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Contribution of throughflows to the ecological interpretation of integral network utility

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ABSTRACT

Ecosystems can be abstracted into models consisting of compartments containing matter or energy, transactional flows of matter or energy between compartments, inputs into the system, and outputs from the system. Although direct transactions are measurable in the field, indirect transactions have been demonstrated to have dominant effects. Integral network utility (**U**) is a summation of all direct and indirect net transactions in a network presented in matrix format and developed as a feature of Network Environ Analysis (NEA). While **U** can provide qualitative information about ecological interactions between compartments, the nonzero-sum nature of indirect net transactions has made ecological interpretation of quantitative network utility challenging. Here we aimed to examine **U** for nine 2- or 3-compartment ecosystem models from a throughflow perspective. For each model, we assigned inputs, outputs, and flows algebraically using flow components traceable across the model, developed corresponding flow (**F**) and throughflow (**T**) matrices based on these values, and used symbolic Matlab to calculate the net adjacent flow intensity matrix (**D**) and **U**. Substituting algebraic combinations of flow components with corresponding throughflow values allowed us to reduce elements of **U** to throughflows to the maximum extent possible. Models with only simple input environs were fully throughflow reducible, while models with more complex input environs exhibited one to three nonreducible elements in **U**. Throughflow reducibility was sufficient, but not necessary, for topological determination of ecological relations of a model, as described by *sign*(**U**). Parametrically determined elements of *sign*(**U**), along with the specific flow components influencing the sign of that element, could be readily identified based on quantitative consideration of nonreducible flow components. We provide an example showing that considering throughflow as a centrality measure can allow the identification of a quantitative basis for network synergism. By allowing identification of specific subsets of transactional flows relating to ecosystem complexity and qualitative differences between human-designed systems in the conventional industrial model and evolved ecological systems, the throughflow perspective of **U** opens avenues for designing more sustainable human systems.

1. Introduction

Network Environ Analysis (NEA), a theoretical approach to the analysis of complex ecological systems, is a key area of research within systems ecology, itself a niche topic in the rapidly expanding area of network ecology (Borrett et al., 2014). Initiated and advanced by Patten (1978) and Matis and Patten (1981), the core of this environmental system theory is algebraic, static (steady state) and linear, descending from economic Input–Output Analysis (Leontief, 1936, 1986). More recently, a dynamic approximation methodology

Abbreviations: NEA, Network Environ Analysis; **U**, (u_{ij}) = integral network utility matrix; **D**, (d_{ij}) = net adjacent flow intensity matrix, or direct utility matrix; **G**, $(g_{ij}) = (f_{ij}/T_j)$ = output environ flow intensity matrix; **G′**, $(g'_{ij}) = (f_{ij}/T_i)$ = input environ flow intensity matrix; **F**, (f_{ij}) = flow matrix; **T**, (T_i) = throughflow matrix.

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(Kazanci and Ma, 2012; Shevtsov et al., 2009) and a particle tracking family of stochastic methodologies (Kazanci et al., 2009; Tollner et al., 2009) have emerged that promise tractable analysis of both non-steady state and nonlinear environs.

Integral network utility $\mathbf{U} = (u_{ij})$ is a matrix measure of the overall relational benefits ($u_{ij} \geq 0$) or costs ($u_{ij} < 0$) expressed between pairs of compartments (i, j) in a system, as derived from transactional matter or energy flows, propagated over paths of all possible lengths, extending to i from j within that system. Mathematically, $\mathbf{U}$ is defined as the sum of powers $m = 0, 1, \ldots, \infty$ of the net adjacent flow intensity matrix $\mathbf{D}$; that is, $\mathbf{U} = \sum_{m=0}^{\infty} \mathbf{D}^m$ (Fath and Patten, 1998; Patten, 1991, 1992). The signs of any selected pair of elements (u_{ij}, u_{ji}) within $\mathbf{U}$ describe the overall relation of i with j in terms of one of nine possible familiar ecological interaction types; for example, (−, −) indicates competition, (+, −) indicates predation, and (+, +) indicates mutualism (Patten, 1991). Recent work on environ utility analysis has also revealed the mathematical basis for previously hypothesized properties of network synergism (Fath and Patten, 1998) and network mutualism (Fath, 2007), further supporting the usefulness of $\mathbf{U}$ in understanding ecological network function.

Throughflow, the sum of adjacent flows and inputs entering (or adjacent flows and outputs leaving) a specific network compartment, plays a direct role in $\mathbf{D}$, and therefore in calculating $\mathbf{U}$ (Patten, 1991, 1992). The sum of all throughflows T_i in a model, or the total amount of matter/energy that travels through a network, is known as *total system throughflow* (Finn, 1976). This holistic network property is related to maximum power, positively correlates with network size and numerous network-level properties, and has been shown to be negatively correlated with the network synergism index in large real-world and computationally-modeled ecosystems despite causing proportional increases in this index in small theoretical models (Buzhdygan et al., 2014; Fath, 2004; Patten, 2014). Some species contribute more strongly than others to total system throughflow, but due to network homogenization, maintaining overall network structure is also necessary to sustain this parameter (Fann and Borrett, 2012). While individual throughflows are node-level properties that should be considered alongside neighborhood- and network-level properties for the purpose of analyzing ecosystems (*sensu* Hines and Borrett, 2014), it is clear that they contribute to network-level properties, at minimum, *via* contributions to total system throughflow. Indeed, throughflows were shown to be present in $\mathbf{U}$ relatively early in the development of utility analysis, when they were employed in demonstrating the mathematical basis for network synergism (Fath and Patten, 1998). This work revealed the presence of throughflows, along with flows, in a throughflow-dimensionalized elaboration of $\mathbf{U}$ for a 3 × 3 complete digraph; it is evident in the resulting matrix, although not directly shown, that throughflows are ubiquitous in $\mathbf{U}$ itself for this nearly-generalized topology (Fath and Patten, 1998). More recently, Fath (2007) implicitly showed the presence of throughflows in $\mathbf{U}$ for five specific network topologies of two, three, or four compartments. In that work, ratios of flows to throughflows, f_{ij}/T_j or f_{ij}/T_i, were condensed into a set of variables g_{ij} and g'_{ij} corresponding to the elements of the output and input environ flow intensity matrices $\mathbf{G}$ and $\mathbf{G}'$, respectively (Leontief, 1986; Patten, 1991), to facilitate the algebraic description of $\mathbf{D}$ and $\mathbf{U}$ matrices for the corresponding networks.

Recent study of utility has employed both numerical and algebraic approaches. Patten and Whipple (2007) examined the extent to which ecological relations derived from $\mathbf{U}$ are determined by the specific links in the model digraph, as opposed to specific flow quantities using numerical computation (also reviewed by Patten, 2014). For some relatively simple ecosystem models, all such relations are determined by the overall structure of the model digraph, without regard to flow values (Patten and Whipple, 2007); that is, they are *topologically determined*. In other models, at least some of the relations are determined by the actual values of the flows f_{ij} within the network, a property described as *parametric determination* (Patten and Whipple, 2007). While numerical methods are highly tractable using computational tools, the resulting numerical values in $\mathbf{U}$ are essentially non-generalizable aggregates. Thus, trial and error is required to identify consistent patterns using this approach. In contrast, Lobanova et al. (2009) used an algebraic approach to carry out similar work in four different three-compartment and three different n-compartment models. The authors identified overall patterns of relations based on the signs of the elements of the resulting $\mathbf{U}$, or *sign*($\mathbf{U}$), then highlighted which elements of *sign*($\mathbf{U}$) would vary parametrically and under what flow conditions *sign*(u_{ij}) would be positive, zero, or negative for the given network topology. This approach is more computationally difficult, but it allows tracking of individual flow components across arithmetical matrix manipulations. Patterns of topological and parametric determination across multiple models are therefore more easily identified and described algebraically.

