Evolutionarily Stable Strategies and Dynamics
Tutorial, Example, and Open Problems

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Abstract

We provide an introduction to the topic of evolutionarily stable strategies and their relations to the stability of the so-called replicator dynamics. We also provide an example of a non trivial mixed ESS in infinite dimemsion, something apparently missing in the literature so far. We end with some open problems.

1 Introduction

The concept of evolutionarily stable strategies, or ESS, has been introduced by John Maynard Smith in a joint paper [5]. Its aim is to investigate the effect of each individual behaving in a selfish manner, on a large population of such individuals, given that the best strategy to use for itself depends on the collective behavior of the population, which itself is composed of many of these same selfish individuals.

The original paper [5] is about the behavior of populations of animals, and this concept has mainly been put forth by researchers in behavioral ecology, hence biologists. Yet, it has attracted the attention of economists, as the same type of question arises concerning a population of economic agents. It would seem to be the right tool also to investigate the behavior of financial markets, where the up and downs of the prices are the result of the individual decisions of a large number of individually rational (?) traders, rather than an exogeneous random phenomenon as hypothezised in 99% of the financial literature, beginning with

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the famous Black and Scholes theory. More recently, it has been applied to the behavior of populations of users on the Internet.

Actually, this is only a revival of an much older form of that concept, namely the so-called Wardrop equilibrium in routing problems, introduced by John G. Wardrop in the context of road traffic [11].

Our intent here is to provide a short introduction to ESS for game theoretists, and then to relate it to the "replicator dynamics". This was introduced by Taylor and Jonker [7] as a plausible model of evolution dynamics. It has since been recognized as a model of the dynamics of learning in sociology for instance.

It should be emphasized here that what behavioral ecologists call "dynamic games" are not dynamic games in the sense generally understood in the ISDG. Rather, the solution of a static game is supposed to say something about the stability of a dynamical equation in which no game is involved.

Typically, if the reward involved in the (static) game is the number of ofsprings —a measure of darwinian "fitness"—, and assuming, to make things simple, that the ofsprings use the same strategy as their parent(s)[1] this dynamical equation modelizes the growth of the various populations depending on the strategy they use. The very concept of ESS was created with these dynamics in mind, to characterize stable points. The idea being that Nature as we observe it should be at a stable point.

We shall see however that the relationship between ESS and stable points of the replicator dynamics is far from simple.

The theory was originally developed in the context we call hereafter finite and linear. Finite refers to the fact that the set of behaviors, or strategies (a game theoretist should say "pure strategies") available to each individual is finite. This leads to matrix games and dynamics in $\mathbb{R}^n$, where things are well understood. But we are also interested in problems where the natural strategy set is infinite, usually continuous. A typical example is as follows.

We consider insect parasitoids who lay their eggs in the eggs of a "host", substituting their own ofspring to that of the host. If the host is a crop pest, the parasitoid may be used to control this pest, a practice now in widespread use, for instance spreading *trychogramma brassicae* to fight against *ostrinia nubilalis*, the European "corn borer".[2] The host eggs are laid in patches by the host female. When a female parasitoid reaches such a patch, it starts attacking eggs one at a time. Yet, it is not able to do so systematically to efficiently exhaust the patch. Rather, from oviposition to oviposition, it moves at random, encountering more and more often

[1] In its simplest form, that theory assumes asexual reproduction. It can, however, be extended to the more common sexual reproduction cycle, using statistical arguments from population genetics.

[2] A small company we are in contact with in Sophia Antipolis produces, and sells, billions of eggs of *trychogramma brassicae* per year.

an egg already parasitized, which it recognizes thanks to pheronomes left behind itself. Hence, the foraging activity becomes less efficient as time goes on, and at some point the animal leaves the patch, leaving some healthy host eggs. The typical *trait*, or *strategy*, we are interested in is the time the animal spends on the patch, a real number, or rather this residence time as a function of the patch quality, a real function.

If this trait is really to be transfered to ofsprings, it is, in genetic terms, a *phenotype*. The three words "strategy", "trait" or "phenotype" will be taken as synonymous hereafter.

2 ESS and classical game theory

2.1 Notations and setup

We consider a compact metric space X the space of *traits* or *phenotypes* or *pure strategies*. Three cases of interest are

- X is finite (the *finite* case), $X = \{x_1, x_2, \ldots, x_n\}$,
- X is a line segment $[a, b] \subset \mathbb{R}$,
- X is a compact subset of $\mathbb{R}^n$.

We shall use letters x, y, for elements of X.

