



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

E.W. Tollner^{a,*}, C. Kazanci^b, J.R. Schramski^c, B.C. Patten^d

^a Driftmier Engineering Center, Biol. & Agr. Engr. Dept, University of Georgia, Athens, GA 30602, United States

^b Driftmier Engineering Center, Faculty of Engineering and Department of Mathematics, University of Georgia, Athens, GA 30602, United States

^c Faculty of Engineering, Driftmier Engineering Center, University of Georgia, Athens, GA 30602, United States

^d Odum School of Ecology, University of Georgia, Athens, GA 30602, United States

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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.

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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–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 Bendricchio, 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-

* Corresponding author. Tel.: +1 706 542 3047; fax: +1 706 542 8806.
E-mail address: btollner@engr.uga.edu (E.W. Tollner).

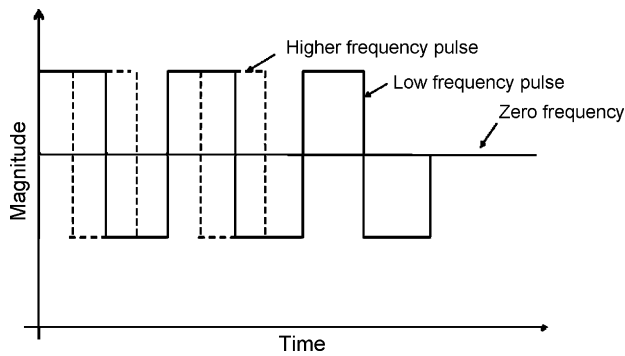


Fig. 1. Steady signal examples with three different frequencies.

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

$$\dot{x}_i = \sum_{j=1}^n \mathbf{f}_{ij} + \mathbf{z}_i - \mathbf{T}_i^{\text{out}}, \quad i = 1, 2, \dots, n, \quad (1)$$

where \mathbf{f}_{ij} are the inter-compartmental flows (oriented from compartment j to i), $\mathbf{T}_i^{\text{out}}$ 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:

$$\dot{\mathbf{x}} + \mathbf{C}\mathbf{x} = \mathbf{z}, \quad (2)$$

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

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

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

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

and

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

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

$$\mathbf{0} + \mathbf{C}\mathbf{x} = \mathbf{z} \quad (6)$$

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:

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

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:

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

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

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

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

$$Y(s) = G(s)U(s) \quad (8d)$$

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 $D = 0$):

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

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, \mathbf{x} becomes a vector of system states, \mathbf{A} is the state-transition matrix, \mathbf{B} is the input distribution matrix which relates input vector \mathbf{u} to change in the state vector $\dot{\mathbf{x}}$, \mathbf{C} relates states (described by vector \mathbf{x}) to the output vector \mathbf{y} , and \mathbf{D} is an input pass-through matrix, taken as zero herein. This nomenclature will apply throughout the remainder of this discussion.

Table 1
Labeled state space matrices for the oyster model.

Matrix A (units = day ⁻¹)						
Filter feeders	-.02	0	0	0	0	0
Dep detritus	0.0079	-.022	0	0.18	0.12	0.0047
Microbiota	0	.0082	-3.39	0	0	0
Meiofauna	0	0.0073	0.50	-0.35	0	0
Dep feeders	0	0.0006	0.50	0.027	-0.15	0
Predators	0.0003	0	0	0	0.011	-0.0099
Matrix B (units = unity)						
Filter feeders	1					
Dep detritus	0					
Microbiota	0					
Meiofauna	0					
Dep feeders	0					
Predators	0					
Matrix C (units of y /units of x , which in this case is unity)						
Filter feeder	1	0	0	0	0	0
Dep detritus	0	1	0	0	0	0
Microbiota	0	0	1	0	0	0
Meiofauna	0	0	0	1	0	0
Dep feeders	0	0	0	0	1	0
Predators	0	0	0	0	0	1

Note: **D** is a 6 × 6 matrix of zeros. Units of *x* in the state equation are kcal/m². Units of inputs are kcal/(m² day).

