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LYAPUNOV FUNCTIONS FOR LOTKA-VOLTERRA SYSTEMS: AN OVERVIEW AND PROBLEMS

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Abstract: The biggest advantage of Lyapunov's function method is that it is "direct", as "increase along orbits", hence one does not need to solve the equation explicitly. The main goal of this paper is to give the short overview of the existing two types: fitness-like and entropy-like Lyapunov functions for generalized Lotka-Volterra systems and to discuss correspondence between the structure of the interaction matrix and these Lyapunov functions. Special attention will be given in case the interaction matrix $A = D_1 B D_2$ where D_1 and D_2 are diagonal matrix, B is symmetrical matrix and to the set of diagonal-symmetrizable matrix.

Keywords: Lotka-Volterra, Lyapunov functions, *D*-symmetrizable.

"Stability is an absolutely universal attribute of nature and therefore it has to be reflected in the basis laws of nature. If the knowledge can be constructed on the basis of small perturbations then scientific thinking could be based on some type of Lyapunov function. In any case this function always exists from postulate of stability".

Chetaev, 1936

1. GENERALIZED LOTKA-VOLTERRA SYSTEMS

A standard mathematical model for the joint evolution of n biological species with spatially homogeneous densities $N_i(t)$ $(i = 1,...,n)$ is the generalized Lotka-Volterra (GLV) food chain systems Pykh (1981a, 1981b, 1983).

$$\dot{N}_i = g_i(N_i)(b_i - r_i(N_i) - \sum_{j=1}^{n} a_{ij} f_j(N_j)), \qquad (1)$$

where:

$$\left.\begin{array}{c} N_i \geq 0, \quad i=1,...,n \\ \partial f_i(N_i)/\partial N_i > 0, \text{when } N_i > 0, \\ g_i(0)=0, \quad i=1,...,n, \\ g_i(N_i)>0 \quad \text{when } N_i>0, \quad i=1,...,n \\ r_i(0)=0 \end{array}\right\} \quad (2)$$

The functions $(b_i - r_i(N_i))$ are the intrinsic or decay rates, and the a_{ij} describe the effect of the j -th population upon the i -th population, which is positive if it enhances and negative if it inhibits the growth. All sorts of interactions can be modeled in this way, including the case when the influence of every species upon the growth rates is nonlinear. The matrix $A=(a_{ij})$ is then called the ***interaction matrix***. If the functions $g_i(N) \equiv f_i(N_i) \equiv N_i \quad r_i(N_i) \equiv 0$ and then we obtain classical Lotka-Volterra (CLV) systems:

$$\dot{N}_i = N_i(b_i - \sum_{j=1}^{n} a_{ij} N_j) \qquad (3)$$

During the past few decades, a lot of work has been done on the problem of stability-complexity relationship in ecosystems model, especially in the case of interactions of predator-prey type, described by the GLV. These kind of equations are of great interest not only for population dynamics or in chemical kinetics, but there importance in ecological modeling and all fields of science, from plasma physics to neural nets. Moreover, the equivalence between the so-called S-systems, i.e., systems of non-linear differential equations which have a wide range of applicability to physical, chemical and biological problems and the Volterra systems has been demonstrated by Hernando-Bermejo (1995).

As an effect of this equivalence, the analytical results obtained in the frame of GLV are of interest not only in the field of mathematical ecology but also in other apparently non-related fields.

It was shown by Pykh (1981a,1983) that GLV systems are equivalent to a pseudo-linear system of differential equations with a matrix preserving its eigenvalues.

