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

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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 (GLV) model via the so-called *quasi-monomial transformation*. This transformation was discovered in the late 1980s at least three times (as far as we can tell, independently) by different authors (Peschel and Mende 1986; Brenig 1988; Gouzé 1990). *Quasi-polynomial* (QP) systems can be recast as a (typically, larger-dimensional) GLV in a straightforward, mechanical manner; several other systems that do not belong to this class can be first transformed into QP systems, and then in turn into GLV. This shows that the Generalized Lotka-Volterra model is not only one of the oldest models in ecology—it was originally proposed in 1920 by Lotka (Lotka 1920a, 1920b), and rediscovered by Volterra in 1926 (Volterra 1926a, 1926b)—, but a somewhat *universal*, *canonical* model, arising in a variety of fields and problems.

The transformation was studied, extended and applied in numerous articles, and summarized in reviews (Hernández-Bermejo and Fairén 1997; Rocha Filho et al. 2005; Brenig 2018) and books (Szederkényi 2012; Szederkenyi, Magyar, and Hangos 2018). Despite the wealth of literature on the subject, applications in theoretical ecology have been so far quite limited (but see Miller and Allesina (2021)).

The goal of this work is to provide a concise, self-contained introduction to the transformation, illustrated by a number of examples taken from the ecological, evolutionary and epidemiological theory, with the hope of popularizing what is a powerful, straightforward approach. The material requires some basic familiarity with differential equations and linear algebra; any advanced concept is explained in detail—though the exposition is not as formal as what found in the mathematical literature. Throughout, we emphasize applications to the problem of determining stability of a biological system via Lyapunov's direct method.

While most of the material is a review or a re-elaboration of published results, we highlight two aspects that are rarely discussed: first, we show that stability can often be proven in a straightforward way by considering that the perturbations of the transformed system are constrained by the perturbations of the original system—and have therefore a characteristic form; second, we discuss at length the (and provide code for) numerical approaches that can be implemented to facilitate the task of proving stability via this transformation.

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We start by deriving the transformation of QP systems into GLV, using the Leslie-Gower predator-prey model as an example; next, we analyze five models taken from the ecological, evolutionary and epidemiological literature, and use the transformation to prove global asymptotic stability; we then show how non-QP systems can be turned into GLV via auxiliary variables or an appropriate rescaling of time; we conclude by briefly presenting more advanced techniques. The Appendix discusses numerical approaches meant to facilitate the application of this methods to systems of interest.

2 Quasi-monomial transformation

2.1 Generalized Lotka-Volterra model

The Generalized Lotka-Volterra model for m interacting populations can be written as:

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

where $\dot{x}_i$ is the derivative with respect to time of the size (or density) of population i, r is a vector of length m containing the intrinsic growth rates (for producers) or mortality rates (for consumers), and A is an $m \times m$ matrix whose coefficients A_{ij} measure the effect of population j on the growth of population i.

This set of equations admits up to 2^m equilibria (i.e., choices of x such that $\dot{x}_i = 0$ for all i), in which some of the populations are present at positive density (called *feasible*), and others are absent. If there is a feasible equilibrium encompassing all populations, it is called the coexistence equilibrium, which we indicate as $x^\star$. If the matrix A has full rank, the coexistence equilibrium is unique and can be computed as $x^\star = -A^{-1}r$. The existence of an equilibrium is necessary, but not sufficient for coexistence in the model. For a review of the GLV system, and closely related models, see Hofbauer and Sigmund (1998).

2.2 Quasi-Polynomial systems

We now introduce a generalization of Eq. 1, defining the class of quasi-polynomial (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 $B = I_n$ (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 allow any B composed of real numbers, we obtain a *quasi-polynomial* (QP) system.

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 coexistence equilibrium for the model is given by $y_1^\star = \frac{\rho_1 \alpha_2}{\rho_2 \alpha_1 + \alpha_2}$ and $y_2^\star = \frac{\rho_1 \rho_2}{\rho_2 \alpha_1 + \alpha_2}$. As we demonstrate below, the equilibrium is globally asymptotically stable—all trajectories starting at positive densities will eventually reach it.
The system differs from GLV in that we have a ratio between the predator and prey in the equation for the predator; it is however a QP system, as seen by defining:

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

2.3 From Quasi-Polynomial to Generalized Lotka-Volterra

For a system in QP form (Eq. 2), we define the set of m *quasi-monomials* as:

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

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 $\dot{\log y_i}$ defines the quasi-monomials in x. Here we concentrate on the most common case in which the number of *quasi-monomials*, m, is larger or equal than the number of equations in the QP system, n, and the matrix B has rank n. In such cases, the GLV embedding will result in a system that is of the same dimension of the original system, or larger. A similar approach can be employed when this is not the case (Hernández-Bermejo and Fairén 1997).

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.

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:

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

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:

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

along with the initial conditions $x(0) = (x_1(0), x_2(0), x_3(0))^T = (y_1(0), y_2(0), y_2(0)/y_1(0))^T$.

2.4 Equivalence between representations

The original QP system and its GLV counterpart are equivalent, in the sense that if $y^\star$ is the coexistence equilibrium of the original system, then there is a coexistence equilibrium for the transformed system, calculated as $x_i^\star = \prod_k (y_k^\star)^{B_{ik}}$. Moreover, the stability of the coexistence equilibrium is unchanged. Mathematically, the two representations are said to be *topologically equivalent*: there is a transformation (technically, a *diffeomorphism* defined by Eq. 5) mapping the phase space of one representation into that for the other (Hernández-Bermejo and Fairén 1997).

