

## Extending ecological network analysis measures to dynamic ecosystem models

C. Kazanci<sup>a,b,\*</sup>, Q. Ma<sup>c</sup>

<sup>a</sup> Faculty of Engineering, University of Georgia, Athens, GA 30602, USA

<sup>b</sup> Department of Mathematics, University of Georgia, Athens, GA 30602, USA

<sup>c</sup> Department of Biological and Agricultural Engineering, University of Georgia, Athens, GA 30602, USA

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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), ascendancy (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

\* Corresponding author at: Faculty of Engineering and Department of Mathematics, University of Georgia, Athens, GA 30602, USA. Tel.: +1 706 542 0863; fax: +1 706 542 8806.

E-mail addresses: [caner@uga.edu](mailto:caner@uga.edu) (C. Kazanci), [maqian12@uga.edu](mailto:maqian12@uga.edu) (Q. Ma).

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  $z = [z_1, \dots, z_n]^T$  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

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

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

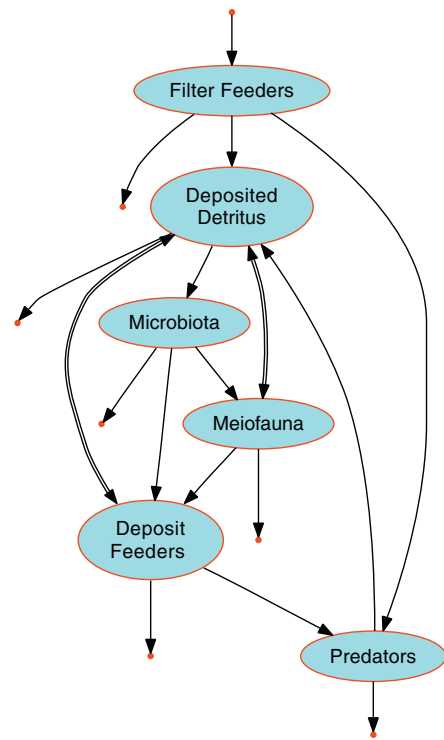


Fig. 1. Network diagram of the intertidal oyster reef ecosystem model (Dame and Patten, 1981) is shown. Flow units are in kcal/m<sup>2</sup>/day, storage units are in kcal/m<sup>2</sup>. The diagram is created by EcoNet (Kazanci, 2007, 2009). The model in EcoNet format is presented in Appendix A.

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.

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

**Table 1**  
Storage analysis matrix  $S$  shown for the intertidal oyster ecosystem model shown in Fig. 1.

	Filter feeders	Deposited detritus	Microbiota	Meiofauna	Deposited feeders	Predators
Filter feeders	48.07	0	0	0	0	0
Deposited detritus	24.04	62.17	12.43	34.93	49.28	29.52
Microbiota	0.06	0.15	0.33	0.08	0.12	0.07
Meiofauna	0.58	1.50	0.72	3.69	1.19	0.71
Deposited feeders	0.39	1.00	1.23	1.07	7.28	0.47
Predators	1.87	1.07	1.32	1.14	7.79	101.52

residence time” is also used to represent the same storage analysis matrix  $S$  (Eisenfeld, 1981).

### 3. A stochastic measure of storage

In this section, we describe a simulation based storage analysis matrix  $S$ . This is a completely different approach than the linear algebraic definition in Eq. (3), and is based on network particle tracking (NPT) simulations. We describe NPT in Section 3.1, followed by the NPT based storage analysis matrix definition in Section 3.2.

#### 3.1. Network particle tracking (NPT)

Network particle tracking (NPT) (Tollner and Kazanci, 2007; Kazanci et al., 2009) is an individual based simulation method, where discrete “packets” of material or energy are labeled and tracked in time as they flow through the model compartments (see Fig. 2). In addition to tracking the storage values of compartments over time (as occurs in a differential equation model), NPT identifies which individual particles represent the storage values of each compartment at any given time. The method is particularly useful at steady state, where differential equation solutions indicate constant storage values over time, giving the illusion that the system has stopped, whereas NPT will demonstrate the continuous movement of particles.

What sets NPT apart from similar individual based algorithms is: (1) NPT deduces its rules on how an individual particle will move directly from the differential equation representation of the model. This eliminates the need for extra parameters or decisions that are required to build most individual-based models. Therefore, causality is preserved. (2) Based on Gillespie’s stochastic algorithm (Gillespie, 1977), NPT is a stochastic method that is compatible with the master equation (Gillespie, 1992, 2000). In other words, the average of many NPT simulations agrees with the differential equation solution.

NPT starts with breaking initial stocks or input flows into discrete packets which we call particles. For example, for a Nitrogen flow model, a particle could represent a Nitrogen atom. Next, based on flow rates, NPT determines which flow is likely to occur and when. A particle is then chosen randomly from the donor compartment and introduced to the recipient compartment. Ecosystem models are open systems and therefore new particles enter the system continuously. So if the chosen flow is an environmental input, a new particle is labeled and introduced to the recipient compartment. NPT keeps the record of pathway history of all particles, including when and where each particle movement occurs. This data is dumped into a text file after the simulation ends.

