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Cycling and reciprocity in weighted food webs and economic networks

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Abstract

Networks of mass flows describe the basic structure of ecosystems as food webs, and of economy as input–output tables. Matter leaving a node in these networks can return to it immediately as part of a reciprocal flow, or completing a longer, multi-node cycle. Previous research comparing cycling of matter in ecosystems and economy was limited by relying on unweighted or few networks. Overcoming this limitation, we study mass cycling in large datasets of weighted real-world networks: 169 mostly aquatic food webs and 155 economic networks. We quantify cycling as the portion of all flows that is due to cycles, known as the Finn Cycling Index (FCI). We find no correlation between FCI and the largest eigenvalues of unweighted adjacency matrices used as a cycling proxy in the past. Unweighted networks ignore the actual flow values that in reality can differ by even 10 orders of magnitude. FCI can be decomposed into a sum of contributions of individual nodes. This enables us to quantify how organisms recycling dead organic matter dominate mass cycling in weighted food webs. FCI of food webs has a geometric mean of 5%. We observe lower average mass cycling in the economic networks. The global production network had an FCI of 3.7% in 2011. Cycling in economic networks (input–output tables and trade relationships) and food webs strongly correlates with reciprocity. Encouraging reciprocity could enhance cycling in the economy by acting locally, without the need to perfectly know its global structure.

KEYWORDS
cycling, economic networks, food webs, industrial ecology, network analysis, reciprocity

1 | INTRODUCTION

Goods and services move between companies and consumers in an economy. Biomass flows between groups of organisms in ecosystems (Hannon, 1973) arise mostly from feeding relationships, and are thus known in ecology as food webs. The flows of mass in both systems define their fundamental, physical structure (Leontief, 1991). Mathematically, they constitute weighted digraphs (directed networks). The mass flows are encoded as weights of links between vertices (nodes) that represent aggregated industries in economic input–output tables or groups of species in ecological food webs (Nebbia, 2000).

Here, we aim to address key questions regarding cycling in weighted ecological and economic networks. How much of the matter flowing in these systems is due to cycling? How much is directly returned in reciprocal flows, compared to longer cycles? Are there any characteristic patterns of mass cycling in these systems? Cycling in real systems is determined by their quantitative, weighted networks. We show that the largest eigenvalues of unweighted adjacency matrices used even in the recent literature (Morris et al., 2021) do not correlate with the actual cycling in weighted networks. We also take a glimpse into networks' internal composition, highlighting how nodes contribute to overall cycling in food webs.

A mass food web has a strongly hierarchical structure, with several very distinct groups of nodes. As carbon makes up most of the mass of organic matter (biomass), its flow is equivalent to the flow of mass in the network. For a particular ecosystem of the size of, for example, a bay, there are two relevant large pools of accessible carbon—the atmosphere and dead organic matter. The atmosphere acts as an external pool of carbon dioxide, which is practically unlimited at the spatial scale of such an ecosystem, as well as over time frames of years. Some organisms, such as phytoplankton, algae, plants, and some bacteria, can assimilate carbon dioxide from the atmosphere. Thus, they are called primary producers and are biomass sources in the system. Dead organic matter is the second, spatially restricted pool of carbon. It is modeled as a part of the food web and referred to as detritus. All the other nodes are consumers, that feed on primary producers, detritus, or other consumers.

Food web flows arise in several distinct processes. Consumption is the basic mass transfer between nodes. The undigested food and dead bodies become detritus. Every living organism respires carbon back into the atmosphere. Some organisms migrate across the ecosystem boundary. Specialized organisms—bacteria, fungi, and invertebrates—recycle dead organic matter (Moore et al., 2004; Szyrmer & Ulanowicz, 1987) and are known as detritivores. They enable the otherwise lost matter to go back to higher-order consumers, decisively impacting the overall cycling of biomass in an ecosystem. This microbial loop (Azam et al., 1983) is particularly important in aquatic ecosystems, utilizing a large fraction of primary production. Further cycles can exist among higher-order consumers, for example, organisms hunting juvenile forms of their predators. In short, a biomass food web is a constant flow of carbon assimilated by primary producers to higher consumers and back into the atmosphere, with an extra part of the flow retained by the virtue of cycling (Patten, 1986).

Ecology (Fath and Patten, 1999) and economics (De Wit et al., 2018; Haas et al., 2015; Katz-Gerro & López Sintas, 2019; Lenzen et al., 2012) have broadly studied the cycling of mass and energy in networks relevant to each field. We quantify cycling with an index proposed by J. T. Finn to estimate the share of cycled matter in the total flow in food webs (Finn, 1976). The Finn Cycling Index (FCI) has been extensively applied in studies of food webs (Christian & Thomas, 2003; Fath et al., 2013; Patten & Higashi, 1995; Higashi et al., 1993; Patten and Higashi, 1984; Ulanowicz, 1983) and socio-economic systems in mass (Alvarez et al., 2014; Fang et al., 2014; Panyam et al., 2019) and monetary units (Picciolo et al., 2017). Its success in capturing all cyclic flows was validated by direct simulations (Kazanci et al., 2009).

The network structure of industrial exchange is particularly relevant to the recent discussion surrounding *circular economy*. The circular economy aims to make production processes more sustainable (Ghisellini et al., 2016; Webster, 2017) by enhancing reuse, recycling, and process integration within and across value chains (Doustmohammadi and Babazadeh, 2020). This concept was first envisaged in the 1990s, in the domain of sustainable resource and waste management (Pearce & Turner, 1990; Schwarz & Steininger, 1997). More recently, it was also mentioned in another field in connection with designing Product Service Systems (Tukker, 2015), in which companies provide services rather than material goods.

