

Equivalence of the realized input and output oriented indirect effects metrics in ecological network analysis

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Abstract

A new understanding of the consequences of how ecosystem elements are interconnected is emerging from the development and application of Ecological Network Analysis. The relative importance of indirect effects is central to this understanding, and the ratio of indirect flow to direct flow (I/D) is one indicator of their importance. Two methods have been proposed for calculating this indicator. The unit approach shows what would happen if each system member had a unit input or output, while the realized technique determines the ratio using the observed system inputs or outputs. When using the unit method, the input oriented and output oriented ratios can be different, potentially leading to conflicting results. However, we show that the input and output oriented I/D ratios are identical using the realized method when the system is at steady state. This work is a step in the maturation of Ecological Network Analysis that will let it be more readily testable empirically and ultimately more useful for environmental assessment and management.

Keywords: environs, network environ analysis, environment, indirect effects, input–output analysis, connectivity, food web, trophic dynamics

1. Introduction

The dominance of indirect effects hypothesis is central to our new understanding of ecosystem ecology revealed through systems analyses like Ecological Network Analysis (ENA) (Ulanowicz, 1986; Fath and Patten, 1999b; Dunne et al., 2002; Belgrano et al., 2005; Bascompte and Jordano, 2007; Jørgensen et al., 2007; McRae et al., 2008; Christian et al., 2009; Baird et al., 2011). While empirical results are also highlighting the important roles of indirect effects (e.g. Wootton, 1994; Berger et al., 2008; Diekötter et al., 2007; Menendez et al., 2007; Letnic et al., 2009; Walsh and Reznick, 2010), network analysis shows how the integral of indirect interactions across a whole web of interactions can transform the effective relationships between species so that they tend to be more positive (Ulanowicz and Puccia, 1990; Patten, 1991; Fath and Patten, 1998; Bondavalli and Ulanowicz, 1999), and more evenly distribute the system resources (Fath and Patten, 1999a; Borrett and Salas, 2010) and control (Schramski et al., 2006, 2007).

When applying ENA, ecologists use the ratio of indirect to direct flows (I/D) to indicate the importance of indirect effects (Higashi and Patten, 1989; Fath and Patten, 1999b; Jørgensen et al., 2007). For example, Borrett et al. (2006) used I/D to show the temporal consistency of the organization of the Neuse River Estuary ecosystem, and Baird et al. (2009) found that indirect effects were dominant in the Sylt-Rømø Bight ecosystem regardless of the model aggregation scheme. Borrett and Freeze (2011) distinguished between two ways of calculating this ratio that they termed the *unit* and *realized* formulations. The unit calculation is the

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traditional approach that is performed after a classic systems analysis technique is applied. In this case, each species is assumed to receive a single unit of boundary flux, and then the direct and indirect flow intensities in the system are summed. This unit calculation shows what the relative indirect flows would be if every node received the same input. It is useful because it facilitates within system comparisons (Whipple et al., 2007) and due to its close relationship to the eigenvalues and vectors of underlying matrices (Borrett et al., 2010). Alternatively, the realized calculation uses the observed boundary flow vector instead of an input vector of ones. This approach was first introduced by Borrett et al. (2006) but was clarified and formalized in Borrett and Freeze (2011). Its analytical advantage is that the system flows are scaled with the observed, typically non-homogeneous boundary fluxes.

Borrett and Freeze (2011) showed that the quantitative and qualitative results could be changed by this shift in perspective, highlighting the importance of the system’s connection to its broader environment. For example, the wet season model of carbon flux in the Everglades graminoid marshes (Ulanowicz et al., 2000; Heymans et al., 2002) exhibits the dominance of indirect effects when analyzed with the realized method ($I/D = 1.2$) but does not when analyzed with the unit approach ($I/D = 0.81$). In this example, both the numerical value of the indicator and its interpretation changed.

An important aspect of ENA throughflow analysis is that it has two orientations: input and output. Conceptually, we can either pull the energy–matter out of the system and trace its origin back through the system to the inputs, or we can push the inputs into the system and then trace where they travel through the system until they exit the system. The first type of analysis is termed the input analysis because in Leontief’s (1966) original application he was determining what raw materials were required as inputs into the economic system to generate a single output, like a car. The second analysis is forward looking in direction, but it is termed the output analysis because we are following the inputs to their output from the system. In this case, it is the output generated that is the focus. Patten exploited this bidirectional analytical feature in the development of his environ concept (Patten, 1978, 1981, 1982) and the subsequent environmental theory. While some ENA components leverage the differences between the input and output orientation (e.g. Patten and Auble, 1981; Ulanowicz and Puccia, 1990; Fath and Patten, 1998; Patten, 1991; Schramski et al., 2006, 2007), the alternative perspectives can generate conflicting and confusing results.

