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Energy Lyapunov Function for Generalized Replicator Equations

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Abstract

Replicator dynamics is an evolutionary strategy well established in different disciplines of biological sciences. It describes the evolution of self-reproducing entities called replicators in various independent models of, e.g., genetics, ecology, prebiotic evolution, and sociobiology. Besides this, replicator selection has been applied to problem solving in combinatorial optimization and to learning in neural networks and also in fluid mechanics, game and laser theory. So, the replicator systems arising in an extraordinary variety of modeling situations. In this report I'll introduce the new class of generalized replicator equations with nonlinear response functions and construct Energy Lyapunov function for this system. Tsallis entropy is considered as an example.

1 An Overview and Introduction

A *replicator* is a fundamental unit in evolutionary processes, representing a population *type*, and characterized by two attributes: $p_i(t)$, its proportion in the population at time t, and its non-negative fitness at time t. A replicator's fitness is a measure of its significance to the future evolution of the population. The proportions of replicators in a population change as a result of their mutual interactions, and their relative fitnesses.

The founding fathers of evolutionary genetics, Fisher, Haldane and Wright used mathematical models to generate a synthesis between Mendelian genetics and Darwinian evolution. Kimura's theory of neutral evolution, Hamilton's kin selection and Maynard Smith's evolutionary game theory are all based on mathematical descriptions of evolutionary dynamics. Concepts like fitness and natural selection are best defined in terms of mathematical equations.

Replicator dynamics is an evolutionary strategy well established in different disciplines of biological sciences. It describes the evolution of self-reproducing entities called replicators in various independent models of, e.g., genetics, ecology, prebiotic evolution, and sociobiology.

The notion of a *replicator* – originally invented by Dawkins [6] – is now used in biology for "*an entity that passes on its structure largely intact in successive replications*" [33]. The origin of life is characterized by the emergence of heritable information that, through the interplay of selection and variation, leads to Darwinian evolution.

Very recently the interest in evolutionary dynamical models has increased dramatically, mainly because in the game theoretic literature it is commonly thought that such models can provide a better understanding of the Nash equilibrium solution concept than traditional static game theory, as well as a description of the non-equilibrium behavior of the players. The replicator dynamics, introduced into the literature by Taylor and Jonker [30] for the special case of two player games in the late seventies of our century, is the classical example of such an evolutionary dynamical model.

Throughout last century the formal analogies between the mathematical models in population dynamics and certain models of different physical or chemical processes have been a source of inspiration both for biologists and physicists. As early as in 1911 Sharpe and Lotka [26] made an analogy between the stable age structure of human populations and an acoustical problem.

Autocatalytic reaction networks which in general involve two classes of catalytic processes – autocatalytic instruction for reproduction and additional material and process specific catalysis – were postulated as models for studies of prebiotic and early biological evolution scenarios [7,8]. In the last decade it turned out that they serve also as models in very different fields like molecular biology, population genetics, theoretical ecology or dynamical game theory [25]. A variety of self-replicating chemical systems have been constructed and investigated experimentally in the past 25 years since Spiegelman's [27].
Besides this fundamental importance in theoretical biology, replicator selection has been applied to

problem solving in combinatorial optimization and to learning in neural networks [3, 15]. Recent results show that the same type of differential equations is also obtained by non-linear coordinate transformations from models in fluid mechanics and laser theory [4].

Recently there has been increasing interest in a more general class of dynamical systems which describe selection consistent with the relative fitness of the strategies, see for example [10, 13].

So, it is clear that replicator systems are a class of first order, nonlinear differential equations, arising in an extraordinary variety of modeling situations.

Recently it has been shown by A. Menon [15] that any first order differential equations model can be non-trivially related to a replicator model.

In this report I'll introduce the new class of generalized replicator equations with nonlinear response functions and construct Energy Lyapunov function for this system.

2 Generalized Replicator Equations

First replicator-like equation was introduced by Fisher [9], who immediately recognized certain formal analogies between the mechanistic models introduced by Boltzmann [2] to analyse physical systems, and the selection models proposed by Darwin [5] to explain adaptation in biological systems. By considering the dynamical system which describes the changes in gene frequency of the population which occurs under natural selection, Fisher proved a directionality theorem, which he called the fundamental theorem of natural selection.

