On a Geometrical Study of Population Ecosystems

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Abstract

We study a class of Lyapunov functions to be applied for investigation of the stability of population ecosystems. In a two dimensional case, a locally geometrical study is given.

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1 Introduction

In this paper, we shall survey some contribution to the geometrical study of mathematical models of ecosystems with emphasis upon some classes of models of interacting species. Initially investigated by A.J. Lotka [**?**] and V. Volterra [**?**], this class of ecosystems plays an important role in mathematical ecology. The models considered in this paper are of the form

$$\dot{x}_i = x_i F_i(x_1, x_2, \ldots, x_n), \quad i = 1, 2, \ldots, n, \tag{1}$$

where x_i is the density of the i^{th} species in the community at time t, and $\dot{x}_i$ denotes $\frac{dx_i}{dt}$. Each F_i is a continuous function from R^n_+, the nonnegative cone in R^n, to R and is sufficiently smooth to guarantee that initial value problems associated with (??) have unique solutions in the population orthant, R^n_+.

As a rule, the stability of such a system is studied by using the eigenvalues of its linear approximation. This method gives answer only concerning the stability relative to infinitesimal perturbations of the initial state. In real cases these systems are subjected to large perturbations. So, the study of stability relative to finite perturbations is useful. This requires an extension from a local property to a global concept. We shall denote by $x^* = (x^*_1, x^*_2, \ldots, x^*_n)$ a steady-state of (??). x^* is said to be *globally* (*asymptotically*) *stable* if for any neighbourhood U of x^*, there exists a neighbourhood W of x^* such that any orbit through W remains forever in U and $x(t) \to x^*$ for all $x \in W$ as the time variable tends to infinity.

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In this period, much effort in studies of ecological models has been directed to local stability analysis and numerical developments [?]. To investigate a global phenomenon such as globally asymptotically stability analytical studies are required.

Based on some ideas of Hsu [?], and using the direct method of Lyapunov [?], we shall study a class of Lyapunov functions to be applied for the study of globally asymptotically stability of systems of the form (??). In a two dimensional case, a locally geometrical study of (**??**) is given. We prove that, in general, totally extinction cannot appear in (**??**) and introduce a Riemannian structure to study it.

2 An extension of the direct method of Lyapunov

We have [?], the following

Definition 2.1 *For (??), a continuous function $V\colon R^n \to R$ is a Lyapunov function if*

1) *V is positive definite with $V(x^*) = 0$;*
2) $\lim\limits_{x_i \to 0^+} V(x) = \infty$; $\lim\limits_{x_i \to \infty} V(x) = \infty$ *for each i, $i = 1, 2, \ldots, n$;*
3) $\dot{V}(x) = \sum\limits_{i=1}^{n} \left(\frac{\partial V}{\partial x_i}\right) x_i F_i(x)$ *is nonpositive for all positive values of x.*

Remark 2.1 *The third condition in Definition* **??** *shows that the time derivative of $V(x)$ along every solution of (??) is nonpositive.*

From LaSalle's extension of the direct method of Lyapunov [?], we have the following

Theorem 2.1 *The positive steady-state x^* of (??) is globally asymptotically stable if there exists a Lyapunov function $V(x)$ such that $\dot{V}(x)$ is nonpositive in the positive orthant and it does not vanish identically along a nontrivial solution of (??) except for the constant solution $x(t) = x^*$.*

Let $V_i(x_i)$ be the Lyapunov function for a stable single species model whose population is x_i. If (??) describes a multispecies system in which each species is self-regulating and the interspecific interactions are relatively weak, then the Lyapunov function can be of the form

$$V(x) = \sum_{i=1}^{n} c_i V_i(x_i), \tag{2}$$

where $c_1, c_2, \ldots, c_n$ are positive constants. These constants are chosen so that $\dot{V}(x)$ is nonpositive in the positive orthant. Hsu [?], suggested that a general expression for $V_i(x_i)$ is of the form

(3) $$V_i(x_i) = \int_{x_i^*}^{x_i} \frac{h_i(s)}{g_i(s)} ds$$

where h_i and g_i have the following properties:

a) h_i and g_i are continuous functions such that for every i, $i = 1, 2, \ldots, n$ we have $h_i(s) < 0$ for all $s \in (0, x_i^*)$, $h_i(x_i^*) = 0$, $h_i(s) > 0$ for all $s \in (x_i^*, \infty)$;

b) $g_i(s) > 0$ for all $s > 0$.

c) h_i and g_i are chosen such that

$$\lim_{x_i \to 0^+} V(x) = \infty; \quad \lim_{x_i \to \infty} V(x) = \infty, \quad i = 1, 2, \ldots, n.$$

Taking into account (??) and (??) we obtain

$$V(x) = \sum_{i=1}^{n} c_i \int_{x_i^*}^{x_i} \frac{h_i(s)}{g_i(s)} ds$$

where h_i and g_i satisfy *a*), *b*) and *c*).

