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When does the variance of replicator fitness decrease?

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Abstract. For the general replicator dynamics with regular relative advantage functions (having non-singular Jacobian and symmetrized Jacobian), it will be shown that the variance of marginal fitness of the replicators strictly decreases along each trajectory of the replicator dynamics near an interior rest point if and only if this rest point is a regular evolutionarily stable state.

1. Introduction

One of the basic questions of Darwinian selection theory is whether there exist any biological quantities that monotonously change during natural selection. The first answer to this question was Fisher's Fundamental Theorem of Natural Selection [5] stating that: "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time." This theorem has been the subject of controversy and exegesis for decades. The historical details of this controversy can be traced from the references in [20, 22, 2, 16]. For very general genetic systems, Ewens [1, 2] gave a more general interpretation of Fisher's theorem than the one that was currently accepted. He stated that the partial increase in mean fitness is equal to the additive genetic variance. Ewens' approach is based on the notion of average effect of the genetic elements, which is an attempt to ascribe, in an optimal way, a fitness notion to genetic elements.

In order to define another monotonously changing biological quantity, we have to recall the notion of relative advantage (see e. g. [14]). This concept comes from evolutionary game theory dealing with frequency dependent selection in asexual populations and describing its phenotypic evolution (see [19, 18]). The relative advantage of a given subpopulation can be defined as the average number of offspring in the considered subpopulation minus that of the whole population (see the formal definition in Section 3). It has been observed that in Fisher's Fundamental Theorem of Natural Selection the relative advantage of the evolutionarily stable state can substitute for average fitness ([10]). Thus, this function is a Lyapunov function for Fisher's selection dynamics and its rate of increase is equal to the genetic variance of the marginal fitness of the alleles.

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In all results mentioned above, the variance of marginal fitness of replicators gives the rate of increase of a certain biological quantity. Therefore, it is natural to ask how this variance behaves in the course of natural selection. I know only one pioneering result answering this question. Svirezhev [23] gave a least action functional for Fisher's selection model. Crow [4] observed that Svirezhev's [23] least action function is the same as the variance of the marginal fitness of the alleles. This means that in Fisher's selection model "Natural Selection chooses such a trajectory from each starting point to the terminal state, on which the integral, over time, of the variance of marginal fitness of the alleles is minimal".

Now I will examine this question from another viewpoint. It is obvious that at the equilibrium state of natural selection the variance of the fitness of replicators is zero. This is why in a neighbourhood of an unstable equilibrium the fitness variance typically increases in the course of natural selection. The question arises: when does the variance of the marginal fitness decrease in the course of natural selection? From the mathematical viewpoint, the main result of this paper will give a condition under which the fitness variance is a local Ljapunov function for the replicator dynamics.

2. Replicator dynamics

In the following, frequency-dependent replicator dynamics will be studied (see [13] pp.147–148). For example, the following three models exhibit replicator dynamics. The first one is the classical Fisher's selection model, in which the alleles are the replicators. The second one is the evolutionary game model where the phenotypes are the replicators. Finally, there is a possible combination of these basic models ([8] see also [3]) in which the alleles are the replicators again. Let n be the number of the replicator types. The phase space of the above three models is the simplex S_n of the n -dimensional frequency vectors. In all models referred to above the " i -type from an i -type" principle is valid. This means that in the production of an i -type replicator the contribution of an i -type replicator is necessary. A consequence of this condition for the inheritance is that the mechanism of replication is supposed to be perfect, in particular, there is no mutation. This is the reason why the *replicator dynamics* has the following form

$$\dot{x}_i = x_i [W_i(x) - xW(x)] \quad (1)$$

where $W_i : S_n \rightarrow \mathbb{R}_+$ denotes the marginal fitness function of the i -replicator and $xW(x) := \sum_{i=1}^n x_i W_i(x)$ is the mean fitness function of the whole replicator population in state x . The fitness is, as usual, the average offspring number of a replicator, and without loss of generality, let us suppose that it is always a positive number.

Example 1. For a random mating population let us recall the classical continuous-time, one-locus multi-allele viability selection model approximating the discrete-time model with non-overlapping generations. Let $\mathbf{A} := (a_{ij})_{i,j=1,\dots,n}$ be the fitness matrix where $a_{ij} > 0$ denotes the fitness of an $A_i A_j$ zygote. The average fitness of the whole population is $xW(x) := x\mathbf{A}x$ and the marginal fitness of the i -th allele is $W_i(x) := e_i\mathbf{A}x$, where e_i ($i = 1, \dots, n$) denotes the i -th basic vector.

