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## How much of the storage in the ecosystem is due to cycling?

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## H I G H L I G H T S

- Finn's cycling index (FCI) computes the cycled ecosystem flow.
- Develop a new storage-based cycling index (SCI).
- SCI utilizes both flow and residence time.
- SCI is vastly different from FCI for most systems.
- SCI is a preferable index for quantifying cycling.

## A R T I C L E I N F O

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## A B S T R A C T

Cycling is the process of reutilization of matter or energy in the ecosystem. As it is not directly measurable, the strength of cycling is calculated based on mathematical models of the ecosystem. For a storage-flow type ecosystem model, throughflow is the total amount of material flowing through all system compartments per unit of time, while storage represents the total standing stock in the system. Finn's cycling index (FCI) is widely used to measure the cycled throughflow, the proportion of throughflow generated by cycling. Thus, although originally named after its author J.T. Finn, FCI can also be called a "flow-based" cycling index. In addition to flow, storage plays an important role in generating network properties, and therefore should be taken into account in measuring cycling. In this paper, we investigate how much of the total standing stock of matter or energy in the ecosystem is due to cycling, and formulate a storage-based cycling index (SCI), by utilizing an individual-based method to simulate the system. SCI utilizes flow values used for FCI and takes into account residence time as well. Therefore, SCI is a preferable index for quantifying cycling in ecosystems.

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## 1. Introduction

Cycling of nutrients in ecosystems (Odum, 1971), such as carbon, phosphorus and nitrogen cycles, has been widely investigated in the last several decades. Despite some disagreement (Odum, 1971), energy also cycles in the ecosystem (Patten, 1985, 1986), but not in as significant amounts as matter. The cycling of energy is mainly accomplished by the flow of energy in dead organic matter to detritus, and back to the system through detritus feeders (Fath and Hales, 2007). Energy cycling can also be realized by the cannibalism (the eating of one's own offspring), which occurs in a variety of taxa, but is especially prevalent in fishes with parental care (FitzGerald, 1992). Many studies on cycling in ecosystems (Fenchel and Blackburn, 1979; DeAngelis, 1980) have been devoted to the empirical description of specific cycling processes, such as the

detailed pathways of carbon, phosphorus and nitrogen cycles. In this paper, we focus on quantifying this important measure for a general ecosystem model of any conservative flow currency, such as biomass, nutrients, energy, or a specific element such as carbon, nitrogen or phosphorus.

According to Odum (1969), cycling is an indicator of maturity of an ecosystem. It reveals the ecosystem's ability to retain matter or energy, and to endure in the face of resource scarcity. Several studies (DeAngelis, 1980; DeAngelis et al., 1989; Loreau, 1994) indicate that increasing material cycling tends to increase the probability that the system will be locally stable. Scotti (2008) points out that increasing the amount of recycled matter tends to increase transfer efficiency and minimize the ecosystem's dependence on external supports. Depending on the flow currency, the effect of cycling may be interpreted differently. For nitrogen and phosphorus, it means efficient utilization of nutrients (Vitousek, 1982). For carbon, high cycling may indicate a stressed system (Wulff and Ulanowicz, 1989). High cycling in a stressed system is mostly through shorter cycles, while the similar cycling values

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tend to be realized through longer paths in mature systems (Baird and Ulanowicz, 1993; Christian et al., 2005; Scotti, 2008). Therefore, quantifying cycling in ecosystems is of great importance to evaluate how well the ecosystem functions. However, measuring the strength of cycling is not trivial. One reason is that, unlike many other ecological indicators, the strength of cycling cannot be measured directly, as its occurrence depends on indirect flows, which are mediated or transmitted through other compartments. For example, even the shortest cycle, such as  $A \rightarrow B \rightarrow A$ , requires indirect flows that are transmitted by  $B$ .

Most efforts on developing a cycling index are based on mathematical models that describe the flow of energy or matter among a variety of species. While cycling can simply be defined as the reutilization of flow material, there are multiple ways to quantify the strength of cycling (Finn, 1976; Patten and Higashi, 1984; Allesina and Ulanowicz, 2004). For example, Finn's cycling index (FCI) (Finn, 1976, 1978) calculates the proportion of total system throughflow of energy or matter that is generated by cycling. Allesina and Ulanowicz (2004) propose a comprehensive cycling index (CCI) that takes into account cycling paths, including simple cycles, compound paths and compound cycles. Simple paths are defined as paths with no repeated compartments; simple cycles are simple paths in which the starting and the ending compartments coincide; compound paths are the paths with repeated compartments; and compound cycles are repeated cycles. A different approach by Ulanowicz (1983) quantifies the amount of cycling by subtracting the structure of cycling from the entire network. All simple cycles are subtracted from the network until the remaining network becomes acyclic.

Among various cycling indices, the most widely accepted and used one is Finn's cycling index (FCI) (Finn, 1976, 1978). This index is part of ecological network analysis (ENA) (Patten, 1978; Fath and Patten, 1999; Ulanowicz, 2004), a system-oriented methodology to analyze within-system interactions (Fath and Borrett, 2006). ENA works with the representations of ecosystems as compartmental models, where compartments and connections represent various species and flows of matter or energy, respectively. ENA defines various quantitative indicators, including FCI, to describe different aspects of the ecosystem. Most of these indicators provide the description of non-observable relations within the system. For example, indirect effect index (IEI) represents the proportion of indirect effects over the total effects (Higashi and Patten, 1989; Ma and Kazanci, 2012a); throughflow analysis (N matrix) (Matamba et al., 2009) and storage analysis (S matrix) (Fath and Patten, 1999), respectively, calculate how the environmental inputs contribute to throughflow and storage of each compartment in the system. Most of these measures involve somewhat unintuitive matrix computations, and are only applicable to steady-state systems, where the flow and storage values stay constant over time. In contrast to the algebraic method used in ENA, an individual-based simulation method, network particle tracking (NPT), has been used to study most ENA indicators and offer simpler and more intuitive interpretations of these properties (Kazanci et al., 2009; Matamba et al., 2009; Ma and Kazanci, 2012a,b). As NPT is based on Gillespie's stochastic algorithm (Gillespie, 1977) for simulating chemical reactions, the mean of different NPT simulations for the same model agrees with the differential equation model. Simulating tracer experiments, NPT discretizes storages of energy or mass into particles (e.g., single atoms and energy quanta) and provides a list of pathways that particles pass through the ecosystem. Furthermore, utilizing NPT, Kazanci and Ma (2012) extend some ENA measures to dynamic models, significantly increasing their applicability.

