi(t)$ defined by (2.12), is a solution and satisfies the initial condition.

Proof Assume $v(x)$ is a continuous and never vanishing function. The tangent of the angle θ , between the field v and the x -axis, is $\frac{1}{v(x)}$. Then the direction the field of $\frac{dx}{dt} = v(x)$ is the same direction of the field of $\frac{dt}{dx} = \frac{1}{v(x)}$ (see Figure 2-3). Their integral curves must coincide. But our field satisfies the premises of Theorem 2.1, it is never parallel to the t -axis because it never vanishes and it maps into itself under all translations along that axis because it is autonomous, then the integral curves can be found by integration alone. An integral curve of the second field is easily found using the Fundamental Theorem of Calculus, and it is

$$t - t_0 = \int_{x_0}^x \frac{d\epsilon}{v(\epsilon)} \quad (2.13)$$

The converse is obvious.

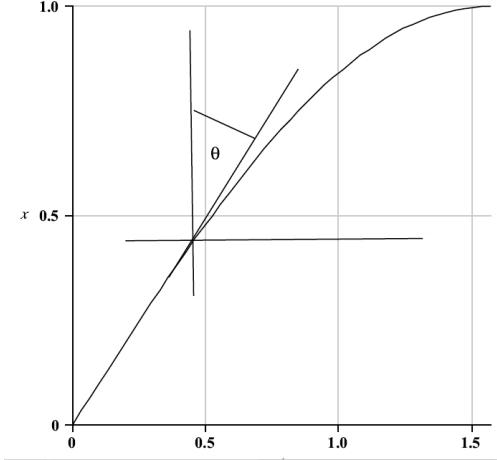


Figure 2-3 The angle θ

2.3 The Main Theorems

We now state and prove the main theorem of this chapter. First we present an important result for the proof.

Differentiability implies locally Lipschitz

Lemma 2.1 $C^1 \Rightarrow L.L$ Let V be any subset of the domain U which is both convex³ and compact⁴. Then a C^1 function f , that is a continuous function with continuous first partial derivatives, defined on a domain $U \subseteq R^m$ satisfies locally the Lipchitz condition. That is $\forall x \in U, \exists V_x$ neighborhood of x such that,

$$\forall y \in V_x, |f(\vec{x}) - f(\vec{y})| \leq k |\vec{x} - \vec{y}|, k \in R^+, k \neq 0 \quad (2.14)$$

Where

$$k = \sup_{x \in V_x} \|f_{*x}\|$$

and f_{*x} represents the derivative of f at the point $x \in U \subseteq R^m$.

Proof Suppose f is C^1 , $f : R^m \rightarrow R$. We construct a new function g as follows:

$$\begin{aligned} g &: R \rightarrow R^m \\ g(\theta) &= \vec{x} + \theta(\vec{y} - \vec{x}) \\ 0 \leq \theta &\leq 1 \end{aligned}$$

Consider now $\alpha(\theta) = f(g(\theta))$. By construction f and g are well defined, their composition α is then a well defined function.

³ A domain in R^n is said to be convex if whenever it contains two points, it also contains the line segment joining the two points

⁴ In R^n , every bounded and closed subset is compact.

Note that $\alpha : R \rightarrow R$ and then we can use the usual chain rule to obtain:

$$\begin{aligned}\alpha'(\theta) &= \nabla f(g(\theta)) \bullet g'(\theta) \text{ and } g'(\theta) = (\vec{y} - \vec{x}) \text{ then} \\ \alpha'(\theta) &= \nabla f(g(\theta)) \bullet (\vec{y} - \vec{x})\end{aligned}\tag{2.15}$$

Then $\alpha'(\theta)$ is continuous because it is the product of continuous functions ($\nabla f(g(\theta))$ is continuous because f is C^1 and g is trivially C^∞ , $(\vec{y} - \vec{x})$ is a continuous constant function). Using the Fundamental Theorem of Calculus and equation (2.15) we obtain:

$$\alpha(1) - \alpha(0) = \int_0^1 (\nabla f(g(\theta)) \bullet (\vec{y} - \vec{x})) d\theta$$

An easy calculation shows that the last equation is equivalent to:

$$f(\vec{y}) - f(\vec{x}) = \int_0^1 (\nabla f(g(\theta)) \bullet (\vec{y} - \vec{x})) d\theta \Rightarrow |f(\vec{y}) - f(\vec{x})| = \left| \int_0^1 (\nabla f(g(\theta)) \bullet (\vec{y} - \vec{x})) d\theta \right|$$

And

$$\left| \int_0^1 (\nabla f(g(\theta)) \bullet (\vec{y} - \vec{x})) d\theta \right| \leq \int_0^1 |(\nabla f(g(\theta)) \bullet (\vec{y} - \vec{x}))| d\theta$$

But

$$|(\nabla f(g(\theta)) \bullet (\vec{y} - \vec{x}))| = \|(\nabla f(g(\theta)))\| \cdot \|\vec{y} - \vec{x}\| \cdot \cos \beta$$

where β is the angle formed by the two vectors $\nabla f(g(\theta))$ and $(\vec{y} - \vec{x})$

Now $\cos \beta \leq 1$ then

$$\int_0^1 |(\nabla f(g(\theta)) \bullet (\vec{y} - \vec{x}))| d\theta \leq \int_0^1 \|(\nabla f(g(\theta)))\| \cdot \|\vec{y} - \vec{x}\| d\theta$$

Finally, note that $\|(\nabla f(g(\theta)))\|$ is bounded because it is a continuous function on a closed interval ($0 \leq \theta \leq 1$) (Rudin, 1976). Let k be:

$$k = \sup_{0 \leq \theta \leq 1} \|(\nabla f(g(\theta)))\|$$

then

$$\int_0^1 \|(\nabla f(g(\theta)))\| \cdot \|\vec{y} - \vec{x}\| d\theta \leq k \|\vec{y} - \vec{x}\|.$$

We conclude that:

$$\forall \vec{x}, \vec{y} \in U, \exists k \in R^+, k \neq 0, \text{ such that } |f(\vec{x}) - f(\vec{y})| \leq k |\vec{x} - \vec{y}|$$

The proof is finished.

C^1 -function v implies C^0 -function $\varphi(t)$

Lemma 2.2 ($v \in C^1 \Rightarrow \varphi \in C^0$) Let V be any subset as in the Lemma 1. Suppose the function $v(t, x)$ in the I.V.P. (2.1) is continuously differentiable (C^1) in a neighborhood of a point (t_0, x_0) of the extended phase space. Then, given any point x sufficiently close to x_0 , there is a neighborhood of t_0 in which a solution $x = \varphi(t)$ (for now we do not know if it exists and it is unique) of the I.V.P. (2.1) is defined and depends continuously on the initial point x_0 , i.e. if $\varphi(t)$ exists, it is a continuous function (C^0).

Proof The proof uses the concept of Picard mappings (contraction mappings). The proof can be red in Arnold's (1978) text.

The Existence, Uniqueness and Continuity Theorems

Theorem 2.4. Let v be a smooth function defined on $U \subseteq R$. The solution $\varphi(t) = x(t)$ of $\dot{x}(t) = v(x)$ with initial condition (t_0, x_0) :

- 1- exists for $\forall t_0 \in R$ and $x_0 \in U$
- 2- is unique in the sense that two solutions with the same initial condition coincide in some neighborhood of t_0
- 3- is given by (2.12) if $v(x_0) \neq 0$ and $\varphi(t) \equiv x_0$ if $v(x_0) = 0$.

Proof Suppose x_0 is not an equilibrium position. Then the theorem is proved by the theorem 2.3.

Suppose $\varphi(t_0) = x_0$ and x_0 is an equilibrium position and $\varphi(t_1) = x_1$ is not an equilibrium position. If such x_1 does not exist then $\varphi(t) \equiv x_0$ is, obviously, the unique solution. Suppose then x_1 exists, we shall arrive to a contradiction.

Let $t_2 \in [t_0, t_1]$ the closest real to t_1 such that $v(\varphi(t_2)) = 0$. We may have $t_0 = t_2$. See Figure 2-4.

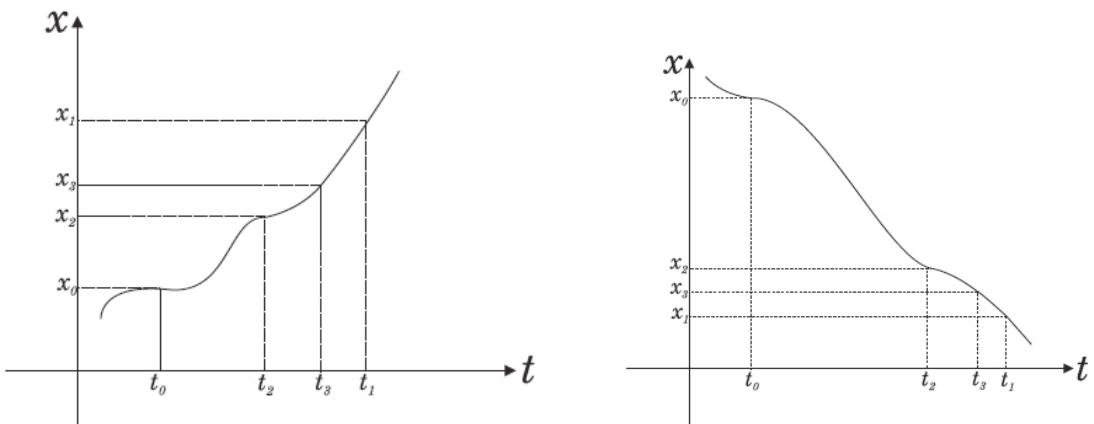


Figure 2-4: There are only two possibilities because v is a C^1 -function.

By (2.13), $\forall t_3 \in (t_2, t_1)$ we have

$$t_3 - t_1 = \int_{x_1}^{x_3} \frac{d\epsilon}{v(\epsilon)}, x_3 = \phi(t_3) \quad (2.16)$$

Remember that by construction $v(\phi(t_3)) \neq 0$.

We show now that

$$t_3 - t_1 = \int_{x_1}^{x_3} \frac{d\epsilon}{v(\epsilon)}, x_3 = \phi(t_3) \rightarrow \infty \text{ when } x_3 \rightarrow x_2 \quad (2.17)$$

By lemma 2.1,

$$\forall \epsilon \in [x_1, x_2] \exists k \in R^+, k \neq 0, \text{ such that } |v(\epsilon) - v(x_2)| \leq k|\epsilon - x_2| \quad (2.18)$$

Thus from (2.17), (2.18) follows:

$$|t_3 - t_1| \geq \left| \int_{x_1}^{x_3} \frac{d\epsilon}{k(\epsilon - x_2)} \right| \quad (2.19)$$

This is obtained by simply looking at the possibilities for the function v . By hypothesis the function $v = v(x)$ is continuous and differentiable at x , therefore it can only be either positive or negative in the range where we seek the solution (see Figure 2-4). If the function is continuous but changes the sign in this range, then the solution $\phi(t)$ would have a jump discontinuity at each critical point of v . This would contradict the Lemma 2.2.

Thus, it is not difficult to calculate that,

$$\left| \int_{x_1}^{x_3} \frac{d\epsilon}{k(\epsilon - x_2)} \right| = |k \cdot (\ln(x_3 - x_2) - \ln(x_1 - x_2))| \quad (2.20)$$

but $\ln(x_1 - x_2)$ is a fixed number and if

$$x_3 \rightarrow x_2, |\ln(x_3 - x_2)| \rightarrow \infty \quad (2.21)$$

Remarking that by construction

$$|t_2 - t_1| \geq |t_3 - t_1| \quad (2.22)$$

Then (2.19), (2.21), and (2.22) $\Rightarrow |t_2 - t_1| \geq \infty$, clearly a contradiction.

Then t_1 cannot exist, and $v(\phi(t)) = 0$ for all t in the domain of definition of ϕ . We have that $\dot{\phi} \equiv 0$ then ϕ is a constant function that satisfies the initial condition so that $\phi(t) = x_0$ is the unique solution.

The proof is finished.