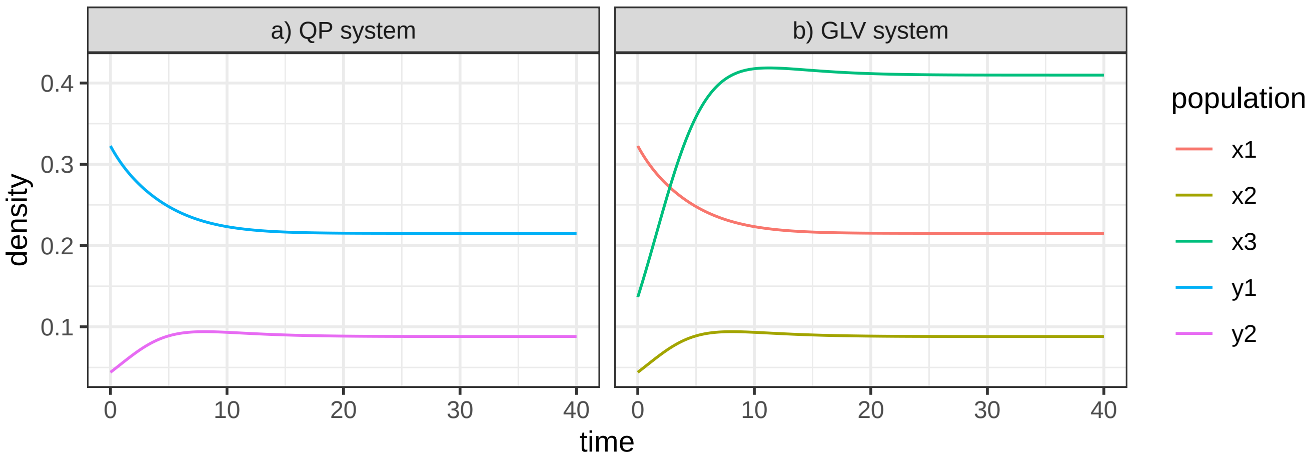

Figure 1: Dynamics for the Leslie-Gower model in its original (QP) formulation and once transformed into a 3-dimensional GLV system. Note that $x_1 = y_1$ and $x_2 = y_2$, and hence the respective trajectories are identical. The relationship $x_3 = x_2/x_1 = y_2/y_1$ is maintained through the dynamics.

Take the original system, with initial conditions $y(0)$; we want to simulate the dynamics of the original and transformed systems. Clearly, the initial conditions of the original system are related to those of the transformed system. We can calculate the initial conditions for the transformed system as:

$$\begin{aligned} x_i(0) &= \prod_k y_k(0)^{B_{ik}} \\ \log x_i(0) &= \sum_k B_{ik} \log y_k(0) \\ \log x_i(0) &= (B \log y_k(0))_i \\ x_i(0) &= \exp(B \log y_k(0))_i \end{aligned} \tag{11}$$

where the functions log and exp are applied element by element when the argument is a vector. As such, we can compute the initial conditions in matrix form as $x(0) = \exp(B \log y(0))$, making sure that the initial conditions of the transformed system are consistent with those of the original system. Take the Leslie-Gower model: in Fig. 1 we report the dynamics of the original and transformed model, showing that the equilibrium, trajectories and stability are consistent between the two representations of the same dynamics.

3 Stability via Lyapunov's direct method

3.1 Lyapunov's direct method

Provided with an $n-$dimensional, autonomous system of differential equations $\dot{y}_i$ having an equilibrium $y^\star = 0$ at the origin $\dot{y}_i|_{y=0} = 0 \, \forall i$, we want to establish the stability of the equilibrium. We use Lyapunov's direct method (also called "second method"), which employs a function (called a *Lyapunov function*) to determine stability or instability in a region of interest (Lyapunov 1992).

Stability. An equilibrium $y^\star$ is stable if for every choice of $\epsilon > 0$, there is a choice of $\delta > 0$ such that if $\|y(0) - y^\star\| < \delta$, then $\|y(t) - y^\star\| < \epsilon$ for every $t \geq 0$ (i.e., we can always identify an $n-$dimensional "ball" around the equilibrium such that trajectories starting in the ball cannot escape the volume defined by another ball).

Asymptotic stability. If an equilibrium is stable and further $y(t) \to y^\star$ as $t \to \infty$, the equilibrium is asymptotically stable (i.e., trajectories starting from a defined region will eventually reach the equilibrium). The set of initial conditions leading to the equilibrium is called the *region of attraction* of the equilibrium. If the region of attraction is the entire space, then the equilibrium is globally asymptotically stable.

Lyapunov's direct method. Take a subset of $\mathbb{R}^n$, $\mathcal{D}$, containing the origin. If one can identify a suitable function V such that a) $V(y^\star) = 0$, b) $V(y) > 0$ for all $y \in D - y^\star$ and c) $\dot{V}(y) < 0$ for all $y \in D - y^\star$, then

$y^\star$ is asymptotically stable. If moreover the trajectories started in $\mathcal{D}$ remain in $\mathcal{D}$ (i.e., $\mathcal{D}$ is an invariant manifold for the dynamics), and $V(y)$ is unbounded in $\mathcal{D}$ (i.e., $\|V(y)\| \to \infty$ when $y \to \partial D$), then $y^\star$ is globally asymptotically stable.

LaSalle's invariance principle. The condition $\dot{V}(y) < 0$ can be often relaxed to $\dot{V}(y) \leq 0$. In such cases, one can apply LaSalle's invariance principle and conclude that any trajectory starting in $\mathcal{D}$ will converge to the *largest invariant set* included in set of points for which $\dot{V}(y) = 0$. In practice, we can prove stability of the equilibrium whenever we can identify a function $V(y)$ such that $\dot{V}(y) \leq 0$, and the equilibrium is the only trajectory contained in the sub-space of $\mathcal{D}$ defined by $\dot{V}(y) = 0$.

For a detailed introduction to Lyapunov's second method, as well as algorithms to build Lyapunov functions, see Nikravesh (2018).

3.2 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:

$$\begin{cases} V_{x_i} = x_i - x_i^\star - x_i^\star \log \frac{x_i}{x_i^\star} \\ V = \sum_i w_i V_{x_i} \end{cases} \tag{12}$$

where the weights $w_1, \dots w_n$ are positive. Note that each function V_{x_i} is clearly positive whenever $x_i > 0$ and $x_i \neq x_i^\star$; moreover $V_{x_i} \to \infty$ whenever $x_i \to \infty$ or $x_i \to 0$ (i.e., the function increases to infinity at the boundaries of the *positive orthant*, $\mathbb{R}^n_+$). As such, if we can find weights such that $\dot{V} = \sum_i w_i \dot{V}_{x_i} \leq 0$, we can attempt proving stability (possibly, by invoking LaSalle's invariance principle). Deriving:

$$\begin{aligned} \dot{V} &= \sum_i w_i \left(\dot{x}_i - x_i^\star \dot{\overline{\log x_i}} \right) \\ &= \sum_i w_i \left(x_i \sum_j A_{ij} \Delta x_j - x_i^\star \sum_j A_{ij} \Delta x_j \right) \\ &= \sum_i w_i \left(\Delta x_i \sum_j A_{ij} \Delta x_j \right) \\ &= \sum_i \Delta x_i w_i \sum_j A_{ij} \Delta x_j \\ &= \sum_i \sum_j w_i A_{ij} \Delta x_i \Delta x_j \end{aligned} \tag{13}$$

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:

$$\dot{V} = \frac{1}{2} \sum_i \sum_j (w_i A_{ij} + A_{ji} w_j) \Delta x_i \Delta x_j = \sum_i \sum_j G_{ij} \Delta x_i \Delta x_j \tag{14}$$

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 $x^\star$.