Both food webs and economic networks consist of nodes internally processing and exchanging matter with each other (Hannon, 1973; Leontief, 1991). This shared basic nature inspired research into how biomimicry in system design could improve human systems. Natural selection has already led to efficiency and robustness improvements of ecosystems beyond what our short history could achieve in human economy. A universal scaling detected in food webs also sparked the idea that they should be regarded as efficient transport networks (Garlaschelli et al., 2003). Mature ecosystems were recognized for achieving a high degree of internal recycling of energy and material. Elements cycle through the biosphere over pathways that can be tight and local (for phosphorus in natural ecosystems) and sometimes broad and global (for carbon in the whole Earth system) (Palmeri et al., 2014). Eugene P. Odum suggested mimicking natural ecosystems as a way to improve human systems (Odum, 1969).

Researchers studied how to improve cycling by mimicking food webs in the context of thermodynamic power cycles (Layton et al., 2012), industrial parks (Layton et al., 2016b), recycling networks (Layton et al., 2016a; Schwarz and Steininger, 1997), and the whole economy in view of the limits to growth (Jørgensen et al., 2015). A low number of links was shown as a potential threat to higher cycling (Lay, 2017). These studies were limited by looking only at unweighted networks, in which weights equal 0 or 1, or by relying on just a few networks. Weighted food webs have significantly different properties from their unweighted simplifications (Scotti et al., 2007). For example, food web flows can span up to 10 orders of magnitude (Okey et al., 2006). We directly compare FCI with the largest eigenvalue of unweighted interaction matrix, called cyclicity (Layton et al., 2012; Layton et al., 2016b; Lay, 2017; Morris et al., 2021) and pathway proliferation (Borrett et al., 2007).

The reciprocity is defined as the fraction of the flow exchanged between two nodes traveling in both directions. Reciprocal and cyclic paths are common in ecological and economic networks. They are related to important features, such as bilateral trade, mutualism, and cooperation (Battiston et al., 2016; Squartini & Garlaschelli, 2011). They depend considerably on the link density (Ruzzenenti et al., 2010; Squartini & Garlaschelli, 2012; Squartini et al., 2013). A more connected network, arguably, increases both the probability of reciprocal links and circular flows. The two-step interactions quantified by the reciprocity were found to differ significantly between weighted and unweighted versions of the same network (Scotti et al., 2007).

In this study, we describe how topology and cycles relate in economy and ecology. We assess the FCI and other relevant network metrics, such as reciprocity, clustering, connectance, cyclicity, on 169 food webs and 155 economic networks. The primary innovative aspects of our study are:

(1) comparing weighted economic and ecological networks with respect to cycling and reciprocity; (2) investigating the relationship of FCI with a portfolio of well-known network metrics; and (3) providing an assessment of the level of cycling (FCI) on the largest sample of ecological and economic networks to date. In the Methods section we describe the reciprocity, cycling, and clustering measures we use. The Results section presents the distributions of FCI values in our datasets, and how network cycling in food webs arises from their specific internal composition. We outline the limitations of the available data and our approach in Discussion, giving a summary and an outlook in Conclusions.

2 | METHODS AND DATA

2.1 | Data

All systems analyzed in this article are represented as weighted and directed networks (digraphs). Nodes (vertices) in food webs represent groups of species connected by flows of biomass (Supplementary Figure 1, in Supporting Information S1). The currency of the flow is the total wet or dry weight or mass of carbon (constituting most of the mass of the organic matter). The dataset of weighted food webs has been compiled from Ecopath with Ecosim models (Christensen and Pauly, 1992) that are collected in Ecobase (Colléter et al., 2013). The Supplementary Information (S1) contains the list of all used networks and their references.

Economic networks under study portray flows of matter or money between sectors of national economies. The economic dataset contains three categories of networks: (1) input–output tables in monetary (IO) or physical units (PIOT); (2) trade tables in units of monetary value, mass, and embodied CO_2 emissions (the amount of CO_2 directly and indirectly emitted to produce traded goods); and (3) multi-regional input–output matrices (MRIO) connecting IO tables from different regions/countries. In the three types of networks, nodes represent, respectively: sectors/industries; countries/regions; and the dyads country industry. In economic networks, self-loops typically account for most of the cycling, but are difficult to compare with food webs, where self-loops are marginal, if not absent; this is why FCI without self-loops has been additionally computed. A description of the sources and criteria used in the construction of the networks is reported in the Supplementary Information (S2).

While monetary data are generally reported and have undergone little manipulation (typically for harmonizing reporting procedures), mass data are the result of either analytical work or econometric conversion (Gaulier and Zignago, 2010). Monetary data are more reliable than mass data, but provide a fundamentally different framework. While mass is partially depleted through production (waste material), value never declines. On the contrary, value accumulates throughout stages of production (value chains). Hence, comparing mass and monetary flows, we highlight the contrast between those two aspects of economic exchange.

2.2 | Methods

We apply measures quantifying reciprocity, cycling, and clustering in weighted directed networks (digraphs) from ecology and economics. A network consists of N nodes that here represent species, industries, countries, or regions. Node i receives a flow F_{ij} from node j. The matrix F consists of real, positive entries. If summation range is not explicitly specified below, it is assumed to run from 1 to N.