We let $\Delta(X)$ denote the set of probability measures over X. In the finite case, we shall also denote it as Δ_n. We notice that in the weak topology, $\Delta(X)$ is compact and the mathematical expectation of any continuous function is continuous with respect to the probability law. We shall use letters p, q, for elements of $\Delta(X)$.

A population of animals is characterized by the probability $p \in \Delta(X)$ governing the traits of its individuals. There is no real need to distinguish whether each individual acts many times, adopting a strategy in $A \subset X$ with probability $p(A)$ —the population is then *monomorphic* and its members are said to use the *mixed strategy* p—, or whether each animal behaves in a fixed manner, but in a polymorphic population, p being the distribution of traits among the population : for any subset $A \subset X$, $p(A)$ is the fraction of the population which has its trait x in A. Then, p also governs the probability that an animal taken randomly in the population behaves a certain way. In the sequel, we shall favor that second interpretation.

We are given a *generating function* $G : X \times \Delta(X) \to \mathbb{R}$ jointly continuous (in the weak topology for its second argument). Its interpretation is that $G(x, p)$ is the *fitness* gained by an individual with trait x in a population characterized by p.

A case of interest, called hereafter the *linear case*, is when G derives from a continuous function $H : X \times X \to \mathbb{R}$ giving the benefit $H(x, y)$ that an animal with trait x gets when meeting an animal with trait y, as the expected benefit for trait x:

$$G(x, p) = \int_X H(x, y)\, \mathrm{d}p(y)\,. \tag{1}$$

Then G and F below are linear in their second argument. But this is not necessary for many results to follow.

The fitness gained by an animal, or a small sub-population, using a mixed strategy q in a population characterized by p is

$$F(q, p) = \int_X G(x, p)\, \mathrm{d}q(x)\,.$$

Notice that if $\delta_x \in \Delta(X)$ denotes the Dirac measure at x, $G(x, p) = F(\delta_x, p)$.

In the linear case, one can be more precise : if this small sub-population represents a fraction ε of the total population, the rest of which uses the mixed strategy p, the total population is characterized by the distribution $(1 - \varepsilon)p + \varepsilon q$.

The most appealing definition of an ESS is as follows ([4]):

Definition 1 *The distribution $p \in \Delta(X)$ is said to be an* ESS *if there exists $\varepsilon_0 > 0$ such that for any positive $\varepsilon \leq \varepsilon_0$,*

$$\forall q \neq p\,, \quad F(p, (1 - \varepsilon)p + \varepsilon q) > F(q, (1 - \varepsilon)p + \varepsilon q)\,.$$

The intent is clear : a small enough mutating sub-population with any new phenotype q will not invade a population governed by p, since it is less fit than the dominating phenotype.

In the nonlinear case, this definition can hardly be used, since nothing is known about the generating function $G(\cdot, (1 - \varepsilon)p + \varepsilon q)$. In the linear case, definition 1 above coincides with the alternative definition of [5]:

Proposition 1 *If F is linear in its second argument, definition 1 is equivalent to definition 2 below.*

Definition 2 *The distribution $p \in \Delta(X)$ is said to be an ESS if*

(I). $\forall q \in \Delta(X)\,, \quad F(q, p) \leq F(p, p)$,

(II). $\forall q \neq p\,, \quad F(q, p) = F(p, p) \Rightarrow F(q, q) < F(p, q)$.

The proof is elementary.

2.2 Relation with classical game theory

It should be emphasized that in the above presentation, we have a game between *strategies* and not between *agents*. We do not distinguish two agents with the same trait. If two agents meet, one playing x the other one y, the first one will have a benefit $H(x,y)$. Whichever it is. The second one will have a benefit $H(y,x) \neq H(x,y)$. (In case H is symmetrical, i.e. $H(x,y) = H(y,x)\ \forall x, y \in X$, the game is said to be *bi-symmetrical*.)

We turn back to a formulation where performance indices are attached to players. Consider a two-player game, between, say, player **1** and player **2**. Both choose their action, say q_1 and q_2, in $\Delta(X)$. Let their respective reward functions, that they seek to maximize, be

$$\begin{aligned} J_1(q_1, q_2) &= F(q_1, q_2)\,, \\ J_2(q_1, q_2) &= F(q_2, q_1)\,. \end{aligned}$$

We have the obvious proposition :

Proposition 2

- *Condition (I) of definition 2 is equivalent to the statement that (p,p) is a Nash equilibrium of this game. For that reason, any p satisfying that condition is called a* Nash point*.*

- *If (p,p) is a strict Nash equilibrium, p is an ESS.*

The proof is elementary.

