When the feasibility of an ecosystem is sufficient for global stability?

Alfredo Porati a,*, Maria Ilde Granero b

a DBSF–Facolta’ di Scienze, Universita dell’Insubria, Via H. Dunant 3, 21100 Varese, Italy
b Dipartimento di Fisica, Universita di Parma Viale delle Scienze, 43100 Parma, Italy

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Abstract

We show via a Liapunov function that in every model ecosystem governed by generalized Lotka–Volterra equations, a feasible steady state is globally asymptotically stable if the number of interaction branches equals $n - 1$, where $n$ is the number of species. This means that the representative graph for which the theorem holds is a ‘tree’ and not only an alimentary chain. Our result is valid also in the case of non-homogeneous systems, which model situations in which input fluxes are present. © 2000 Elsevier Science Inc. All rights reserved.

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1. Introduction

During the past few decades, much work has been done on the problem of stability–complexity relationship in model ecosystems, especially in the case of interactions of predator–prey type, described by the so-called generalized Lotka–Volterra equations (GLVEs).

These kind of equations are of great interest not only in Population Dynamics or in Chemical Kinetics, but their importance in ecological modeling “...equals its ubiquity in all fields of science, from plasma physics to neural nets” [1]. 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 [1,2].

As an effect of this equivalence, the analytical results obtained in the frame of GLVEs are of interest not only in the field of Mathematical Ecology but also in other apparently non-related fields.
In the present work, we shall show that the feasible (if present) steady state of a wide class of Lotka–Volterra systems is globally asymptotically stable if simple conditions on the representative graph are satisfied, regardless of the number of interacting ‘species’.

We also consider the case of non-homogeneous systems, introducing an external supplementation, a case that has been studied by Gard [3] and Roy and Solimano [4]. In real ecosystems this is the case, for example, of transport of pelagic eggs and free embryos of fishes (but also crabs and bivalves) from the place where they spawned to the feeding grounds [5].

2. Analysis of the model

Many authors have focused their attention on the stability of alimentary chains: Freedman and Waltman [6] demonstrate that the feasible steady state of a Lotka–Volterra food chain with carrying capacity at the lowest trophic level, is locally asymptotically stable. Harrison [7] demonstrates that, under the same conditions (feasibility of the steady state and self-regulation of the primary species), the steady state is globally asymptotically stable. Similar results, valid not only for linear alimentary chains, but also for more complex food-webs, have been achieved previously, in the case of classical Lotka–Volterra models (without self-regulation) [8] and then for GLV models [9,10]. In the present work, we shall show that, in a wide class of GLV systems, the feasibility of steady states is sufficient for global asymptotic stability if simple conditions on the representative graph are satisfied, conditions that are valid also when constant input fluxes are introduced.

Let us consider a system of the form

\[
\dot{N}_i = \Phi_i - b_i N_i - a_{ii} N_i^2 + \sum_{j=1}^{n} a_{ij} N_i N_j, \quad j \neq i \quad (i = 1, \ldots, n).
\]

The input fluxes \(\Phi_i \geq 0\) can be considered either as a constant immission of individuals, replacing the usual birth-rate term, or as a positive source supplied from outside.

The \(a_{ii} \geq 0\) are the intraspecific interaction coefficients, and \(a_{ij} (a_{ij} a_{ji} \leq 0, \; i \neq j)\) are interspecific interaction coefficients. No conditions are imposed on the sign of \(b_i\), provided that all the \(b_i\) are different from 0.

System (1), when

(i) \(\Phi_i = 0 \forall i\), and at least one of \(a_{ii}\) is different from 0, represent a GLV system

(ii) \(a_{ii} = 0 \forall i\), but at least one of \(\Phi_i\) is positive, represent a Volterra system, without self-regulation, but with at least one input flux.

In the following, we shall call ‘feasible’ a positive steady-state \(N^*\) of (1) (i.e., \(N^*_i > 0 \forall i\)).

We have investigated the conditions under which the feasible steady states are globally asymptotically stable. A sufficient condition is given by the following.

**Theorem.** Every feasible steady state of system (1), for which at least one of the conditions (i) or (ii) is satisfied, is globally asymptotically stable if the number of interaction branches equals \(n - 1\).

To demonstrate the theorem, let us state the following:

**Lemma.** Every feasible steady state of the antisymmetric form of system (1) is globally asymptotically stable under the same conditions required for the theorem.
Proof. The antisymmetric form of system (1) is
\[
\dot{N}_i = \Phi_i - b_i N_i - a_{ii} N_i^2 + \beta_i^{-1} \sum_{j=1}^{n} \alpha_{ij} N_i N_j \quad (i = 1 \ldots n),
\]
where \( \beta_i > 0, a_{ii} \geq 0, \alpha_{ij} = -\alpha_{ji}, \) and \( a_{ij} = \beta_i^{-1} \alpha_{ij}. \)

Generalizing a method analogous to the one of Goel et al. [11], we introduce the variables \( v_i \) defined by \( N_i = N_i^* \exp v_i, \) where \( N^* \in \mathbb{R}_+^n. \) Taking into account the steady-state equations of (2), we obtain
\[
\frac{d}{dt} \sum_{i=1}^{n} \beta_i N_i^* (\exp v_i - v_i) = - \left[ \sum_{i=1}^{n} \Phi_i \beta_i \frac{(\exp v_i - 1)^2}{\exp v_i} + \sum_{i=1}^{n} \beta_i a_{ii} N_i^* (\exp v_i - 1)^2 \right].
\]

The function \( \Psi = \sum_{i=1}^{n} \beta_i N_i^* (\exp v_i - v_i) \) has a negative derivative along the trajectories of system (2). Consider now the function \( V = \Psi - \sum_{i=1}^{n} \beta_i N_i^*; \) when \( \Phi_i \neq 0 \) or \( a_{ii} \neq 0 \) for one \( i \) at least, \( V \) is a positive definite function (\( V > 0 \) in every set of \( v_i, \) \( i = 1, \ldots, n \) different from the origin and \( V = 0 \) in the origin) whose derivative \( \dot{V} = \Psi \) is a negative definite function (\( \dot{V} < 0 \) in every set of \( v_i, \) \( i = 1, \ldots, n \) different from the origin, and \( \dot{V} = 0 \) in the origin).