FCI is defined using an algebraic formula. While this algebraic definition of cycling is computationally efficient for steady-state models, it is rather hard to build an intuitive link between the

concept of cycling and the formula itself. For example, Allesina and Ulanowicz (2004) state that "FCI is a biased counting of cycling, because it does not include all flows engaged in recycling". While FCI does indeed compute the fraction of cycled throughflow through all indirect flows, this fact is not immediately recognizable from its algebraic formula. Using NPT, Kazanci et al. (2009) confirm that FCI does actually compute the fraction of all particles' revisits to compartments (system throughflow due to cycling) over the total number of visits (total system throughflow). This pathway-based computation of FCI is much more intuitive than its algebraic formula. Furthermore, NPT simulations are not limited to steady-state networks, and therefore, are able to extend FCI to dynamic models as well.

While this pathway-based method confirms the accuracy of FCI, it also exposes a significant limitation of FCI, that it only counts the number of revisits but disregards how long these revisits are. For example, given that particle A revisits compartment "Producers" spending 2 days there and that particle B also revisits the same compartment "Producers" staying for 10 days, these two revisits are regarded equally by FCI. Our intuition is that the revisit with longer residence time should contribute more to the strength of cycling. That means particle B's contribution to cycling is four times greater than that of particle A. To eliminate this discrepancy, we propose a new cycling index that weights each visit with its corresponding residence time.

Using NPT simulations, we demonstrate the computation of a weighted cycling index, utilizing both flow rate and residence time. The product of flow rate and residence time is the storage value. Therefore, this new weighted cycling index computes the proportion of storage generated by cycling, and therefore is called storage-based cycling index (SCI). For steady-state networks, we also construct an algebraic formula for SCI that agrees with the pathway-based calculation. Previously, Patten and Higashi (1984) proposed an approximation to a storage-based cycling index using Markovian techniques. However, due to the cumbersome nature of the involved computation, this work is not utilized nearly as much as FCI (cited only 29 times, whereas FCI was cited 475 times). In this paper, we introduce both a pathway-based definition and an algebraic formulation for SCI, which provide a much more intuitive interpretation, and an efficient computation for steady-state systems, respectively.

FCI and SCI measure the amount of cycling from the perspective of flow rate and storage, respectively. We compare FCI and SCI for sixteen seasons' nitrogen flow models for the Neuse River estuary, North Carolina, USA (Christian and Thomas, 2003). For these models, SCI is more sensitive to the seasonal changes occurring in the system. A comparison between FCI and SCI is also shown with thirty-six published ecological network models, which have a variety of network sizes. Their values for a specific ecological network can differ significantly. SCI utilizes all the information used for computing FCI, and also takes into account the residence time, which is an important network property. Herendeen (1989) has indicated that the residence time of nutrients can be affected by cycling. Patten (1985) also shows the importance of storage in generating network properties, such as in diversifying path structure and increasing flows in networks. Patten also concludes that energy storage as biomass is the root cause of ecosystem energy cycling. Therefore, storage should be taken into account in measuring of cycling (Patten and Higashi, 1984). We propose SCI as a desirable cycling index for ecosystems.

FCI and SCI, initially defined as system-level measures, can be utilized to quantify the cycling strength for a single compartment in the system as well. In other words, one can compute how much of the throughflow or storage of a specific compartment is due to cycling. In Section 5, we provide the computation of compartmental FCI and SCI and discuss their relationship for steady-state networks.

## 2. Finn's cycling index (FCI): a flow-based cycling index

### 2.1. Definition of FCI

Computation of Finn's cycling index (FCI) relies solely on the flow rates of the ecological system, including environmental inputs ( $\mathbf{z}$ ), outputs ( $\mathbf{y}$ ) and flows among compartments ( $F$ ). Besides flows, the storage value ( $x$ ) represents the amount of currencies stored in each compartment. Assuming there are  $n$  compartments in the system, all the flows and storages are denoted as follows:

- $z_i$  : Rate of environmental input to compartment  $i$
- $y_i$  : Rate of environmental output from compartment  $i$
- $x_i$  : Storage value at compartment  $i$
- $F_{ij}$  : Rate of direct flow from compartment  $j$  (columns of  $F$ ) to compartment  $i$  (rows of  $F$ )

where  $i, j = 1, 2, \dots, n$ . Throughflow  $T_i$  is the rate of material (or energy) moving through compartment  $i$ . Input throughflow is defined as the sum of flow rates into compartment  $i$  from other compartments and the environment. And output throughflow is the sum of flow rates from compartment  $i$  to other compartments and the environment. For a system at steady state, input and output throughflows are equal:

$$T_i = \sum_{j=1}^n F_{ij} + z_i = \sum_{j=1}^n F_{ji} + y_i. \tag{1}$$

The total system throughflow (TST) is the sum of throughflow  $T_i$  for all compartments in the system. The idea of FCI is to divide TST into two parts: one contributed by flow material's initial visits, and the other generated through revisits or cycling, called  $TST_c$ . The fraction  $TST_c/TST$  is defined as FCI. The derivation of the algebraic formula is described below.