It immediately follows, by a theorem due to Von Neumann [10, assertion (17:D) p. 161][3] in the finite case, and noticed at least since the early 50's in the infinite case (see [3])[4]

Theorem 1 *Let p be an ESS, then*

(I). $\forall x \in X\ ,\ G(x,p) \leq F(p,p)$*,*

(II). let $N = \{x \in X \mid G(x,p) < F(p,p)\}$, then $p(N) = 0$.

A proof completely similar to (but slightly distinct from) the existence proof of the Nash equilibrium lets one state the following result, which applies here :

Theorem 2 *Let P be a compact space, $F : P \times P \to \mathbb{R}$ be a continuous function, concave in its first argument. Then there exists at least one $p \in P$ satisfying condition (I) of definition 2.*

[3] This was probably in the 1928 paper of J. Von Neumann, but we did not check

[4] Von Neumann's proof applies to zero sum games. Its extension to a Nash equilibrium is trivial, and can be found, e.g., without claim of novelty, in [3]

Proof Continuity and concavity of F and compactness of X together insure that the *best response* point-to-set mapping $p \mapsto \mathrm{argmax}_q F(q,p)$ is non empty and convex, and the continuity in the second argument that the same map is u.s.c., so that according to Kakutani's fixed point theorem, there exists a fixed point p. ▮

However, condition (II) of Definition 2 will be seen to be a second order condition. It may fail to be satisfied by any Nash point, resulting in a game without ESS.

2.3 Further analysis of the linear finite case

2.3.1 Characterization in terms of the game matrix

In the finite linear case, the problem is entirely defined by the matrix $A = (a_{ij})$ with $a_{ij} = H(x_i, x_j)$, as

$$G(x_i, p) = (Ap)_i\,, \quad F(q,p) = \langle q, Ap\rangle = q^t Ap\,.$$

We rephrase theorem 1 in that context. To do so, introduce the notation $\mathbb{1}$ to mean a vector (of appropriate dimension) the entries of which are all ones, and the notation for vectors u and v of same dimension $u < v$ to mean that the vector $v - u$ has all its coordinates strictly positive.

We obtain the following more or less classical results :

Theorem 3 *In the finite linear case, the two conditions of definition 2 are respectively equivalent to (I) and (II) below.*

(I). There exists a partition $X = X_1 \cup X_0$, $|X_1| = n_1$, $|X_0| = n_0$, such that, reordering the elements of X in that order and partitioning $\mathbb{R}^n$ accordingly, there exists a vector $p_1 \in \Delta_{n_1}$, a real number α and a vector $\beta \in \mathbb{R}^{n_0}$ such that,

$$p = \begin{pmatrix} p_1 \\ 0 \end{pmatrix}, \quad Ap = \begin{pmatrix} \alpha\mathbb{1} \\ \beta \end{pmatrix}, \quad \beta < \alpha\mathbb{1}\,. \tag{2}$$

(II). Partitioning A accordingly in

$$A = \begin{pmatrix} A_{11} & A_{10} \\ A_{01} & A_{00} \end{pmatrix},$$

$$\forall q_1 \in \Delta_{n_1}\backslash\{p_1\}\,, \quad \langle q_1 - p_1, A_{11}(q_1 - p_1)\rangle < 0\,. \tag{3}$$

(Notice that the vectors $\mathbb{1}$ in the second and third expression of (2) do not have the same dimension. Notice also that p_1 may still have some null coordinates.)

Proof For condition (I), this is just a rephrasing of theorem 1. Concerning condition (II), the vectors $q \in \Delta(\mathbb{R}^n)$ such that $F(q,p) = F(p,p)$ are all the vectors of the form

$$q = \begin{pmatrix} q_1 \\ 0 \end{pmatrix}, \quad q_1 \in \Delta_{n_1} .$$

As a matter of fact, for all such vectors, $\langle q, Ap\rangle = \alpha$. So that condition (I) of definition 2 says that $\forall q_1 \in \Delta_{n_1}\backslash\{p_1\}$, $\langle q_1 - p_1, A_{11}q_1\rangle < 0$. But we have seen that $\langle q_1 - p_1, A_{11}p_1\rangle = 0$. Therefore, we may substract that quantity to get (II) above. ∎

Remark 1 *Equation (2) above can also be written in terms of a so-called* complementarity condition*:*

$$\mathbb{1}\alpha - Ap \geq 0\,,$$
$$p^t(\mathbb{1}\alpha - Ap) = 0\,.$$

Theorem 2 above says that there always exists at least one solution of equations (2). The question thus for any such solution is to know whether it satisfies condition (II) of the definition. Or whether none does. To further discuss that question, let $p_2 \in \mathbb{R}^{n_2}$ be the vector of the non zero entries of p_1, so that, reordering the elements of X_1 if necessary,

$$p_1 = \begin{pmatrix} p_2 \\ 0 \end{pmatrix}.$$

Let also A_{22} be the corresponding sub-matrix of A, and $B := A_{22} + A_{22}^t$.