In Fig. 3, we show a sample NPT simulation output for the intertidal oyster reef ecosystem model (Patten, 1986). The results include *pathway*, *flow time* and *residence time* data. We define the pathway of a particle as an ordered list of compartments visited by that particle. Flow time indicates the exact time when a particle flows from one compartment (or the environment) to another one (or the environment). Simulation start time is set as the

reference ( $t=0$ ). Time units are defined by the model, therefore depend on the model. For the oyster reef model, time units are days. This work does not focus on a particular model. Therefore, we simply use the generic term *time units* ( $tu$ ). Residence time represents how long a particle stays in a particular compartment it visits. Therefore it is defined as the difference between two consecutive flow time values. For example, Fig. 3 indicates that Particle 144 enters compartment 1 at  $t=0.5 tu$  and leaves at  $t=9.7 tu$ . Hence its residence time at compartment 1 is  $9.2 tu$ .

#### 3.2. NPT based storage analysis

To compute the storage analysis matrix  $S$  using NPT, we need both the pathway and the residence time data. Recall that  $S_{ij}$  represents the amount of storage generated at compartment  $i$  by a unit environmental input into compartment  $j$ . Next, we show the computation of  $S_{61}$  using the NPT data shown in Fig. 3:

Note that all three particles enter the ecosystem at *Filter feeders* (compartment 1), and  $S_{61}$  represents how much storage is created by these particles at *Predators* (compartment 6). Only two out of the three particles (144 and 146) end up visiting compartment 6, and they stay for 7.6 and 6.7  $tu$  respectively. Therefore:

$$S_{61} \approx \frac{7.6 + 0 + 6.7}{3} = 4.77 \quad (4)$$

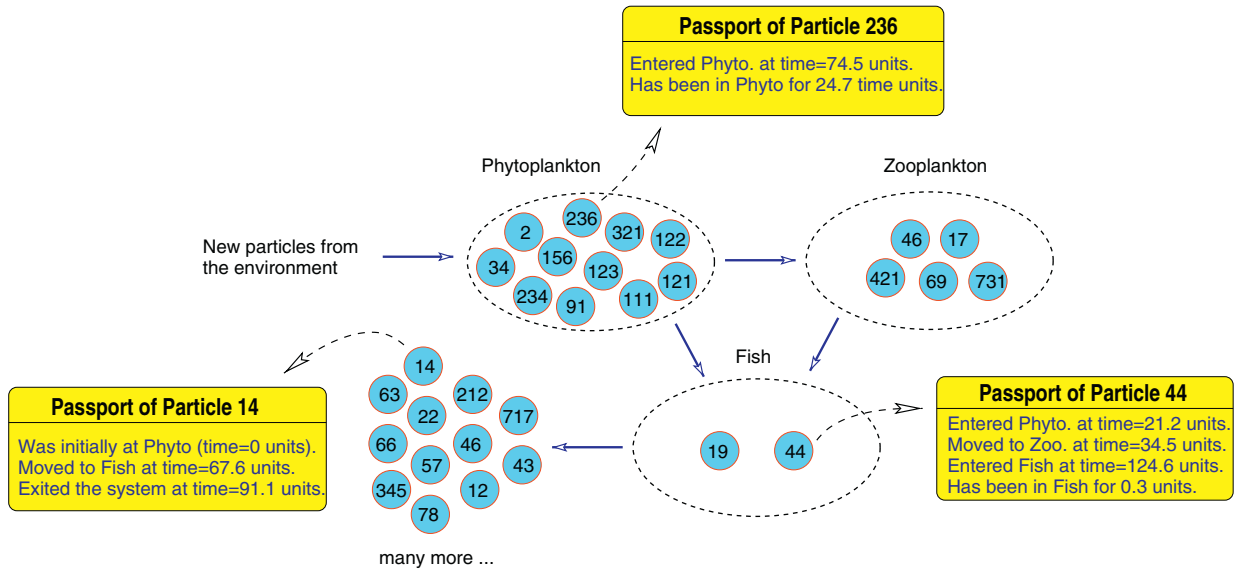
*Deposited detritus* (compartment 2) get visited more than *Predators*, and all three particles visit this compartment at least once before they exit the system. Therefore we can compute  $S_{21}$  as follows:

$$S_{21} \approx \frac{(7.1) + (9.5 + 5.5) + (4.2 + 7.0)}{3} = 11.1 \quad (5)$$

There is a significant discrepancy between the values we have just computed above ( $S_{61} \approx 4.77$ ,  $S_{21} \approx 11.1$ ) and the values given in Table 1 ( $S_{61} = 1.87$ ,  $S_{21} = 24.04$ ). This is mainly due to our computation being based on only three pathways. NPT is a stochastic simulation method, therefore the NPT based computation of  $S$  is an approximation. However, any desired accuracy can be achieved by using more pathways. We address accuracy and convergence issues towards the end of this section.

Actually, the process of computing  $S$  is slightly more involved, because rarely an ecosystem model will have environmental inputs into all its compartments. For example, computing  $S_{42}$  for the oyster reef ecosystem model poses a problem because no particle enters *Deposited detritus* (compartment 2) from the environment.

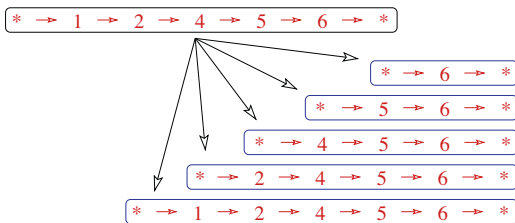
In order to compute the full  $S$  matrix, we use the Markov assumption that whether a particle enters a compartment from the environment, or from another compartment, it will behave the exact same way afterwards (Barber, 1978a,b; Higashi, 1986). In other words, past pathway history of a particle does not affect its future behavior. Therefore we need not make any distinction between environmental inputs and inter-compartmental inputs to compute  $S$  using the NPT simulation output. To utilize this idea, we treat each particle pathway as multiple pathways as shown in Fig. 4. Applying this expansion to all three pathways in Fig. 3 results



**Fig. 2.** Three-compartment model depicting particles and their transport information. A record of the trajectory and timing of each particle from its entry to (potentially) its exit is given in the particle “passports”.