A node can also exchange matter with the outside environment. In food webs, ecologists distinguish between the mass taken from the outside of the modelled ecosystem as imports, the respiration of living organisms exiting into the atmosphere, and other exports outside the ecosystem (e.g., due to fishing). These quantities are explicitly present in the data as node properties. In economic networks, the information about the exchange with the environment is frequently missing or incomplete. We add the flow into or out of the system calculated as the flow needed to balance system flows around each node.

The amount of matter leaving a node i, T_i, is given by

$$T_i = \sum_{j=1}^{N} F_{ji} + O_i, \tag{1}$$

where O_i is the flow leaving the system from node i. A probability that a unit of mass moves from node i to node j in one step is given by a respective entry of an $N \times N$ transition matrix G

$$G_{ji} = F_{ji}/T_i. \tag{2}$$

A sum of powers of G expresses the transition probability from i to j in at most S steps (Norris, 1998; Bharucha-Reid, 2012):

$$U^{(S)} = (u_{ij}^{(S)})_{1 \le i,j \le N} = \sum_{q=0}^{S} G^q = I + G^1 + \cdots G^S. \tag{3}$$

We introduce the cycling index of a vertex as the probability of flow passing through a node i to return statistically (directly or indirectly) to it within S steps, formally:

$$\gamma_i^{(S)} = \frac{u_{ii}^{(S)} - 1}{u_{ii}^{(S)}}. \tag{4}$$

The mass of $\gamma_i^{(S)} T_i$ passes through a node i and returns to it within S steps. The (global) Cycling Index (CI) of the network (i.e., the fraction of total throughflow that returns, directly or indirectly, to a starting node) within S steps is given by:

$$CI^{(s)} = \frac{\sum_i \gamma_i^{(S)} T_i}{\sum_j T_j}. \tag{5}$$

Since G is a sub-stochastic matrix, its power series converges for $S \rightarrow \infty$ (Solow, 1952):

$$U^{(\infty)} = (I - G)^{-1}. \tag{6}$$

The FCI (Finn, 1976) accounts for mass returning over all possible paths of all possible lengths, that is, for $S = \infty$,

$$FCI = \frac{\sum_i \gamma_i^{(\infty)} T_i}{\sum_j T_j}. \tag{7}$$

FCI takes values between 0 and 1. The lower limit is achieved when no flow starting at any node comes back to the same node at any path length (there are no directed cycles). The upper limit represents a system where all flows come back to the starting node. In the further text we also compare the few-step cycling $CI^{(2)}$, $CI^{(3)}$, $CI^{(4)}$ with the FCI.

The simplest type of cycling is a reciprocal exchange of mass between two nodes. The network *reciprocity r* (Squartini et al., 2013) measures the fraction of such overlapping bilateral flows among all flows:

$$r = \frac{\sum_i \sum_j \min[F_{ij}, F_{ji}]}{\sum_k \sum_k F_{kl}}. \tag{8}$$

If all flows are perfectly reciprocated, then $r = 1$. If there are no nodes connected by flows in both directions, $r = 0$.

We evaluate the *weighted clustering coefficient* averaged over all the nodes of the network (Fagiolo, 2007) for all possible triplets:

$$cc_i^{tot} = \frac{\sum_{j \neq i} \sum_{k \neq j,i} (F_{ij}^{1/3} + F_{ji}^{1/3})(F_{jk}^{1/3} + F_{kj}^{1/3})(F_{ki}^{1/3} + F_{ik}^{1/3})}{2[k_i^{tot}(k_i^{tot} - 1) - 2k_i^{\leftrightarrow}]}. \tag{9}$$

For cyclic motifs (directed paths):

$$cc_i^{cyc} = \frac{\sum_{j \neq i} \sum_{k \neq j,i} (F_{ij} F_{jk} F_{ki})^{1/3}}{k_i^{in} k_i^{out} - k_i^{\leftrightarrow}}, \tag{10}$$

where the in-degree k_i^{in} and out-degree k_i^{out} count the incoming and outgoing flows. The reciprocal degree $k_i^{\leftrightarrow}$ is the number of bidirectional connections.

Simpler network measures rely just on the unweighted interaction matrix A. The interaction matrix can be obtained by replacing non-zero entries with 1 in the flow matrix F. The *connectance* (Yodzis, 1980) is the fraction of possible flows that are non-zero:

$$c_i = \frac{\sum_{j \neq i} A_{ij}}{N^2}. \tag{11}$$

Cyclicity, or the Perron–Frobenius eigenvalue is the largest real eigenvalue λ_{max} of A. It has also been called pathway proliferation (Borrett et al., 2007). It was expected to mark the strength of cycling. For comparison, we also compute the Perron–Frobenius eigenvalue of the transition probability matrix G.

TABLE 1 Two-step Cycling Index (Equation 5), Finn Cycling Index (Equation 7), reciprocity (r^w), and connectance (c) of economic networks and food webs in mass and monetary units. We calculated FCI for the World Trade in CO_2 without self-loops which disproportionately distort the measure, and marked it with *. We use abbreviations MRIO for Multi-Regional Input–Output, and PIOT for Physical Input–Output Table

