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Extending ecological network analysis measures to dynamic ecosystem models

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ABSTRACT

Ecological network analysis measures such as cycling index, indirect effects, and storage analysis provide insightful information on ecosystem organization and function, which can be extremely useful for environmental management and control. These system-wide measures focus on indirect relations among system compartments, providing a holistic approach. Unfortunately, the application of these useful measures are restricted to steady state models. Seasonal changes, environmental impacts, and climate shifts are not accommodated by the current methodology, which greatly limits their application. The novel methodology introduced in this paper extends the application of these useful but limited measures to dynamic compartmental models. This method relies on network particle tracking simulation, which is an agent based algorithm, whereas the current methods utilize steady-state flow rates and compartment storage values. We apply this new methodology to storage analysis, which quantifies how much storage is generated at any compartment within the system by a unit external input into another compartment. Also called *compartmental mean residence time*, this measure is widely used in environmental sciences, pharmacokinetics and nutrition, to assess the interaction between system boundary (e.g. drug intake, pollution, feeding) and internal compartments (e.g. tissues, crops, species). Storage analysis is chosen for demonstration because it is applicable to a limited class of dynamic models (linear and donor-controlled), which gives us an opportunity to verify our new method. The methodology introduced here is also applicable to Finn's cycling index, indirect effects index, throughflow analysis, and possibly other network analysis based indicators as well.

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1. Introduction

Compartmental models are widely used to represent living systems, such as genetic networks, biochemical pathways, and ecosystems. Various software products (Clauset et al., 1987; Ramsey et al., 2005; Kazanci, 2007) exist for modeling real-life phenomena, with built-in simulation and analysis tools. These models enable researchers to capture system-wide behavior, which may be counter-intuitive and difficult to predict. Such behavior is generally due to the inherent complexity of network models. Effects of indirect connections among compartments and feedback cycles often exceed the effects of direct connections, producing unexpected behavior: a predator can have a significant positive effect upon its prey (Bondavalli and Ulanowicz, 1999); a protein may have a negative auto-regulatory role on its own expression (O'hare and Hayward, 1985). Various measures have been identified that capture system-wide properties and function of network models, such as connectivity distribution (Jeong et al., 2000), response to perturbations (Ueda et al., 2004), cycling (Finn, 1976; Kazanci et al., 2009), indirect effects (Higashi and Patten, 1986; Patten, 1995), ascendency (Ulanowicz, 1986; Patten, 1995; Patrício et al., 2004), etc. Some of these measures were based on economic input–output analysis (Hannon, 1973; Patten et al., 1976a; Finn, 1976).

An important system-wide property, storage analysis (Matis and Patten, 1981; Hearon, 1981; Fath and Patten, 1999), traces the storage value of a compartment back to the system input. Storage analysis consists of a matrix S, which is a linear map from system boundary inputs (z) to compartment storage values (x). In particular, S_{ij} represents how much storage is generated in compartment i by a unit boundary input into compartment j, through all direct and indirect connections. Storage analysis is potentially useful for research in environmental sciences (Mackay and MacLeod, 2002), pharmacokinetics (Cheng and Jusko, 1988; Plusquellec and Houin, 1990), ecology (Matis and Patten, 1981) and nutrition (Green and Green, 1990), where compartmental models are heavily utilized to assess the interaction between system boundary and internal compartments.

Traditionally, storage analysis has been useful for studying systems at steady state. However, this methodology is not applicable to evolving systems, which limits its application, as many

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essential and interesting issues involve change, such as environmental impacts, climate change, and regime shifts. In this paper, we present a novel simulation-based definition for storage analysis matrix S. This new definition agrees with the current definition for steady state systems. However, the new definition is applicable to dynamic, evolving systems, greatly increasing the applicability of this useful methodology. Beyond dynamic storage analysis, this new approach also provides an arbitrarily close approximation to input based residence time distribution (Yu and Wehrly, 2004; Hearon, 1972).

The new definition is based on network particle tracking (NPT) (Kazanci et al., 2009) simulations, an agent-based method applicable to compartmental models. NPT simulations have been previously used to study Finn's cycling index (Finn, 1977, 1978, 1982) and throughflow analysis (Patten, 1978). Similar to storage analysis, both measures are only applicable to steady state systems. While similar simulation-based definitions have been developed for these two measures (Kazanci et al., 2009; Matamba et al., 2009), both are only valid for steady state systems. Methodology described in this paper can be applied to any simulation-based measure (including Finn's cycling index and throughflow analysis), to extend their application to evolving, dynamic systems.