A canonical form for general MIMO systems in state space is:

$$P_{can} = \begin{bmatrix} A & B \\ C & D \end{bmatrix} \quad (9)$$

where **A**, **B**, **C**, and **D** are control system canonical matrices and **P_{can}** is a partitioned matrix with the same dimensions as those for corresponding scalars given with Eq. (7). The canonical system **P_{can}** is useful for checking dimensions of the state matrices, and input and output vectors. The **A** matrix is a square matrix similar to the **C** matrix of Eq. (2) (not to be confused with the **C** matrix of the response function of Eq. (7b) herein) used in Network Environ Analysis (Patten, 1978; Matis and Patten, 1981; Fath and Patten, 1999; Schramski, 2006) as developed from the linear differential equations of compartmental analysis.

4. Analysis results

Two small ecosystem models shown in Fig. 2 will serve to assess the effect of pulse frequency, observability–controllability, and interactions among inputs and outputs. The Dame and Patten (1981) oyster reef energy model (Fig. 2a) represents a one-input–six-output system. The Edmisten (1970) tropical rain forest nitrogen model (Fig. 2b) has two inputs and three outputs. Details of the published food web analysis of each model were input to the Kazanci (2007) EcoNet software for analysis. Donor control was assumed. EcoNet produced the diagrams of each model portraying the modeled states and connectivity shown in Fig. 2a and b. EcoNet also computed standard environ analysis outputs, including the key matrices of the analysis (Patten, 1978, 1981, 1982; Fath and Patten, 1999; Schramski, 2006). EcoNet also provided an interface for importing this information into Matlab (Mathworks, 2007). This research was conducted with extended Matlab 2007 using the ‘control systems toolbox’ of this software.

The environ analysis input, output, and the NEA **C** matrix were then converted into the control system canonical form of Eq. (1) using a Matlab script file, ‘EcoStateSpace.m’ (available from the author). Control analysis was performed using this script file as well. An example is shown below.

Forming canonical matrices: Eq. (9) canonical matrices were first constructed. The **A** matrix corresponds to the environ analysis **C** matrix. The **B** matrix contains rows equal to the number of states

and columns equal to the number of inputs. Zeros and ones were used in **B** to enable the appropriate inputs, *z*, from *u* to be applied to the appropriate state vector elements when rules of matrix multiplication are followed. The (matrix) product **B*****u** gives a *z* vector with number of rows equal to number of states. The input–output balance for each state variable is described in the matrices **A** and **B**.

The control model **C** matrix, Eq. (7b), has columns equal to the number of states and rows equal to the number of outputs. In theory, the output is a linear combination of the state exchanges (**C** matrix) plus pass-throughs (**D** matrix). It was assumed for present purposes that the desired output was the state at time *t*, resulting in **C** being an identity matrix and **D** being a matrix of zeros with rows equal to the number of outputs and columns equal to the number of inputs. The state space formulations for the oyster and tropical forest systems are shown in Tables 1 and 2.

Invariant analysis: The initial assessment of any system begins with stability or eigenvalue analysis. We regard eigenvalues and a related analysis, the singular value decomposition (SVD), as the first major generalization involved in going from SISO to MIMO systems.

Table 2
Labeled state space matrices for the tropical forest model.

Matrix A (units = day ⁻¹)					
Leaves	-17.7	0	10.2	0	0
Fib. roots	0	-18.7	0	16	0
Wood	0	3.6	-10.2	0	6.6
Loose litter	16	0	0	-16	0
Mineral soil	0	9.2	0	0	-9.2
Matrix B (units = unity)					
Leaves	1				0
Fib. roots	0				1
Wood	0				0
Loose litter	0				0
Mineral soil	0				0
Matrix C (units of y over units of x , which in this case is unity).					
Leaves	1	0	0	0	0
Fib. roots	0	1	0	0	0
Wood	0	0	1	0	0
Loose litter	0	0	0	1	0
Mineral soil	0	0	0	0	1

Note: **D** is a 5 × 5 matrix of zeros. Units of *x* in the state equation are g/m². Units of inputs are g/(m² day).

