Stability of ecological and epidemiological models via representation as Generalized Lotka-Volterra dynamics

A Preprint

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Abstract

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1 Introduction

Several models for ecological, evolutionary, and epidemiological dynamics can be recast as a Generalized Lotka-Volterra model via the so-called *quasi-monomial transformation*. This fact was discovered at least three times (as far as we can tell, independently) by different authors in the late '80s (Peschel and Mende 1986).

2 Generalized Lotka-Volterra model

$$\dot{x}_i = x_i \left(r_i + \sum_{j=1}^{m} A_{ij} x_j \right) \tag{1}$$

3 Quasi-Polynomial systems

We now introduce a generalization of Eq. 1, defining the class of quasi-polynomial systems (QP-systems):

$$\dot{y}_i = y_i \left(s_i + \sum_{j=1}^{m} M_{ij} \prod_{k=1}^{n} y_k^{B_{jk}} \right) \tag{2}$$

where we have n equations, $\dot{y}_1, \ldots, \dot{y}_n$. The vector s is of length n, M is a matrix of size $n \times m$ containing real coefficients, and B a matrix of size $m \times n$, also containing real coefficients. If $n = m$, and thus both M and B are square matrices, and further that $B = I_n$ (the identity matrix of size n), the model reduces to the Generalized Lotka-Volterra model in Eq. 1 with $r = s$ and $A = M$. If B contains only integers, Eq. 2 defines a *polynomial* system of differential equations; relaxing this condition to admit B composed of real numbers, we obtain a *quasi-polynomial* (QP-) system.

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QP-representation of Leslie-Gower predator-prey model

The Leslie-Gower model is simple variation on the classic Lotka-Volterra predator-prey model. We have two equations:

$$\begin{cases} \dot{y}_1 = y_1(\rho_1 - y_1 - \alpha_1 y_2) \\ \dot{y}_2 = y_2\left(\rho_2 - \alpha_2 \frac{y_2}{y_1}\right) \end{cases} \tag{3}$$

with y_1 representing the prey, y_2 the predator, and all coefficients are assumed to be positive. The system differs from GLV in that we have a ratio between the predator and prey in the equation for the predator. The system is however in QP form, as seen by defining:

$$s = \begin{pmatrix} \rho_1 \\ \rho_2 \end{pmatrix} \quad M = \begin{pmatrix} -1 & -\alpha_1 & 0 \\ 0 & 0 & -\alpha_2 \end{pmatrix} \quad B = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ 1 & -1 \end{pmatrix} \tag{4}$$

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4 From Quasi-Polynomial to Generalized Lotka-Volterra

We define a set of m *quasi-monomials*:

$$x_j = \prod_{k=1}^{n} y_k^{B_{jk}} \tag{5}$$

A simple way to identify quasi-monomials for any system that can be written in QP form is to consider the per capita dynamics:

$$\dot{\log} y_i = \frac{\dot{y}_i}{y_i} = s_i + \sum_{j=1}^{m} M_{ij} \prod_{k=1}^{n} y_k^{B_{jk}} \tag{6}$$

As such, the set of variables, or product of powers of variables, appearing in the equations for the equations $\dot{\log} y_i$ defines the quasi-monomials x.

Quasi-monomials for the Leslie-Gower model

For the Leslie-Gower model in Eq. 3 we identify three quasi-monomials:

$$\begin{cases} x_1 = y_1^1\, y_2^0 = y_1 \\ x_2 = y_1^0\, y_2^1 = y_2 \\ x_3 = y_1^{-1}\, y_2^1 = \frac{y_2}{y_1} \end{cases} \tag{7}$$

Now we show how the $n-$dimensional QP-system of differential equations in Eq. 2 can be recast as an $m-$dimensional GLV system in Eq. 1. By chain rule, we have:

$$\begin{aligned}
\dot{x}_j &= \sum_k B_{jk}\, \dot{y}_k\, y_k^{(B_{jk}-1)} \prod_{l \neq k} y_l^{B_{jl}} \\
&= \sum_k B_{jk} \frac{\dot{y}_k}{y_k} \prod_l y_l^{B_{jl}} \\
&= \sum_k B_{jk} \frac{\dot{y}_k}{y_k} x_j \\
&= x_j \sum_k B_{jk} \frac{\dot{y}_k}{y_k} \\
&= x_j \left(\sum_k B_{jk} s_k + \sum_k B_{jk} \sum_l M_{kl} \prod_l y_l^{B_{kl}} \right) \\
&= x_j \left(\sum_k B_{jk} s_k + \sum_k B_{jk} \sum_l M_{kl} x_l \right) \\
&= x_j \left((Bs)_j + \sum_l (BM)_{jl} x_l \right) \\
&= x_j \left(r_j + \sum_l A_{jl} x_l \right)
\end{aligned} \tag{8}$$

where we have defined $A = BM$ and $r = Bs$; $(Bs)_j$ is the j^{th} element of the vector Bs and $(BM)_{jl}$ is the coefficient in row j and column l of the matrix BM.