	Year	Networks	Nodes	$CI^{(2)}$	FCI	r^w	c
Mass Flows							
Food webs		169	7−125	0.063	0.091 ± 0.085	0.22	0.28
EXIOBASE (world)	2011	1	5424	0.035	0.037	0.02	0.17
EXIOBASE (countries)	2011	42	113	0.061	0.071 ± 0.058	0.01	0.32
PIOT, various	1990, 2015	4	12−16	0.12	0.13 ± 0.021	0.06	0.4
World Trade (BACI)	1998−2015	1	203	0.03	0.05 ± 0.004	0.36	0.53
World Trade (EORA), CO_2	2000−2016	1	42	0.034*	$0.06^* \pm 0.01$	0.02	0.99
China EIO	2012	1	900	0.21	0.26	0.25	0.8
China MRIO, CO_2	2012	30	30	0.24	0.32 ± 0.09	0.28	0.9
Monetary Flows							
World Trade	1998−2015	1	208	0.06	0.19 ± 0.03	0.7	0.5
WIOD, world	2000−2014	1	2408	0.14	0.17 ± 0.01	0.32	0.1
WIOD, countries	1995−2011	43	34	0.02	0.09 ± 0.65	0.25	0.8
US IO	1947−2016	1	42/66	0.15	0.27 ± 0.001	0.27	0.8
UK IO	1998−2015	1	97	0.12	0.20 ± 0.01	0.36	0.7
China IO	1992−2012	1	45	0.21	0.29 ± 0.003	0.25	0.89
Italy MRIO	2014	20	37	0.19	0.23 ± 0.05	0.27	–

The properties of nodes in food webs are heavily influenced by their trophic level. Trophic level counts intermediate nodes between a given consumer and resources entering the system. The trophic level (Odum and Heald, 1975) of a node i is defined as:

$$\begin{cases} 1 \\ 1 + \sum_{j=1}^{n} \frac{F_{ij}}{\sum_{k=1}^{n} F_{ik}} \tau_j \end{cases} \tag{12}$$

3 | RESULTS

Mass cycling in aquatic food webs has a very broad and skewed distribution that reflects the diversity of these networks. Their number of nodes and connectance vary greatly, from 7 to 125 nodes and from 11% to 53% (Table 1). The share of mass cycled in food webs takes values between 0.3% and 33%. The majority of networks display FCI lower than 6%. Its distribution is closer to lognormal than to normal. Thus, we choose the geometric mean of 5.1% (Figure 4) to quantify the "typical" extent of cycling in food webs.

Much of the biomass cycling can be attributed to reciprocal flows. Reciprocity ranges from 0.7% to 56% with a geometric mean of 16%. At the network level, reciprocity is a very good predictor of biomass cycling, as can be seen in Figure 1. This clear power law relationship is estimated with ordinary least squares regression as

$$\text{FCI} \propto r^{1.209 \pm 0.040}. \tag{13}$$

The correlation between reciprocity and FCI is very strong, with the fit R^2 equal to 0.85.

The nature of cycling in food webs becomes visible in the way individual nodes contribute to the sum that is the network FCI. The differing distributions of FCI values of various groups of nodes are presented in Figure 2. Especially, the cycling of nodes at trophic levels higher than two can be well fit by a lognormal distribution, with chi-square an order of magnitude below other standard distributions. Lognormality would indicate that node-level FCI values could originate as products of many independent random positive variables.

We observe that the recycling of dead organic matter (detritus) completely dominates cycling in food webs. The detrital FCI values with the geometric mean of 1.7×10^{-3} are typically two orders of magnitude above consumers at the second trophic level (geometric mean 9.4×10^{-6}), and
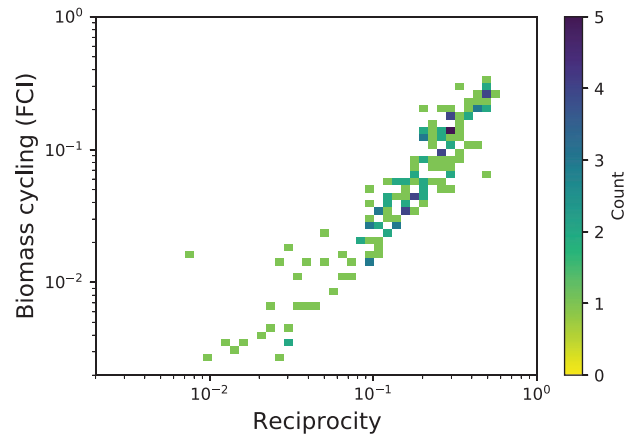
FIGURE 1 A histogram of values of reciprocity and FCI of all analyzed food webs. Color indicates the number of networks that fell into bins defined by reciprocity and FCI intervals (Underlying data are available in the FoodWebs tab of Supporting Information S3)
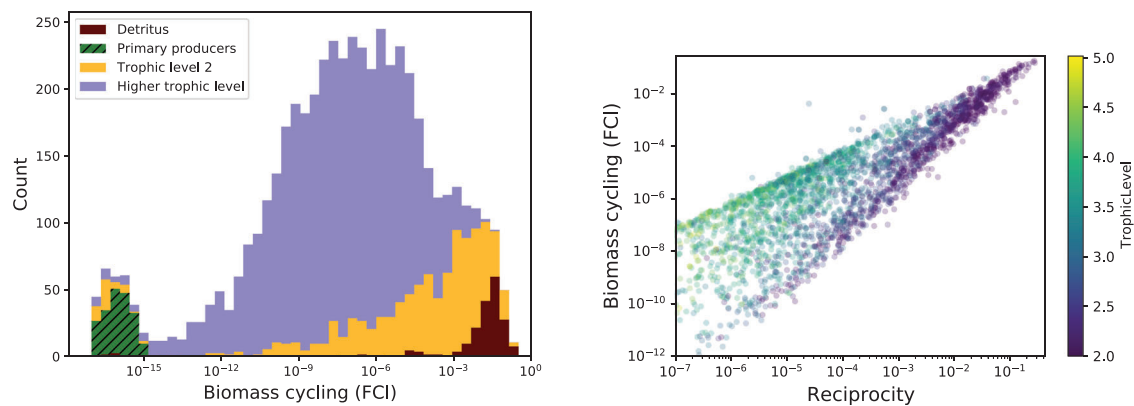