The absolute fitness of the zygote $\boldsymbol{A}_i\boldsymbol{A}_j$, denoted as w_{ij} is defined as the relative or fractional number of offspring per unit time that the genotype will produce that will grow to maturity and themselves reproduce.

The state of the genetical system at time t is simply the vector $p(t)=(p_1(t),\ldots,p_n(t))$, which is clearly constrained to lie in the standard simplex σ in n-dimensional Euclidean space $\mathbb{R}^n$:

$$\sigma=\left\{p\in\mathbb{R}^n : p_i\geq 0,\quad i=1,...,n,\ \mathbf{e}^T p=1\right\}.$$

Here and in the sequel, the letter **e** is reserved for a vector of appropriate length, consisting of unit entries $\left(\text{hence } \mathbf{e}^T p=\sum_{i=1}^n p_i\right)$. The original Fisher's selection equation of haploid genotypes evolution is, then, written as:

$$\dot{p}_i = p_i\left(\sum_{j=1}^n w_{ij}p_j-\sum_k\sum_j w_{kj}p_k p_j\right)\quad i=1,...,n \qquad (1)$$

where the dot is derivative w.r.t. time. The population state is then given as a point in simplex σ. Fisher took into account only zygote fitness. In this case $w_{ij}=w_{ji}$ i.e. matrix $W=(w_{ij})=W^T$. The difference between symmetric and nonsymmetrical matrices W is crucial. Indeed in the symmetric case the quadratic form $p(t)^T Wp(t)$ is increasing along trajectories of the selection dynamics (1) – this is the Fundamental Theorem of Selection going back to R. A. Fisher.

Theorem 1 (Fisher [9]) *If $W=W^T$ then the function $p(t)^T Wp(t)$ is strictly increasing with increasing t along any non-stationary trajectory $p(t)$ under (1). Furthermore, any such trajectory converges to a stationary point.*

Fisher claimed that the theorem was an analog of Boltzmann's principle of entropy increase, and thus to be an analog of the Second Law. These claims have later been re-evaluated.

This theorem is tantamount to saying that mean fitness is an Energy Lyapunov function of the dynamical system (1). Let me recall that a single–valued function which is continuous and has continuous partial derivatives is called the Energy Lyapunov function (ELF) for dynamical system if it is monotonically increasing along the trajectories of this dynamical systems [16]. So, if we know ELF for dynamic system under consideration then we know practically everything about evolution of this system.

In 1969 V.A. Ratner [23] showed that if we take into account also gamete selection when the fitness matrix $G=DW$, where $D=diag(d_i)$ is diagonal matrix with $d_i>0$ and W is symmetrical matrix. In this case Fisher's theorem is a false. But, it was shown by Pykh [19, 22] that there exists an analog of Fisher's theorem. Let us denote by $\langle\cdot,\cdot\rangle$ the inner product of the two vectors.

Theorem 2 (Pykh [21]) *If matrix G has the next form: $G=D_1BD_2$, where B is symmetrical, D_1 and D_2 are diagonal matrices and matrix $D=D_1^{-1}D_2>0$ then the function $E:\sigma\to\mathbb{R}^1$*

$$E(p)=\frac{p^T D_2BD_2p}{\langle d,p\rangle^2} \qquad (2)$$

is ELF for system (6). □

It is obvious that equations (1) as well as Fokker-Planck, Frobenius-Perron and Master equations belong to a class of so-called evolution equations for probability densities (EPD). In this report I try to introduce the more general form of the evolution equations in the class of ordinary differential equation. From my point of view this equation should have the next form:

$$\dot{p}_i = h(p)\left(\varphi_i(p) - \frac{\psi_i(p)}{\sum_{j=1}^{n}\psi_j(p)}\sum_{j=1}^{n}\varphi_j(p)\right) \quad i = 1,\dots,n \quad (3)$$

where $p \in \sigma$, and functions φ_i and $\psi_i : \sigma \to \mathbb{R}^1_+$ satisfy the next conditions:

$$\varphi_i(p) \geq 0,\ \psi_i(p) = 0,\ h(p) > 0 \text{ if } p \in \sigma^i \ i = 1,\dots,n \quad (4)$$

where $\sigma^i = \{p : p \in \sigma,\ p_i = 0\}$ is the face of σ corresponding to the number i. Naturally, we suppose what $\sum_{j=1}^{n}\psi_j(p) > 0$ when $p \in \sigma$. From relations (4) and the fact that $\sum_{i=1}^{n}\dot{p}_i \equiv 0$ on the simplex σ it follows that σ is a forward invariant set of system (3).

