TOTAL FLOWS IN ECOSYSTEMS

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ABSTRACT

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Ever since it was introduced to ecology over a decade ago, economic input–output analysis has been a tool useful in defining the structure of ecosystems. The central element in this theory hitherto has been the Leontief structure matrix, which is commonly thought to express the total direct and indirect flows between any two compartments of a system. However, the Leontief calculus focusses upon the contributions towards the exports from the system and does not explicitly compute the ecologically more interesting bilateral exchanges that occur within the flow network. It is possible to define a matrix of 'total flows' which provides a more convenient starting point for such tasks as sensitivity analyses, description of cycles, identification of key compartments, optimal resource reallocation, and definition of trophic status. The matrix of total flows can be considered the kernel for a more nearly canonical version of input–output analysis.

1. INTRODUCTION

"Ecology is the study of the relationships of organisms with one another and with their non-living environment" (Odum, 1959). Exactly how to quantify the relationships among organisms is a matter of some debate, but a growing number of systems ecologists now regard the magnitudes of flows of material and energy between the various components of an ecosystem as appropriate measure of such relationships. In so doing they do not infer that, for example, the amount of carbon flowing from zebra to lion is a complete description of every detail of the complicated relationship of that particular predator and prey interaction any more than the dollar exchange between an auto manufacturer and the steel industry portrays the intricacies

of the corresponding business transaction. But the common assumption is that the ethologies and physiologies of predator and prey are embodied in the measured carbon flow in the same way that, say, manufacturing technologies, union-labor relationships and availability of materials are implicit in the volume of commodities and cash exchanged between supplier and consumer.

The analogy between ecology and economics is especially appropriate in that the study of the networks of economic exchanges has a longer history than does the systematic study of ecological flows. 'Input–output analysis', or the characterization of both direct and indirect influences in economic communities began with Leontief (1936, 1951) and reached its zenith over 20 years ago. Just when interest in economic matrix methodologies was beginning to wane, Hannon (1973) introduced input–output analysis (IOA) into ecological studies.Viewed afresh from the new perspective of mathematical ecologists, IOA was employed for a number of novel applications. Patten et al. (1976) emphasized the newfound capability to assess indirect effects in ecosystem networks. An organism might be directly in communication (i.e., exchanging matter or energy) with only a few other species. But those compartments in turn are linked with perhaps a different set of species, and this second set with still others in an infinite causal regression. IOA seemed to quantify the cumulative effects of a potentially infinite number of pathways of cause in the elements of a simple two dimensional matrix, the Leontief structure matrix. This structure matrix afforded a more complete description of the environment experienced by each species, whence the title 'environ' or niche descriptor.

As IOA deals with the transfers of medium in discrete steps, it conveniently can be used to define the trophic status of an element in a network (Levine, 1980). Alternatively, discrete trophic levels can be assumed, and the nodes of the network can be apportioned to these trophic compartments (Ulanowicz and Kemp, 1979).

Most ecosystem networks contain closed cycles, and the presence of these cycles is implicit in the diagonal elements of the Leontief structure matrix. These diagonal values can be used to calculate the actual amount of cycling present in the network, purportedly a significant indicator of the degree of system development (Finn, 1976).

Finally, because the elements of the structure matrix appear to indicate the fraction of a given compartmental output which flows to any other compartment, the generic techniques of sensitivity analysis can be applied to the structure matrix to assess the relative significance of each flow in the network (Bosserman, 1981).

Unfortunately, the authors are aware of no instance in which these novel adaptations of IOA by ecologists have been implemented by economists.

2. TOTAL FLOW

During the early developmental stages of any discipline, elements and methods evolve opportunistically and sometimes haphazardly. However, there usually comes a time when it pays to look at the body of theory, identify the core elements, and ask how the remaining elements can be most efficiently related to that kernel. One should also explore the possibility that some other core elements will permit a simple, or canonical, exposition of the theory.

In IOA the central element has always been the structure matrix, of Leontief inverse. This matrix is calculated solely from the intramural system transfers (intermediate flows) and final outputs (final demands). Among n compartments there exist at most n^2 nonnegative flows, z_{ij}, from any compartment i to any other compartment j ($i \neq j$), or to itself ($i = j$). These form the components of an $n \times n$ matrix of direct flows, Z. The final outputs to the external world appear as the n elements of a column vector, Y. The total outputs from each compartment are defined to be the elements of a vector X and are calculated by summming all the intramural outputs and adding the external output, i.e.

$$X = ZJ + Y \tag{1}$$

where J is an n-dimensional column vector of 1's.