Corollary 4

- *A necessary condition for a solution of equation (2) to be an ESS is that the restriction of the quadratic form $\langle q_2, Bq_2\rangle$ to the orthogonal subspace of $\mathbb{1}$ in $\mathbb{R}^{n_2}$ be negative definite, which implies that B necessarily has at most one non negative eigenvalue*[5]*.*

- *A sufficient condition is that the restriction of the quadratic form $\langle q_1, A_{11}q_1\rangle$ to the orthogonal subspace to $\mathbb{1}$ in $\mathbb{R}^{n_1}$ be negative definite, and therefore afortiori that $A_{11} + A_{11}^t$ be a negative definite matrix.*

Another easy corollary is that the number of ESS is bounded by n. More precisely, we have the following statement :

Corollary 5 *If there is an ESS in the relative interior of a face of Δ_n, there is no other ESS in that face, and in this statement Δ_n is itself an $n-1$-dimensional face. (In particular, if there is an ESS in the relative interior of Δ_n, it is* the *unique ESS.)*

[5]Some authors have mistakenly replaced *at most one* by *exactly one*.

Although this corollary can be directly derived from the above analysis, it follows trivially from the theorem on the stability of the replicator dynamics to follow.

2.4 Evolutionarily robust strategies

A related useful concept is as follows:

Definition 3

- *A strategy $p \in \Delta(X)$ is called a* locally superior strategy *(LSS) if there exists a neighborhood N of p in $\Delta(X)$ such that,*

$$\forall q \in N \backslash \{p\}\,, \quad F(p,q) > F(q,q)\,. \tag{4}$$

- *A strategy locally superior strategy in the weak topology is called an* evolutionarily robust strategy *(ERS)*

It should be emphasized that the concept of LSS depends on the topology used on $\Delta(X)$, which is a non trivial issue in the infinite cases, hence the specialization to ERS.

This concept is stronger than that of ESS, as shown by the following result:

Theorem 6

i. A LSS in any topology for which a convex combination of measures is continuous in its coefficient (and in particular an ERS), is an ESS (according to definition 1).

ii. In the finite linear case, an ESS is a LSS (i.e. both concepts are equivalent).

Proof

i. Assume p is a LSS. Take any $q \in \Delta(X)$. By the continuity assumption, there exists an $\varepsilon_0 > 0$ small enough to insure that, for any positive $\varepsilon \leq \varepsilon_0$, $(1-\varepsilon)p + \varepsilon q$ belongs to N in Definition 3 so that (4) stands. Therefore

$$F(p,(1-\varepsilon)p + \varepsilon q) - F((1-\varepsilon)p + \varepsilon q, (1-\varepsilon)p + \varepsilon q) > 0\,.$$

Now, F is always linear with respect to its first argument. Hence, this yields

$$\varepsilon[F(p,(1-\varepsilon)p + \varepsilon q) - F(q,(1-\varepsilon)p + \varepsilon q)] > 0\,,$$

which, upon dividing through by the positive ε is precisely definition 1.

ii. Assume X is finite, thus $\Delta(X) = \Delta_n$ can be taken to be a subset of $\mathbb{R}^n$. Let p be an ESS, belonging to the relative interior of a face $\mathcal{F}$ of Δ_n. Let B be the boundary of Δ_n deprived of the relative interior of $\mathcal{F}$. It is compact. Take $r \in B$, and for any r let $r_\varepsilon := (1-\varepsilon)p + \varepsilon r$. For any $r \in B$, there exists an ε_0 such that it holds that

$$\forall \varepsilon \in (0, \varepsilon_0)\,, \quad F(p, r_\varepsilon) > F(r, r_\varepsilon)\,.$$

More precisely, define the *invasion barrier* of r as the function $b(r) = \sup\{\varepsilon_0 \in [0,1]\}$ such that the above inequality holds. Concerning it, we have the following :

Lemma 1 *The function b is continuous and everywhere positive on the compact set B.*

Proof Write

$$F(p, r_\varepsilon) - F(r, r_\varepsilon) = F(p-r, p) - \varepsilon F(p-r, p-r)\,.$$

The first term in the rhs is non negative by hypothesis. If the second one is negative, then $b(r) = 1$. By hypothesis also, this is always the case if r is a best response to p, i.e. if $F(p-r, p) = 0$. If $F(p-r, p) > 0$ and $F(p-r, p-r) > 0$, then $b(r) = \min\{1, F(p-r,p)/(F(p-r,p-r)\}$, which is continuous. ∎

Hence b reaches its minimum, say $\hat{\varepsilon}$ over B.

