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Control system approaches to ecological systems analysis: Invariants and frequency response

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ABSTRACT

The steady-state assumption is a mainstay for the analysis of ecological systems with more than three or four states. However, it is well accepted in ecology that inputs to large systems come in pulses assumed to have a reasonably constant magnitude and frequency. Steady pulse inputs and the use of electro-chemical–mechanical control systems methodology enables limited short term dynamic responses of ecological systems of a scale often occurring in systems of potential engineering importance to be analyzed. This paper explores and presents a survey of multi-input–multi-output (MIMO) control systems analysis of ecosystem network models to better understand pulse frequency issues and further develop experimentally verifiable approaches to testing the MIMO concept. The analysis process is demonstrated using two network model exemplars. Two aspects of MIMO analyses appear relevant to understanding ecological systems: (1) Eigenvalue invariant analyses and singular value decomposition (SVD) analyses enable assessment of stability and relative strength of states. Eigenvalues reflect time constants and provide a check on experimentally determined system matrices. (2) Analysis of SVD versus frequency for each output indicates maximum pulse frequencies that allow system components to benefit from pulsing. As a group, MIMO analyses complement other analytical methods and provide a theoretical systems focus convenient for analyzing ecosystems from an engineering perspective.

1. Introduction

Control theory has been applied to relatively simple linear biological problems solvable with analytical techniques. Milsum (1966) and Jones (1973) applied single in-single out control theory to various problems on the human and animal scale analytically. Analytical and numerical tools available have made huge advances since their work, which enables studies of more complex multi-in–multi-out biochemical process at the human–animal scale and also at the cellular scale (Ingalls et al., 2006). More advanced non-linear analysis has been explored, especially for simpler systems (e.g., see Apreutesei, 2006), however, these approaches become practically intractable for larger systems of potential engineering interest. Thus, our emphasis is on linear systems analysis with its wide array of available solution options.

Linear Ecosystem analysis has roots in cybernetics, which is also the parent discipline of electro-chemical–mechanical control systems. A popular control system textbook of its time, Dorf (1980) cites ecosystem modeling work underway in that period. Due to the multiple inputs and outputs that typify ecosystems, control theory and systems ecology diverged. Patten (1978) and colleagues adopted the control system format and thinking and assumed steady state to develop *network environ analysis* (*NEA*) (Patten, 1978; Barber et al., 1979; Fath and Patten, 1999; Schramski, 2006). Ulanowicz (1986, 1997, 2000) developed a similar approach, *ascendency analysis*, featuring the use of information theory. We anchor our controls concepts to NEA mainly because we are most familiar with this analysis approach.

There has been much discussion in ecology about how to make models. Ecological models are gross simplifications of complex systems, whose details due to size and complexity are impossible to describe (Jorgensen and Bendoricchio, 2001). The latter authors indicate it is important to start modeling with a well defined question that circumscribes key elements and processes. Ecological models are always under-defined and as such unmodeled components and processes have a high likelihood of contributing to observed dynamics.

Network environ analysis (NEA) is the background for this review. A brief summary of the input-driven, time-forward methodology follows. (A reverse-time, output referenced analy-

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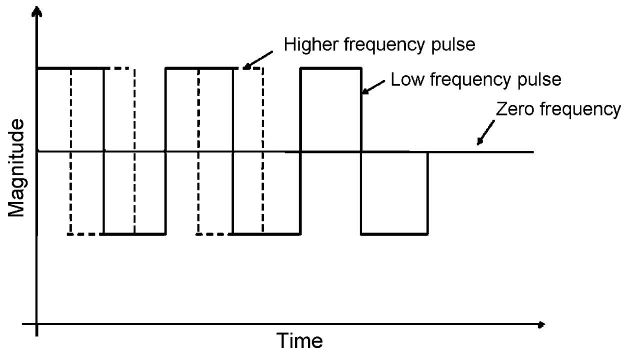

Fig. 1. Steady signal examples with three different frequencies.

sis also exists but is not needed for present purposes.) The scalar dynamical equation is:

$$\dot{x}_i = \sum_{\substack{j=1\\ \text{in}}}^{n} \mathbf{f}_{ij} + \mathbf{z}_i - \mathbf{T}_i^{\text{out}}, \quad i = 1, 2, \ldots, n, \tag{1}$$

where $\mathbf{f}_{ij}$ are the inter-compartmental flows (oriented from compartment j to i), $\boldsymbol{T}_i^{\text{out}}$ is throughflow, the sum of each compartment's outflows, and $\mathbf{z}_i$ is the inflow to each compartment from the environment. A linear matrix equation corresponding to Eq. (1) is:

$$\dot{\boldsymbol{x}} + \boldsymbol{Cx} = \boldsymbol{z}, \tag{2}$$

where **C** can be specifically interpreted in terms of turnover rates (Matis and Patten, 1981; Schramski, 2006):

$$[C] \equiv \begin{bmatrix} -(\rho_1 - \rho_{11}) & \rho_{12} & \cdots & \rho_{1n} \\ \rho_{21} & -(\rho_2 - \rho_{22}) & \cdots & \vdots \\ \vdots & \cdots & \ddots & \vdots \\ \rho_{n1} & \cdots & \cdots & -(\rho_n - \rho_{nn}) \end{bmatrix} \tag{3}$$