Since throughflows can be described as sums of individual inputs and flows (or outputs and flows), previous observations raise the question of the extent to which a given ecological network's $\mathbf{U}$ can be described in terms of algebraic combinations of its throughflows. For example, Fath and Patten (1998) noted that individual flows could be replaced with throughflows in $\mathbf{U}$ for a three-compartment resource competition model but did not carry out this substitution to the maximum extent possible (see Eq. (16) therein). Preliminary work on this and other simple ecosystem models suggested to us the likelihood that $\mathbf{U}$ may be entirely reducible to algebraic combinations of throughflows for at least some model topologies. In the current work, we therefore sought to identify network topologies in which elements of $\mathbf{U}$ can be reduced entirely to combinations of throughflows. For each of nine different simplified two- or three-compartment ecosystem models, we notated inputs, outputs, and internal flows as arithmetic combinations of algebraic flow component variables stoichiometrically balanced for consistency with static conditions. We then employed a symbolic computation approach to calculate $\mathbf{U}$ for each model. By substituting combinations of variables with their throughflow equivalents, we reduced elements of $\mathbf{U}$ to throughflows to the maximum extent possible. Further analysis based in abstract algebra aided the identification of which network topologies did and did not produce $\mathbf{U}$ completely reducible to throughflows, and we looked for common features among each type of network. We also identified which matrix elements and specific flow parameters were critical in determining qualitative relations between compartments. Finally, we considered how this "throughflow perspective" deepens current ecological interpretation of integral network utility and, more generally, the understanding of ecological networks.

2. Methods

2.1. Model structures

Nine model structures, comprised of two 2-compartment models and seven 3-compartment models, were developed for analysis. Many of these models have previously been analyzed in other contexts; e.g., Fath and Patten (1998) deal with a special (numerical) case of Model 3 and the general (algebraic) case for Model 4; Fath (2007) addresses general cases for Models 1, 3, and 4; Lobanova et al. (2009) examine Models 3, 4, 6, and 7. All models were dissipative in that each compartment contained an output. Both two-compartment models contained

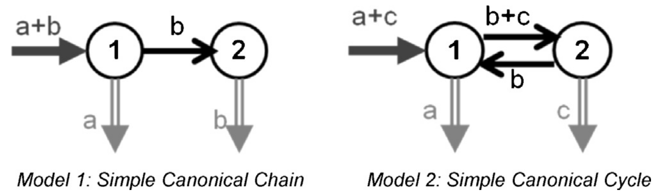

Fig. 1. Two-compartment dissipative models used to calculate algebraic utility matrices. Black, numbered circles indicate compartments, and black arrows indicate internal (i.e., intercompartmental) flows. Black bold arrows indicate inputs, while gray open arrows indicate outputs. Associated letters indicate algebraic values of the nearest input, output, or flow.

a single input, with one model representing a simple canonical chain, i.e., flow between compartments was unidirectional, and the other representing a simple canonical cycle, i.e., flows in both directions between compartments existed (Fig. 1). Analogous three-compartment models, a three-compartment chain and a three compartment cycle, each with one input, were included (Models 3 and 7, respectively; Fig. 2). Two types of competition models were developed, one in which two compartments directly competed for flows from a single, third compartment (Model 4), and one in which a single compartment gained flows from two different compartments (Model 5; Fig. 2). Model 6 built upon the resource competition model by including an additional flow from one competitor to the other, representing intraguild predation (Fig. 2). Finally, Models 8 and 9 built additional complexity into the three-compartment cycle of Model 7 by adding an additional input and a reverse flow between two compartments, respectively (Fig. 2). Collectively, these models are not exhaustive of all possible two- and three-compartment dissipative models, but they address different levels of complexity in terms of both inputs and patterns of flows.

Unlike previous analyses by Lobanova et al. (2009), Fath (2007), and Fath and Patten (1998), each of the nine models herein were described not in terms of algebraic forms of individual inputs, outputs, and flows, but rather as algebraic decompositions of the overall model, labeled as *a*, *b*, *c*, and so forth (Figs. 1 and 2). Thus, inputs, outputs, and flows shared individual algebraic subcomponents (i.e., *flow components*) with each other within a given model, allowing a more parsimonious analysis of the movement of matter or energy through it (Luper et al., 2011). Cross-comparisons of the same variables across different models should therefore not be assumed valid.

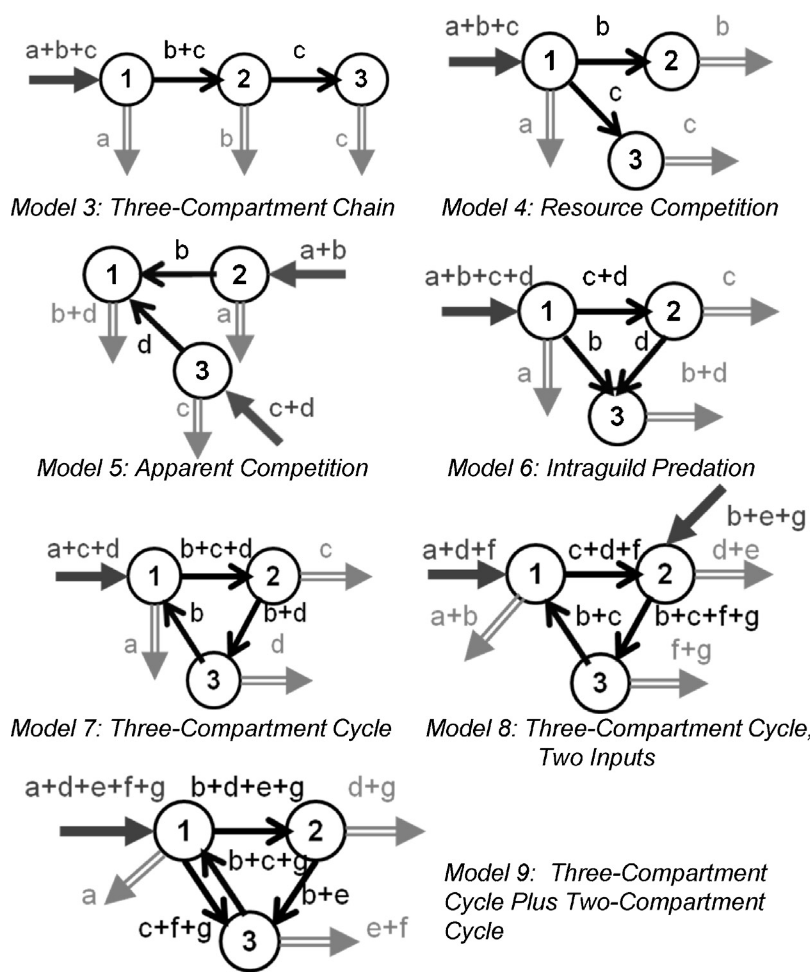

Fig. 2. Three-compartment dissipative models used to calculate algebraic utility matrices. Compartments, flows, inputs, and outputs are designated as in Fig. 1.

2.2. Symbolic computation

Flow matrices $\mathbf{F}_m$ were developed by inspection of the algebraic flows within each model m in accordance with the approach developed by Patten (1978); that is, each element f_{mij} is the flow from compartment j to compartment i within m. Corresponding throughflow matrices $\mathbf{T}_m$ were developed similarly, with each element T_{mi} algebraically representing the throughflows for compartment i within m (Patten, 1978). From each $\mathbf{F}_m$ and $\mathbf{T}_m$, the corresponding net adjacent flow intensity (direct utility) matrix $\mathbf{D}_m$ was algebraically computed using Symbolic Matlab (MathWorks, Inc.; Natick, MA, USA) such that the elements $d_{mij} = (f_{mij} - f_{mji})/T_{mi}$ (Patten, 1991). Finally, the integral utility matrix $\mathbf{U}_m$ was algebraically computed in Symbolic Matlab as $(\mathbf{I}_m - \mathbf{D}_m)^{-1}$, where $\mathbf{I}_m$ is the $n \times n$ identity matrix for model m, consisting of n compartments (Patten, 1991). This approach to calculating $\mathbf{U}_m$ assumes that the infinite series $\mathbf{U}_m = \sum_{n=0}^{\infty} \mathbf{D}_m^n$ converges, which requires that $\mathbf{I}_m - \mathbf{D}_m$ is invertible (Patten, 1991, 1992). This, in turn, has been proven to hold if and only if $|\lambda_i| < 1$, where λ_i is the ith eigenvalue of $\mathbf{D}_m$, for all i from 1 to n (Kawasaki's Convergence Theorem, Patten, 1991).