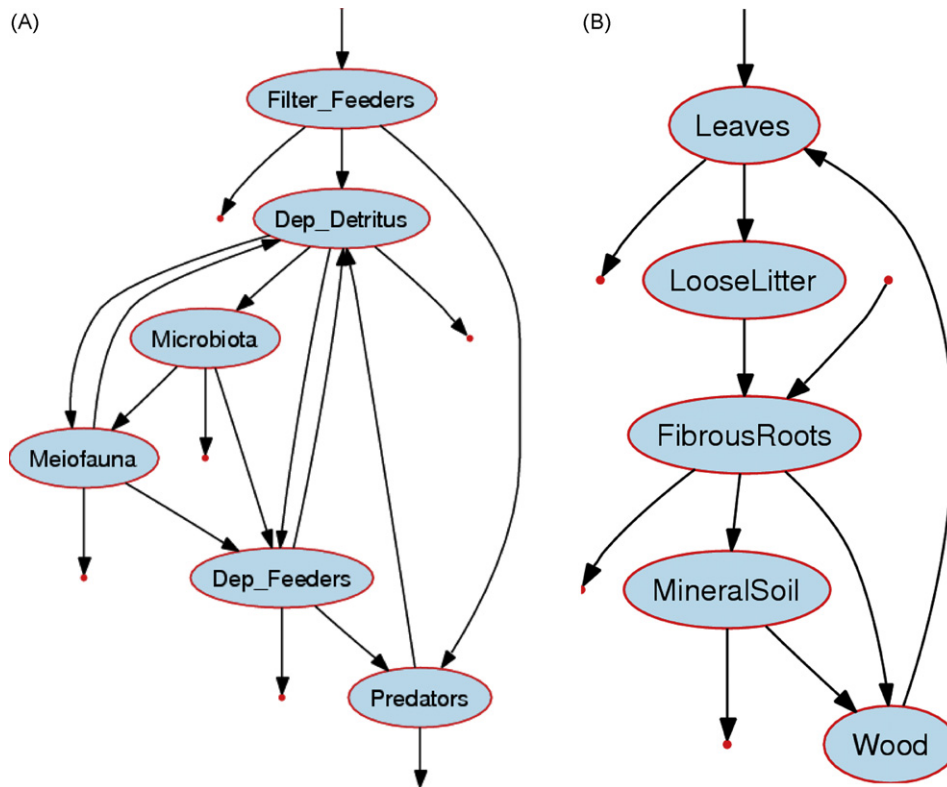


Fig. 2. (a) Modeled states and connectivity of the Dame and Patten (1981) oyster reef energy model. Dimensional units, kcal/(m² day) (b). Modeled states and connectivity of the Edmisten (1970) tropical forest nitrogen model. Dimensional units, g N/(m² day).

An analysis of eigenvalues of the **A** (or NEA's **C**) matrix provides a look at the fundamental poles of a control system. Systems with all negative eigenvalues are inherently stable regardless of inputs. Since **A** is square, it can be analyzed for eigenvalues by finding the roots of the characteristic equation $c(\lambda)$:

$$c(\lambda) = \det[\mathbf{A} - \lambda\mathbf{I}] = 0 \tag{10a}$$

where λ is the set of eigenvalues and $c(\lambda)$ is a polynomial of order equal to the size of the **A** matrix.

Borrett et al. (2006) discuss system eigenvalues and their calculation with respect to environ analysis. Eigenvalues are inversely related to time constants. Thus, high eigenvalues indicate small time constants and low eigenvalues indicate larger time constants. In a donor controlled system, the time constant is a product of flow 'resistance' and state storage, thus the high eigenvalues (low time constants) usually associate with a small resistance \times storage product and small eigenvalues (high time constants) associate with high resistance \times storage. Smaller eigenvalues cause larger time lags between the input signal and resulting output response. The number of eigenvalues is equal to the number of first-order-equivalent number of states, with higher order states expanded to a system of first-order states. Eigenvalues may repeat or be zero, which in theory leads to control-related issues. Common control system analysis software (e.g., see Mathworks, 2007) routinely provides system eigenvalues.