The function \( V \) is a well-known Liapunov function that in the classical Volterra system (\( \Phi = 0, \forall i, a_{ii} = 0, \forall i \)) is a constant of motion, (\( \dot{V} = 0 \)), and in the generalized Volterra system (\( \Phi = 0, \forall i, a_{ii} \neq 0 \) at least for one \( i \)) ensures the global asymptotical stability (\( \dot{V} \) negative definite). It is interesting to note that the introduction of fluxes \( \Phi_i \) is a stabilizing factor, because, also when all the \( a_{ii} = 0, \) the system is asymptotically stable, which is not true in the classical case.

Proof of the theorem. The theorem will be proven when we satisfy the (sufficient) conditions to put system (1) in the antisymmetric form (2). One can easily see the possibility of determining the numbers \( \beta_i \) if the conditions
\[
a_{ij} \beta_i + a_{ji} \beta_j = 0 \quad (i \neq j; \ i, j = 1, \ldots, n).
\]
are satisfied.

These relations can be obviously satisfied in the case of alimentary chains (as pointed out, when no input fluxes are present, by Huang and Morowitz [12] and Harrison [7]), but the implications of (4) regards a wider class of systems, for which the alimentary chain represents only a subclass.

System (4) is a linear homogeneous system of \( s = \binom{n}{2} \) equations in the \( n \) unknowns \( \beta_i. \) A non-trivial solution for such a system exists only when all the minors of order \( n \) of the coefficient matrix equal 0. When these conditions are satisfied, it is possible to find (in infinitely many ways) the \( \beta_i \) and to put system (1) into the antisymmetric form (2). Under these conditions, all the feasible steady states of (1) will be globally asymptotically stable.

If in the representative graph of system (1) all the interaction branches are present (i.e., all the \( a_{ij} \) are different from 0), the number of minors to be 0 in order to have non-trivial solutions for (4) equals \( v = \binom{n}{2}, \) and \( v \) is a rapidly increasing number as \( n \) increases. Of course, when the number of interaction branches decreases, \( v \) also decreases, and in particular, when the number of branches in the graph of (1) is \( n - 1, \) (a ‘tree’ in the language of graph theory), system (4) consists of a
linear homogeneous system of \( n - 1 \) equations in \( n \) unknowns, thus infinitely many non-trivial solutions are possible, and the theorem is then proven.

3. Conclusions

The more remarkable result is the following:

In a connected community of \( n \) ‘species’ governed by Eq. (1), global asymptotic stability is ensured if the steady state is feasible and the number of interaction branches equals \( n - 1 \), i.e., when the connectedness \( C \) (i.e., the ratio between the existing number of branches and the maximum number of interactions) equals \( 2/n \). In fact this theorem holds not only for simple alimentary chains, for which the condition \( C = 2/n \) is obviously satisfied, but also for graphs representing more complicated and perhaps more interesting interactions in an ecological community. For example, also in the simple case of \( n = 3 \), three directed and connected graphs (di-graphs), all globally stable when feasible, are possible, and when \( n = 4 \), the number of stable trees is 8 (see Fig. 1), and this number increases very rapidly with \( n \). The fact that we are certain that when \( C = 2/n \) all the feasible solutions of system (1) are also globally asymptotically stable, make it possible in the case of random simulations (see for example [13,14]), where the analysis of stability of a very large number of systems is necessary to reduce computational times. In this case, it is only sufficient to verify the feasibility of the steady states of (1) and it is not necessary to look for the sign of the real parts of the eigenvalues.

Fig. 1. The set of all digraphs with \( n = 3 \) and with \( n = 4 \), for which the feasibility of the steady state ensures global asymptotic stability.
Moreover, the theorem is valid for any (also very large) number of species and for every value of interaction coefficients. This means that we have no limitation due to a specific relation between the number of species and interaction strength, limitation present in linear systems (semicircular law) as pointed out by May [15].

It appears interesting to compare the purely mathematical result of the theorem with the structure of real community food-webs.

In Cohen et al. [16] the predation matrices and the list of organisms in 113 real food-webs are presented. Looking at predation matrices it may be seen that, in most cases the number of branches is very low when compared with its possible maximum value. As a consequence, the connectedness $C$ is $\ll 1$, and, in some few cases, is $C = 2/n$, i.e., the number of branches equals $n - 1$ (see Fig. 2). Moreover, the listed species are not necessarily trophic species, in the sense of “a collection of organism that have the same diets and the same predators” [16]. This implies that the number of ‘species’ can be splitted into a greater number and, taking into account the alimentary preferences, $C$ can assume the value $2/n$ for which the theorem holds. In particular, this is true for communities of fishes. As said by Nikolsky [5]: “…every species of fish is adapted to feeding on a particular food, its sensory organs are adapted to seeking out this food, its buccal cavity to seizing it, its intestine to digesting it…”.

References


Fig. 2. Two real community food webs (reported in [16]): a salt marsh, Georgia (left) and a temporary freshwater rockpool in France (right).