Importantly, these are sufficient, but not necessary conditions for stability—while weights that make G negative definite might not exist, the system could still be stable, and a Lyapunov function of a different form could prove the result.

3.3 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 positive 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. 14 if the matrix G is not negative (semi-)definite.

The search for weights that make G negative semi-definite (called *admissibility*) has been a focus of the literature on Lyapunov functions for GLV and QP systems (Figueiredo, Gleria, and Rocha Filho 2000; Gléria, Figueiredo, and Rocha Filho 2003). Note however that, when we represent an $n-$dimensional QP-system using an $m-$dimensional GLV system, the quasi-monomials x_i are functions 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 $\Delta x_i = \prod_k y_k^{B_{ik}} - \prod_k (y_k^\star)^{B_{ik}}$.

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. 14 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. 12 for the QP-representation of the Leslie-Gower model (Eq. 10). A convenient choice of weights is $w = (0, \rho_1\alpha_1/\alpha_2 + 1, \rho_2)^T$, yielding:

$$G = \frac{1}{2}(D(w)A + A^T D(w)) = \begin{pmatrix} 0 & 0 & \frac{\rho_2}{2} \\ 0 & 0 & -\frac{\alpha_2}{2} \\ \frac{\rho_2}{2} & -\frac{\alpha_2}{2} & -\rho_2\alpha_2 \end{pmatrix} \tag{15}$$

We can calculate $\dot{V}$ as:

$$\begin{aligned} \dot{V} &= \sum_i \sum_j G_{ij} \Delta x_i \Delta x_j \\ &= \Delta x_3(\rho_2 \Delta x_1 - \alpha_2 \Delta x_2 - \rho_2 \alpha_2 \Delta x_3) \end{aligned} \tag{16}$$

Note that the function above can assume positive values when we are free to choose the Δx_i however we wish. For example, take all parameters to be equal to one and $\Delta x_3 = 1$, $\Delta x_2 = 1$ and $\Delta x_1 = 3$; then $\dot{V} = 1$. However, we are not free to choose the perturbations arbitrarily, because they need to be consistent with our definition of the quasi-monomials. Substituting $\Delta x_1 = y_1 - y_1^\star$, $\Delta x_2 = y_2 - y_2^\star$ and $\Delta x_3 = y_2/y_1 - y_2^\star/y_1^\star$ shows that the function V does not grow in time when perturbations are admissible:

$$\dot{V} = -\frac{(\rho_2 + y_1)(\rho_2 y_1 - \alpha_2 y_2)^2}{\alpha_2 y_1^2} \leq 0 \tag{17}$$

To prove stability, we need to show that the equilibrium is the only trajectory contained in the manifold (i.e., space) defined by $\dot{V} = 0$. In such case, $\rho_2 y_1 = \alpha_2 y_2$; substituting in the equation for the predator we find $\dot{y_2}|_{\dot{V}=0} = 0$, meaning that only trajectories for which y_2 is constant are contained in the space defined by $\dot{V} = 0$. This in turn means that y_1 must also be constant, proving that the equilibrium $y^\star$ is the only trajectory contained in $\dot{V} = 0$ and therefore the global asymptotic stability of the equilibrium.

4 Examples: quasi-polynomial systems

In this section we present five simple examples in which dynamics are defined by a quasi-polynomial system of differential equations. We prove stability using the quasi-monomial transformation in conjunction with the candidate Lyapunov function in Eq. 12. See Rocha Filho et al. (2005) for other relevant examples.

4.1 Growth under Allee effect

To set the stage for more complex derivations, we analyze the simple case of a single population experiencing an Allee effect: when the density of a population is below the critical threshold α, the population declines; between $\alpha < y < \beta$, it grows; and, finally, it declines if the density is above β. Growth in this model can be represented as a cubic polynomial:

$$\dot{y} = y(y-\alpha)(\beta - y) = y(-\alpha\beta + (\alpha+\beta)y - y^2) \tag{18}$$

Clearly, there are three equilibria, corresponding to the absence of the population, $y^\star = \alpha$, and $y^\star = \beta$. It is also fairly simple to show (for example using a graphical method, or a quadratic Lyapunov function) that any initial condition $y(0) < \alpha$ leads to the extinction of the population, while any initial density above α defines trajectories converging to β. We want to show that the equilibrium $y^\star = \beta$ is asymptotically stable for any trajectory starting at $y(0) > \alpha$. First, we rewrite the system in QP form, and then turn it into a two-dimensional GLV system:

$$\begin{aligned} x = \begin{pmatrix} y \\ y^2 \end{pmatrix} \quad s = (-\alpha\beta) \quad M = \begin{pmatrix} \alpha+\beta & -1 \end{pmatrix} \quad B = \begin{pmatrix} 1 \\ 2 \end{pmatrix} \\ r = Bs = \begin{pmatrix} -\alpha\beta \\ -2\alpha\beta \end{pmatrix} \quad A = BM = \begin{pmatrix} \alpha+\beta & -1 \\ 2(\alpha+\beta) & -2 \end{pmatrix} \end{aligned} \tag{19}$$

Clearly, the matrix A has rank one. Now we consider the matrix $G = \frac{1}{2}(D(w)A + A^T D(w))$:

$$G = \begin{pmatrix} w_1(\alpha+\beta) & (\alpha+\beta)w_2 - \frac{1}{2}w_1 \\ (\alpha+\beta)w_2 - \frac{1}{2}w_1 & -2w_2 \end{pmatrix} \tag{20}$$

along with the perturbation $\Delta x = (y - y^\star, y^2 - y^{\star 2})^T = (y-\beta, y^2-\beta^2)^T$. We find:

$$\dot{V} = -(y-\alpha)(\beta-y)^2(w_1 + 2w_2(\beta+y)) \tag{21}$$

Because $(\beta-y)^2(w_1+2w_2(\beta+y)) > 0$ for any choice of $w_1 > 0$ and $w_2 > 0$, then the function $\dot{V}$ is negative whenever $y > \alpha$ and $y \neq \beta$, proving stability (given that if $y(0) > \alpha$, then $y(t) > \alpha$ for every t).