The system singular value decomposition (SVD) is used to compare magnitudes of effects indicated by eigenvalues. Without going into details, the SVD is computed by evaluating the square root of the eigenvalues of the matrix product of transpose of the **A** matrix by itself¹. SVD values are also routinely provided by controls sys-

Table 3a
Oyster reef eigenvalues.

-3.39	0	0	0	0	0
0	-0.0098	0	0	0	0
0	0	-0.15	0	0	0
0	0	0	-0.36	0	0
0	0	0	0	-0.16	0
0	0	0	0	0	-0.02

Note: The SVDs for the oyster system ranged from 3.46 to 0.0086, giving a condition of 401.09.

Table 3b
Tropical forest eigenvalues.

-1.89	0	0	0	0
0	-12.2 + 10.09i	0	0	0
0	0	-12.2 - 10.09i	0	0
0	0	0	-22.21 + 3.5i	0
0	0	0	0	-22.21 - 3.5i

Note: The SVDs for the tropical forest system ranged from 30.39 to 1.89, giving a condition of 16.07.

tems analyses software. The system condition is a ratio of the largest to smallest SVD values and this value may correlate with the range of scales present in the system. In electro-chemical-mechanical controls, high conditions (e.g., greater than 100 or so) are generally undesirable due to extreme sensitivity and lack of robustness while low condition values (e.g., less than 10 or so) are generally more robust to input or process perturbations.

The eigenvalues of the example systems shown in Tables 3a and 3b have negative real parts, indicating these

¹ More generally, for any square matrix **A**, the singular values of **A** are the square roots of the eigenvalues of **A**^H**A**, where **A**^H refers to the Hermetian conjugate, which is

the transpose of **A** with opposite signs for the imaginary component of any complex element of **A**. Bay (1999) gives a more general approach for the SVD evaluation of non-square matrices.

systems are asymptotically stable. The oyster model had several small eigenvalues, suggesting high storage time constants in their dynamics. The tropical forest model had larger eigenvalues (suggesting low storage time constants; see Table 3b), some with imaginary elements, indicating potential for damped oscillatory behavior. Most ecological models analyzed to date have negative eigenvalues, suggesting that the corresponding real networks are inherently stable. Small eigenvalues raise the possibility of a lack of TF robustness (e.g., would a small perturbation due to sampling error cause a positive eigenvalue?), which provides a launch point for future enquiries. The SVD values of the oyster system ranged from 3.49 down to 0.0086, giving a condition of 401, while the forest system SVD values ranged from about 30.39 to 1.89, giving a condition of about 16. High condition numbers in electro-chemical–mechanical systems are suggestive of systems with low robustness or likelihood of going unstable in the presence of perturbations. Condition in ecological systems may be proportional to the range of modeled time scales; thus, high condition numbers may well be desirable in ecosystems. The results above suggest that the oyster system as modeled had a wider range of scales than did the modeled forest system.

Frequency response: The state space form of the system may be transformed into a polynomial matrix of transfer functions (TFs) using Eqs. (8c) and (8d). The polynomial matrix $G(s)$ is a matrix of the TFs from each input–output combination (Glad and Ljung, 2000). A polynomial TF matrix for a hypothetical system with three inputs and three outputs is shown in Eq. (11).

$$G(s) = \begin{bmatrix} \frac{1}{s+1} & \frac{4}{s+3} & \frac{-1}{s+10} \\ \frac{s+2}{-5} & \frac{s+1}{-3} & \frac{s+1}{0.1} \\ \frac{1}{s+1} & \frac{1}{s+3} & \frac{1}{s+1} \end{bmatrix} \quad (11)$$

Eq. (11) is presented, fully realizing that it is a form of a system not generally recognized by ecological scientists. Each element of Eq. (11) represents a transfer function (TF) from input i to output j . In other words, the path from input i to output j is represented by $TF(ij)$. Essential features of the TFs are (1) roots of the numerator, known as zeros (each elemental TF has none in Eq. (11)); (2) roots of the denominator, known as poles (each elemental TF has one in Eq. (11)); and, (3) the order of the numerator and denominator, which is the highest power. The denominator order represents the order of the homogenous differential equation and the numerator represents the order of the forcing function (always less than the order of the differential equation). The denominator roots correspond to eigenvalues of the system and the zeros are important for anticipating dynamic behavior. Note that the positive sign associated with each denominator factor or pole indicates a negative eigenvalue when, for example, $s+1 (=0)$ is written as $s=-1$. Numerator factors or zeros indicate the presence of derivatives in the forcing functions. All the elements of Eq. (11) are first-order in the denominator and zero-order in the numerator. Each element in Eq. (11) represents a first-order differential equation with a constant forcing function.