Particle	Pathway	* → 1 → 2 → 4 → 5 → 6 → *
144	Flow time	0.5 9.7 16.8 20.4 27.2 34.8
	Residence time	9.2 7.1 3.6 6.8 7.6
Particle	Pathway	* → 1 → 2 → 5 → 2 → 4 → *
145	Flow time	1.2 10.3 19.8 28.0 33.5 41.6
	Residence time	9.1 9.5 8.2 5.5 8.1
Particle	Pathway	* → 1 → 2 → 4 → 2 → 3 → 4 → 5 → 6 → *
146	Flow time	2.3 9.2 13.4 17.2 24.2 33.5 39.6 44.1 50.8
	Residence time	6.9 4.2 3.8 7.0 9.3 6.1 4.5 6.7

**Fig. 3.** Partial output of a network particle tracking (NPT) simulation is shown for the intertidal oyster reef ecosystem model (see Fig. 1). Numbers 1–6 correspond to compartments *Filter Feeders*, *Deposited Detritus*, *Microbiota*, *Meiofauna*, *Deposited Feeders* and *Predators* respectively. The simulation output includes *pathway*, *flow time* and *residence time* data for each particle. “\*” represents the environment. NPT tracks all particles starting from their entrance into the ecosystem, until they return to the environment. A typical NPT simulation contains more than  $10^5$  particle pathways. In general, such a simulation takes less than 5 s on a typical desktop computer (equipped with a single dual core CPU).



**Fig. 4.** To compute storage analysis matrix  $S$ , each pathway in NPT output is viewed as multiple pathways as shown above. Here, pathway of particle 144 from Fig. 3 is expanded into five separate pathways. Such expansion enables us to compute  $S_{ij}$  even if there is no environmental input into compartment  $j$ .

in 15 new pathways, yielding 18 pathways in total.<sup>1</sup> This increase in the number of effective pathways also increases the accuracy of our computation of  $S$ . We name this new set *contracted pathways*.

<sup>1</sup> As a rule, a pathway with  $n$  compartments generate  $n$  many contracted pathways. The three pathways in Fig. 3 contain 18 compartments in total, and therefore, generate 18 contracted pathways.

We carry out the same computation of  $S$  as we did in Eq. (4) on contracted pathways. Since any compartment receives an environmental input or an inter-compartmental input, it is possible to compute the full  $S$  matrix for any ecosystem model. For example, to compute  $S_{42}$  using the contracted pathways, first we determine how many contracted pathways start with *Deposited detritus* (compartment 2). Note that compartment 2 appears five times in Fig. 3, therefore five contracted pathways will start with *Deposited detritus*. Then we add up the total residence time at *Meiofauna* (compartment 4) for these five (contracted) pathways, and compute  $S_{42}$  as follows:

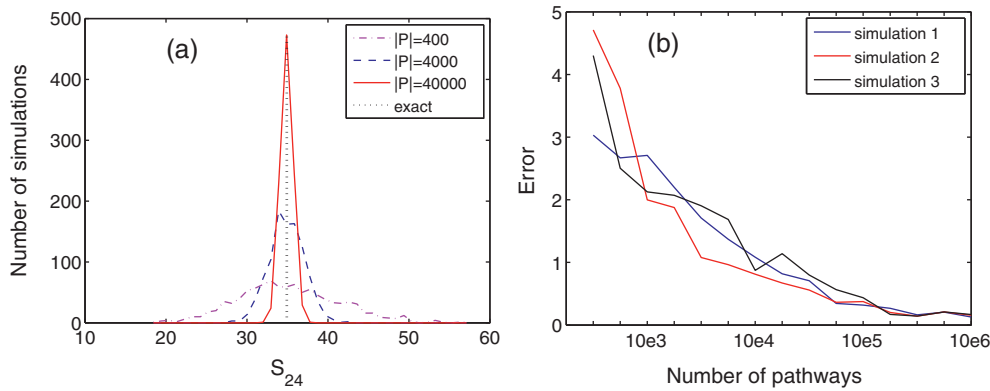
$$S_{42} \approx \frac{(3.6) + (8.1) + (8.1) + (3.8 + 6.1) + (6.1)}{5} = 7.16 \quad (6)$$

In general, we compute  $S$  as follows:

$$S_{ij} \approx \frac{1}{|\mathcal{P}_j|} \sum_{p \in \mathcal{P}_j} \text{Sum of residence times at comp. } i \text{ for pathway } p \quad (7)$$

where  $\mathcal{P}_j$  is a list of contracted pathways that start with compartment  $j$ , and  $|\mathcal{P}_j|$  represents the number of contracted pathways in this list. The larger the value  $|\mathcal{P}_j|$ , the more accurate the computation. Since NPT is a stochastic individual-based method, each