First, the flow intensity matrix  $G$  is obtained by normalizing the flow matrix  $F$  by the throughflow  $T$ :

$$G_{ij} = \frac{F_{ij}}{T_j} \tag{2}$$

$G$  is actually a one-step probability transition matrix, where  $G_{ij}$  represents the probability of transitioning from compartment  $j$  to compartment  $i$  in one step.  $[G^m]_{ij}$  represents the fraction of the flow material from  $j$  to  $i$  in exactly  $m$  steps ( $j \rightarrow \dots \rightarrow i$ ). The sum of

all powers of  $G$  defines the throughflow analysis matrix  $N$ :

$$N = \underbrace{I}_{\text{Boundary}} + \underbrace{G}_{\text{Direct}} + \underbrace{G^2 + G^3 + \dots}_{\text{Indirect}} = (I - G)^{-1} \tag{3}$$

where  $I$  is the identity matrix.  $N_{ij}$  represents the throughflow generated at compartment  $i$  by per unit input at compartment  $j$ . By definition, diagonal values  $N_{ii}$  represent the amount of throughflow generated at compartment  $i$  by one unit input into compartment  $i$ . Another interpretation from the perspective of flow material is the number of times the discretized input (e.g., carbon atom, energy quantum) entering at  $i$  will go through  $i$  on average. A unit input into compartment  $i$  contributes to its throughflow ( $T_i$ ) at least once due to the initial visit. Therefore by definition,  $N_{ii}$  is larger than or equal to 1. Then, the difference  $(N_{ii} - 1)$  represents the amount of throughflow generated at compartment  $i$  only through cycling. Based on this idea, Finn (1978) defines his cycling index as the fraction of the total system throughflow (TST) due to cycling ( $TST_c$ ):

$$FCI = \frac{TST_c}{TST} = \frac{1}{TST} \sum_{i=1}^n T_i \frac{N_{ii} - 1}{N_{ii}}. \tag{4}$$

### 2.2. An easier interpretation of FCI from the perspective of pathways

Kazanci et al. (2009) provide a much simpler and intuitive interpretation for FCI using the individual-based simulation method called network particle tracking (NPT). It is based on Gillespie's stochastic algorithm (Gillespie, 1977; Doob, 1945), which is a variety of a dynamic Monte Carlo method (Meng and Weinberg, 1994; Metropolis and Ulam, 1949). As shown in Fig. 1, NPT discretizes storages of energy or matter into small particles such as single carbon atoms or energy quanta, which are determined by the modeler. Then, 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. This method traces movements of these particles, and stores their pathways as an ordered list of compartments they visit as they flow through the system. By converting flow rates (inputs, outputs and inter-compartmental flows) into a list of particle pathways, NPT offers a different way to view the system from the perspective of a single unit of flow material, such as a single carbon atom, or an energy quantum.

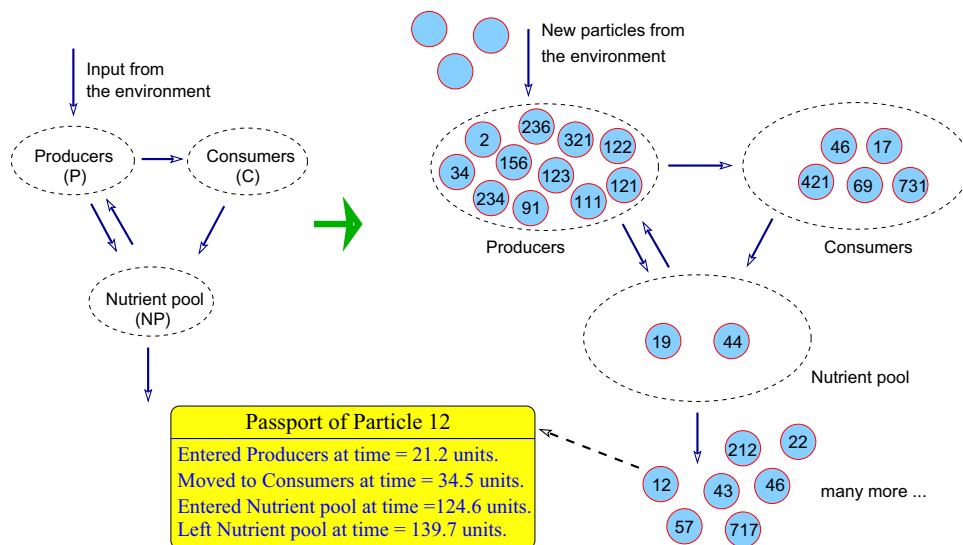


Fig. 1. NPT discretizes storages of energy or matter into small particles such as single carbon atoms or energy quanta, then traces movements of these particles, and stores the pathways they pass through in the system.

NPT has been used to re-investigate, verify and extend the applicability of several NEA measures. For example, Kazanci et al. (2009), Matamba et al. (2009) and Kazanci and Ma (2012) show that the pathway-based computations and conventional algebraic formulations coincide for FCI, throughflow analysis (N matrix), and storage analysis (S matrix). Using NPT, Ma and Kazanci (2012a) show that the original definition of indirect effects ratio ( $I/D$ ) differs from its intended meaning, and provide a revised formulation. Extending the applicability of ecological network analysis to dynamic models has been discussed in Kazanci and Ma (2012), using storage analysis as an example.

Here we describe the computation of FCI using particle pathways. Fig. 2 is a sample output of NPT, including the pathways of three particles. As shown in Fig. 2, each particle visits a list of compartments before leaving the system. Letters P, C, and NP represent the three compartments “Producers”, “Consumers”, and “Nutrient pool” in Fig. 1, respectively. The total number of compartments visited by these three particles is 13. Some particles may visit the same compartment multiple times because of cycling. In Fig. 2, these revisits caused by cycling are underlined. The number of revisits due to cycling is 4. Therefore,  $FCI = 4/13 \approx 0.3077$ . The sample output containing three pathways is used to demonstrate the idea of this method. More pathways will be needed for an accurate computation of FCI. As the number of pathways in the computation increases, the pathway-based computation of FCI converges to the conventional algebraic formulation (Eq. (4)). Kazanci et al. (2009) show that for a four-compartment network,  $10^5$  pathways are required for an accurate computation. It takes less than a second to simulate this many pathways on a modern dual-core 3 GHz computer. Therefore, high accuracy can be achieved by increasing the number of pathways being used, without consuming too much simulation time.