Let us introduce the *relative advantage function of the replicators*

$$g : S_n \rightarrow \mathbb{R}^n, \quad g_i(x) := W_i(x) - xW(x). \tag{2}$$

One of the basic tenets of Darwinism says: if a replicator type has greater fitness than the average over the whole population then it will propagate. Thus, the sign of g_i indicates whether the relative frequency of an i -replicator increases or decreases. Using this notation, replicator dynamics (1) can be re-written in the following form

$$\dot{x}_i = x_i g_i(x) \tag{3}$$

Let us observe that, according to the replicator dynamics, the rate of increase of the frequency of an i -replicator is proportional to its frequency and its relative advantage over the whole population.

In what follows, only the interior rest point of the replicator dynamics (1) will be investigated, so we consider $x^* \in \text{int}S_n$ for which $g_i(x^*) = 0$ for all $i = 1, \dots, n$. Using the above condition, an easy calculation shows that the Jacobian matrix of the right-hand side of replicator dynamics (1) can be written as

$$\mathbf{L}_{x^*} = \mathbf{X}\mathbf{G}_{x^*} \tag{4}$$

where \mathbf{L}_{x^*} is the matrix of the linearization of the replicator equation (1) about x^* , \mathbf{G}_{x^*} is the Jacobian matrix of the relative advantage function of the replicators at x^* and \mathbf{X} is a diagonal matrix with entries $x_{ii} := x_i^*$. Now let us introduce a notion to be used later on: a matrix \mathbf{A} is said to be *T-negative definite*, if it is negative definite on the tangent space T of the simplex, i.e. if

$$\xi \mathbf{A} \xi < 0 \text{ whenever } \xi \in \mathbb{R}^n, \quad \sum_{i=1}^n \xi_i = 0 \text{ and } \xi \neq 0.$$

It is well known that the n -dimensional simplex is invariant with respect to the replicator dynamics (see e.g. [25]). Thus, it is a sufficient condition for the asymptotic stability of a rest point of the replicator dynamics that the matrix \mathbf{L}_{x^*} is *T-negative definite*. (It is easy to see that \mathbf{L}_{x^*} is *T*-invariant.)

Alternatively, the *T*-negative definiteness of \mathbf{G}_{x^*} or of the Jacobian of the fitness vector implies asymptotic stability. In the case of linear marginal fitness functions this reduces to the well-known fact that an interior ESS is asymptotically stable under the replicator dynamics.

3. Evolutionarily stable state

Now we recall a function that can be used to compare two states of a replicator population. For two replicator distributions $p, x \in S_n$, the *relative advantage of p over x* is defined as

$$\Psi_p : S_n \rightarrow \mathbb{R}, \quad \Psi_p(x) := pW(x) - xW(x) \tag{5}$$

where $W(x)$ denotes the marginal fitness vector. This notion was originally introduced in evolutionary game theory (see e.g. [14]). The quantity Ψ gives the difference between the fitness of a p -subpopulation and the average fitness of the whole population. In theoretical evolutionary biology the following notion is fundamental:

Definition 1. A state x^* is evolutionarily stable if the relative advantage of x^* over x is strictly positive whenever x is close enough to x^* .

See e.g. [19, 18, 15, 21]. It is well known that if a state x^* is evolutionarily stable then it is an asymptotically stable rest point of the replicator dynamics. For Fisher's model and the evolutionary game model see [13, 15, 25]; for the combination of these basic models (see Example 3 below), we refer the reader to [8], for the general non-linear case to [21]. It is well known that if a state x^* is evolutionarily stable then x^* is also a Nash equilibrium, i.e. $x^*W(x^*) \geq xW(x^*)$ for all $x \in S_n$. Furthermore, if $x \in \text{int}S_n$ then $x^*W(x^*) = xW(x^*)$ for all $x \in S_n$.