Theorem 1. Let $r_i(N_i) \equiv 0, i=1,...,n,$. If the system (1) has equilibrium point $\hat{N}=(\hat{N}_1,...,\hat{N}_n) \in Int\mathbb{R}_+^n$ then there exists a diffeomorphism $\varphi : \mathbb{R}_+^n \to R^n$

$$N=\varphi(x), \qquad x=\varphi^{-1}(N)$$

such that the system (4) is diffeomorphic to the next system:

$$\dot{x} = -\Phi(x)\hat{A}\Phi^{-1}(x)x \qquad x \in R^n \qquad (4)$$

where R^n is an open subset in $\mathbb{R}^n$, and $\Phi(x) \in Int\mathbb{D}_n^+$, where $\mathbb{D}_n^+$ is the set of nonnegative diagonal matrices, $\hat{A} = A\Psi(\hat{N}), \;\; \Psi(\hat{N}) \in Int\mathbb{D}_n^+$.□

It is clear that all eigenvalues of matrix $\Phi(x)\hat{A}\Phi^{-1}(x)$ are independent of values of vector $x \in R^n$.

Example. It is easily shown that in the case of classical Lotka-Volterra system equations (3) take the form:

$$\dot{x}_i = -(1-x_i)\sum_{j=1}^{n} a_{ij}\hat{N}_j(1-x_j)^{-1}x_i \qquad x \in R^n$$

where $R^n = \{x : x_i < 1, i=1,...,n\}$,

$N_i = \hat{N}_i/(1-x_i)$,

$x_i = (1-\hat{N}_i)/N_i, \qquad i=1,...,n.$

Next important model in theoretical population ecology is the generalized Fisher equations (Pykh 1983):

$$\dot{p}_i = p_i(g_i(p) - \theta(p)) \qquad i=1,...,n \qquad (5)$$

where $p = col(p_1,...,p_n)$ is an n dimensional state vector defined on the unit simplex:

$$\sigma = \left\{ p : \sum_{i=1}^{n} p_i = 1, p \geq 0 \right\},$$

$g_i(p)$ is the fitness of i-th phenotype, and $\theta(p) = \sum_{i=1}^{n} p_i g_i(p)$ is the mean fitness of population. Systems (5) also known as replicator equation. Good survey of the subject has been made by Sigmund (1998).

The classical Fisher's model could be obtained from (5) if the functions $g_i(p)$ are linear:

$$g_i(p) = \sum_{j=1}^{n} g_{ij} p_{j.}$$

that is

$$\dot{p} = P(G(p) - e\theta(p)) \qquad (6)$$

where $P = diag(p_1,...,p_n)$ is $n \times n$ diagonal matrix, $e = col(1,...,1), G = (g_{ij})$ is an $n \times n$ fitness matrix and $\theta(p) \equiv pGp^T \equiv \langle p, Gp \rangle$ is the population fitness.

Pykh (1981a, 1983) showed that for each system (6) there exists Lotka-Volterra equation with a flow-invariant hyperplane. In particular it is shown that if vector $\hat{q}$ satisfies the equation $\hat{q}^T G = \langle \hat{q}, e \rangle \hat{\theta} e^T$ i.e. vector $\hat{q}$ is dual in relation to the vector $\hat{p}$ then function:

$$h(p, M, t) = \sum_{i=1}^{n} \hat{q}_i \ln p_i + \langle e, \hat{q} \rangle \ln M - \langle e, \hat{q} \rangle \hat{\theta} t$$

is the first integral of extended generalized Fisher's system:

$$\dot{p} = P(Gp - e\theta(p)),$$
$$\dot{M} = M\theta(p).$$

where M is total population density.

In other words along any trajectories of this system $h(p, M, t) \equiv const$. Without loss of generality it may be assumed that $\langle e, \hat{q} \rangle = 1$. It is clear that in steady-state $\hat{\theta} = 0$ and if $\hat{q} \in Int\sigma$ then we receive the conservation law:

$$I(p(t), \hat{q}) - \ln M(t) = const$$

where $I(p, \hat{q})$ is the relative entropy (Kullback, et. al. 1951) of distributions p and $\hat{q}$.