In this short communication we show that while the input and output oriented unit I/D can differ in quantitative and qualitative nature, the realized input and output oriented I/D are always identical. We first show this result numerically for a set of network ecosystem models drawn from the literature. We then provide a mathematical proof for why this relationship will generally hold when the models are at steady state. We conclude this paper by arguing that this identity bolsters the utility of the realized metric for (1) testing the generality of network hypotheses like the dominance of indirect effects (Salas and Borrett, 2011), (2) applying the ecological insights of this type of ENA to the original system, and (3) comparing ecosystems’ organization (Baird et al., 1991, 2009; Borrett et al., 2006; Borrett and Osidele, 2007; Whipple et al., 2007).

2. Ecological Network Analysis

ENA is well described in the literature (e.g., Patten et al., 1976; Ulanowicz, 1986, 2004; Fath and Patten, 1999b; Fath and Borrett, 2006; Schramski et al., 2010), but we recount the input and output throughflow analyses here as this is essential for our discussion. Borrett and Freeze (2011) focused on the distinction between the idealized and realized forms of the I/D ratio. Here we focus on contrasting the input and output oriented analyses.

2.1. Model Input

Ecologists apply ENA to network models of energy–matter storage and flux in ecosystems. These models are alternatively referred to as compartment models or energy–matter budgets. In the general form of these models, n nodes represent species, groups of species, or abiotic components, and the L weighted directed edges represent the flow of energy–matter generated by some ecological process (e.g., consumption, excretion, harvesting). Let $\mathbf{F}_{n \times n} = (f_{ij})$ represent the observed flow from ecosystem compartment j to compartment i (e.g., $j \rightarrow i$), $\mathbf{z}_{n \times 1}$ be a vector of node inputs originating from outside the system, and $\mathbf{\bar{y}}_{1 \times n}$ be a vector

of flows from each node that exit the system. Sometimes the outputs are subdivided into those that are thermodynamically degraded and those that reflect high quality energy–matter exported from the system (e.g., Ulanowicz, 1986). For the analysis presented here, we lump these losses together because once they cross the system boundary our analysis is blind to their fate, making this distinction less critical.

ENA throughflow analysis assumes that the model traces a single conserved currency (e.g., energy, nitrogen, phosphorus), and that the system is at a steady state (inputs equal outputs). The steady state assumption is crucial for the throughflow path decomposition (Borrett et al., 2010).

For this research, we examined 50 ecosystem network models that represent 35 distinct primarily freshwater and marine ecosystems (Table 1). The models exhibit a range of sizes ($4 \leq n \leq 125$), connectance (number of direct links divided by the total possible number of links; $0.03 \leq (C = L/n^2) \leq 0.40$), and recycling (Finn Cycling Index (Finn, 1980), which is the proportion of total system throughflow derived from recycled flux; $0 \leq FCI \leq 0.51$). The core of these trophically-based networks is a food web, but other ecological processes are included and model compartments may represent non-living resource pools such as particulate organic carbon. We applied Allesina and Bondavalli’s (2003) AVG2 balancing algorithm to 15 models that were not initially at steady state because this technique tends to generate the least distortion of network properties. This is the same set of models used in several recent network studies (Borrett and Salas, 2010; Borrett and Freeze, 2011; Salas and Borrett, 2011), and the model data are available from <http://people.uncw.edu/borretts/research.html>.

2.2. Throughflow Analysis

Input and output oriented throughflow analysis have three main steps. First, we determine the throughflow vector \vec{T} , which is the total amount of energy–matter flowing into or out of each node. This can be calculated from the initial model information as follows:

$$T_i^{\text{in}} \equiv \sum_{j=1}^n f_{ij} + z_i \quad (i = 1, 2, \dots, n), \text{ and} \quad (1)$$

$$T_j^{\text{out}} \equiv \sum_{i=1}^n f_{ij} + y_j \quad (j = 1, 2, \dots, n). \quad (2)$$

At steady state, $T_i^{\text{in}} = (T_j^{\text{out}})^T = \vec{T}_{n \times 1} = (T_j)$. From this vector, we derive the first whole-system indicator, total system throughflow ($TST = \sum_{j=1}^n T_j$). TST indicates the total magnitude of flow activity.