2.3. Limitations of FCI

In the previous subsection, we observe that FCI only counts the number of compartments visited by particles. The number of compartment visits corresponds to flow rates. Therefore, FCI only depends on the flow rates. This fact is also demonstrated by the

Particle 1 Pathway \* → P → NP → P → C → NP → \*  
 Particle 2 Pathway \* → P → C → NP → P → NP → \*  
 Particle 3 Pathway \* → P → C → NP → \*

Fig. 2. Sample output of NPT: pathways of three particles. Letters P, C, and NP within the pathways represent three compartments “Producers”, “Consumers”, and “Nutrient pool”, respectively. “\*” denotes the environment.

algebraic definition of FCI in Eq. (4), as all the terms in the equation, including  $T$  and  $N$ , are only flow-related. Thus, if a network’s flow rates are fixed, the FCI will remain constant, regardless of how the storages of compartments vary. In other words, two networks with the same flow rates but different storages will have the same strength of cycling according to FCI. While FCI is named after its author, J.T. Finn, interpreting FCI as “flow-based” cycling index is perhaps more descriptive.

Fig. 3 shows two conceptual ecosystems with exactly the same environmental input ( $z$ ), flow matrix ( $F$ ) and environmental output ( $y$ ). In this example, the only difference between these two systems is the storage of the compartment “Producers”. In Fig. 3(a), “Producers” has the storage of 50 units which is higher than that in “Consumers” (20 units). As observed in most ecosystems, the biomass of lower trophic levels is larger than that of higher levels, following the well-known ecological pyramid of biomass (Odum, 1971). In Fig. 3(b), “Producers” has the storage value of 5 units, which is even lower than that of “Consumers” (20 units). Therefore, it follows an inverted pyramid (Jackson, 2006), which also occurs in real life. For example, in some water ecosystems, the total amount of major producers, such as phytoplankton, is usually smaller than the standing stock of the consumers. This can be explained by the short life span of phytoplankton in the water ecosystem. They are consumed fast but also reproduce quickly, ensuring enough food supply for consumers.

Because of the same flow rates, FCI (using Eq. (4)) for these two systems in Fig. 3 are exactly the same:  $FCI = 0.0422$ . However, as we have discussed earlier, these two systems represent totally different ecosystems in real life. As the producers in (b) have shorter life span than those in (a), the flow material in system (b) has a shorter residence time. Shorter residence time may mean lower ability of retaining biomass or energy within the system, or less efficient utilization of nutrients. This indicates that (b) might have weaker cycling than (a). Such differences due to storage or residence time are ignored by FCI, raising the need for a new cycling index. In addition, what we can directly observe in real ecosystems is mostly the storage (biomass in trees, grass, animals, etc.), but rarely the flows (the movement of biomass from one species to another, such as sheep preyed upon by wolves). Storage plays an important role in ecosystem function (Patten, 1985). Thus, a new cycling index that quantifies the amount of the storage generated by cycling can potentially be more useful in certain situations, especially when the focus of research is on the storage or the ecosystem evolves significant changes of storage. For example, carbon storage and cycling (Pregitzer and Euskirchen, 2004; Hazen et al., 2012) has been an active research topic in ecology. In these studies, storage is a property that cannot be ignored, thus a storage-based cycling index is preferable than a flow-based one. Another example is eutrophication. Eutrophication involves a great increase of plant

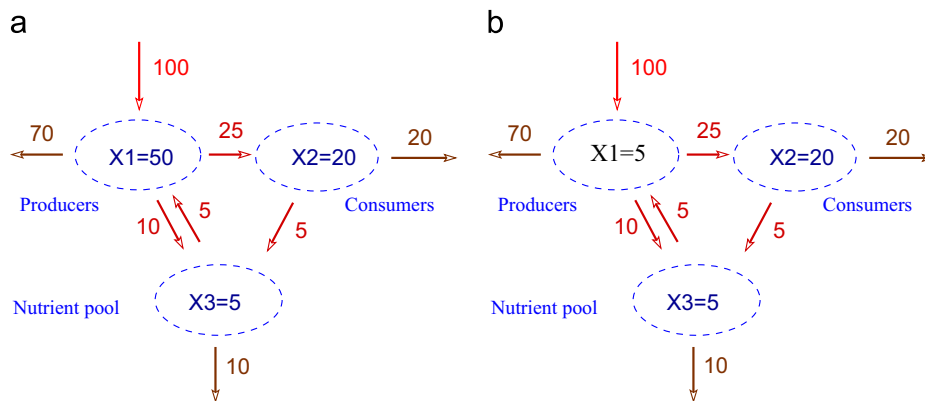


Fig. 3. Two simple conceptual ecosystems with the same flow rates, but different storages.

Particle 1	Pathway	*	>	P	→	NP	→	<u>P</u>	→	C	→	<u>NP</u>	→	*
	Flow time			0.5		9.7		16.8		20.4		27.2		34.8
	Residence time					9.2		7.1		<u>3.6</u>		6.8		<u>7.6</u>
Particle 2	Pathway	*	→	P	→	C	→	NP	→	<u>P</u>	→	<u>NP</u>	→	*
	Flow time			1.2		10.3		19.8		28.0		33.5		41.6
	Residence time					9.1		9.5		8.2		<u>5.5</u>		<u>8.1</u>
Particle 3	Pathway	*	→	P	→	C	→	NP	→	*				
	Flow time			2.3		9.2		13.4		17.2				
	Residence time					6.9		4.2		3.8				

Fig. 4. Sample NPT output, including pathways, flow times and residence times. The letters P, C, and NP within the pathways represent the three compartments “Producers”, “Consumers”, and “Nutrient pool”, respectively. “\*” denotes the environment.

biomass in the ecosystem. As FCI does not reflect changes of storage, SCI can possibly serve as an indicator to detect eutrophication.

