Cycling in ecological networks: Finn's index revisited

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Abstract

A chief cybernetic feature of natural living systems is the recycling of nutrients, which tends to enhance stability and is one of the principal causes of ecosystem complexity. In 1976, Finn proposed a simple and effective measure (later known as the Finn cycling index [FCI]) to assess the quantitative importance of cycles in ecosystems. This index was successfully applied as a gauge of ecosystem health and maturity in a wide variety of studies.

It turns out, however, that FCI is biased as a measure of cycling in ecosystems, because it does not include all flows engaged in recycling. A new, more inclusive version of the index is possible. What is called the comprehensive cycling index (CCI) accounts for all of the fluxes generated by cycling. Computing the new measure requires a large amount of time, however, even with ad-hoc software. To obviate the necessity for such heavy computation, a linear transformation of the FCI into the CCI is proposed.
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Keywords: Cycle; Network analysis; Finn cycling index; Residence time; Leontief matrix

1. Introduction

> ... went on saying to herself, in a dreamy sort of way, 'Do cats eat bats? Do cats eat bats?' and sometimes, 'Do bats eat cats?' for, you see, as she couldn't answer either question, it didn't much matter which way she put it.
>
> Lewis Carrol, Alice's Adventures in Wonderland

Energy and matter cycle in ecosystems. This phenomenon, which has been widely examined in literature (see for example, Ulanowicz, 1983; Patten and Higashi, 1984; Patten, 1985; Essington and Carpenter, 2000; Christian and Thomas, 2003), is one of an ecosystem's most important features, because it affects the residence time of nutrients (Herendeen, 1989), acts as a buffer for fluctuations in energy supply (Loreau, 1994), augments stability (DeAngelis et al., 1989), and greatly affects ecosystem functioning.

Although the presence of trophic cycles was discovered early in ecological studies (Hutchinson, 1948), the first method for actually quantifying the amount of cycling matter/energy was not introduced until the end of the 1970s, by Finn (1976), in the context of ecological network analysis (ENA) (Baird and Ulanowicz, 1989; Christensen and Pauly, 1992; Fath and Patten, 1999). What became known as Finn's cycling index (FCI) accounts for the percentage of all fluxes that is generated by cycling, and has been applied in a wide range of ecological studies (e.g. Bodini and Bondavalli, 2002; Christian and Thomas, 2003; Fath, 2004; Heymans et al., 2004; Manickchand-Heileman et al., 2004).

Finn's seminal work has been extended by Patten and Higashi (1984), to incorporate biomass storages into the computation via Markovian techniques. The computation was further improved by Han (1997) through his definition of cycling matrix; in a similar fashion, Szyrmer (1984), expressed the cycling contribution of each compartment to the "total flow". Yet another approach was initiated by Ulanowicz (1983) who devised a procedure to extract cycled flows from the network and compare their activities with the remaining unidirectional flows.

The chief advantage of FCI has been its simplicity, as its computation requires but a single matrix inversion. Furthermore, being a percentage, it is dimensionless, a feature that allow ecologists to compare directly diverse ecosystems.

Here we examine the FCI using Leontief matrices, and show how FCI, in all its implementations, underestimates

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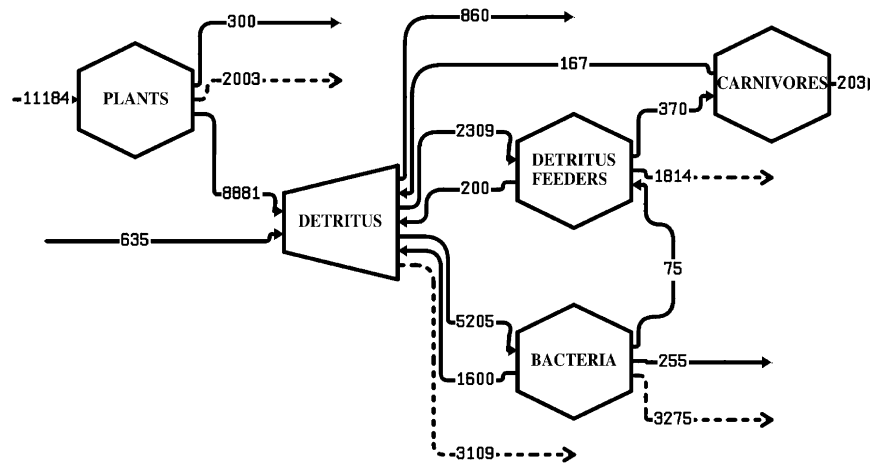ulan@cbl.umces.edu (R.E. Ulanowicz).