Obviously, $\Psi_p(x) = (p - x)g(x)$. Thus, the state x^* is evolutionarily stable if and only if it is a local minimum of the function $\Psi_{x^*}(x) = (x^* - x)g(x)$. If the state $x^* \in \text{int}S_n$ is a Nash equilibrium then we have $\text{grad}\Psi_{x^*}(x) = -g(x^*) = 0$. For the Hessian matrix of Ψ_{x^*} at x^* put $H\Psi_{x^*} = -(\mathbf{G}_{x^*} + \mathbf{G}_{x^*}^T)$. If $x^* \in \text{int}S_n$ is a regular ESS then $H\Psi_{x^*}$ is necessarily positive semi-definite on T . Later on, I will need two strengthened versions of Definition 1:

Definition 2. A state $x^* \in \text{int}S_n$ is said to be regular evolutionarily stable if $\text{grad}\Psi_{x^*}(x) = -g(x^*) = 0$ and the Hessian matrix at x^* $H\Psi_{x^*} = -(\mathbf{G}_{x^*} + \mathbf{G}_{x^*}^T)$ is T -negative definite.

Definition 2 has been introduced by Taylor & Jonker [24] who remarked that: "generically, every ESS is regular". In geometrical terms, regularity means that the function $\Psi_{x^*}(x) = (x^* - x)g(x)$ has a minimum at x^* and is strictly convex near x^* .

Definition 3. A Nash equilibrium state $x^* \in \text{int}S_n$ is said to be regular if \mathbf{G}_{x^*} is non-singular on the tangent space of S_n , i.e. $\mathbf{G}_{x^*}\xi \neq 0$ for all $\xi \in \mathbb{R}^n$, $\sum_{i=1}^n \xi_i = 0$ and $\xi \neq 0$.

Based on the non-singularity of the Jacobian of the pay-off, different regularity concepts for a Nash equilibrium of a game in normal form were also introduced in [12, 26] cf. [15].

Remark 1. Since $\xi\mathbf{G}_{x^*}\xi < 0$ implies that $\mathbf{G}_{x^*}\xi \neq 0$, each regular ESS is also a regular Nash equilibrium. The converse implication does not hold since for a non-symmetric matrix \mathbf{G}_{x^*} , $\xi(\mathbf{G}_{x^*} + \mathbf{G}_{x^*}^T)\xi \neq 0$ in general does not imply that $\mathbf{G}_{x^*}\xi \neq 0$.

Example 2. It is well known that for the linear fitness functions (i.e., when $W_i(x)$ is linear in x) an interior ESS is always regular (see [24, 11]). In Fisher's selection model and in the evolutionary matrix game the corresponding marginal fitness functions are linear.

Example 3. In this example let us consider a Mendelian population with a dominant-recessive inheritance system, in which n -alleles at a single locus uniquely determine n possible individual phenotypes and each pure phenotype is represented by a homozygote. This sexual population can realise all possible phenotypic

states ([7]). Let us consider an evolutionary matrix game in this Mendelian population. In this situation, the marginal fitness function of each allele is non-linear. For describing the terminal state of the evolution in this situation, the notion of evolutionarily stable allele distribution (ESAD) is defined ([8, 9]). Let us suppose that in phenotypic terms there exists a totally mixed terminal state of the evolution. (This means that there exists an interior ESS.) It is easy to see that if there exists a totally mixed ESS, and the inheritance system is the one defined above, then the interior ESAD is a regular ESS.

4. The variance of replicator fitness

For a state $x \in S_n$, the variance in fitness, namely, the variance of the marginal fitness of the replicators, is defined as follows

$$v : S_n \rightarrow \mathbb{R}, v(x) := \sum_{i=1}^n x_i [W_i(x) - xW(x)]^2. \tag{6}$$

This variance can be re-written in the following form:

$$v(x) = \sum_{i=1}^n x_i g_i^2(x). \tag{7}$$

The variance equals zero only at equilibrium and at other states it is strictly positive. This implies that the variance attains a minimum on S_n at each equilibrium state. This implies that $\text{grad}v(x^*) = 0$ (for $x^* \in \text{int}S_n$) and the Hessian matrix of the variance at equilibrium state is necessarily positive semi-definite on T . The question arises when the variance is *strictly* convex at its minimum point. The answer is given below.