Via the quasi-monomial transformation in Eq. 5 we have turned the $n-$dimensional QP-system in Eq. 2 into an $m-$dimensional GLV system in Eq. 1.

GLV representation of the Leslie-Gower model

We can represent the Leslie-Gower model in Eq. 3 as a three-dimensional GLV model defined by the quasi-monomials in Eq. 7 and:

$$r = Bs = \begin{pmatrix} \rho_1 \\ \rho_2 \\ \rho_2 - \rho_1 \end{pmatrix} \quad A = BM = \begin{pmatrix} -1 & -\alpha_1 & 0 \\ 0 & 0 & -\alpha_2 \\ 1 & \alpha_1 & -\alpha_2 \end{pmatrix} \tag{9}$$

Note that A is rank deficient, given that the third row can be written as the difference between the second and first row. Rank-deficiency of A is expected whenever $m > n$ (as here, where we went from two to three equations).

The GLV representation of the model becomes:

$$\begin{cases} \dot{x}_1 = x_1(\rho_1 - x_1 - \alpha_1 x_2) \\ \dot{x}_2 = x_2(\rho_2 - \alpha_2 x_3) \\ \dot{x}_3 = x_3(\rho_2 - \rho_1 + \alpha_1 x_1 - \alpha_2 x_3) \end{cases} \tag{10}$$

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5 Stability in Generalized Lotka-Volterra

5.1 Lyapunov's direct method

Provided with a dynamical system $\dot{y}_i$

5.2 Candidate Lyapunov function for Generalized-Lotka Volterra

Before proceeding, we note that if Eq. 1 has a feasible (i.e., positive) coexistence equilibrium, then $r = -Ax^\star$, and as such we can rewrite the equations more compactly as $\dot{x}_i = x_i \sum_j A_{ij}(x_j - x_j^\star) = x_i \sum_j A_{ij} \Delta x_j$, where we have defined the deviation from equilibrium $\Delta x_j = x_j - x_j^\star$.

We now consider the candidate Lyapunov function proposed by Goh:

$$\begin{cases} V_{x_i} = x_i - x_i^\star - x_i^\star \log \frac{x_i}{x_i^\star} \\ V = \sum_i w_i V_{x_i} \end{cases} \tag{11}$$

where each $V_{x_i} > 0$ for any positive $x_i \neq x_i^\star$ and zero at the equilibrium. The weights $w_1, \dots w_n$ are non-negative, and at least one is positive. In such cases, V is radially unbounded. If we can find weights such that $\dot{V} = \sum_i w_i \dot{V}_{x_i} \leq 0$, we can prove stability (possibly, through LaSalle's invariance principle). Deriving:

$$\begin{aligned} \dot{V} &= \sum_i w_i \left(\dot{x}_i - x_i^\star \dot{\log x_i} \right) \\ &= \sum_i w_i \left(x_i \sum_j A_{ij} \Delta x_j - x_i^\star \sum_j A_{ij} \Delta x_j \right) \\ &= \sum_i w_i \left(\Delta x_i \sum_j A_{ij} \Delta x_j \right) \\ &= \sum_i \Delta x_i w_i \sum_j A_{ij} \Delta x_j \\ &= \sum_i \sum_j w_i A_{ij} \Delta x_i \Delta x_j \end{aligned} \tag{12}$$

Note that in the sum over i and j, only the symmetric part of the matrix $D(w)A = (w_i A_{ij})$ matters (the skew symmetric part cancels). It is therefore convenient to define a new, symmetric matrix $G = \frac{1}{2}(D(w)A + A^T D(w))$, so that our expression becomes:

$$\dot{V} = \frac{1}{2} \sum_i \sum_j (w_i A_{ij} + A_{ji} w_j) \Delta x_i \Delta x_j = \sum_i \sum_j G_{ij} \Delta x_i \Delta x_j \tag{13}$$

A symmetric matrix G satisfying $z^T G z = \sum_i \sum_j G_{ij} z_i z_j < 0$ for every $z \neq 0$ is called *negative definite.* If the sum can be zero for some $z \neq 0$, G is called *negative semi-definite.* A symmetric, negative definite matrix has all eigenvalues real and negative; in a negative semi-definite matrix eigenvalues can be zero. As such, if we can identify suitable, positive (nonnegative) weights w such that G is negative (semi-)definite, then $\dot{V} \leq 0$ and we can prove the stability of the equilibrium $x^\star$.