An inverse Laplace transform will take one back to the state form shown in Eqs. (7a,b); however, the inverse transform must be taken using the system as a whole, which provides the canonical matrices **A**, **B**, **C**, **D** shown in Eq. (9), because of interconnections in the generalized ecological system. As will be seen from discussions below, Eq. (11) is indeed a very simple system.

TFs to outputs from the two compartments receiving inputs of the Fig. 2a oyster model (1 × 6) are presented in Table 4. The poles (denominator roots) of the denominator correspond to system eigenvalues (within rounding error) while poles (numerator roots) correspond to zeros. Table 4 was simplified by cancelling

Table 4
Simplified transfer function $G(s)$ matrix elements for the oyster model.

From input “Filter Feeders” to outputs (column 1 of the $G(s)$ matrix)...
Filter feeders = $\frac{1}{s+0.0208}$
Dep. detritus = $\frac{0.0079}{(s+0.02)(s+0.015)}$
Microbiota = $\frac{0.00006}{(s+3.39)(s+0.015)(s+0.02)}$
Meiofauna = $\frac{0.00006(s+3.95)}{(s+3.39)(s+0.36)(s+0.02)(s+0.015)}$
Dep. feeders = $\frac{0.000005(s+10.44)(s+0.47)}{(s+3.39)(s+0.36)(s+0.16)(s+0.02)(s+0.015)}$
Predators = $\frac{0.0003}{(s+0.016)(s+0.010)}$

Note: since the output $y(s)$ is simply the state $x(s)$, the gains have dimensions of unity.

terms approximately equal. In addition to the eigenvalues being negative (compare the denominator roots to values in Table 3a), the zeros (respective numerators of Table 3a) are also negative and real. The numerator zeros, where present, tend to accelerate the system response. In elements where only some of the eigenvalues appear in the denominator, cancellations with numerator roots occurred. It is surmised that the multiple short-range feedback paths in the oyster model (see Fig. 2a) may account for the cancellations. The predator to filter feeder element was zero as one would expect from the lack of a path from other elements back to the filter feeders. The denominator is one or two orders greater than that of the numerator, implying that system dynamics between input and output is first or second order.

TF elements for the input compartments of the Fig. 2b tropical forest model are presented in Table 5. The second-order denominator terms represent complex eigenvalues (that have negative real components). The second-order numerator terms in the tropical forest model are substantial, perhaps due to the single but multi-element feedback path in the tropical forest model (Fig. 2b). As with the oyster model, the tropical forest system is also first or second order.

The singular value decomposition (SVD) diagram provides a Bode-like diagram that represents each input in a MIMO system. Tools for making the plot are readily available (e.g., Mathworks, 2007). The frequency response can be assessed using the SVD diagrams shown in Figs. 3 and 4 (oyster) and 4 (tropical forest). This diagram provides a panorama of scales operating within the respective systems. Frequencies where the curves break downward are known as corner frequencies. The slope of the curve beyond the corner frequency indicates the effective system order, which in both cases here is first order as indicated by the one-to-one slope. The oyster model frequency response decays at frequencies above approximately 10^{-3} cycles per day. The forest model decays at $\sim 10^{-1}$ cycles per day (input to leaves) and ~ 1 cycle per day (input

Table 5
Transfer function $G(s)$ matrix elements for the tropical forest model.