2. Storage analysis and residence time

Storage analysis (Matis and Patten, 1981) investigates the relation between input flows and compartment storage values. The storage matrix S represents a linear mapping between the environmental input rates and the final storage values of each compartment. For instance, given one unit of mass or energy input to a system at compartment j, S_{ij} represents how much storage is generated at compartment i as a result of this input. The linear relationship between environmental input rates and storage values at steady state is described by the following equation:

$$Sz = x^* \tag{1}$$

where $z = [z_1, \ldots, z_n]^T$ is the vector of environmental input flow rates to each compartment, and x^* is a vector of the steady state storage values of all compartments.

Traditionally, storage analysis has provided a way of studying ecosystem models at steady state. This useful but limited application of storage analysis is due to the way it is defined using linear algebra, as follows (Matis and Patten, 1981; Fath and Patten, 1999):

$$\frac{dx}{dt} = Cx + z \tag{2}$$

where

$$C_{ij} = \begin{cases} \dfrac{F_{ij}}{x_j}, & i \neq j \\ \dfrac{-T_i}{x_i}, & i = j \end{cases}$$

Here, F_{ij} represents the flow rate from compartment j to i at time t. Throughflow $T_i = z_i + \sum_k F_{ik}$ represents the rate of total input a compartment receives from other compartments and the environment. For donor controlled systems, C stays constant. For non-donor controlled systems, C is a function of x.

For an ecosystem model at steady state, the storage values of all compartments remain constant over time and the rate of change of these values equal to zero ($dx/dt = 0$). This leads to the derivation of the storage analysis matrix as a function of C, which also remains constant over time:

$$\begin{aligned} 0 &= Cx^* + z \\ -Cx^* &= z \\ x^* &= \underbrace{-C^{-1}}_{=S} z \end{aligned} \tag{3}$$

This way, the storage analysis matrix S is determined exclusively by the flow rates (F) and steady state storage values (x^*), and is independent of initial conditions or environmental input flow rates.

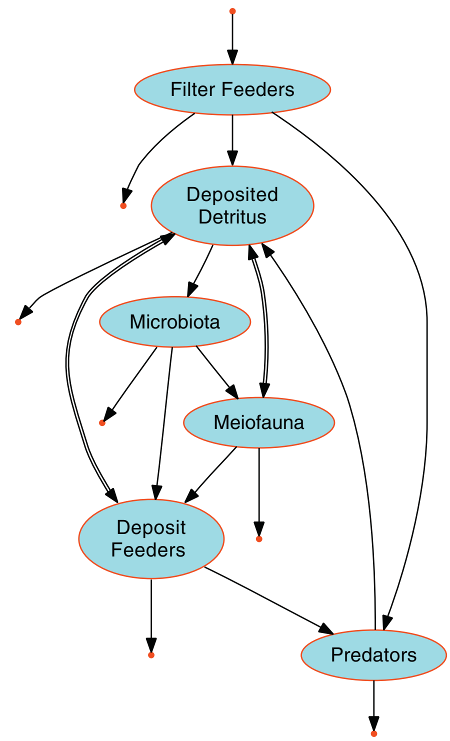

Fig. 1. Network diagram of the intertidal oyster reef ecosystem model (Dame and Patten, 1981) is shown. Flow units are in kcal/m^2/day, storage units are in kcal/m^2. The diagram is created by EcoNet (Kazanci, 2007, 2009). The model in EcoNet format is presented in Appendix A.

We use the intertidal oyster reef ecosystem model (Patten, 1986) shown in Fig. 1 as an example to demonstrate storage analysis. Simulating the oyster reef ecosystem model using EcoNet (Kazanci, 2007, 2009; Schramski et al., 2011), we get the S matrix shown in Table 1. The first row of S contains all zeroes except for the first term because *Filter feeders* do not receive input from any other compartment. All other entries are nonzero, meaning that energy flows from any compartment to any other through direct or indirect pathways. S_{12} = 24.04 represents that a unit of input to *Filter feeders* contributes to *Deposited detritus* 24.04 units of storage over time. For further information on storage analysis or computing S for steady state models is available in Fath and Patten (1999) and Patten (1978).

Storage analysis is related to residence time, which quantifies how long a given substance remains in a particular compartment of a biogeochemical cycle. For ecosystems, residence time represents the amount of time the flow material spends in a certain compartment, which is associated with storage value of this compartment and the flow rates to connected compartments. For steady state systems, it is computed as the ratio of compartment storage value to throughflow (x_i/T_i).

Storage analysis could be considered as a "more detailed" residence time measure, one which is environmental input based and compartment specific. Indeed, the term "compartmental mean