Remark 2.2 *The simplest expressions for the functions h_i and g_i are $h_i(s) = s - x_i^*$ and $g_i(s) = s$.*

Using these functions and based on Theorem **??** we can state

Theorem 2.2 *A positive steady-state of* (??) *at x^* is globally asymptotically stable if there exist positive constants $c_1, c_2, \ldots, c_n$ such that the function*

$$\dot{V}(x) = \sum_{i=1}^{n} c_i (x_i - x_i^*) F_i(x)$$

is negative semidefinite in the positive orthant and $\dot{V}$ does not vanish identically along a nontrivial solution of (??) *except for the constant solution $x(t) = x^*$.*

Remark 2.3 *It can be shown that for a general model of a population*

(4) $$\dot{x} = xF(x),$$

where $F \colon R_+ \to R$ is a continuous function, a Lyapunov function is

$$V(x) = x - x^* - \ln \frac{x}{x^*},$$

and $\dot{V}(x) = (x - x^*)F(x)$.

So, the positive steady-state x^* of (??) is globally asymptotically stable if $F(x) > 0$ for all $x \in (0, x^*)$ and $F(x) < 0$ for all $x \in (x^*, \infty)$.

Let us consider now a community of n interacting species modelled by a Lotka-Volterra system. This system is of the form (??) where

(5) $$F_i(x_1, x_2, \ldots, x_n) = b_i + \sum_{k=1}^{n} a_{ik} x_k, \quad i = 1, 2, \ldots, n.$$

Here b_i, $-a_{ii}$ are positive constants and a_{ik}, $i \neq k$ are constants with any sign. As we shall see later, any arbitrary sign for a_{ik}, $i \neq k$, allows us a greater flexibility for the interactions between the i^{th} and k^{th} species in the community. If we define $A = (a_{ik})$ and $b = (b_1, b_2, \ldots, b_n)$ then it can be shown that $x^* = -A^{-1}b^t$ is a steady-state of system. Let us suppose that $x^* \in R_+^n$ is positive and $C = \text{diag}(c_1, c_2, \ldots, c_n)$. Using Theorem **??** we can investigate the stability of the steady-state $x^* > 0$ of this system. By Remark **??** we deduce that

$$V(x) = \sum_{i=1}^{n} c_i (x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*})$$

can be used as a Lyapunov function. Clearly, $V(x)$ satisfies the conditions $V(x^*) = 0$, $V(x) > 0$ for all $x \in R_+^n$, $x \neq x^*$, $V(x) \to \infty$ as $x \to \infty$ and $x \to 0$. We have

$$\begin{aligned}\dot{V}(x) &= \sum_{i=1}^{n} c_i (x_i - x_i^*)(b_i + \sum_{k=1}^{n} a_{ik} x_k) \\ &= \sum_{i=1}^{n} c_i (x_i - x_i^*)(\sum_{k=1}^{n} a_{ik}(x_k - x_k^*)) \\ &= \frac{1}{2}(x - x^*)^t (CA + A^t C)(x - x^*).\end{aligned}$$

Let the matrix $CA + A^t C$ be negative semidefinite. Then, it is clear that $x = x^*$ is asymptotically stable. In fact, the basin of atraction of x^* is R_+^n. Therefore we have outlined a proof of this result

Theorem 2.3 *The steady-state x^* is globally assymptotically stable if there exists a positive diagonal matrix C such that $CA + A^t C$ is negative semidefinite and the function*

$$\dot{V}(x) = \frac{1}{2}(x - x^*)^t (CA + A^t C)(x - x^*)$$

does not vanish identically along a nontrivial solution.