If we put $\psi_i(p) = p_i$, $h(p) = 1$, then from (3) we receive EPD proposed by Pykh [18]:

$$\dot{p}_i = \varphi_i(p) - p_i\sum_{j=1}^{n}\varphi_j(p) \qquad i = 1,\dots,n$$

If we put $\psi_i(p) = p_i$, $\varphi_i(p) = p_i g_i(p)$, $h(p) = 1$ then we receive replicator equation which has been introduced into game theory by Taylor and Jonker [30]:

$$\dot{p}_i = p_i\left(g_i(p) - \sum_{j=1}^{n}p_j g_j(p)\right) \qquad i = 1,\dots,n$$

In this report we'll restrict our consideration with special case when

$$\varphi_i(p) = f_i(p_i)\sum_{j=1}^{n}w_{ij}f_j(p_j) \qquad i = 1,\dots,n$$

$$\psi_i(p) = f_i(p_i)$$

where

$$f_i(0) = 0$$

$$\partial f_i / \partial p_i > 0$$

$W = (w_{ij})$ - the interaction matrix.

In this case the equation (3) takes the form:

$$\dot{p}_i = h(p)f_i(p_i)\left(\sum_{j=1}^{n}w_{ij}f_j(p_j) - \theta^{-1}(p)\sum_{jk}w_{jk}f_j(p_j)f_k(p_k)\right) \quad (5)$$

where $\theta(p) = \sum_{i=1}^{n}f_i(p_i) = \langle \mathbf{e}, f(p)\rangle$.

Note that if $f_i(p_i) = p_i, h(p) = 1$ then we receive Fisher's equation (1). It is clear that equations (5) are replicator equations with non-linear response functions [12, 28, 29]. We'll title equations (5) as generalized replicator equations (GRF).

3 Fixed Points

For the next it'll be convenient to use matrix notation. In these terms equations (5) take the form

$$\dot{p} = h(p)\mathcal{D}(f)\left(Wf - \mathbf{e}\theta^{-1}(p)\langle f, Wf\rangle\right) \quad (6)$$

where $\mathcal{D}(f) = diag(f_1(p_1),\dots,f_n(p_n))$.

We'll say that fixed point $\hat{p}$ of equation (6) is nontrivial if $\hat{p} \in \mathrm{Int}\sigma$.

Theorem 3 *The system (6) has a unique nontrivial (interior) equilibrium* $\hat{p} \in \mathrm{Int}\sigma$ *if and only if* $W^{-1}\mathbf{e}$ *is either strictly positive or strictly negative.*

Proof: If $\hat{p}$ is nontrivial fixed point let us denote $\hat{f} = (f_1(\hat{p}_1),\dots,f_n(\hat{p}_n))$. The reader will easily prove that from equation $\dot{p} = 0$ directly follows that

$$\frac{\hat{f}}{\langle \hat{f}, \mathbf{e}\rangle} = \frac{W^{-1}\mathbf{e}}{\langle \mathbf{e}, W^{-1}\mathbf{e}\rangle}. \quad (7)$$

This completes the proof. □

It is easily to receive the equation for $\hat{p}$ from (7). Let us denote vector $W^{-1}\mathbf{e}$ by q, i.e.

$$q = W^{-1}\mathbf{e}$$

and consider an auxiliary system:

$$f_i\left(\hat{p}_i\right) = \lambda q_i \qquad i = 1,\dots,n \tag{8}$$

where λ is an auxiliary parameter.