Now, for any $q \neq p \in \Delta_n$, there is a $r \in B$ and a positive ε such that $q = r_\varepsilon$. It easily follows that $b(q) > b(r) \geq \hat{\varepsilon}$. Thus, $\hat{\varepsilon}$ is a *uniform invasion barrier*. Now, since p is not in B which is compact, it is at a finite distance of B, hence the set $\{r_\varepsilon \mid r \in B,\ \varepsilon \in (0, \hat{\varepsilon})\}$ contains a neighborhood of p in Δ_n, where, thus, $F(p,q) > F(q,q)$.

∎

3 Example

3.1 The example

There does not seem to be a completely worked out, non trivial example of an ESS in infinite dimension in the literature[6]. We provide an examle of an ERS, thus also an ESS. It is inspired by an example of game on the square in [2].

[6]At least with a continuous kernel H. The war of attrition is an example with a discontinuous kernel. But then defining Lebesgue integrals with arbitrary measures becomes a problem.

3.1.1 A reference ESS

Let $X = [0,1]$, λ be a positive number less than one, and

$$H(x,y) = \max\{x-y, \lambda(y-x)\}\,.$$

We want to prove the following result, the proof of which occupies the rest of this section.

Theorem 7 *The strategy*

$$p = \frac{\lambda}{1+\lambda}\delta_0 + \frac{1}{1+\lambda}\delta_1$$

is a superior strategy, i.e.

$$\forall r \neq p \in \Delta(X) \quad F(p,r) \geq F(r,r)$$

If so, p is both an ERS and a ESS.

Notice first that p is equalizing :

$$\forall x \in [0,1]\,, \quad G(x,p) = \frac{\lambda}{1+\lambda}H(x,0) + \frac{1}{1+\lambda}H(x,1) = \frac{\lambda}{1+\lambda}\,.$$

3.1.2 A comparison strategy r

Let r be an arbitrary measure on $X = [0,1]$. It immediatly follows from the fact that $x \mapsto H(x,y)$ is convex for all y the following important fact:

Proposition 3 *The function $x \mapsto G(x,r)$ is convex.*

We need to define the following two numbers:

$$x_0 = \inf\{x \in X \mid r([0,x]\} \geq \frac{\lambda}{1+\lambda}\,,$$
$$x_1 = \sup\{x \in X \mid r([x,1])\} \geq \frac{1}{1+\lambda}\,.$$

We have the obvious fact :

Proposition 4 *$x_0 = 0$ and $x_1 = 1$ if and only if $r = p$.*

3.2 Cases $r(\{0\}) \geq \lambda/(1+\lambda)$ or $r(\{1\}) \geq 1/(1+\lambda)$

Lemma 2 *If $x_0 = 0$ or $x_1 = 1$ but $r \neq p$, $F(p,r) > F(r,r)$.*

Proof Let us first assume that $r_0 := r(\{0\}) \geq \lambda/(1+\lambda)$, so that $x_0 = 0$, but $r \neq p$. Notice that $\lambda(1-r_0) \leq \lambda/(1+\lambda) = r_0$. As a consequence we get that

$$G(0,r) = \lambda \int_{(0,1]} y r(\mathrm{d}y) = \lambda(1-r_0) - \lambda \int_{(0,1]} (1-y) r(\mathrm{d}y) < \lambda(1-r_0) \leq r_0\,,$$
$$G(1,r) = r_0 + \int_{(0,1]} (1-y) r(\mathrm{d}y) \geq r_0\,.$$

Hence, $G(0,r) < G(1,r)$. Thus, by the convexity of $G(\cdot,r)$, it follows that $\forall x \in [0,1)$, $G(x,r) < G(1,r)$. And since the weight of r over $(0,1]$ is not entirely concentrated at 1,

$$F(p,r) - F(r,r) = (\frac{\lambda}{1+\lambda} - r_0)G(0,r) + \frac{1}{1+\lambda}G(1,r) - \int_{(0,1]} G(x,r) r(\mathrm{d}y)$$
$$> (\frac{\lambda}{1+\lambda} - r_0)G(0,r) + \frac{1}{1+\lambda}G(1,r) - (1-r_0)G(1,r)$$
$$= (\frac{\lambda}{1+\lambda} - r_0)[G(0,r) - G(1,r)] > 0\,.$$