2.3.1 General Case of a First Order Initial Value Problem

When we have a general first order I.V.P. as follows:

$$\begin{cases} \dot{x} = v(t, x), x \in R^m \\ x(t_0) = x_0, (t_0, x_0) \in R \times U \subseteq R^m \end{cases} \quad (2.23)$$

We are interested in the following questions:

- 1- Under what conditions can we be sure that a solution t (2.23) exists?
- 2- Under what conditions can we be sure that, if the solution exists, it is unique?

In the previous section we gave answers to these questions when the process is autonomous. The goal of these proofs was mainly geometrical intuitive treatment. For the general case the answers may be found in Arnold's (1978) book or for the simple case $m=1$ in Boyce and Di Prima's (1977). The proofs contain a technique for constructing approximate solutions based in contraction mappings. These mappings are a generalization of the Picard's mappings (successive Picard's approximations). It is not our interest to repeat these proofs but we will state the theorems when $m=1$. Then, we will present several examples illustrating the applications of these theorems.

Theorem 2.5 (Existence) Suppose that v is a continuous function defined in a region $R = \{(t, x), a - \delta < t < a + \delta, b - \varepsilon < x < b + \varepsilon\}$ such that $(t_0, x_0) \in R$. Then there exists a number δ_0 , possibly smaller than δ , so that a solution to the following I.V.P. exists.

$$\begin{cases} \dot{x} = v(t, x) \\ x(t_0) = x_0 \end{cases} \quad (2.24)$$

Theorem 2.6 (Uniqueness) Suppose that v and $\frac{\partial v}{\partial x}$ are both continuous functions defined in a region $R = \{(t, x), a - \delta < t < a + \delta, b - \varepsilon < x < b + \varepsilon\}$ such that $(t_0, x_0) \in R$. Then there exists a number δ_1 , possibly smaller than δ_0 in the Theorem 2.5, such that the solution $x = \varphi(t)$ guaranteed by the Theorem 2.5 is the unique solution to the I.V.P. (2.24) for $\forall x, x_0 - \delta_1 < x < x_0 + \delta_1$.

Theorem 2.7 (Continuity and Differentiability-Picard-Lindelöf) Suppose that v is a C^2 function, i.e a function with two first partial derivatives continuous functions, defined in a region $R = \{(t, x), a - \delta < t < a + \delta, b - \varepsilon < x < b + \varepsilon\}$ such that $(t_0, x_0) \in R$. Then the solution $x = \varphi(t)$ guaranteed by the Theorems 2.5 and 2.6 to the I.V.P. (2.24) for $\forall x, x_0 - \delta_1 < x < x_0 + \delta_1$ is a C^1 function, i.e a continuous and differentiable function.

2.4 Examples

Example 2.5 The following I.V.P.

$$\begin{cases} \dot{x} = t - x \\ x(1) = 0 \end{cases} \quad (2.25)$$

corresponds to a process modelled by a linear differential equation where $v(t,x)$ is a C^∞ -function. Then its solution exists, it is unique and it is a smooth function. Figure 2-5 shows this and other solutions corresponding to distinct initial conditions and its associated direction field. We used the software Maple11® to plot it.

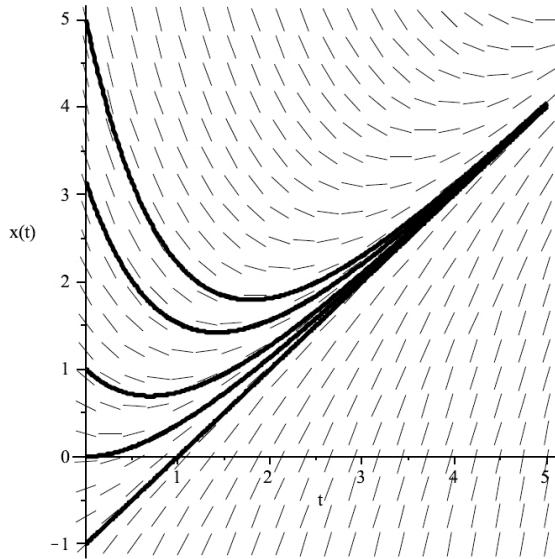


Figure 2-5: PVI $\dot{x} = t - x$; solutions for $x(1) = 0; x(0) = 1, \pi, 5$.

The solution of the I.V.P. is

$$x = \varphi(t) = t - 1 \quad (2.26)$$

and the values of a, δ in the Theorems 2.5, 2.6, 2.7 are: $a = 0, \delta = \infty$.

Example 2.6 The following I.V.P.

$$\begin{cases} \dot{x} = 1 + x^2 \\ x(0) = 0 \end{cases} \quad (2.27)$$

corresponds to an autonomous process modelled by a nonlinear differential equation where $v(t,x)$ is a C^∞ -function. Then its solution exists, it is unique and it is a smooth function. Figure 2-6 shows this and other solutions corresponding to distinct initial conditions and its associated direction field. We used the software Maple11® to plot it.

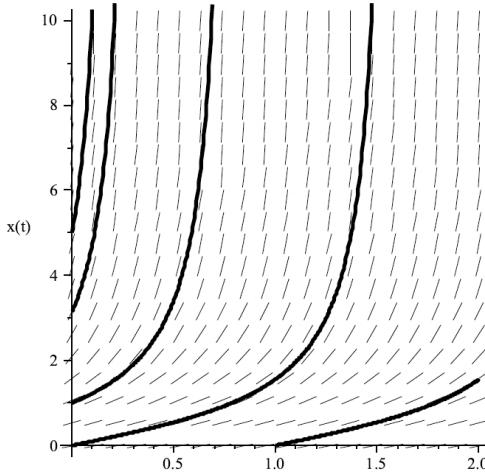


Figure 2-6: PVI $\dot{x} = 1 + x^2$; solutions for $x(1) = 0; x(0) = 1, \pi, 5$.

The solution of the I.V.P. is

$$x = \varphi(t) = \tan t \quad (2.28)$$

and the values of a, δ in the Theorems 2.5, 2.6, 2.7 are: $a = 0, \delta = \frac{\pi}{2}$.

Example 2.7 The following I.V.P.

$$\begin{cases} \dot{x} = \frac{3-x}{2} \\ x(0) = x_0 \end{cases} \quad (2.29)$$

corresponds to an autonomous process modelled by a linear differential equation where $v(t, x)$ is a C^∞ -function. Then its solution exists, it is unique and it is a smooth function. Figure 2-7 shows this and other solutions corresponding to distinct initial conditions and its associated direction field. We used the software Maple11® to plot it.

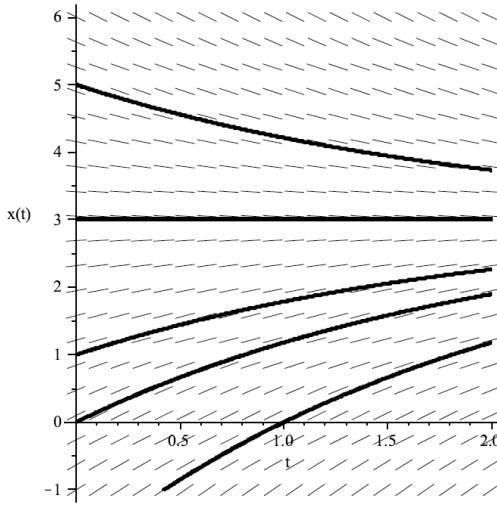


Figure 2-7: PVI $\dot{x} = \frac{3-x}{2}$; **solutions for** $x(1)=0; x(0)=0,1,3,5.$

The solution of the I.V.P. for $x(0)=0$ is

$$x = \varphi(t) = 3 - 3e^{-\frac{1}{2}t} \quad (2.30)$$

and the values of a, δ in the Theorems 2.5, 2.6, 2.7 are: $a = 0, \delta = \infty$.

Example 2.8 The following I.V.P.

$$\begin{cases} \dot{x} = 1 - 2tx \\ x(0) = x_0 \end{cases} \quad (2.31)$$

corresponds to an nonautonomous process modelled by a nonlinear differential equation where $v(t,x)$ is a C^∞ -function. Then its solution exists, it is unique and it is a smooth function. Figure 2-8 shows this and other solutions corresponding to distinct initial conditions and its associated direction field. We used the software Maple11® to plot it.

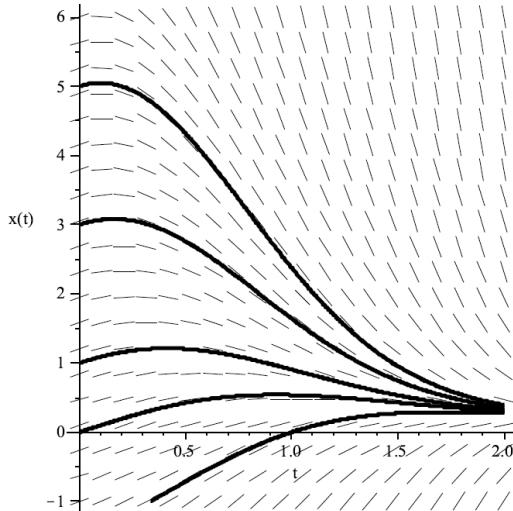


Figure 2-8: PVI $\dot{x} = 1 - 2tx$; solutions for $x(1) = 0; x(0) = 0, 1, 3, 5$

The solution of the I.V.P. is not easy to obtain in this case. We used Maple11®.

$$x = \varphi(t) = -\frac{1}{2}\sqrt{\pi}e^{-t^2} \operatorname{erf}(t) \quad (2.32)$$

where $\operatorname{erf}(t)$ is the error function $\operatorname{erf}(z) \doteq \frac{2}{\sqrt{\pi}} \int_0^z e^{-t^2} dt$, see Figure 2.9.

The values of a, δ in the Theorems 2.5, 2.6, 2.7 are: $a = 0, \delta = \infty$.

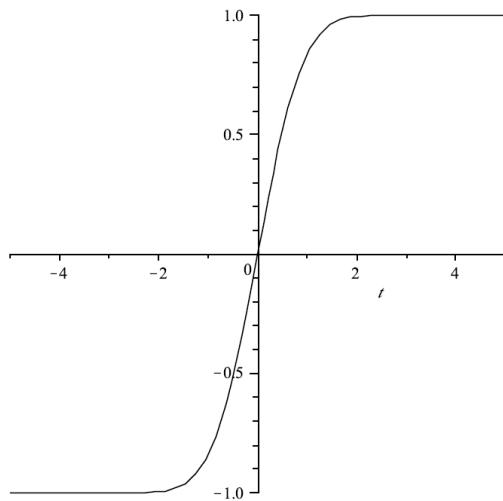


Figure 2-9: the error function $\operatorname{erf}(z) \doteq \frac{2}{\sqrt{\pi}} \int_0^z e^{-t^2} dt$

Example 2.9 The following I.V.P.

$$\begin{cases} \dot{x} = \frac{x}{2} + e^{-t} \\ x(0) = x_0 \end{cases} \quad (2.33)$$

corresponds to a nonautonomous process modelled by a nonlinear differential equation where $v(t,x)$ is a C^∞ -function. Then its solution exists, it is unique and it is a smooth function. Figure 2-10 shows this and other solutions corresponding to distinct initial conditions and its associated direction field. We used the software Maple11® to plot it.

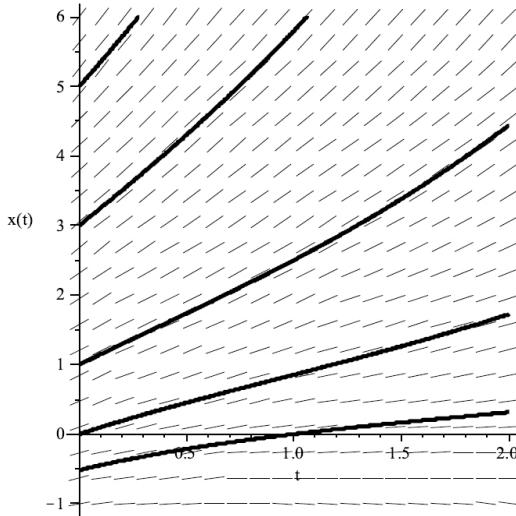


Figure 2-10: PVI $\dot{x} = \frac{x}{2} + e^{-t}$; solutions for $x(1) = 0; x(0) = 0, 1, 3, 5$.

The solution of the I.V.P. for $x(0) = 0$ are

$$x = \frac{2}{3}e^{\frac{t}{2}} - \frac{2}{3}e^{-t} \quad (2.34)$$

and the values of a, δ in the Theorems 2.5, 2.6, 2.7 are: $a = 0, \delta = \infty$.