From input “Leaves” to output at indicated compartments (column 1 of the $G(s)$ matrix)...
Leaves = $\frac{(s+10.2)(s+9.2)(s+16)(s+18.7)}{(s+1.9)(s^2+45.48s+529.4)(s^2+24.43s+251)}$
Fibrous roots = $\frac{256(s+10.2)(s+9.2)}{(s+1.9)(s^2+45.48s+529.4)(s^2+24.43s+251)}$
Mineral soil = $\frac{2355.2(s+10.2)}{(s+1.9)(s^2+45.48s+529.4)(s^2+24.43s+251)}$
From input “Fibrous Roots” to output at indicated compartments (column 2 of the $G(s)$ matrix)...
Leaves = $\frac{36.72(s+16)(s+26.07)}{(s+1.9)(s^2+45.48s+529.4)(s^2+24.43s+251)}$
Fibrous roots = $\frac{(s+17.7)(s+16)(s+10.2)(s+9.2)}{(s+1.9)(s^2+45.48s+529.4)(s^2+24.43s+251)}$
Mineral soil = $\frac{9.2(s+10.2)(s+16)(s+17.7)}{(s+1.9)(s^2+45.48s+529.4)(s^2+24.43s+251)}$

Note: since the output $y(s)$ is simply the state $x(s)$, the gains have dimensions of unity.

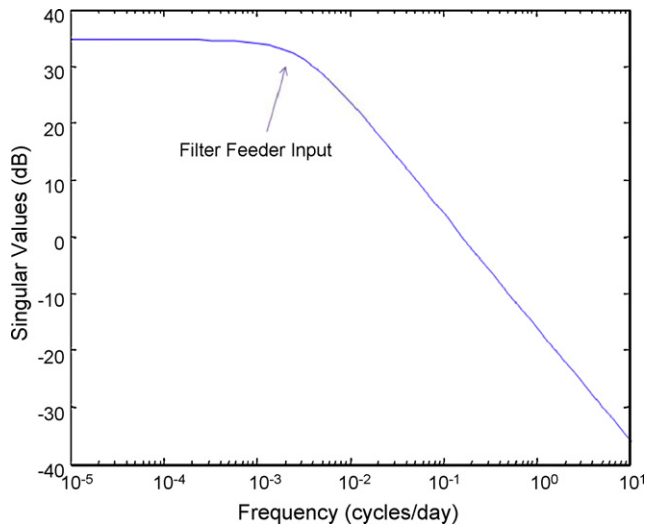


Fig. 3. SVD diagram for the oyster model.

to fibrous roots). The other inflections in the forest model SVD diagram indicate other higher frequency transformations occurring at other states in the model. This implies that pulse periods are approximately 1000 days for the oyster system and approximately 10 days for the forest system. It would be interesting to observe what would happen if the oyster reef model were perturbed every three years (approx. 1000 days), or when leaves were pulsed every 10 days to the forest system. The 10-day frequency leads one to conclude that the readily available nitrogen from the leaves was substantially depleted in 10 days. More recalcitrant forms of nitrogen would be more slowly available and would take a longer time (e.g., a year or so) to be released into the system. The range of frequencies present in the system appears to correlate with the inference of larger SVD condition numbers correlate with wider range of scales present in systems as modeled.

Pulse input plots are shown for the oyster system in Fig. 5 and the tropical forest system in Fig. 6. These figures visually portray the output response to an impulse input at each input, based on the TF elements in Table 4 (oyster model) and Table 5 (tropical forest model). The dynamics shown in the respective impulse plots is consistent with responses expected for first or second-order systems. Compartments with an input and an output respond very fast (e.g., filter feeders and predators in the oyster model; leaves and

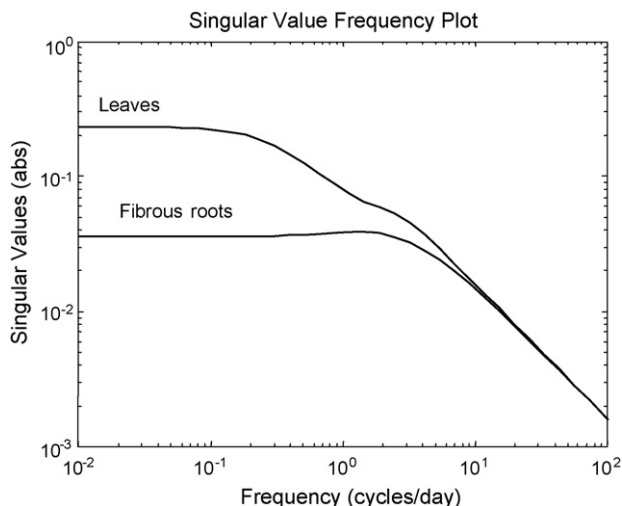


Fig. 4. SVD diagram for the tropical forest model.