4.2 Leslie-Gower without intraspecific competition

Take the Leslie-Gower model above and set the coefficient modeling intraspecific competition to zero. The model simplifies to:

$$\begin{cases} \dot{y}_1 = y_1(\rho_1 - \alpha_1 y_2) \\ \dot{y}_2 = y_2\left(\rho_2 - \alpha_2 \frac{y_2}{y_1}\right) \end{cases} \tag{22}$$

The model has a feasible equilibrium $y_1^\star = \alpha_2\rho_1/(\alpha_1\rho_2)$, $y_2^\star = \rho_1/\alpha_1$, and we want to prove that the equilibrium is globally attractive. We can identify two quasi-monomials (i.e., in this case $n = m$). As such, we can recast the model as a GLV with two equations. We define:

$$\begin{aligned} x = \begin{pmatrix} y_2 \\ \frac{y_2}{y_1} \end{pmatrix} \quad s = \begin{pmatrix} \rho_1 \\ \rho_2 \end{pmatrix} \quad M = \begin{pmatrix} -\alpha_1 & 0 \\ 0 & -\alpha_2 \end{pmatrix} \quad B = \begin{pmatrix} 0 & 1 \\ -1 & 1 \end{pmatrix} \\ r = Bs = \begin{pmatrix} \rho_2 \\ \rho_2 - \rho_1 \end{pmatrix} \quad A = BM = \begin{pmatrix} 0 & -\alpha_2 \\ \alpha_1 & -\alpha_2 \end{pmatrix} \end{aligned} \tag{23}$$

These parameters define a predator-prey GLV model in which the predator experiences intraspecific competition. The coexistence equilibrium is stable, as shown by considering the candidate Lyapunov function with weights $w = (1/\alpha_2, 1/\alpha_1)^T$, and the perturbations $\Delta x = (\Delta x_1, \Delta x_2)^T = (y_2 - y_2^\star, y_2/y_1 - y_2^\star/y_1^\star)^T = (\Delta y_2, (y_2 y_1^\star - y_1 y_2^\star)/(y_1 y_1^\star))^T$. Deriving with respect to time, we obtain:

$$\dot{V} = \frac{1}{2}\Delta x^T (D(w)A + A^T D(w))\Delta x = -\frac{\alpha_2}{\alpha_1}\Delta x_2^2 = -\frac{\alpha_2}{\alpha_1}\left(\frac{y_2 y_1^\star - y_1 y_2^\star}{y_1 y_1^\star}\right)^2 \leq 0 \tag{24}$$

Thus, $\dot{V} \leq 0$, with equality attained when $y_2 y_1^\star - y_1 y_2^\star$; when this is the case, the equation $\dot{y}_2 = 0$, and therefore the equilibrium is the only trajectory contained in the space defining $\dot{V} = 0$ and thus is globally stable.

4.3 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:

$$\begin{cases} \dot{y}_1 = \delta - \delta y_1 - \beta y_1 y_2 = y_1 \left(-\delta + \delta \dfrac{1}{y_1} - \beta y_2\right) \\ \dot{y}_2 = -(\delta+\gamma) y_2 + \beta y_1 y_2 = y_2 \left(-(\delta+\gamma) + \beta y_1\right) \\ \dot{y}_3 = \gamma y_2 - \delta y_3 = y_3 \left(-\delta + \gamma \dfrac{y_2}{y_3}\right) \end{cases} \tag{25}$$

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:

$$\begin{gathered} x = \begin{pmatrix} y_1 \\ y_2 \\ \frac{1}{y_1} \\ \frac{y_2}{y_3} \end{pmatrix} \quad s = \begin{pmatrix} -\delta \\ -\delta-\gamma \\ -\delta \end{pmatrix} \quad M = \begin{pmatrix} 0 & -\beta & \delta & 0 \\ \beta & 0 & 0 & 0 \\ 0 & 0 & 0 & \gamma \end{pmatrix} \quad B = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ -1 & 0 & 0 \\ 0 & 1 & -1 \end{pmatrix} \\ r = Bs = \begin{pmatrix} -\delta \\ -\delta-\gamma \\ \delta \\ -\gamma \end{pmatrix} \quad A = BM = \begin{pmatrix} 0 & -\beta & \delta & 0 \\ \beta & 0 & 0 & 0 \\ 0 & \beta & -\delta & 0 \\ \beta & 0 & 0 & -\gamma \end{pmatrix} \end{gathered} \tag{26}$$

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:

$$\dot{V} = \frac{1}{2}\Delta x^T (D(w)A + A^T D(w))\Delta x = -\delta \frac{(y_1 - y_1^\star)^2}{y_1 y_1^\star} \leq 0 \tag{27}$$

Note that this choice of weights does not result in a negative semi-definite matrix: the nonzero eigenvalues of $G = \frac{1}{2}(D(w)A + A^T D(w))$ 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 $\dot{V} = 0$. We find that $\dot{y}_2|_{\dot{V}=0} = 0$, meaning that y_2 must be constant for a trajectory to be contained in the space defined by $\dot{V} = 0$; but if both y_1 and y_2 are constants, then y_3 must be constant as well given that $y_1 + y_2 + y_3 = 1$, concluding the proof.