Fig. 1. Schematic of the network of trophic transfers in the Cone Spring ecosystem. Incoming edges represent imports, while outgoing ones denote exports and dissipations (dotted).

the magnitude of cycling flows in ecosystems. We begin by introducing the FCI in its original derivation and discuss its subsequent emendations. Finally, we show how, using a different approach, one can compute precisely the full amount of cycling in natural systems. We compare the latter procedure with the earlier calculations and show how FCI culminates in a biased estimation of the importance of cycling. Hence, this statistically significant bias must be corrected in order to assess an ecosystem's status with precision.

2. Materials and methods

2.1. Network models

Ecological network analysis depicts ecosystems as being comprised of compartments (black boxes) that exchange energy/matter with each other. These compartments can represent species, trophospecies (Yodzis and Winemiller, 1999), nutrient pools, trophic levels, etc., according to the aim of the investigation. The pictorial representation of the ecosystems is as a network, that is, a directed, weighted graph (Bang-Jensen and Gutin, 2000). The oriented, weighted links (edges) account for the flows between compartments in terms of a specific currency (usually grams of $Cy^{-1} m^{-2}$). Three virtual compartments are introduced to accommodate the expression of flows entering or leaving the system, that is, imports (incoming flows), outputs (flows to other systems) and dissipations (waste).

When the inflows exactly balance outflows over each compartment, the network is said to be in steady state (no increase nor decrease of biomass).

Such a network scheme can be readily be formalized in terms of matrices and vectors. Most often, the representation will consist of a single square matrix (T) representing the flows between compartments, and three vectors to accommodate flows of the virtual, external compartments (Z, imports; E, exports, D, dissipations).

Fig. 1 depicts the fluxes occurring in a simple five-compartments network, Cone Spring (Tilly, 1968). The matrix and three vectors would be:

$$
\begin{bmatrix} \text{Plants} \\ \text{Bacteria} \\ \text{Det. Feed.} \\ \text{Carnivores} \\ \text{Detritus} \end{bmatrix}, \quad
Z = \begin{bmatrix} 11\,184 \\ 0 \\ 0 \\ 0 \\ 635 \end{bmatrix}, \quad
E = \begin{bmatrix} 300 \\ 255 \\ 0 \\ 0 \\ 860 \end{bmatrix},
$$

$$
D = \begin{bmatrix} 2003 \\ 3275 \\ 1814 \\ 203 \\ 3109 \end{bmatrix}, \quad
T = \begin{bmatrix}
0 & 0 & 0 & 0 & 8881 \\
0 & 0 & 75 & 0 & 1600 \\
0 & 0 & 0 & 370 & 200 \\
0 & 0 & 0 & 0 & 167 \\
0 & 5205 & 2309 & 0 & 0
\end{bmatrix}
$$

Using matrices and vectors we can write the steady state equation as:

$$T_{.i} + Z_i = T_{i.} + E_i + D_i, \quad \forall i \tag{1}$$

where $T_{.i}$ represents the sum of the ith column, and $T_{i.}$, the sum of the ith row. Continuing with the same notation, $T_{..}$ becomes the sum of all the elements in the matrix.

We define the right-hand side of the equation as the inflow vector (S) and the left-hand side as the outflow vector (S'). When the steady state has been achieved, $S = S'$.

2.2. Leontief matrix

Leontief (1963) developed what has become commonly known as *input–output analysis* to estimate the amount of raw materials and services required to produce a certain quantity of goods. Augustinovics (1981) extended this method in the opposite direction to approximate what production (output) should result from a given quantity of input (materials and services). Both the methods have been introduced into ecology via ENA (Hannon, 1973). Both approaches require that one calculates inverse matrices,

which then can be used to portray sundry aspects of the input–output problem.

