



Theory of materials and energy flow analysis in ecology and economics

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Abstract

Materials and energy flow analysis (MEFA) has been widely utilized in ecology and economics, occupying unique positions in both disciplines. The various approaches to materials and energy flow analysis in ecology are reviewed, the focus being on the linear network system introduced from input–output economics. After its introduction in the early 1970s, the calculus and system definition for materials and energy flow analysis have been diversified, causing problems in comparing the results of different studies. This paper uses a materials and energy flow analysis framework that is a generalization of the major approaches in ecology and economics to illuminate the differences and similarities between the approaches on the basis of a set of consistent principles. The analysis often shows that seemingly different calculus and interpretations employed by different approaches eventually lead to the same outcome. Some issues of interpretations that conflict or require cautious interpretation are further elaborated. A numerical example is presented to test the generalized framework, applying major analytical tools developed by other approaches. Finally, some parallels, convergents, and divergents of the perspectives of ecology and economics and their implications for endogenized resources economy are discussed as they are reflected in the materials and energy flow analysis frameworks.

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1. Introduction

Since Lotka (1925) and Lindeman (1942), materials and energy flows have been among the central issues in ecology (Lindeman, 1942; Lotka, 1925). Energy

flows in ecological systems have often been presented in the form of so-called Lindeman spines, which illustrate uptake, utilization, and dissipation of energy in a chain-like diagram. A more comprehensive representation of energy flows based on a network structure rather than a chain was introduced in the 1970s (Heal and MacLean, 1975). It was Hannon (1973) who first introduced the use of a system of linear equations,

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taken from input–output economics, to analyze the structure of energy utilization in an ecosystem (Hannon, 1973). Using an input–output framework, the complex interactions between trophic levels or ecosystem compartments can be modeled, taking all direct and indirect relationships between components into account.

Shortly after its introduction, Hannon's approach was adopted by various ecologists. Finn (1976, 1977) developed a set of analytical measures to characterize the structure of an ecosystem using a rather extensive reformulation of the approach proposed by Hannon (1973) successfully demonstrating how some key properties of a complex network system could be extracted (Finn, 1976, 1977). Finn's cycling index (FCI), for instance, is still one of the most frequently applied indicators in ecological network analyses. The contributions by Finn (1976, 1977) have led the materials and energy flow analysis framework to be more widely utilized in general ecological applications (Baird et al., 1991; Baird and Ulanowicz, 1989; Heymans and Baird, 1995; Heymans and Baird, 2000a,b; Heymans and McLachlan, 1996; Loreau, 1998; Szyrmer and Ulanowicz, 1987; Vasconcellos et al., 1997). For instance, Baird et al. (1991) evaluated E.P. Odum's definition of ecosystem maturity using FCI. The analysis of six marine ecosystems by Baird et al. (1991) showed that FCI and system maturity were inversely correlated. The result was generally confirmed by Vasconcellos et al. (1997) on 18 marine trophic models.

Another important development in the materials and energy flow analysis tradition in ecology is *environ* analysis. Patten (1982) proposed the term *environ* to refer to the relative interdependency between ecosystem components in terms of nutrient or energy flows. Results of *environ* analysis are generally presented as a comprehensive network flow diagram, which shows the relative magnitudes of materials or energy flows between the ecosystem components through direct and indirect relationships (Levine, 1980; Patten, 1982; Patten et al., 1990).

R.E. Ulanowicz and colleagues have broadened the value of materials and energy flow analysis both theoretically and empirically. A comprehensive study on Chesapeake Bay by Baird and Ulanowicz (1989) found that the extended diets of bluefish and striped bass they calculated showed considerable differences, although, as both are pelagic piscivores, the differences in their

direct diets are not apparent. The finding helped to explain why the concentration of the pesticide Kepone detected in the flesh of bluefish was much higher than that in striped bass. The methodology used in Baird and Ulanowicz (1989) is based on, for instance, Szyrmer and Ulanowicz (1987).

Finally, a number of researchers have contributed to further enriching and broaden the materials and energy flow analysis in ecology. Higashi (1986a) and Han (1997a) concerned the residence time of materials in ecological systems, and Higashi (1986b) and Han (1997b) further extended the ecological network analysis. Savenkoff et al. (2001) and Allesina and Bondavalli (2003) developed procedures for balancing input–output network data.

These important developments in the materials and energy analysis tradition in ecology were rather isolated from major developments in network analysis in economics, notably Input–Output Analysis (IOA). Szyrmer and Ulanowicz (1987) wrote:

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

An economist perhaps could have made a similar statement. Because of the lack of interaction with input–output economics and the different needs of ecologists, the materials and energy flow analysis tradition in ecology has followed its own path, resulting in considerable differences in its appearance from that used in economics. Furthermore, the system definitions and calculi used by different studies are surprisingly different from each other, hampering a fruitful communication among ecologists themselves.

The present paper reviews the tradition of materials and energy flow analysis (MEFA) in ecology focussing on the input–output formulation of ecological network analysis (ENA). The existing approaches are analyzed and compared by means of a MEFA framework that represents a generalization of the major approaches. The analysis presented here may be used as a point of departure in facilitating a common language and dialogue between and among the network flow analysts in ecology and economics.

In this paper, bold characters represent matrices (upper case) and vectors (lower case), while lower case italics are used for scalars and elements of the corre-

sponding matrix or vector (with subscripts). Prime (′) denotes transpose of matrices or vectors. Hat (^) diagonalizes vectors. Italics of i, j , and m are used as indices for ecosystem components and k for energy or nutrient inputs from outside the system.

2. The tradition of materials and energy flow analysis in ecology

The calculi and the system definitions of major MEFA approaches in ecology are summarized below, emphasizing their similarities and differences.

2.1. Hannon (1973)

The system that Hannon (1973) concerns is a freshwater ecosystem at an aggregated level. Let p_{ij} be the amount of energy consumed by j feeding on i for a given period.¹ Note that the flow is oriented from i to j (in later matrices this will become from row elements to column elements), and that p_{ij} includes not only the energy flow within the ecosystem components but also primary energy flows from outside the ecosystem. The net system loss of energy is called respiration in Hannon (1973) and denoted by r .² The total production of energy e is calculated by

$$e_i = \sum_j p_{ij} + r_i, \quad (1)$$

where the total production of energy by i equals the total consumption by ecosystem components plus the net energy loss by the system. Let g_{ij} be the amount of energy consumed by the ecosystem component j feeding on i per unit production of energy by j , such that $p_{ij} = g_{ij}e_j$. Note here that the concept that Hannon (1973) describes is fully output-referenced one, just

like economic IOA. By substituting p_{ij} in Eq. (1) we obtain

$$e_i = \sum_j g_{ij}e_j + r_i, \quad (2)$$

Using matrix formalism, Eq. (2) is written as

$$\mathbf{e} = \mathbf{G}\mathbf{e} + \mathbf{r}, \quad (3)$$

and is solved for \mathbf{e} by

$$\mathbf{e} = (\mathbf{I} - \mathbf{G})^{-1}\mathbf{r}, \quad (4)$$

where \mathbf{I} refers to an identity matrix with relevant dimension. Eq. (4) can be used to calculate the amount of production by each ecosystem component required to produce a given amount of net system output. With the diagonalized respiration vector $\hat{\mathbf{r}}$, the same equation generates the energy flow matrix, showing the direct and indirect energy flows between ecosystem components and primary energy sources for a given net system output.

It should be noted that, strictly speaking, the above exposition of MEFA calculus by Hannon (1973) differs from those used most commonly in input–output analysis. Hannon (1973) included primary energy inputs such as solar energy as part of the intermediate part of the system. In input–output economics, this corresponds to including the production and consumption of “labor” within the intermediate part of the system. Such a treatment, called “closure toward primary input”, was not unknown to economists but was not a common practice either. Except for the fact that the primary inputs are endogenized in the system, the approach by Hannon (1973) so far generally conforms to those used in input–output economics.³

What is very peculiar in Hannon (1973) but has not been fully acknowledged by his followers is the following:

Multiplying each component’s coefficients by the direct energy flow from that component [...] reveals the relative dependence of each component on the two energy sources.

Hannon (1973) does not provide a mathematical notation for the operation quoted above, but presents the

¹ Section 2 uses the original notation used in the studies referred to, as long as they do not conflict with each other, for the convenience of tracing back the original references. A new set of notations is introduced in Section 3; the relations between them and the notations used by the studies referred to in Section 2 are shown in Table 2.

² Energy is lost by an ecosystem component via respiration, export, and changes in stock. Hannon (1973) referred to these three mechanisms of net system loss of energy collectively as “respiration” (Hannon, 1973, p. 538).