2.3. Reduction of $\mathbf{U}_m$ and algebraic substitution of T_{mi}

For each model m, we first reduced the elements of $\mathbf{U}_m$ to their corresponding throughflows, T_{mi}, to the greatest extent possible using substitutions within Symbolic Matlab. However, this program does not appear to carry out complex substitutions, as this approach failed to identify many T_{mi} that could be identified and computed by hand. Thus, algebraic substitution of the elements of $\mathbf{U}_m$ with the corresponding T_{mi} was largely carried out by hand, with intermittent use of Symbolic Matlab to confirm that parts of a given matrix element could be further simplified as had been achieved without computational software. Software that guarantees decompositions to unique, minimal-variable throughflow sets is still in need of development. Truly unique solutions are not possible for models in which one or more T_{mi} is a subset of another, leaving the most elegant algebraic formulation of $\mathbf{U}_m$ as the one which employs the fewest total variables. We define any model m for which the elements of $\mathbf{U}_m$ could be completely reduced to algebraic combinations of throughflows as *throughflow reducible*. Each model for which at least one element of the corresponding $\mathbf{U}_m$ seemed not to be completely reduced in this way was further analyzed using a commutative algebraic approach to demonstrate whether or not the entries of that $\mathbf{U}_m$ could be written as algebraic combinations of its T_{mi}. If the simplified algebraic results were supported by this second method, we considered the model *throughflow nonreducible*.

3. Calculation

3.1. Flow and throughflow matrices for algebraic models

For Model 1, the flow matrix $\mathbf{F}_1$ and throughflow matrix $\mathbf{T}_1$ are described as follows:

$$\mathbf{F}_1 = \begin{bmatrix} 0 & 0 \\ b & 0 \end{bmatrix}; \quad \mathbf{T}_1 = \begin{bmatrix} a+b \\ b \end{bmatrix}. \tag{1}$$

The corresponding matrices for Model 2 are:

$$\mathbf{F}_2 = \begin{bmatrix} 0 & b \\ b+c & 0 \end{bmatrix}; \quad \mathbf{T}_2 = \begin{bmatrix} a+b+c \\ b+c \end{bmatrix}. \tag{2}$$

The remaining models form 3×3 $\mathbf{F}_m$ matrices and 3×1 $\mathbf{T}_m$ matrices:

$$\mathbf{F}_3 = \begin{bmatrix} 0 & 0 & 0 \\ b+c & 0 & 0 \\ 0 & c & 0 \end{bmatrix}, \quad \mathbf{T}_3 = \begin{bmatrix} a+b+c \\ b+c \\ c \end{bmatrix} \quad \text{for the three-compartment chain;} \tag{3}$$

$$\mathbf{F}_4 = \begin{bmatrix} 0 & 0 & 0 \\ b & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, \quad \mathbf{T}_4 = \begin{bmatrix} a+b+c \\ b \\ c \end{bmatrix} \quad \text{for the resource competition model;} \tag{4}$$

$$\mathbf{F}_5 = \begin{bmatrix} 0 & b & d \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, \quad \mathbf{T}_5 = \begin{bmatrix} b+d \\ a+b \\ c+d \end{bmatrix} \quad \text{for the apparent competition model;} \tag{5}$$

$$\mathbf{F}_6 = \begin{bmatrix} 0 & 0 & 0 \\ c+d & 0 & 0 \\ b & d & 0 \end{bmatrix}, \quad \mathbf{T}_6 = \begin{bmatrix} a+b+c+d \\ c+d \\ b+d \end{bmatrix} \quad \text{for the intraguild predation model;} \tag{6}$$

$$\mathbf{F}_7 = \begin{bmatrix} 0 & 0 & b \\ b+c+d & 0 & 0 \\ 0 & b+d & 0 \end{bmatrix}, \quad \mathbf{T}_7 = \begin{bmatrix} a+b+c+d \\ b+c+d \\ b+d \end{bmatrix} \quad \text{for the three-compartment cycle;} \tag{7}$$

$$\mathbf{F}_8 = \begin{bmatrix} 0 & 0 & b+c \\ c+d+f & 0 & 0 \\ 0 & b+c+f+g & 0 \end{bmatrix}, \quad \mathbf{T}_8 = \begin{bmatrix} a+b+c+d+f \\ b+c+d+e+f+g \\ b+c+f+g \end{bmatrix} \quad \text{for the two-input cycle.} \tag{8}$$

Finally, the three-compartment cycle with reversed two-compartment cycle corresponds to:

$$\mathbf{F}_9 = \begin{bmatrix} 0 & 0 & b+c+g \\ b+d+e+g & 0 & 0 \\ c=f+g & b+e & 0 \end{bmatrix}; \quad \mathbf{T}_9 = \begin{bmatrix} a+b+c+d+e+f+g \\ b+d+e+g \\ b+c+e+f+g \end{bmatrix}. \tag{9}$$

3.2. Direct utility matrices

As previously stated, the $\mathbf{D}_m$ matrices consist of elements $d_{mij} = (f_{mij} - f_{mji})/T_{mi}$, where m denotes the model, i indicates matrix row, and j indicates matrix column. Based on the $\mathbf{F}_m$ and $\mathbf{T}_m$ described in Section 3.1, we find that:

$$\mathbf{D}_1 = \begin{bmatrix} 0 & -b/(a+b) \\ 1 & 0 \end{bmatrix}; \tag{10}$$

$$\mathbf{D}_2 = \begin{bmatrix} 0 & -c/(a+b+c) \\ c/(b+c) & 0 \end{bmatrix}; \tag{11}$$

$$\mathbf{D}_3 = \begin{bmatrix} 0 & -(b+c)/(a+b+c) & 0 \\ 1 & 0 & -c/(b+c) \\ 0 & 1 & 0 \end{bmatrix}; \tag{12}$$

$$\mathbf{D}_4 = \begin{bmatrix} 0 & -b/(a+b+c) & -c/(a+b+c) \\ 1 & 0 & 0 \\ 1 & 0 & 0 \end{bmatrix}; \tag{13}$$

$$\mathbf{D}_5 = \begin{bmatrix} 0 & b/(b+d) & d/(b+d) \\ -b/(a+b) & 0 & 0 \\ -d(c+d) & 0 & 0 \end{bmatrix}; \tag{14}$$

$$\mathbf{D}_6 = \begin{bmatrix} 0 & -(c+d)/(a+b+c+d) & -b/(a+b+c+d) \\ 1 & 0 & -d/(c+d) \\ b/(b+d) & d/(b+d) & 0 \end{bmatrix}; \tag{15}$$

$$\mathbf{D}_7 = \begin{bmatrix} 0 & -(b+c+d) & b/(a+b+c+d) \\ 1 & 0 & -(b+d)/(b+c+d) \\ -b/(b+d) & 1 & 0 \end{bmatrix}. \tag{16}$$

Recalling from Eq. (8) that $T_{82} = b+c+d+e+f+g$, we have for Model 8:

$$\mathbf{D}_8 = \begin{bmatrix} 0 & -(c+d+f)/(a+b+c+d+f) & (b+c)/(a+b+c+d+f) \\ (c+d+f)/T_{82} & 0 & -(b+c+f+g)/T_{82} \\ -(b+c)/(b+c+f+g) & 1 & 0 \end{bmatrix} \tag{17}$$