The fundamental assumption upon which IOA rests is that any input to a compartment will appear proportionately among the various outputs of that compartment. In matrix terms, if X is an $n \times n$ diagonal matrix with diagonal entries equal to the elements of vector X, then:

$$Z = A\hat{X} \tag{2}$$

where A is an $n \times n$ matrix of constant structural coefficients (called technical coefficients in economics or stoichometric coefficients in chemistry). Because $\hat{X}J = X$, substitution of eqn. (2) into eqn. (1) yields:

$$X = AX + Y \tag{3}$$

Solving eqn. (3) for X in terms of Y and A gives:

$$X = (I - A)^{-1}Y \tag{4}$$

where I is the $n \times n$ identity matrix.

The matrix relating the total outputs to the final outputs is called the structure matrix and will be denoted here by D, that is:

$$D = (I - A)^{-1} \tag{5}$$

Because matrix A has been properly normalized, it is possible to expand the structure matrix as an infinite series (Miller and Blair, 1985) in the manner:

$$(I - A)^{-1} = I + A + A^2 + A^3 + \dots \qquad (6)$$

Now, if $\hat{Y}$ represents a diagonal matrix with the components of vector Y along the diagonal, then the i–j component of $A\hat{Y}$ represents the amount of total output of i which exits the system at j after the first round of transfers. Similarly, the i–j component of $A^2\hat{Y}$ represents that amount which exits the system at j two rounds of transfers after it emerged from i. It follows that the amount issuing from i and eventually exiting from j after all possible transfers will be represented by the i, jth element of the matrix:

$$F = (D - I)\hat{Y} \qquad (7)$$

Economists are primarily interested in what leaves a system—the final outputs or demands. However, final outputs are relatively less interesting to ecologists to whom they appear as respiration or other losses. The intramural ecological outputs usually evoke greater interest in ecology. Reflecting upon the opening sentence of this paper, it becomes evident that the ecologist is more interested in the total effect which the output from i has on the total output of j. This gross amount of flow can be estimated by scaling up F from the final outputs $\hat{Y}$ to the total outputs $\hat{X}$, so that the matrix, Z^G, of overall or gross flows from all i to all j takes the form:

$$Z^G = (D - I)\hat{X} \qquad (8)$$

In a system without cycling the elements of Z^G will represent the total influence which compartment i has upon compartment j, and one stands ready to base ecological judgements about total influence upon this matrix. However, real ecosystem networks contain cycles of material and energy, and the presence of cycles confounds the meaning of Z^G. Part of the gross flow from i to j is cycled back to i. As in any causal circle, the gross flow represents not only the influence of i upon j, but also that of j upon i. Is there any way to isolate that influence upon j which is proper to compartment i? Such an influence will be called the *total flow* from i to j and designated by the matrix Z^T. *

To calculate the components of Z^T it is best to reformulate the question, "What is the total unidirectional influence of i upon j?" as, "What happens if i is prevented from influencing j?" In general the output of i can

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* Throughout this paper superscripts T and T′ denote corresponding total flow and coefficient matrices. They do not denote matrix transposition.

indirectly flow to j via any of the other compartments of the system. Hence, to prevent i from influencing j it becomes necessary to decouple j from *all* its intramural inputs. That is, one imagines that all the internal inputs to j come instead from outside the system. Operationally, this is equivalent to zeroing all the elements in the jth column of the matrix A. Call the resultant matrix A_j.

A structure matrix corresponding to altered configuration can be calculated as:

$$D_j = (I - A_j)^{-1} \tag{9}$$

and a corresponding vector of total outputs as:

$$X_j = D_j Y \tag{10}$$

Now that i does not have to support (or influence) j, the ith element of X_j is always smaller than or equal to the corresponding element of X. The vector difference, $X - X_j$, represents the amounts of each output which go to sustain the output of j. Hence, the matrix of total flows, Z^T, has the difference vector, $X - X_j$, in column j.