**Fig. 5.** Convergence of the NPT-based stochastic storage analysis matrix  $S$  to the deterministic conventional computation of  $S$  is shown for the oyster reef ecosystem model. (a) Variation of the simulation-based  $S_{24}$  is shown based on 1000 simulations. With increasing pathway data, the distribution converges to a single peak that coincides with the exact value  $S_{24} = 34.93$  computed with the conventional methodology, shown with the vertical dotted line. (b) Frobenius norm of the difference between  $S$  and  $S$  converges to zero with increasing pathway data, which correlates with simulation time. The result holds for three different NPT simulations.

simulation will produce a different output, which raises some questions: (1) How does the computation of  $S$  vary with respect to different simulations of the same model? (2) How much pathway data ( $|\mathcal{P}_j|$ ) is needed on average to obtain an accurate value for  $S_{ij}$ ? Since NPT is based on Gillespie's stochastic algorithm (Gillespie, 1977), the mean of different NPT simulations for the same model should agree with the differential equation model. Therefore, given enough pathway data, both the conventional and the NPT-based definitions for the storage analysis matrix  $S$  should agree. However, feasibility of computation could still be an issue. In other words, how long does the NPT-based computation take to get an accurate answer? We illustrate this issue in Fig. 5 using the oyster reef ecosystem model shown in Fig. 1 as an example.

To answer these questions, we simulated the oyster reef ecosystem model 1000 times, each time generating  $|\mathcal{P}| = 400 \pm 50$  pathways. Here  $\mathcal{P}$  represents the set of all pathways. For each of these 1000 simulations, we computed the storage analysis matrix  $S$ . Then we repeated for  $|\mathcal{P}| \approx 4000$  and  $|\mathcal{P}| \approx 40,000$  pathways. For each case, we created a histogram for  $S_{24}$  based on 1000 simulations (see Fig. 5a) showing the variation of the values computed. The choice of  $S_{24}$  is arbitrary, as any other entry of the  $S$  matrix displays similar behavior. The dotted vertical line in Fig. 5a shows the exact value of  $S_{24} = 34.93$ . We observe a large variation in values computed for  $|\mathcal{P}| \approx 400$ , ranging from  $S_{24} \approx 18$  to  $S_{24} \approx 52$ . This is due to the scarce data provided by each NPT simulation. Although the variation is large, the mean of computed values is 35.13, which is close to the exact value of  $S_{24} = 34.93$ . We observe that the variation decreases for  $|\mathcal{P}| \approx 4000$  and even more so for  $|\mathcal{P}| \approx 40,000$ , where the distribution takes the shape of a sharp peak that coincides with the exact value of  $S_{24} = 34.93$ . Because NPT is a stochastic algorithm, there is no exact control on the number of pathways each simulation will produce. Therefore the numbers of pathways ( $|\mathcal{P}|$ ) presented here are approximate figures. Similar results would be observed if we had compared the output for  $|\mathcal{P}| = 100, 1000$  and  $10,000$ .

Fig. 5a shows that the NPT based computation of  $S_{24}$  converges to its exact value as larger pathway data is used. To show that this is the case for all entries of the  $S$  matrix, we compute error between the conventional and the NPT-based computation of  $S$  using the Frobenius norm,<sup>2</sup> which is an entry-wise

extension of the most widely used vector norm (Euclidean norm) to matrices:

$$\text{Error} = E(S, \hat{S}) = \left\| \frac{S - \hat{S}}{S} \right\|_F = \sqrt{\sum_i \sum_j \left| \frac{S_{ij} - \hat{S}_{ij}}{S_{ij}} \right|^2} \quad (8)$$

In this equation,  $S$  and  $\hat{S}$  represent the NPT-based (see Eq. (7)) and conventional (see Eq. (3)) computation of the storage analysis matrix. By definition, if this error term  $E(S, \hat{S})$  converges to zero, all entries of  $\hat{S}$  have to converge to  $S$ . To demonstrate the convergence of  $\hat{S}$  to  $S$ , we ran three NPT simulations of the oyster reef ecosystem model to generate  $10^6$  pathways. For each simulation, we computed  $\hat{S}$  using increasing number of pathways, starting from  $10^1$  up to  $10^6$ . Fig. 5b shows that for all three simulations, the error  $E(S, \hat{S})$  converges to zero with increasing number of pathways, despite the stochastic behavior of the NPT-based computation.

#### 4. Dynamic storage analysis

NPT based definition of  $S$  (see Eq. (7)) depends solely on the output of an NPT simulation. This simulation may belong to an ecosystem at steady state, in transition to a steady state, oscillating between states, or even a chaotic ecosystem. Therefore the NPT based  $S$  can be computed for dynamic ecosystems, unlike the conventional definition (see Eq. (3)) which is only valid for steady state systems. However, our current definition (see Eq. (7)) only allows us to compute a constant storage matrix  $S$  that represents an “average” behavior over a time interval  $[0, t]$ . In this section, we describe a method to compute a true dynamic storage analysis matrix function  $S(t)$ , where  $S(a)$  represents the instantaneous storage analysis matrix at time  $t = a$ .

##### 4.1. Need for a new definition

Before constructing the NPT-based definition, perhaps we need to clarify the meaning of “dynamic storage analysis matrix”, and study why it is cumbersome to extend the conventional algebraic definition to dynamic ecosystem models. Repeating the steps in Eq. (3) to derive  $S$  for a dynamic ecosystem, we get:

$$\begin{aligned} \dot{x}(t) &= C(x)x(t) + z(t) \\ -C(x)x(t) &= z(t) - \dot{x}(t) \\ x(t) &= [-C(x)^{-1}][z(t) - \dot{x}(t)] \end{aligned} \quad (9)$$

Assume that we define the dynamic storage analysis matrix as  $S(t) = -C(x(t))^{-1}$ , similar to the steady state definition. Note that

<sup>2</sup> Frobenius norm is a component-wise  $L^2$ -norm, and is more suitable for error analysis in our case compared to the standard  $L^2$  (induced) matrix norm.