### 3. Storage-based cycling index (SCI): a residence time-weighted cycling index

In this section, we develop a storage-based cycling index to quantify the amount of total standing stocks in the system due to cycling. Pathway-based computations of FCI provide a more intuitive interpretation than algebraic approaches. NPT simulations generate pathway and residence time information for each particle flowing in the system, thus becoming a suitable tool to develop a storage-based cycling index. Fig. 2 only provides the pathway information, whereas Fig. 4 shows the complete simulation output for the same three particles, including pathways, flow times and residence times. “Flow time” indicates the times when the particle enters the system, moves from one compartment to another, and leaves the system. “Residence time” indicates the duration a particle stays in each compartment, computed as the difference between the entrance and exit times. For example,

$$\begin{aligned}
 SCI &= \frac{\text{Residence time of repeated visits}}{\text{Residence time of all visits}} = \frac{\overbrace{(3.6 + 7.6)}^{\text{Particle 1}} + \overbrace{(5.5 + 8.1)}^{\text{Particle 2}}}{\underbrace{(9.2 + 7.1 + 3.6 + 6.8 + 7.6)}_{\text{Particle 1}} + \underbrace{(9.1 + 9.5 + 8.2 + 5.5 + 8.1)}_{\text{Particle 2}} + \underbrace{(6.9 + 4.2 + 3.8)}_{\text{Particle 3}}} \\
 &= 0.2768.
 \end{aligned}
 \tag{5}$$

particle 3 in Fig. 4 enters the system at compartment P (Producers) at time=2.3 units, then moves to compartment C (Consumers) at time=9.2, moves to compartment NP (Nutrient pool) at time=13.4 units, and finally leaves the system at compartment NP (Nutrient pool) at time=17.2 units. It passes through three compartments in total and stays in compartments P, C, and NP for 6.9 units, 4.2 units and 3.8 units, respectively. The time unit here can be in hours, days, or years, determined by the modeler, based on the available empirical data. In Fig. 2, all the compartments revisited by each particle are underlined. In Fig. 4, we underline both the revisited compartments and the corresponding residence times in these compartments.

The reason why the mall is more crowded on black Friday is not only that more people visit the mall, but also the fact that they stay longer to browse and take advantage of various deals. Similarly, the storage of a compartment is determined by two factors: throughflow and residence time. The number of particles' visits to compartment *i* corresponds to its throughflow at *i* ( $T_i$ ). The sum of residence times for all visits constitutes the storage at *i* ( $x_i$ ).

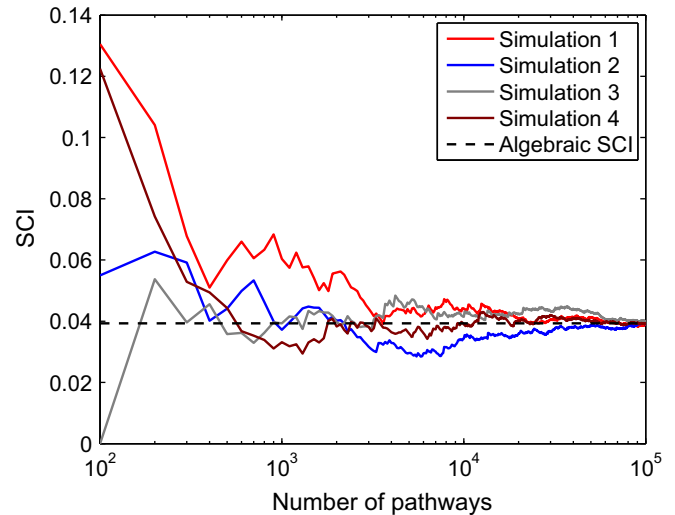


Fig. 5. Computation of SCI using NPT simulations in Eq. (5) converges to the result using Eq. (7).

In Fig. 4, both particles 1 and 2 revisit compartment P (Producers) once. Particle 2 stays in compartment P (5.5 units) longer than particle 1 (3.6 units). Given the number of revisits is equal for the two particles, their contribution to the storage is proportional to their residence time in compartment P. The computation of FCI counts the number of revisits but disregards how long these revisits are. Thus, FCI quantifies the cycled throughflow. To derive the storage-based cycling index, we should weight each visit with the corresponding residence time.

The sum of residence times in these revisited compartments constitutes the total storage due to cycling. The sum of residence times in all compartments is the total storage generated by both first and repeated visits. Therefore, a storage-based cycling index (SCI) is computed as follows:

Using the same three pathways, SCI is different from FCI ( $FCI = 4/13 = 0.3077$ ). While this pathway-based computation of SCI is intuitive and easy to understand, an algebraic formulation, which is vastly easier to compute, is also desirable for steady-state networks. As the computation of FCI (Eq. (4)) is in terms of compartmental throughflow  $T$  and throughflow matrix  $N$ , one straightforward way to construct SCI formulation is to replace these flow-based terms with the storage-based terms. Throughflow ( $T$ ) can be replaced by storage values ( $x$ ). Ecological Network Analysis (Fath and Patten, 1999) provides a storage-based alternative ( $S$ ) to the throughflow analysis matrix  $N$ , where  $S_{ij}$  represents the storage generated at compartment *i* by per unit input at compartment *j*. From the perspective of particles,  $S_{ij}$  is the sum of its residence times at *i* given that the particle enters the system at *j*. The algebraic formulation of the storage analysis matrix  $S$  is defined below. Further information on the pathway-based computation and interpretation of  $S$  is provided in Kazanci and Ma (2012):

$$S = -C^{-1}
 \tag{6}$$

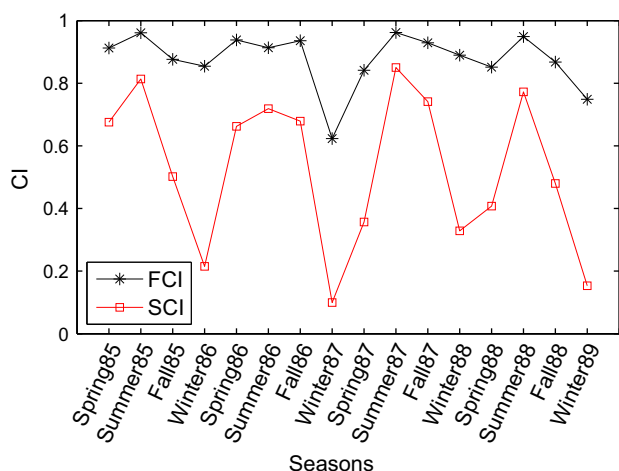


Fig. 6. SCI and FCI of sixteen seasons' nitrogen flow in Neuse River estuary, North Carolina (Christian and Thomas, 2003).