3 Stability via Poincaré transformation

Let $\dot{V}$ be the function in Theorem **??**. We remark that is desirable for $\frac{\partial F_1}{\partial x_1}(x^*)$ to be nonpositive. If it is positive, Hsu recomments to subject (1.1) to the following Poincaré transformation [**?**],

$$x_1 = \frac{1}{y_1}, \quad x_k = \frac{y_k}{y_1}, \quad k = 2, 3, \ldots, n. \tag{6}$$

We obtain

$$\begin{aligned}&\dot{y}_1 = -y_1 F_1(\frac{1}{y_1}, \frac{y_2}{y_1}, \ldots, \frac{y_n}{y_1}) \\ &\dot{y}_k = y_k (F_k - F_1), \quad k = 2, 3, \ldots, n.\end{aligned} \tag{7}$$

Remark 3.1 *The transformation* (??) *maps* x^* *into* y^* *as follows*

$$y^* = (\frac{1}{x_1^*}, \frac{x_2^*}{x_1^*}, \ldots, \frac{x_n^*}{x_1^*}).$$

Now, if we apply Theorem **??** we find

$$\dot{V}(y) = -c_1(y_1 - y_1^*)F_1 + \sum_{k=2}^{n} c_k(y_k - y_k^*)(F_k - F_1). \tag{8}$$

In this context, we get

Theorem 3.1 *The steady-state* y^* *is globally asymptotically stable if there exists positive constants* $c_1, c_2, \ldots, c_n$ *such that the function* (??) *is negative semidefinite in the positive orthant and* $\dot{V}(y)$ *does not vanish identically along of non-trivial solution of* (??).

We wish now to consider the system [**?**],

$$\dot{x}_1 = X(x_1, x_2); \quad \dot{x}_2 = Y(x_1, x_2) \tag{9}$$

where

$$\begin{aligned} X(x_1,x_2) &= -2(\alpha_2 + \alpha_1 L)x_1x_2 - (L\alpha_2 - \alpha_1)x_2^2 - (\alpha_1 - L\alpha_2)x_1^2 + \lambda x_1 \\ Y(x_1,x_2) &= -2(\alpha_1 - \alpha_2 L)x_1x_2 + (\alpha_2 + L\alpha_1)x_1^2 - (\alpha_2 + L\alpha_1)x_2^2 + \lambda x_2. \end{aligned}$$

This system describes a 2-coral community model of scleractinian corals. It can be shown that

$$x_1^* = \frac{\lambda(\alpha_1 - \alpha_2 L)}{(\alpha_1 - \alpha_2 L)^2 + (\alpha_2 + \alpha_1 L)^2}; \quad x_2^* = \frac{\alpha_2 + \alpha_1 L}{\alpha_1 - \alpha_2 L} x_1^* \tag{10}$$

is a positive steady-state of (??). Moreover, by Theorem **??** and a theorem of Antonelli and Lin [**?**], we get

Theorem 3.2 *The system* (??) *exhibits a positive steady-state at* (x_1^*, x_2^*) *given by* (??). *Moreover, this steady-state is unique and globally asymptotically stable for the set* R_+^2.

4 A locally geometrical study

According to [**?**], *extinction* occurs in (**??**) if there is a solution $(x_1, x_2, \ldots, x_n)$ of (**??**) with $x_i(0) > 0$, $i = 1, \ldots, n$ and having a component x_j which satisfies $\lim_{t \to \tau} x_j(t) = 0$ for some τ in $(0, +\infty)$.

Let us consider a community of $n \geq 2$ mutually competing species that is a system (**??**) whose function F in (**??**) has the coefficients such that a_{ik}, a_{ki}, $i \neq k$ are both negative, that is

(11) $$\dot{x}_i = x_i(b_i - \sum_{j=1}^{n} a_{ij}x_j), \quad i = 1, \ldots, n.$$

Consider also the auxiliary function $\rho(t) = x_1(t)x_2(t)\cdots x_n(t)$ and its total time derivative along trajectories of (**??**). We have

$$\dot{\rho}(t) = \rho\left[\sum b_i - (\sum a_{i1})x_1 - (\sum a_{i2})x_2 - \cdots - (\sum a_{in}\Big) x_n\right]$$

Let us suppose that total extinction occurs. Then there exists a T such that whenever $t \geq T$

$$x_1(t) < \frac{\sum b_i}{(n+1)\sum a_{i1}}; \ldots ; x_n < \frac{\sum b_i}{(n+1)\sum a_{in}}.$$

It follows that for $\eta = \frac{1}{n+1}\sum b_i$ we have $\dot{\rho} \geq \rho\eta$, therefore $\rho(t) \geq \rho(T)e^{\eta(t-T)}$, $t \geq T$. This implies that $\lim\limits_{t\to\infty} \rho(t) = \infty$. We get the following result which states that complete extinction cannot occur in (??).