$S(t)$  no longer maps boundary inputs ( $z(t)$ ) to compartment storages ( $x(t)$ ) because of the extra “ $-\dot{x}(t)$ ” term. In fact,  $S(t)$  maps the difference between the environmental inputs and the change in storage values ( $\dot{x}(t)$ ), to storage values, which is hardly a practical measure. What we need is a matrix function  $S(t)$ , where  $S_{ij}(t)$  represents the instantaneous storage contribution to compartment  $i$  by unit boundary input at compartment  $j$ .

One issue with this definition is that all off-diagonal entries of  $S(t)$  will be zeros ( $S_{ij}(t)=0$  for all  $i \neq j$ ), because it takes time for any boundary input to flow to another compartment, and then contribute to its storage. An instantaneous approximation to a phenomenon that takes a finite, non-zero amount of time to occur will be inaccurate. An example is trying to capture a snapshot of a moving scene at night with a camera at 1/1000 s. The result will be a completely dark picture, since 1/1000 s is not long enough for accurate exposure in low ambient light. In fact, any steady state measure that depends on indirect effects (Higashi and Patten, 1986; Patten, 1995), such as Finn’s cycling index (Kazanci et al., 2009; Finn, 1978) and throughflow analysis (Patten et al., 1976; Matamba et al., 2009), will have the same issue when one tries to extend their definitions to dynamic systems using instantaneous approximations.

Another issue with this definition is the inherent assumption that storage occurs instantaneously. Storage depends not only on the amount of particles that reside in a compartment, but also on the residence time of those particles. The same amount of storage can be created by 10 particles staying in a compartment for a day, or 240 particles staying for an hour. Therefore we revise the previous definition by applying the instantaneous approximation only to the environmental inputs, as follows:

Let  $S_{ij}([a, b])$  represent the amount of storage created at compartment  $i$  over time  $([a, \infty])$ , by a unit input into compartment  $j$  over the time interval  $[a, b]$ . Then we define the dynamic storage analysis matrix function  $S(t)$  as follows:

$$S(t) = \lim_{h \rightarrow 0} S([t - h, t + h]) \tag{10}$$

In this latter definition, we do not care when the storage contribution occurs. It can be at any time. However, since we are dealing with open systems, all particles will leave the system sooner or later. Therefore we can revise the definition above and use a value  $M$  instead of  $\infty$  ( $[a, M]$  instead of  $[a, \infty]$ ) where  $M$  is some large finite value.

In this section, we extended the definition of a steady state measure, storage analysis, to dynamic ecosystem models. The same procedure can be applied to other steady state measures that depend on indirect relations among compartments, such as throughflow analysis (Patten, 1978), Finn’s cycling index (Finn, 1976) and indirect effects ratio (Higashi and Patten, 1986).

#### 4.2. Dynamic storage analysis

Utilizing this new definition for dynamic storage analysis, we

$$S_{ij}(t) \approx S([t - h, t + h]) = \frac{\sum_{p \in \mathcal{P}_j(t-h, t+h)} p}{|\mathcal{P}_j(t - h, t + h)|} \tag{12}$$

describe the computation of  $S(t)$  based on the output of NPT simulations. Similar to numerical differential equation solutions (e.g. Euler, Runge-Kutta, etc.), our computation of  $S(t)$  will be based on a discrete time-step value  $h$ . Smaller  $h$  values are preferred for higher accuracy. To compute an approximate value of  $S_{ij}(t)$ , we first set a time interval  $[t - h, t + h]$ . Then we label those particles entering compartment  $j$  during this time period, and add up their storage contribution to  $i$ . Here is how  $S(t)$  is computed:

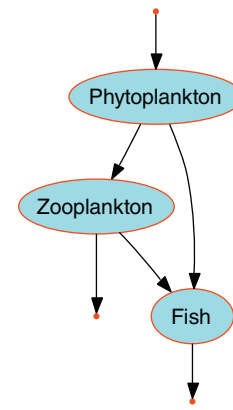


Fig. 6. Simplistic lake model with three compartments, modeling biomass flow.

Step 1: Simulate the model with NPT until all the particles that move during the time window  $[t - h, t + h]$  leave the system.

Step 2: To compute  $S_{ij}(t)$ , we find out all contracted pathways of the form

$$* \rightarrow j \rightarrow \dots \rightarrow i \rightarrow \dots \rightarrow *$$

where the first flow “ $* \rightarrow j$ ” occurs during  $[t - h, t + h]$ .

Step 3: To get an estimated value for  $S_{ij}(t)$ , we add up all residence times at compartment  $i$  for each contracted pathway, and divide this sum by the number of contracted pathways. This value is the average storage contribution (at compartment  $i$ ) of one unit environmental input at compartment  $j$ .