³ It is notable that Hannon no longer endogenizes primary energy inputs in his later contributions.

result in a table. Using matrix notation, the description in Hannon (1973) can be rewritten as

$$\mathbf{\Pi} = (\mathbf{I} - \mathbf{G})^{-1}\hat{\mathbf{e}}, \tag{5}$$

if we limit ourselves to the part involving primary energy sources.⁴ Obviously, post-multiplication of the total production value (\mathbf{e}) to the Leontief inverse is not a common practice in input–output economics. In Hannon (1973), the resulting matrix $\mathbf{\Pi}$ is interpreted as *the distribution of primary energy inputs over ecosystem components*. This issue will be further elaborated in another part of this paper.

2.2. Finn (1976,1977) and Patten et al. (1976)

The MEFA framework proposed by Hannon (1973) was adapted by Finn (1976, 1977) with substantial reformulation. The method proposed by Finn (1976, 1977) uses large concatenated matrices and introduces various new terms. The approach in Finn (1977) explicitly incorporates changes in stock, relaxing the steady-state condition generally imposed in a network system. Furthermore, the direction of flows represented in the matrices proposed by Finn (1976, 1977) is the opposite of that in Hannon (1973). Let \mathbf{P} describe the energy or materials flows within an ecosystem and between the ecosystem and its environment

$$\mathbf{P} = \begin{bmatrix} \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{P}_{21} & \mathbf{P}_{22} & \mathbf{0} \\ \mathbf{0} & \mathbf{P}_{32} & \mathbf{0} \end{bmatrix}, \tag{6}$$

where \mathbf{P}_{21} describes the flows to the system from the environment, \mathbf{P}_{22} those within the system, and \mathbf{P}_{32} those from the system to the environment and the changes in stock.⁵ Detailed descriptions of all submatrices can be found in Appendix A. The elements in \mathbf{P} are divided by its non-zero row sum, and the result is denoted by \mathbf{Q}^* .

$$\mathbf{Q}^* = \begin{bmatrix} \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{Q}_{21}^* & \mathbf{Q}_{22}^* & \mathbf{0} \\ \mathbf{0} & \mathbf{Q}_{32}^* & \mathbf{0} \end{bmatrix}. \tag{7}$$

⁴ Table 5 in Hannon (1973).

⁵ In the original formulation by Finn (1976, 1977), the term *changes in stock* is divided into two, negative and positive, and distributed into \mathbf{P}_{21} and \mathbf{P}_{32} , respectively. For the sake of simplicity, they have here been reduced to one term by varying signs.

Matrix \mathbf{Q}^* is further inverted to form $\mathbf{N}^* = (\mathbf{I} - \mathbf{Q}^*)^{-1}$.

$$\mathbf{N}^* = \begin{bmatrix} \mathbf{I} & \mathbf{0} & \mathbf{0} \\ \mathbf{N}_{21}^* & \mathbf{N}_{22}^* & \mathbf{0} \\ \mathbf{N}_{31}^* & \mathbf{N}_{32}^* & \mathbf{I} \end{bmatrix} \tag{8}$$

Finn (1977) used the term *Transitive Closure Inflow matrix* for \mathbf{N}^* . The meaning of the elements in \mathbf{N}^* is rather difficult to see from Eq. (8). Patten et al. (1976) interpret \mathbf{N}_{22}^* as the total production by ecosystem components necessary for the system net output, which is equivalent to the part in $(\mathbf{I} - \mathbf{G})^{-1}$ that represents exchanges within ecosystem components. The famous Finn’s cycling index (FCI) appears in the diagonal of \mathbf{N}_{22}^* . Finn (1977) called this type of analysis *creaon* flow analysis.

Finn (1977) also proposed another approach, called *genon* flow analysis. According to Finn (1977), genon flow analysis shows the structure of the distribution of primary inputs over ecosystem components and net system output. Recall the quotation from Hannon (1973) and Eq. (5), which proposes the same analysis. However, the procedure proposed by Finn (1976, 1977) is completely different from that of Hannon (1973). Finn divided the elements in \mathbf{P} by its column sum instead of its row sum, which results in \mathbf{Q}^{**} , and then proceeded to the inversion, $\mathbf{N}^{**} = (\mathbf{I} - \mathbf{Q}^{**})^{-1}$.⁶

$$\mathbf{N}^{**} = \begin{bmatrix} \mathbf{I} & \mathbf{0} & \mathbf{0} \\ \mathbf{N}_{21}^{**} & \mathbf{N}_{22}^{**} & \mathbf{0} \\ \mathbf{N}_{31}^{**} & \mathbf{N}_{32}^{**} & \mathbf{I} \end{bmatrix} \tag{9}$$

Matrix \mathbf{N}^{**} is called the *Transitive Closure Outflow matrix*. According to Patten et al. (1976), the i - j th element of \mathbf{N}_{22}^{**} shows the amount of i produced by a unit flow originating from j . The element, the i - j th element of \mathbf{N}_{32}^{**} , is the amount of system net output or stock change of i enabled by a unit flow from j (see also Bailey et al., 2004a, 2004b).

A number of questions arise. First, the calculus used by Finn (1976, 1977) for genon analysis is very different from that used by Hannon (1973), although both seem to share the same goal of revealing the structure of

⁶ In Hannon (1973), the coefficient matrix \mathbf{G} is prepared by $g_{ij} = p_{ij}/e_j$ but the operation used for the preparation of \mathbf{Q}^{**} by Finn (1976, 1977), which is equivalent to $g_{ij} = p_{ij}/e_i$ in Hannon’s system, does not even appear.

materials or energy distribution. Second, the interpretation of the submatrices in \mathbf{N}^{**} by Patten et al. (1976) is not exactly about the distribution of inputs, which is supposed to be the intention (recall the interpretation of \mathbf{N}_{22}^{**} by Patten et al. (1976)). Has either Hannon (1973) or Finn (1976, 1977) failed to achieve what was intended? Or is the interpretation by Patten et al. (1976) misleading? Obviously, the answers to both questions cannot be negative at the same time. This issue will be elaborated later in this paper.

2.3. Szyrmer and Ulanowicz (1987)

Szyrmer and Ulanowicz (1987) separated primary inputs and system net outputs from the exchanges between ecosystem components. Consider a system

$$\mathbf{x} = \mathbf{Ax} + \mathbf{y}, \tag{10}$$

where x_i denotes the total production (either materials or energy) by ecosystem component i , a_{ij} the direct input from i used to produce one unit of output by j , and y_i the amount of i that leaves the system to environment. The equation is then solved for \mathbf{x} by

$$\mathbf{x} = (\mathbf{I} - \mathbf{A})^{-1}\mathbf{y}, \tag{11}$$

which is a standard form in input–output economics. Szyrmer and Ulanowicz (1987) then rightly point out the difference in perspective between economics and ecology by saying that

Economists are primarily interested in what leaves a system — the final outputs or demands. However, final outputs are relatively less interesting to ecologists [. . .]. [. . .] the ecologist is more interested in the total effect which the output from i has on the total output of j .

The above quoted part leads to a new measure *gross flow*. According to Szyrmer and Ulanowicz (1987), the gross flow from i to j is estimated by “scaling up” the final output \mathbf{y} in (11) to the total production \mathbf{x} such that

$$\mathbf{Z}^G = (\mathbf{D} - \mathbf{I})\hat{\mathbf{x}}, \tag{12}$$

where \mathbf{D} refers to $(\mathbf{I} - \mathbf{A})^{-1}$ in (11) (cf. Eq. (5)). Szyrmer and Ulanowicz (1987) also proposed another measure called *total flows*. According to them, the question in the total flow is “What happens if i is prevented from influencing j ?”. They found that this ques-

tion can be answered by the equation

$$z_{ij}^T = \left[\frac{d_{ij} - \delta_{ij}}{d_{ij}} \right] x_j, \tag{13}$$

where d_{ij} are the corresponding elements in \mathbf{D} , δ_{ij} the elements of the identity matrix, and x_j the total production of j . Szyrmer and Ulanowicz (1987) argued that the network properties are more closely related to the total flow than other input–output measures and further that the structure of input–output analysis appears more “nearly canonical” when built around total flows than the Leontief inverse.

2.4. Patten (1982)

The most comprehensive analysis of the interrelationships between ecosystem components in the MEFA framework might be environ analysis (for a comprehensive review, see Fath and Patten, 1999). Environ analysis reveals the relative interdependencies between ecosystem components with regard to materials and energy flows. Input environ analysis shows the relative materials or energy requirements by components per unit of net system output. Output environ analysis concerns the relative materials and energy distribution per unit of primary input.

The rather complex accounting structure by Finn (1976) exhibits analytical power when it comes to the environ analysis. The input environ analysis and the output environ analysis are carried out in one step for each net system output m or primary inputs k by

$$\mathbf{E}^{A,m} = \hat{\mathbf{N}}_m^* \mathbf{Q}^*, \tag{14}$$

and

$$\mathbf{E}^{\Omega,k} = \hat{\mathbf{N}}_k^{**} \mathbf{Q}^{**}, \tag{15}$$

respectively. Matrix $\hat{\mathbf{N}}_m^*$ is a diagonalized m th row in matrix \mathbf{N}^* , where m is an index for system net outputs, and matrix $\hat{\mathbf{N}}_k^{**}$ is a diagonalized k th column in matrix \mathbf{N}^{**} , where k is an index for primary inputs. The i - j th element of $\mathbf{E}^{A,m}$ represents the amount of materials or energy flow from j to i that is required to produce one unit of net system output from m . Likewise the i - j th element of $\mathbf{E}^{\Omega,k}$ concerns the amount of energy or materials flow from j to i that is enabled by one unit of primary input from k .