Theorem 4.1 *For any solution* $(x_1(t), \ldots, x_n(t))$ *of a mutually competing system with* $x_1(0) > 0, \ldots, x_n(0) > 0$ *the limits* $\lim\limits_{t\to\infty} x_i(t) = 0$, $i = \overline{1,n}$ *cannot occur simultaneously.*

In the following we consider $n = 2$ and we would like to point out how to use the local Riemannian geometrical structure and information geometry for studying the qualitative fluctuations of our system. We have

Proposition 4.1 *The two dimensional mutually competing system is Hamiltonian if and only if the following conditions hold*

$$b_1 + b_2 = 0, \quad a_{21} + 2a_{11} = 0, \quad a_{12} + 2a_{22} = 0.$$

In this case we find the Hamiltonian

(12) $$H(x_1, x_2) = x_1x_2(b_1 - a_{11}x_1 + a_{22}x_2).$$

We easily check that $H(x_1, x_2)$ verifies the Hamilton equations

$$\frac{\partial H}{\partial x_2} = \frac{dx_1}{dt}, \quad -\frac{\partial H}{\partial x_1} = \frac{dx_2}{dt}.$$

We shall denote by (x_1^*, x_2^*) the nontrivial steady-states of (**??**). For our purpose we make the expansion around (x_1^*, x_2^*) of H given by (**??**) according to Taylor formula to the second order. We obtain

$$-a_{11}x_2^*(x_1-x_1^*)+a_{22}x_1^*(x_2-x_2^*)+(b_1-2a_{11}x_1^*+2a_{22}x_2^*)(x_1-x_1^*)(x_2-x_2^*) = H-H_0.$$

We now introduce the Boltzman-Gibbs entropy, in fact the absolute uncertainty of a state P

$$S(P) = -\int_{\Omega} P \ln P d\sigma,$$

where Ω is the state space, P is the density function of a random vector (X, Y), and $S(P)$ is considered as an absolute information (entropy). Also, we introduce the Kullbak entropy or the relative information

$$S(Q|P) = \int_{\Omega} P(\ln P - \ln Q) d\sigma. \tag{13}$$

Expression (**??**) is called the relative uncertainty of P with respect to Q and represents an information distance between P and Q. Let us consider a two dimensional differentiable manifold M of class C^∞ with local coordinates u : $(u^1 = X, \quad u^2 = Y)$ and local metric defined by $S(Q|P)$ of C^∞ class. Thus $P(X, Y) \to P(u)$, $Q(X, Y) \to Q(u)$, and they are functions of C^∞ class. The form (??) may be transformed into the following expression

$$S(u, v) = S(P(v)|P(u)) = \int_M P(u)(\ln P(u) - \ln P(v)) d\omega. \tag{14}$$

If we take into account that

$$\int_M P(u) d\omega = \int_M P(v) d\omega = 1$$

we obtain

$$\int_M \frac{\partial P}{\partial u^\alpha} d\omega = 0, \quad \int_M \frac{\partial^2 P}{\partial u^\alpha \partial u^\beta} d\omega = 0, \quad \alpha, \beta \in \{1, 2\}.$$

Then the first and the second derivatives of (**??**) with respect to u are found to be given by

$$\frac{\partial S}{\partial u^i}|_{u=v} = 0, \quad \frac{\partial^2 S}{\partial u^i \partial u^k}|_{u=v} =< \frac{\partial \ln P}{\partial u^i} \frac{\partial \ln P}{\partial u^k} >= 2g_{ik} \tag{15}$$

We remark that (**??**) is positive definite, therefore the symmetric matrix $g = (g_{ik})$ is positive definite. In particular, $\det(g) > 0$ or $\mathrm{rank}(g) = 2$. Thus we may locally write $ds^2 = g_{\alpha\beta} du^\alpha du^\beta \geq 0$, where ds is the information distance between the states parametrized by u and $u + du$ in the two dimensional state manifold M. Therefore, M becomes locally a Riemannian manifold.

We introduce now the Gibbs distribution [**?**]

$$P(x_1, x_2) = Z^{-1}(x_1, x_2) \exp(-H(x_1, x_2) + H(x_1^*, x_2^*)), \tag{16}$$

where $Z(x_1, x_2)$ can be written as

$$Z(x_1, x_2) = \iint_{-\infty}^{+\infty} \exp(-H(x_1, x_2) + H(x_1^*, x_2^*)) dx_1\, dx_2.$$

If we suppose that $b_1 + a_{11}a_{22}x_1^* x_2^* + 2a_{22}x_2^* - 2a_{11}x_1^* > 0$ then

$$Z = \frac{\pi}{\sqrt{b_1 + a_{11}a_{22}x_1^* x_2^* + 2a_{22}x_2^* - 2a_{11}x_1^*}}.$$

If we use the expression (**??**) in (**??**) then we can compute the metric tensor and Gauss curvature.

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