Second, we calculate the input $\mathbf{G}'_{n \times n} = (g'_{ij})$ and output $\mathbf{G}_{n \times n} = (g_{ij})$ direct flow intensities from node j to i . These are defined as

$$g'_{ij} \equiv f_{ij}/T_i^{\text{in}}, \text{ and} \quad (3)$$

$$g_{ij} \equiv f_{ij}/T_j^{\text{out}}. \quad (4)$$

Here, g'_{ij} is the fraction of input at receiver node i contributed from the donor node j , while g_{ij} is the fraction of output throughflow at donor node j contributed to node i . The subtle distinction between the input and output oriented direct flow intensities in equations (3 and 4) is whether the observed flow is normalized by the throughflow of the receiving node (input case) or the donating node (output case). The g'_{ij} and g_{ij} values are dimensionless and the column sums of the matrices must lie between 0 and 1 because of thermodynamic constraints of the original model (see Borrett et al., 2010, for details).

Third, we determine the *integral flow intensities* $\mathbf{N}' = (n_{ij})$ (input) and $\mathbf{N} = (n_{ij})$ (output) as

$$\mathbf{N}' \equiv \sum_{m=0}^{\infty} \mathbf{G}'^m = \underbrace{\mathbf{I}}_{\text{Boundary}} + \underbrace{\mathbf{G}'^1}_{\text{Direct}} + \underbrace{\mathbf{G}'^2 + \dots + \mathbf{G}'^m + \dots}_{\text{Indirect}}, \quad (5)$$

and

$$\mathbf{N} \equiv \sum_{m=0}^{\infty} \mathbf{G}^m = \underbrace{\mathbf{I}}_{\text{Boundary}} + \underbrace{\mathbf{G}^1}_{\text{Direct}} + \underbrace{\mathbf{G}^2 + \dots + \mathbf{G}^m + \dots}_{\text{Indirect}}. \quad (6)$$

In equations (5 and 6), $\mathbf{I} = (i_{ij})$ is the matrix multiplicative identity and the elements of \mathbf{G}'^m and \mathbf{G}^m are the fractions of boundary flow that travels from node j to i over all pathways of length m . The exact values of \mathbf{N}' and \mathbf{N} can be found using the following identities because given our model definitions the power series must converge. Thus,

$$\mathbf{N}' = (\mathbf{I} - \mathbf{G}')^{-1}, \text{ and} \quad (7)$$

$$\mathbf{N} = (\mathbf{I} - \mathbf{G})^{-1}. \quad (8)$$

The n'_{ij} and n_{ij} elements represent the intensity of boundary flow that passes from j to i over all pathways of all lengths. These values integrate the boundary, direct, and indirect flows.

The differences between \mathbf{N}' and \mathbf{N} results from the input and output perspectives. However, we can use either of these integral flow matrices to recover T as follows:

$$\vec{T} = \vec{y}\mathbf{N}', \quad (9)$$

$$\vec{T} = \mathbf{N}\vec{z}. \quad (10)$$

2.3. Unit and Realized Indirect Effects

There are two methods of calculating I/D used in ENA to quantify the importance of indirect flows. We refer to these as the *unit* and *realized* methods. The unit method assumes that each node receives a single unit of input, which we will represent as a vector of ones with length equal to the number of nodes $[1]_{n \times 1}$ or output $[1]_{1 \times n}$. The unit input and output I/D metrics are calculated as follows.

$$I/D_{\text{unit, input}} = \frac{\sum_{i=1}^n ([\vec{1}]_{1 \times n} (\mathbf{N}' - \mathbf{I} - \mathbf{G}'))_i}{\sum_{i=1}^n ([\vec{1}]_{1 \times n} \mathbf{G}')_i} \quad (11)$$

$$I/D_{\text{unit, output}} = \frac{\sum_{i=1}^n ((\mathbf{N} - \mathbf{I} - \mathbf{G}) [\vec{1}]_{n \times 1})_i}{\sum_{i=1}^n (\mathbf{G} [\vec{1}]_{n \times 1})_i} \quad (12)$$

In contrast, the realized method uses the observed boundary vectors \vec{z} or \vec{y} .

$$I/D_{\text{realized, input}} = \frac{\sum_{i=1}^n (\vec{y}(\mathbf{N}' - \mathbf{I} - \mathbf{G}'))_i}{\sum_{i=1}^n (\vec{y}\mathbf{G}')_i} \quad (13)$$

$$I/D_{\text{realized, output}} = \frac{\sum_{i=1}^n ((\mathbf{N} - \mathbf{I} - \mathbf{G})\vec{z})_i}{\sum_{i=1}^n (\mathbf{G}\vec{z})_i} \quad (14)$$

As [Borrett and Freeze \(2011\)](#) discuss, the magnitude of the boundary flow vectors, be it a unit vector $[\vec{1}]_{n \times 1}$ or the observed boundary vectors \vec{z} or \vec{y} , cancels in the ratio measure. However, the different distribution of boundary flows differentially excites the flow intensities in the integral flow matrices. It is the distribution of the boundary inputs and outputs that is key.