Finally, recalling from Eq. (9) that $T_{91} = a+b+c+d+e+f+g$, we have for Model 9:

$$\mathbf{D}_9 = \begin{bmatrix} 0 & -(b+d+e+g)/T_{91} & (b-f)/T_{91} \\ 1 & 0 & -(b+e)/(b+d+e+g) \\ -(b-f)/(b+c+e+f+g) & (b+e)/(b+c+e+f+g) & 0 \end{bmatrix}. \tag{18}$$

3.3. Integral utility matrices

The $\mathbf{U}_m$ matrices are calculated as $(\mathbf{I}_n - \mathbf{D}_m)^{-1}$, where $\mathbf{I}_n$ is the $n \times n$ identity matrix, $n = 2$ when $m = 1$ or 2, $n = 3$ when m is any of 3–9, and $\mathbf{A}^{-1}$ is the inverse matrix of $\mathbf{A}$, such that $\mathbf{AA}^{-1} = \mathbf{I}$. Thus, based on the $\mathbf{D}_m$ from Section 3.2, we can calculate both flow-based and simplified, throughflow-based forms of $\mathbf{U}_m$:

$$\mathbf{U}_1 = \frac{1}{a+2b}\begin{bmatrix} a+b & -b \\ a+b & a+b \end{bmatrix} = \frac{1}{T_{11}+T_{12}}\begin{bmatrix} T_{11} & -T_{12} \\ T_{11} & T_{11} \end{bmatrix}; \tag{19}$$

$$\mathbf{U}_2 = \frac{1}{(a+b+c)(b+c)+c^2}\begin{bmatrix} (a+b+c)(b+c) & -c(b+c) \\ c(a+b+c) & (a+b+c)(b+c) \end{bmatrix} = \frac{1}{T_{21}T_{22}+c^2}\begin{bmatrix} T_{21}T_{22} & -cT_{22} \\ cT_{21} & T_{21}T_{22} \end{bmatrix}; \tag{20}$$

$$\mathbf{U}_3 = \frac{1}{(b+c)^2+(a+b+c)(b+2c)}\begin{bmatrix}(a+b+c)(b+2c) & -(b+c)^2 & c(b+c)\\ (a+b+c)(b+c) & (a+b+c)(b+c) & -c(a+b+c)\\ (a+b+c)(b+c) & (a+b+c)(b+c) & (b+c)(a+2b+2c)\end{bmatrix}$$
$$= \frac{1}{T_{32}^2+T_{31}(T_{32}+T_{33})}\begin{bmatrix}T_{31}(T_{32}+T_{33}) & -T_{32}^2 & T_{32}T_{33}\\ T_{31}T_{32} & T_{31}T_{32} & -T_{31}T_{32}\\ T_{31}T_{32} & T_{31}T_{32} & T_{32}(T_{31}+T_{32})\end{bmatrix}; \tag{21}$$

$$\mathbf{U}_4 = \frac{1}{a+2b+2c}\begin{bmatrix}a+b+c & -b & -c\\ a+b+c & a+b+2c & -c\\ a+b+c & -b & a+2b+c\end{bmatrix} = \frac{1}{T_{41}+T_{42}+T_{43}}\begin{bmatrix}T_{41} & T_{41} & -T_{43}\\ T_{41} & T_{41}+T_{43} & -T_{43}\\ T_{41} & -T_{42} & T_{41}+T_{42}\end{bmatrix}; \tag{22}$$

$$\mathbf{U}_5 = \frac{1}{(b+d)(a+b)(c+d)+d^2(a+b)+b^2(c+d)}\begin{bmatrix}(b+d)(a+b)(c+d) & b(a+b)(c+d) & d(a+b)(c+d)\\ -b(b+d)(c+d) & (a+b)\left((b+d)(c+d)+d^2\right) & -bd(c+d)\\ -d(b+d)(a+b) & -bd(a+b) & (c+d)((b+d)(a+b)+b^2)\end{bmatrix}$$
$$= \frac{1}{T_{51}T_{52}T+d^2T_{52}+b^2T_{53}}\begin{bmatrix}T_{51}T_{52}T_{53} & bT_{52}T_{53} & dT_{52}T_{53}\\ -bT_{51}T_{53} & T_{52}(T_{51}+T_{53}+d^2) & -bdT_{53}\\ -dT_{51}T_{52} & -bdT_{52} & T_{53}(T_{51}+T_{52}+b^2)\end{bmatrix}' \tag{23}$$

$$U_6 = \frac{1}{(a+b+c+d)(c+d)(b+d)(c+d)^2+(b+d)+d^2(a+b+c+d)+b^2(c+d)}$$
$$\times\begin{bmatrix}(a+b+c+d)((c+d)(b+d)+d^2) & -(c+d)((c+d)(b+d)+bd) & (c+d)(b+d)(b-d)\\ (a+b+c+d)((c+d)(b+d)-bd) & (c+d)((a+b+c+d)(b+d)+b^2) & -(b+d)((c+d)(b+d)+d(a+b))\\ (a+b+c+d)(c+d)(b+d) & (c+d)(d(a+b+c+d)-b(c+d)) & (c+d)(b+d)(a+b+2c+2d)\end{bmatrix}$$
$$= \frac{1}{T_{61}T_{62}T_{63}+T_{62}^2T_{63}+d^2T_{61}+b^2T_{62}}\begin{bmatrix}T_{61}(T_{62}T_{63}+d^2) & -T_{62}(T_{62}T_{63}+bd) & T_{62}T_{63}(d-b)\\ T_{61}(T_{62}T_{63}-bd) & T_{62}(T_{61}T_{62}+b^2) & -T_{63}(T_{62}T_{63}+d(T_{61}-T_{62}))\\ T_{61}T_{62}T_{63} & T_{62}(dT_{61}-bT_{62}) & T_{62}T_{63}+(T_{61}-T_{62})\end{bmatrix}; \tag{24}$$

$$\mathbf{U}_7 = \frac{1}{(b+d)(a+b+c+d)(b+c+d)+(b+c+d)^2(b+d)+(a+b+c+d)(b+d)^2+b^2(b+c+d)}$$
$$\times\begin{bmatrix}(a+b+c+d)(b+d)(2b+c+2d) & -(b+c+d)(b+d)(c+d) & (b+c+d)(b+d)(2b+d)\\ (a+b+c+d)(b+d)(2b+c+2d) & (b+c+d)((a+b+c+d)(b+d)+b^2) & (b+d)((a+b+c+d)(b+d)-b(b+c+d))\\ d(a+b+c+d)(b+c+d) & (b+c+d)((a+b+c+d)(b+d)+b(b+c+d)) & (b+c+d)(b+d)(a+2b+2c+2d)\end{bmatrix}$$
$$= \frac{1}{T_{73}(T_{71}T_{72}+T_{72}^2+T_{71}T_{73})+b^2T_{72}}\begin{bmatrix}T_{71}T_{73}(T_{72}+T_{73}) & -T_{72}T_{73}(T_{72}-b) & T_{72}T_{73}(T_{73}+b)\\ T_{71}T_{73}(T_{72}+b) & T_{72}(T_{71}T_{73}+b^2) & -T_{73}(T_{71}T_{73}-bT_{72})\\ T_{71}T_{72}(T_{73}-b) & T_{72}(T_{71}T_{73}+bT_{72}) & T_{72}T_{73}(T_{71}+T_{72})\end{bmatrix}; \tag{25}$$

$$\boldsymbol{U}8=\frac{1}{(b+c+f+g)\left((a+b+c+d+f)(b+c+d+e+f+g)+(c+d+f)^2\right)+(b+c+d+e+f+g)\left((a+b+c+d+f)(b+c+f+g)+(b+c)^2\right)}\begin{bmatrix}u_{811}&u_{812}&u_{813}\\u_{821}&u_{822}&u_{823}\\u_{831}&u_{832}&u_{833}\end{bmatrix},\text{ where} \tag{26a}$$