Example 2.10 The following I.V.P.

$$\begin{cases} \dot{x} = x^3 \\ x(0) = 0 \end{cases} \quad (2.35)$$

corresponds to an autonomous process modelled by a linear differential equation where $v(t,x)$ is not even a C^1 -function. There is not an unique solution. Figure 2-11 shows two solutions and its associated direction field. We used the software Maple11® to plot it.

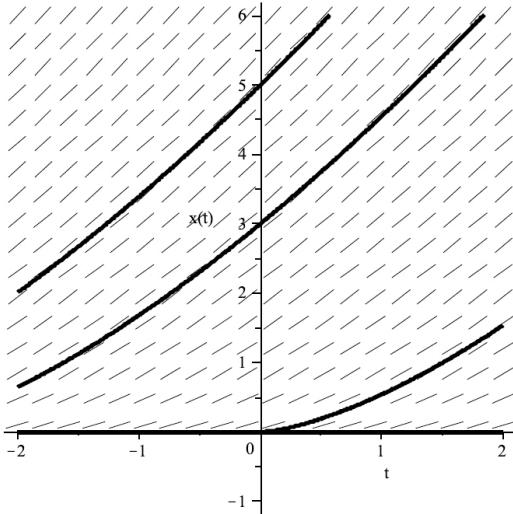


Figure 2-11: PVI $\dot{x} = x^{\frac{1}{3}}$; solutions for $x(0) = 0, 3, 5$.

The general solutions of the I.V.P. for $x(t_0) = 0$ are

$$\psi(t) \equiv 0 \quad (2.36)$$

and

$$\varphi(t) = \begin{cases} 0 & \text{if } 0 \leq t \leq t_0 \\ \left[\frac{2}{3}(t - t_0) \right]^{\frac{3}{2}} & \text{if } t \geq t_0 \end{cases} \quad (2.37)$$

The theorems 2.5, 2.6, 2.7 are not applicable. The nonuniqueness of the solution of the problem (2.35) does not contradict these theorems since

$$\frac{\partial}{\partial x} v(t, x) = \frac{\partial}{\partial x} x^{\frac{1}{3}} = \frac{1}{3} x^{-\frac{2}{3}} \quad (2.38)$$

and this function is not continuous, nor even defined when $x = 0$. Hence the theorems do not apply in any region containing some part of the t -axis.

Example 2.11 The following I.V.P.

$$\begin{cases} \dot{x} = rx\left(1 - \frac{x}{K}\right) \\ x(t_0) = x_0 \end{cases} \quad (2.39)$$

corresponds to an autonomous process modelled by a nonlinear differential equation where $v(t, x)$ is a C^∞ -function. Then its solution exists, it is unique and it is a smooth function. This problem is known in Biology as the logistic growth in Population Dynamics, where $x = \varphi(t)$ is the population of a given species at time t and r is called

its intrinsic growth rate. Thus $x = \varphi_1(t) \equiv 0, x = \varphi_2(t) \equiv K$ are constant equilibrium solutions, the zeros of the direction field are critical points.

Figure 2-12 shows some solutions corresponding to $K = 3, r = \frac{1}{2}$ and its associated direction field. We used the software Maple11® to plot it.

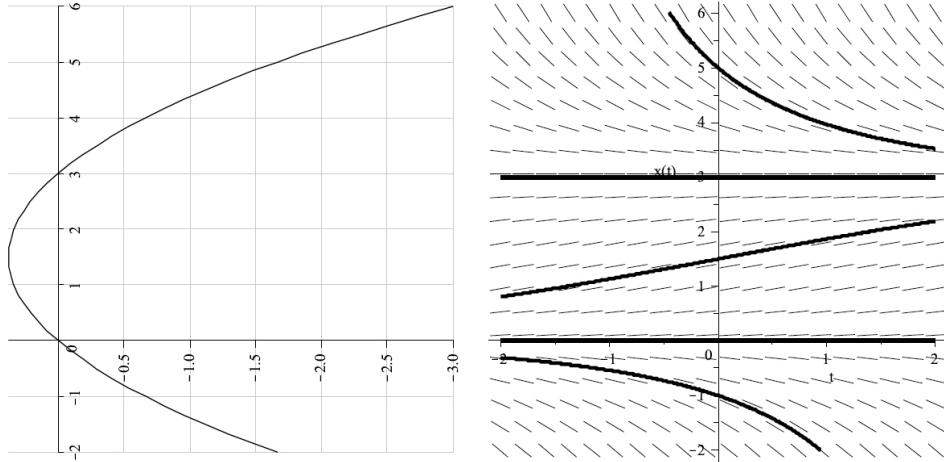


Figure 2-12: PVI $\dot{x} = \frac{1}{2}x(1 - \frac{x}{3})$; **solutions for** $x(1) = 0; x(0) = 0, 1, 3, 5$.

The solution of the I.V.P. for $x(0) = x_0$ are

$$x = \frac{x_0 K}{x_0 + (K - x_0)e^{-rt}} \quad (2.34)$$

and the values of a, δ in the Theorems 2.5, 2.6, 2.7 are: $a = 0, \delta = \infty$.

2.5 Discussion.

This chapter served as a basic introduction to ordinary differential equations (ODE). We began with very simple notions in order to set a common language. We used V.I Arnold (1978) proofs and notation because it has a strong intuitive geometric component. The fundamental result that we completely proved is the existence and uniqueness of the solution of an autonomous ODE. We stated other generalizations of this result. The chapters ends with different examples illustrating the use of the theory presented. This material is simple but important for readers without experience in the field. As we will see, the theory of ODE is the most important tool of EGT: all the other results that we will discuss in this work rely in this theory. Usually, game theorists only reference this results. We wanted to include, at least, the basic ideas for mathematical completeness of the document.

3. Evolutionary Game Theory: Static Analysis

Fitness of an individual is not constant, it depends strongly on his, as well as the others, proportion on the population. This assertion seems obvious in every day life. EGT arises when we assume its validity and it is thus “the most comprehensive way to look at the world” (Nowak,2006b). In this section we begin by introducing an example of EGT, the famous Prisoner’s Dilemma, then we describe in 3.2 the relation between Game Theory (GT) and EGT. After this motivation in section 3.3 we formalize two basic notions of games: the Nash equilibrium and evolutionary stable strategies. Finally in section 3.4 we present a discussion of the results and implications of the chapter. The presentation is mostly based on Nowak (2006b) and Weibull (1995) both well resumed by Armao (unpublished).

3.1 Prisoner’s Dilemma

The following example is the most known game in GT. It is appealing because it is a simple model of every day human life situations and its results are, usually, unexpected. As we will see, EGT makes a huge conceptual advance allowing to apply this model (and many others) to biology in general.

Two suspects of having committed a crime are in jail. Each of them must decide whether keep quiet (cooperate, noted C) or confess (defect,D). The judge offers the following deal: if one of you confesses and the other not, the first becomes a witness and goes free while the other must stay in jail for 10 years. If both confess, you stay each 7 years in prison. If both of you keeps quiet, you stay around a year in prison until the process is achieved. They cannot communicate between them.

What should they do?

Put into the language of game theory the situation is represented by the following *payoff matrix* where the matix element (i,j) represents the payoff received by the player in row i playing against the player in row j :

$$\begin{array}{cc} & \begin{matrix} C & D \end{matrix} \\ \begin{matrix} C & \\ D & \end{matrix} & \begin{pmatrix} -1 & -10 \\ 0 & -7 \end{pmatrix} \end{array} \quad (3.1)$$

It is obvious that, independently of what the other will do, confessing is always the best choice (go free instead of 1 year, 7 years instead of 10 years). So if the prisoners analyze rationally their situation they should both confess and will spend 7 years in prison each. But, note that, if they would have cooperated, non confessing, they sentence would be only a year. This is the dilemma.

Rationality leads to mutual defection a worst scenario than mutual cooperation, that seems to be irrational. In fact, as we will see, defecting is a Nash equilibrium.

What happens if we do not assume rational players?

The same: defection will be favored. To prove this simple fact we must consider the fitness depending on frequency scenario. Fortunately, the situation in which EGT is useful.

Assume then a population where the proportion of the cooperators is given by x and the proportion of the defectors by $1-x$. If we assume random encounters and that (3.1) describes the payoff for the possible encounters the average payoff for a cooperator will be f and for a defector g defined as follows:

$$\begin{aligned} f(x) &= -x - 10(1-x) \\ g(x) &= -7(1-x) \end{aligned} \tag{3.2}$$

Then $g(x) \geq f(x), \forall x \in [0,1]$ which means that given that natural selection promotes the survival of the fittest, (see remark 2.1 of chapter2) it will tend to eliminate cooperators of the population.

We have then proved that rational and irrational settings should lead to defection. But in fact there is cooperation in the real world now and since its beginning: replicating molecules had to cooperate to form the first cells, single cells to form multicellular organisms, humans to form cities, and many other examples prove this fact (Nowak, 2006b). How can we explain the evolution of cooperation?

Martin Nowak's current classic paper "Five Rules for the Evolution of Cooperation" (Nowak, 2006a) makes a modern account of the explanations for the evolution of cooperation. The mechanisms presented are: Kin Selection (where the individuals involved are related), Direct Reciprocity (where the same two individuals are assumed to play the game repeatedly), Indirect Reciprocity (mostly applied to humans and where there is a reputation for each member of the population), Network Reciprocity (where the population is not assumed to be well mixed but spatially structured) and Group Selection (where group of cooperators might more successful than a group of defectors).

In spite of being completely different mechanisms for explaining the evolution of a certain trait, the wonderful fact is that all of them can be modeled by a 2×2 payoff matrix such as (3.1) and can be analyzed by the standard framework of EGT. This fact becomes more impressive if we recognize cooperation as well as reproduction, selection and mutation as one the fundamental principles of evolution. It is then crucial to have a basic understanding of the fundamental concepts of EGT in order to acquire a powerful tool for advancing in the use of mathematics to study evolutionary biology.

3.2 Game Theory and Evolutionary Game Theory

In this part we formalize the similitudes and differences between GT and EGT. The past section provide us an adequate background for this discussion. As we saw, GT relies on rationality of the individuals involved. Traditionally it has been divided between cooperative and non cooperative games. In the first kind of games, cooperation is not a problem to explain: it is a premise, the players can explicitly

make agreements in order to maximize their payoffs. In the second kind, cooperation is not previously assumed. The rational part of the Prisoner's Dilemma is a typical non cooperative game. In general, GT has been used in economics to model the interactions between humans in scenarios where there are diverging interests. EGT does not presume any degree of consciousness of the players. This, fortunately, does not mean that it is an independent area of work. Instead, EGT relies in GT results and builds upon them.

We make here a brief review of Darwinian evolution, area where EGT has become an essential theoretical and practical tool. Individuals have genotypes that determine their phenotype (that for us includes physical and behavioral traits). For simplicity, we make this over simplification because we know that the environment of an individual, let it be a bacteria or a child, is as important as its genotype in its development. Genotypes are not chosen by the individuals but imposed by heritage. Similarly, in their turn to reproduce, sexually or asexually, they will impose their genes to their offspring. Phenotypes determine fitness of the individuals. Fitness is a direct measure of reproductive success in our context. Natural selection means that the fittest survives. EGT permits a framework where fitness is not constant, it depends on the composition of the population (see (3.2)). Mutations, "errors" during reproduction in some level, introduce genetic diversity in the population. Until here, the three classical blocks of the theory of evolution have been mentioned: selection, mutation, and reproduction. For us, cooperation is the fourth block.

EGT then models "games" between "players". The players have fixed strategies (probably by their genotype) and the result of the game is a determined payoff for the players involved. These payoff depend on the strategies used by the players. We also assume that the probability of an encounter between a player using strategy i versus a player using strategy j is determined by the proportions of these strategies in the population. For example in this model, strategy j is not more prone to interact with another having strategy j .

An evolutionary dynamic arises when we include time and study the change of the proportions of the strategies when time passes. In our presentation, this dynamic will depend on games and particularly on EGT properties. ODE will make the bond between static games and the dynamic process in continuous time.