4.4 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:

$$\begin{cases} \dot{z}_i = \kappa_i - \delta_i z_i - z_i \sum_j C_{ij} y_j \\ \dot{y}_i = -\mu_i y_i + y_i \epsilon_i \sum_j C_{ji} z_j \end{cases} \tag{28}$$

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: $x = (z, y, 1/z)^T$. This allows us to rewrite the system in Eq. 28 as a QP-system defined by:

$$s = \begin{pmatrix} -\delta \\ -\mu \end{pmatrix} \quad M = \begin{pmatrix} 0_{n\times n} & -C & D(\kappa) \\ D(\epsilon)C^T & 0_{n\times n} & 0_{n\times n} \end{pmatrix} \quad B = \begin{pmatrix} I_n & 0_{n\times n} \\ 0_{n\times n} & I_n \\ -I_n & 0_{n\times n} \end{pmatrix} \tag{29}$$

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:

$$r = Bs = \begin{pmatrix} -\delta \\ -\mu \\ \delta \end{pmatrix} \quad A = BM = \begin{pmatrix} 0_{n\times n} & -C & D(\kappa) \\ D(\epsilon)C^T & 0_{n\times n} & 0_{n\times n} \\ 0_{n\times n} & C & -D(\kappa) \end{pmatrix} \tag{30}$$

We now consider the candidate Lyapunov function in Eq. 12 with weights $w = (1_n, 1/\epsilon, 0_n)$. Our matrix G becomes:

$$G = \frac{1}{2}(D(w)A + A^T D(w)) = \begin{pmatrix} 0_{n\times n} & 0_{n\times n} & \frac{1}{2}D(\kappa) \\ 0_{n\times n} & 0_{n\times n} & 0_{n\times n} \\ \frac{1}{2}D(\kappa) & 0_{n\times n} & 0_{n\times n} \end{pmatrix} \tag{31}$$

The matrix is clearly not negative semi-definite (just take $n = 1$). 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. 14 reduces to:

$$\dot{V} = \sum_i k_i (z_i - z_i^\star) \left(\frac{1}{z_i} - \frac{1}{z_i^\star} \right) = -\sum_i \frac{k_i}{z_i z_i^\star} (z_i - z_i^\star)^2 \leq 0 \tag{32}$$

Note that when $\dot{V} = 0$ the resources are all at equilibrium; but this implies that the consumers must also be at equilibrium, because all $\dot{y}_i|_{\dot{V}=0} = \dot{y}_i|_{z=z^\star} = 0$.

4.5 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:

$$\begin{cases} \dot{y}_1 = y_1(2y_3^2 + y_1 y_3 - 2y_1 y_2 - y_2^2) \\ \dot{y}_2 = y_2(2y_1^2 + y_1 y_2 - 2y_2 y_3 - y_3^2) \\ \dot{y}_3 = y_3(2y_2^2 + y_2 y_3 - 2y_1 y_3 - y_2^2) \end{cases} \tag{33}$$

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:

$$x = \begin{pmatrix} y_1^2 \\ y_2^2 \\ y_3^2 \\ y_1 y_2 \\ y_1 y_3 \\ y_2 y_3 \end{pmatrix} \tag{34}$$

and parameters

$$s = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix} \quad M = \begin{pmatrix} 0 & -1 & 2 & -2 & 1 & 0 \\ 2 & 0 & -1 & 1 & 0 & -2 \\ -1 & 2 & 0 & 0 & -2 & 1 \end{pmatrix} \quad B = \begin{pmatrix} 2 & 0 & 0 \\ 0 & 2 & 0 \\ 0 & 0 & 2 \\ 1 & 1 & 0 \\ 1 & 0 & 1 \\ 0 & 1 & 1 \end{pmatrix} \tag{35}$$

As such, the model in Eq. 33 with three variables ($n = 3$, 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 ($m = 6$), and parameters:

$$r = Bs = 0_m \quad A = BM = \begin{pmatrix} 0 & -2 & 4 & -4 & 2 & 0 \\ 4 & 0 & -2 & 2 & 0 & -4 \\ -2 & 4 & 0 & 0 & -4 & 2 \\ 2 & -1 & 1 & -1 & 1 & -2 \\ -1 & 1 & 2 & -2 & -1 & 1 \\ 1 & 2 & -1 & 1 & -2 & -1 \end{pmatrix} \tag{36}$$

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. 12 function with weights $w = (1, 1, 1, 2, 2, 2)^T$ and considering the perturbations $\Delta x = (y_1^2 - {y_1^\star}^2, y_2^2 - {y_2^\star}^2, y_3^2 - {y_3^\star}^2, y_1 y_2 - y_1^\star y_2^\star, y_1 y_3 - y_1^\star y_3^\star, y_2 y_3 - y_2^\star y_3^\star)^T$, we obtain:

$$\begin{aligned} \dot{V} &= -\frac{2}{3}\left(y_1^2 + y_2^2 + y_3^2 - y_1 y_2 - y_1 y_3 - y_2 y_3\right) \\ &= -\frac{1}{3}\left((y_1 - y_2)^2 + (y_1 - y_3)^2 + (y_2 - y_3)^2\right) \leq 0 \end{aligned} \tag{37}$$

The derivative is thus negative for any y but the equilibrium point, proving the stability of the equilibrium.

5 Examples: non quasi-polynomial systems

Several other models can be turned into QP system by introducing some auxiliary functions, or simply rescaling time. We provide an example of each.

5.1 Facultative mutualism with Type-II functional response

We consider a very simple model of facultative mutualism:

$$\begin{cases} \dot{z}_1 = z_1 \left(\rho_1 - \alpha_1 z_1 + \beta_1 \frac{z_2}{(\gamma_2 + z_2)}\right) \\ \dot{z}_2 = z_2 \left(\rho_2 - \alpha_2 z_2 + \beta_2 \frac{z_1}{(\gamma_1 + z_1)}\right) \end{cases} \tag{38}$$

This model is not in QP form. We therefore need to create *auxiliary variables* in order to recast the system as a (typically, larger) QP model. We can then apply the same machinery and turn it into a (typically, even larger!) GLV model.

A convenient choice is to choose $y_3 = 1/(\gamma_1 + z_1)$, because $\frac{\partial y_3}{\partial z_1} = -\frac{1}{(\gamma_1+z_1)^2} = -y_3^2$, and as such $\dot{y}_3 = -y_3^2 \dot{z}_1$, guaranteeing that the result will be a QP system.