3. Results

We present our results in two parts. The first section shows the numerical results of applying ENA and the alternative formulations of I/D to the 50 network models. The second section summarizes the analytical work that generalizes this result.

3.1. Numerical Results

Figure 1 compares the input and output oriented I/D values of the network models. Panel (a) illustrates the variation that can occur between the input and output oriented I/D values when using the idealized formulation. The adjusted r^2 value for a linear regression fit to this data set is 0.82, and the Pearson's correlation coefficient is 0.91. To ensure our balancing routine did not heavily influence our results, we also calculated the Pearson's correlation coefficient for only the 35 models not balanced and found it to be 0.92. Panel (b) shows the one to one correspondence between the input and output I/D values when we use the realized formulation. These values are identical and have a Pearson's correlation coefficient of 1.

3.2. Analytical Results

The steady state assumption actually implies very strong compatibility conditions on the powers of \mathbf{G} and \mathbf{G}' , namely that for each nonnegative integer m , the sizes of $\mathbf{G}^m \bar{\mathbf{z}}$ and $\bar{\mathbf{y}} \mathbf{G}'^m$ must coincide in the sense that we have the equality

$$\sum_{i=1}^n (\mathbf{G}^m \bar{\mathbf{z}})_i = \sum_{i=1}^n (\bar{\mathbf{y}} \mathbf{G}'^m)_i, \quad (15)$$

as demonstrated in the proof of Lemma 6.3 in Appendix A.

The terms of the numerator and denominator of realized I/D each are of the form found on the left hand side in equation (15) for realized output I/D or of the form found on the right hand side in equation (15) for realized input I/D. It follows that at steady state, the realized input I/D and output I/D must be identical. This mathematical generalization of the numerically observed results is recorded in Theorem 6.4 of Appendix A.

4. Discussion

In this note we show that using the realized formulation the input and output oriented I/D values are identical when the system is at steady state. Like Bata et al. (2007), this work provides a conceptual and mathematical condensation for Ecological Network Analysis. This is part of a methodological maturation process in which investigators are finding relationships amongst the alternative analyses (input vs. output or throughflow vs. storage) and reconsidering initial assumptions that have become canalized (e.g. Schramski et al., 2010; Matamba et al., 2009). Here, we are not fully pruning the analytical options, but clarifying the consequences of alternative methods. When an investigator selects to use the realized method as described by Borrett and Freeze (2011), one advantage is that the input and output values are identical.

The realized formulation of I/D functions as one description of the internal organization of the ecosystem. It is intuitively satisfying that our understanding of this organization does not change because our point of view switches (input or output). Further, as the realized formulation considers both the internal system organization and the external environmental connection, it characterizes the complete system as it was initially described by the model builders. Thus, the realized metric is most appropriate for testing the generality of systems ecology hypotheses like the dominance of indirect effects (Salas and Borrett, 2011), applying ENA insights back to the original system (Zhang et al., 2010a,b), and comparing ecosystem organization (Baird et al., 1991; Whipple et al., 2007; Ray, 2008).

A limitation of this work is that the realized input and output I/D should only be identical when the observed system is at steady state, as shown in the mathematical proof. This means systems not at steady state will likely have different relative contributions of indirect flows when observed forward through the

network instead of backwards through the network. This is evident when we recall equations (9) and (10) and that $T^{in} = T^{out}$ at steady state. Without this identity (i.e., not at steady state), there is no reason to expect the mathematical decomposition of the input and output throughflow into boundary, direct, and indirect flows to be identical. We suspect that network particle tracking as implemented in EcoNet (Kazanci, 2007; Tollner et al., 2009) will be useful for further exploring the consequences of these input and output perspective differences.

This work is one more essential step in the maturation of the ecosystem and environmental theory developing in association with Ecosystem Network Analysis (e.g. Abarca-Arenas and Ulanowicz, 2002; Allesina and Ulanowicz, 2004; Borrett et al., 2010; Kaufman and Borrett, 2010; Schramski et al., 2010). Multiple lines of investigation are building confidence in ENA results including the initial empirical validation by Dame and Christian (2008) and the agreement between the Eulerian approach used here and the Lagrangian approach of network particle tracking (Matamba et al., 2009), but continued rigorous empirical testing of network ecology hypotheses is essential. Loehle (1987) points out that this theory maturation is essential so that theory predictions clarify to the point that robust empirical test be successful.

5. Acknowledgments

This paper benefited from discussions with B.C. Patten and the careful reviews J. R. Schramski, A. Stapleton, and two anonymous reviewers. This work was supported in part by UNCW and NSF (DEB-1020944). AKS was supported by the James F. Merritt fellowship from the UNCW Center for the Marine Science.