3.3 Evolutionary Game Theory: Fundamentals

We begin here by introducing the fundamental notions that will support our discussion, and that will set the framework to introduce Nash equilibria (NE) and Evolutionary Stable Strategies (ESS) in games without a dynamical structure. This will establish a point of reference for the posterior discussion. We use Weibull (1995) notation and base our presentation on Armao's work (unpublished).

3.3.1 Preliminaries

EGT relies mostly on *finite games in normal form*. These are games where there is a set $I = \{1, \dots, n\}$ of *players*, n a positive integer. Each player i has a set $S_i = \{1, \dots, m_i\}$, his *finite set of pure strategies*, for some integer $m_i \geq 2$. A *pure strategy profile* is a

vector $s = (s_1, \dots, s_n)$ where s_i is a pure strategy for player i . The pure-strategy space S of the game is the cartesian product of the player's pure strategy sets, that is $S = \times_i S_i$.

Now, for $s \in S$ and $i \in I$, let $\pi_i(s) \in \mathbb{R}$ be the associated payoff to player i . For us, this payoff is the *fitness* of player i . The i -th player's *pure strategy payoff function* is defined as $\pi_i : S \rightarrow R$. The *combined pure strategy payoff function of the game* is $\pi : S \rightarrow R^n$ such that $\pi(s) = (\pi_1(s), \dots, \pi_n(s))$.

In summary a game in normal form can be fully described by the triplet $G = (I, S, \pi)$. Introducing *mixed strategies* we improve the applicability of the theory. A mixed strategy for a player i is a probability distribution over the set S_i . We can represent a mixed strategy x_i as a vector in R^{m_i} where its h -th coordinate x_{ih} is the probability assigned by x_i to the player's h th pure strategy.

Note that $\sum_{h=1}^{m_i} x_{ih} = 1$ and that a pure strategy k is a particular mixed strategy x_i where $x_{ik} = 1$ and $x_{ih} = 0$ for all $h \neq k$. The *mixed strategy space of player i* is then equivalent to an $(m_i - 1)$ dimensional Δ_i simplex, the set $\Delta_i = \{x_i \in R_+^{m_i} : \sum_{h=1}^{m_i} x_{ih} = 1\}$.

The *vertices* of this simplex are the pure strategies.

In the same way we did for pure strategies, we define a *mixed strategy profile* as a vector $x = (x_1, \dots, x_n)$ where each x_i is a mixed strategy for player i . The set of all mixed strategy profiles is the *mixed strategy space of the game* noted $\Theta = \times_{i \in I} \Delta_i$. We remark, but no prove, that Θ is a $(m - n)$ -dimensional *polyhedron* in R^m where m is the total number of pure strategies in the game.

The set $C(x_i) = \{h \in S_i : x_{ih} > 0\}$ is called the *support* of x_i . In words, the support of a mixed strategy is the set of all pure strategies to which it assigns non-zero probabilities. This is a concept commonly used in EGT.

In the evolutionary context we are interested mainly in games where the players have the same set of pure strategies and the payoffs are independent of which player plays each strategy. These games are called *symmetric* games. The prisoner's dilemma is such a game. In our work we focus on the theory concerning symmetric games, the general normal-form games does not make an essential contribution and imposes a more complex notation. The full treatment can be found in Weibull (1995).

We turn now our attention to the *expected payoff* $u_x(y)$ of an x -strategist versus a y -strategist. For simplicity remember that we are in a two players symmetric normal form game and x, y are mixed strategies, that is probability distributions over the set $S = \{e_1, \dots, e_n\}$ of pure strategies. Then:

$u_x(y) = \sum_{i=1}^n \sum_{j=1}^n x_i y_j \pi(s_i, s_j) = \sum_{i,j=1}^n x_i y_j a_{ij} = x.Ay$ where $a_{ij} = \pi(s_i, s_j)$ are the elements of the *payoff matrix A*.

It is clear that this function is a bilinear form.

3.3.2 Nash Equilibrium

The following function will be crucial to the Nash equilibrium existence proof.

Definition 3.1. Given $y \in \Delta_n$ an opponent's strategy, a player's *best reply* is given by:

$$B(y) = \{x \in \Delta_n \mid x.Ay \geq e_i.Ay, \forall e_i \in S\}.$$

A best reply to a strategy y is then the set of strategies such that no other strategies available give her a higher payoff against y . Note that this set is, at least, non empty. Furthermore, note the best reply requires only to check profitable pure-strategy deviations because no mixed strategy x can have a higher payoff to a player than any of her pure best replies to y being a convex combination of pure strategies and by the linearity of $u_x(y)$ in x .

Definition 3.2. A *Nash equilibrium* occurs when each players strategy is a best reply to his opponent's strategy that is $(x,y) \in B(y) \times B(x) \subset \Delta_n^2$. Particularly we are interested in *symmetric Nash equilibria* (x,x) in which both players use the same strategy, formally the requirement is $x.Ax \geq e_i.Ax \quad \forall e_i \in S$. If the preceding inequality is strict then $B(x) = \{x\}$ and x is said to be a *strict Nash equilibrium*.

Note the following: a mixed strategy Nash equilibrium cannot be a strict Nash equilibrium. That is because the payoff to a mixed strategy is linear in the probability assigned to the pure strategies in its support and then no profitable deviation can be achieved by changing the weight of the pure strategies (if this occurred it couldn't be a Nash equilibrium). So a mixed strategy can deviate to another probabilistic combination of its support strategies without altering her payoff and thus the inequality in the past definition cannot be strict.

We prove now the main result of this chapter, the existence of symmetric Nash equilibria in symmetric games. The proof is based on Kakutani Fixed Point Theorem a generalization of Brouwer Fixed Point theorem. We state but not prove the theorem, see Kakutani (1941) for a proof.

Theorem: Kakutani Fixed Point. Let S be a nonempty, convex and compact subset of a Euclidean space, and $\varphi : S \rightarrow P(S)$ a set valued function. If φ has convex nonempty images and a closed graph, then it has a fixed point $x \in \varphi(x)$.

Remember that φ has a *closed graph* if $(\{\sigma_\alpha\}, \{\sigma'_\alpha\}) \rightarrow (\sigma, \sigma')$ with $\sigma'_\alpha \in \varphi(\sigma_\alpha) \Rightarrow \sigma' \in \varphi(\sigma)$ (Armao, (unpublished)).

Theorem: Existence of Symmetric Nash Equilibria. Every finite symmetric two-player game has a symmetric Nash equilibrium.

The outline of the proof is given by Armao (unpublished).

Proof By definition of a player's best reply set function, β , and of a symmetric Nash equilibrium we need only to prove that this set function has a fixed point. We prove now that $\beta : \Delta_n \rightarrow P(\Delta_n)$, where $P(\Delta_n)$ is the set of all subsets of Δ_n , satisfies the requirements of Kakutani's theorem and thus has a fixed point, what we need.

i) $\Delta_n = \{x \in R_+^n : \sum_{i=1}^n x_i = 1\}$, the domain of β is trivially nonempty and convex. It is a closed and bounded subset of R^n then it is compact. The domain satisfies the requirements.

ii) As we saw $u_x(y)$, the expected payoff function, is a linear function on $x \in \Delta_n$ then it is continuous. A continuous function on a compact set attains a maximum, w . That is, $w \cdot Ay \geq x \cdot Ay \quad \forall x \in \Delta_n \Rightarrow w \in \beta(y)$. So for, $\forall y \in \Delta_n, \beta(y)$ is non empty .

iii) Now let $y \in \Delta_n$ and $\{x^1, \dots, x^k\} \in \beta(y)$. That is $\forall i \in \{1, \dots, k\}$, we have $x^i \cdot Ay = \lambda \geq x \cdot Ay, \forall x \in \Delta_n$. And suppose $\{a_1, \dots, a_k\}$ is a positive set of real numbers satisfying $\sum_{i=1}^k a_i = 1$. Then $(\sum_{i=1}^k a_i x^i) \cdot Ay = \sum_{i=1}^k a_i (x^i \cdot Ay) = \sum_{i=1}^k a_i \lambda = \lambda$. So $\forall y \in \Delta_n, \beta(y)$ is convex .

iv) It remains to show that β has a closed graph. Suppose by contradiction that $\{x^k, y^k\} \rightarrow (x, y)$, with $x^j \in \beta(y^j)$ and that $x \notin \beta(y)$. Then there exists an $\varepsilon > 0$ and an $w \in \Delta_n$ such that $w \cdot Ay > x \cdot Ay + 3\varepsilon$. Now, by the continuity of the bilinear payoff function and the convergence $\{x^k, y^k\} \rightarrow (x, y)$, we have for j sufficiently large the following:

$w \cdot Ay^j > w \cdot Ay - \varepsilon$ and $x \cdot Ay > x^j \cdot Ay^j - \varepsilon$. Combining the inequalities we get:
 $w \cdot Ay^j > w \cdot Ay - \varepsilon > x \cdot Ay + 2\varepsilon > x^j \cdot Ay^j + \varepsilon$, and this contradicts the fact that $x^j \in \beta(y^j)$.

So β has a closed graph.

We conclude that by Kakutani's theorem, β must have a fixed point x , precisely a symmetric Nash equilibrium of the game.

The proof is finished.

We state here the general version of Nash's existence theorem. The proof is an extension of the particular case presented above, we remark that we do not have here a symmetric Nash equilibrium.

Theorem: Nash Existence Theorem. Every finite normal-form game has a Nash equilibrium.

The notion of Nash equilibrium is one of the cornerstones of economic theory, underlying most of modern economics (Weibull, 1995). Probably its importance is due to the ease of its formulation, its intuitive understanding and its presence in every game. Nevertheless it has some weakness, for example in spite of knowing it exists we don't know how to get explicitly to a Nash equilibrium. There has been many attempts to improve Nash equilibrium's defects creating new notions of equilibriums (Perfection, Properness, Essentiality can be found in Weibull (1995)) but none of these has attempted to fully replace the classic Nash equilibrium concept. In spite of this, Maynard Smith and Price (1973) introduced a new concept useful in biological contexts, the notion of an Evolutionarily Stable Strategy. This one proved to be an interesting advance in the application of EGT to evolutionary biology and is presented in the following subsection.

3.3.3 Evolutionarily Stable Strategies

Evolutionary biologists are interested in the maintenance or not of new mutations or invaders arriving to an environment relatively stable. This can be thought in genetical terms inside a population, will be a new mutation prevail in the population or will it disappear?. An ecological approach can also be taken: will be an immigrant, with a special feature, arriving to a new island successful?

Based on our presentation of Nash equilibriums, one will be tempted to say that a Nash equilibrium is a strategy such that if it is used by the majority of the population it cannot be invaded by a new mutation or invader. But, unfortunately, the situation is not so simple.

Suppose we have a population using a strategy that is a strict Nash equilibrium. Is it possible to have an invasion of this strategy? Well, no. Given that the initial strategy is the unique best reply to itself the intruder will be quickly erased by natural selection. But remember, that only pure strategies may be strict Nash equilibriums. Evidently, we are interested in the more general approach permitted by mixed strategies. Suppose now that we have an initial population using a Nash mixed strategy. In this scenario, the intruders may earn the same payoff versus the initial strategy that this strategy with itself. If the intruders earn a higher payoff than the initial strategy against themselves, then natural selection may favor the invasion of the population. Thus, a Nash equilibrium does not assure the evolutionarily stability of a strategy.

There is a precise form of evolutionary equilibrium that may be represented by mixed strategies and if used in a population it is uninvadable: an Evolutionary Stable Strategy (ESS). Our intuition leads us to situate this ESS somewhere between a Nash equilibrium and a strict Nash equilibrium.

We remark here two aspects to take into account.

First, a population invaded by a small number of the same type of intruders is, intuitively, equivalent to a mixed strategy of a single individual. The probability assigned to a pure strategy is the share of the resident population and the probability

assigned to the other pure strategy (“the type of the intruders”) is the infinitesimal share of the invaders.

Second, the following discussion is restricted to symmetric two player games and thus a Nash Equilibrium is a synonym of symmetric Nash Equilibrium.

We formalize now this discussion.