where

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

In the formula of FCI (Eq. (4)), by subtracting the first visit,  $N_{ii} - 1$  represents the total number of revisits to compartment  $i$ . The corresponding storage-based measures  $RT_i$  and  $S_{ii}$ , respectively, represent the particles' residence time at compartment  $i$  for the first visit, and the cumulative residence time including all revisits. Then,  $S_{ii} - RT_i$ , analogous to  $N_{ii} - 1$ , is the sum of residence times of revisits (excluding the first visit). Therefore,  $(S_{ii} - RT_i)/S_{ii}$  indicates the proportion of residence time caused by cycling. Based on the algebraic formula of FCI (Eq. (4)), simply by substituting throughflow ( $T_i$ ) with storage values ( $x_i$ ), and  $(N_{ii} - 1)/N_{ii}$  with  $(S_{ii} - RT_i)/S_{ii}$ , the SCI formulation that computes the fraction of total system storage (TSS) due to cycling ( $TSS_c$ ) is proposed as follows:

$$SCI = \frac{TSS_c}{TSS} = \frac{1}{TSS} \sum_{i=1}^n x_i \frac{S_{ii} - RT_i}{S_{ii}} \quad (7)$$

where TSS (total system storage) is computed as the sum of storage values  $x_i$  of all compartments in the system. To further demonstrate that this formula agrees with the pathway-based computation in Eq. (5), both methods are utilized to compute SCI for the three-compartment steady-state model in Fig. 3(a). The SCI computed using Eq. (7) is 0.0393. We also compute SCI using four simulations of NPT (Fig. 5). As NPT is a stochastic simulation method, the pathways of different simulations are not the same. But as we increase the number of pathways (from  $10^2$  to  $10^5$ ), SCI from all four simulations accurately converge to the same value of 0.0393, matching the algebraic formulation (Eq. (7)), indicating the agreement between the two very different methods. For a given model, the computational resources needed for an accurate computation of SCI are difficult to predict, as it depends on a number of parameters, including, but not limited to, network size and connectivity. For the Everglades Graminoids Wet Season model (Ulanowicz et al., 2000) with 66 compartments and 857 flows, accurate computations (1% relative error) of SCI requires about  $10^6$  pathways, which takes about one minute to simulate on an ordinary dual-core 3 GHz desktop computer. For smaller models, pathway-based SCI can be computed in a couple of seconds.

As we have shown earlier, the same FCI value (0.0422) for the two ecosystems in Fig. 3 means that 4.22% of the total system

throughflow is due to cycling. Using Eq. (7), the SCI for models (a) and (b) are 0.0393 and 0.0268, respectively, indicating that 3.93% and 2.68% of the total biomass in system (a) and (b) are due to cycling. Not only the interpretations, but also the values of FCI and SCI are indeed very different. As the producer in (b) has shorter life span than that in (a), the turnover rate of producer in (b) is much higher. Therefore, SCI provides potentially useful information that is not indicated by FCI. For example, assuming that the environmental input contains pollutants, the lower cycling index in (b) indicates that the system with higher turnover rate will be affected less by the pollutants.

Based on some equivalent relations between flow rates, storage values, and residence times, an alternative representation of Eq. (7) can be derived. The storage value of a compartment equals the product of its residence time and throughflow:  $x_i = RT_i \times T_i$ . For compartmental models, a similar relation exists between the storage matrix  $S$  and throughflow matrix  $N$ :  $S_{ij} = N_{ij} \times RT_i$ . Therefore, the term  $(S_{ii} - RT_i)/S_{ii}$  can be reduced to  $(N_{ii} - 1)/N_{ii}$ . Replacing  $x_i$  with  $RT_i \times T_i$ , SCI can be rewritten as

$$SCI = \frac{TSS_c}{TSS} = \frac{1}{\sum_{i=1}^n RT_i T_i} \sum_{i=1}^n RT_i T_i \frac{N_{ii} - 1}{N_{ii}} \quad (8)$$

In this formula, the numerator represents the residence time of recycled throughflow, and the denominator is the residence time of all throughflow. Comparing Eq. (4) for FCI and Eq. (8) for SCI, we clearly see that SCI is obtained by weighting FCI with residence times. In other words, SCI is actually a residence time-weighted FCI. If the residence time is the same for all compartments in the system, the values of FCI and SCI will be the same. However, it is rarely the case in real ecosystems. Different compartments hold particles for different periods of time. Therefore, SCI would predict a different impact of recycling than FCI.

Two formulas in Eqs. (7) and (8) are equivalent and agree with the pathway-based method for steady-state models. However, ecosystems are rarely at steady state. Flows and storage values change over time, often fluctuating daily and/or seasonally. Thus, for highly dynamic models, algebraic formulas of FCI and SCI may not be appropriate. Fortunately, one significant advantage of pathway-based definitions is their applicability to both steady-state and dynamic models.

#### 4. Numerical difference of FCI and SCI

As demonstrated in the last section, both the computation and interpretation of FCI and SCI are different. Then, another question of interest is how much can FCI and SCI values vary for a given ecosystem model. To illustrate how FCI and SCI can be different, we compare the two indices for sixteen seasons' nitrogen flow models for the Neuse River estuary, North Carolina, USA (Christian and Thomas, 2003). All sixteen models have identical structures, but different flow and storage values. Fig. 6 shows the seasonal changes in FCI and SCI values, from spring 1985 through winter 1989. FCI values indicate a high level of cycling overall, with little variation between seasons. Comparing with SCI, we observe that the recycled storage is much lower than recycled flow. Furthermore, SCI fluctuates in a wide range between 0.10 and 0.85, showing a clear distinction among seasons, unlike FCI. Riley (2000) states that sensitivity to change is an important characteristic of a good indicators. SCI, taking into account of both flow and residence time, is more sensitive to seasonal changes that occur in the Neuse River estuary.

To further compare the two indices for a variety of networks, we compute SCI and FCI for thirty-six ecological networks gathered from the literature. All of these networks are at steady state. Table 1 provides the reference, flow currency and flow unit for

**Table 1**  
Comparison of FCI and SCI for thirty-six ecological network models. The percent difference between FCI and SCI is computed as the absolute difference between two values, divided by the average of these two values:  $(FCI - SCI) / ((FCI + SCI) / 2) \times 100$ . Connectance is computed as the ratio of the number of actual intercompartmental links ( $d$ ) to the number of possible intercompartmental links:  $d / (\# \text{ Compartments})^2$ .