For example, to compute  $S_{61}(1)$  over  $[0.5, 1.5]$  with the sample NPT output shown in Fig. 3, we focus on the contracted pathways of the form  $* \rightarrow 1 \rightarrow \dots \rightarrow 6 \rightarrow \dots \rightarrow *$ . Based on these three pathways, we get totally eighteen contracted pathways (five for particle 144, five for particle 145, eight for particle 146). Only three of these contracted pathways start with compartment 1 (one for particle 144, one for particle 145, one for particle 146). For these three contracted pathways, the first flow ( $* \rightarrow 1$ ) occurs at times 0.5, 1.2 and 2.3, respectively. Only the first two of these time values belong to the interval  $[0.5, 1.5]$ . Therefore we can only use these two specific pathways (that correspond to particles 144 and 145) for this computation. For the first contracted pathway, particle 144 enters compartment 1 at 0.5  $tu$  and stays in compartment 6 for 7.6  $tu$ . Particle 145 enters compartment 1 at 1.2  $tu$  and does not visit compartment 6 at all. Therefore:

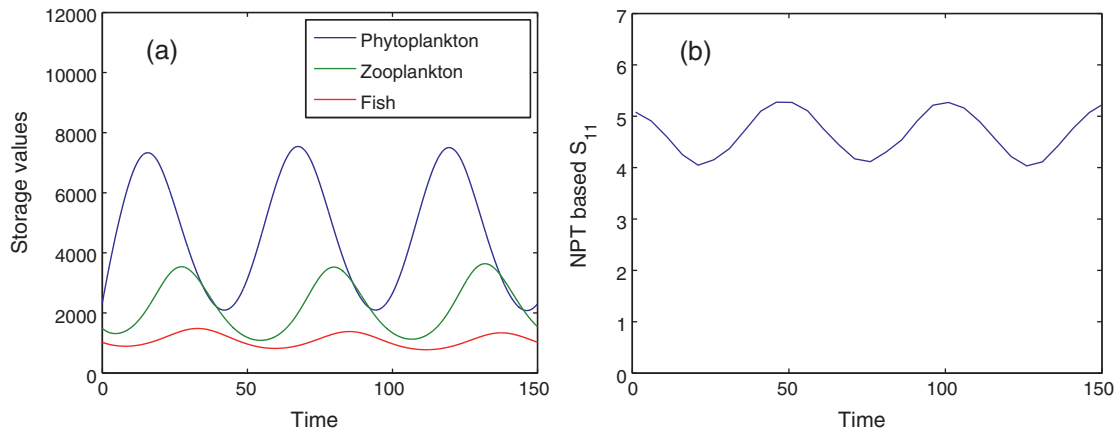
$$S_{61}(1) \approx \frac{(7.6) + (0)}{2} = 3.8 \tag{11}$$

In general, we compute  $S$  as follows:

$$\text{(Sum of residence times at compartment } i \text{ for pathway } p) \tag{12}$$

where  $\mathcal{P}_j(t - h, t + h)$  is a list of extended pathways that start with compartment  $j$ , where the particle enters compartment  $j$  during the time interval  $[t - h, t + h]$ .  $|\mathcal{P}_j(t - h, t + h)|$  represents the number of items in this list.

We demonstrate this method using the simplistic lake model shown in Fig. 6. The three compartment lake model consists of three compartments: phytoplankton, zooplankton and fish. The model accounts for the biomass flow among these compartments,



**Fig. 7.** (a) Time course of biomass storage, simulated using the differential equations (see Eq. (13)) for the simplistic lake model (Fig. 6). The oscillations are indicative of the seasonal changes. (b) The first entry of the dynamic storage analysis matrix  $S_{11}(t)$  computed for this model.

simulating the annual changes of biomass in the lake. The differential equation system is as follows:

$$\begin{aligned} \dot{P} &= 1000 + 600 \sin\left(\frac{t}{8.3}\right) - 2.5 \times 10^{-5}PZ - 2.5 \times 10^{-5}PF - 0.15P \\ \dot{Z} &= 2.5 \times 10^{-5}PZ - 2.5 \times 10^{-5}ZF - 0.1Z \\ \dot{F} &= 2.5 \times 10^{-5}PF + 2.5 \times 10^{-5}ZF - 0.08F \end{aligned} \quad (13)$$

The predatory relations among the three compartments are modeled using Lotka–Volterra type (Lotka, 1925; Volterra, 1926) predator–prey equations (Berryman, 1992). Phytoplankton compartment gets time varying environmental input ( $1000 + 600 \sin(t/8.3)$ ), which represents the fluctuating availability of nutrients and sunlight with seasonal variation. Fig. 7a shows the time course of compartmental storage values. Successive peaks of storage values for the three compartments are in accordance with their trophic level in the lake ecosystem. Fig. 7b shows one element of the dynamic storage analysis matrix  $S(t)$ , computed using  $h = 10 tu$ . We observe that the period of oscillations in Fig. 7a and b coincide with each other (about 50 tu).  $S_{11}(t)$  represents how much storage is generated at compartment 1 (phytoplankton) by a unit input into itself. Comparing Fig. 7a and b we observe a negative correlation between  $S_{11}$  and the storage value of phytoplankton. This is because any input received by phytoplankton at its lowest storage value is more likely to be retained longer, as its storage value increases over time. Similarly, at its peak storage value, any input phytoplankton receives is more likely to be lost as its storage value declines. This inverse relation indicates that more complicated and insightful results might be observed for larger systems with feedback cycles.

Fig. 7 demonstrates the very first example of dynamic storage analysis for a non-linear ecosystem model with time dependent coefficients in the literature. Therefore we do not have any comparison or verification opportunity due to the lack of alternative methodology. However, under certain assumptions, the conventional methodology works for a rather narrow class of dynamic models. We use such a model to test our results.