FIGURE 2 The network FCI value is a sum of more easily interpretable contributions of individual nodes. Left: a histogram of contributions to FCI among all food web nodes. The nodes are divided into subgroups: primary producers (green, striped), detritus (red), consumers at the second trophic level (yellow), and consumers at higher trophic levels (blue). Right: reciprocity and FCI contributions of all nodes at trophic level two and higher. Color denotes the trophic level (Underlying data are available in Supporting Information S4)

five orders of magnitude above consumers at higher trophic levels (geometric mean 2.2×10^{-8}). The strong hierarchy of cycling values is explained by the fact that organisms feeding on detritus, such as fungi and bacteria, can recycle and feed a significant fraction of primary production back into the system (Azam et al., 1983; Patten, 1986).

Reciprocity strongly influences FCI at node level in roughly two ways, depending on the trophic level. High reciprocity nodes at the second trophic level have FCI values clustered around a central power law trend, as visible in the right panel of Figure 2. At lower reciprocity (less than 10^{-2}) a second statistically significant trend becomes visible. For given reciprocity, the FCI of nodes at higher trophic levels is higher than those at the second trophic level, and follows a less steep power law. At the second trophic level, the direct exchange with one of the possibly numerous detrital nodes dominates the cycling. At higher trophic levels though, multiple indirect pathways to detrital nodes become available.

We observe that cyclicity, an alternative measure of cycling, fails to predict FCI values. We compare the values of cyclicity, (pathway proliferation) $\lambda_{max}(A)$, and FCI for the food web dataset. The lack of any significant relationship is clear in Figure 3 and quantified by Spearman correlation coefficient of about -1%. On the other hand, the largest eigenvalue of the transition matrix G (Equation 2) can roughly predict FCI values. Much of the information about cycling is already encoded in this eigenvalue. The neglect of the actual values of flows makes such prediction impossible for cyclicity.

Reciprocity and FCI in food webs are closely related, by Equation 13. This relationship can be explained by the predominance of two-step cycles in FCI (Figure 4). They are topologically akin to reciprocity, involving pairwise mutual flows.

The cycling of all economic networks is normally distributed (see SM3), differently from food webs. In economic networks, the cycling of money is an order of magnitude larger than the cycling of resources. Of the 32 Gt of matter processed in the world by 5424 nodes (country industry), with 17% connectance in 2011, only 3.7% were cyclical flows (EXIOBASE dataset, see SM2).
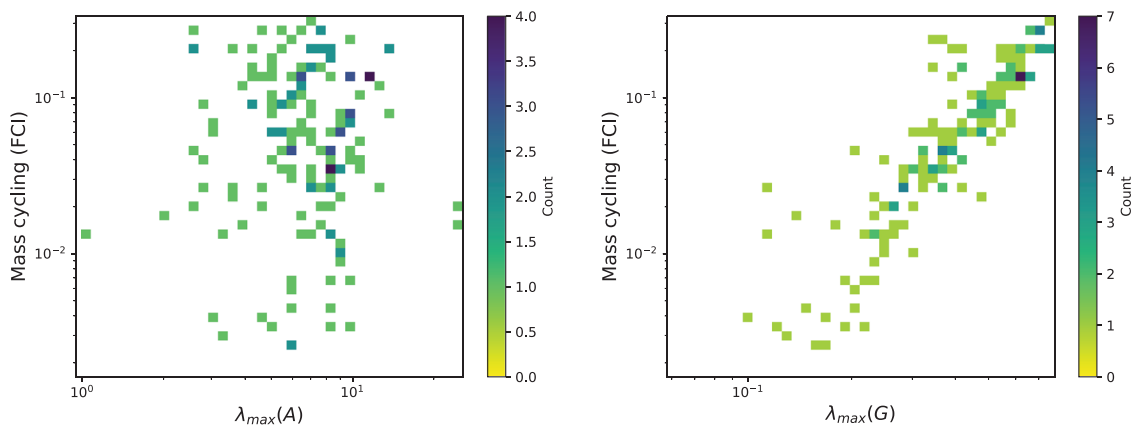
FIGURE 3 Cyclicity (pathway proliferation) does not correlate with mass cycling once flow values are accounted for. Left: values of the largest eigenvalue of unweighted interaction matrix A and FCI for each food web. Right: values of the largest eigenvalue of weighted transition matrix G and FCI for each food web (Underlying data are available in Supporting Information S4)
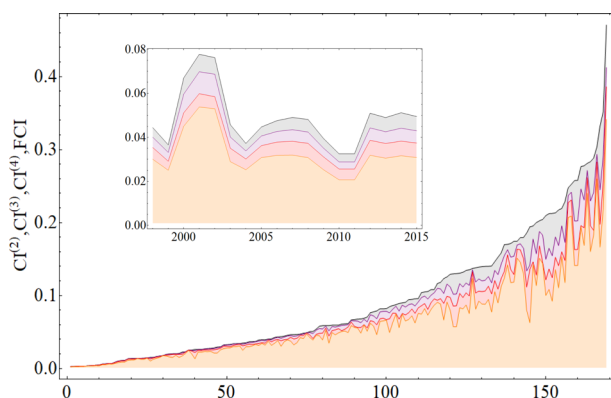