Model	Flow currency	Flow unit	#Compartments	#Nonliving compartments	Connectance	FCI	SCI	Difference (%)
Lake Oneida (pre-ZM) (Miehls et al., 2009a)	Carbon	G/M <sup>2</sup> /Year	74	3	0.221	1.08E-4	5.99E-5	57.29
Lake Oneida (post-ZM) (Miehls et al., 2009a)	Carbon	G/M <sup>2</sup> /Year	76	3	0.216	1.34E-4	1.14E-4	16.13
Lake Quinte (pre-ZM) (Miehls et al., 2009b)	Carbon	G/M <sup>2</sup> /Year	74	3	0.209	8.78E-4	8.03E-4	8.92
Lake Quinte (post-ZM) (Miehls et al., 2009b)	Carbon	G/M <sup>2</sup> /Year	80	3	0.209	0.006	0.011	-58.82
St. Marks Seagrass, site 3 (January) (Baird et al., 1998)	Carbon	Mg/M <sup>2</sup> /Day	51	3	0.048	0.007	0.021	-100.00
Everglades Graminoids Wet Season (Ulanowicz et al., 2000)	Carbon	G/M <sup>2</sup> /Year	66	3	0.181	0.018	0.049	-92.54
St. Marks Seagrass, site 4 (February) (Baird et al., 1998)	Carbon	Mg/M <sup>2</sup> /Day	51	3	0.077	0.035	0.086	-84.30
Everglades Graminoids Dry Season (Ulanowicz et al., 2000)	Carbon	G/M <sup>2</sup> /Year	66	3	0.181	0.037	0.095	-87.88
Cypress Dry Season (Ulanowicz et al., 1997)	Carbon	G/M <sup>2</sup> /Year	68	3	0.120	0.043	0.007	144.00
Cypress Wet Season (Ulanowicz et al., 1997)	Carbon	G/M <sup>2</sup> /Year	68	3	0.118	0.044	0.009	132.08
Northern Benguela Upwelling (Heymans and Baird, 2000)	Carbon	Mg/M <sup>2</sup> /Day	24	2	0.201	0.047	0.088	-60.74
Swarkops Estuary (Baird et al., 1991)	Carbon	Mg/M <sup>2</sup> /Day	15	3	0.156	0.056	0.082	-37.68
Ems Estuary (Baird et al., 1991)	Carbon	Mg/M <sup>2</sup> /Day	15	3	0.164	0.059	0.225	-116.90
Crystal Creek (Ulanowicz, 1986)	Carbon	Mg/M <sup>2</sup> /Day	21	1	0.186	0.066	0.084	-24.00
St. Marks Seagrass, site 2 (February) (Baird et al., 1998)	Carbon	Mg/M <sup>2</sup> /Day	51	3	0.076	0.083	0.208	-85.91
Florida Bay Dry Season (Ulanowicz et al., 1998)	Carbon	Mg/M <sup>2</sup> /Year	125	3	0.126	0.084	0.124	-38.46
St. Marks Seagrass, site 2 (January) (Baird et al., 1998)	Carbon	Mg/M <sup>2</sup> /Day	51	3	0.068	0.086	0.214	-85.33
Crystal River (thermal) (Ulanowicz, 1986)	Carbon	Mg/M <sup>2</sup> /Day	21	1	0.136	0.090	0.118	-26.92
Mangrove Estuary Wet Season (Ulanowicz et al., 1999)	Carbon	G/M <sup>2</sup> /Year	94	3	0.152	0.095	0.049	63.89
Mangrove Estuary Dry Season (Ulanowicz et al., 1999)	Carbon	G/M <sup>2</sup> /Year	94	3	0.152	0.097	0.049	65.75
St. Marks Seagrass, site 1 (February) (Baird et al., 1998)	Carbon	Mg/M <sup>2</sup> /Day	51	3	0.083	0.109	0.256	-80.55
Oyster Reef (Dame and Patten, 1981)	Energy	Kcal/M <sup>2</sup> /Day	6	1	0.333	0.110	0.092	17.82
Neuse Estuary Flow Model, Late Summer 1998 (Baird et al., 2004)	Carbon	Mg/M <sup>2</sup> /Day	30	5	0.093	0.112	0.365	-106.08
Chesapeake Mesohaline Ecosystem (Baird, 1989)	Carbon	Mg/M <sup>2</sup> /Day	15	3	0.182	0.116	0.301	-88.73
Neuse Estuary Flow Model, Early Summer 1997 (Baird et al., 2004)	Carbon	Mg/M <sup>2</sup> /Day	30	5	0.088	0.116	0.337	-97.57
Neuse Estuary Flow Model, Early Summer 1998 (Baird et al., 2004)	Carbon	Mg/M <sup>2</sup> /Day	30	5	0.084	0.120	0.349	-97.65
St. Marks Seagrass, site 1 (January) (Baird et al., 1998)	Carbon	Mg/M <sup>2</sup> /Day	51	3	0.075	0.125	0.312	-85.58
Neuse Estuary Flow Model, Late Summer 1997 (Baird et al., 2004)	Carbon	Mg/M <sup>2</sup> /Day	30	5	0.111	0.126	0.365	-97.35
Aggregated Baltic Ecosystem (Wulff and Ulanowicz, 1989)	Carbon	Mg/M <sup>2</sup> /Day	15	3	0.164	0.129	0.211	-48.24
Baltic Sea (Baird et al., 1991)	Carbon	Mg/M <sup>2</sup> /Day	15	3	0.165	0.130	0.221	-51.85
Somme Estuary (Rybarczyk and Nowakowski, 2003)	Carbon	G/M <sup>2</sup> /Year	9	1	0.296	0.139	0.204	-37.90
Florida Bay Wet Season (Ulanowicz et al., 1998)	Carbon	G/M <sup>2</sup> /Year	125	3	0.124	0.144	0.193	-29.08
Chesapeake Bay Mesohaline Network (Baird, 1989)	Carbon	Mg/M <sup>2</sup> /Year	36	3	0.093	0.194	0.066	98.46
Bothnian Bay (Sandberg et al., 2000)	Carbon	Mg/M <sup>2</sup> /Year	12	2	0.201	0.264	0.409	-43.09
Bothnian Sea (Sandberg et al., 2000)	Carbon	G/M <sup>2</sup> /Year	12	2	0.215	0.327	0.482	-38.32
Narragansett Bay (Monaco and Ulanowicz, 1997)	Carbon	Mg/M <sup>2</sup> /Year	32	1	0.152	0.505	0.758	-40.06

each of these ecological networks. The percent difference between FCI and SCI is computed as the absolute difference between two values, divided by the average of these two values:

$$\frac{FCI - SCI}{(FCI + SCI) / 2} \times 100.$$

The column titled "Difference (%)" in Table 1 shows that FCI can vastly differ from SCI.