In Section 2, we mention that  $S = -C^{-1}$  in Eq. (3) is constant if all flows in the model are donor controlled, that is,  $f_{ij} = c_{ij}x_j$  where  $c_{ij}$  is constant for all  $i, j$ . Note that this is true for even dynamic ecosystem models. So, if we compute  $S(t)$  for a dynamic ecosystem model with donor controlled flows,  $S_{ij}(t)$  should stay constant over time, for all  $i, j$ .

To verify our definition of  $S(t)$ , we build a simplistic model, which has the same network structure and similar storage changes over time as with the lake model in Figs. 6 and 7a. We change the flow type to donor-controlled and keep the seasonal changing input.

Although the flow dynamics are different, we adjusted the parameters of this new model so that the time course plots of two models are very similar (Figs. 7a and 8a). Here is the differential equation system for this model:

$$\begin{aligned} \dot{P} &= 1000 + 600 \sin\left(\frac{t}{8.3}\right) - 0.08P - 0.01P - 0.1P \\ \dot{Z} &= 0.08P - 0.05Z - 0.1Z \\ \dot{F} &= 0.01P + 0.05Z - 0.1F \end{aligned} \quad (14)$$

We compute the dynamic storage analysis matrix for this new model. As all the compartmental flows are donor controlled, we expect to observe constant values for  $S(t)$  that do not vary over time, despite the fact that storage values of all compartments will be changing in a similar way to the previous model. Results agree with our prediction. Fig. 8b shows that  $S_{11}(t)$  stays constant over time, indicating that no matter when the particles enter the system, their contribution to the storage value of phytoplankton remains the same regardless of time. While we only provide the time course figure for  $S_{11}(t)$ , the remaining eight entries of the  $S(t)$  matrix depict the exact same behavior.

#### 4.3. Verification and accuracy

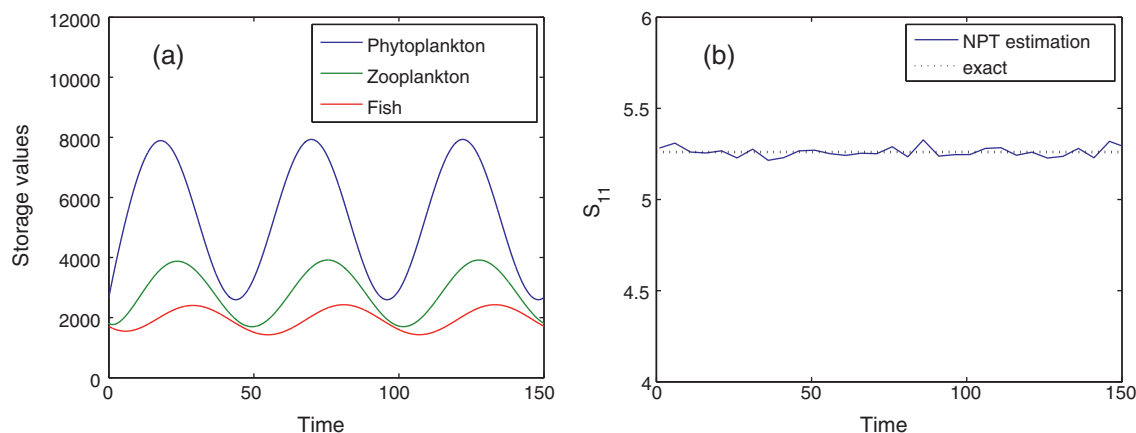
We have previously discussed the accuracy of NPT based storage analysis matrix computation for steady state ecosystem models (see Fig. 5), and concluded that this new method has good convergence properties, and that  $S$  can be feasibly computed with arbitrary accuracy. This conclusion is valid for the dynamic case as well. However, the computation of  $S(t)$  includes one more parameter ( $h$ ) which is related to the following approximation:

$$S(t) = \lim_{h \rightarrow 0} S(t-h, t+h) \approx S(t-h, t+h) \text{ when } h \text{ is small} \quad (15)$$

How small should  $h$  be chosen so that  $S(t)$  is computed accurately? This is an important concern, especially if  $S(t-h, t+h)$  changes rapidly as  $h \rightarrow 0$ , which means that  $S(t)$  could vary greatly when  $h$  is small, which negates the purpose of the approximation in Eq. (15). Fortunately this is not the case, because the instantaneous approximation to  $S(t)$  is defined as the average value of  $S(t)$  over the interval  $[t-h, t+h]$ :

$$S(t) \approx S(t-h, t+h) = \frac{1}{2h} \int_{t-h}^{t+h} S(t) dt \quad (16)$$

Therefore the error term  $|S(t-h, t+h) - S(t)|$  is going to be exactly zero if the change in  $S(t)$  is linear (with respect to time). In other words, no matter how fast or steep the change in  $S$  is, as long as



**Fig. 8.** (a) Time course of biomass storage, simulated using the differential equations (see Eq. (14)) for the simplistic lake model (Fig. 6). (b) The first entry of the dynamic storage analysis  $S_{11}(t)$  computed for this model.

it is close to linear, the approximation above will be almost exact.  $S_{11}(t)$  presented in Figs. 7b and 8b were computed using  $h = 10$ . Decreasing the value of  $h$  to 5 yielded no visible difference in  $S(t)$ .