5.3 Stability in QP-systems

In the Generalized Lotka-Volterra model in Eq. 1, the variables x_i can in principle take any positive value (at least as an initial condition), and therefore each Δx_i is radially unbounded: $\Delta x_i \in [-x_i^\star, \infty)$; moreover, we can set (again, at least initially) each x_i to any arbitrary value, irrespective of the value of the rest of the x_j. In such a setting, it is therefore difficult to prove stability via Eq. 13 if the matrix G is not negative (semi-)definite.

Note however that, when we represent an $n-$dimensional QP-system using an $m-$dimensional GLV system, the quasi monomials x_i are function of the original variables y_i. This in turn means that the perturbations in the GLV system are a function of the perturbations in the original system: in particular $\Delta x_i = \prod_{k=1}^n y_k^{B_{ik}} - \prod_{k=1}^n (y_k^\star)^{B_{ik}}$.

In practice, this means that not all perturbations Δx are allowed—rather, only those compatible with the definition of the quasi-monomials. In turn, this means that we could (and often will) find nonnegative weights in Eq. 13 such that $\dot{V} \leq 0$ and yet the matrix G *is not negative semi-definite*. In such cases, G *acts* like a negative semi-definite matrix on the *admissible* perturbations, i.e., those abiding by the form specified by the quasi-monomials.

Stability of the Leslie-Gower model

We consider the candidate Lyapunov function in Eq. 11 for the QP-representation of the Leslie-Gower model (Eq. 10). A convenient choice of weights is $w = (0, \rho_1\alpha_1 + \alpha_2, \rho_2\alpha_2)^T$, yielding:

$$G = \frac{1}{2}(D(w)A + A^T D(w)) = \begin{pmatrix} 0 & 0 & \frac{\rho_2\alpha_2}{2} \\ 0 & 0 & -\frac{\alpha_2^2}{2} \\ \frac{\rho_2\alpha_2}{2} & -\frac{\alpha_2^2}{2} & -\rho_2\alpha_2^2 \end{pmatrix} \tag{14}$$

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6 Examples

6.1 A susceptible-infected-recovered model with demography

We consider a simple S-I-R model in which mortality in all classes is counterbalanced by the birth of susceptible individuals:

$$\begin{cases} \dot{y_1} = \delta - \delta y_1 - \beta y_1 y_2 = y_1\left(-\delta + \delta\frac{1}{y_1} - \beta y_2\right) \\ \dot{y_2} = -(\delta+\gamma)y_2 + \beta y_1 y_2 = y_2\left(-(\delta+\gamma) + \beta y_1\right) \\ \dot{y_3} = \gamma y_2 - \delta y_3 = y_3\left(-\delta + \gamma\frac{y_2}{y_3}\right) \end{cases} \tag{15}$$

where y_1 represents the proportion of susceptible individuals in the population, y_2 that of the infected/infectious individuals, and y_3 the recovered individuals. The parameter δ serves both as a birth rate for the population, and as the mortality rate in each compartment, β is the transmission rate, and γ the recovery rate. We have $y_1 + y_2 + y_3 = 1$. It is well known that if the critical threshold $\mathcal{R}_0 = \frac{\beta}{\gamma+\delta} > 1$, the model has a globally stable endemic equilibrium in which a constant proportion of individuals is infected.

At the endemic equilibrium, we have $y_1^\star = 1/\mathcal{R}_0$, $y_2^\star = (\mathcal{R}_0 - 1)\delta/(\delta+\gamma)$, and $y_2^\star = (\mathcal{R}_0 - 1)\gamma/(\delta+\gamma)$, such that the equilibrium is feasible only if $\mathcal{R}_0 > 1$.