We therefore define $y_1 = z_1$, $y_2 = z_2$, $y_3 = 1/(\gamma_1 + z_1)$ and $y_4 = 1/(\gamma_2 + z_2)$, resulting in a four-dimensional QP system:

$$\begin{cases} \dot{y}_1 = y_1 \left(\rho_1 - \alpha_1 y_1 + \beta_1 y_2 y_4\right) \\ \dot{y}_2 = y_2 \left(\rho_2 - \alpha_2 y_2 + \beta_2 y_1 y_3\right) \\ \dot{y}_3 = -y_3^2 \dot{y}_1 = y_3(-\rho_1 y_1 y_3 + \alpha_1 y_1^2 y_3 - \beta_1 y_1 y_2 y_3 y_4) \\ \dot{y}_4 = -y_4^2 \dot{y}_2 = y_4(-\rho_2 y_2 y_4 + \alpha_2 y_2^2 y_4 - \beta_2 y_1 y_2 y_3 y_4) \end{cases} \tag{39}$$

We now proceed as before: we identify seven quasi-monomials, and represent the system as a GLV model:

$$\begin{gathered} s = \begin{pmatrix} \rho_1 \\ \rho_2 \\ 0 \\ 0 \end{pmatrix} \quad B = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 \\ 2 & 0 & 1 & 0 \\ 0 & 2 & 0 & 1 \\ 1 & 1 & 1 & 1 \end{pmatrix} \quad M = \begin{pmatrix} -\alpha_1 & 0 & 0 & \beta_1 & 0 & 0 & 0 \\ 0 & -\alpha_2 & \beta_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & -\rho_1 & 0 & \alpha_1 & 0 & -\beta_1 \\ 0 & 0 & 0 & -\rho_2 & 0 & \alpha_2 & -\beta_2 \end{pmatrix} \\ x = \begin{pmatrix} y_1 \\ y_2 \\ y_1 y_3 \\ y_2 y_4 \\ y_1^2 y_3 \\ y_2^2 y_4 \\ y_1 y_2 y_3 y_4 \end{pmatrix} \quad r = \begin{pmatrix} \rho_1 \\ \rho_2 \\ \rho_1 \\ \rho_2 \\ 2\rho_1 \\ 2\rho_2 \\ \rho_1 + \rho_2 \end{pmatrix} \quad A = \begin{pmatrix} -\alpha_1 & 0 & 0 & \beta_1 & 0 & 0 & 0 \\ 0 & -\alpha_2 & \beta_2 & 0 & 0 & 0 & 0 \\ -\alpha_1 & 0 & -\rho_1 & \beta_1 & \alpha_1 & 0 & -\beta_1 \\ 0 & -\alpha_2 & \beta_2 & -\rho_2 & 0 & \alpha_2 & -\beta_2 \\ -2\alpha_1 & 0 & -\rho_1 & 2\beta_1 & \alpha_1 & 0 & -\beta_1 \\ 0 & -2\alpha_2 & 2\beta_2 & -\rho_2 & 0 & \alpha_2 & -\beta_2 \\ -\alpha_1 & -\alpha_2 & \beta_2 - \rho_1 & \beta_1 - \rho_2 & \alpha_1 & \alpha_2 & -\beta_1 - \beta_2 \end{pmatrix} \end{gathered} \tag{40}$$

Despite the complicated appearance, it is possible to prove the stability of the model in a straightforward way: choose the first two weights (w_1, w_2) to be positive, and all other weights to be zero. The matrix $G = \frac{1}{2}(D(w)A + A^T D(w))$ becomes very sparse, yielding:

$$\dot{V} = \Delta x^T G \Delta x = w_1 \Delta x_1 (\beta_1 \Delta x_4 - \alpha_1 \Delta x_1) + w_2 \Delta x_2 (\beta_2 \Delta x_3 - \alpha_2 \Delta x_2) \tag{41}$$

Substituting the perturbations measured in the QP, and then the original coordinates, $\Delta x_1 = \Delta y_1 = \Delta z_1$, $\Delta x_2 = \Delta y_2 = \Delta z_2$, $\Delta x_3 = y_1 y_3 - y_1^\star y_3^\star = z_1/(\gamma_1 + z_1) - z_1^\star/(\gamma_1 + z_1^\star) = \gamma_1 \Delta z_1/((\gamma_1 + z_1)(\gamma_1 + z_1^\star))$, $\Delta x_4 = \gamma_2 \Delta z_2/((\gamma_2 + z_2)(\gamma_2 + z_2^\star))$, the expression reduces to:

$$\dot{V} = -\alpha_1 w_1 \Delta z_1^2 - \alpha_2 w_2 \Delta z_2^2 + \Delta z_1 \Delta z_2 \left(\frac{\gamma_2 \beta_1 w_1}{(\gamma_2 + z_2)(\gamma_2 + z_2^\star)} + \frac{\gamma_1 \beta_2 w_2}{(\gamma_1 + z_1)(\gamma_1 + z_1^\star)} \right) \tag{42}$$

Naturally, the first two terms are negative (as long as the two weights are positive), and the coefficients in parenthesis are positive. As such whenever $\Delta z_1 \Delta z_2 \le 0$, $\dot{V} \le 0$. When this is not the case, we can bound the function from above by noticing that the term in parenthesis is maximal when $z_1 \to 0$ and $z_2 \to 0$:

$$\begin{aligned} \dot{V} &\le -\alpha_1 w_1 \Delta z_1^2 - \alpha_2 w_2 \Delta z_2^2 + \Delta z_1 \Delta z_2 \left(\frac{\beta_1 w_1}{(\gamma_2 + z_2^\star)} + \frac{\beta_2 w_2}{(\gamma_1 + z_1^\star)} \right) \\ &\le -\alpha_1 w_1 \Delta z_1^2 - \alpha_2 w_2 \Delta z_2^2 + \Delta z_1 \Delta z_2 \left(w_1 \frac{\alpha_1 z_1^\star - \rho_1}{z_2^\star} + w_2 \frac{\alpha_2 z_2^\star - \rho_2}{z_1^\star} \right) \\ &\le -\alpha_1 w_1 \Delta z_1^2 - \alpha_2 w_2 \Delta z_2^2 + \Delta z_1 \Delta z_2 \left(w_1 \frac{\alpha_1 z_1^\star}{z_2^\star} + w_2 \frac{\alpha_2 z_2^\star}{z_1^\star} \right) \end{aligned} \tag{43}$$