2. ENERGY LYAPUNOV FUNCTIONS FOR GENERALIZED LOTKA-VOLTERRA AND FISHER'S EQUATIONS

A Lyapunov function is some kind of mathematical quantity that is maximized by a particular dynamical system as it changes according to whatever rules it works by. A general methodology in the stability analysis of an equilibrium of a nonlinear dynamical system is to find a suitable Lyapunov function. This is in general a very difficult task, but for mechanical systems there often is a natural candidate Lyapunov function, namely the energy function.

The most important feature of Lyapunov's direct method cannot be overemphasized: the method does not require any knowledge about the precise time evolution of the ecosystems; the mere existence of a bounded function that is increasing along every solution suffices to characterize the system's long-time behavior. As a consequence, one can analyze the long-time dynamics of an ecosystem without actually solving its equations of dynamics. The existence of a Lyapunov function is thus of great conceptual as well as technical importance.

Lyapunov's method suffers, however, from one serious flaw: no systematic technique is known to decide whether a dynamical system admits a Lyapunov function or not. Finding Lyapunov functions requires experience, intuition, and luck. Fortunately, a wealth of knowledge on both practical and theoretical issues has been accumulated over the years.

A single–valued function $E(N)$ which is continuous and has continuous partial derivatives is called the Energy Lyapunov function (ELF) for dynamical system (Meyer, 1968) if it is monotonically increasing along the trajectories of this dynamical systems. So, if we know ELF for dynamic system under consideration then we know practically everything about evolution of this system.

For generalized L-V system two main types of ELF exist.

Theorem 2. (Pykh, 1981b, 1983) If matrix A has the next form: $A = D_1 B D_2$, where B is symmetrical, D_1 and D_2 are diagonal matrices and matrix $D = D_1^{-1} D_2 \geq 0$, then the function:

$$E(N) = b^T D f(N) - \frac{1}{2} f^T(N) D_2 B D_2 f(N) - \sum_{i=1}^{n} d_i \int_0^{N_i} \left(r_i(x) \frac{df_i(x)}{dx} \right) dx, \quad (7)$$

is ELF for system (1). □

Evidently that function (7) is similar to well known Lur'e – Postnikov function: square form plus integral from nonlinearity. Note that function (7) is more general than the similar function proposed later by Cohen and Grossberg (1983).

Corollary. Let the conditions of Theorem 2 be satisfied. If system (1) has equilibrium point $\hat{N} \in Int\mathbb{R}_+^n$ and matrix:

$$\hat{B}_r = D_2 B_2 D_2 + diag\left(d_i \left(\frac{\partial r_i}{\partial N_i}\right)\left(\frac{\partial f_i}{\partial N_i}\right)^{-1}_{N=\hat{N}} \right)$$

is positive definite, then there exist a region $\Omega \ni \hat{N}$ where the equilibrium $\hat{N}$ is asymptotically stable. □

Theorem 3. (Pykh, 1981b, 1983) If system (1) has equilibrium point $\hat{N} \in Int\mathbb{R}_+^n$ and the matrix

$$-A_r(N) = -A - diag\left(\frac{\hat{r}_i - r_i(N_i)}{\hat{f}_i - f_i(N_i)} \right)$$

is D-dissipative with matrix D=diag(d_i) i.e. $N^T D A_r(N) N \geq 0, \quad \forall N \in \mathbb{R}_+^n$ then the function:

$$E_d(N) = \sum_{i=1}^{n} d_i \int_{\hat{N}_i}^{N_i} \frac{\hat{f}_i - f_i(x_i)}{g_i(x_i)} dx \quad (8)$$

is ELF for system (1). □

Corollary. If matrix $-A_r(N)$ is positive *D*-dissipative i.e. $D = diag(d_i) > 0,$ then equilibrium point $\hat{N}$ is globally stable in $\mathbb{R}^n_+$. □

So, for a wide class of interaction matrices *A* we find two types of ELF. More clearly it follows from the example of classical Lotka – Volterra systems that

$$r_i(N) \equiv 0, \qquad f_i(N_i) \equiv g_i(N_i) \equiv N_i$$

In this case from (7) and (8) we obtain:

$$E = b^T DN - \frac{1}{2} N^T D_2 BD_2 N \quad \text{(Mac Arthur, 1969)}$$

$$E_d = -\sum_{i=1}^{n} d_i (N_i - \hat{N}_i \ln N_i) \quad \text{(Volterra, 1931)}$$