A plot of SCI versus FCI is shown in Fig. 7. The dashed line indicates SCI=FCI. We observe that SCI can be very different from FCI for most of these models. For example, several networks at around (0.1, 0.4) have SCI that is almost four times of their FCI. On the other hand, the network at around (0.2, 0.05) has SCI that is about 1/4 of its FCI. This implies that it would be incorrect to use FCI to compute the contribution of recycled particles to storage in a food web.

## 5. Compartmental cycling index

While it is often used as a system-wide property, the cycling index can be better characterized by highlighting the contribution of each compartment. For example, pollutants existing within an ecosystem may repeatedly visit the same species due to cycling.

System-wide cycling indices quantify the effect of pollution in the system as a whole, but do not provide much information on how strong the effect of pollution is for each species, or compartment. For such analysis focusing on single species (or compartment), a compartmental cycling index is more meaningful.

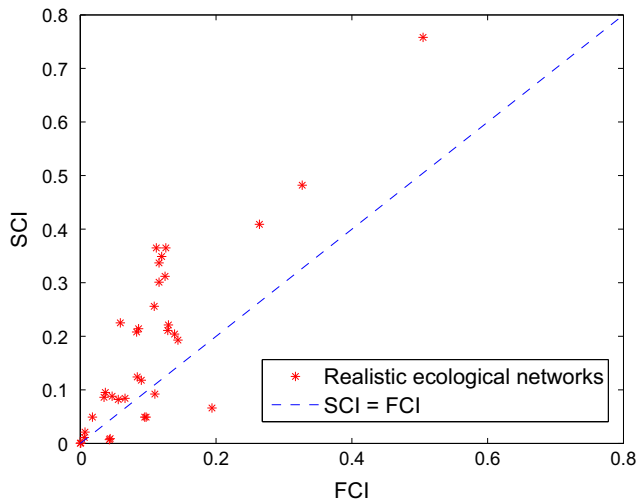
System-wide FCI and SCI are actually computed by summing up the strength of cycling in all compartments. Their formulations can easily be reduced to represent the strength of cycling for a single compartment  $j$ . For a single compartment  $j$ , TST (total system throughflow) is replaced by the  $T_j$  (throughflow at compartment  $j$ ). Then the FCI for  $j$  can be defined as:

$$FCI_j = \frac{1}{\sum_{i=j} T_i} \sum_{i=j} T_i \frac{N_{ii} - 1}{N_{ii}} = \frac{1}{T_j} T_j \frac{N_{jj} - 1}{N_{jj}} = \frac{N_{jj} - 1}{N_{jj}}. \quad (9)$$

Similarly, SCI (Eq. (7)) can be modified to represent compartmental storage-based cycling:

$$SCI_j = \frac{1}{\sum_{i=j} x_i} \sum_{i=j} x_i \frac{S_{ii} - RT_i}{S_{ii}} = \frac{1}{x_j} x_j \frac{S_{jj} - RT_j}{S_{jj}} = \frac{(N_{jj} - 1) RT_j}{N_{jj} RT_j} = \frac{N_{jj} - 1}{N_{jj}}. \quad (10)$$

For steady-state models, residence time ( $RT_j$ ) of an atom, or an energy quantum, is constant for each compartment  $j$ . Once the residence time is out of the equation, compartmental FCI (Eq. (9)) and SCI (Eq. (10)), although they have different meanings, are



**Fig. 7.** SCI vs FCI. Each star represents a real ecological network in Table 1. The dashed line indicates  $SCI = FCI$ .

numerically equivalent for the same compartment. For dynamic models, however, the compartmental FCI and SCI values may differ as they change over time (Kazanci and Ma, 2012).

## 6. Discussion and conclusion

The main contribution of this work is the introduction of a new storage-based cycling index (SCI). Finn's original formulation of the cycling index (FCI) has been used by many researchers from a wide range of disciplines. However, we believe a storage-based cycling index does indeed have a wide range of potential applications, some of which are mentioned in the previous sections.

SCI has been conceived two decades ago (Patten and Higashi, 1984). However, the cumbersome formulation using Markov chains hindered its widespread adaptation. In this paper, we provide a simple algebraic formulation similar to FCI, in addition to a pathway-based formulation that makes this useful but limited formulation applicable to dynamic systems. Many interesting research problems concern change, therefore the quasi-steady state assumption does not always hold. Studies of climate change, environmental impacts, regime shifts do need a dynamic formulation.

An interesting point is the vast time difference of over three decades between this paper studying SCI and the original work on FCI by Finn (1976), which makes us wonder why the work presented in this paper was not published earlier. One reason we anticipate is the inherent difficulty of utilizing matrix algebra to study and formulate complex system-wide measures involving indirect effects. A recent development, network particle tracking (NPT), has been an invaluable tool in this regard. It is compelling that the pathway-based formulations of cycling, as well as other ecological network analysis measures, which are based on counting arguments applied to the output of a stochastic individual-based simulation algorithm (NPT), agree with the rather rigid algebraic formulations. This correspondence, or backwards compatibility, enables us to investigate new useful formulations of ecosystem measures, using the flexible medium of pathway data, with the possibility of a corresponding algebraic formulation for easy computation.

While cycling index is originally proposed as a measure for ecological network analysis, the concept of cycling is applicable to, and carries different meanings in other fields, such as reinfection

in epidemiology (Gomes et al., 2004), the reuse of materials in industry (Bailey et al., 2008), and the recycling of drug within body in pharmacokinetics (Hatanaka et al., 1998), to name a few. Our computation of cycling index for ecosystems is applicable to these areas as well.

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