A similar proof applies for the case $x_1 = 1$. ∎

3.3 Case $r(\{0\}) < \lambda/(1+\lambda)$ and $r(\{1\} < 1/(1+\lambda)$

Let us therefore investigate now the case where $0 < x_0$ and $x_1 < 1$. We need a new lemma:

Lemma 3 *For all $r \in \Delta(X)$, $x_0 \leq x_1$ and $r((x_0,x_1)) = 0$. If $x_0 < x_1$, then $r([0,x_0]) = \lambda/(1+\lambda)$ and $r([x_1,1]) = 1/(1+\lambda)$.*

Proof If $x_1 < x_0$, there is an x in between. It follows from the definition of x_0 and x_1 that if $x < x_0$, $r([0,x]) < \lambda/(1+\lambda)$, and also that if $x > x_1$, $r([x,1]) < 1/(1+\lambda)$, hence $r([0,x)) > \lambda/(1+\lambda)$. Thus $r([0,x)) > r([0,x])$, a contradiction.

It follows from the definition that $r([0,x_0]) \geq \lambda/(1+\lambda)$, and that $r([x_1,1]) \geq 1/(1+\lambda)$. Assume that $x_0 < x_1$, it follows that both inequalities are equalities, and that $r((x_0,x_1)) = 0$. An equality which is trivially true if $x_0 = x_1$. ∎

We must distinguish the case $x_0 < x_1$ and the case $x_0 = x_1$.

3.3.1 Case $x_0 < x_1$

Define

$$a = \int_{[0,x_0]} x r(\mathrm{d}x)\,, \quad b = \int_{[x_1,1]} (1-x) r(\mathrm{d}x)\,.$$

For any $x \in [x_0, x_1]$, we get

$$G(x,r) = \int_{[0,x_0]} (x-y)r(\mathrm{d}y) - \lambda \int_{[x_1,1]} [(1-y)-(1-x)]r(\mathrm{d}y)\,.$$

Hence, using the above notations

$$\forall x \in [x_0, x_1]\,, \quad G(x,r) = \frac{\lambda}{1+\lambda} - a - \lambda b\,.$$

Very similar calculations also yield

$$G(0,r) = \frac{\lambda}{1+\lambda} + \lambda a - \lambda b\,, \quad \text{and} \quad G(1,r) = \frac{\lambda}{1+\lambda} - a + b\,.$$

We use the convexity of $G(\cdot, r)$ to get

$$G(x,r) \le \begin{cases} G(0,r) - \dfrac{x}{x_0}[G(0,r) - G(x_0,r)] & \text{if } x \le x_0\,, \\ G(1,r) - \dfrac{1-x}{1-x_1}[G(1,r) - G(x_1,r)] & \text{if } x \ge x_1\,. \end{cases}$$

Use the above expressions to get $G(0,r) - G(x_0,r) = (1+\lambda)a$ and $G(1,r) - G(x_1,r) = (1+\lambda)b$, and integrate remembering that $r((x_0,x_1)) = 0$ to find

$$F(r,r) \le \frac{\lambda}{1+\lambda} G(0,r) + \frac{1}{1+\lambda} G(1,r) - (1+\lambda)\left[\frac{a^2}{x_0} + \frac{b^2}{1-x_1}\right]\,.$$

We recognize $F(p,r)$ in the first two terms of the r.h.s., to conclude that

$$F(r,r) - F(p,r) \le -(1+\lambda)\left[\frac{a^2}{x_0} + \frac{b^2}{1-x_1}\right] < 0\,, \tag{5}$$

which, in view of proposition 4 proves the result.

3.3.2 Case $x_0 = x_1$

If $x_0 = x_1$, we need to introduce $r_0 : r(\{x_0\})$ and $\alpha \in [0,1]$ such that

$$r([0,x_0)) = \frac{\lambda}{1+\lambda} - \alpha r_0\,, \quad r((x_0,1]) = \frac{1}{1+\lambda} - (1-\alpha) r_0\,.$$

Define now

$$a = \int_{[0,x_0)} x r(\mathrm{d}x) + x_0 \alpha r_0\,, \quad b = \int_{(x_0,1]} (1-x) r(\mathrm{d}x) + (1-x_0)(1-\alpha) r_0\,.$$

Proposition 4 still holds true.