Proposition 1. *If a state $x^* \in \text{int} S_n$ is a regular equilibrium then the variance of fitness is a strictly convex function on the simplex of frequency vectors at $x^* \in \text{int}S_n$.*

Proof. Using the formula (A1) of the Appendix (with $f_i(x) = x_i g(x)$ for $i = 1, \dots, n$) we get that the Hessian matrix \mathbf{V}_{x^*} of the fitness variance $v(x)$ at x^* is

$$\mathbf{V}_{x^*} = \mathbf{L}_{x^*}^T \mathbf{G}_{x^*} + \mathbf{G}_{x^*}^T \mathbf{L}_{x^*} \tag{8}$$

Using the symmetry of \mathbf{X} and equality (4) we obtain

$$\mathbf{L}_{x^*}^T \mathbf{G}_{x^*} = \mathbf{G}_{x^*}^T \mathbf{X}^T \mathbf{G}_{x^*} = \mathbf{G}_{x^*}^T \mathbf{X} \mathbf{G}_{x^*} = \mathbf{G}_{x^*}^T \mathbf{L}_{x^*}. \tag{9}$$

Thus, the matrix $\mathbf{L}_{x^*}^T \mathbf{G}_{x^*}$ is symmetric, which implies

$$\mathbf{V}_{x^*} = 2\mathbf{L}_{x^*}^T \mathbf{G}_{x^*} = \mathbf{G}_{x^*}^T \mathbf{X} \mathbf{G}_{x^*}. \tag{10}$$

The matrix \mathbf{V}_{x^*} is known to be positive semi-definite on T , so \mathbf{V}_{x^*} is positive definite with respect to the tangent space of the simplex if and only if the matrix \mathbf{G}_{x^*} is of full rank on T . Since $\mathbf{L}_{x^*} = \mathbf{X} \mathbf{G}_{x^*}$ has no zero eigenvalue associated with an eigenvector in T and \mathbf{X} is positive definite, \mathbf{G}_{x^*} restricted to T is of full rank. \square

Remark 2. From Remark 1 it follows that, if $x^* \in \text{int}S_n$ is a regular ESS, then at x^* the variance of the marginal fitness is strictly convex.

5. When does the variance decrease?

Now I am in a position to formulate the main result of this paper:

Theorem 1. *If an interior rest point x^* is a regular ESS then the variance of the fitness strictly decreases along all trajectories of the replicator dynamics near x^* .*

Proof. A sufficient condition for the strict decrease of the variance close to the rest point $x^* \in \text{int}S_n$ is that the variance is a strict local Ljapunov function for the replicator dynamics (1). This means that the derivative with respect to the dynamics (1) of the variance has to be negative near the rest point. Formally, we have to show that for the function $\Phi : S_n \rightarrow \mathbb{R}; \Phi(x) := \sum_{i=1}^n \left(\frac{\partial v(x)}{\partial x_i}\right) x_i g_i(x)$ we have $\Phi(x) < 0$ for all $x \neq x^*$ in some neighbourhood of $x^* \in \text{int}S_n$. If the function Φ has a strict maximum at $x^* \in \text{int}S_n$ and $\Phi(x^*) = 0$ then it is obviously locally negative definite at x^* . This maximality is guaranteed by the following two conditions. The first order necessary condition, $\text{grad}\Phi(x^*) = 0$, is satisfied since $\text{grad}v(x^*) = 0$ and $g(x^*) = 0$. The second order sufficient condition is that the Hessian matrix of $\Phi(x)$ at x^* has to be T -negative definite. In order to verify the latter condition, let \mathbf{H}_{x^*} denote the Hessian matrix of $\Phi(x)$ at x^* . Using formula (A1) of the Appendix we get

$$\mathbf{H}_{x^*} = \mathbf{V}_{x^*}\mathbf{L}_{x^*} + \mathbf{L}_{x^*}^T\mathbf{V}_{x^*}.$$

From equality (10), we get

$$\mathbf{H}_{x^*} = 2\mathbf{L}_{x^*}^T \left(\mathbf{G}_{x^*} + \mathbf{G}_{x^*}^T \right) \mathbf{L}_{x^*}.$$

Since $(\mathbf{G}_{x^*} + \mathbf{G}_{x^*}^T)$ is a T -negative definite matrix, it is enough to verify that if \mathbf{L}_{x^*} restricted to T is of full rank then \mathbf{H}_{x^*} is T -negative definite. Now, to arrive a contradiction, let us suppose that there exists a $\xi \in \mathbb{R}^n$ with $\sum_{i=1}^n \xi_i = 0$ and $\xi \neq 0$ such that $\mathbf{L}_{x^*}\xi = 0$, which can be rewritten as $\mathbf{L}_{x^*}\xi = \mathbf{X}\mathbf{G}_{x^*}\xi = 0$. The T -negativeness of \mathbf{G}_{x^*} implies that $\sigma := \mathbf{G}_{x^*}\xi \neq 0$. If $\mathbf{X}\mathbf{G}_{x^*}\xi = 0$ then $\mathbf{X}\xi = 0$, which contradicts the positive definiteness of \mathbf{X} on \mathbb{R}^n . Summing up: T -negativeness of \mathbf{H}_{x^*} implies the above negativity property of the function Φ . The latter means that if $x^* \in \text{int}S_n$ is a regular ESS then the variance of the fitness of the replicators is a negative definite Ljapunov function. □