Table 1
Comparison between system definitions of MEFA approaches

	Physical input–output analysis	Hannon (1973)	Finn (1977), Patten (1982)	Szyrmer and Ulanowicz (1987)
Flows within structural matrix	Inter-industry exchanges	Inter-ecosystem component exchanges, primary energy inputs	Inter-ecosystem component exchanges, primary energy inputs, changes in stocks, exports	Inter-ecosystem component exchanges
Flows outside the structural matrix	Final demand, primary resource inputs, wastes	Exports, changes in stock, respiration	–	Exports, respiration,
Multiple primary inputs	Generally no	Yes	No	No
Stock changes	Explicit	Implicit	Explicit	No
Bi-directional analysis	No	No	Yes	No

3. A generalized framework for materials and energy flow analysis

In the development of MEFA approaches in ecology, little attention has so far been paid to horizontal integration and comparison between studies. Except for a few well-known indicators such as FCI, different studies often employ different sets of indicators, hampering communications and comparisons between results. The differences in system definitions are another source of difficulties in comparing and understanding the approaches (Table 1). In input–output economics, statistical bureaus have started to produce physical input–output tables (PIOTs) in recent decades, providing another basis for the MEFA approach to economic systems (Kratena et al., 1992; Kratterl and Kratena, 1990; Pedersen, 1999; Stahmer et al., 2003; Suh, 2004).

In this section, I introduce a generalized framework for MEFA that embraces existing approaches in both ecology and economics. The generalized MEFA framework is then used to illuminate the relationships between and within the existing approaches.

Fig. 1 shows a flow diagram of a generalized system. Each flow in the system that is denoted by an arrow may represent either a materials or an energy flow. The term used for each flow varies depending on the type of flow. For instance, r would be best referred to as “respiration” in an energy flow model, whereas “residues” or “wastes” would be used in a nutrients or materials flow model in both ecological and economic applications. The flow w denotes primary inputs from outside the system, such as solar energy or net nutrient inflows and

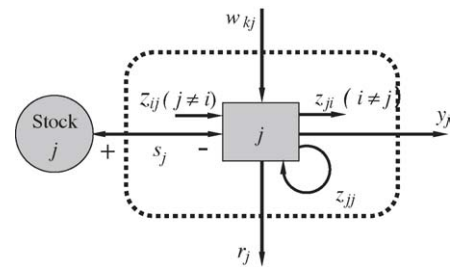


Fig. 1. A flow diagram of a generalized input–output system. w_{kj} : primary input from k to j ; Z_{ij} ($i \neq j$): flow from i to j ; z_{ji} ($i \neq j$): flow from j to i ; z_{jj} : flow from j to j ; r_j : waste (dissipative) flow to outside the system from j ; y_j : usable (non-dissipative) flow to outside the system from j ; s_j stock change ($s_j > 0$ increase in stock, $s_j < 0$ decrease in stock).

resource extraction. Similarly, y refers to outputs like fishing catches, the amount harvested or final demand, z to the materials or energy flows between the ecosystem components or industries, and s to the changes in stock size, which can be positive, negative, or zero.⁷ The broken line represents the overall system boundary. Note that treating the stock reserves as an exogenous component implies a relaxation of the steady-state condition required to satisfy mass and energy balances at all lev-

⁷ In input–output economics, the flows w , y , Z , and s are generally referred to as primary inputs, final demand, intermediate inputs and inventory adjustments, respectively. By differentiating its sign, the term s can represent both increase and decrease in stock using only one term. It should be noted that stock changes take place within the system but they are noted here as if they take place outside the system. Such a treatment, which is commonly used in economic IOA, is made rather for computational convenience and balancing purposes, and when modelling steady-state system they should be set to zeros.

From	To	Ecosystem component	Waste or respiration	Catch or export	Stock change	sum
Ecosystem component		Z	r	y	s	x
Exogenous input		W				
Sum		x'				

Fig. 2. Basic accounting framework for generalized input–output system.

els of the system. Such a treatment is widely used in economic IOA in treating inventory changes.

However, as a general description of the system used in both economics and ecology, the generalized MEFA framework can be adapted differently for deferent applications. For instance, the stock change can be set to 0 for steady-state modelling, and the system boundary can be defined in such a way that it distinguishes between the system and its environment.

The generalized MEFA framework is based on the duality of input-side balance and output-side balance. At the overall system level, the total inputs to the system equal the total outputs from the system:

$$\sum_{i,j} w_{ij} + \sum_j s_j = \sum_j (r_j + y_j). \tag{16}$$

The system is in a steady-state condition when $s_j = 0$ for all j . The same input–output balance holds at component level, such that

$$\sum_i (z_{ij} + w_{ij}) = \sum_j z_{ji} + s_j + r_j + y_j. \tag{17}$$

Eq. (17) says that the total input to an ecosystem component equals the total output plus change in stock. In a balanced accounting framework, the left-hand side (LHS) and the right-hand side (RHS) of (17) are simply the column sum and row sum, respectively, of the table shown in Fig. 2.

The generality of the system definition presented above allows a more flexible system boundary definition. The broken line in Fig. 1 may be further extended to internalize cross-boundary flows such as w , r or y , while Eqs. (16) and (17), and the system definition above, still hold. For instance, closing the system toward primary inputs can be achieved by treating the materials or energy sources such as bread fed or solar energy as one of the ecosystem components (see e.g. Hannon, 1973 and Suh, 2004). This means that w

becomes zero and the dimension of \mathbf{Z} is augmented accordingly.

Similarly, the system can be closed toward the outputs, y and r by treating the recipients of the materials or energy as part of the ecosystem compartments.

The LHS and RHS of Eq. (17) refer to the total production by the component on the basis of the input balance and output balance, respectively. In matrix notation, these relationships are written as

$$\mathbf{i}'\mathbf{Z} + \mathbf{i}'\mathbf{W} = \mathbf{x}' \tag{18}$$

and

$$\mathbf{Z}\mathbf{i} + \mathbf{v} = \mathbf{x}, \tag{19}$$

respectively, where $\mathbf{v} = \mathbf{s} + \mathbf{y} + \mathbf{r}$, \mathbf{x} is the total production, and \mathbf{i} is a summation operator, a column vector in the relevant dimension with 1s for all elements.⁸ Let $\mathbf{Z} = \hat{\mathbf{x}}\bar{\mathbf{A}} = \mathbf{A}\hat{\mathbf{x}}$, where $\hat{\mathbf{x}}$ refers to a diagonalized matrix of vector \mathbf{x} . An element in $\bar{\mathbf{A}}$, \bar{a}_{ij} shows the fraction of i directly distributed to j , whereas a_{ij} shows the amount of i directly required to produce one unit of j . Then (18) and (19) become

$$\mathbf{x}'\bar{\mathbf{A}} + \mathbf{i}'\mathbf{W} = \mathbf{x}' \tag{20}$$

and

$$\mathbf{A}\mathbf{x} + \mathbf{v} = \mathbf{x}, \tag{21}$$

respectively. Rearranging (20) and (21) yields

$$\mathbf{x}' = \mathbf{i}'\mathbf{W}(\mathbf{I} - \bar{\mathbf{A}})^{-1} \tag{22}$$

and

$$\mathbf{x} = (\mathbf{I} - \mathbf{A})^{-1} \mathbf{v}, \tag{23}$$

respectively. The input-side balance in (18), (20), and (22) is a physical version of the *supply-driven* model by Ghosh, while the output-side balance in (19), (21), and (23) is the *demand-driven* model by Leontief (Ghosh, 1958; Leontief, 1941). In particular, the i - j th element of $(\mathbf{I} - \bar{\mathbf{A}})^{-1}$ shows the amount of j produced relying on the input from i , while that of $(\mathbf{I} - \mathbf{A})^{-1}$ shows the amount of i required to produce one unit of net system output j . Under the assumption that the input–output structure of the materials and energy flow is fixed, one

⁸ Using $\hat{\mathbf{v}} = [\mathbf{s} \ \mathbf{y} \ \mathbf{r}]$ allows the three components of the total net system output to be distinguished as well.