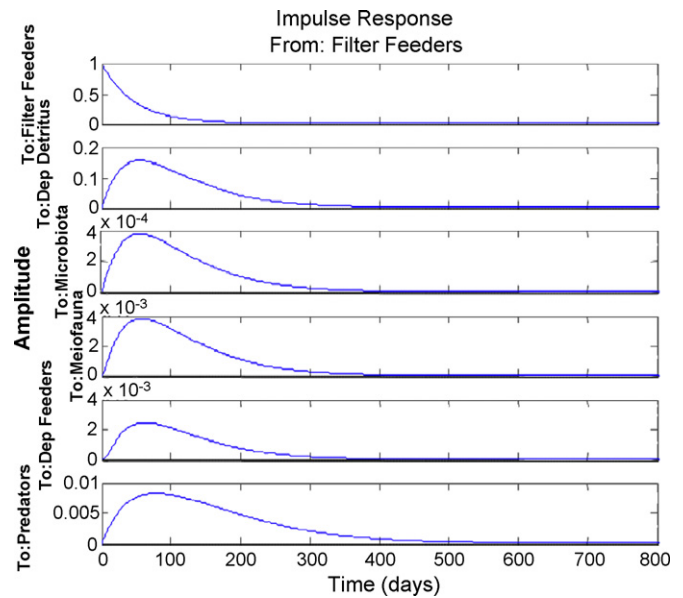


Fig. 5. Impulse response of the oyster system.

fibrous roots in the tropical rain forest model). The more compartments that separate input and outputs (as can be seen in Fig. 2), the longer the lag in the output response as one would expect. Complexity in the diagrams due to cycling (see Fig. 2) resulted in the tendency for more complex shaped impulse responses (see the response from filter feeders to deep feeders in the oyster model and from leaves to fibrous roots in the forest model). The time required for a pulse to pass through the system based on the compartment with the longest response time, should determine the frequency (e.g., 1/time) corresponding to the corner frequency as shown in Figs. 3 and 4.

Pulses with frequencies less than the corner frequency would transmit the impulse throughout the system with little attenuation, while higher frequency (e.g., shorter time period) pulses would be attenuated. The forest was expected to have an annual period of one year or a frequency of approximately 0.003 cycles per day due to the annual leaf fall. The modeled dynamics processed the leaves much faster. The oyster system period reached beyond an annual cycle. It seems likely that operation at a frequency at or below the breakpoint frequency would lead to maximum system robustness.

We have as yet not addressed pulse magnitudes. The food web analysis involves an implicit steady-state assumption, hence the system and the corresponding state space and frequency space representations would carry forward this assumption. It is likely that some cyclical variations occurred in the food web analysis such that some pulsing was in effect represented. Tentatively, we suggest that the plus or minus pulse departure from the long term average not be more than 10% or 15%. This topic requires additional research.

One example where pulsing has proved necessary is in waste treatment by wetlands (e.g., see Crites and Tchobanoglous, 1998). Systems are alternately operated and rested on a weekly to monthly basis, which could provide a platform for an interesting study. Systems operated without rest periods tended to collapse in short times. It would be very interesting to have an energy analysis and a nitrogen analysis for a treatment wetland to assess utility of these modeling approaches for providing design insights.

In general, there are many kinds of mathematical analyses tools originally developed and used for engineering purposes that are now available for application to the growing set of complex systems problems represented by human interactions with environment.