Given a matrix of exchanges T, one can normalize its columns by dividing each coefficient T_{ij} by its corresponding inflow S_i. Doing this produces the so-called *fractional inflow matrix G*, the columns of which also happen to portray the "diet" compositions of their respective predator compartments. The column sum will be exactly 1 whenever the compartment relies solely on internal transfers for its sustenance, and less than 1 whenever an Import flows into that compartment.

If we multiply this matrix for itself, producing G^2, we obtain a matrix whose coefficients describe the fraction of the total flow that emanates from the row compartment that reaches the column compartment over all pathways consisting of exactly two steps. In similar manner, G^3 will trace the fate of flows over all pathways of exactly 3 steps, and so forth. If the system contains cycles, matrix G^n will tend toward zero as $n \rightarrow \infty$, because the coefficients become vanishingly small after only a few steps (but never vanish completely due to cycling). Recalling that the geometric series

$$\sum_{n=0}^{\infty} q^n = 1 + q + q^2 + \cdots = \frac{1}{1-q}$$

whenever $-1 < q < 1$, it is possible to demonstrate (Higashi et al., 1991) that, whenever $0 \geq G_{ij} \geq 1$, then

$$\sum_{n=0}^{\infty} G^n = G^0 + G + G^2 + \cdots = [I - G]^{-1} = L \quad (2)$$

where $G^0 = I$ (the identity matrix), and L is the Leontief inverse matrix.

For the Cone Spring ecosystem, these matrices take on the values:

$$G = \begin{bmatrix} 0 & 0 & 0 & 0 & 0.773 \\ 0 & 0 & 0.032 & 0 & 0.139 \\ 0 & 0 & 0 & 1 & 0.017 \\ 0 & 0 & 0 & 0 & 0.014 \\ 0 & 1 & 0.969 & 0 & 0 \end{bmatrix}$$

and

$$L = \begin{bmatrix} 1 & 0 & 0 & 0 & -0.773 \\ 0 & 1 & -0.032 & 0 & -0.139 \\ 0 & 0 & 1 & -1 & -0.017 \\ 0 & 0 & 0 & 1 & -0.014 \\ 0 & -1 & -0.969 & 0 & 1 \end{bmatrix}^{-1}$$

$$= \begin{bmatrix} 1 & 0.933 & 0.933 & 0.933 & 0.933 \\ 0 & 1.169 & 0.201 & 0.201 & 0.201 \\ 0 & 0.039 & 1.039 & 0.039 & 0.039 \\ 0 & 0.018 & 0.018 & 1.018 & 0.018 \\ 0 & 1.207 & 1.207 & 1.207 & 1.207 \end{bmatrix}$$

To illuminate the coefficients of the Leontief matrix, Higashi et al. (1991) stated that each coefficient represents

the average number of times a quantum of energy/matter entering the column compartment will visit the designated row member. As one can readily see from (2), the number of times a quantum entering ith will visit ith compartment (the diagonal elements) is at least 1. Coefficients greater than unity indicate that the compartment participates in cycles.

2.3. The FCI and its improvements

The Finn cycling index (Finn, 1976) utilizes the Leontief matrix to assess the amount of material cycling within the ecosystem. The formula, derived from the inverse matrix L is straightforward and simple:

$$CI = \sum_{i=1}^{n} \frac{S_i}{TST} \frac{l_{ii} - 1}{l_{ii}} \quad (3)$$

where l_{ii} is the ith coefficient along the diagonal of the Leontief matrix, and S_i is the inflow to the ith compartment. The definition of the "total system throughput" (TST) varies among authors: in Finn's original work it stood for $T_{..} + Z_{.}$, the sum of the internal transfers plus the imports (in the steady state condition one could also write $T_{..} + E_{.} + D_{.}$), whereas Ulanowicz (1986) and Patten and Higashi (1984) define TST in more comprehensive fashion as $T_{..} + Z_{.} + E_{.} + D_{.}$—the sum of *all* fluxes occurring in the ecosystem. For clarity and comparison we will adopt this latter definition in what follows.