$$\begin{bmatrix}u_{811}\\u_{821}\\u_{831}\end{bmatrix}=\begin{bmatrix}(a+b+c+d+f)(b+c+f+g)(2b+2c+d+e+2f+2g)\\(a+b+c+d+f)(b+c+f+g)(b+2c+d+f)\\(a+b+c+d+f)((b+c+f+g)(c+d+f)-(2b+2c+d+e+f+g))\end{bmatrix}, \tag{26b}$$

$$\begin{bmatrix}u_{821}\\u_{822}\\u_{823}\end{bmatrix}=\begin{bmatrix}(b+c+d+e+f+g)(b+c+f+g)(-b+d+f)\\(b+c+d+e+f+g)\left((a+b+c+d+f)(b+c+f+g)+(b+c)^2\right)\\(b+c+d+e+f+g)((a+b+c+d+f)(b+c+f+g)+(b+c)(c+d+f))\end{bmatrix},\quad\text{and} \tag{26c}$$

$$\begin{bmatrix}u_{831}\\u_{832}\\u_{833}\end{bmatrix}=\begin{bmatrix}(b+c+f+g)((b+c+f+g)(c+d+f))+(b+c)(b+c+d+e+f+g)\\-(b+c+f+g)((a+b+c+d+f)(b+c+f+g)-(b+c)(c+d+f))\\(b+c+f+g)((a+b+c+d+f)(b+c+d+e+f+g)+(c+d+f)^2)\end{bmatrix}. \tag{26d}$$

$$\mathbf{U}_8=\frac{1}{T_{83}(T_{81}T_{83}+(T_{81}-(a+b))^2)+T_{82}(T_{81}T_{83}+(b+c))}\times\begin{bmatrix}T_{81}T_{83}(T_{82}+T_{83}) & T_{82}T_{83}((T_{81}-(a+b))-(b+c)) & T_{83}(T_{83}(T_{81}-(a+b))+T_{82}(b+c))\\ T_{81}T_{83}((T_{81}-(a+b))+(b+c)) & T_{82}(T_{81}T_{83}+(b+c)^2) & -T_{83}(T_{81}T_{83}-(T_{81}-(a+b))(b+c))\\ T_{81}(T_{83}(T_{81}-(a+b))-T_{82}(b+c)) & T_{82}(T_{81}T_{83}+(b+c)(T_{81}-(a+b))) & T_{83}(T_{81}T_{82}+(T_{82}-(a+b))^2)\end{bmatrix}. \tag{27}$$

$$\boldsymbol{U}9=\frac{1}{(a+b+c+d+e+f+g)(b+d+e+g)(b+c+e+f+g)+(b+d+e+g)^2(b+c+e+f+g)+(a+b+c+d+e+f+g)(b+e)^2+(b+d+e+g)(b-f)^2}\begin{bmatrix}u_{911}&u_{912}&u_{913}\\u_{921}&u_{922}&u_{923}\\u_{931}&u_{932}&u_{933}\end{bmatrix},\text{ where} \tag{28a}$$

$$\begin{bmatrix}u_{911}\\u_{921}\\u_{931}\end{bmatrix}=\begin{bmatrix}(a+b+c+d+e+f+g)((b+d+e+g)(b+c+e+f+g)+(b+e)^2)\\(a+b+c+d+e+f+g)((b+d+e+g)(b+c+e+f+g)+(b+e)(b-f))\\(a+b+c+d+e+f+g)(b+d+e+g)(e+f)\end{bmatrix}, \tag{28b}$$

$$\begin{bmatrix}u_{912}\\u_{922}\\u_{932}\end{bmatrix}=\begin{bmatrix}-(b+d+e+g)((b+d+e+g)(b+c+e+f+g)-(b+e)(b-f))\\(b+d+e+g)((a+b+c+d+e+f+g)(b+c+e+f+g)+(b-f)^2)\\(b+d+e+g)((a+b+c+d+e+f+g)(b+e)+(b+d+e+g)(b-f))\end{bmatrix},\quad\text{and} \tag{28c}$$

$$\begin{bmatrix}u_{913}\\u_{923}\\u_{933}\end{bmatrix}=\begin{bmatrix}(b+d+e+g)(b+c+e+f+g)(2b+e-f)\\-(b+c+e+f+g)((a+b+c+d+e+f+g)(b+e)-(b+d+e+g)(b-f))\\(b+d+e+g)(b+c+e+f+g)(a+2b+c+2d+2e+f+2g)\end{bmatrix} \tag{28d}$$

$$\mathbf{U}_9=\frac{1}{T_{91}T_{92}T_{93}+T_{92}^2T_{93}+T_{91}(b+e)^2+T_{92}(b-f)^2}\times\begin{bmatrix}T_{91}(T_{92}T_{93}+(b+e)^2) & -T_{92}(T_{92}T_{93}-(b+e)(b-f)) & T_{92}T_{93}((b+e)+(b-f))\\ T_{91}(T_{92}T_{93}+(b+e)(b-f)) & T_{92}(T_{91}T_{93}+(b-f)^2) & -T_{93}(T_{91}(b+e)-T_{92}(b-f))\\ T_{91}T_{92}(e+f) & T_{92}(T_{91}(b+e)+T_{92}(b-f)) & T_{92}T_{93}(T_{91}+T_{92})\end{bmatrix}. \tag{29}$$

3.4. Determination of throughflow nonreducibility

The initial calculations in Section 3.3 indicate that Models 2, 5, 6, 7, 8, and 9 may not be throughflow reducible. Considering each result as an ideal membership problem may provide further insight as to the throughflow reducibility of $\mathbf{U}_m$ for these models. In the following proofs, the graded lexicographical order (grlex) is used for the ordering on the polynomial rings. First, given the result for $\mathbf{U}_2$, let I_2 be the ideal generated by entries of $\mathbf{T}_2$, namely $a+b+c$ and $b+c$ (Eq. (28)), over $\mathbb{C}[a, b, c]$. The corresponding matrix for $a+b+c$ and $b+c$ is:

$$\begin{bmatrix} 1 & 1 & 1 \\ 0 & 1 & 1 \end{bmatrix} \tag{30}$$

Based on an observation given in Section 5.5 of Becker and Weispfenning (1993), the row reduced echelon form of this matrix:

$$\begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 1 \end{bmatrix} \tag{31}$$

gives a corresponding Groeber basis for I_2 as $G_2 = \{a, b+c\}$. Alternatively, we can employ computer software such as *Mathematica* to get the same Groebner basis. By Corollary 2 in Section 2.6 of Cox et al. (2007), division of any polynomial in I_2 by G_2 must be zero. However, by the division algorithm over $\mathbb{C}[a, b, c]$ described in Section 2.3 of Cox et al. (2007), the remainder of the division on c^2 by G_2 is c^2, not zero. Hence, c^2, a term that is found in the denominator of the scalar part of $\mathbf{U}_2$, is not in I_2. This proves that not all entries of $\mathbf{U}_2$ can be written as algebraic combinations of T_{21} and T_{22}; thus $\mathbf{U}_2$ is not throughflow reducible.

Next, consider the matrix $\mathbf{U}_5$. Let I_5 be the ideal generated by $b+d$, $a+b$, and $c+d$ over $\mathbb{C}[a, b, c, d]$. By the same procedure applied above (Becker and Weispfenning, 1993), $G_5 = \{a–d, b+d, c+d\}$ is a Groebner basis for I_5. Further, according to the division algorithm (Cox et al., 2007), the remainder of the division of d^2 by G_5 is d^2. Thus, d^2, which is found in the denominator of the scalar part of $\mathbf{U}_5$, is not in I_5 by Corollary 2 of Section 2.6 of Cox et al. (2007); thus, $\mathbf{U}_5$ is not throughflow reducible.