It's clear that function E_d is very similar to the generalized Boltzmann entropy (Chakrabarti 1997):

$$S_g = K \sum_{i=1}^{n} \left[(N_i - \hat{N}_i) - N_i \ln \frac{N_i}{\hat{N}_i} \right]$$

and the only difference is coefficients d_i which we may consider as weighing coefficients taking into account the traits of population under consideration.

As I pointed out above there exists an equivalence relationship between systems (3) and (6). Therefore we may expect that for system (6) there exists ELF by analogy with Theorems 2 and 3. This has been shown to be true (Pykh, 1983).

Theorem 4. (Pykh 1983) If matrix G has the next form: $G = D_1 BD_2$, where *B* is symmetrical, D_1 and D_2 are diagonal matrices and matrix $D = D_1^{-1} D_2 > 0$ then the function $E : \sigma \to \mathbb{R}^1$

$$E(p) = \frac{p^T D_2 BD_2 p}{\langle d, p \rangle^2} \qquad (9)$$

is ELF for system (6). □

Corollary. Let the conditions of Theorem 4 be satisfied. If system (6) has equilibrium point $\hat{p} \in Int\sigma$ and $\theta(\hat{p}) > 0,$ then necessary and sufficient condition for the point $\hat{p}$ to be globally stable in $Int\sigma$ is that the matrix *B* has $(n-1)$ negative eigenvalues. □

In order to formulate the next theorem I need the following definition.

Definition. Matrix *G* is called *D*-dissipative on $\sigma^0 = \left(x : \sum_{i=1}^{n} x_i = 0, -\hat{p}_i \le x_i \le 1 - \hat{p}_i, \quad i = 1,...,n \right)$ if there exists such diagonal matrix *D* that $x^T ADx < 0$ for $x \in \sigma^0$, and positive D-dissipative if $D = diag(d_i) > 0.$ □

Theorem 5. (Pykh, 1983) If system (6) has the equilibrium point $\hat{p} \in Int\sigma$ and the matrix *G* is positive *D*-dissipative on σ^0 with the matrix $D^{-1} = diag(d_i^{-1})$ then function

$$E_d(p) = \sum_{i=1}^{n} d_i \hat{p}_i \ln \frac{p_i}{\hat{p}_i} - \langle d, \hat{p} \rangle \ln \langle d, p \rangle \qquad (10)$$

is ELF for system (6) and equilibrium point $\hat{p}$ is stable in $Int\sigma$. □

It is evident that if $d_i = 1, \quad i = 1,...,n$ then $E_d(p) = I(p, \hat{p})$, where $I(p, \hat{p})$ is Kullback's relative entropy or directed divergence between the two distribution p and $\hat{p}$.

So, it will be natural if we call our function $E_d(p)$ as ***weighted relative entropy***. Note, that meaning of the coefficients d_i depend from fitness matrix $G = (g_{ij})$, and represents in an integrated form the value of different species groups.

It is obvious also that if the matrix $G = G^T$ then $d_i = 1, \quad i = 1,...,n,$ and for function (9) we obtain: $E(p) = p^T Gp$, i.e. $E(p)$ is well-known Fisher's fitness, first introduced in population genetics by Fisher (1930).

Thus it will be natural if we will consider functions (7), (9) as fitness-like functions and (8), (10) as entropy-like functions. Both functions are Energy Lyapunov functions and evolution of the systems under consideration goes in the direction of their increase i.e. may be considered as the ecosystems goal functions. Function *E* takes into account the connections between the structure of a system and it's dynamics and in particular species interaction strengths affect on community evolution. Function E_d depends on structure of a system in an indirect way through the coefficients $d_i \quad i = 1,...,n$ and components of equilibrium vector and this function may be used as a distance measure between current value of systems variables and its steady-state. Note, also, that if we know ELF for a dynamic system then this system can be presented in universal form (R.I.McLachlan, et. al. 1988) which makes the conservation (dissipation) property manifest.