Patten and Higashi (1984) extended the cycling index to incorporate the notion of storage. This was done to decouple the network analysis measures from the assumption of steady state. This modified index of cycling index can be equated to the FCI whenever storages are changing.

Han (1997) estimated the importance of cycles in ecological networks by splitting the Leontief matrix into two separate matrices, one accounting for cycling and the other for unidirectional flows. This cycling matrix was obtained via matrix multiplication:

$$L_C = L \times C \quad (4)$$

where C is a matrix that has coefficients 0 in the off-diagonal positions and $(l_{ii} - 1)/l_{ii}$ along the diagonal. For the Cone Spring ecosystem, Han's matrices become:

$$C = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0.145 & 0 & 0 & 0 \\ 0 & 0 & 0.0375 & 0 & 0 \\ 0 & 0 & 0 & 0.018 & 0 \\ 0 & 0 & 0 & 0 & 0.172 \end{bmatrix},$$

$$L_C = \begin{bmatrix} 0 & 0.1349 & 0.035 & 0.0165 & 0.16 \\ 0 & 0.169 & 0.0075 & 0.0036 & 0.0345 \\ 0 & 0.0056 & 0.039 & 0.0007 & 0.0067 \\ 0 & 0.0026 & 0.0007 & 0.018 & 0.0031 \\ 0 & 0.1745 & 0.0453 & 0.0213 & 0.207 \end{bmatrix}$$

L_C presents the fluxes generated by cycles (the diagonal elements of the Leontief matrix). By subtracting L_C from L

one arrives at a matrix to represent the non-cycling flows, L_{NC}:

$$L_{NC} = L - L_C \begin{bmatrix} 1 & 0.7981 & 0.898 & 0.9165 & 0.773 \\ 0 & 1 & 0.1935 & 0.1974 & 0.1665 \\ 0 & 0.0334 & 1 & 0.0383 & 0.0323 \\ 0 & 0.0154 & 0.0173 & 1 & 0.0149 \\ 0 & 1.0325 & 1.1617 & 1.1857 & 1 \end{bmatrix}$$

We wish to point out that the presence of coefficients greater than 1 in the last matrix implies that the Han's cycling matrix does not encompass all the contributions of cycling to the overall flows. In fact, in any acyclic network, all the coefficients of the L matrix will be less than or equal to one. The Han procedures will be amended presently.

Ulanowicz (1983) attempted to reveal the importance of cycles in ecological networks by writing an algorithm that identifies all the simple cycles in a network, weights them according to their probabilities of completion, and extracts them from the network. The final result consists of two flux matrices, one that is constituted only of cycles, and another that is composed only of non-recursive fluxes. This latter matrix can be regarded as an acyclic version of the original network.

2.4. Paths taxonomy and Leontief layers

Using the nomenclature introduced into ecosystems research by Patten (1985), we define a *path* to be an ordered sequence of alternating compartments and edges. A path represents a possible walk that a quantum of energy/matter would take in going from the starting compartment to the ending one. Paths can be divided into four categories.

1. *simple paths* → paths with no repeated compartments;
2. *simple cycles* → simple paths in which the starting and the ending compartments coincide;
3. *compound paths* → paths with repeated compartments;
4. *compound cycles* → repeated cycles.

Graphical examples illustrating the taxonomy of paths are presented in Fig. 2.

As we compute the powers of the G matrix, we are tracing all the possible paths from row to column compartments in n sequential steps. It seems only natural, therefore, to decompose the power series of matrices according to the classification of pathways. That is, we may consider that every power of G is obtained summing up four different matrices each one representing a different type of pathways, i.e.

$$G^i = P^i + C^i + \Pi^i + \Xi^i \tag{5}$$

where P^i accounts for all i-length simple paths; C^i accounts for i-length simple cycles; Π^i accounts for i-length compound paths; Ξ^i accounts for i-length compound cycles.