We write the model as a four-dimensional GLV system, and probe the stability of the endemic equilibrium assuming that it is positive. First, we identify the quasi-monomials and associated matrices and vectors:

$$x = \begin{pmatrix} y_1 \\ y_2 \\ \frac{1}{y_1} \\ \frac{y_2}{y_3} \end{pmatrix} \quad s = \begin{pmatrix} -\delta \\ -\delta-\gamma \\ -\delta \end{pmatrix} \quad M = \begin{pmatrix} 0 & -\beta & \delta & 0 \\ \beta & 0 & 0 & 0 \\ 0 & 0 & 0 & \gamma \end{pmatrix} \quad B = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ -1 & 0 & 0 \\ 0 & 1 & -1 \end{pmatrix}$$
$$r = \begin{pmatrix} -\delta \\ -\delta-\gamma \\ \delta \\ -\gamma \end{pmatrix} \quad A = \begin{pmatrix} 0 & -\beta & \delta & 0 \\ \beta & 0 & 0 & 0 \\ 0 & \beta & -\delta & 0 \\ \beta & 0 & 0 & -\gamma \end{pmatrix} \tag{16}$$

Now consider the candidate Lyapunov function with weights $w = (1,1,0,0)^T$, and the perturbations $\Delta x = (y_1 - y_1^\star, y_2 - y_2^\star, 1/y_1 - 1/y_1^\star, y_2/y_3 - y_2^\star/y_3^\star)^T$. Deriving with respect to time, we obtain:

$$\dot{V} = \frac{1}{2}\Delta x^T (D(w)A + A^T D(w))\Delta x = -\delta\frac{(y_1 - y_1^\star)^2}{y_1 y_1^\star} \leq 0 \tag{17}$$

Note that this choice of weights does not result in a negative semi-definite matrix: the nonzero eigenvalues of $(D(w)A + A^T D(w))$ are $\pm\delta/2$.

Because $\dot{V} = 0$ whenever $y_1 = y_1^\star$, to prove stability we need to make sure that the equilibrium is the only trajectory contained in the set of points satisfying $\dot{V} = 0$.

LaSalle's

6.2 Stability of a consumer-resource model with inputs

We consider a model with $2n$ equations, equally divided into resources (z_i) and consumers (y_i). The model can be written as:

$$\begin{cases} \dot{z}_i = \kappa_i - \delta_i z_i - z_i \sum_j C_{ij} y_j \\ \dot{y}_i = -\mu_i y_i + y_i \epsilon_i \sum_j C_{ji} z_j \end{cases} \tag{18}$$

where κ_i is the input to resource i, δ_i its degradation rate, C_{ij} the consumption of i by consumer j, μ_i the mortality rate of consumer i, and ϵ_i the efficiency of transformation of resources into consumers. We want to show that, whenever a feasible equilibrium exists, it is globally stable.

We identify $3n$ quasi-monomials: $x_i = z_i$ for $i \in \{1, \dots, n\}$, $x_i = y_i$ for $i \in \{n+1, \dots, 2n\}$, and finally $x_i = 1/z_i$ for $i \in \{2n+1, \dots, 3n\}$. This allows us to rewrite the system in Eq. 18 as a QP-system defined by:

$$s = \begin{pmatrix} -\delta \\ -\mu \end{pmatrix} \quad M = \begin{pmatrix} 0_{n\times n} & -C & D(\kappa) \\ D(\epsilon)C^T & 0_{n\times n} & 0_{n\times n} \end{pmatrix} \quad B = \begin{pmatrix} I_n & 0_{n\times n} \\ 0_{n\times n} & I_n \\ -I_n & 0_{n\times n} \end{pmatrix} \tag{19}$$

where $0_{n\times n}$ is a matrix of size $n \times n$ containing zeros, I_n is the identity matrix of size n and $D(\theta)$ the diagonal matrix with θ on the diagonal. We rewrite the system as a $3n-$dimensional GLV defined by:

$$r = Bs = \begin{pmatrix} -\delta \\ -\mu \\ \delta \end{pmatrix} \quad A = BM = \begin{pmatrix} 0_{n\times n} & -C & D(\kappa) \\ D(\epsilon)C^T & 0_{n\times n} & 0_{n\times n} \\ 0_{n\times n} & C & -D(\kappa) \end{pmatrix} \tag{20}$$

We now consider the candidate Lyapunov function in Eq. 11 with weights $w = (1_n, 1/\epsilon, 0_n)$. Our matrix G becomes:

$$G = \frac{1}{2}(D(w)A + A^T D(w)) = \begin{pmatrix} 0_{n\times n} & 0_{n\times n} & \frac{1}{2}D(\kappa) \\ 0_{n\times n} & 0_{n\times n} & 0_{n\times n} \\ \frac{1}{2}D(\kappa) & 0_{n\times n} & 0_{n\times n} \end{pmatrix} \tag{21}$$