The proof for matrix $\mathbf{U}_6$ is exactly similar to the $\mathbf{U}_5$ case. Let I_6 be the ideal generated by $a+b+c+d$, $c+d$, and $b+d$ over $\mathbb{C}[a, b, c, d]$. Again, by the same procedure applied in former case, $G_6 = \{a–d, b+d, c+d\}$ is a Groebner basis for I_6. Then the division algorithm again implies that the remainder of the division of d^2, a term found in the denominator of the scalar part of $\mathbf{U}_6$, by G_6 is d^2. Thus, d^2 is not in I_6 by Corollary 2 of Section 2.6 in Cox et al. (2007). Hence $\mathbf{U}_6$ is also not throughflow reducible.

Now, considering the matrix $\mathbf{U}_7$, let I_7 be the ideal generated by $a+b+c+d$, $b+c+d$, and $b+d$ over $\mathbb{C}[a, b, c, d]$. Then, $G_7 = \{a, b+d, c\}$ is a Groebner basis for I_7 according to the same method used previously. The remainder of the division of b, a term found in over half of the entries of $\mathbf{U}_7$, by G_7 is $-d$. Therefore, b is not in I_7 by Corollary 2 of Section 2.6 in Cox et al. (2007), and $\mathbf{U}_7$ is not throughflow reducible.

We can consider the matrix $\mathbf{U}_8$ next. Let I_8 be the ideal generated by $a+b+c+d+f$, $b+c+d+e+f+g$, and $b+c+f+g$ over $\mathbb{C}[a, b, c, d, e, f, g]$. Now, $G_8 = \{a-e-g, b+c+f, d+e\}$ is a Groebner basis for I_8. By the division algorithm noted previously, the remainder of the division of $a+b$, which is found in the denominator of the scalar part of $\mathbf{U}_8$, by G_8 is $-c+e-f+g$. Hence by Corollary 2 of Section 2.6 in Cox et al. (2007), $\mathbf{U}_8$ is not throughflow reducible.

Finally, given the matrix $\mathbf{U}_9$, let I_9 be the ideal generated by $a+b+c+d+e+f+g$, $b+d+e+g$, and $b+c+e+f+g$ over $\mathbb{C}[a, b, c, d, e, f, g]$. By the same procedure we applied previously (Becker and Weispfenning, 1993), $G_9 = \{a+d, b+d+e+g, c-d+f\}$ is a Groebner basis for I_9. The remainder of the division of $e+f$, which is found in at least one of the entries of $\mathbf{U}_9$, by G_9 is $e+f$ by the division algorithm (Cox et al., 2007). Thus, by Corollary 2 of Section 2.6 in Cox et al. (2007), $\mathbf{U}_9$ is not throughflow reducible. In summary, none of the $\mathbf{U}_m$ for $m = 2, 5, 6, 7, 8$, and 9 are throughflow reducible.

4. Results and discussion

4.1. Throughflow reducibility of $\mathbf{U}_m$ requires simple input environs

We define here as *throughflow reducible* any NEA matrix for which all elements can be described using only algebraic combinations of the throughflows from the ecological network used to derive that matrix. As seen in Section 3.3, the integral utility matrices $\mathbf{U}_1$, $\mathbf{U}_3$, and $\mathbf{U}_4$ are all throughflow reducible. Algebraic descriptions of the six remaining $\mathbf{U}_m$ appeared to be not throughflow reducible, in that each matrix required the inclusion of at least one individual flow component. Division of at least one flow component term found in $\mathbf{U}_m$ by a Groebner basis G_m, for $m = 2, 5, 6, 7, 8$ and 9, always produced a remainder, indicating that these $\mathbf{U}_m$ were not throughflow reducible.

Models 2 and 7, both representing simple cycles with one input to the network, each required a single flow component in combination with throughflows to describe their respective $\mathbf{U}_m$. Models 5 and 6, representing apparent competition and intraguild predation, respectively, required two flow components and the throughflows to describe $\mathbf{U}_5$ and $\mathbf{U}_6$. Finally, Models 8 and 9, the two-input cycle and the three-compartment/two-compartment cycle combination, respectively, each required three flow components beyond the throughflows to describe their respective $\mathbf{U}_m$. In Models 5, 6, and 7, the non-reducible flow components were equivalent to full internal flows found within those models. However, this was not the case for Models 2, 8, and 9, indicating that, at least with respect to integral utility, the use of flow components to examine throughflow non-reducibility is more parsimonious than using the "complete" flows f_{ij}.

Interestingly, the topological characteristics of these nine models correlate with the throughflow reducibility of their corresponding $\mathbf{U}_m$. The three throughflow reducible models (Models 1, 3, and 4) each exhibit the simplest possible network transactions. Recall that *input* and *output* denote entering and exiting boundary flows into compartments originating and terminating, respectively, outside the defined system. Let *inflow* and *outflow* denote incoming and outgoing flows from and to, respectively, other interior compartments. The throughflow reducible Models 1, 3, and 4, then, contain only compartments that receive either a single input or single inflow, while partitioning the incoming material among an output and zero to two outflows. In contrast, Models 2, 7, and 8 each exhibit an input and inflow for Compartment 1, and Model 8 also has an input and inflow into Compartment 2. Models 5 and 6 exhibit two inflows to Compartment 1 and Compartment 3, respectively. In Model 9, Compartment 1 has both an input and inflow, and Compartment 3 exhibits two inflows. Thus, throughflow reducibility of $\mathbf{U}_m$ appears to relate directly to the type of input environs found in Model m, and more specifically, the level of complexity for input environs of path length one. Patten (1981) and Patten and Auble (1980, 1981) have previously described environs as *extended niches* or *superniches*, with environs of path length one in the inflow or outflow direction more specifically described as ecological *input niches* or *output niches*, respectively. The exclusive presence of simple (i.e., unpartitioned) input niches therefore appears to generate throughflow reducibility in $\mathbf{U}_m$ of dissipative ecological network models, while more complex ones require the inclusion of specific flows.

That the topology of input niches influences the throughflow reducibility of the corresponding $\mathbf{U}_m$ leads to the question of whether output niche topology may also influence throughflow reducibility. In this case, the conditions must be considered from a holistic perspective rather than on output niches of individual compartments. In particular, both throughflow reducible and non-reducible $\mathbf{U}_m$ are seen for models in which the compartments produce either one output only, or one output and one or more outflows; e.g., Models 3 and 5. The presence of a threshold number of outflows within a model, or high network connectivity, appears to be sufficient for throughflow nonreducibility, as n-compartment models exhibiting n or more total outflows were not throughflow reducible. This was not a necessary condition for nonreducibility, however, as Model 5 has $n-1$ outflows for $n=3$.

4.2. Parametrically-determined qualitative relations between compartments

The current work builds directly on that of Patten and Whipple (2007) and Lobanova et al. (2009), and indirectly on other work (Fath, 2007; Fath and Patten, 1998) in that the nine models for which $\mathbf{U}_m$ was calculated can be identified as having topologically-determined or parametrically-determined ecological relations, described by $sign(\mathbf{U}_m)$. To reiterate, topologically-determined relations are those depending only on the structure of the model, while parametrically-determined relations require the consideration of flow values. Since internal flows are assumed to be greater than zero (i.e., allowing any $f_{ij}=0$ generates a different topology than that of the model under consideration), all throughflows and flow variables are also greater than zero for the $\mathbf{D}_m$ and $\mathbf{U}_m$ calculated here. Thus, both two-compartment models have topologically-determined relations of:

$$sign(\mathbf{U}_n)=\begin{bmatrix} + & - \\ + & + \end{bmatrix},$$

where $n=1$ or 2. The results for Model 1 are consistent with those of Fath (2007). The results for Model 2 are inconsistent with the conclusions drawn by Patten and Whipple (2007), who suggested that cycling itself produces parametrically determined $sign(\mathbf{U})$ when inputs were present. In the underlying analysis for that work, however, Model 2 was never explicitly examined; instead, a three-compartment cycle akin to Model 7, with varying numbers and positions of inputs, was considered. Interestingly, this work identified the necessity of an input for parametric determination, as the three-compartment cycle without inputs had a topologically determined $sign(\mathbf{U})$ (Patten and Whipple, 2007). This highlights the importance of considering inputs as well as internal flows in any comprehensive analysis of $sign(\mathbf{U})$, and in the current work, we consider different numbers of inputs as indicating different model topologies.