Table 2
Relationships between symbols for basic matrices in MEFA studies^a

Previous symbols	Symbols in this paper	Meaning	Reference for the previous study
G	$\begin{bmatrix} \mathbf{A} & \mathbf{0} \\ \mathbf{B} & \mathbf{0} \end{bmatrix}$	Structural coefficient for the system that is closed toward primary inputs	Hannon (1973)
e	$\begin{bmatrix} \mathbf{x} \\ \mathbf{Wi} \end{bmatrix}$	Total production for the system that is closed toward primary inputs	Hannon (1973)
P₂₁	$\hat{\mathbf{w}}$	Diagonalized primary input	Finn (1976, 1977)
P₂₂	\mathbf{Z}'	Materials or energy flows between ecosystem components	Finn (1976, 1977)
P₃₂	$\begin{bmatrix} \hat{\mathbf{y}} \\ \hat{\mathbf{s}} \end{bmatrix}$	Diagonalized net system output vector	Finn (1976, 1977)
Q₂₁*	$\hat{\mathbf{B}}$	Diagonalized primary input coefficient vector	Finn (1976, 1977)
Q₂₂*	\mathbf{A}'	Transposed structural coefficient matrix	Finn (1976, 1977)
Q₃₂*	$\begin{bmatrix} \mathbf{I} \\ \mathbf{I} \end{bmatrix}$	Identity matrices	Finn (1976, 1977)
Q₂₁**	\mathbf{I}	An identity matrix	Finn (1976, 1977)
Q₂₂**	$\bar{\mathbf{A}}'$	Transposed Ghosh structural coefficient matrix	Finn (1976, 1977)
Q₃₂**	$\begin{bmatrix} \hat{\mathbf{y}}\hat{\mathbf{x}}^{-1} \\ \hat{\mathbf{s}}\hat{\mathbf{x}}^{-1} \end{bmatrix}$	Normalized net system output and changes in stock size	Finn (1976, 1977)

^a Other symbols are either defined in the text or can be used directly without loss of consistency.

can calculate the total direct and indirect production of ecosystem components for an arbitrary primary input or net system output using Eqs. (22) and (23).

Let $\mathbf{B} = \mathbf{W}\hat{\mathbf{x}}^{-1}$ and $\mathbf{C} = \hat{\mathbf{x}}^{-1}\hat{\mathbf{v}}$, denoting the normalized primary input matrix and the normalized net system output vector, respectively.⁹ The equation

$$\mathbf{v}' = \mathbf{i}'\mathbf{W}(\mathbf{I} - \bar{\mathbf{A}})^{-1}\mathbf{C} \quad (24)$$

may then be used to calculate the amount of net system output enabled by the primary input. Similarly, the equation

$$\mathbf{Wi} = \mathbf{B}(\mathbf{I} - \mathbf{A})^{-1}\mathbf{v} \quad (25)$$

calculates the primary inputs required for the net system output. It should also be noted that the supply-driven model by Ghosh has been interpreted as an *allocative* model. This line of interpretation of the supply-driven model is discussed in the next section.

⁹ A diagonalized form of the relevant vector is more useful for understanding the internal structure than the sum. For instance, if $\hat{\mathbf{B}}_k = \hat{\mathbf{W}}_k\hat{\mathbf{x}}^{-1}$, $\hat{\mathbf{v}}$ and $\hat{\mathbf{W}}_k$ are used instead of \mathbf{B} , \mathbf{v} , and $\mathbf{i}'\mathbf{W}$, respectively, the results of Eqs. (22)–(25) show the same information but are distributed over the ecosystem components and the type of primary input, k .

4. Interrelations between existing MEFA approaches

In this section, the interrelations between existing MEFA approaches are derived by means of the generalized MEFA framework presented in the previous section.

4.1. A system closed toward primary inputs

The relationship between the matrix symbols in earlier studies and the generalized MEFA framework is summarized in Table 2. Using Table 2, Eq. (4), which is used in Hannon (1973), can be converted into

$$\begin{bmatrix} \mathbf{x} \\ \mathbf{Wi} \end{bmatrix} = \begin{bmatrix} \mathbf{I} - \mathbf{A} & \mathbf{0} \\ -\mathbf{B} & \mathbf{I} \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{v} \\ \mathbf{0} \end{bmatrix}. \quad (26)$$

With the help of LU decomposition,¹⁰ the inverse of the concatenated matrices in Eq. (26) can be shown to

¹⁰ LU decomposition is a mathematical technique where a matrix is decomposed into lower (L) and upper (U) triangular matrices. Using LU decomposition, inverses of some concatenated matrices are easily derived analytically.

be

$$\begin{bmatrix} \mathbf{x} \\ \mathbf{Wi} \end{bmatrix} = \begin{bmatrix} (\mathbf{I} - \mathbf{A})^{-1} & \mathbf{0} \\ \mathbf{B}(\mathbf{I} - \mathbf{A})^{-1} & \mathbf{I} \end{bmatrix} \begin{bmatrix} \mathbf{v} \\ \mathbf{0} \end{bmatrix}, \quad (27)$$

so that the overall operation becomes equivalent to

$$\begin{bmatrix} \mathbf{x} \\ \mathbf{Wi} \end{bmatrix} = \begin{bmatrix} (\mathbf{I} - \mathbf{A})^{-1} \mathbf{v} \\ \mathbf{B}(\mathbf{I} - \mathbf{A})^{-1} \mathbf{v} \end{bmatrix}. \quad (28)$$

Observe the identity between the submatrices in Eq. (28) and Eqs. (23) and (25) of the generalized MEFA framework. Thus, the calculus used by Hannon (1973) is a special case of the generalized MEFA framework. From this general relationship, it can also be observed that endogenizing the primary input does not alter the general results (see also Suh, 2004).

4.2. Transitive closure matrices

Using Table 2, Eq. (7) can be rewritten using the notation of generalized MEFA framework as

$$\mathbf{Q}^* = \begin{bmatrix} \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \hat{\mathbf{D}} & \mathbf{A}' & \mathbf{0} \\ \mathbf{0} & \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \mathbf{I} & \mathbf{0} \end{bmatrix}. \quad (29)$$

Using LU decomposition, the block matrices in the Transitive Closure Inflow matrix, $\mathbf{N}^* = (\mathbf{I} - \mathbf{Q}^*)^{-1}$ can be broken down into

$$\mathbf{N}^* = \begin{bmatrix} \mathbf{I} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ (\mathbf{I} - \mathbf{A}')^{-1} \hat{\mathbf{B}} & (\mathbf{I} - \mathbf{A}')^{-1} & \mathbf{0} & \mathbf{0} \\ (\mathbf{I} - \mathbf{A}')^{-1} \hat{\mathbf{B}} & (\mathbf{I} - \mathbf{A}')^{-1} & \mathbf{I} & \mathbf{0} \\ (\mathbf{I} - \mathbf{A}')^{-1} \hat{\mathbf{B}} & (\mathbf{I} - \mathbf{A}')^{-1} & \mathbf{0} & \mathbf{I} \end{bmatrix}. \quad (30)$$

Apparently, matrix \mathbf{N}^* does not need all of its space, as only two submatrices are meaningful in terms of information contents. Transposing the block elements in the matrix gives $(\mathbf{N}_{21}^*)' = \hat{\mathbf{B}}(\mathbf{I} - \mathbf{A})^{-1}$ and $(\mathbf{N}_{22}^*)' = (\mathbf{I} - \mathbf{A})^{-1}$, which are identical to the key elements in (23) and (25) of the generalized MEFA framework.

Now consider the Transitive Closure Outflow matrix, $\mathbf{N}^{**} = (\mathbf{I} - \mathbf{Q}^{**})^{-1}$, where

$$\mathbf{Q}^{**} = \begin{bmatrix} \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{I} & \bar{\mathbf{A}}' & \mathbf{0} \\ \mathbf{0} & \hat{\mathbf{x}}^{-1} \hat{\mathbf{y}} & \mathbf{0} \\ \mathbf{0} & \hat{\mathbf{x}}^{-1} \hat{\mathbf{s}} & \mathbf{0} \end{bmatrix}. \quad (31)$$

Using the similar procedure it can easily be shown that

$$\mathbf{N}^{**} = \begin{bmatrix} \mathbf{I} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ (\mathbf{I} - \bar{\mathbf{A}}')^{-1} & (\mathbf{I} - \bar{\mathbf{A}}')^{-1} & \mathbf{0} & \mathbf{0} \\ \hat{\mathbf{x}}^{-1} \hat{\mathbf{y}} (\mathbf{I} - \bar{\mathbf{A}}')^{-1} & \hat{\mathbf{x}}^{-1} \hat{\mathbf{y}} (\mathbf{I} - \bar{\mathbf{A}}')^{-1} & \mathbf{I} & \mathbf{0} \\ \hat{\mathbf{x}}^{-1} \hat{\mathbf{s}} (\mathbf{I} - \bar{\mathbf{A}}')^{-1} & \hat{\mathbf{x}}^{-1} \hat{\mathbf{s}} (\mathbf{I} - \bar{\mathbf{A}}')^{-1} & \mathbf{0} & \mathbf{I} \end{bmatrix}. \quad (32)$$

Transposing the block elements gives $(\mathbf{N}_{22}^{**})' = (\mathbf{I} - \bar{\mathbf{A}})^{-1}$, $(\mathbf{N}_{32}^{**})' = (\mathbf{I} - \bar{\mathbf{A}})^{-1} \hat{\mathbf{y}} \hat{\mathbf{x}}^{-1}$, and $(\mathbf{N}_{42}^{**})' = (\mathbf{I} - \bar{\mathbf{A}})^{-1} \hat{\mathbf{s}} \hat{\mathbf{x}}^{-1}$, which are again identical to the key elements in (22) and (24) of the generalized MEFA framework. The interpretation by Patten et al. (1976) of an element $(\mathbf{N}_{22}^{**})_{ij}$, which is the amount of i produced by a unit flow originating from j , is generally in line with the interpretation in the generalized MEFA framework as well.