3. *D*-SYMMETRIZABLE MATRIX

Let $\mathbb{B}_n$ be a set of $n \times n$ nondegenerate symmetrical matrices and $\mathrm{Y} = diag(y_i),\quad \mathrm{X} = diag(x_i)\quad i = 1,...,n.$ As follows from Theorems 2 and 4 the problem of existence energy Lyapunov functions is reduced to the solution of matrix inclusion:

$$\mathrm{XAY} \in \mathbb{B}_n \tag{11}$$

It is clear that, if this inclusion has the solution then $A = X^{-1}BY^{-1},$ where $B \in \mathbb{B}_n$. In this case we will say that *A* is *D*-symmetrizable matrix and positive *D*-symmetrizable matrix if the constraints $x_i y_i > 0,\quad i = 1,...,n$ be fulfilled. It is obvious that from (11) we have the system from $n(n-1)/2$ equations:

$$a_{ij} x_i y_j = a_{ji} x_j y_i \qquad i \neq j;\quad i, j = 1,...,n. \tag{12}$$

with respect to 2*n* variables $x_i, y_i, i = 1,...,n.$ It is easy to prove that even if *n* = 3 the inclusion (11) has no solutions in the general case of arbitrary a_{ij}. Note that if XAY is symmetric, than also $X^{-1}XAYX^{-1} = AYX^{-1}$ is symmetric. Hence there exists a diagonal matrix $Z = YX^{-1}$, such that *AZ* is symmetric. Thus system (12) reduces to the next linear system:

$$a_{ij} z_j = a_{ji} z_i \qquad i \neq j;\quad i, j = 1,...,n \tag{13}$$

Denote by $\tilde{A}$ $n \times n(n-1)/2$ rectangle matrix of the system (13). It is clear that the matrix *A* is diagonal symmetrizable if and only if rang $\tilde{A} < n.$ But verify this condition for large *n* is rather difficult. It turns out that in this case it's possible to obtain the explicit form of the solution (13) and restriction to coefficients of the matrix *A*. This problem was solved by Volterra for the sign-antisymmetric matrix *A* i.e. then $a_{ij} a_{ji} \leq 0\quad i, j = 1,...,n;\ i \neq j.$ But his method can be fully extended to the case of sign-symmetric matrix *A* with $a_{ij} a_{ji} \geq 0\quad i, j = 1,...,n;\quad i \neq j.$

Theorem 5 (Volterra 1931). Consider system (13). Assume that *A* is sign-antisymmetric. Then the system (13) has a solution $Z > 0$ iff for any sequence of integers $i_1,...,i_k$ such that $1 \leq i_r \leq n,\quad r = 1,...,k$ it is true that

$$a_{i_1 i_2} a_{i_1 i_3} ....a_{i_k i_1} = (-1)^k a_{i_2 i_1} a_{i_3 i_2} ....a_{i_1 i_k}. \quad \square \tag{14}$$

Volterra's proof of this theorem without change can be transfer to the situation when *A* is sign-symmetric.

Theorem 6. Consider system (13) . Assume that *A* is sign-symmetric. Than the system (13) has a solution $Z > 0$ iff for any sequence if integers $i_1,...,i_k$ such that $1 \leq i_r \leq n,\quad r = 1,...,k$ it is true that

$$a_{i_1 i_z} a_{i_2 i_3} ....a_{i_k i_1} = a_{i_2 i_1} a_{i_3 i_2} ....a_{i_1 i_k}. \quad \square \tag{15}$$

We won't repeat the Volterra's proof but note that later this results was obtain by Parter and Youngs (1962) on the basis of graph theory.