FIGURE 4 Contribution of paths of different length to FCI in 169 food webs. The S-step cycling index CI^S captures the fraction of flow returning to the same node within S steps, see Equation 5). The subsequent curves indicate CI^2 (orange), CI^3 (red), CI^4 (purple), and the total FCI (gray). The inset displays an analogous FCI breakdown for the world trade network (WTW, in mass units), between the years 1998 and 2015 (Underlying data are available in Supporting Information S3: FoodWebs, WTW-WD)

Mass cycling as described by FCI gives a lower estimate of global recycling than measures used in previous studies. These set the global recycling level to 6%, for a total processed mass of 62 Gt in 2010 (Haas et al., 2015), 9% in 2017 for a total of 92 Gt (De Wit et al., 2018) and 8.6% in 2019[1]. FCI reflects the cycling of matter passing through all nodes. The Global Circularity Metric of (De Wit et al., 2018) looks only at the total system inputs and outputs and estimates them based on different sources than used here. Other major differences with our study concern the aggregation level of data (and the attribution of byproducts), the analytical framework, the inclusion of regenerative flows, and the methods used for assessing the reused inputs (Mayer et al., 2019). In our analysis mass flows are homogeneously considered and sectors with hybrid accounting (mixing monetary, energy, and mass units, see SM2) are excluded. These differences make a direct comparison difficult and show that the uncertainty of a recycling estimate can be large. A systematic and comprehensive review of the diverse approaches is a question that demands further investigation.

We assess mass cycling within individual countries by splitting the EXIOBASE global exchange network into subnetworks and studying them separately. The average mass cycling of 42 countries in 2011 was 0.071, but only 2.6×10^{-3} when self-loops were omitted. The corresponding monetary exchange had FCI of 0.26, but 0.08 without self-loops. The large impact of self-loops shows the importance of cycling within each industry sector aggregating manifold companies into one node. The mass cycling has a significantly wider range, from 2.6×10^{-3} in Cyprus to 0.25 in Luxembourg. Monetary cycling varies from 0.027 in Hungary to 0.15 in Indonesia. Generally, high-income countries have a higher level of mass FCI compared to low- or medium-income countries (see Figure 5).

The level of cycling for individual countries is an order of magnitude higher compared to the global economy. Cycling differs also by two orders of magnitude among countries. This reflects differences in the structure or the national economies, and their embedding in the global production network. Highly interconnected and globalized value chains are expected to lower the FCI of an individual country, but more research is needed.
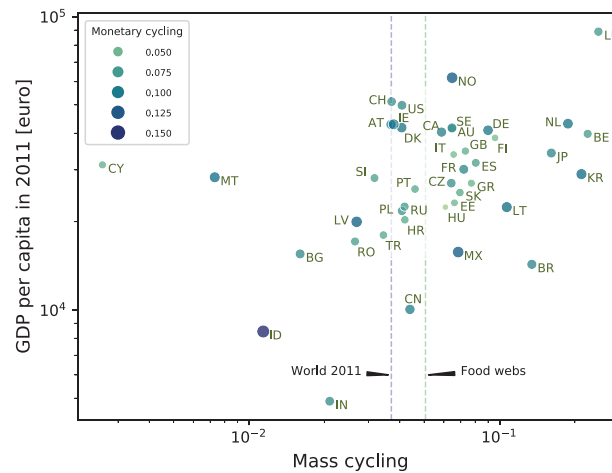
FIGURE 5 Mass cycling (FCI) in 43 countries and their GDP per capita in 2011, as portrayed by EXIOBASE. They are compared with the FCI of the whole world economy in 2011 (blue line) and the geometric mean of food web FCI (green line). Bubble size and color reflect the monetary cycling of countries (Underlying data are available in Supporting Information S3: EXIOBASE_WIOD)

Countries differ not only by values of FCI, but also in the way their cycling changes over time. The FCI of the United States has decreased over time, whereas that of China and the United Kingdom has increased, similarly to that of the World MRIO (WIOD, World Input–Output Tables, see SM3).

The world trade network exchanged 13 billion tonnes of matter in 2011, 19% of all the matter processed that year. Between 1998 and 2015 an average of 4.7% consisted of matter that left and returned to the same country in the form of a whole or intermediate product. Several countries even have FCI that is higher than the majority of food webs. The four physical input–output tables (PIOT) considered exhibit a level of cycling around 10%. However, these systems differ by their scale and the type of mass that was quantified.

The level of mass FCI seems to be unrelated to both the level of income of the country or the level of FCI in monetary units (see Figure 5); nevertheless, as a general, almost ubiquitous rule, mass cycling is one order of magnitude smaller than monetary cycling in IO, MRIO, and trade networks. It indicates that, while mass is dissipated throughout production chains, value is accrued. Two-thirds of the cycled mass in food webs, on average around 69%, is cycled among two compartments (two-step cycling or $CI^{(2)}$). In socio-economic networks, the share of $CI^{(2)}$ ranges from 42% of the UK IO up to an average of 78% of EXIOBASE MRIO matrices and roughly 30% for the world trade network (Figure 4).