Overall, it is shown that the calculus used by Finn (1976, 1977) is also a special case of the generalized MEFA framework.¹¹

4.3. Distribution of primary inputs over ecosystem components

The previous section has shown the genon flow analysis to be equivalent to the supply-driven model by Ghosh, and has confirmed that the interpretation by Patten et al. (1976) of genon flow is equivalent to that of Ghosh. In the present section I elaborate on the proposition by Hannon (1973) on the distribution of primary

¹¹ B.C. Patten noted that T.J. Finn and Patten himself did not recognize the existence of the work by Ghosh (1958) as well as the inherent duality between the input- and output-balanced systems (supply-driven and demand-driven, respectively) at University of Georgia, Athens in the 1970s when they developed these models.

inputs and its relationship with the approaches taken by others.

Using Table 2, Eq. (5) used for the calculation of primary energy distribution can be rewritten as

$$\mathbf{\Pi} = \mathbf{B}(\mathbf{I} - \mathbf{A})^{-1}\hat{\mathbf{x}}. \tag{33}$$

The formula does not resemble any of those discussed so far. Recall that Finn’s genon flow analysis is also described as a model for the distribution of inputs, although the interpretation by Patten et al. (1976) was slightly different. Perhaps it may be helpful to compare Finn’s genon flow model with Hannon’s proposition. The total flows in the genon flow analysis by Finn (1976, 1977) can be calculated by

$$\mathbf{W}(\mathbf{N}_{22}^{**})' = \mathbf{W}(\mathbf{I} - \bar{\mathbf{A}})^{-1}, \tag{34}$$

the RHS of which is completely different from that of Eq. (33). Although they do not appear to be, Eqs. (33) and (34) are identical (see the Appendix B for a proof). Thus, the seemingly quite different approach used by Hannon (1973) to calculate the distribution of primary inputs over ecosystem components is in fact identical to that used in Finn’s genon flow analysis. Then it turned out that the apparently different interpretations by Patten et al. (1976) and Hannon (1973) have been made on the same equation. Recall that the interpretation by Patten et al. (1976) of Eq. (34) is that it gives the amount of ecosystem components produced by the amount of primary inputs, while the interpretation by Hannon (1973) of (33) is that it concerns the distribution of primary inputs over ecosystem components. Which interpretation is right?

It can be easily shown, using an example, that the calculus used in (33) and (34) is not about the distribution of inputs in the general sense of the term “distribution”.

Let us examine the simple and aggregated system shown in Fig. 3. Here there are self-loops denoted by z_{11} and z_{22} showing the flows directed to their origins. Such self-loops are employed due to the statistical resolution: if two species or industries are connected through material and energy flows but are not distinguished as a distinctive compartment, such flows are noted with self-loops. Another example could be, in principle, cannibalistic behavior, of which the occurrence in real life

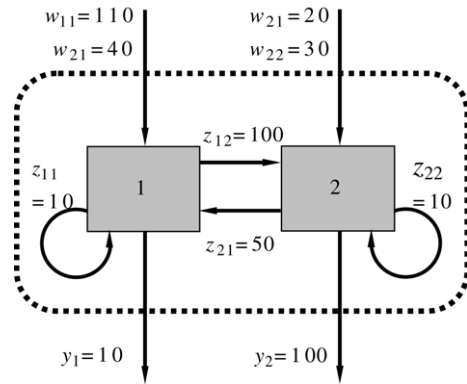


Fig. 3. An example of a two-component system.

situation might be minimal.¹² Eq. (33) or (34) results in

$$\mathbf{\Pi} = \begin{bmatrix} 147 & 96 \\ 63 & 64 \end{bmatrix}. \tag{35}$$

According to Hannon (1973) this means that 147 and 96 units of the first primary input are distributed over the first and the second components, respectively, and 63 and 64 of the second primary inputs over the first and second components, respectively. However, the total system inputs of the first and second primary inputs amount to only 150 and 50 units, respectively. This disqualifies the interpretation of $\mathbf{\Pi}$ as the mere distribution of inputs, since what has been distributed is more than what is supplied.

Here I analyze the meaning of $\mathbf{\Pi}$ by means of its components. First, the operation $\mathbf{B}(\mathbf{I} - \mathbf{A})^{-1}$ results in a matrix (or a row vector, depending on the dimension of \mathbf{B}), one of whose elements shows the amount of each primary input directly and indirectly required to produce one unit of net system output. In a balanced system where $\mathbf{i}'\mathbf{W} + \mathbf{i}'\mathbf{Z} = \mathbf{i}'\mathbf{x}$, the column sum of $\mathbf{B}(\mathbf{I} - \mathbf{A})^{-1}$ is invariably the vector \mathbf{i}' , and the elements in each column indicate the proportion of primary inputs directly and indirectly required to produce one unit of its output. Post-multiplying $\hat{\mathbf{x}}$ will then result in the

¹² The diagonal elements of \mathbf{A} matrix have been a point of theoretical discussion in economics. Georgescu-Roegen (1971, p. 256ff), for instance, argues that the diagonal elements should be zero. In practice, however, the diagonal elements are positive in most of the aggregated IO accounts due to the limitations of industry classification.

amount of the total production that is produced relying on each of the primary inputs. In other words, the element $(\mathbf{\Pi})_{ki}$ represents the amount of i that is enabled by the primary input k , which confirms the interpretation by Patten et al. (1976). Second, consider a diagonalized vector of the k th row of \mathbf{B} , $\hat{\mathbf{B}}_k$. The i - j th element of $\hat{\mathbf{B}}_k(\mathbf{I} - \mathbf{A})^{-1}$ then shows the amount of input k directly and indirectly required for i to generate one unit of system net output from j . By post-multiplying $\hat{\mathbf{x}}$ instead of $\hat{\mathbf{y}}$, the exchanges between the ecosystem components are counted double, as production of one ecosystem component requires producing other components. As $\mathbf{B}(\mathbf{I} - \mathbf{A})^{-1} \hat{\mathbf{x}}$ consists of the column sums of $\hat{\mathbf{B}}_k(\mathbf{I} - \mathbf{A})^{-1}$ for all k , the element $(\mathbf{\Pi})_{ki}$ can be interpreted as the gross amount of primary input k that is directly or indirectly required by the whole system to produce the total amount of i . Therefore, the value $(\mathbf{\Pi})_{11} = 147$, for instance, can be interpreted as (1) the amount of production by the first component enabled by the first primary input or (2) the gross amount of the first primary input required by the whole system to produce the total amount of the first component, which are, in any case, not exactly about distribution of primary inputs.

Does this mean that the interpretation of (34) by Hannon (1973) is misleading? Below, I argue that it is not in certain cases. It is well known that the inverse matrix in (33) and (34) can be expanded into a power series form. Using the identity $\mathbf{A}\hat{\mathbf{x}} = \hat{\mathbf{x}}\bar{\mathbf{A}}$ and the power series, Eqs. (33) and (34) can be written as

$$\mathbf{\Pi} = \mathbf{B}\hat{\mathbf{x}}(\mathbf{I} + \bar{\mathbf{A}} + \bar{\mathbf{A}}^2 + \bar{\mathbf{A}}^3 + \dots), \tag{36}$$

which becomes

$$\mathbf{\Pi} = \mathbf{W} + \mathbf{BZ} + \mathbf{BZ}\bar{\mathbf{A}} + \mathbf{BZ}\bar{\mathbf{A}}^2 + \mathbf{BZ}\bar{\mathbf{A}}^3 + \dots \tag{37}$$

The first term already shows the total primary input to the system. The second, a fraction of the first, shows the total primary inputs required for the whole intra-system exchanges. The third, a fraction of the second, shows the amount of the first tier distribution of the primary inputs, and so on. Thus, the values in $\mathbf{\Pi}$ are accumulative amounts of primary inputs, which means that in a system with strong direct or indirect internal cycling, as is the case in the above example, the magnitudes of the elements in $\mathbf{\Pi}$ are grossly amplified.