Definition 3.3. $x \in \Delta_n$ is an *ESS* if $\forall y \in \Delta_n, y \neq x$ there exists an *invasion barrier* $\bar{\varepsilon}(y) \in (0,1)$ such that $\forall \varepsilon \in (0, \bar{\varepsilon}(y))$:

$$x.A(\varepsilon y + (1 - \varepsilon)x) > y.A(\varepsilon y + (1 - \varepsilon)x)$$

This inequality respects our biological intuition: a strategy x is an ESS if for every “mutant” strategy y there is an invasion barrier (that is, a proportion of the population) such that if the proportion of y is below this barrier, x has a higher expected payoff (fitness) than y , which will be then eliminated by natural selection. From this definition, one may suppose that a more “powerful” ESS strategy may have higher invasions barriers than a “weak” ESS strategy. A natural question is if for a fixed ESS the set $\{\bar{\varepsilon}(y) : \forall y \in \Delta_n\}$ has a minimum, that is a fixed universal invasion barrier. The interesting and, maybe, unexpected answer is yes. This fact will be formally stated later.

For the moment, let’s see how the ESS relates with Nash equilibria. Initially, note that an ESS is a (symmetric) Nash equilibrium. Suppose, by contradiction, that x is an ESS and it is not a best reply to itself. Then there exists y such that $x.Ax < y.Ax$, hence if there is a share ε , sufficiently small, of y and $1 - \varepsilon$ of x by the linearity of the payoff function we would have that $x.A(\varepsilon y + (1 - \varepsilon)x) < y.A(\varepsilon y + (1 - \varepsilon)x)$ which contradicts the fact that x is an ESS. But, a Nash equilibrium does not guarantee ESS. Suppose x is a Nash equilibrium and y is another best reply to x (which is possible because the equilibrium is not strict). Then if x is not a best reply to y that y to itself, it is evident that y may invade an x population. Then x is not an ESS. In order to be an ESS, x must have the additional property of being a best reply to y that y to itself.

We have then proved the following result.

Proposition 3.1. x is an ESS if the following two conditions holds:

- i) $x.Ax \geq y.Ax \Leftrightarrow x.Ax \geq e_i.Ax, \forall y \in \Delta_n, \forall i \in \{1, \dots, n\}$
- ii) if $y \neq x$ and $x.Ax = y.Ax$ then $x.Ay > y.Ay$.

Now note that if a strategy is a strict Nash equilibrium, condition i) of the past proposition is strictly satisfied making condition ii) trivially true.

We define a final type of strategy: x is a *weak ESS* if the inequality in ii) is not strict.

The conclusion is then the following proposition.

Proposition 3.2. The following chain of implications holds for a strategy in a symmetric two player game:

Strict Nash \Rightarrow ESS \Rightarrow weak ESS \Rightarrow Nash .

We now introduce some useful characteristics of the support of an ESS.

Proposition 3.3. If x is an ESS and y is a strategy such that $C(y) \subset C(x)$, then y is not a Nash equilibrium.

Proof. If x is an ESS then it is a Nash equilibrium, so it must be indifferent to any combination of its support strategies. In particular: $x.Ay = y.Ay$, then by condition ii) of Proposition 3.1, $x.Ay > y.Ay$, hence y is not a Nash equilibrium.

Proposition 3.3 offers a corollary that will define the structure of the ESS of a game.

Corollary 3.3.1. The set of ESS of a finite game is finite. Moreover, if an ESS is in the interior of the simplex it is the unique Nash equilibrium of the game.

Proof. Since the number of pure strategies is finite, the number of subsets of pure strategies is also finite. The latter is precisely the number of different supports of the game, then by proposition 3.3 the number of ESS must be finite. For the second assertion, just note that if an ESS is in the interior of the simplex its support is the complete set of pure strategies. Then every other strategy's support is a subset of this one and by proposition 3.3 it cannot be a Nash equilibrium.

We finally give two more common characterizations of ESS and important for the dynamical analyses. For the first one we begin by defining a concept previously mentioned implicitly.

Definition 3.4. A strategy x has a *uniform invasion barrier* if the inequality in definition 3.1 holds for a minimal $\bar{\varepsilon}$ throughout the simplex and every $\varepsilon \in (0,1)$.

We here state but not prove the following equivalence, see Weibull (1995) for proof. The mathematical proof is fairly complicated and does not contribute to our biological approach of EGT. Instead, we remark the consequences that do have evolutive implications.

Theorem 3.1. x is an ESS if and only x has a uniform nonzero invasion barrier.

Shortly this theorem assures that for an ESS there is a nonzero threshold such that any invading strategy below it, is eliminated by natural selection. But, one must be very cautious of the limits of this result: it does not say that an ESS is necessarily resistant simultaneously to *various* type of intruders. Weibull (1995) gives a simple illustration of this fact:

Example 3.1. Suppose a population is composed entirely by x an ESS with uniform invasion barrier $\bar{\varepsilon}$, and that two intruders y, z invade the population with respective proportions α, β such that $\alpha + \beta < \bar{\varepsilon}$. The resulting population is:

$$w = (1 - \alpha - \beta)x + \alpha y + \beta z \Leftrightarrow (1 - \bar{\varepsilon})x + \bar{\varepsilon}y' \text{ where } y' = \frac{\alpha y + \beta z}{(\alpha + \beta)} \text{ and } \bar{\varepsilon} = \alpha + \beta. \text{ This equivalence is easily verified.}$$

Then by definition of $\bar{\varepsilon}$, x earns a higher payoff than the fictitious strategy y' . And by the linearity of the payoff function, at least one of y or z must do worse than x but nothing assures that both do, so one may in fact do better than x in this scenario and invade the population.

The second characterization of an ESS is due to Hofbauer et al. (1979). Recall proposition 3.3 and its corollary where we proved that an interior ESS is globally superior to every intruder in the sense that it earns a higher payoff against all the intruders than these earn against themselves. The following result will prove that any ESS is at least locally superior, that means that it earns a higher payoff against all the intruders in some neighborhood that these intruders earn against themselves.

We formalize this discussion.

Definition 3.5. $x \in \Delta_n$ is *locally superior* if it has a neighborhood U such that $x.Ay > y.Ay, \forall y \neq x \in U$.

Proposition 3.4. x is an ESS if and only if it is locally superior.

This proof is a simple application of definition 3.3 and theorem 3.1, it is due to Armao (unpublished). We develop it to illustrate the use of the introduced notions and because it will be useful in a dynamical context.

Proof. Let x be an ESS and $\bar{\varepsilon}$ its uniform invasion barrier given by the theorem 3.1. Then, by definition 3.3 the following sequence of equivalences holds for $\forall \varepsilon \in (0, \bar{\varepsilon}), \forall y \in \Delta_n$:

$$\begin{aligned} &x.A(\varepsilon y + (1 - \varepsilon)x) > y.A(\varepsilon y + (1 - \varepsilon)x) \quad (i) \\ (i) &\Leftrightarrow \varepsilon(x.A(\varepsilon y + (1 - \varepsilon)x)) > \varepsilon(y.A(\varepsilon y + (1 - \varepsilon)x)) \text{ (multiplying each side by } \varepsilon) \\ (i) &\Leftrightarrow (1 - \varepsilon)x.A(\varepsilon y + (1 - \varepsilon)x) + \varepsilon(x.A(\varepsilon y + (1 - \varepsilon)x)) > (1 - \varepsilon)x.A(\varepsilon y + (1 - \varepsilon)x) + \varepsilon(y.A(\varepsilon y + (1 - \varepsilon)x)) \\ &\text{(adding } (1 - \varepsilon)x.A(\varepsilon y + (1 - \varepsilon)x)) \end{aligned}$$

and it is easily verified now that:

$$(i) \Leftrightarrow x.A(\varepsilon y + (1 - \varepsilon)x) > (\varepsilon y + (1 - \varepsilon)x).A(\varepsilon y + (1 - \varepsilon)x)$$

Then x is locally dominant in $U = \{\varepsilon y + (1 - \varepsilon)x \mid \forall y \in \Delta_n, \forall \varepsilon \in (0, \bar{\varepsilon})\}$, what we wanted.

The sequence is reversible, so the proof is finished.

3.4 Discussion

In this chapter we began by introducing the Prisoner's Dilemma that served us to illustrate the conceptual differences between GT and EGT. Posteriorly, we introduced the language of EGT. This may be a heavy notation for a reader unused. In spite of that, it is necessary to keep the terms clear and one gets used with time. We then made the proof of the Nash existence theorem in symmetric two player games. The generalization of this result, which is stated, is probably the main contribution of the Nobel prize John F.Nash to the field. We finally worked on Evolutionary Stable Strategies defined by Maynard Smith and that are a refinement of the Nash Equilibrium. ESS hold a lot of biological intuition and thus we recommend for the biology interested to spend most of the time in this subsection.

4. Evolutionary Game Theory: Dynamic Concepts

In the present chapter we introduce a new element that will allow us to study biological as well as many other problems more accurately: time. Note that in the past chapter for defining Nash equilibriums (NE) and ESS we only needed to work on some inequalities and this mathematical procedure remained valid even for the theorems describing NE and ESS. In the present chapter, when time is explicitly involved in our discussion, we need to introduce ODE's. This may imply sometimes a higher mathematical complexity that is rewarded by the powerful applications of the dynamic approach. In this sense we rely strongly on the definitions and results of the first chapter, and the reader is invited to check these concepts if necessary. As expected, a game and its payoffs will be the determining factor of the equations involved.

The chapter is organized as follows: in section 4.1 we begin by a short discussion that illustrates the motivation of the dynamic approach and introduce the precise framework to study such a system. Then in section 4.2, we describe the different equilibrium states that may be attained in the long run of a particular system. Section 4.3 is the core of the chapter: we present the link between static and dynamic concepts. The chapter ends with a presentation of the replicator dynamics in 4.4, the most used dynamic model, and with a discussion of the complete chapter and its implications in section 4.5.

The presentation is based on Weibull (1995) and Armao (unpublished).

4.1 Preliminaries

4.1.1 General Motivation

The Nash equilibrium and its refinement ESS were particularly useful for studying the evolutionary performance of mutations. Basically, they permitted us to answer the following question: what would be the fate, prevail or disappear, of a new strategy (a "mutation") invading a population where the majority of the individuals use a particular strategy?

Instead the dynamic approach focus on the selection mechanism of evolutionary processes. For this we will turn our attention to the change in time of the proportion of some entities, pure strategies mainly, in a population. We will see which remain and which disappear if any, and it is in this sense that selection is studied. Fortunately, the dynamic model does not rule out possible mutations, as we will see by means of determining dynamic stability of stationary states (i.e: states where selection has already acted and stabilized the composition of the population). Taking care of some formalities we may study simultaneously selection and mutation. Reproduction is implicitly involved here because the change of time of the proportion of the entities implies that these may increase or decrease and for this to occur some kind of birth-death rate process must be involved.

Recalling remark 2.1 of chapter 2 we will have then the complete traditional fundamental blocks of the theory of evolution, included here: mutation, selection and reproduction.

We begin by describing the population where the process takes place. In the evolutionary stability and static ambient of chapter 3 individuals were assumed to have pure or mixed strategies (for example, imposed by their genotypes in the biological context). Here we use Weibull (1995) treatment where we restrict the dynamic to pure strategies and mixed strategies are intuitionnally equivalent to population states $x=(x_1,\dots,x_n)$ where x_i is the proportion of the population using pure strategy e_i (remember that in a mixed strategy x_i is the probability assigned by an individual to pure strategy e_i).

In this population, pairwise interactions, represented by games, still occur and determine individuals fitness. Fitness univocally determines reproductive success. Then the entities we mentioned above are the pure strategies that reproduce continuously over time depending on their fitness (and here ODE's will be the appropriate tool). This reproduction is without errors. What is crucial here is to keep in mind that the fitness of the individuals (that is, pure strategies) is not constant, as population changes so does the payoff of the games. That is precisely, the main contribution of EGT to study biological evolution.

The notion of support of a mixed strategy translates naturally to the notion of support of a population state, consisting of the pure strategies present in the population in some determinate time.

We formalize this discussion.

Definition 4.1 A *game dynamics* is defined by n autonomous ODE's given by:

$\dot{x}_i = x_i g_i(x_1,\dots,x_n) \quad \forall i = 1,\dots,n$, where $x=(x_1,\dots,x_n) \in \Delta_n$ is a population state and $g : X \rightarrow \mathbb{R}^n$ is the *growth-rate* function of the dynamic.