It is obvious from definition that $q_i > 0 \quad i = 1,\dots,n$, therefore

$$\hat{p}_i = f_i^{-1}\left(\lambda q_i\right) \qquad i = 1,\dots,n \tag{9}$$

where $f_i^{-1}(\cdot)$ denotes the local inverse branch of f_i. Take into account that $\langle \hat{p}, \mathbf{e} \rangle = 1$ we receive equation for λ:

$$\sum_{i=1}^{n} \hat{f}_i^{-1}\left(\lambda q_i\right) = 1 \tag{10}$$

Thus equations (9) and (10) give us the unique nontrivial fixed point of the system (6). Evidently, that we can apply Theorem 3 to all faces of the simplex σ and hence receive all fixed points of the system (6).

Note that for the verifying the inequality $W^{-1}\mathbf{e} > 0$ it is possible to use Hawkins-Simon condition [11] or Spectral Radius condition [17].

4 Lyapunov Function for GRF

The Lyapunov function method is mostly used to study convergence and stability of a dynamic system. Using this method, the evolution of this system is related to the arising to a maximum of such Lyapunov function. Note also that Lyapunov function can in turn be used to derive bounds on various robust performance measure of the system under consideration. Such a function assigns a number to each possible global state of the dynamical system in such a way that as the system changes state over time, the value of the function continually increases.

In this way, Pykh [19, 20, 21, 22] presents two types of ELF: fitness-like and entropy-like Lyapunov functions for generalized Lotka-Volterra and Fisher's equations. The main aim of this paper is to present fitness-like Lyapunov function for generalized replicator equation.

Theorem 4 *If matrix W is symmetrical, then the function*

$$E_f\left(p\right) = \frac{\left\langle f\left(p\right), Wf\left(p\right)\right\rangle}{\theta^2\left(p\right)} \tag{11}$$

increases along all solutions of the system (6) outside the fixed points i.e. this function is ELF for system (6).

Proof: Let us calculate the derivative of $E_f\left(p\right)$ along solutions of system (6). For $\operatorname{grad} E_f\left(p\right)$ we receive:

$$\operatorname{grad} E_f\left(p\right) = \frac{2}{\theta^2\left(f\right)} \mathcal{D}\left(\frac{\partial f}{\partial p}\right)\left(Wf - \mathbf{e}\frac{\left\langle f, Wf\right\rangle}{\theta\left(f\right)}\right)$$

where $\mathcal{D}\left(\dfrac{\partial f}{\partial p}\right) = \operatorname{diag}\left(\partial f_1/\partial p_1,\dots,\partial f_n/\partial p_n\right)$.

It can be seen now that (6) may be given the form

$$\dot{p} = G\left(f\left(p\right)\right)\operatorname{grad} E_f\left(p\right) \tag{12}$$

where the $G\left(f\left(p\right)\right)$ are

$$G\left(f\left(p\right)\right) = h\left(p\right)\mathcal{D}\left(f\right)\frac{\theta^2\left(f\right)}{2}\mathcal{D}^{-1}\left(\frac{\partial f}{\partial p}\right) > 0.$$

This implies that the derivative of E_f along the solution of (6) is nonnegative, i.e. $\dot{E}_f\left(p\left(t\right)\right) \geq 0$, and the set $\dot{E}_f\left(p\right) = 0$ consist only of equilibria. □

Note that from this theorem it follows that the system (6) is "linear-gradient system" [14].

Now we can formulate stability theorem.

Theorem 5 *If system (6) has the nontrivial fixed point $\hat{p} \in \operatorname{Int}\sigma$, then the necessary and sufficient condition for the point $\hat{p}$ to be global stable in $\operatorname{Int}\sigma$ is that the matrix W has $(n-1)$ negative eigenvalues.*

Proof: From Lyapunov stability theory it follows that the fixed point $\hat{p}$ is global stable in $\operatorname{Int}\sigma$ if the function

$$\left(E_f\left(p\right) - E_f\left(\hat{p}\right)\right)$$

is negative in $\operatorname{Int}\sigma$. Let us consider the normalized transformation [21] defined by the next formula

$$x_i\left(p\right) = f_i\left(p\right)/\theta\left(p\right) \qquad x\left(p\right) \in \sigma. \tag{14}$$

Later this transformation was introduced as "twisted" or "escort" distribution [1, 32].