Now in the context of ecological applications, suppose that the predator–prey relationship in an ecosys-

tem is unidirectional, that is, the direction of mass and energy flows goes only from lower to higher trophic levels. In other words, the structural coefficient matrix \mathbf{A} can be arranged in such a way that the lower or upper triangle of the matrix becomes a zero matrix, which was also the case in Hannon (1973). In the case of zero or minimal internal cycling, each term in Eq. (37) implies the uni-directional sequence of primary input distribution, showing the cascade distribution structure of primary inputs. Thus, the interpretation of Eq. (33) by Hannon (1973) is valid in ecological applications in case the predator–prey relationship is uni-directional.¹³

4.4. Gross flow and total flow

Using Table 2, the gross flow matrix in Eq. (12) becomes

$$\mathbf{Z}^G = (\mathbf{I} - \mathbf{A})^{-1}\hat{\mathbf{x}} - \hat{\mathbf{x}}. \tag{38}$$

According to Szyrmer and Ulanowicz (1987), the i - j th element of the gross flow matrix, z_{ij}^G , refers to the effect that an output from i has on the total output j . Observe that the first term in the RHS of (38) is close to Hannon’s proposal for the distribution of primary inputs in Eq. (33), except for the normalized primary input coefficient \mathbf{B} . Applying the power series expansion to (36) and (37), \mathbf{Z}^G is expanded to

$$\mathbf{Z}^G = \mathbf{Z} + \mathbf{Z}\bar{\mathbf{A}} + \mathbf{Z}\bar{\mathbf{A}}^2 + \mathbf{Z}\bar{\mathbf{A}}^3 + \dots, \tag{39}$$

showing the cascade distribution of ecosystem components outputs through intra-system exchanges. Again, the values are in accumulative form and thus require cautious interpretation when added up. In the words of Patten et al. (1976), z_{ij}^G may be interpreted as the accumulated production of j enabled by the output from i , which is generally in line with the definition by Szyrmer and Ulanowicz (1987).

Szyrmer and Ulanowicz (1987) argued that the total flows are more closely related to the network properties. Eq. (13), used for the calculation of total flows by

¹³ S. Allesina and B.C. Patten pointed out that predator–prey relationships are in general not uni-directional especially for those include detritus compartment. S. Allesina further noted that omnivory could generate cycles and, especially in fish, dividing compartments in age structure could yield to cannibalism leading cycles.

Szyrmer and Ulanowicz (1987), can be rewritten as

$$\mathbf{Z}^T = (\mathbf{D} - \mathbf{I})\hat{\mathbf{x}}(\hat{\mathbf{D}}^d)^{-1}, \tag{40}$$

where $\mathbf{D} = (\mathbf{I} - \mathbf{A})^{-1}$ and \mathbf{D}^d is a vector with the diagonal elements of \mathbf{D} .¹⁴ Using \mathbf{Z}^G in Eq. (38), Eq. (40) can be rewritten as

$$\mathbf{Z}^T = \mathbf{Z}^G(\hat{\mathbf{D}}^d)^{-1}, \tag{41}$$

so that the total flow matrix is simply a scaled-down version of the gross flow matrix based on the degree of self-cycling that appears in the diagonal of \mathbf{D} . In general, one can regard the total flow as a version of the gross flow \mathbf{Z}^G , with the amplification effects due to self-cycling removed.¹⁵

4.5. Environ analysis

The calculus of environ analysis is very similar to the structural path analysis (SPA) proposed in economics by Defourny and Thorbecke (Defourny and Thorbecke, 1984). SPA was proposed as a tool to analyze the paths in the circulation of monetary flows in an economy through consumption, production and income distribution. This has been further extended to describe energy or other physical flows (see e.g. Lenzen, 2003; Suh, 2002; Treloar, 1997).

Using Table 2 and Section 4.2 of the present paper, the input environ between ecosystem components induced by one unit of net system output of i is calculated in the generalized MEFA framework as

$$\mathbf{E}^{A,i} = \mathbf{A}\hat{\mathbf{D}}_i. \tag{42}$$

Input enviros from the primary input k due to a unit of net system output of i can be found from the i th column of $\hat{\mathbf{B}}_k(\mathbf{I} - \mathbf{A})^{-1}$, that has already appeared in Section

3. Calculation of the output Environ due to one unit of primary input to i between the ecosystem components is done by

$$\mathbf{E}^{\Omega,i} = \hat{\mathbf{D}}_i\bar{\mathbf{A}}, \tag{43}$$

where $\hat{\mathbf{D}}_i$ is the diagonalized vector of the i th row in $(\mathbf{I} - \bar{\mathbf{A}})^{-1}$. The output enviros to net system output and changes in stock can be found from the i th rows of $(\mathbf{I} - \bar{\mathbf{A}})^{-1}\hat{\mathbf{y}}\hat{\mathbf{x}}^{-1}$ and $(\mathbf{I} - \bar{\mathbf{A}})^{-1}\hat{\mathbf{s}}\hat{\mathbf{x}}^{-1}$, respectively, that appeared in Section 3 as well.

In general, each of the intra-system output Enviro from i to j due to the system net output m can be derived using the simple scalar notation

$$e_{ij}^{A,m} = a_{ij}d_{jm}. \tag{44}$$

Similarly, each of the intra-system input enviros from i to j due to the primary input k is calculated by

$$e_{ij}^{\Omega,k} = \bar{d}_{ki}\bar{a}_{ij}, \tag{45}$$

where \bar{d}_{ki} is k - i th element of $\bar{\mathbf{D}} = (\mathbf{I} - \bar{\mathbf{A}})^{-1}$ (see the example in the next section).

Overall, environ analysis is successfully translated into the generalized MEFA framework, and it is shown that the framework is able to perform the analysis in more compact manner.

5. A numerical example

Table 3 and Fig. 4 show an example of a MEFA problem involving five ecosystem components and two types of primary input.

Two types of dependency coefficients can be defined: supply-driven dependency and demand-driven dependency. Supply-driven dependency is calculated from Eq. (22) by $(\mathbf{I} - \bar{\mathbf{A}})^{-1} - \mathbf{I}$ (Table 4), while demand-driven dependency is derived from (23) by $(\mathbf{I} - \mathbf{A})^{-1} - \mathbf{I}$ (Table 5).

The i - j th cell in Table 4 shows the production of j induced by one unit of availability of i , and the i - j th cell in Table 5 shows the net amount of i required to produce one unit of j . The negative element in Table 4 shows that one unit of availability of Plants actually reduces the stock size of plants because the availability of Plants partly depends on its stock. Finn's Cycling Index appears in the diagonal of the two tables. The sum

¹⁴ In Szyrmer and Ulanowicz (1987), another total flow matrix appears, for which the authors refer to Augustinovic (1970) as its methodological reference. Although Szyrmer and Ulanowicz (1987) did not explicitly show it, one may deduce from a table that the authors used $(\hat{\mathbf{D}}^d)^{-1}\mathbf{Z}^G$ for its calculation. The equivalence of this operation with that in (Augustinovic, 1970), which is basically about Ghosh's supply-driven model, however, is not confirmed.

¹⁵ Accordingly, the total intermediate output matrix, $\hat{\mathbf{x}}^{-1}\mathbf{Z}^T$ in Szyrmer and Ulanowicz (1987) can be reduced to $[(\mathbf{I} - \bar{\mathbf{A}})^{-1} - \mathbf{I}](\hat{\mathbf{D}}^d)^{-1}$, the ij th element of which shows the net fraction of i distributed over j .

Table 3
Input data for the numerical example (kCal/m²-year)^a

	(1)	(2)	(3)	(4)	(5)	Exports (y)	Respiration (r)	Changes in stock (s)	Total production (x)
(1) Plants	0	0	0	0	8881	300	2003	-200	10984
(2) Bacteria	0	0	75	0	1600	255	3275	0	5205
(3) Detritus feeders	0	0	0	370	200	0	1814	0	2384
(4) Omnivores	0	0	0	0	167	0	203	500	870
(5) Detritus	0	5205	2309	0	0	860	3109	0	11483
Primary input of bread (w ₁)	0	0		500	0				
Primary input of sunlight (w ₂)	10984	0	0	0	635				
Total production (x')	10984	5205	2384	870	11483				

^a Modified from EcoNetwrk database on Cone Spring (<http://www.glerl.noaa.gov/EcoNetwrk/EcoNetwrk.html>). Originally developed in the systems ecology classes at University of Georgia (Williams and Crouthamel, 1972).