Based on this definition we can make some important observations.

First note the following: $\frac{\dot{x}_i}{x_i} = \lim_{\Delta t \rightarrow 0} \left(\frac{\Delta x_i / \Delta t}{x_i} \right) = \lim_{\Delta t \rightarrow 0} \left(\frac{\Delta x_i}{x_i} \right) \cdot \left(\frac{1}{\Delta t} \right) = g_i(x)$, thus each

i component of the growth-rate function g is just the growth rate per time unit of strategy i .

Second, now we have formalized the fact that the dynamic approach takes on account only the present pure strategies (that is all $x_i \neq 0$) and cannot "insert" new mutants (if $x_i = 0$ for some t , then the strategy e_i will never appear in the dynamic). But still we may take care of mutation studying the stability of the system (section 4.2).

Third, we remark that g depends only on x , the current state of the population, so the past and the future don't influence the dynamic.

Fourth and final observation: the natural expectation is that the growth-rate is somehow related to the single or multiple games underlying the dynamic. This will be shortly made explicit but we need first to make some restrictions on g .

4.1.2 Regular Game Dynamics

Evolutionary we are more interested in long run behaviors rather than in the particular trajectories to attain them, as Armao (unpublished) says: “for it is the outcome –not the pathway- of evolution that is of chief interest” . For this to happen we need two conditions: that the system of equations introduced in definition 4.1 has an unique solution (it would make little evolutive sense to have many possible outcomes) and that this solution stays always in the simplex (this is a formal requirement because it makes no sense a share of population superior than 1 or negative). By Picard-Lindelöf’s theorem (section 2.3 of chapter 2), to assure existence and uniqueness of a solution we need Lipschitz continuity of the system introduced in definition 4.1 and note that this is satisfied if g is Lipschitz continuous. Shortly, we will prove that the second condition, remaining on the simplex, is satisfied if $\forall x \in \Delta_n, g(x)x = 0$.

We have then reduced the dynamics we are interested in to the *regular* game dynamics.

Definition 4.2. A *regular game dynamics* is a game dynamics where g , its growth-rate function, satisfies:

- i) g is Lipschitz continuous
- ii) $\forall x \in \Delta_n, g(x)x = 0$

4.1.3 The Solution

We precise now what we are looking for: the solution of a system of ODE’s, in mathematical terms, or the long run state of a population under a selection dynamic in biological terms.

Definition 4.3. A *solution mapping* of a regular game dynamics is a function $\varepsilon : \mathbb{R} \times \Delta_n \rightarrow \Delta_n$ such that:

- i) $\varepsilon(0, x) = x$
- ii) $\dot{\varepsilon}_i(t, x) = \varepsilon_i(t, x)g_i(\varepsilon(t, x)), \forall t \in \mathbb{R}, i = 1, \dots, n$
- iii) $\varepsilon(t, \varepsilon(s, x)) = \varepsilon(t + s, x), \forall x \in \Delta_n, \forall t, s \in \mathbb{R}$
- iv) ε is continuous.

The first property just indicates that at the beginning we are in the initial state. The second one is required in order to ε be in fact a solution of the regular game dynamics. Third condition is a consequence of the ODE’s being autonomous (time independent). Fourth condition is a nice mathematical condition to have.

The following proposition will describe the main properties of a regular dynamics.

Proposition 4.1. Any regular game dynamics admits a unique solution mapping $\varepsilon, \forall x_0 \in \Delta_n$ where x_0 represents the initial state at $t = 0$. Moreover, the simplex Δ_n is invariant under the dynamic in the sense that if $x_0 \in \Delta_n$ then $\varepsilon(t, x_0) \in \Delta_n, \forall t \in \mathbb{R}$. The same holds for its boundary, interior and vertices.

Proof.

-The first part is an immediate consequence of Picard-Lindelöf's theorem (theorem 4 of chapter 2) that can be used because g is Lipschitz continuous.

-We prove now the invariance of Δ_n .

Note that the regular game dynamic preserves the sum of the components for any vector $\varepsilon(t, x_0) = x \in X$. For this we prove that the change with time of this sum is zero:

$$\frac{d}{dt} \left(\sum_{i=1}^n \varepsilon_i(t, x_0) \right) = \sum_{i=1}^n \dot{x}_i = \sum_{i=1}^n x_i \cdot g_i(x) = x \cdot g(x) = 0, \text{ the last equality by the regularity of } g.$$

Thus, it only remains to show that each $\varepsilon_i(t, x_0) \geq 0$, because if the sum of the components is constant the only possible way to leave the simplex is by having a component superior than 1 that must be compensated by a negative component of the same magnitude.

By contradiction, suppose there exists $t' \in \mathbb{R}$ such that $\varepsilon_i(t', x_0) < 0$ for some i . The continuity of ε implies that $\varepsilon_i(t_0, x_0) = 0$ for some $t_0 \in \mathbb{R}$. Note $x_1 = \varepsilon(t_0, x_0)$. Suppose we set $x_i = \eta_i(t, x_1) = 0$ for all $t \in \mathbb{R}$ and solve the dynamic for all $j \neq i$. This contradicts Picard-Lindelöf's theorem, because we have two different solutions ε, η (they differ on $t = t'$) through x_1 .

We have then proved the simplex is invariant under the regular game dynamic.

-We prove now the invariance of the boundary of Δ_n , that is $bd(\Delta_n) = \{x \in \Delta_n \mid x_i = 0, \text{ for at least one } i = 1, \dots, n\}$. This is easy to show:

$x \in bd(\Delta_n) \Rightarrow \varepsilon_i(0, x) = 0 \Rightarrow \dot{\varepsilon}_i(0, x) = 0$, for at least one $i = 1, \dots, n$, where the first and second implication follow from conditions i) and ii) od definition 4.3 respectively.

-Finally by definition the interior of Δ_n , $int(\Delta_n) = (bd(\Delta_n))^C$. It must then invariant by the invariance of the simplex and the boundary. Each vertex is invariant just by definition of the game dynamic, because $x_i = 0 \Rightarrow \varepsilon_i(t, x) = 0$ for any time t .

The proof is finished.

There is now an elegant equivalence between the static normal form game $G = (I, S, \pi)$ and the triplet $D = (\mathbb{R}, \Delta_n, \varepsilon)$ where \mathbb{R} denote the time space, Δ_n the state space and ε the solution mapping.

4.2 Equilibrium States

In order to study our object of interest, the long run behavior of D , we begin by noting that a population state is stationary if and only if it does not change with time. That is if the growth rate g_i of each x_i present in the population is zero. In spite of that, we need more information to answer simple problems that may arise: what will happen with the dynamic if small perturbations are induced to a stationary state? The system will come back to that state or will it change to another one? Are there more than one kind of stationary states?

In this section we pretend to answer these questions, and we begin with a precise definition of stationarity and then a statement of the basic concepts of stability. It is important to note that the material presented here is precisely the way dynamical systems allow us to deal with the effect of mutations that we model as perturbations of the stationary state. We can make a parallel between the past chapter and this section: the small proportion of new strategist invaders are equivalent to the small perturbation and the initial population using a determined strategy is equivalent to the stationary population state.

Definition 4.4. A *stationary* state under a solution ε is a state $x \in \Delta_n$ such that $\varepsilon(t, x) = x$ for all $t \in \mathbb{R}$.

The following proposition that we do not prove (it is quite complicated and does not contribute to our understanding of the problem) has been described as an useful consequence of this definition.

Proposition 4.2. If $x, y \in \Delta_n$ and $\lim_{t \rightarrow \infty} \varepsilon(t, x) = y$, then y is stationary and y is called the limit of x .

The proof solely uses the definition of an induced solution mapping and may be found in Weibull (1995). Weibull's remark following the proof is important and invites to do not over estimate it: the convergence does not imply, obviously, that the state y is reached in a finite time. More surprising it may be that if the state is not initially in a stationary state, it will never reach one: if $x \neq y$ and $\lim_{t \rightarrow \infty} \varepsilon(t, x) = y$ then y is stationary but $\varepsilon(t, x) \neq y, \forall t \geq 0$ because we have already the unique solution through y given by Picard-Lindelöf's theorem $\varepsilon(t, y) = y, \forall t \geq 0$. Thus, the only way that the solution reaches a stationary state it is that $x = y$, that is the easy case where we begin in a stationary state.

We present now two classical notions of stability: Lyapunov stability (LS or stability for short) and asymptotic stability (AS) . LS is weaker in the sense that it requires that no small perturbation induces a movement away from the initial stationary state while AS requires that any small perturbation induces a movement toward the initial stationary state. AS implies then LS. Formally:

Definition 4.5. A state $x \in \Delta_n$ is *Lyapunov stable* in D if for every neighborhood U of x there is $x' \in U' \subseteq U$, such that $\varepsilon(t, x') \in U, \forall t \geq 0$. A state $x \in \Delta_n$ is

asymptotically stable if it is Lyapunov stable and if there is a neighborhood V of x such that $\forall y \in V \cap \Delta_n, \lim_{t \rightarrow \infty} \varepsilon(t, y) = x$.

The following proposition characterizes the relation between these states.

Proposition 4.3. $AS \Rightarrow LS \Rightarrow \text{stationary}$.

Proof. The first implication is by definition. For the second one, suppose by contradiction that $x \in \Delta_n$ is LS and it is not stationary. Then there exists some $t \in \mathbb{R}, y \neq x \in \Delta_n$ such that $\varepsilon(t, x) = y$. y and x are at a finite distance. We have then a neighborhood W of x (for example the ball centered in x with radius one half the distance between x and y) that the system leaves in a finite time t , a contradiction.

Armao proposes an interesting corollary of this proposition. The stationary states may be classified in three categories and we describe each of them:

- 1- Stationary and unstable (not LS): states that are not robust in any way to small perturbations. These states are of little interest in evolutionary studies because they do not resist any kind of mutation.
- 2- Stationary and only LS: states that apparently resist small perturbations but that may be in “danger” because they may be driven away by neutral drift to other stationary and unstable states or stay in infinite oscillations.
- 3- Stationary and AS: states really resistant to small perturbations because selection counteracts them by taking the system as close as possible to the initial state.

Intuitively we have then an analogy between AS and ESS in the sense that they both are stable (dynamic and statically respectively) to mutations or perturbations.

4.3 Dynamic and Static Connection

At this point haven't made any relation between game payoffs and growth rates functions. This is why no formal connection between static concepts of games and dynamic concepts has appeared (the last assertion in the preceding section is only an intuition). In this section, we relate the static and dynamic approaches proving interesting results. For this we need to make some requirements on the relation between the growth function and the payoffs. We start presenting a general class of dynamics statisfying these requirements, the weak payoff positive dynamics, and then discuss a subclass of these, the payoff monotonic dynamics, that permit new natural stronger connections.

4.3.1 Weak Payoff Positivity.

The first relation we demand is not too much to ask: we need that if some pure strategies earn a payoff superior to the average payoff of the population, at least one of these pure strategies has a strictly growth rate.

Formally, we begin by noting: $B(x) = \{e_i \in \Delta_n \mid e_i \cdot A.x > x \cdot A.x\}$.

Definition 4.6. A regular game dynamics is *weakly payoff positive* if $\forall x \in \Delta_n, B(x) \neq \emptyset \Rightarrow g_i(x) > 0$ for some corresponding $e_i \in B(x)$.

It turns out that weakly payoff positive dynamics (wpp for short) are the largest class of games dynamics for which we can relate dynamical equilibria states as Nash equilibria of the underlying game. This result is very important because it will allow us to restrict our search of equilibria in the dynamics to a precise set of the static approach and, moreover, under certain conditions we are free to move between static and dynamic concepts.

Theorem 4.1: Folk Theorem of Evolutionary Game Theory. In wpp game dynamics D with underlying game G the following holds:

- a) If $x \in \text{int}(\Delta_n)$ is stationary in $D \Rightarrow x$ is a symmetric Nash equilibrium in G
- b) If $x \in \Delta_n$ is Lyapunov stable in $D \Rightarrow x$ is a symmetric Nash equilibrium in G
- c) If $x \in \Delta_n$ is the limit of some $y \in \text{int}(\Delta_n)$ in $D \Rightarrow x$ is a symmetric Nash equilibrium in G

Proof.