Cycling correlates much stronger with reciprocity than with connectance or clustering coefficient. The relevant Spearman correlation coefficients are shown in Figure 6. The only exceptions are the IO tables of the United States and the United Kingdom. This hints at the important difference between country-wide and global economies. The higher the reciprocity, the higher the cycling in all the considered network sets except WIOD, that represents world monetary flows from 2000 to 2014. The FCI values of these flows were steadily increasing over time, despite falling reciprocity. Reciprocity directly contributes to the two-step cycling index $CI^{(2)}$. Yet, even the difference between FCI and $CI^{(2)}$ correlates strongly with the reciprocity.

Correlations between cycling and connectance highlight the differences among the studied networks. They are strongly positive in world monetary exchange (WIOD), but strongly negative in the monetary World Trade; moderately positive in food webs, but insignificant in EXIOBASE world mass exchanges.

The similarly strong and positive relationships between cycling and reciprocity in economic networks and food webs hint at a possible universal law connecting topology and mass dissipation.

4 | DISCUSSION

The generality of cycling and reciprocity patterns observed in food webs and economic networks relies on the availability and the reliability of empirical data. The 169 food webs considered account for a great diversity of mostly aquatic ecosystems around the globe. The most common continental shelves are followed by open ocean, upwellings, bays/fjords, and coastal lagoons. The main reason the aquatic ecosystems are greatly overrepresented could be their significance in fishery management (Pauly et al., 1998) and the historical collapse of fisheries (Frank et al., 2005). Furthermore, many of the food webs model managed areas, such as fisheries, already significantly impacted by humans. It has been noted that their important properties, such as biomass distribution, might differ from pristine ecosystems (McCauley et al., 2018).
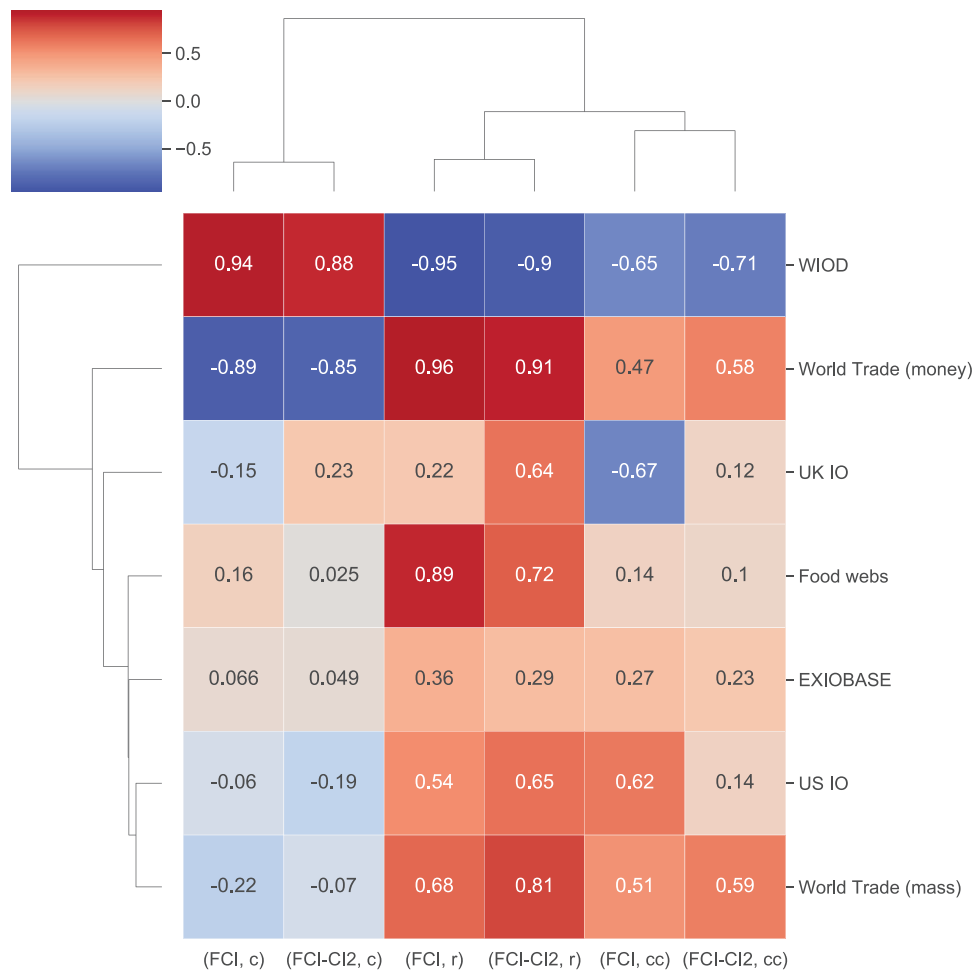
FIGURE 6 Spearman correlation coefficients between cycling and other structural indicators. Rows correspond to sets of networks and columns to pairs of indicators for which the correlation has been computed. *c* stands for connectance (11), *r* for reciprocity (8), and *cc* for the weighted clustering coefficient (9). Rows and columns were ordered according to similarity with clustering shown through dendrograms above and on the left of the heatmap (Underlying data are available in Supporting Information S3)

Cycling in economic networks can be studied at various levels of aggregation. Here, we focused on the macroeconomic perspective, relevant for the circular economy concept. The global scale is also the most appropriate for cycling studies, as current supply chains are strictly intercontinental (Picciolo et al., 2017).

We showed the advantage of FCI over unweighted cycling measures. The network FCI is also a sum of contributions of individual nodes. By decomposing FCI we observed how cycling originates at the node level and quantified the underlying cycling structure in food webs. This cannot be achieved with alternative cycling measures, such as the largest eigenvalue of the adjacency matrix (Borrett et al., 2007).