6. Appendix A

The steady state assumption that $\vec{T}^{in} = (\vec{T}^{out})^T$ means that $T_\ell^{in} = T_\ell^{out}$ for all indices ℓ . We have the following proposition as an immediate consequence.

Proposition 6.1. *When the observed system is at steady state, we have that $\sum_i (\mathbf{G}\vec{z})_i = \sum_i (\vec{y}\mathbf{G}')_i$.*

Proof. Note that

$$\begin{aligned}
\sum_i (\mathbf{G}\vec{z})_i &= \sum_i \left[\sum_j \left(z_j \frac{f_{ij}}{T_j^{\text{out}}} \right) \right] \\
&= \sum_{i,j} \left(z_j \frac{f_{ij}}{T_j^{\text{in}}} \right) \\
&= \sum_{i,j} \left[\left(T_j^{\text{in}} - \sum_k (f_{jk}) \right) \frac{f_{ij}}{T_j^{\text{in}}} \right] \text{ (by equation (1))} \\
&= \sum_{i,j} (f_{ij}) - \sum_{i,j,k} \left(\frac{f_{ij} f_{jk}}{T_j^{\text{in}}} \right) \\
&= \sum_{i,j} (f_{ij}) - \sum_{j,k} \left[\frac{f_{jk}}{T_j^{\text{in}}} \sum_i (f_{ij}) \right] \\
&= \sum_{i,j} (f_{ij}) - \sum_{j,k} \left[\frac{f_{jk}}{T_j^{\text{in}}} (T_j^{\text{out}} - y_j) \right] \text{ (by equation (2))} \\
&= \sum_{i,j} (f_{ij}) - \sum_{j,k} (f_{jk}) + \sum_{j,k} \left(\frac{f_{jk}}{T_j^{\text{out}}} y_j \right) \\
&= \sum_{j,k} \left(\frac{f_{jk}}{T_j^{\text{out}}} y_j \right) \\
&= \sum_k \left[\sum_j \left(y_j \frac{f_{jk}}{T_j^{\text{out}}} \right) \right] \\
&= \sum_k (\vec{y}\mathbf{G}')_k.
\end{aligned}$$

□

We extend the observation of Proposition 6.1.

Lemma 6.2. *For each integer $m \geq 2$, we have that*

$$(\mathbf{G}^m \vec{z})_i = \sum_{\ell_1, \dots, \ell_m} \left[z_{\ell_m} \cdot \frac{f_{i\ell_1}}{T_{\ell_1}^{\text{out}}} \cdot \prod_{n=1}^{m-1} \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_{n+1}}^{\text{out}}} \right) \right]$$

and

$$(\vec{y}\mathbf{G}'^m)_i = \sum_{\ell_1, \dots, \ell_m} \left[y_{\ell_m} \cdot \frac{f_{\ell_1 i}}{T_{\ell_1}^{\text{in}}} \cdot \prod_{n=1}^{m-1} \left(\frac{f_{\ell_{n+1} \ell_n}}{T_{\ell_{n+1}}^{\text{in}}} \right) \right].$$

Proof. We observed in the proof of Proposition 6.1 that

$$(\mathbf{G}\vec{z})_i = \sum_j \left(z_j \frac{f_{ij}}{T_j^{\text{out}}} \right).$$

It follows that

$$\begin{aligned}
(\mathbf{G}^2 \vec{z})_i &= (\mathbf{G}(\mathbf{G} \vec{z}))_i \\
&= \sum_j \left((\mathbf{G} \vec{z})_j \frac{f_{ij}}{T_j^{\text{out}}} \right) \\
&= \sum_j \left[\left(\sum_k z_k \frac{f_{jk}}{T_k^{\text{out}}} \right) \frac{f_{ij}}{T_j^{\text{out}}} \right] \\
&= \sum_{j,k} \left(z_k \frac{f_{ij}}{T_j^{\text{out}}} \frac{f_{jk}}{T_k^{\text{out}}} \right) \\
&= \sum_{\ell_1, \ell_2} \left(z_{\ell_2} \frac{f_{i\ell_1}}{T_{\ell_1}^{\text{out}}} \frac{f_{\ell_1\ell_2}}{T_{\ell_2}^{\text{out}}} \right),
\end{aligned}$$

and by iteration we obtain the stated formula for $(\mathbf{G}^m \vec{z})_i$. The formula for $(\vec{y} \mathbf{G}'^m)_i$ is similarly obtained. \square

The following lemma makes use of Lemma 6.2 to extend the observations of Proposition 6.1.