Moreover, $G^0 = P^0 = I$, and $C^0 = \Pi^0 = \Xi^0 = \Pi^1 = \Xi^1 = 0$, that is simple cycles start with G^1, whereas com-
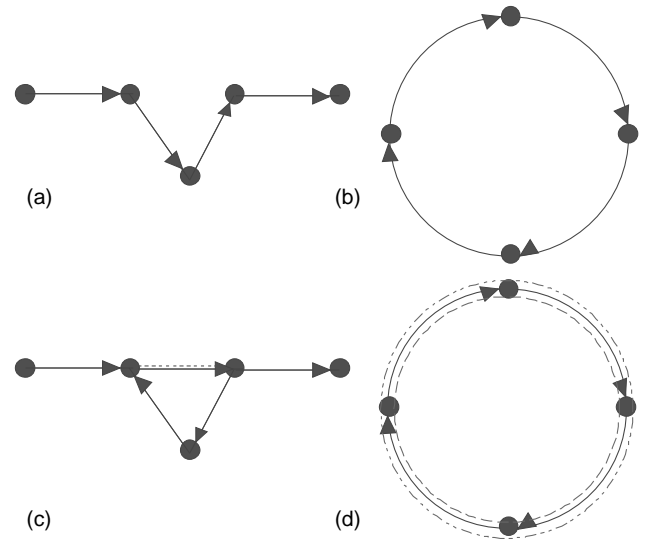

Fig. 2. Taxonomy of pathways: simple paths (a); simple cycles (b); compound paths; (c) and compound cycles (d). Dotted lines stand for repeated edges.

pound paths and cycles require at least two steps. Simple paths may have a maximum of $n - 1$ steps, where n is the number of compartments. The maximum length of simple cycles maximum would be n, while both compound paths and compound cycles could be infinitely long. Cycles are involved in three out of the four matrices defined, namely C^i, Π^i and Ξ^i. In fact, every compound path embeds at least one cycle. Along the diagonal of Leontief matrix we account for only the contributions due to simple and compound cycles. This implies that, even if compound paths are originated by cycles, they will not contribute to the Finn cycling index as currently defined.

Now, if we define

$$\sum_{i=0}^{n-1} P^i = I + P^1 + P^2 + \cdots + P^{n-1} = P_{All} \tag{6}$$

then we can decompose the Leontief matrix into cycling and non-cycling components:

$$L = L_{Cyc} + L_{NCyc} \tag{7}$$

where

$$L_{Cyc} = L - L_{NCyc} = L - P_{All} \tag{8}$$

because P_{All} represents all the contributions that cannot be ascribed to cycles. (Han (1997) performed the same decomposition, but only separated out simple and compound cycles.)

2.5. A comprehensive cycling index

Having calculated the L_{Cyc} matrix, one can now extend the FCI to include *all* the cycling paths. We choose to call this new index the comprehensive cycling index (CCI):

$$\text{CCI} = \sum_{i=1}^{n} \frac{S_i}{\text{TST}} \sum_{j=1}^{n} \frac{l_{\text{Cyc }ij}}{l_{\cdot j}} = \sum_{i=1}^{n} \frac{S_i}{\text{TST}} \sum_{j=1}^{n} \frac{l_{ij} - p_{\text{All }ij}}{l_{\cdot j}} \qquad (9)$$

As with the FCI, this index is dimensionless and represents the fraction of *all* flows that are generated by cycles. One may apply CCI in the same way one currently uses FCI, CCI being simply an amended version of the latter.

The chief practical problem with CCI is that there is no simple way to calculate P_{All}. Even with efficient software the computation of P_{All} can require an enormous amount of time, because even an ecological network with far fewer than one hundred compartments can contain billions of simple pathways.