Hence we can represent function $E\left(p\right)$ in the form

$$E_f(p) = \langle x(p), Wx(p) \rangle \qquad (15)$$

It was shown by Pykh [18, 21] that square-form on the simplex σ is negative-defined if it's matrix has $(n-1)$ negative eigenvalues. □

5 Equivalence Theorem and Power Law Distributions

We have been interested to find the conditions when the normalized transformation (14) has a one-to-one inverse. It will be reasonable if we try to find inverse transformation in the next form:

$$p_i = \frac{\eta_i(x_i)}{\vartheta(x)}, \qquad \vartheta(x) = \sum_{i=1}^{n} \eta_i(x_i) \qquad (16)$$

where unknown functions $\eta_i : [0,1] \to \mathbb{R}_+^1, \ \ i = 1,\dots,n.$

Theorem 6 The system of equations (14) and (16) has unique solution $\eta(x) = (\eta_1(x_1)),\dots,\eta_n(x_n)$ if and only if the functions $f_i(p_i)$ has the next power-law form

$$f_i(p_i) = d_i p_i^{\alpha}$$

where $d_i > 0, \ \ i = 1,\dots,n, \ \ \alpha > 0.$

Proof: From (14) and (16) we receive the next system of functional equations:

$$x_i = \frac{f_i\left(\eta_i(x_i)\vartheta^{-1}(x)\right)}{\sum_{j=1}^{n} f_j\left(\eta_j(x_j)\vartheta^{-1}(x)\right)} \qquad i = 1,\dots,n \qquad (17)$$

It is obvious that the solution of this system have to satisfy the next conditions:

$$f_i\left(\eta_i(x_i)\vartheta^{-1}(x)\right) = \gamma\left(\vartheta^{-1}(x)\right)x_i \qquad i = 1,\dots,n \qquad (18)$$

where the function $\gamma : \mathbb{R}_+^1 \to \mathbb{R}_+^1$. System (18) is the generalized functional Cauchy equation and it has the unique solution only if $f_i(p_i) = d_i p_i^{\alpha}$. In this case $\eta_i(\cdot) = f_i^{-1}(\cdot)$ i.e.

$$\eta_i(x_i) = d_i^{-\frac{1}{\alpha}} x_i^{\frac{1}{\alpha}} \qquad i = 1,\dots,n.$$

From here we receive for the inverse transformation:

$$p_i = \frac{d^{-\frac{1}{\alpha}} x_i^{\frac{1}{\alpha}}}{\vartheta(x)}, \quad \vartheta(x) = \sum d_i^{-\frac{1}{\alpha}} x_i^{\frac{1}{\alpha}}$$

This complete the proof. □

6 Example

Let us consider the next generalized replicator equation:

$$\dot{p}_i = \frac{1-q}{q} p_i^{1-q} \left(p_i^{1-q} - \theta^{-1}(p) \sum_{j=1}^{n} p_j^{2(1-q)} \right) \ i = 1,\dots,n \quad (19)$$

where $q < 1$. It is clear that this system of equations corresponds to the system (5), if we put $f_i(p_i) = p_i^{1-q}$, $W = I$, $h(p) = (1-q)/q$. Very interesting fact that Tsallis entropy [31]:

$$S_q = \left(\sum_{i=1}^{n} p_i^q - 1 \right) \Big/ (1-q)$$

is the Energy Lyapunov function for the system (19). Really, it is easy to prove that if we calculate the derivative of $S_q(p)$ along the solutions of the system (19), then

$$\frac{d}{dt} S_q(p) = \theta(p) \left(1 - n\, \theta^{-2} \sum_{j=1}^{n} p_j^{2(1-q)} \right) \geq 0.$$

Note, that this statement is true also when $q > 1$, but in this case the system (19) is not the generalised replicator equation, and it is defined only in the $\mathrm{Int}\sigma$.

7 Problems

1. To construct fitness-like Energy Lyapunov function for generalized replicator equation in the case when interaction matrix W is nonsymmetrical.

2. To construct entropy-like Energy Lyapunov function for system (6) with stable nontrivial fixed point.

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