This outline of how to calculate Z^T was helpful in expositing the origin and nature of total flows. However, the algorithm is computationally cumbersome and requires the inversion of n separate matrices. Equation (8), by comparison, requires only one inversion. It turns out (Szyrmer, 1984) that the elements of Z^T can be calculated directly from the elements of D according to the formula:

$$z_{ij}^T = \left[(d_{ij} - \delta_{ij})/d_{jj} \right] x_j \tag{11}$$

where δ_{ij} are the elements of the identity matrix (which $= 0$ for $i \neq j$ and $= 1$ for $i = j$).

Finally, it should be mentioned that total flows could likewise have been derived using the intramural flows and exogenous inputs (the Augustinovics (1970) approach). Szyrmer (1984) shows that the consequent total flow matrix, $Z^{T'}$, is not in general equal to Z^T. The difference may be ascribed to the influence of cycling. (See Section 4)

3. THE UTILITY OF TOTAL FLOWS

At this point it is fair to ask, "If the total flows are implicit in the calculation of the gross flows, why go to the trouble of defining them?" In short, the answer is that properties of the network are more closely related to the total flows than they are to either the direct flows or the gross flows. Which is to say that the structure of input–output analysis appears more

nearly canonical when built around total flows than when centered on the Leontief inverse. Total flows also allow for a more natural ranking of the ecological importance of each component in the system.

A major advantage of total flows is that they more clearly define the role of cycling in the network. Using rather complicated calculations based on the Leontief inverse, Finn (1976) was able to compute the aggregate amount of total throughput which was being cycled. However, the very same index appears explicity as a weighted average of the diagonal elements of the total flow matrix.

Trophic analysis is traditionally based on the distance of a given compartment from the primary inputs (Levine, 1980). It might be inferred that the trophic distance between two compartments is measured by the difference in their respective trophic measures, but the trophic metric does not behave in such a way. One may use total flow to assess the bilateral trophic relationship between any two compartments.

Total flows are also of considerable help in defining measures of complexity (Szyrmer, 1986) and identifying optimal network reallocations (in preparation).

4. AN EXAMPLE OF TOTAL FLOWS

A convenient example with which to demonstrate the calculation of total flows is the Cone Spring ecosystem (Tilly, 1968) as adapted for IOA by Williams and Crouthamel (1972). Cone Spring is a cold, shallow spring-fed brook located near Conesville, Iowa. It is small in areal extent (141 m^2) with well-defined boundaries, relatively homogeneous spatial structure, nearly constant temperature and a stable physical and chemical environment.

Tilly argued that the analysis of populations, tedious and cumbersome as it is, would have been too detailed; whereas limiting the study to a trophic chain would have deleted some important information. Therefore, the ecosystem is aggregated into five 'food-web segments' (see Fig. 1) as follows:

(1) *Autotrophic plants*—consisting mainly of three species which interact while sharing the biotope in space and time.

(1) *Detritus*—nonliving organic material which forms the base of the foodweb in Cone Spring. It serves as substrate for the bacteria and food for the detritus feeders.

(3) *Bacteria*—playing the dual role of primary consumers and decomposers.

(4) *Detritus feeders*—mainly invertebrates which consume the detritus–bacteria amalgam.

(5) *Carnivores*—The highest trophic compartment in this system preying upon the detritus feeders. Through excretion and death they contribute to the detrital compartment.
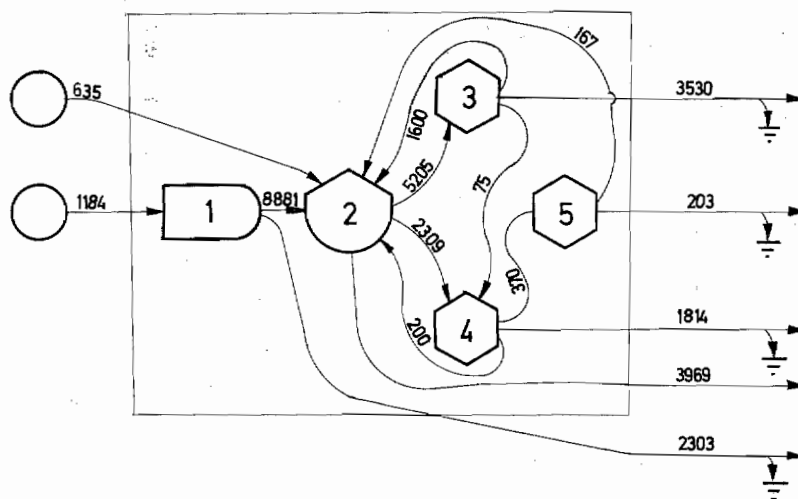
Fig. 1. Energy flow in Cone Spring ecosystem, measured in kcal m^{-2} year^{-1}. 1 = autotrophs, 2 = detritus, 3 = bacteria, 4 = detritus feeders, 5 = carnivores. Ground symbols represent losses to respiration.