Next, Models 3–5 all clearly have topologically-determined relations, consistent with previous work (Fath, 2007; Fath and Patten, 1998; Lobanova et al., 2009; Patten and Whipple, 2007):

$$sign(\mathbf{U}_3)=\begin{bmatrix} + & - & + \\ + & + & - \\ + & + & + \end{bmatrix},\quad sign(\mathbf{U}_4)=\begin{bmatrix} + & - & - \\ + & + & - \\ + & - & + \end{bmatrix},\quad \text{and}\quad sign(\mathbf{U}_5)=\begin{bmatrix} + & + & + \\ - & + & - \\ - & - & + \end{bmatrix}.$$

The four remaining models require additional consideration, as multiple matrix elements in the corresponding $\mathbf{U}_m$ contain individual flows subtracted individually or multiplied with other flows or throughflows. It is possible that such elements may vary from negative to positive based on these flows' values. For Model 6, the integral utility is represented as in Eq. (24):

$$\frac{1}{T_{61}T_{62}T_{63}+T_{62}^2T_{63}+d^2T_{61}+b^2T_{62}}\begin{bmatrix} T_{61}(T_{62}T_{63}+d^2) & -T_{62}(T_{62}T_{63}+bd) & T_{62}T_{63}(d-b) \\ T_{61}(T_{62}T_{63}-bd) & T_{62}(T_{61}T_{63}+b^2) & -T_{63}(T_{62}T_{63}+d(T_{61}-T_{62})) \\ T_{61}T_{62}T_{63} & T_{62}(dT_{61}-bT_{62}) & T_{62}T_{63}(T_{61}+T_{62}) \end{bmatrix}.$$

Recognizing that the scalar is positive, we can readily see that over half the elements in $\mathbf{U}_6$ are topologically determined:

$$sign(\mathbf{U}_6)=\begin{bmatrix} + & - & ? \\ ? & + & ? \\ + & ? & + \end{bmatrix}.$$

The remaining four elements depend on the signs of:

$$d-b,\quad T_{61}-T_{62},\quad T_{62}T_{63}-bd,\ \text{and}\ dT_{61}-bT_{62}.$$

First, $d-b$ may be negative if $b>d$, zero if $b=d$, or positive if $b<d$. This implies that the element (1, 3) is parametrically determined by the relative values of b and d. Next, given that $T_{61}=a+b+c+d$ and $T_{62}=c+d$, we know that $T_{61}-T_{62}=a+b>0$. This, in turn, implies that element (2, 3) is negative, since the element includes a multiplier of $-T_{63}$. Third, since $T_{63}=b+d$, we also know that:

$$T_{62}T_{63}-bd=bc+cd+bd+d^2-bd=bc+cd+d^2>0.$$

Thus, the element (2, 1) is positive. Finally,

$$dT_{61}-bT_{62}=ad+bd+cd+d^2-bc-bd=ad+cd+d^2-bc.$$

This term, and therefore element (3, 2), may be negative, zero, or positive, depending on the relative magnitudes of the flow variables. In particular, it will be positive whenever $d\geq b$, but it may be positive, negative, or zero based on the values of a and c when $d<b$. Thus,

two elements of $\mathbf{U}_6$ are parametrically determined, one by the relative magnitude of two flows, and the other by the relative magnitudes of four flows:

$$sign(\mathbf{U}_6) = \begin{bmatrix} + & - & (b,d)? \\ + & + & - \\ + & (a,b,c,d)? & + \end{bmatrix},$$

and in particular,

$$sign(\mathbf{U}_6) = \begin{bmatrix} + & - & + \\ + & + & - \\ + & + & + \end{bmatrix} \text{ for } b < d, \quad \begin{bmatrix} + & - & 0 \\ + & + & - \\ + & + & + \end{bmatrix}, \text{ for } b = d, \quad \text{and} \quad \begin{bmatrix} + & - & - \\ + & + & - \\ + & (a,b,c,d)? & + \end{bmatrix} \text{ for } b > d.$$

This result is broadly consistent with previous findings (Lobanova et al., 2009; Patten and Whipple, 2007), but differs somewhat from previous considerations of the possible states of the parametrically determined elements, as Lobanova et al. (2009) did not explicitly include the possibility of null-signed elements.

For Model 7, the integral network utility matrix $\mathbf{U}_7$ is represented as in Eq. (25):

$$\frac{1}{T_{73}(T_{71}T_{72}+T_{72}^2T_{71}T_{73})+b^2T_{72}} \begin{bmatrix} T_{71}T_{73}(T_{72}+T_{73}) & -T_{72}T_{73}(T_{72}-b) & T_{72}T_{73}(T_{73}+b) \\ T_{71}T_{73}(T_{72}+b) & T_{72}(T_{71}T_{73}+b^2) & -T_{73}(T_{71}T_{73}-bT_{72}) \\ T_{71}T_{72}(T_{73}-b) & T_{71}(T_{71}T_{73}+bT_{72}) & T_{72}T_{73}(T_{71}+T_{72}) \end{bmatrix}.$$

Here, the scalar is again clearly positive, and we have:

$$sign(\mathbf{U}_7) = \begin{bmatrix} + & ? & + \\ + & + & ? \\ ? & + & + \end{bmatrix},$$

where the three unknown signs depend on the signs of:

$$T_{72}-b, \qquad T_{71}T_{73}-bT_{72}, \quad \text{and} \quad T_{73}-b.$$

By simple substitution, we know that $T_{72}-b=c+d$ and that $T_{73}-b=d$, so the corresponding matrix elements (1, 2) and (3, 1) have negative and positive topologically-determined signs, respectively. Finally,

$$T_{71}T_{73}-bT_{72}=(a+b+c+d)(b+d)-b^2-bc-bd=ab+ad+bd+cd+d^2,$$

which is always positive. Since the remainder of element (2, 3) consists of a negatively-signed throughflow, the element overall is negative. Thus, $sign(\mathbf{U}_7)$ is topologically determined:

$$sign(\mathbf{U}_7) = \begin{bmatrix} + & - & + \\ + & + & - \\ + & + & + \end{bmatrix}.$$

This topological determination of $sign(\mathbf{U}_7)$ is consistent with the findings of Lobanova et al. (2009), but may be considered to differ from the conclusions of Patten and Whipple (2007), who indicated that simple cycles could be subject to exogenous parametric determination. It is important to note, however, that the description of exogenous parametric determination previously described includes the possibility of differing locations and numbers of inputs, which inherently involves changing the overall network's connectedness with the external environment. Thus, the results for $sign(\mathbf{U}_2)$ and $sign(\mathbf{U}_7)$ suggest that it may not be cycling *per se* which gives rise to parametric determination, but rather changes in the topology of inputs.