Theorem 2. *Let us suppose that $x^* \in \text{int} S_n$ is an interior equilibrium and that the matrices \mathbf{G}_{x^*} and $(\mathbf{G}_{x^*} + \mathbf{G}_{x^*}^T)$ have no zero eigenvalue on T . If the variance of fitness decreases along all trajectories of the replicator dynamics near x^* , then x^* is a regular evolutionarily stable state.*

Proof. If the variance of fitness of the replicators strictly decreases along all trajectories of the replicator dynamics near an interior rest point then $\Phi(x) \leq 0$ for all $x \in S_n$ near x^* , so the Hessian of Φ at x^* i.e. $\mathbf{H}_{x^*} = 2\mathbf{G}_{x^*}^T\mathbf{X}(\mathbf{G}_{x^*} + \mathbf{G}_{x^*}^T)\mathbf{X}\mathbf{G}_{x^*}$ is T -negative semi definite. Since \mathbf{G}_{x^*} has no zero eigenvalue and \mathbf{X} is positive definite $(\mathbf{G}_{x^*} + \mathbf{G}_{x^*}^T)$ is T -negative semi definite, and hence also T -negative definite since it has no zero eigenvalue. □

6. Conclusions

Under a mild regularity assumption on the relative advantage function, a “second order fundamental theorem” for replicator selection is given: the variance of the fitness of the replicator strictly decreases along all trajectories of the replicator dynamics near a rest point if and only if this rest point is a regular evolutionarily stable state. This means that near to the “terminal state of the evolution” the fitness variance decreases independently of the starting point. From the mathematical viewpoint, Theorem 1 gives a new proof of the local asymptotical stability of a regular evolutionarily stable state, using the variance of marginal fitness as a local Ljapunov function. The main point is that the Ljapunov function proposed here appears to be biologically interpretable. In the background of this result are the mathematical forms of the replicator dynamics (2) and the fitness variance (7). I note that the regularity assumptions are valid in the overwhelming majority of cases of non-linear marginal fitness functions.

Finally, I would like to point out that while Fisher’s fundamental theorem holds only for symmetric matrices, or those fitness functions that are Shahshahani gradients ([13] ch.24.), the “second order fundamental theorem” also applies to non-symmetric matrices, and non-linear fitness functions.

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Appendix

Calculus. The Hessian matrix of the product of two functions can be given as follows: let $f, g : \mathbb{R}^n \rightarrow \mathbb{R}^n$ be two vector-vector functions and let h be their scalar product $h : \mathbb{R}^n \rightarrow \mathbb{R}$, $h(x) := f(x)g(x)$. Let \mathbf{H}_x denote the Hessian matrix of the function h at x , formally $\mathbf{H}_x := \left(\frac{\partial^2 h(x)}{\partial x_i \partial x_j} \right)_{i,j=1,\dots,n} \in \mathbb{R}^{n \times n}$. Let $\mathbf{F}_x := \left(\frac{\partial f_i(x)}{\partial x_j} \right)_{i,j=1,\dots,n} \in \mathbb{R}^{n \times n}$ and $\mathbf{G}_x := \left(\frac{\partial g_i(x)}{\partial x_j} \right)_{i,j=1,\dots,n} \in \mathbb{R}^{n \times n}$ be the Jacobian matrix of the functions f and g , respectively. Now let us consider $x^* \in \mathbb{R}^n$ with $f(x^*) = 0$ and $g(x^*) = 0$. An easy calculation shows that

$$\frac{\partial^2 h(x^*)}{\partial x_i \partial x_j} = \sum_k \frac{\partial f_k(x^*)}{\partial x_i} \frac{\partial g_k(x^*)}{\partial x_j} + \sum_k \frac{\partial f_k(x^*)}{\partial x_j} \frac{\partial g_k(x^*)}{\partial x_i}.$$

So, matrix \mathbf{H}_{x^*} is given by

$$\mathbf{H}_{x^*} = \mathbf{F}_{x^*}^T \mathbf{G}_{x^*} + \mathbf{G}_{x^*}^T \mathbf{F}_{x^*}. \quad (\text{A1})$$

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