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Dynamic environ analysis of compartmental systems: A computational approach

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ABSTRACT

Ecosystems are often modeled as stocks of matter or energy connected by flows. Network environ analysis (NEA) is a set of mathematical methods for using powers of matrices to trace energy and material flows through such models. NEA has revealed several interesting properties of flow–storage networks, including dominance of indirect effects and the tendency for networks to create mutually positive interactions between species. However, the applicability of NEA is greatly limited by the fact that it can only be applied to models at constant steady states. In this paper, we present a new, computationally oriented approach to environ analysis called dynamic environ approximation (DEA). As a test of DEA, we use it to compute compartment throughflow in two implementations of a model of energy flow through an oyster reef ecosystem. We use a newly derived equation to compute model throughflow and compare its output to that of DEA. We find that DEA approximates the exact results given by this equation quite closely – in this particular case, with a mean Euclidean error ranging between 0.0008 and 0.21 – which gives a sense of how closely it reproduces other NEA-related quantities that cannot be exactly computed and discuss how to reduce this error. An application to calculating indirect flows in ecosystems is also discussed and dominance of indirect effects in a nonlinear model is demonstrated.

1. Introduction

Compartment models (Matis et al., 1979) are widely used to represent ecological networks of *stocks*, x_i (i = 1, 2, . . ., n), and *flows*, f_{ij} (i, j = 1, 2, . . ., n), of conserved substances (energy or matter). The flows are generated by boundary *inputs*, z_j, and they terminate in boundary *outputs*, y_i. *Throughflows* are the sums of inflows, T_i^{in}, and outflows, T_i^{out}, to and from each stock. Within-model environments of the compartments are *environs* (Patten, 1978). These may be found using the system's mathematical description by *network environ analysis* (NEA), a set of methods derived from Leontief (1936, 1966) input–output analysis. NEA has revealed several interesting properties of flow–storage networks, including dominance of indirect effects (Patten, 1984; Higashi and Patten, 1989) and the tendency for networks to create mutually positive interactions between species (Patten, 1991).

At least three aspects of dynamical behavior limit the applicability of present NEA methods. (1) The methodology can only be applied to models at constant steady states where inputs balance outputs. This greatly limits the range of applicability because (2) not all models reach constant steady states, and (3) those that do may also have significant, but unanalyzable, transient behavior. Previous attempts to respond to these limitations and develop methods for non-steady-state linear (Hippe, 1983) as well as nonlinear (Hallam and Antonios, 1985) systems have not found use, in part because of their mathematical difficulty.

This paper describes a computational approach to dynamic environ analysis. Like NEA, the dynamic methodology can be applied to any compartment model that satisfies two properties. First, either all compartments that have an input must have a boundary output or, failing that, every block of compartments that receives an input must have a boundary output (Fadeev and Fadeeva, 1963). Second, at least one compartment must receive input from outside the system to prevent system descent to the zero state (although zero-input transient dynamics from a nonzero initial state may be of interest, and could be analyzed using DEA).

2. The method

2.1. Overview of standard environ analysis

For a compartmental system, let $\mathbf{x}_{n\times 1} = (x_i)$, $\mathbf{z}_{n\times 1} = (z_j)$, and $\mathbf{y}_{n\times 1} = (y_i)$ be stock, input, and output vectors, respectively; let $\mathbf{1}_{n\times 1}$ be a vector of ones, and $\mathbf{F}^{\mathrm{T}}$ the transpose of the matrix of flows, $\mathbf{F}_{n\times n} = (f_{ij})$. We define $\bar{\mathbf{F}}$ as the flow matrix $\mathbf{F}$ with negative throughflows on the diagonal, so $\bar{f}_{ij} = f_{ij}$ for $i \neq j$ and $\bar{f}_{ii} = -T_i$. Then, for a

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system at steady state, input- and output-driven ordinary differential equation descriptions of model dynamics, in matrix notation, are

$$\frac{d\boldsymbol{x}}{dt} = 0 = \bar{\mathbf{F}} \cdot \mathbf{1} + \mathbf{z} \tag{1a}$$

$$0 = -\bar{\mathbf{F}}^{\mathrm{T}} \cdot \mathbf{1} - \mathbf{y} \tag{1b}$$

The first equation represents time-forward dynamics generated by input, **z**. The second denotes reverse-time trace-back dynamics beginning at output, **y**, which serves as the forcing condition. (The flows **z** and **y** may be termed boundary flows.) In Eq. (1b), taking the transpose of $\bar{\boldsymbol{F}}$ orients it to backward movement of time, signified by the negative signs of both terms.

Standard NEA converts boundary inputs (in output-environ analysis) and outputs (in input-environ analysis) into steady-state throughflows, $\mathbf{T}_{n\times 1} = (T_i^{\mathrm{in}}) = (T_i^{\mathrm{out}})$, and storages (stocks), $\mathbf{x}_{n\times 1} = (x_i)$, employing flow intensity matrices, $\mathbf{N}_{n\times n}$ and $\mathbf{N}'_{n\times n}$ for throughflow analysis, and $\mathbf{S}_{n\times n}$ and $\mathbf{S}'_{n\times n}$ for storage analysis:

$$\boldsymbol{T} = \boldsymbol{N}\boldsymbol{z} = \boldsymbol{N}'\boldsymbol{y} \tag{2a}$$

$$\boldsymbol{x} = \boldsymbol{S}\boldsymbol{z} = \boldsymbol{S}'\boldsymbol{y}. \tag{2b}$$

Here, $\mathbf{N} = (\mathbf{I} - \mathbf{G}_{n\times n})^{-1}$, $\mathbf{N}' = (\mathbf{I} - \mathbf{G}'_{n\times n})^{-1}$, $\mathbf{S} = -\mathbf{C}_{n\times n}{}^{-1}$, and $\mathbf{S}' = -\mathbf{C}'_{n\times n}{}^{-1}$, where $\mathbf{I}_{n\times n}$ is the multiplicative identity matrix, and the elements of **G** and **C** are $g_{ij} = f_{ij}/T_j$ and $c_{ij} = f_{ij}/x_j$, and those of **G**′ and **C**′ are, $g_{ij}' = f_{ij}/T_i$ and $c_{ij}' = f_{ij}/x_i$. Both **G** and **G**′ are dimensionless, while **C** and **C**′ have the dimensions of reciprocal time; note that **C** is the familiar "community matrix" used in population and community ecology.

