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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.

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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.

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