Lemma 6.3. *For each integer $m \geq 0$, we have that*

$$\sum_{i=1}^n (\mathbf{G}^m \vec{z})_i = \sum_{i=1}^n (\vec{y} \mathbf{G}'^m)_i.$$

Proof. The case $m = 0$, namely that $\sum_i z_i = \sum_i y_i$, follows directly from the steady-state assumption, and the case $m = 1$ was observed in Proposition 6.1. Suppose then that $m \geq 2$.

Observe that we have the following identity by re-indexing the left-hand side via $\ell_t \mapsto \ell_{t+1}$ for $1 \leq t \leq m-1$, $\ell_m \mapsto \ell_1$, followed by renaming ℓ_1 to ℓ_{m+1} and then i to ℓ_1 :

$$\sum_{i, \ell_1, \dots, \ell_m} \left[f_{i\ell_1} \cdot \prod_{n=1}^{m-1} \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] = \sum_{\ell_1, \dots, \ell_{m+1}} \left[f_{\ell_1 \ell_2} \prod_{n=2}^m \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] \quad (16)$$

From Lemma 6.2 it follows that

$$\begin{aligned}
\sum_i (\mathbf{G}^m \vec{z})_i &= \sum_{i, \ell_1, \dots, \ell_m} \left[z_{\ell_m} \cdot \frac{f_{i\ell_1}}{T_{\ell_1}^{\text{out}}} \cdot \prod_{n=1}^{m-1} \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_{n+1}}^{\text{out}}} \right) \right] \\
&= \sum_{i, \ell_1, \dots, \ell_m} \left[\left(T_{\ell_m}^{\text{out}} - \sum_{\ell_{m+1}} f_{\ell_m \ell_{m+1}} \right) \cdot \frac{f_{i\ell_1}}{T_{\ell_1}^{\text{out}}} \cdot \prod_{n=1}^{m-1} \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_{n+1}}^{\text{out}}} \right) \right] \text{ (recall that } \vec{T}^{\text{in}} = \vec{T}^{\text{out}} \text{)} \\
&= \sum_{i, \ell_1, \dots, \ell_m} \left[f_{i\ell_1} \cdot \prod_{n=1}^{m-1} \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] - \sum_{i, \ell_1, \dots, \ell_{m+1}} \left[f_{i\ell_1} \prod_{n=1}^m \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] \\
&= \sum_{i, \ell_1, \dots, \ell_m} \left[f_{i\ell_1} \cdot \prod_{n=1}^{m-1} \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] - \sum_{\ell_1, \dots, \ell_{m+1}} \left[\left(\sum_i f_{i\ell_1} \right) \prod_{n=1}^m \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] \\
&= \sum_{i, \ell_1, \dots, \ell_m} \left[f_{i\ell_1} \cdot \prod_{n=1}^{m-1} \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] - \sum_{\ell_1, \dots, \ell_{m+1}} \left[(T_{\ell_1}^{\text{out}} - y_{\ell_1}) \prod_{n=1}^m \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] \\
&= \sum_{i, \ell_1, \dots, \ell_m} \left[f_{i\ell_1} \cdot \prod_{n=1}^{m-1} \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] - \sum_{\ell_1, \dots, \ell_{m+1}} \left[f_{\ell_1 \ell_2} \prod_{n=2}^m \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] + \sum_{\ell_1, \dots, \ell_{m+1}} \left[y_{\ell_1} \cdot \prod_{n=1}^m \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] \\
&= \sum_{\ell_1, \dots, \ell_{m+1}} \left[y_{\ell_1} \cdot \prod_{n=1}^m \left(\frac{f_{\ell_n \ell_{n+1}}}{T_{\ell_n}^{\text{out}}} \right) \right] \text{ (by equation (16))} \\
&= \sum_{i, \ell_1, \dots, \ell_m} \left[y_{\ell_m} \cdot \frac{f_{\ell_1 i}}{T_{\ell_1}^{\text{in}}} \cdot \prod_{n=1}^{m-1} \left(\frac{f_{\ell_{n+1} \ell_n}}{T_{\ell_{n+1}}^{\text{in}}} \right) \right] \text{ (relabelling } \ell_{m+1} \text{ as } i \text{)} \\
&= \sum_i (\vec{y} \mathbf{G}'^m)_i.
\end{aligned}$$

□

Theorem 6.4. *Realized input and output I/D are identical when the observed system is at steady state.*

Proof. Lemma 6.3 implies the equality of the denominators of realized input and output I/D as well as equality of corresponding summands of the numerators of realized input and output I/D . □