Finally, choosing $w_1 = 1/(\alpha_1 z_1^2)$ and $w_2 = 1/(\alpha_2 z_2^2)$, we obtain:

$$\begin{aligned}\dot{V} &\leq -\frac{1}{(z_1^\star)^2}\Delta z_1^2 + 2\Delta z_1 \Delta z_2 \frac{1}{z_1^\star z_2^\star} - -\frac{1}{(z_2^\star)^2}\Delta z_2^2 \\ &\leq -\left(\frac{\Delta z_1}{z_1^\star} - \frac{\Delta z_2}{z_2^\star}\right)^2 \\ &\leq 0\end{aligned} \tag{44}$$

5.2 Rosenzweig-MacArthur model with competing prey

Sometimes, we do not need to introduce auxiliary variables to turn our model of interest into a QP system. For example, consider the Rosenzweig-MacArthur model in which a predator consumes two prey that are competing for resources:

$$\begin{cases}\dot{z}_1 = z_1(\rho_1 - C_{11}z_1 - C_{12}z_2) - \beta_1 \frac{z_1 z_3}{\gamma + z_1 + z_2} \\ \dot{z}_2 = z_2(\rho_2 - C_{21}z_1 - C_{22}z_2) - \beta_2 \frac{z_2 z_3}{\gamma + z_1 + z_2} \\ \dot{z}_3 = z_3 \left(-\delta + \epsilon \frac{\beta_1 z_1 + \beta_2 z_2}{\gamma + z_1 + z_2}\right)\end{cases} \tag{45}$$

If we choose a variable rescale of time $t = \tau(\gamma + z_1 + z_2)$, which is akin to multiplying all equations by $(\gamma + z_1 + z_2) > 0$, the resulting system is in QP form:

$$\begin{cases}\dot{y}_1 = y_1(\rho_1 - C_{11}y_1 - C_{12}y_2)(\gamma + y_1 + y_2) - \beta_1 y_1 y_3 \\ \dot{y}_2 = y_2(\rho_2 - C_{21}y_1 - C_{22}y_2)(\gamma + y_1 + y_2) - \beta_2 y_2 y_3 \\ \dot{y}_3 = y_3\left(-\delta(\gamma + y_1 + y_2) + \epsilon(\beta_1 z_1 + \beta_2 z_2)\right)\end{cases} \tag{46}$$

We therefore define:

$$s = \begin{pmatrix}\rho_1\gamma \\ \rho_2\gamma \\ -\delta\gamma\end{pmatrix} \quad B = \begin{pmatrix}1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \\ 2 & 0 & 0 \\ 0 & 2 & 0 \\ 1 & 1 & 0\end{pmatrix} \quad M = \begin{pmatrix}\rho_1 - \gamma C_{11} & \rho_1 - \gamma C_{12} & -\beta_1 & -C_{11} & -C_{12} & -(C_{11} + C_{12}) \\ \rho_2 - \gamma C_{21} & \rho_2 - \gamma C_{22} & -\beta_2 & -C_{21} & -C_{22} & -(C_{21} + C_{22}) \\ \epsilon\beta_1 - \delta & \epsilon\beta_2 - \delta & 0 & 0 & 0 & 0\end{pmatrix} \quad x = \begin{pmatrix}y_1 \\ y_2 \\ y_3 \\ y_1^2 \\ y_2^2 \\ y_1 y_2\end{pmatrix} \tag{47}$$

The model can give rise to complex dynamics (e.g., even for a single predator and prey we can have stable limit cycles). We therefore choose parameters in which a coexistence equilibrium exists, is feasible, and, as we will prove, globally stable.

$$\delta = 13 \quad \epsilon = 9 \quad \gamma = 4 \quad \rho = \begin{pmatrix}15 \\ 18\end{pmatrix} \quad \beta = \begin{pmatrix}3 \\ 8\end{pmatrix} \quad C = \begin{pmatrix}20 & 5 \\ 4 & 18\end{pmatrix} \tag{48}$$

Substituting the values for the variables, and computing $r = Bs$ and $A = BM$, we obtain the six-dimensional GLV system defined by:

$$r = \begin{pmatrix}60 \\ 72 \\ -52\end{pmatrix} \quad A = \begin{pmatrix}-65 & -5 & -3 & -20 & -5 & -25 \\ 2 & -54 & -8 & -4 & -18 & -22 \\ 14 & 59 & 0 & 0 & 0 & 0 \\ -130 & -10 & -6 & -40 & -10 & -50 \\ 4 & -108 & -16 & -8 & -36 & -44 \\ -63 & -59 & -11 & -24 & -23 & -47\end{pmatrix} \tag{49}$$

6 Advanced topics

6.1 Rescaling time

In the example above, we have rescaled time to obtain a QP system. When we start from a QP system, we can always rescale time by a quasi-monomial of choice, and this rescaling maps a QP system into another QP system. Equilibria and stability are unchanged. Suppose that for the original system there is no choice of positive weights that can be used to prove stability via the candidate Lyapunov function proposed by Goh; an appropriate time rescale could yield a system for which the candidate Lyapunov function is applicable. As such, rescaling time extends the applicability of the candidate Lyapunov function.

To proceed with a quasi-monomial rescaling of time, it is convenient to rewrite the QP system by introducing a new equation for y_{n+1} such that $y_{n+1}(0) = 1$ and $\dot{y}_{n+1} = 0$. This extra equation can be thought as representing the "external environment," which does not change through the dynamics. Having defined this extra equation, we can rewrite the dynamics in Eq. 2 in a more compact form:

$$
\begin{aligned}
\dot{y}_i &= y_i \left(s_i + \sum_{j=1}^{m} M_{ij} \prod_{k=1}^{n} y_k^{B_{jk}} \right) \\
\dot{y}_i &= y_i \left(s_i y_{n+1} + \sum_{j=1}^{m} M_{ij} \prod_{k=1}^{n} y_k^{B_{jk}} \right) \\
\dot{y}_i &= y_i \left(\sum_{j=1}^{m+1} \tilde{M}_{ij} \prod_{k=1}^{n+1} y_k^{\tilde{B}_{jk}} \right)
\end{aligned}
\tag{50}
$$

where $\tilde{M}$ is the matrix M with the addition of another column containing the vector s; $\tilde{B}$ is the matrix B with the addition of a row of zeros:

$$
\tilde{M} = \left(\; M \mid s \; \right) \quad \tilde{B} = \left(\frac{B}{0_n} \right) \tag{51}
$$

with this notation at hand, we want to rescale time such that $t = \tau \prod_k y_k^{\theta_k}$, and as such $\frac{dy}{d\tau} = \frac{dy}{dt} \prod_k y_k^{\theta_k}$. Because we are multiplying all equations by a quasi monomial ($\prod_k y_k^{\theta_k}$), if the original system was quasi-polynomial, the system with rescaled time is also QP. In fact, we can compactly define the new QP system as:

$$
\tilde{s} = 0_n \quad \tilde{M} = \left(\; M \mid s \; \right) \quad \approx\!\!\!\!\!B = \left(\frac{B}{0_n} \right) + 1_{(m+1 \times n)} D(\theta) \tag{52}
$$

i.e., we have added a constant θ_k to each column in $\tilde{B}$. To show that this transformation can extend the applicability of the candidate Lyapunov function by Goh, we consider two cases of the simplest situation, in which we start from a GLV system.

To start, we take the GLV system:

$$
r = \begin{pmatrix} 47/10 \\ 43/10 \end{pmatrix} \quad A = \begin{pmatrix} 0 & -2/5 \\ 9 & -47/10 \end{pmatrix} \tag{53}
$$

This is also a QP system with $s = r$, $M = A$ and $B = I_3$. The system has a feasible, locally stable equilibrium. However, for any choice of positive $w = (w_1, w_2)^T$, at least one eigenvalue of $G = \frac{1}{2}(D(w)A + A^T D(w))$ is positive. It is therefore impossible to prove stability using Goh's candidate Lyapunov function. To prove stability, we rescale time. First, we form the augmented matrices:

$$
\tilde{M} = \begin{pmatrix} 0 & -2/5 & 47/10 \\ 9 & -47/10 & 43/10 \end{pmatrix} \quad \tilde{B} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ 0 & 0 \end{pmatrix} \tag{54}
$$

We have two special choices for rescaling time: for example, if we choose $\theta_1 = -1, \theta_2 = 0$ we are rescaling time such that now the first species serves as the external environment; choosing $\theta_1 = 0, \theta_2 = -1$ would set the second species as the external environment. With the first choice, we obtain:

$$\tilde{\tilde{B}} = \begin{pmatrix} 0 & 0 \\ -1 & 1 \\ -1 & 0 \end{pmatrix} \quad \tilde{\tilde{M}} = \tilde{\tilde{B}}\tilde{M} = \begin{pmatrix} 0 & 0 & 0 \\ 9 & -43/10 & -2/5 \\ 0 & 2/5 & -47/10 \end{pmatrix} \tag{55}$$

This means that if we rescale time such that one of the rows of $\tilde{\tilde{B}}$ is zero, we end up with a transformed GLV system with the same number of equations. I.e., the GLV system with rescaled time, and having defined $y_1 = x_2/x_1$ and $y_2 = 1/x_1$ is GLV with:

$$r = \begin{pmatrix} 9 \\ 0 \end{pmatrix} \quad A = \begin{pmatrix} -43/10 & -2/5 \\ 2/5 & -47/10 \end{pmatrix} \tag{56}$$

Notice that the off-diagonal part of A is skew-symmetric, and the diagonal is negative, ensuring stability. The Lyapunov function proposed by Goh can be applied choosing unit weights.

Through this special transformation, we have connected two seemingly different GLV models—which have the same stability properties—such that it is impossible to prove stability using the usual function in the former, and trivial in the latter. For any system of n equations, one can attempt n such special time rescalings, each zeroing a different row of $\tilde{B}$.

Now a more complex case, in which the time rescaling yields a larger-dimensional (but rank-deficient) system. Consider the competitive GLV system defined as:

$$s = \begin{pmatrix} 13/10 \\ 2/5 \\ 2 \end{pmatrix} \quad M = \begin{pmatrix} -1/2 & -1/3 & 0 \\ 0 & -1/3 & -51/50 \\ -1 & 0 & -1/4 \end{pmatrix} \tag{57}$$

The system has a feasible equilibrium, and a simple calculation shows that it is locally stable. However, one can prove that there is no suitable choice of weights such that the candidate Lyapunov function proposed by Goh is guaranteed to decrease in time: for example, compute the characteristic polynomial of $G = \frac{1}{2}(D(w)M + M^T D(w))$ and notice that the coefficients cannot be of the same sign.

We therefore compute $\tilde{M}$ and $\tilde{B}$ as:

$$\tilde{M} = \begin{pmatrix} -1/2 & -1/3 & 0 & 13/10 \\ 0 & -1/3 & -51/50 & 2/5 \\ -1 & 0 & -1/4 & 2 \end{pmatrix} \quad \tilde{\tilde{B}} = \begin{pmatrix} \theta_1 + 1 & \theta_2 & \theta_3 \\ \theta_1 & \theta_2 + 1 & \theta_3 \\ \theta_1 & \theta_2 & \theta_3 + 1 \\ \theta_1 & \theta_2 & \theta_3 \end{pmatrix} \tag{58}$$

Now we are free to choose the three coefficients defining the time rescaling $(\theta_1, \theta_2, \theta_3)$ as well as the four positive weigths (w_1, w_2, w_3, w_4). Each choice corresponds to a matrix $\tilde{G}$ $\tilde{G} = \frac{1}{2}(D(\tilde{w})\tilde{\tilde{B}}\tilde{M} + \tilde{M}^T\tilde{\tilde{B}}^T D(\tilde{w}))$, and if we can find a combination of weights and scales such that $\tilde{G}$ is negative semi-definite, we have provent the stability of the equilibrium. In this case, there are infinitely many choices: for example, take the weights to be $w_1 = 21$, $w_2 = 5$, $w_3 = 2$, and $w_4 = 12$. Then choose the values for θ that are the only real solution satisfying $\det G = 0$: $\theta = -\frac{1}{63941}(47565, 2136, 500)^T$. We obtain a matrix $\tilde{G}$ in which an eigenvalue is zero, and all others are negative, proving the stability of the original system.

6.2 Other approaches to stability for Lotka-Volterra

Conclusions

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