Table 4
Supply-driven dependency matrix $(\mathbf{I} - \bar{\mathbf{A}})^{-1} - \mathbf{I}$

	(1)	(2)	(3)	(4)	(5)	Exports (y)	Respiration (r)	Changes in stock (s)	Sum
(1) Plants	0	0.44	0.20	0.03	0.97	0.03	0.18	-0.02	1.83
(2) Bacteria	0	0.17	0.09	0.01	0.37	0.05	0.63	0	1.32
(3) Detritus feeders	0	0.06	0.03	0.16	0.14	0	0.76	0	1.15
(4) Omnivores	0	0.10	0.05	0.01	0.23	0	0.23	0.57	1.20
(5) Detritus	0	0.54	0.25	0.04	0.19	0.07	0.27	0	1.37

in Table 4 shows that unit increase in the availability of Plants increases the overall production in the system the most. In terms of gross input requirements, Detritus Feeders require the largest direct and indirect energy inputs to produce one unit of themselves. By multiplying the total primary inputs and total net system output one can easily calculate the actual amount instead of the coefficients. For instance, the cascade distribution of primary inputs or the production of ecosystem compo-

nents enabled by each primary production is calculated by Eq. (33) or Eq. (34).

$$\mathbf{\Pi} = \begin{bmatrix} 0 & 52 & 24 & 504 & 115 \\ 10984 & 5153 & 2360 & 366 & 11368 \end{bmatrix}$$

Gross flow and the total flow matrices by Szyrmer and Ulanowicz (1987) are shown in Tables 6 and 7. These tables show that the outputs from Plants and Detritus have the largest accumulated production in the overall system.

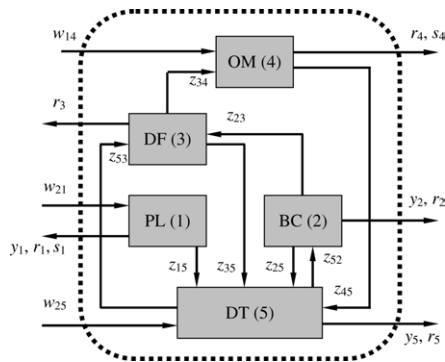


Fig. 4. An example of a MEFA problem. Arrows show direct interactions. PL: plants; BC: bacteria; DF: Detritus feeders; OM: Omnivores; DT: Detritus.

Table 5
Demand-driven dependency matrix $(\mathbf{I} - \bar{\mathbf{A}})^{-1} - \mathbf{I}$

	(1)	(2)	(3)	(4)	(5)
(1) Plants	0	0.92	0.92	0.39	0.92
(2) Bacteria	0	0.17	0.20	0.08	0.17
(3) Detritus feeders	0	0.03	0.03	0.44	0.03
(4) Omnivores	0	0.02	0.02	0.01	0.02
(5) Detritus	0	1.19	1.19	0.51	0.19
Primary input of bread (w ₁)	0	0.01	0.01	0.58	0.01
Primary input of sunlight (w ₂)	1.00	0.99	0.99	0.42	0.99
Sum	1.00	3.33	3.36	2.43	2.33

Table 6
Gross flow matrix, Z^G

	(1)	(2)	(3)	(4)	(5)	Sum
(1) Plants	0	4809	2203	342	10610	17964
(2) Bacteria	0	871	474	74	1922	3341
(3) Detritus feeders	0	147	67	380	324	918
(4) Omnivores	0	90	41	6	200	337
(5) Detritus	0	6218	2848	442	2235	11743

Table 7
Total flow matrix, Z^T

	(1)	(2)	(3)	(4)	(5)	Sum
(1) Plants	0	4120	2142	339	8881	15482
(2) Bacteria	0	746	461	73	1609	2889
(3) Detritus feeders	0	126	65	378	271	840
(4) Omnivores	0	78	40	6	167	291
(5) Detritus	0	5327	2770	439	1871	10407

Table 8
Input environs matrix, $E^{A,5}$

	(1)	(2)	(3)	(4)	(5)	Export (y)
(1) Plants	0	0	0	0	0.924	0
(2) Bacteria	0	0	0.001	0	0.167	0
(3) Detritus feeders	0	0	0	0.007	0.021	0
(4) Omnivores	0	0	0	0	0.017	0
(5) Detritus	0	0.167	0.027	0	0	1

Environ analyses were carried out using Eqs. (42) and (43) and those in Section 3. By way of example, input and output environs were calculated for the output from Detritus and the input to Omnivores, respectively. The resulting input and output environ matrices are shown in Tables 8 and 9. Figs. 5 and 6 illustrate these two environs. Fig. 5 shows the relative inputs re-

Table 9
Output Environ matrix, $E^{\Omega,1}$

	(1)	(2)	(3)	(4)	(5)
(1) Plants	0	0	0	0	0
(2) Bacteria	0	0	0.0015	0	0.032
(3) Detritus feeders	0	0	0	0.0074	0.004
(4) Omnivores	0	0	0	0	0.1934
(5) Detritus	0	0.1039	0.0461	0	0
Primary input of bread (w_1)	0	0	0	1	0

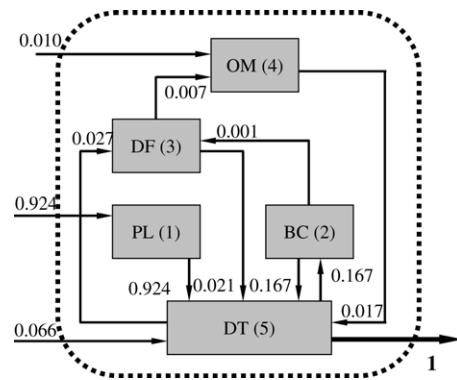


Fig. 5. Input Environs per unit export of Detritus.

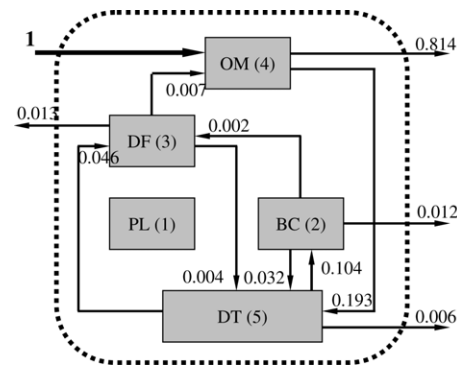


Fig. 6. Output Environs per unit of primary input to Omnivores.

quired to generate one unit export from Detritus, and Fig. 5 shows the relative outputs enabled by one unit of external input to Omnivores. The input environ analysis, for instance, makes it clear that the external input to Plant and Plant to Detritus flow are critical path that constitute most of the exports from Detritus with their high input environs of 0.924.

6. Discussion and conclusions

This paper has analyzed MEFA methodologies in ecological studies, and presented a generalized MEFA framework that embraces ecological as well as economic systems. Using the generalized MEFA framework, it has interpreted and compared existing methods, while discussing a few critical issues of interpretations and calculi as well. Finally, it has demonstrated the generalized MEFA framework by

means of a numerical example. Below I discuss a few issues arising from the analyses.

6.1. Possibilities and limitations of linear frameworks

The MEFA framework presented here is basically, like economic input–output analysis, a system of linear equations, and is certainly not a one-size-fits-all tool. There are important limitations, which clearly restrict application of the analysis. Most of all, caution needs to be exerted when the results of MEFA are applied for the purpose of prediction. First, the framework assumes that the input–output relationship is linear and fixed. In reality, the relationship between the network components of an ecosystem is by no means linear or fixed. A predator–prey relationship in a food web, for instance, changes over time for a variety of reasons, including changes in patterns of competition, seasonal changes, and, most fundamentally, behavioral indeterminacy (Yodzis, 1988). Although the MEFA framework is perfectly correct as a snapshot of reality for certain period of time, it has a serious limitation as a predictive model, especially for a non-linear, indeterminate system. In other words, an analysis based on a linear MEFA framework is often irrelevant for predicting the behavior of such a system beyond the marginal perturbation, although it is perfectly relevant to understanding the system. Thus the terms “effect” or “influence” should be used with the utmost caution in a dynamic context (see Loehle, 1990; Patten, 1990 for a debate). Second, even though the underlying mechanism of ecosystem behavior in terms of the changes in materials or energy supply is nearly linear and fixed, the real system may not behave as analyzed, as there may be other constraints. An ecosystem is generally a multi-constrained system, and the relationship through one nutrient or energy flow works only until the system hits another constraint (see Gaedke et al., 2002; Sundareshwar et al., 2003 for such cases).

I believe, however, that there is still an important role for linear frameworks in ecology. First, they provide a basic accounting scheme for network structure. The complexity, non-linearity, and inherent indeterminacy of ecosystem behavior does not reduce the need for more basic data, which is always a basis for further sophistication. The lack of a common architecture for the presentation of basic data has often been pointed

out (see e.g. Cohen et al., 1993). The linear system is a well-defined, efficient way of presenting fundamental data for a network structure (e.g. Christensen and Pauly, 1992; Heymans and Baird, 2000b). Second, the framework enables a number of important analytical perspectives that has been proposed and utilized in unraveling the complex interdependencies between ecosystem components. Dealing with a complex system often requires a set of indicators that reveal some key properties of the system. By virtue of its common structure, the linear framework provides a number of universal indicators that can be applied to different systems and enable better inter-system comparison.