In all the integrals over $[0,1]$, write

$$\int_0^1 \phi(x)r(\mathrm{d}x) = \\ \int_{[0,x_0)} \phi(x)r(\mathrm{d}x) + \phi(x_0)\alpha r_0 + \phi(x_0)(1-\alpha)r_0 + \int_{(x_0,1)} \phi(x)r(\mathrm{d}x)\,.$$

We have for instance

$$\begin{aligned} G(0,r) = {} & \lambda \int_{[0,x_0)} yr(\mathrm{d}y) + \lambda\alpha x_0 r_0 + \lambda(1-\alpha)x_0 r_0 \\ & -\lambda \int_{(x_0,1]} (1-y)r(\mathrm{d}y) + \frac{\lambda}{1+\lambda} - \lambda(1-\alpha)r_0 \\ = {} & \lambda a - \lambda b + \tfrac{\lambda}{1+\lambda}\,. \end{aligned}$$

We obtain thus the same formula as in the preceding case. Similar calculations also give the same formulas as previously for $G(x_0,r)$ and $G(1,r)$, and lead to the same conclusion (5). And this completes the proof of the theorem.

4 Replicator dynamics

Some authors ([8, 9]) define an ESS (in the finite case) as a stable point p of the *replicator dynamics* introduced in [7]. We shall see that this is *not* an equivalent definition Since we already have two, we do not take this third one as a definition, and investigate this topic in more detail.

4.1 Population dynamics

We have a population described by the number $n(x)$ of individuals of phenotype x, or more precisely, in the continuous case, $n(x)$ is the density, with respect to the Lebesgue measure, of individuals with phenotype x. Then, the distribution of the population according to our previous description, has a density[7]

$$q(x) = \frac{n(x)}{N}\,, \quad N = \int_X n(y)\mathrm{d}y\,. \tag{6}$$

Make the (overly simplistic) assumptions that

- $G(x,q)$ is the excess of the number of ofsprings over the number of deaths per unit time of individuals of phenotype x in a population governed by q,

[7]We restrict here our attention to distributions with densities with respect to the Lebesgue measure. Most calculations can be extended to a more general distribution.

- individuals get ofsprings with the same phenotype as theirs.

This last assumption seems to restrict this theory to asexual reproduction. Yet, a more evolved analysis of population genetics with sexual reproduction shows that a similar result may be proved.

Let all the above quantities vary with time, and "dot" denote time derivative. It follows that

$$\dot{n}(t,x) = G(x,q(t))n(t,x)\,.$$

And differentiating (6), by a simple calculation,

$$\dot{q}(t,x) = q(t,x)[G(x,q(t)) - F(q(t),q(t))]\,. \tag{7}$$

In particular, in the finite case, this simplifies in

$$\dot{q}_i = q_i[G(x_i,q) - F(q,q)]\,. \tag{8}$$

Notice first that a consequence of (7) is that

$$q(t,x) = q(0,x)\exp\left(\int_0^t [G(x,q(s)) - F(q(s),q(s))]\,\mathrm{d}s\right)$$

so that if all $q(0,x)$ are non-negative, this is preserved over time. Moreover, one sees that, as should be, $\int_X q(t,x)\mathrm{d}x$ is invariant. The conclusion of these two remarks is the following:

Proposition 5 *Under the replicator dynamics,*

- $\Delta(X)$ *is invariant, as well as its interior,*
- *the faces of* $\Delta(X)$ *are invariant as well as their interiors.*

4.2 Stability of the replicator dynamics and ESS

It is known (see, e.g. [6, 1] for a much more detailed analysis) that in the finite linear case, the relationship between these two concepts is as in the next theorem.

Theorem 8 *In the finite linear case,*

- *every stable point of (7) is a Nash point.*
- *Every ESS is a locally*[8] *asymptotically stable point of (7), and its attraction basin contains the relative interior of the lowest dimensional face of* $\Delta(X)$ *it lies on.*

[8]relative to the face we are referring to

Two particular cases of that theorem are as follows :

Corollary 9 *In the finite linear case,*

- *If an ESS is an interior point of $\Delta(X)$ it is globally stable in the interior of $\Delta(X)$.*
- *Every pure strategy, whether an ESS or not, is a rest-point of (7). The above theorem implies nothing more for pure ESS.*

Proof of the theorem To prove the necessity, assume p is not an Nash point. Then, there exists i such that $G_i(p) > F(p,p)$. By continuity, and compacity, there is a neighborhood $\mathcal{V}$ of p and a positive δ such that $\forall q \in \mathcal{V}$, $G_i(q) - F(q,q) > \delta$, hence $\dot{q}_i > \delta q_i$, and q can therefore not have a limit in that neighborhood.