Another alternative, the storage-based cycling index (Ma and Kazanci, 2014) takes into account stock values of mass in nodes. In published food webs though, the estimates of detrital biomass are frequently unavailable. Moreover, the reported stock values may not be causally connected with cycling in the current ecosystem. Many of the food webs in the dataset describe areas with significant human impacts. These impacts are recent compared to the timescales at which organic matter accumulates in wetlands or at the sea bottom. Thus, the sampled detrital biomass might have originated in an ecosystem differing from the modeled one. The flows, however, fully belong to the current ecosystem.

Studies of well-resolved empirical systems can give the best guidance in improving cycling, but the modelers' assumptions also impact the realism of conclusions. Both the biosphere and the human economy vary in time, and are far from equilibrium. Food webs are approximate static pictures of populations of organisms. Therefore, no biomass accumulates in any of the nodes: the incoming and outgoing flows balance each other. This balance condition sets them apart from, for example, monetary input–output tables.

The exact currency of flows studied also gives rise to several limitations of cycling studies. In economy, when flows represent the total mass, no distinction is made about the type of flow, that is, the nature of the material. Therefore, one ton of outgoing flow of iron can return in the form of one ton of plastic. This limitation becomes clearer when goods with composite materials are considered. Our economic cycling estimates are upper

bounds on the present recycling of resources, representing an average over separate resource categories/elements. On the contrary, FCI in food webs is a good indicator of the level of mass cycling. Wet and dry weight food webs are essentially just carbon networks, as carbon provides the most of the weight of any organic compound.

A simultaneous study of how the most relevant elements flow through a system could explain its level of cycling. In food webs, the populations grow to a size limited by the scarcest element and carrying capacity constraints. Nitrogen and phosphorus play such a limiting role in most aquatic ecosystems. Their relative scarcity in body mass makes carbon and total mass networks in our study characterized by lower FCI values than known from nitrogen and phosphorus networks (Scharler et al., 2016).

Various elements can impose differing limits on recycling. We have quantified the importance of specialized organisms recycling dead organic matter in food webs. Bacteria and fungi required millions of years to evolve abilities to break down otherwise indigestible chemical compounds, such as lignin (Floudas et al., 2012). The difficulty of recycling different elements in human economy is also unequal (Brunner, 2013). Such technological challenges limit the improvements possible by manipulating the network structure alone.

A possible improvement of mass cycling could originate locally, through enhanced reciprocity. We observed a strong empirical correlation between reciprocity and cycling. Its deeper, causal explanation is beyond the scope of the present analysis. Higher reciprocity might be inhibited by geographical, political, or economic factors, among which the most plausible is the structure of the economy. The correlation by itself does not guarantee that enhancing reciprocity alone in an existing system is a feasible procedure to achieve an arbitrarily high cycling. In particular, it depends on how the exchanging dyads are coupled to the rest of the network.

Can we use FCI as a metric to assess the level of circularity in economy? It should certainly not be replaced by any unweighted simplifications, but certain caveats remain. Our analysis only accounts for flows arising from monetary transactions. This includes, for example, the waste disposal industry and production processes that rely on other sectors instead of extracting resources directly from the environment. However, it excludes any reuse and material-saving processes by firms or consumers that could result in an increase in the FCI.

Further research could explore the impact of system boundaries on cycling. The identification of flows crossing the system boundary in an industrial network significantly affects calculations. For example, if world trade accounts for 20% of all mass processed globally, as much as 80% of this mass crosses the system boundary.

5 | CONCLUSIONS

Implementing nature's lesson (Jørgensen et al., 2015; Schwarz and Steininger, 1997) by observing ecological complexity to draw conclusions for the humans' sake might not be possible in the oversimplified sense of *recycling everything* (Ayres, 2004). Nonetheless, nature, differently from human made systems, refined its processes and structures for million of years. It accomplished a better strategy, as shown by our results, to sustain cycles of matter.

A circular economy requires vast improvements in the efficiency of production chains. It means a global sustainable-oriented interdependence of sectors/countries. Locally, a circular design of process and products is needed. Data-based studies of mass cycling in networks benefit this goal. We have described mass cycling through FCI that highlights how nodes contribute to the network cycling. We have shown that studies of cycling in unweighted networks fail to predict the actual portion of all flows that is due to cycles. This explains differences between these two indicators noted in the recent literature (Morris et al., 2021). Sound inferences require relying on weighted indicators, such as FCI.

Our results show a strong correlation of FCI with reciprocity in real-world weighted networks, observed for the datasets of 169 weighted food webs as well as 155 economic networks. We have additionally quantified to which extent organisms recycling dead organic matter dominate mass cycling in weighted food webs. We have noted that in food webs reciprocity and FCI are related through a power law. Socio-economic networks on average lag far behind food webs in mass recycling and would thus benefit from a redesign that considers biomimicry and other evolutionary approaches. Differently from food webs, the relationship between reciprocity and FCI is ubiquitous and more evenly distributed among nodes of economic networks. Even the difference between FCI and CI[2] correlates strongly with the reciprocity. It shows that the impact of reciprocity on cycling stretches beyond the direct two-step cycles.

In addition to recycling waste and minimizing pollution, policies could promote reciprocity and collaboration among network's compartments, such as economic partners, subsidiaries, or countries. This can be local and incremental and does not require a global knowledge of the system. Such a strategy is simpler than designing an optimized network in a top-down process.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All the processed data are available as supporting information (S3 and S4). The data that support the findings of this study are derived from public domain resources, listed in Supporting Information S1 and S2.

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