The matrix is clearly non negative semi-definite. And yet, when we consider the perturbations: $\Delta x = (z - z^\star, y - y^\star, 1/z - 1/z^\star)^T$, the derivative with respect to time in Eq. 13 reduces to:

$$\dot{V} = \sum_i k_i (z_i - z_i^\star) \left(\frac{1}{z_i} - \frac{1}{z_i^\star} \right) = -\sum_i \frac{k_i}{z_i z_i^\star} (z_i - z_i^\star)^2 \leq 0 \tag{22}$$

TODO LaSalle's

6.3 Reducing nonlinearities in a model with higher-order interactions

The last few years have seen a resurgence in the interest for so-called higher-order interactions. When including interactions of more than two populations at a time, dynamics can be altered dramatically. For example, Grilli *et al.* showed stabilization for the replicator equation when three or more players interact. The simplest model is that for a replicator equation describing a three-player game of rock-paper-scissors:

$$\begin{cases} \dot{y}_1 = y_1(2y_3^2 + y_1y_3 - 2y_1y_2 - y_2^2) \\ \dot{y}_2 = y_2(2y_1^2 + y_1y_2 - 2y_2y_3 - y_3^2) \\ \dot{y}_3 = y_3(2y_2^2 + y_2y_3 - 2y_1y_3 - y_2^2) \end{cases} \tag{23}$$

with dynamics occurring on the simplex $y_1 + y_2 + y_3 = 1$. The system has a single feasible equilibrium $y_i^\star = \frac{1}{3} \quad \forall i$. Note that the system is in QP-form as defined by the monomials:

$$x = \begin{pmatrix} y_1^2 \\ y_2^2 \\ y_3^2 \\ y_1y_2 \\ y_1y_3 \\ y_2y_3 \end{pmatrix} \tag{24}$$

and parameters

$$\lambda = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix} \quad M = \begin{pmatrix} 0 & -1 & 2 & -2 & 1 & 0 \\ 2 & 0 & -1 & 1 & 0 & -2 \\ -1 & 2 & 0 & 0 & -2 & 1 \end{pmatrix} \quad B = \begin{pmatrix} 2 & 0 & 0 \\ 0 & 2 & 0 \\ 0 & 0 & 2 \\ 1 & 1 & 0 \\ 1 & 0 & 1 \\ 0 & 1 & 1 \end{pmatrix} \tag{25}$$

As such, the model in Eq. 23 with three variables (equivalent to two equations, given the constrain of dynamics happening in the simplex) and higher-order interactions can be recast as a GLV model with six variables, and parameters:

$$r = B\lambda = \vec{0} \quad A = BM = \begin{pmatrix} 0 & -2 & 4 & -4 & 2 & 0 \\ 4 & 0 & -2 & 2 & 0 & -4 \\ -2 & 4 & 0 & 0 & -4 & 2 \\ 2 & -1 & 1 & -1 & 1 & -2 \\ -1 & 1 & 2 & -2 & -1 & 1 \\ 1 & 2 & -1 & 1 & -2 & -1 \end{pmatrix} \tag{26}$$

Note that matrix A has eigenvalues $-\frac{3}{2}(1 \pm 3\sqrt{3})$ and an additional four eigenvalues equal to zero (i.e., it has rank 2, the number of independent equations in the original system).

By choosing the candidate Lyapunov in Eq. 11 function with weights $\gamma = (1, 1, 1, 2, 2, 2)^T$ and considering the perturbations $\Delta x = (y_1^2 - y_1^{\star 2}, y_2^2 - y_2^{\star 2}, y_3^2 - y_3^{\star 2}, y_1y_2 - y_1^\star y_2^\star, y_1y_3 - y_1^\star y_3^\star, y_2y_3 - y_2^\star y_3^\star)^T$, we obtain:

$$\dot{V} = -\frac{2}{3}\left(y_1^2 + y_2^2 + y_3^2 - y_1y_2 - y_1y_3 - y_2y_3\right) \leq 0 \tag{27}$$

A good proof of this? It is definitely true

The derivative is thus negative for any $0 < y_i < 1$ but the equilibrium point, proving the stability of the equilibrium.

You can insert references. Here is some text (Kour and Saabne 2014b, 2014a) and see Hadash et al. (2018).

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