2.6. Network models

Because of the large amount of computation required, we analyzed only small to medium size networks (5–50 compartments), in our search for any relationship between FCI and CCI. The 23 ecosystems chosen for the analysis were comprised almost entirely of models of this size, both published and unpublished. The collection included both aquatic and terrestrial networks with different levels of resolution, and even duplicated some systems in their aggregated forms. For example, we intentionally chose the Chesapeake network in both its original 36-compartment manifestation (Baird and Ulanowicz, 1989) and in its 15-compartment aggregated form (Wulff and Ulanowicz, 1989), because the process of aggregation creates self-cycles that can significantly increase the FCI (Ulanowicz and Kemp, 1979), and we wished to compare this inflation with whatever the corresponding effect might be on the CCI.

3. Results

We computed the P^i matrices for all of the 23 systems chosen and applied (8) to each ecosystem network to compute the cycling matrix. From this cycling matrix we then computed the CCI, and compared the resulting value with the corresponding FCI. For example, with the Cone Spring ecosystem one can trace all the path matrices and, by subtraction, the corresponding cycling matrices $G^i - P^i$ as follows:

$$P^0 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix},$$

$$G^0 - P^0 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

$$P^1 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0.773 \\ 0 & 0 & 0.031 & 0 & 0.139 \\ 0 & 0 & 0 & 1 & 0.017 \\ 0 & 0 & 0 & 0 & 0.015 \\ 0 & 1 & 0.969 & 0 & 0 \end{bmatrix},$$

$$G^1 - P^1 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

$$P^2 = \begin{bmatrix} 0 & 0.773 & 0.750 & 0 & 0 \\ 0 & 0 & 0.135 & 0.031 & 0 \\ 0 & 0.017 & 0 & 0 & 0 \\ 0 & 0.015 & 0.015 & 0 & 0 \\ 0 & 0 & 0.031 & 0.969 & 0 \end{bmatrix},$$

$$G^2 - P^2 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0.139 & 0 & 0 & 0 \\ 0 & 0 & 0.017 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.156 \end{bmatrix}$$

$$P^3 = \begin{bmatrix} 0 & 0 & 0.024 & 0.749 & 0 \\ 0 & 0 & 0 & 0.135 & 0.4E-3 \\ 0 & 0.015 & 0 & 0 & 0 \\ 0 & 0 & 0.4E-3 & 0 & 0 \\ 0 & 0 & 0 & 0.031 & 0 \end{bmatrix},$$

$$G^3 - P^3 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0.121 \\ 0 & 0.001 & 0.005 & 00 & 0.022 \\ 0 & 0 & 0.015 & 0.017 & 0.003 \\ 0 & 0 & 0 & 0.014 & 0.002 \\ 0 & 0.156 & 0.151 & 0 & 0.015 \end{bmatrix}$$

We can then compute the matrix $P_{\text{All}} = \sum_{i=0}^{n-1} P^i$, and $L_{\text{Cyc}} = L - P_{\text{All}} = \sum_{i=0}^{n} C^j + \sum_{k=0}^{\infty} \Pi^k + \sum_{l=0}^{\infty} \Xi^l$ to be:

$$P_{\text{All}} = \begin{bmatrix} 1 & 0.77 & 0.77 & 0.77 & 0.77 \\ 0 & 1 & 0.17 & 0.17 & 0.14 \\ 0 & 0.03 & 1 & 1 & 0.03 \\ 0 & 0.01 & 0.01 & 1 & 0.01 \\ 0 & 1 & 1 & 1 & 1 \end{bmatrix},$$

$$L_{\text{Cyc}} = \begin{bmatrix} 0 & 0.160 & 0.160 & 0.160 & 0.160 \\ 0 & 0.169 & 0.034 & 0.034 & 0.029 \\ 0 & 0.006 & 0.038 & 0.038 & 0.006 \\ 0 & 0.003 & 0.003 & 0.017 & 0.003 \\ 0 & 0.207 & 0.207 & 0.207 & 0.207 \end{bmatrix}$$

Finally, applying (9), we obtain CCI = 0.0744. The corresponding Finn's cycling index turns out to be 0.663.