Therefore if the coefficients of matrix *A* and *G* satisfy the conditions (15) then functions (7) and (9) is ELF for systems (1) and (6) respectively. i. e. dynamics of this system is convergent (Hirsch 1982, Fiedler and Gedeon 1997, Gedeon 1999).

When we deal with application of the systems (1) in ecology it is obvious that in the general case strong relation (15) is not fulfilled. This raises the question: under which conditions the matrix *A* is *D*-symmetrizable without constraints on it's coefficients? We will say what the matrix *A* is robust *D*-symmetrizable if it is *D*-symmetrizable without constraints on it's coefficients. Without loss of generality we may consider only ***indecomposable*** matrix *A* which has at least one nonzero off-diagonal coefficient in each row and column.

Theorem 7. The indecomposable, combinatorially symmetric matrix *A* (i.e. if $a_{ij} \neq 0$ implies $a_{ji} \neq 0)$ is robust *D*-symmetrizable if and only if the number of it's off-diagonal coefficients is equal to 2(*n*-1). □

Proof. If the number off-diagonal coefficients of the matrix *A* is equal to 2(*n*-1) then the matrix $\tilde{A}$ has size $(n-1) \times n.$ Hence rang $\tilde{A} < n$ and the system (13) has nonzero solution. If the number off-diagonal coefficients of the matrix *A* is greater than 2(*n*-1) then size of the matrix *A* is greater than $n \times n$ and condition: rang $\tilde{A} < n$ of solvability the systems (13) give us constraints to it's coefficients. □

Let us consider two interesting examples of the robust *D*-symmetrizable matrix.

Example 1. If the matrix *A* is tridiagonal and $a_{ij} \neq 0$ $i, j = 1,...,n,\quad |i - j| = 1$ then the matrix inclusion (11) has the next set of solutions:

$$x_1 = y_1 \frac{x_2 a_{21}}{y_2 a_{12}} \qquad x_2 = x_2$$
$$x_k = y_k \frac{x_2}{y_2} \frac{\prod_{i=2}^{k} a_{i,i-1}}{\prod_{i=2}^{k} a_{i-1,i}} \qquad k = 3,...,n \tag{16}$$

where we may choose arbitrarily values of $x_2 \neq 0,\ y_i \neq 0,\ i = 1,...,n\ (or\quad x_i \neq 0,\ i = 1,...,n).$

Proof. Validity of the (12) may be verify by direct calculation. □

From (12) it follows that tridiagonal matrix A is positive D-symmetrizable iff

$$\frac{\prod_{i=1}^{k} a_{i,i+1}}{\prod_{i=1}^{k} a_{i+1,i}} > 0 \qquad \forall k = 1,...,n-1 \qquad (17)$$

Corollary. If matrices of systems (1) and (6) are tridiagonal and (17) is fulfilled, then there exists an Energy Lyapunov functions for these systems. It is obvious from (16) that, as we pointed out above, the matrix A is D-symmetrizable with only one diagonal matrix.

Example 2. Let us consider interaction matrix A between one and multispecies. As was shown (Li, et al., 1999) in this case the matrix A has the next form:

$$A = \begin{pmatrix} a_{11} & a_{12} & a_{13} \cdots & a_{1n} \\ a_{21} & a_{22} & 0 \cdots & 0 \\ a_{31} & 0 & a_{33} \cdots & 0 \\ \vdots & \vdots & \vdots \ \ddots & \vdots \\ a_{n1} & 0 & 0 \cdots & a_{nn} \end{pmatrix} \qquad (18)$$

It is obvious that the matrix A is robust D-symmetrizable and systems (13) has the next solution:

$$z_i = \frac{a_{1i}}{a_{i1}} z_1 \qquad i = 2,...,n$$

Thus the matrix (18) is positive D-symmetrizable iff $a_{1i} / a_{i1} > 0, \quad i = 2,...,n$.

Problems:

1. To find another classes of positive D-symmetrizable matrices.
2. To establish correspondence between the structure of the interaction matrix A and Energy Lyapunov functions (7) and (8).

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