The estimated flows (in kcal m^{-2} year^{-1}) among the compartments comprise the elements of the Z matrix and appear in Table 1 along with the vector of final outputs, Y (respiration and export) and the vector of exogenous inputs, W. These are the fundamental data from which all other quantities may be calculated—namely X (from (1), A from (2), D from (5) Z^G from (8), and finally Z^T from (11).

The gross flows, Z^G, are displayed in Table 2. Of course, each element in this matrix is equal to or greater than the corresponding direct flow. Hence, 80% of the overall flow from detritus to detritus feeders (2–4) is direct, whereas only 16% of the gross flow from bacteria to carnivores occurs in a single step, and none of the considerable flow from plants to detritus feeders is an immediate transfer.

The matrix of total flows, Z^T, contains elements which are intermediate to the direct flows and the gross flows (see Table 3). That these values of Z^T lie closer to Z^G than to Z is a reflection of the relatively small degree of cycling in the Cone Spring network (some 16% of total throughput appears as cycling).

The total flows calculated using the input approach, $Z^{T'}$, are shown in Table 4. As mentioned earlier, the difference between Z^T and $Z^{T'}$ is

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1 kcal m^{-2} year^{-1} = 4.1868 kJ m^{-2} year^{-1} ≈ 133 × 10^{-6} J m^{-2} s^{-1} = 133 × 10^{-6} W m^{-2}.

TABLE 1

Cone Spring ecosystem: matrix of direct flows, Z, the final output vector, Y, and the vector of exogenous inputs, W (kcal m^{-2} year^{-1})

	Autotrophic plants (1)	Detritus (2)	Bacteria (3)	Detritus Feeders (4)	Carnivores (5)	Final output
Autotrophic plants (1)	0	8881	0	0	0	2303
Detritus (2)	0	0	5205	2309	0	3969
Bacteria (3)	0	1600	0	75	0	3530
Detritus feeders (4)	0	200	0	0	370	1814
Carnivores (5)	0	167	0	0	0	203
Exogenous inputs	11184	635	0	0	0	

attributable to the presence of cycling in the system (Z^T and $Z^{T'}$ being identical in the absence of cycling). For example, from the output perspective 8881 units of flow issuing from the plants eventually (directly in this

TABLE 2

Matrix of gross flows, Z^G (kcal m^{-2} year^{-1})

	Autotrophic plants (1)	Detritus (2)	Bacteria (3)	Detritus feeders (4)	Carnivores (5)
Autotrophic plants (1)	0	10717.08	4857.98	2225.06	345.33
Detritus (2)	0	2373.53	6280.87	2876.77	446.48
Bacteria (3)	0	1945.22	881.73	478.71	74.30
Detritus feeders (4)	0	443.24	200.91	92.02	484.18
Carnivores (5)	0	200.95	91.09	41.72	6.48

TABLE 3

Matrix of total flows, Z^T (kcal m^{-2} year^{-1})

	Autotrophic plants (1)	Detritus (2)	Bacteria (3)	Detritus feeders (4)	Carnivores (5)
Autotrophic plants (1)	0	8881.00	4154.16	2142.30	339.35
Detritus (2)	0	1967.00	5371.27	2769.96	438.78
Bacteria (3)	0	1611.35	753.81	460.96	73.02
Detritus feeders (4)	0	367.00	171.67	88.53	377.64
Carnivores (5)	0	167.00	78.12	40.28	6.38

case) reach the detritus. The perspective from the receiver (input) side is different in that, of all the inputs to the detritus, 10 717 units can be traced back to the plants. The difference arises from the cycling which passes through the other three compartments.