- a) Suppose $x \in \text{int}(\Delta_n)$ is stationary in D . Then $\dot{x}_i = x_i \cdot g_i(x) = 0$ and $x_i \neq 0$ for all i because $x \in \text{int}(\Delta_n)$.

Then $g_i(x) = 0, \forall i \Rightarrow B(x) = \emptyset \Rightarrow e_i \cdot A.x \leq x \cdot A.x, \forall i \Rightarrow x$ is Nash in G .

- b) Let $x \in \Delta_n$, a Lyapunov stable state. Then by proposition 4.3 x is stationary. Then $g_i(x) = 0$ whenever the corresponding $e_i \in S(x)$, the support of x . Suppose by contradiction x is not a Nash equilibrium. Then $B(x) \neq \emptyset$ and by wpp there is some $e_j \in B(x)$ such that $g_j(x) > 0$. Then $e_j \notin S(x) \Rightarrow x_j = 0$. By continuity of g , there is a $\delta > 0$ and a neighborhood $U \subseteq \Delta_n$ of x such that $g_j(y) > \delta, \forall y \in U$. Then, recalling the game dynamics, we have $\dot{\varepsilon}_j(t, y) = \varepsilon_j(t, y) \cdot g_j(\varepsilon(t, y))$. Hence for any $y \in U$ and all times $t > 0$ such that

$$\varepsilon(t, y) \in U : \log \left(\frac{\varepsilon_j(t, y)}{\varepsilon_j(0, y)} \right) = \int_0^t g_j(\varepsilon(\tau, y)) d\tau > \int_0^t \delta d\tau \Rightarrow \varepsilon_j(t, y) > y_j e^{\delta t}. \text{ Thus}$$

$x_j = 0$ and yet $\varepsilon_j(t, y)$ grows exponentially from any $y \in U$ such that $\varepsilon(t, y) \in U$, so x is not Lyapunov stable, a contradiction. x must be Nash in G .

- c) Suppose $y \in \text{int}(\Delta_n)$ and $\varepsilon(t, y) \xrightarrow[t \rightarrow \infty]{} x$ in a wpp dynamics. By proposition 4.2, x is stationary. Suppose by contradiction x is not Nash. Then $B(x) \neq \emptyset$ and there is some $e_j \in B(x)$ such that $g_j(x) > 0, e_j \notin S(x) \Rightarrow x_j = 0$. Since g is continuous, there exists some neighborhood $U \subseteq \Delta_n$ of x such that $g_j(y) > 0, \forall y \in U$. Also, as $\varepsilon(t, y) \xrightarrow[t \rightarrow \infty]{} x$, there is a time T such that

$\varepsilon(t,y) \in U$ for all $t \geq T$. Note now that $y \in \text{int}(\Delta_n)$ implies that $y_j \neq 0$ and since $x_j = 0$ there must be some $t \geq T$ such that $\dot{\varepsilon}_j(t,y) < 0$, a contradiction of the positivity of g_j on U . Then x is Nash in G .

The Folk Theorem gives us a connection between dynamic equilibria classifying them at least as strong as the static Nash equilibrium. There are more relations between growth rate functions and payoffs, particularly the payoff monotonic are of great interest because they are a wide subclass satisfying stronger bonds between static-dynamic approaches.

4.3.2 Payoff Monotonicity.

We now impose to the growth rate function a higher value for strategies more successful. This natural requirement is a subclass of the wpp dynamics and will have interesting properties concerning the long run state of dominated strategies.

Definition 4.7. A regular game dynamics is *payoff monotonic* if for any e_i, e_j and all $x \in \Delta_n$ we have: $e_i.A.x > e_j.A.x \Leftrightarrow g_i(x) > g_j(x)$.

Now we prove that payoff monotonic dynamics are a subclass of the wpp.

Proposition 4.4. Monotonic \Rightarrow wpp

Proof. Let $x \in \Delta_n$. Assume a monotonic dynamic and $B(x) \neq \emptyset$.

First, suppose all the pure strategies in the support of x earn the same payoff, then all their growth rates must be the same, by monotonicity: $e_i.A.x = e_j.A.x \Leftrightarrow g_i(x) \leq g_j(x)$ and the role of i, j may be reversed proving that $g_i(x) = g_j(x)$. And this common growth rate must be zero by regularity: $g(x).x = g_i(x).(x_1 + \dots + x_n) = 0 \Rightarrow g_i(x) = 0, \forall i$. Hence, if $e_i \in B(x)$, then $e_i.A.x > e_j.A.x$ for any $e_j \in S(x)$ (they earn all the same payoff $x.A.x = e_j.A.x$) and by monotonicity $g_i(x) > g_j(x) = 0$, what we wanted.

Second, suppose that not all pure strategies in the support of x earn the same payoff. By regularity $g_i(x) > 0$ for some i . We can choose a strategy e_j that maximizes the payoff $e_j.A.x$ and clearly this $e_j \in B(x)$. By monotonicity, and recalling that $g_i(x) > 0$ for some i , $g_j(x) > 0$, what we wanted.

Thus every monotonic dynamic are wpp.

We prove now that any monotonic dynamic wipes out some “weak” strategies in the sense of low payoff earning. These strategies are the strictly dominated strategies dominated by pure strategies. Formally,

Definition 4.8. A strategy $x \in \Delta_n$ is said to be *dominated* by $y \in \Delta_n$ if $x.A.z \leq y.A.z, \forall z \in \Delta_n$. If the inequality is strict, x is said to *strictly dominated* by y , otherwise it is said to *weakly dominated* by y .

Proposition 4.5. If a strategy e_i is strictly dominated by a pure strategy, then the population share $\varepsilon_i(t, x^0)$ converges to zero in any payoff monotonic dynamics, from any interior initial state $x^0 \in \text{int}(\Delta_n)$.

Proof. Suppose that $e_i.A.x < e_j.A.x, \forall x \in \Delta_n$. Then by monotonicity $g_i(x) - g_j(x) < 0, \forall x \in \Delta_n$. By continuity of g and compactness of Δ_n , there exists some $\varepsilon > 0$ such that $g_i(x) - g_j(x) < -\varepsilon, \forall x \in \Delta_n$. Suppose that $x^0 \in \text{int}(\Delta_n)$ and note that in any regular dynamics the following holds:

$$\frac{d}{dt} \left(\frac{\varepsilon_i(t, x)}{\varepsilon_j(t, x)} \right)_{t=0} = \frac{\dot{x}_i}{x_j} - \frac{x_i \dot{x}_j}{x_j x_i} = (g_i(x) - g_j(x)) \frac{x_i}{x_j}.$$

$$\text{In particular: } \frac{d}{dt} \left(\frac{\varepsilon_i(t, x^0)}{\varepsilon_j(t, x^0)} \right) < -\varepsilon \cdot \left(\frac{\varepsilon_i(t, x^0)}{\varepsilon_j(t, x^0)} \right), \forall t \geq 0.$$

And hence, $\left(\frac{\varepsilon_i(t, x^0)}{\varepsilon_j(t, x^0)} \right) < \left(\frac{x_i^0}{x_j^0} \right) \cdot e^{-\varepsilon t}, \forall t \geq 0$. The right part of the last inequality clearly tends to 0 as $t \rightarrow \infty$. We have that $0 < \varepsilon_i(t, x^0), \varepsilon_j(t, x^0) < 1, \forall t \geq 0$. Then $\lim_{t \rightarrow \infty} \left(\frac{\varepsilon_i(t, x^0)}{\varepsilon_j(t, x^0)} \right) = 0 \Rightarrow \varepsilon_i(t, x^0) \rightarrow 0$, what we wanted to show.

Weibull interestingly remarks that this result is of particular importance because it shows that under monotonic dynamics selection acts against irrational behaviors in the sense of reducing as much as possible the proportion of pure strategies earning lower payoffs. Note also that is crucial to have an initial state in the interior of the simplex, consider the extreme case of a strictly dominated strategy e_i in a population where $\varepsilon_i(t, x^0) = 1$, that is no other pure strategies are present in the initial state, then the proportion of e_i will be always 1.

Samuelson and Zhang (1992) strengthen the above proposition. We need first a natural extension of definition 4.8:

Definition 4.9. A pure strategy e_i is not *iteratively strictly dominated* if it is not strictly dominated in the original game G , nor in G^1 the game obtained by the deletion of strictly dominated strategies in G , nor in similar the similarly defined game G^2 and so on until no more strategies can be eliminated. Since the number of players and pure strategies are finite, this procedure or iterated elimination must stop after a finite number of rounds.

Samuelson and Zhang's stronger result is:

Proposition 4.6. If a strategy e_i does not survive the iterated elimination of pure strategies dominated by pure strategies, then the population share $\varepsilon_i(t, x^0)$ converges to zero in any payoff monotonic dynamics, from any interior initial state $x^0 \in \text{int}(\Delta_n)$.

Finally, we present to the interested reader the conditions under which any pure strategy dominated by another strategy (not necessarily pure) is eliminated in the dynamics. We need a *convex monotonic dynamic* for this to occur, a result due Hofbauer and Weibull (1996). Intuitively a convex monotonic dynamic is a subclass of monotonic dynamics, where the ranking of pure versus mixed strategies growth rates respects their difference in payoff (for the monotonic dynamic we only demand this for pure versus pure strategies).

Armao suggests a weakness of the above discussion: in fact we have proved that long term stationary behaviors that are reachable are rational, but what about irrational behaviors? Formally they are not allowed to evolve.

We finish our discussion by precising the set of stationary states of any monotonic game dynamics. This will give us an interesting insight into new relations between Nash equilibria and stationary notes, remembering that the Folk theorem already gave us a powerful description.

Proposition 4.7. $\Delta_n^0 = \{x \in \Delta_n \mid e_i.A.x - x.A.x = 0, \forall e_i \in S(x)\}$ is the set of stationary states under any monotonic dynamics.

Proof. Suppose $x \in \Delta_n^0$. Then $e_i.A.x = x.A.x, \forall e_i \in S(x)$. By monotonicity there exists $\mu \in \mathbb{R}$ such that $g_i(x) = \mu, \forall e_i \in S(x)$. But then $g(x)x = \mu \Rightarrow \mu = 0 \Rightarrow g_i(x) = 0$. Then, x is stationary what we wanted.

Now suppose $y \in \Delta_n$ is stationary. Then $g_i(y) = 0, \forall e_i \in S(y)$. By monotonicity this implies that there exists $\lambda \in \mathbb{R}$ such that $e_i.A.y = \lambda, \forall e_i \in S(y)$. But then $y.A.y = \sum_i y_i.(e_i.A.y) = \lambda \Rightarrow y \in \Delta_n^0$.

The proof is finished.

An immediate corollary of this proposition is that the set of Nash equilibria of G is a subset of Δ_n^0 and moreover the set of interior Nash equilibria of G is precisely the set of interior Nash equilibria (Weibull (1995) for a formal proof of these claims). Also, in a finite game this proposition promotes the possibility of an explicit computation of the stationary states, given that the number of supports sets is finite (it is 2^n) and for each of these the system $e_i.A.x = x.A.x, \forall e_i \in S(x)$ has exactly the same number of equations as unknowns, $x_i, \forall e_i \in S(x)$. As Armao well notes, despite of its interesting consequences the proposition does not tell us anything about one subject of extreme importance: the stability of stationary states (that is evolutive robustness in variable environments).

As expected, there are many other growth rate functions related with payoff. Particularly, our main reference Weibull, presents the payoff positive dynamics and an extensive discussion of discrete time dynamics. We consider that the material presented in this subsection is a complete introduction and the interested reader is invited to investigate further developments.

Now, we work on a common application of the material presented: the replicator dynamics.

4.4 Replicator Dynamics

The replicator dynamics was the product of the first application of differential equations to evolutionary game dynamics. This was done by Taylor and Jonker (1978). In the following thirty years it has been used as a simple way to understand the use of the theory presented in this chapter and has produced advanced results in many scientific areas. Particularly in biology the replicator dynamics is a model of the “survival of the fittest” and as proved by Hofbauer and Sigmund (1998) it is in fact equivalent to the Lotka-Volterra equations, widely applied in ecology. We begin by deriving this dynamics following Weibull (1995).