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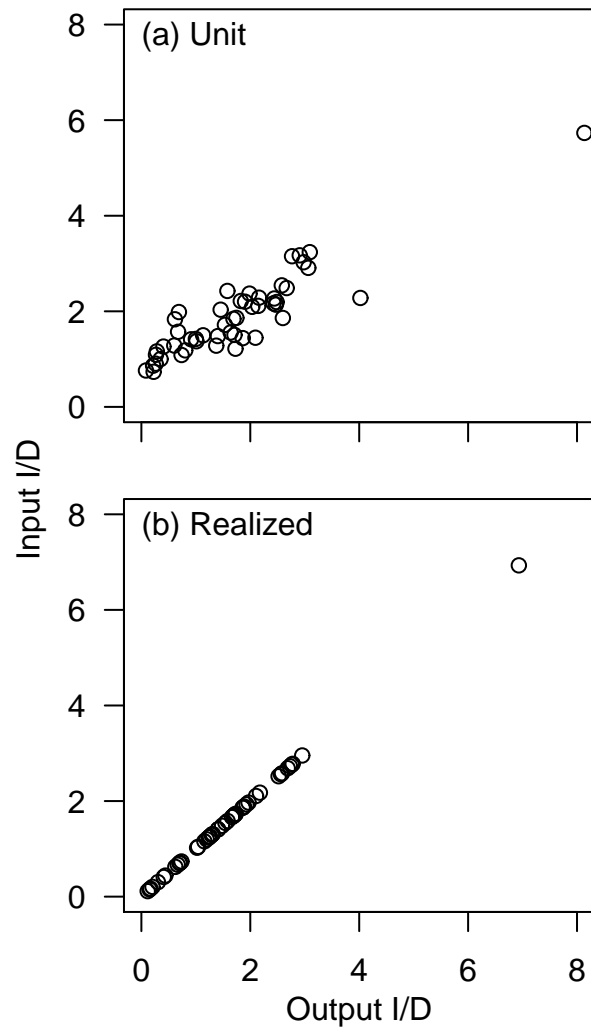


Figure 1: Relationship between input and output oriented measures of the ratio of indirect-to-direct effects calculated using the (a) unit and (b) realized metrics.

Table 1: Fifty trophically-based ecosystem network models.