The total flow matrix explicitly shows the ultimate exchanges between any two components. When normalized by the appropriate total throughputs the

TABLE 4

Matrix of total flows from input perspective, $Z^{T'}$ (kcal m^{-2} year^{-1})

	Autotrophic plants (1)	Detritus (2)	Bacteria (3)	Detritus feeders (4)	Carnivores (5)
Autotrophic plants (1)	0	10716.74	4857.67	2224.92	345.31
Detritus (2)	0	1967.00	5205.00	2384.00	370.00
Bacteria (3)	0	1663.02	753.81	409.40	63.54
Detritus feeders (4)	0	426.42	193.28	88.53	370.00
Carnivores (5)	0	198.04	89.77	41.12	6.38

TABLE 5

Total intermediate input coefficients, A^{T}

	Autotrophic plants (1)	Detritus (2)	Bacteria (3)	Detritus feeders (4)	Carnivores (5)
Autotrophic plants (1)	0	0.933	0.933	0.933	0.933
Detritus (2)	0	0.171	1.000	1.000	1.000
Bacteria (3)	0	0.145	0.145	0.172	0.172
Detritus feeders (4)	0	0.037	0.037	0.037	1.000
Carnivores (5)	0	0.017	0.017	0.017	0.017

resulting fractions measure the bilateral interdependencies. For example, when the columns of the total flow matrix, $Z^{\mathrm{T}'}$, are normalized by the total throughputs,

$$Z^{\mathrm{T}'} = A^{\mathrm{T}}\hat{X} \qquad (12)$$

the i-jth component of the resulting matrix of total intermediate inputs, A^{T}, represents the fraction of the jth input that comes directly or indirectly from i. In similar manner, when the rows of Z^{T} are normalized,

$$Z^{\mathrm{T}} = \hat{X}B^{\mathrm{T}} \qquad (13)$$

the $i-j$th entry in the total intermediate output matrix, B^{T}, represents the fraction of the ith output that eventually reaches j. The values of A^{T} and B^{T} for Cone Spring are shown in Tables 5 and 6, respectively.

Table 4 shows that, for example, the detritus (2) and the detritus feeders (4) are mutually interdependent. However, the relationship is rather skewed. The detritus feeders are entirely dependent upon the detritus ($a_{24}^{\mathrm{T}} = 1.0$), whereas less than 4% of the detritus originates with the detritus feeders. Donorship between these two species is more nearly equitable, as can be seen from Table 5. Some 24% of the detritus is ultimately processed by the detritus feeders, and about 15% of the detritus feeder production winds up in the detrital pool.

In complementary fashion $(1-a_{ij}^{\mathrm{T}})$ and $(1 - b_{ij}^{\mathrm{T}})$ provide the degrees to which i is independent of j with respect to inputs and outputs, respectively. For example, the carnivores possess no independence from the detritus or the detritus feeders.

TABLE 6

Total intermediate output coefficients, B^T

	Autotrophic plants (1)	Detritus (2)	Bacteria (3)	Detritus feeders (4)	Carnivores (5)
Autotrophic plants (1)	0	0.794	0.371	0.192	0.030
Detritus (2)	0	0.171	0.468	0.241	0.038
Bacteria (3)	0	0.310	0.145	0.089	0.014
Detritus feeders (4)	0	0.154	0.072	0.037	0.158
Carnivores (5)	0	0.451	0.211	0.109	0.017

Shifting towards a more system-wide perspective, the question naturally arises as to how to rank the contributions of each compartment towards the total activity of the system, i.e., which are the key compartments? In IOA, where exogenous supplies and demands captivate the attention of most economists, the marginal sums of the Leontief and Augustinovics inverses provide ready yardsticks of importance. However, in keeping with the theme emphasized here that intramural activity is the natural focus of ecology, the marginal sums of Z^T and $Z^{T'}$ become more appropriate indicators of the size of the role each compartment plays in the total activity of the community. It should also be noted that the method by which these matrices could be calculated is reminiscent of a perturbation or sensitivity analysis, thereby making the total flows even more pertinent to the identification of key elements.