For the sufficiency, restrict the attention to the subspace $\mathbb{R}^{n_2}$ of corollary 4 above, where all coordinates of p are strictly positive, and further to $\Delta := \Delta_{n_2}$. And consider the Lyapunov function

$$V(q) = \sum_i p_i \ln \frac{p_i}{q_i}\,.$$

It is zero at p, its gradient at p is $\nabla V(p) = -\mathbb{1}$, so that for any $q \in \Delta$, $\langle \nabla V(p), q - p\rangle = 0$, and its hessian matrix at any q is $\mathrm{D}^2 V(q) = \mathrm{diag}\{p_i/q_i^2\} > 0$. Thus its restriction to Δ is indeed a valid Lyapunov function. And trivially, on a trajectory

$$\frac{\mathrm{d}V(q(t))}{\mathrm{d}t} = -\sum_{i=1}^{n_2} p_i[G(x_i,q) - F(q,q)] = -F(p,q) + F(q,q)$$

which is by hypothesis negative on Δ_{n_2}. ∎

One sees that the result on the number of ESS in that case is a trivial consequence of this theorem.

Using the theorem 6, it follows further that

Corollary 10 *In the finite linear case, the basin of attraction of an ESS contains a neighborhood in Δ_n of the relative interior of the lowest dimensional face of Δ_n on which that ESS lies.*

4.3 Stability of the replicator dynamics the infinite case

Little is known about the stability of the replicator dynamics in the infinite case, and the general case is still open. The main point is that the natural generalization of the classical Lyapunov function would be

$$V(q) = \int_X p(x) \ln \frac{p(x)}{q(x)}\,\mathrm{d}x\,.$$

Indeed, $\forall q \in \Delta(X)\backslash\{p\}$, $V(q) > 0$. As a matter of fact, using the fact that for any $x \neq 0$, $\ln x < x - 1$, we get

$$V(q) = -\int_X p(x) \ln \frac{q(x)}{p(x)} \, \mathrm{d}x > -\int_X p(x) \left(\frac{q(x)}{p(x)} - 1 \right) \mathrm{d}x = 0$$

for any $q \neq p$ in $\Delta(X)$.

It is a simple matter to compute its time derivative along a trajectory of the replicator dynamics, and get

$$\dot{V}(q(t)) = F(q(t), q(t)) - F(p, q(t)) \,,$$

which is negative in a weak neighborhood of p if it is a ERS. But this $V(\cdot)$ is not continuous with respect to the weak topology. So that even assuming that p is an ERS, one cannot conclude.

Some special results are known. We have for instance :

Theorem 11 *If the game is linear and bi-symmetrical, any ERS is a weakly locally stable point of the replicator dynamics.*

Proof We use the Lyapunov function $V(q) = F(p,p) - F(q,q)$. The first point is to prove that it is indeed a positive function for any $q \neq p$ in a neighborhood of p. As a matter of fact, using the symmetry of F,

$$F(p,p) - F(q,q) = [F(p,p) - F(q,p)] + [F(p,q) - F(q,q)]$$

p being a ERS, it is an ESS, and the first bracket is always nonnegative. The second bracket is also nonnegative in a weak neighborhood of p by the definition of an ERS. Moreover, if the first bracket is null, the second is strictly positive by the definition of an ESS.

Let us compute the time derivative of $V(q(t))$ on a trajectory of the replicator dynamics. By linearity and symmetry, we have

$$\dot{V}(q(t)) = -2F(q, \dot{q}) = -2 \iint H(x,y) q(x) q(y) [G(y,q) - F(q,q)] \, \mathrm{d}x \, \mathrm{d}y \,.$$

Integrating in x "inside", this gives

$$\dot{V}(q(t)) = -2 \int G(y,q)[G(y,q) - F(q,q)] q(y) \, \mathrm{d}y \,,$$

hence, $\dot{V}(q(t)) =$

$$= -2 \int [G(y,q) - F(q,q)]^2 q(y) \, \mathrm{d}y + 2 \int F(q,q)[G(y,q) - F(q,q)] q(y) \, \mathrm{d}y \,.$$

The first integral is positive as the integral of a square with a positive measure, the second one is easily seen to be zero. Hence $\dot{V}(q(t)) < 0$ for any $q \neq p$ ∎

5 Conclusion

This is only a partial overview of the full topic of the relationship between ESS, related concepts, and the stability of the replicator dynamics. The second author is preparing a full augmented survey (augmented with original results). An outstanding open problem is the question of the local stability, in an appropriate topology, of an ESS or ERS (or, for that matter *non invadable* or any better suited concept) in the continuous trait space case. Having worked on that topic, we offer no conjecture !

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