Model	units	n^\dagger	C^\dagger	TST^\dagger	FCI^\dagger	Source
Lake Findley	gC m ⁻² yr ⁻¹	4	0.38	51	0.30	Richey et al. (1978)
Mirror Lake	gC m ⁻² yr ⁻¹	5	0.36	218	0.32	Richey et al. (1978)
Lake Wingra	gC m ⁻² yr ⁻¹	5	0.40	1,517	0.40	Richey et al. (1978)
Marion Lake	gC m ⁻² yr ⁻¹	5	0.36	243	0.31	Richey et al. (1978)
Cone Springs	kcal m ⁻² yr ⁻¹	5	0.32	30,626	0.09	Tilly (1968)
Silver Springs	kcal m ⁻² yr ⁻¹	5	0.28	29,175	0.00	Odum (1957)
English Channel	kcal m ⁻² yr ⁻¹	6	0.25	2,280	0.00	Brylinsky (1972)
Oyster Reef	kcal m ⁻² yr ⁻¹	6	0.33	84	0.11	Dame and Patten (1981)
Somme Estuary	mgC m ⁻² d ⁻¹	9	0.30	2,035	0.14	Rybarczyk et al. (2003)
Bothnian Bay	gC m ⁻² yr ⁻¹	12	0.22	130	0.18	Sandberg et al. (2000)
Bothnian Sea	gC m ⁻² yr ⁻¹	12	0.24	458	0.27	Sandberg et al. (2000)
Ythan Estuary	gC m ⁻² yr ⁻¹	13	0.23	4,181	0.24	Baird and Milne (1981)
Baltic Sea	mgC m ⁻² d ⁻¹	15	0.17	1,974	0.13	Baird et al. (1991)
Ems Estuary	mgC m ⁻² d ⁻¹	15	0.19	1,019	0.32	Baird et al. (1991)
Svarkops Estuary	mgC m ⁻² d ⁻¹	15	0.17	13,996	0.47	Baird et al. (1991)
Southern Benguela Upwelling	mgC m ⁻² d ⁻¹	16	0.23	1,774	0.19	Baird et al. (1991)
Peruvian Upwelling	mgC m ⁻² d ⁻¹	16	0.22	33,496	0.04	Baird et al. (1991)
Crystal River (control)	mgC m ⁻² d ⁻¹	21	0.19	15,063	0.07	Ulanowicz (1986)
Crystal River (thermal)	mgC m ⁻² d ⁻¹	21	0.14	12,032	0.09	Ulanowicz (1986)
Charca de Maspalomas Lagoon	mgC m ⁻² d ⁻¹	21	0.13	6,010,331	0.18	Almunia et al. (1999)
Northern Benguela Upwelling	mgC m ⁻² d ⁻¹	24	0.21	6,608	0.05	Heymans and Baird (2000)
Neuse Estuary (early summer 1997)	mgC m ⁻² d ⁻¹	30	0.09	13,826	0.12	Baird et al. (2004b)
Neuse Estuary (late summer 1997)	mgC m ⁻² d ⁻¹	30	0.11	13,038	0.13	Baird et al. (2004b)
Neuse Estuary (early summer 1998)	mgC m ⁻² d ⁻¹	30	0.09	14,025	0.12	Baird et al. (2004b)
Neuse Estuary (late summer 1998)	mgC m ⁻² d ⁻¹	30	0.10	15,031	0.11	Baird et al. (2004b)
Gulf of Maine	g ww m ⁻² yr ⁻¹	31	0.35	18,382	0.15	Link et al. (2008)
Georges Bank	g ww m ⁻² yr ⁻¹	31	0.35	16,890	0.18	Link et al. (2008)
Middle Atlantic Bight	g ww m ⁻² yr ⁻¹	32	0.37	17,917	0.18	Link et al. (2008)
Narragansett Bay	mgC m ⁻² yr ⁻¹	32	0.15	3,917,246	0.51	Monaco and Ulanowicz (1997)
Southern New England Bight	g ww m ⁻² yr ⁻¹	33	0.03	17,597	0.16	Link et al. (2008)
Chesapeake Bay	mgC m ⁻² yr ⁻¹	36	0.09	3,227,453	0.19	Baird and Ulanowicz (1989)
St. Marks Seagrass, site 1 (Jan)	mgC m ⁻² d ⁻¹	51	0.08	1,316	0.13	Baird et al. (1998)
St. Marks Seagrass, site 1 (Feb)	mgC m ⁻² d ⁻¹	51	0.08	1,591	0.11	Baird et al. (1998)
St. Marks Seagrass, site 2 (Jan)	mgC m ⁻² d ⁻¹	51	0.07	1,383	0.09	Baird et al. (1998)
St. Marks Seagrass, site 2 (Feb)	mgC m ⁻² d ⁻¹	51	0.08	1,921	0.08	Baird et al. (1998)
St. Marks Seagrass, site 3 (Jan)	mgC m ⁻² d ⁻¹	51	0.05	12,651	0.01	Baird et al. (1998)
St. Marks Seagrass, site 4 (Feb)	mgC m ⁻² d ⁻¹	51	0.08	2,865	0.04	Baird et al. (1998)
Sylt Rømø Bight	mgC m ⁻² d ⁻¹	59	0.08	1,353,406	0.09	Baird et al. (2004a)
Graminoids (wet)	gC m ⁻² yr ⁻¹	66	0.18	13,677	0.02	Ulanowicz et al. (2000)
Graminoids (dry)	gC m ⁻² yr ⁻¹	66	0.18	7,520	0.04	Ulanowicz et al. (2000)
Cypress (wet)	gC m ⁻² yr ⁻¹	68	0.12	2,572	0.04	Ulanowicz et al. (1997)
Cypress (dry)	gC m ⁻² yr ⁻¹	68	0.12	1,918	0.04	Ulanowicz et al. (1997)
Lake Oneida (pre-ZM)	gC m ⁻² yr ⁻¹	74	0.22	1,638	< 0.01	Miehls et al. (2009a)
Lake Quinte (pre-ZM)	gC m ⁻² yr ⁻¹	74	0.21	1,467	< 0.01	Miehls et al. (2009b)
Lake Oneida (post-ZM)	gC m ⁻² yr ⁻¹	76	0.22	1,365	< 0.01	Miehls et al. (2009a)
Lake Quinte (post-ZM)	gC m ⁻² yr ⁻¹	80	0.21	1,925	0.01	Miehls et al. (2009b)
Mangroves (wet)	gC m ⁻² yr ⁻¹	94	0.15	3,272	0.10	Ulanowicz et al. (1999)
Mangroves (dry)	gC m ⁻² yr ⁻¹	94	0.15	3,266	0.10	Ulanowicz et al. (1999)
Florida Bay (wet)	mgC m ⁻² yr ⁻¹	125	0.12	2,721	0.14	Ulanowicz et al. (1998)
Florida Bay (dry)	mgC m ⁻² yr ⁻¹	125	0.13	1,779	0.08	Ulanowicz et al. (1998)

[†] n is the number of nodes in the network model, $C = L/n^2$ is the model connectance when L is the number of direct links or energy-matter transfers, $TST = \sum \sum f_{ij} + \sum z_i$ is the total system throughflow, and FCI is the Finn Cycling Index (Finn, 1980).