6.2. Parallels and convergents in economics and ecology

Szyrmer and Ulanowicz (1987) raised the question whether the novel adaptations of input–output analysis made by ecologists were ever applied in economics. Having analyzed the MEFA approaches in ecology, I could find many “parallels and convergents” between the developments introduced by economists and ecologists. The name of A. Ghosh, who proposed the supply-driven model in 1958, is almost completely unknown in ecological literature. But although the two disciplines are thus relatively isolated from each other, exactly the same problem formulation as that used by Ghosh (1958) appears from the very beginning of its introduction by Hannon (1973) and has been independently proposed by others in variety of forms, notably by Finn (1976, 1977), Patten et al. (1976) and Szyrmer and Ulanowicz (1987). Another example may be the structural path analysis (SPA) by Defourny and Thorbecke (1984), who introduced it to analyze monetary flows in an economic system. Although it is quite evident that the SPA method was developed independently from ecological literature, many of its elements can be found in the environ analysis. Thus, there are considerable overlaps between the relatively independent developments introduced by input–output economists and ecologists. Unfortunately, however, most of them fail to utilize the findings of others. Given that there are many interesting parallel developments of MEFA in ecology and input–output economics, a good communication between the two disciplines would be fruitful for both.

However, in exploring each other’s disciplines, economists and ecologists need to be aware that there

is a fundamental discrepancy between their views in addressing their systems, as is discussed in the next subsection.

6.3. *Conflicts of paradigm between ecology and economics*

One observation of the present analysis is the contrast in specialization in MEFA approaches between ecology and input–output economics. Independent proposals of MEFA framework in ecology often reach Ghosh’s supply-driven model, while the demand-driven model by Leontief has been the general practice in input–output economics (cf. Pauly and Christensen, 1995). Why has the supply-driven model been specialized as an MEFA framework in ecology? The answer may be helpful in revealing the fundamental difference between the views of the two disciplines in looking at their systems.

The supply-driven model and the demand-driven model are two facets of a network structure. The former shows the impact that the availability of inputs has upon production, while the latter shows the impact that the output has upon its production. In other words, the supply-driven model in ecology shows the change in production at higher trophic levels, or predators, that is induced by changes in availability at a lower trophic level, or prey, or the changes in overall activity rates induced by nutrient or energy inflows. On the other hand, the demand-driven model in economics concerns with the impacts of consumer demand upon the production of commodities. In an ecosystem, however, quantifying the impacts of final demand on production is like asking the question, “how much phytoplankton will be produced due to the increase in fish catches?”, which is quite improbable.¹⁶ The factor that governs the whole system in ecology is primary inputs from nature, showing the dependence of the ecological system on nature. The specialization of demand-driven model in economics implies the view that final consumption rather than the primary supply from nature is the driver that runs an economics system. In that sense, the demand-

driven model is operated *as if* an economic system is free from the inputs from outside such as natural resources and solar energy.

Perhaps, the two conflicting paradigms have been able to coexist because our human ecology has not yet faced a major input-side constraint. The prices of major natural resources have been actually decreasing over the past decades, and there are views that technology development will ultimately lead to an invention of ‘backstop technology’, which will literally free the economic system from input-side constraints. Whether or not the depletion of resources will happen, or what does it imply for the intra- and inter-generation equity has long been a theoretical discussion in resources economics, and I do not have much to add to that (Dasgupta and Heal, 1974; Solow, 1974a; Solow, 1974b). However, interestingly, the recycling rates for major metal resources are steadily rising world wide, and there are substantial institutional changes towards a more recycling-oriented economy at least in Europe.¹⁷ These movements would eventually change our economy more tied to resource availability through recycling, where supply-driven paradigm and findings in ecology will play an important role. In terms of the theory of ecosystem development by E.P. Odum, for instance, these developments toward an endogenized resources economy implies a step towards system maturity in the course of ecological succession (Odum, 1969). According to Odum (1969), ecological succession “culminates in a stabilized ecosystem in which maximum biomass (or high information content) and symbiotic function between organisms are maintained per unit of available energy flow”. The implications of the theories and knowledge developed in ecology, including Odum’s theory of ecosystem development, for an endogenized resources economy are yet to be explored.

6.4. *A meeting point: industrial ecology and future research needs*

There are some positive movements toward a more ecological paradigm in industry and economics, the

¹⁶ A slightly different question that is more relevant to a static relationship than to impacts in a dynamic sense would be “how much phytoplankton is required due to the increase in fish catches?”, which is perhaps a more plausible question (see also Pauly and Christensen, 1995).

¹⁷ Two very important steps in this development would be the European Union guidelines on waste electrical and electronic equipment (WEEE) and end of life vehicle (ELV). These guidelines set the required rate of recycling for electronic equipment and motor vehicles.

rise of the new discipline of industrial ecology being one of them (Ayres and Ayres, 1996; Frosch and Gallopoulos, 1989; Graedel and Allenby, 1995). In industrial ecology, closing the materials cycle within the economy by means of symbiotic functions between industrial processes is among the greatest interests. This will be an important direction for future research on utilizing the findings of ecology to achieve a sustainable society. Interesting developments in industrial ecology include the physical input–output tables (PIOTs) and substance flow analysis (SFA) projects. Over the last decade, national bureaus that collect economic statistics have started to compile PIOTs. PIOTs show the materials and energy terms of our economy, linking production, consumption, and disposal of products and services with their embedding physical reality (Kratena et al., 1992; Kratterl and Kratena, 1990; Pedersen, 1999; Stahmer et al., 2003). Large-scale substance flow analysis (SFA) studies have recently been finished or are currently underway in a number of countries (Kyzia, 2003; Lennox et al., 2004; Spatari et al., 2003; van der Voet et al., 2000; Bailey et al., 2004a, 2004b). These initiatives will broaden our current understanding on materials and energy cycles

in our economy and environment and the findings in MEFA in ecology will be valuable resources.

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Appendix A

The accounting framework in Finn (1977).

	w_{11}	w_{1n}	$-\dot{x}_{1-}$	$-\dot{x}_{n-}$	$z_{,1}$	$z_{,n}$	$y_1 \cdots y_n$	$\dot{x}_{1+} \cdots \dot{x}_{n+}$
w_{11}														
\vdots														
w_{1n}														
$-\dot{x}_{1-}$														
\vdots														
$-\dot{x}_{n-}$														
$z_{,1}$	w_{11}	0	...	0	$-\dot{x}_{1-}$	0	...	0	f_{11}	f_{12}	...	f_{1n}		
$z_{,2}$	0	w_{12}		0	0	$-\dot{x}_{2-}$		0	f_{21}	f_{22}		f_{2n}		
\vdots	\vdots		\ddots	\vdots	\vdots		\ddots	\vdots	\vdots		\ddots	\vdots		
$z_{,n}$	0	0	...	w_{1n}	0	0	...	$-\dot{x}_{n-}$	f_{n1}	f_{n2}	...	f_{nn}		
y_1									y_1	0	...	0		
\vdots									0	y_2		0		
\vdots									\vdots		\ddots	\vdots		
y_n									0	0	...	y_n		
\dot{x}_{1+}									\dot{x}_{1+}	0	...	0		
\vdots									0	\dot{x}_{2+}		0		
\vdots									\vdots		\ddots	\vdots		
\dot{x}_{n+}									0	0	...	\dot{x}_{n+}		

In Finn (1977), the row index refers to the recipient and the column index to the supplier. w : primary input, \dot{x}_- : decrease in stock, z : intra-system exchanges, y : net system output, \dot{x}_+ : increase in stock. Blank areas are zero cells (notations have been modified to avoid confusion).

Appendix B

Proposition. $\Pi = \mathbf{W}(\mathbf{N}_{22}^{**})'$

Proof. From Section 3, $\hat{\mathbf{x}}\bar{\mathbf{A}} = \mathbf{A}\hat{\mathbf{x}}$. Substituting \mathbf{A} in Eq. (33)

$$\begin{aligned}\Pi &= \mathbf{B}(\mathbf{I} - \hat{\mathbf{x}}\bar{\mathbf{A}}\hat{\mathbf{x}}^{-1})^{-1}\hat{\mathbf{x}} = \mathbf{B}[\hat{\mathbf{x}}^{-1}(\mathbf{I} - \hat{\mathbf{x}}\bar{\mathbf{A}}\hat{\mathbf{x}}^{-1})]^{-1} \\ &= \mathbf{B}(\hat{\mathbf{x}}^{-1} - \bar{\mathbf{A}}\hat{\mathbf{x}}^{-1})^{-1} = \mathbf{B}[(\mathbf{I} - \bar{\mathbf{A}})\hat{\mathbf{x}}^{-1}]^{-1} \\ &= \mathbf{B}\hat{\mathbf{x}}[(\mathbf{I} - \bar{\mathbf{A}})]^{-1} = \mathbf{W}(\mathbf{I} - \bar{\mathbf{A}})^{-1} = \mathbf{W}(\mathbf{N}_{22}^{**})' \quad \square\end{aligned}$$

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