In particular, the column sums of Z^T can be used to measure the contributions of the outputs of the various nodes to the total system activity. Summing the columns of Z^T in Table 3, one finds that the largest total intermediate output derives from the detritus (12 994 kcal m^{-2} year^{-1}, or about 42% of the total output). This dominance of the detritus accords with the ecologist's description of Cone Spring as having a "detrital-based ecosystem". It contrasts, however, with the results one would obtain by relying on the corresponding Leontief analysis, which identifies bacteria as ultimately contributing the greatest amount to total output (39%, as compared to 31% from the detritus). This switch in designation of key compartment is due entirely to the change in perspective afforded by total flow

TABLE 7

Ratios of total production : total consumption, τ_{ij}

	Autotrophic plants (1)	Detritus (2)	Bacteria (3)	Detritus feeders (4)	Carnivores (5)
Autotrophic plants (1)	0	0	0	0	0
Detritus (2)	0	1.00	3.23	6.50	2.22
Bacteria (3)	0	0.31	1.00	2.39	0.81
Detritus feeders (4)	0	0.15	0.42	1.00	9.21
Carnivores (5)	0	0.45	1.23	0.11	1.00

analysis. The Leontief calculus gauges the importance of the elements in terms of their contributions to the final outputs (at which the bacteria visibly excel), whereas the analysis introduced here evaluates the influence of each compartment to the overall activity of the community (which is clearly characterized by the cycling of detritus).

Knowing the entire picture of flow sources and destinations within a system allows one to make definitive statements about trophic relationships *within* the flow network. The trophic relationship of i to j depends on the ratio of the amount of flow leaving i which flows to j to the amount leaving j that ultimately serves as input to i. Quantitatively, an index τ_{ij} may be defined as,

$$\tau_{ij} = z_{ij}^{T}/z_{ji}^{T'} \tag{14}$$

The values of τ_{ij} for Cone Spring are shown in Table 7. As can be seen $\tau_{ij} = 1/\tau_{ji}$, which indicates mutual reciprocity of the trophic relationship. (If i is a net supplier for j, then j must be a net consumer of i.)

Several interesting relationships appear from Table 7. When Levine's trophic positions are calculated for the elements of the Cone Spring network the values for bacteria, detritivores and carnivores are 3.37, 3.40 and 4.40, respectively. Whereas bacteria and detritivores are seen to be nearly equidistant from the primary inputs, it is clear from the τ_{ij} that the detritivores dominate the bilateral exchange. What is perhaps more suprising is that the bacteria dominate their trophic exchanges with the carnivores ($\tau_{53} > \tau_{35}$). In fact, one observes a cyclical pattern of dominance, bacteria > carnivores >

detritivores > bacteria. Ulanowicz (1983) has suggested that closed cycles of direct flows are indicative of cybernetic feedback. It is interesting to note that the cycle just enumerated does not exist at the level of direct flows. If, as Higashi and Patten (1986) argue, the indirect flows can at times dominate the direct interactions, then the cycles of trophic dominance obtained from total flows may be more appropriate indicators of cybernetic behavior.

In any event, the total amount of flow being cycled within the system has been proposed as an index of cybernetic feedback (Odum, 1969). Finn (1976) showed how one may use the Leontief inverse to calculate the fraction of total throughput which occurs as cycled flow. The cycling flows are related in nonlinear fashion to the diagonals of the Leontief inverse. In total flow analysis this relationship becomes an identity, that is, the amount of flow being recycled is precisely the sum of the diagonals of the Z^T matrix! To obtain the Finn cycling index one simply normalizes this sum by the total system throughput.

5. SUMMARY AND CONCLUSIONS

Input–output analysis has been fashioned by economists to answer questions about indrect effects of initial supplies or final demands upon sectors of the economy. Until now the mathematical framework of IOA has been borrowed intact by ecologists to study indirect effect in ecosystems. However, the kinds of questions ecologists ask about living communities bear more upon the intramural relationships which species or other ecosystem components have one another. Using the formulations of Leontief and Augustinovics to treat indirect flows between components is mathematically (and ofttimes conceptually) cumbersome.

The actual amounts of direct and indirect flows between compartments may be portrayed explicitly as the components of a matrix of total flows. Any question pertaining to the bilateral indirect relationship between two components is best addressed using this matrix. Key ecosystem elements are more naturally defined by the total flows. Furthermore, cybernetic relationships (e.g., cycles of flows and flow dominance involving more than two compartments) are more directly demonstrated by the structure of the total flow matrix.

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