The full results from the 23 networks are depicted in Fig. 3. One notes as how FCI is always less than or equal
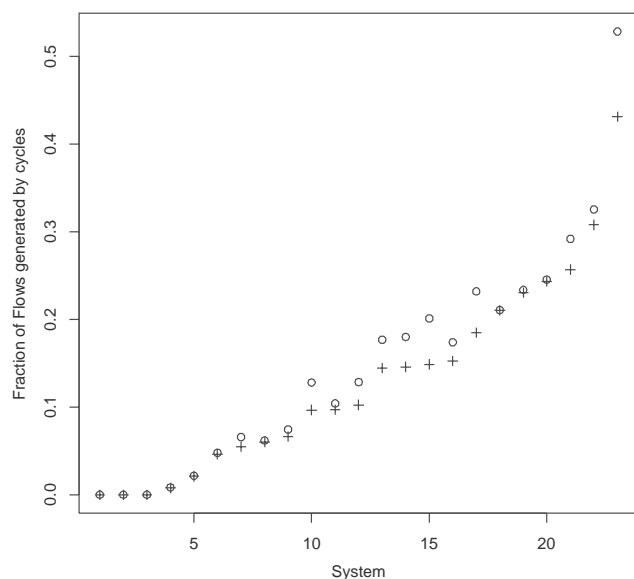
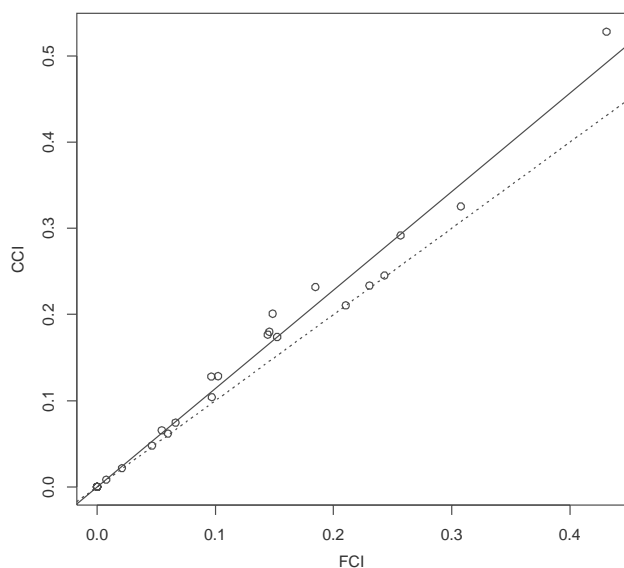Fig. 3. Values of CCI (circles) and FCI (crosses) computed for the chosen 23 ecological networks.

Fig. 4. The linear model CCI $= \alpha$FCI. The dotted line is the bisector of the first quadrant.

to CCI. When FCI $= 0$, then CCI $= 0$. The differences between the indices seem to increase with the amount of cycling, as expected.

Plotting FCI versus CCI reveals that the two indices appear to be linearly dependent. Using a linear model, we found that CCI $=$ FCI$\cdot 1.142$ (standard error $= 0.022$, $P < 2e - 16^{***}$) and that the regression is very tight ($R^2 = 0.9915$, $F_{1,22} = 2694$, $P = 0$) (Fig. 4).

4. Discussion and conclusion

Although it has been widely applied, FCI appears to be biased as a measure of the importance of cycling in ecolog-

ical networks. While the difference between FCI and CCI (the exact amount of flows generated by cycles) is negligible for networks that are nearly acyclic, the disparity increases as the number of cycles and their importance rises. The two indices seem to be strongly correlated in a nearly linear fashion. Such linearity might be due in part to the fact that every compound path is composed of one or more cycles that are attached to one or more segments of straight chains. The probability of transiting such a compound path could, therefore, be expressed as the probability of completing the cycles multiplied by a coefficient that accounts for the probability of traversing the straight segments. The linearity between FCI and CCI seems to imply that every cycle "creates" compound paths that, when summed, augment the cycled flow by some 14% on average. This increment is practically constant over all the networks considered, and probably reflects the low efficiency of trophic transfers.

The linear relationship between the two measures has one major practical advantage. It means that the costly computation of P_{All} is not required after all. One may approximate the actual amount of flow generated by cycling (CCI) simply by inflating the commonly used FCI by some 14.2%.

Acknowledgements

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