Here ρ_{ij} and ρ_i are total and partial turnover rates, respectively:

$$c_i = \rho_i \equiv \frac{\tau_i^{\text{out}}}{x_i}, \quad i = 1, 2, \ldots, n, \tag{4}$$

and

$$c_{ij} = \rho_{ij} \equiv \frac{f_{ij}}{x_j}, \quad i, j = 1, 2, \ldots, n. \tag{5}$$

Steady-state NEA is predicated on $\dot{x} = 0$:

$$\mathbf{0} + \boldsymbol{Cx} = \boldsymbol{z} \tag{6}$$

Perturbations about steady state such as shown in Fig. 1 are important. Jorgensen and Mitsch (1989) and Odum (1989) include pulsing about homeostatic set points in a list of recommended features for ecosystem design. Magnitudes and frequencies of pulses are not discussed by these authors. Electro-chemical–mechanical control methodology provides possibilities for operationalizing the 'pulse' ecological engineering principle.

2. Objectives

The overall objective of this work is to further operationalize the Jorgensen and Mitsch (1989) and Odum (1989) principles of ecological engineering through examination of pulse frequencies and their possibilities of input and output coupling in ways that lend them to experimental verification. Using two multi-input–multi-output (MIMO) ecological system exemplars, we examine system invariants, such as eigenvalues and singular values, in this initial examination of multi-in–multi-out controls in ecological contexts.

3. Control systems representation of ecological systems

To gain an understanding of control system theory, we begin with the scalar case of a single input, single output (SISO) first-order system representing a single compartment in a typical input–output multi-compartment network model (Matis et al., 1979). The system state equation appears as a nonhomogeneous linear differential equation:

$$\begin{aligned} \dot{x} &= Ax + Bu \\ y &= Cx + Du \end{aligned} \tag{7a,b}$$

where x represents the state (typically dimensioned as mass or energy density), u is the input ($Bu = z$ in Eq. (6), dimensioned as mass or energy density per unit time), y is the output (dimensioned depending on what is desired, taken herein as the same as the state variable x), and A, B, C, and D are coefficients. A has units of reciprocal time, B is dimensionless, and C and D are dimensioned to convert x and u, respectively, to the desired information variable y. Eq. (7a), an extension of Eq. (2), is a mass balance state-transition expression in which a linear function of state, Ax, denotes state interchanges and losses to outputs, and matrix B distributes inputs, u, within the system interior. Eq. (7b) is a response function that serves as information about system outputs, y. The Laplace transform of equations (7) produces a corresponding frequency form:

$$\begin{aligned} sX(s) &= AX(s) + BU(s) \\ Y(s) &= CX(s) + DU(s) \end{aligned} \tag{8a,b}$$

in which the differential Eq. (7a) is transformed to the algebraic form of 8a, and the algebraic Eq. (7b) becomes 8b. This may be written as

$$Y(s) = [C(s - A)^{-1}B + D]U(s) \tag{8c}$$

where the bracketed terms comprise a transfer function (TF) matrix, $G(s)$:

$$Y(s) = G(s)U(s) \tag{8d}$$

In Eqs. (8), $U(s)$, $Y(s)$ and $X(s)$ represent the Laplace transformed input, output, and state, respectively. Details on the derivation of equations (8) are given in such control theory texts as Bay (1999) and Šiljak (1991). In the first-order SISO system, $Y(s)$ represents the transformed output and $U(s)$ the transformed input. The variable s is a complex number that may be represented by $a + i\omega$, with ω the frequency in radians per unit time and a is a real constant often set equal to zero. As an example, a first-order SISO open-loop TF may appear as (with $D = 0$):

$$Y(s) = \frac{CB}{s - A}U(s) \tag{8e}$$

The general approach to understanding Eq. (8c) with respect to the pulse question is to put frequencies $j\omega$ in place of s to compare the magnitudes of input versus output pulses as frequency changes. A standard plot known as the Bode diagram portrays this information.

Eqs. (7) can also represent any number of inputs or outputs, which is essential for applying control system analysis to ecological systems. For MIMO systems, **x** becomes a vector of system states, **A** is the state-transition matrix, **B** is the input distribution matrix which relates input vector **u** to change in the state vector $\dot{\boldsymbol{x}}$, **C** relates states (described by vector **x**) to the output vector **y**, and **D** is an input pass-through matrix, taken as zero herein. This nomenclature will apply throughout the remainder of this discussion.