4.4.1 Derivation and Properties.

Recall that the payoffs of a game determine in EGT the fitness of an individual and that fitness is, for us, number of offspring (per unit of time, a useful and not so unreal assumption). Also, reproduction here means that an individual inherits his single parent’s strategy without errors. It takes place continuously (in opposition to discrete time models) and then the birthrate of individuals using strategy e_i at any time t where the population state is $x(t)=x$ is:

$\beta + e_i \cdot A \cdot x$, where $\beta \geq 0$ is the background of fitness of all the individuals in the population, β accounts for everything but the game that may affect the fitness of the individuals. Note $\delta \geq 0$ the death rate of all individuals. Then if $p_i(t) = p_i$ is the number of individuals playing the strategy e_i at t , we have:

$\dot{p}_i = (\beta + e_i \cdot A \cdot x) p_i$ and if, $p(t) = p = \sum_i p_i$ is the total population and $x_i(t) = x_i = \frac{p_i}{p}$ the share of individuals i , at t :

$$\dot{x}_i = (e_i \cdot A \cdot x - x \cdot A \cdot x) x_i$$

This is easy to check noting that: $p_i x_i = p_i$ and then derivating both sides of the equality.

Thus in the replicator dynamics those strategies e_i such that $e_i \cdot A \cdot x > x \cdot A \cdot x$ augment their share, that is, strategies with associated payoff greater than the average grow. Similarly, strategies with payoff lower than the average, decline. It is in this sense that this dynamic is known as the “simplest”. As usual, simple models are powerful and intuitive.

Armao derives this dynamic in an equivalent way and ends with an interesting notation:

$\dot{x}_i = (f_i(x) - \phi(x))x_i$, where f_i is the fitness of the strategy e_i function of the population state x and $\phi(x)$ is the average fitness of the population.

We characterize now the replicator dynamics.

Proposition 4.8. The replicator dynamics is a regular monotonic dynamic.

Proof. Regularity follows from the definition:

$$x.g(x) = \sum_i x_i.(e_i.Ax - x.Ax) = \sum_i (e_i x_i).Ax - \sum_i x_i.(x.Ax) = x.Ax - x.Ax = 0.$$

Let's check now monotonicity:

$$e_i.Ax > e_j.Ax \Leftrightarrow e_i.Ax - x.Ax > e_j.Ax - x.Ax \Leftrightarrow g_i(x) > g_j(x).$$

So proposition 4.8 allows us to use the Folk Theorem, and relate the stationary dynamic states with Nash equilibria. In fact, stronger results apply to the replicator dynamics. The following theorem describes them, it was due to Taylor and Jonker (1978) and refined by Hofbauer, Schuster and Sigmund (1979), which we state here but not prove. The second part of the theorem is usually presented as an independent result but it is an immediate corollary and we include it here together.

Theorem 4.2. Any state $x \in \Delta_n$ ESS of an underlying game is an asymptotically stable state in the replicator dynamics. Moreover, if x is an ESS and $x \in \text{int}(\Delta_n)$, then $\varepsilon(t, x^0)_{t \rightarrow \infty} \rightarrow x, \forall x^0 \in \text{int}(\Delta_n)$.

Interestingly theorems 4.1 and 4.2 apply to the replicator dynamics constructing two way implications. The first one, allows to describe asymptotic stable states of the dynamic as Nash equilibria of the underlying game. And with the second one, we can depart from an ESS (a refinement of the NE) of the static game and assure asymptotic stability in the replicator dynamics. The second part of 4.2 describes an interior ESS as a globally stable state in the replicator dynamic.

There are many others growth rates functions but the replicator dynamics is a complete and useful example. Finally, just for reference, we shortly describe other possible dynamics.

Weibull presents the discrete time versions of the replicator dynamics, that may be applied to some biological entities, and other models more apt to economics (replication by imitation and where communication is basic).

Armao works on a quite different model of dynamic, called The Viability Updating. Interestingly its assumptions and characteristics are completely different: it acts on small group interactions, not pairwise interactions, recreating, in Armao's words, the "gregarious" aspect of evolution (in the sense that a strategy is reinforced if it is

surrounded by the same strategy). Furthermore, the Viability Updating is not even wpp and thus the “rational” results of the Folk theorem are not necessarily valid. Irrational strategies may be successful here.

Now, we turn to the application of the replicator dynamics to our main interest games: symmetric two player games.

4.4.2 An Application: Symmetric games.

Suppose $A = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$ is a standard payoff matrix for a 2x2 player’s symmetric game with two pure strategies. We are interested in classifying the different outcomes of this game based on the entries of A and following the replicator dynamics.

For simplicity, note $x = x_1$ and $1 - x = x_2$ the share of the two strategies. By proposition 4.1 the states $x = 0, x = 1$ are stationary. There may be interior stationary states but we can study completely the behavior of the dynamic by observing what occurs when small perturbations are induced to a $x = 0, x = 1$ state (that is a relative small number of one of the strategies invades a population with majority of it using the other strategy).

We define the following possibilities:

Definition 4.10. There are four evolutionary behaviors based on the matrix A for any two strategy dynamics. We assume $\varepsilon > 0$ arbitrarily small.

- 1- Strategy 1 is *dominant* if it is asymptotically stable (AS) , or if it is stable and the other strategy is unstable. That is: $\dot{x} \geq 0$ for $x \geq 1 - \varepsilon$ and $\dot{x} \leq 0$ for $x \leq \varepsilon$, with strict inequality holding at least once. The statement is equivalent for strategy 2 being dominant.
- 2- Strategies 1 and 2 are *bistable* if they are each AS: $\dot{x} > 0$ for $x \geq 1 - \varepsilon$ and $\dot{x} < 0$ for $x \leq \varepsilon$.
- 3- Strategies 1 and 2 *coexist* if they are both unstable: $\dot{x} < 0$ for $x \geq 1 - \varepsilon$ and $\dot{x} > 0$ for $x \leq \varepsilon$.
- 4- Strategies 1 and 2 are *neutral* if they are both stable but not AS: $\dot{x} = 0$ for $x \geq 1 - \varepsilon$ and $x \leq \varepsilon$.

We apply now the replicator dynamic to the two player game and use the different notions of the past definition.

$$\dot{x} = x(ax + (1 - x)b + x(ax + (1 - x)b) + (1 - x)(cx + (1 - x)d))$$

Where, $x_1 A x = ax + (1 - x)b$ and $x A x = x(ax + (1 - x)b) + (1 - x)(cx + (1 - x)d)$.

Which simplifies into:

$$\dot{x} = x(1-x)(ax + (1-x)b - cx - d(1-x)) \Leftrightarrow \dot{x} = x(1-x)((a-b-c+d)x + b-d).$$

Thus, in the replicator dynamics of a standard 2x2 game, the stationary states may be:

$$\dot{x} = 0 \Rightarrow x_1 = 0, x_2 = 1 \text{ or } x_3 = \frac{d-b}{a-b-c+d}.$$

The two first states are then pure strategies that represent stationary states. The third one is of interest if it is in the interior of the simplex (that is if: $0 < \frac{d-b}{a-b-c+d} < 1$).

Then selection must drive the dynamic toward the interior equilibrium or one of the vertices. We classify then the strategies based on this interior equilibrium following Nowak (2006).

Proposition 4.9. The following describes the evolutionary behavior of the replicator dynamics based on A :

There are four evolutionary behaviors based on the matrix A for any two strategy dynamics. We assume $\varepsilon > 0$ arbitrarily small.

- 1- Strategy 1 is *dominant* if $a \geq c$ and $b \geq d$, with strict inequality in at least one case. Similarly for dominance of strategy 2.
- 2- Strategies 1 and 2 are *bistable* if $a > c$ and $b < d$. The interior state is unstable.
- 3- Strategies 1 and 2 *coexist* if $a < c$ and $b > d$. The interior state is globally stable.
- 4- Strategies 1 and 2 are *neutral* if $a = c$ and $b = d$. Biologically this case has no interest.

In fact Proposition 4.9 is the converse of the theorem 4.2: any AS state in the replicator dynamics is an ESS of the underlying game. Just note that by proposition 3.1, the first condition holds for a pure strategy ESS and the third condition corresponds to a mixed strategy ESS.

4.5 Discussion

In this chapter we began by defining a game dynamic. This approach includes time as a defining factor and emphasizes the role of selection in the evolutionaery process. We described the solution of such a dynamic, that is a direct application of the second chapter's results. We justified the fact that we were interested in the long run behavior of the solution not the path that it takes. This is why we spent a section studying the different equilibrium states that may be attained in our dynamics. The stability of

these states resulted the way to evaluate the role of mutations in this context. Section 4.3, particularly, the Folk Theorem is the bridge between the static and dynamic approaches. Interestingly, this bridge has both mathematical and biological consequences, and it is highly recommended to fully understand the mathematical procedure that ends with biological formal interpretations. We finished presenting the replicator dynamics, an important application.

5. Conclusions

In this work we presented the fundamentals of evolutionary game theory. The second chapter included all the material needed to prove the Picard Lindelof's theorem of existence and uniqueness of the solution of some ordinary differential equations (ODE). This result, as we saw, was needed for formal completeness of the mathematical procedure to describe the behavior of dynamic models. Third chapter recovered two basic concepts of static game theory: Nash equilibrium and Evolutionary Stable Strategies, in particular we worked on Nash's theorem assuring us the existence of precise equilibria in some standard games. Then in the fourth chapter we made some links, using the ordinary differential equations of the beginning, between the static notions and stationary evolutive states of a population. This was mediated by different kind of functions defined by the payoffs of the underlying games. We were mainly interested in the stability of those states and the fate of poor strategies. We reviewed, finally, the replicator dynamics, a simple but widely used evolutive dynamic.

We were conscient of the magnitude of the definitions, theorems and applications of this field. In spite of this, we tried to choose the basic material in order to have a self contained document. Apart of the pleasure of discovering the mathematics involved, we had always in mind the biologic use of the theory presented. Undoubtedly, this influenced the mentioned choice. And, for this reason also, we tried to keep the material in terms reachable by a non-mathematical audience without loosing rigor, convinced that if biologists use these tools their work will be, formally, much powerful. To complete this goal, in this chapter we make a brief account of the applications of EGT to biology, hoping to give a last motivation for biologists to study this area. Economy had largely enjoyed the benefits of this interdisciplinary work. Even if biology has already started, it is important to keep reducing the gap between the theoretical and practical advances. For this to happen, it is preferable that biologists have a clear understanding of the theoretical background. Misunderstandings and lost of time may be avoided (see Binmore (2010) for painful examples). Particularly, mathematical biologists have a big responsibility: they are the best suited to move into the two sciences and “move” the information between them as fast,natural and clear as possible.

5.1. Applications

Since the late eighties, EGT became a common language for the study of biological issues. Especially, animal behavior saw many advances in areas such as: Social Foraging, Animal Contests, Habitat Selection, Communication and many others. Dugatkin and Reeve gathered together the advances in their book Game and Theory and Animal Behavior (Dugatkin and Reeve, 1998). As far as we know, fewer applications have been done in botanics (see Falster and Westoby, 2003). Recently, microorganisms became common models in this field, they are well suited because they are easy to manage in the laboratory and many generations, including the genotypes and phenotypes, may be followed in small time (see for example Jiricny et.al, 2010 and Gore et.al, 2009). Some criticized the absence of genetics considerations in EGT and, for example, the reduced view of asexual reproduction in

the dynamics requiring reproduction. Hammerstein (1996) addresses well this problems.

We began the presentation of game theory with the Prisoner's Dilemma. This game represented the paradox of the evolution of cooperation. We argued then that Nowak's (2006a) work resolved this paradox in five distinct but all elegant ways (in a mathematical and biological sense). This issue, the evolution of cooperation, is by far the most studied problem. The reader is now prepared to analyze the five mechanisms through the scope of EGT. For those of us who believe that cooperation is essential for understanding where we come from and where are we going, this is an amazing achievement. Apparent and hopefully we are many: Nowak's paper is the most highly cited paper in a multidisciplinary field in this year and it has been designated as a current classic (<http://www.sciencewatch.com/dr/cc/10-febcc/>, the 8th of July, 2010).

In summary, mathematics is now permeating biology with EGT. There are still many challenges ahead and the common work of scientists of both areas is a prerequisite for produce new advances. For an excellent review of the past-future of the field we recommend McGill and Brown (2007).

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