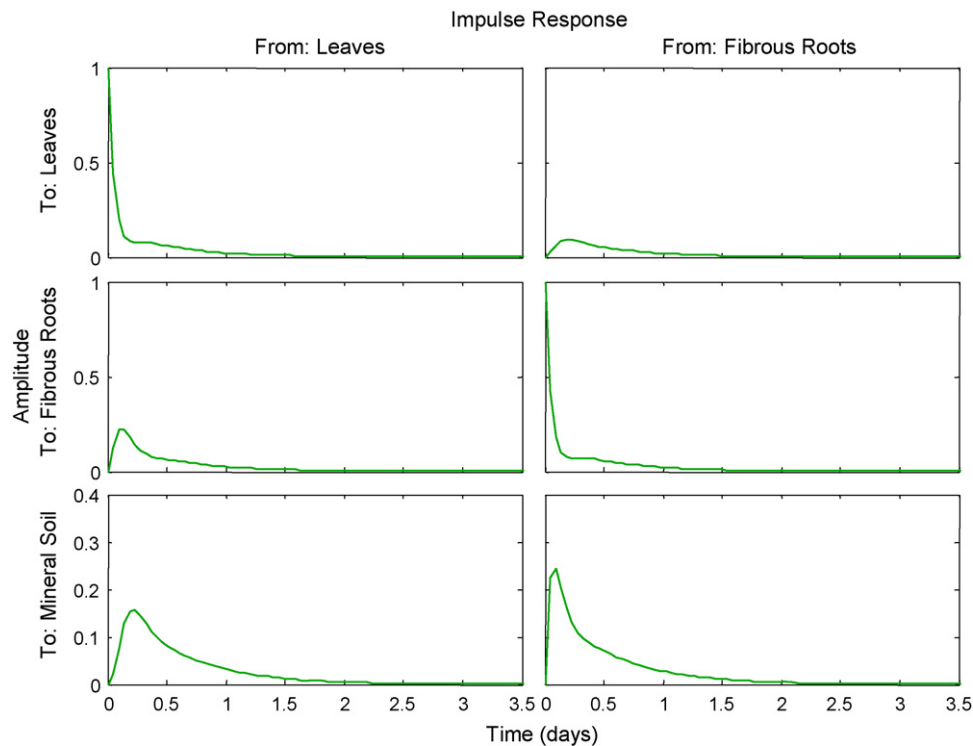


Fig. 6. Impulse response of the tropical forest system.

These include both linear and nonlinear analysis. We envision looking at a variety of techniques for nonlinear analysis, including Pontrjagin's principle, in future work. The Pontrjagin principle sits at the pinnacle of a hierarchy of advanced techniques building on Lyapunov theory, Lagrangian analysis, and Hamiltonian analysis. Each of these embeds assumptions that are just that. Model specificity increases as one goes up this hierarchy. Each will involve extensive numerical and symbolic tools that are coming available. In this paper, we start at the general level and reserve the future explorations to future papers. These approaches will all find application in ecosystem analysis as well as the parallel developments of control theory application in other biological modeling problems previously discussed.

That the compartmental models NEA intersect the control models of engineering is fortuitous because it makes possible the exploration of established methods to the new set of modern-day problems.

5. Summary findings and implications

In control analyses, as discussed herein, eigenvalues provide insights into stability, potential for oscillatory behavior, data validity checks, and the range of time constants in a system. Positive eigenvalues indicate instability and signals that a compartment model may have errors that should be re-examined. Pulsing of systems relaxes the steady-state assumption common in model investigations and opens the door to other forms of analysis. For example, frequency response analysis identifies the pulse frequency for maximum propagation through the system. Corner frequency on the SVD plot is the upper limit of pulse frequency a system can fully track before the response falls off. In the two small models examined, the corner frequencies fell within 0.1–10 times the reciprocal time unit in the data collection and analysis. The SVD condition number appears to correlate with the range of scales present in systems. The time required for an input impulse to propagate through the system was generally consistent with the

break frequency from the SVD diagram. Pulse analysis lends itself to experimentation using, for example, spiked inputs of labeled materials. The linear control analysis presented here offers a rationale for specifying pulse intervals.

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