Accuracy will be of concern only if  $(d^2S(t))/(dt^2)$  is significantly large. This only happens for extremely sudden changes, and are rather rare for ecosystems. Even in such cases, choosing smaller  $h$  values guarantees accurate results. If a specific model is prone to sudden changes, then an adaptive algorithm can be devised that can choose the appropriate  $h$  value automatically, based on the same idea used for adaptive ODE solvers such as Runge-Kutta-Fehlberg (Hull et al., 1972).

## 5. Conclusion and future work

In this paper, we present a novel simulation based approach to compute storage analysis for compartmental models. The simulations (NPT) are stochastic, whereas the conventional methodology is deterministic. Linear algebra is used for conventional residence time studies, whereas we use combinatorics and intuitive counting arguments. Despite these vast differences, both definitions of the same measures equal each other (see Fig. (5)), which attest to the accuracy and reliability of this new method.

Furthermore, the new definition in this paper is not restricted with the limitations of the current methodology. Change is often the focus of essential research problems such as environmental impacts and climate shifts. The same simulation-based definition applies to dynamic systems, which greatly extends the applicability of storage analysis. Similar simulation-based definitions exist for Finn's cycling index (Kazanci et al., 2009), throughflow analysis (Matamba et al., 2009), indirect effects index (Patten, 1986; Ma and Kazanci, 2012), and are being developed for other network properties. Similar to storage analysis, all these measures are only applicable to steady state systems. The method presented in this paper can be used for all ecological network properties with simulation based definitions, to extend their applicability to dynamic models.

Previous efforts to extend the applicability of ecological network properties to dynamic models exist (Hippe, 1983; Shevtsov et al., 2009). Hippe (1983) proposes a differential equation based approach, which is only applicable to donor-controlled flows. Therefore the simple system that we study in Fig. 8 cannot be used with this method. While the method proposed by Shevtsov et al. (2009) does not have this limitation, the methodology presented in this paper is superior in terms of accuracy and scalability.

This method does not replace, but complement the conventional methodology, which is preferable for steady state systems.

The conventional methodology is easier to use, as no simulations are necessary. The results are exact values, only limited by computational precision, whereas the simulation based method only provides approximate values. Not everyone has quick access to NPT simulations. Therefore we plan to integrate simulation-based results to EcoNet (<http://eco.engr.uga.edu>), a free online software for modeling, simulation and analysis (Kazanci, 2007, 2009; Schramski et al., 2011). This integration would make this rather computationally heavy method accessible to a wide range of scientists and disciplines, increasing its adoption and utilization for current and future ecosystem models.

Accuracy is another concern with this new method, as the results contain errors due to approximations involved. However, it is possible to get arbitrarily accurate results using larger pathway data sets. The cost, as with other numerical methods, is the computation time. In our experience, the computation time has always been in the order of seconds and minutes at most (on a regular desktop computer with two 2.5 GHz cores). However, the computation time will increase with system size and complexity, which also brings the issue of scalability. The method fares well in this regard. We have run a simulation for a model with 3000 compartments involving  $9 \times 10^9$  particles. This unusually large model (Small et al., 2009) was built to study the effect of consumer stoichiometric regulation on nutrient spiraling in streams. The very fact that we were able to run a simulation for such a model confirms its applicability to large and complex systems. The computing time will be less of an issue in near future, with the current technological advances in hardware and software.

Our future work will focus on extending this novel methodology to other network properties (e.g. Finn's cycling index, Indirect effects index), as well as application to specific ecosystem models validating its use as a practical empirically-based methodology.

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## Appendix A. Intertidal oyster reef ecosystem model in EcoNet format

Energy flows in an Intertidal oyster reef ecosystem model (Dame and Patten, 1981) is shown in EcoNet (Kazanci, 2007, 2009; Schramski et al., 2011) format. Flow units are in kcal/m<sup>2</sup>/day, storage units are in kcal/m<sup>2</sup>.

```
* ->Filter_Feeders c=41.4697
```

```
Filter_Feeders ->Dep_Detritus c=0.0079
```

```
Filter_Feeders ->Predators c=0.0003
```

```
Dep_Detritus ->Microbiota c=0.0082
```

```
Dep_Detritus ->Meiofauna c=0.0073
```

```
Dep_Detritus ->Dep_Feeders c=0.0006
```

```
Microbiota ->Meiofauna c=0.5
```

```
Microbiota ->Dep_Feeders c=0.5
```

```
Meiofauna ->Dep_Detritus c=0.1758
```

```
Meiofauna ->Dep_Feeders c=0.0274
```

```
Dep_Feeders ->Dep_Detritus c=0.1172
```

```
Dep_Feeders ->Predators c=0.0106
```

```
Predators ->Dep_Detritus c=0.0047
```

```
Filter_Feeders -> * c=0.0126
```

```
Dep_Detritus -> * c=0.0062
```

```
Microbiota -> * c=2.3880
```

```
Meiofauna -> * c=0.1484
```

```
Dep_Feeders -> * c=0.0264
```

```
Predators -> * c=0.0052
```

```
Filter_Feeders = 2000; Dep_Detritus = 1000; Microbiota = 2.4121;
```

```
Meiofauna = 24.121; Dep_Feeders = 16.274; Predators = 69.237
```

The text above can be directly entered into EcoNet web interface at <http://eco.engr.uga.edu> to generate Fig. 1 and the same results in Table 1. More information on EcoNet and its model structure is available on its website.

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