Inputs, **z**, outputs, **y**, and throughflows, **T**, have the same dimensions, therefore **N** and **N**′, Eq. (2a), are dimensionless transformations from boundary flows, **z** and **y**, to interior throughflows, **T**. Both Eqs. (2a) and (2b) have infinite power series equivalents that reflect trajectories of the boundary flows over all interior pathways of all lengths traveled in reaching the points where the steady-state throughflows, **T**, are registered. For Eq. (2a), these series are

$$\boldsymbol{T} = [\boldsymbol{I} + \boldsymbol{G} + \boldsymbol{G}^2 + \cdots + \boldsymbol{G}^k + \cdots]\boldsymbol{z} \tag{3a}$$

$$= [\boldsymbol{I} + \boldsymbol{G}' + \boldsymbol{G}'^2 + \cdots + \boldsymbol{G}'^k + \cdots]\boldsymbol{y} \tag{3b}$$

2.2. The dynamic case

The equation that governs the dynamics of a single compartment k is

$$\frac{dx_k}{dt} = T_k^{\mathrm{in}}(t) - T_k^{\mathrm{out}}(t) \tag{4}$$

where $T_k^{\mathrm{in}}(t)$ and $T_k^{\mathrm{out}}(t)$ are functions that represent rates of input to and output from compartment k at time t. Note that $T_k^{\mathrm{in}}(t)$ is a combinations of environmental and inter-compartmental flows:

$$T_k^{\mathrm{in}} = \sum_{i=1}^{n} f_{ki}(t) + z_k(t) \tag{5}$$

Combining Eqs. (4) and (5), we get, for $i \neq k$,

$$\sum_{i=1}^{n} f_{ki} + z_k = T_k^{\mathrm{out}} + \frac{dx_k}{dt} \tag{6}$$

As before, we define **G**, the flow matrix normalized with respect to throughflows (T_k^{out}), as $g_{ik} = f_{ik}/T_k^{\mathrm{out}}$. Replacing **F** with **G** in Eq. (6), we get

$$z_k - \frac{dx_k}{dt} = T_k^{\mathrm{out}} - \sum_{i=1}^{n} g_{ki} T_i^{\mathrm{out}} \tag{7}$$

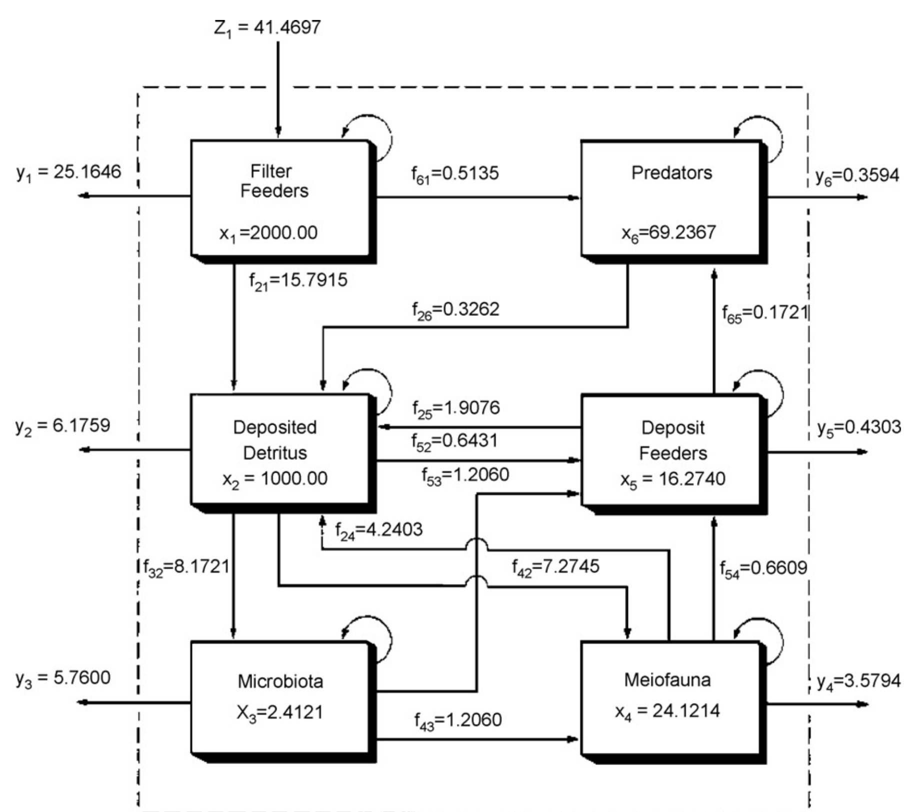

Fig. 1. Energy flows in an oyster reef ecosystem. The stock and flow values are for a constant steady state. Note that only Compartment 1 receives direct boundary inflow. From Patten (1985).