Model 8 differs from Model 7 only in that it is more strongly connected to the external environment due to the presence of an additional input. Further insights can therefore be gained on the interpretation of exogenous parametric determination by examining $sign(\mathbf{U}_8)$. Next, the integral utility matrix for Model 8 was calculated as in Eq. (26):

$$U_8 = \frac{1}{T_{83}(T_{81}T_{83}+(T_{81}-(a+b))^2)+T_{82}(T_{81}T_{83}+(b+c)^2)} \times \begin{bmatrix} T_{81}T_{83}(T_{82}+T_{83}) & T_{82}T_{83}((T_{81}-(a+b))-(b+c)) & T_{83}(T_{83}(T_{81}-(a+b))+T_{82}(b+c)) \\ T_{81}T_{83}((T_{81}-(a+b))+(b+c)) & T_{82}(T_{81}T_{83}+(b+c)^2) & -T_{83}(T_{81}T_{83}-(T_{81}-(a+b))(b+c)) \\ T_{81}(T_{83}(T_{81}-(a+b))-T_{82}(b+c)) & T_{82}(T_{81}T_{83}+(b+c)(T_{81}-(a\_b))) & T_{83}(T_{81}T_{82}+(T_{82}-(a+b))^2) \end{bmatrix}.$$

We can readily see that the scalar for $\mathbf{U}_8$ is always positive. Furthermore, from $\mathbf{T}_8$ (Eq. (8)), we know that $T_{81}=a+b+c+d+f$. This implies that $T_{81}-(a+b)=c+d+f$, so that we have:

$$sign(\mathbf{U}_8) = \begin{bmatrix} + & ? & + \\ + & + & ? \\ ? & + & + \end{bmatrix},$$

where the three unknown signs depend on the signs of:

$$(T_{81}-(a+b))-(b+c), \qquad T_{81}T_{83}-(T_{81}-(a+b))(b+c), \quad \text{and} \quad (T_{81}-(a+b))-T_{82}(b+c).$$

Based on substitution of T_{81}, we know that:

$$T_{81}-(a+b)-(b+c)=c+d+f-b-c=d+f-b,$$

which may be positive, negative, or zero, depending on the values of b, d, and f. In particular, both this portion and the overall value of (1, 2) will be positive when $d+f>b$, zero when $d+f=b$, and negative when $d+f<b$. Next, given that $T_{83}=b+c+f+g$, we know that:

$$T_{81}T_{83}-(T_{81}-(a+b))(b+c)=(a+b+c+d+f)(b+c+f+g)-(c+d+f)(b+c)=ab+ac+af+ag+b^2+bc+bf+bg+cf+cg+df+dg+f^2+fg,$$

which must always be positive. The corresponding matrix element (2, 3) is therefore topologically determined as negative based on its leading sign. Finally, based on substitution of T_{82}, we also have:

$$(T_{81}-(a+b))-T_{82}(b+c)=c+d+f-(b+c+d+e+f+g)(b+c)=(1-(b+c))(c+d+f)-(b+c)(b+e+g),$$

which may be positive, negative, or zero based on the values of flows b through g. In particular, when we have $b+c\geq 1$, the corresponding element (3, 1) will be negative; when $b+c<1$, the corresponding matrix element to be positive, negative, or zero, depending on the values of all flows other than a.

In summary, the signs of two elements in $\mathbf{U}_8$ are parametrically determined:

$$sign(\mathbf{U}_8)=\begin{bmatrix} + & (b,d,f)? & + \\ + & + & - \\ (b,c,d,e,f,g)? & + & + \end{bmatrix}.$$

All but one flow is incorporated into the parametric determinations overall in Model 8. However, if we know that $d+f>b$, $d+f=b$, or $d+f<b$, then we have:

$$sign(\mathbf{U}_8)=\begin{bmatrix} + & + & + \\ + & + & - \\ (b,c,d,e,f,g)? & + & + \end{bmatrix}, \quad sign(\mathbf{U}_8)=\begin{bmatrix} + & 0 & + \\ + & + & - \\ (b,c,d,e,f,g)? & + & + \end{bmatrix}, \quad \text{or} \quad sign(\mathbf{U}_8)=\begin{bmatrix} + & - & + \\ + & + & - \\ (b,c,d,e,f,g)? & + & + \end{bmatrix},$$

respectively.

Similarly, if we know that $b+c\geq 1$, we have:

$$sign(\mathbf{U}_8)=\begin{bmatrix} + & (b,d,f)? & + \\ + & + & - \\ - & + & + \end{bmatrix}.$$

Overall, this parametric determination of $sign(\mathbf{U}_8)$ contrasts with the topological determination of $sign(\mathbf{U}_7)$. That the determination of ecological relations differs between these two models, which both contain a single three-compartment cycle, further supports the idea that cycling itself is not the topological property which confers parametric determination, as initially suggested by Patten and Whipple (2007). However, the parametric determination of $sign(\mathbf{U}_8)$ can be interpreted to support the previous concept of exogenous parametric determination (Patten and Whipple, 2007), insofar as the number of inputs (one for Model 7, two for Model 8) clearly influences elements (1, 2) and (3, 1) for the cycling models' respective $sign(\mathbf{U}_m)$. However, a broader interpretation of exogenous parametric determination, in which all variables associated with a model's inputs influence parametric determination of $sign(\mathbf{U}_m)$, does not appear to be valid for these cases, as a is not involved in parametric determination of $sign(\mathbf{U}_8)$. Thus, since the number of inputs differentially influences the determination types of Models 7 and 8, we suggest that the concept of exogenous determination be restricted to comparisons between models differing in their input topologies.

Finally, the integral utility matrix for Model 9 was described in Eq. (27) as:

$$\mathbf{U}_9=\frac{1}{T_{91}T_{92}T_{93}+T_{92}^2T_{93}+T_{91}(b+e)^2+T_{92}(b-f)^2}$$
$$\times\begin{bmatrix} T_{91}(T_{92}T_{93}+(b+e)^2) & -T_{92}(T_{92}T_{93}-(b+e)(b-f)) & T_{92}T_{93}((b+e)+(b-f)) \\ T_{91}(T_{92}T_{93}+(b+e)(b-f)) & T_{92}(T_{91}T_{93}+(b-f)^2) & -T_{93}(T_{91}(b+e)-T_{92}(b-f)) \\ T_{91}T_{92}(e+f) & T_{92}(T_{91}(b+e)+T_{92}(b-f)) & T_{92}T_{93}(T_{91}+T_{92}) \end{bmatrix}.$$

The scalar for the matrix is guaranteed to be positive, because the one segment that introduces a potential negative value is squared. Given this, we also know that:

$$sign(\mathbf{U}_9)=\begin{bmatrix} + & ? & ? \\ ? & + & ? \\ + & ? & + \end{bmatrix},$$

where the five unknown signs depend on the signs of:

$$T_{92}T_{93}-(b+e)(b-f),\qquad (b+e)+(b-f),\qquad T_{92}T_{93}+(b+e)(b-f),\qquad T_{91}(b+e)-T_{92}(b-f),\quad \text{and}\quad T_{91}(b+e)+T_{92}(b-f).$$

First, based on substitution of T_{92} and T_{93} in accordance with Eq. (9), we know that:

$$T_{92}T_{93}-(b+e)(b-f)=(b+d+e+g)(b+c+e+f+g)-(b^2+be-bf-ef)=bc+bd+be+2bf+2bg+cd+ce+cg+de+df+e^2+2ef+2eg+fg+g^2,$$

which must always be positive. This leaves the overall matrix element (1, 2) topologically determined as negative based on its leading sign. Next, we have:

$$(b+e)+(b-f)=2b+e-f,$$

which will be positive when $2b+e>f$, zero when $2b+e=f$, and negative when $2b+e<f$. Thus, the corresponding element (1, 3) is parametrically determined. Third, we have:

$$T_{92}T_{93}+(b+e)(b-f)=(b+d+e+g)(b+c+e+f+g)+b^2+be-bf-ef=2b^2+bc+bd+3be+2bg+cd+ce+cg+de+df+dg+e^2+2eg+fg+g^2,$$

which, along with its corresponding element (2, 1), is topologically determined as positive. Next, the sign of (2, 3) depends on:

$$T_{91}(b+e)-T_{92}(b-f)=(a+b+c+d+e+f+g)(b+e)-(b+d+e+g)(b-f)=ab+bc+2bf+ae+be+ce+de+e^2+2ef+eg+df+fg.$$

This portion it is always positive; with a negative leading sign, the corresponding matrix element is therefore topologically determined as negative. The last parameterization is:

$$T_{91}(b+e)+T_{92}(b-f)=(a+b+c+d+e+f+g)(b+e)+(b+d+e+g)(b-f)=ab+2b^2+bc+2bd+3be+2bg+ae+ce+de+e^2+eg-df-fg=(b+e)(a+2b+c+e)+(2b+e-f)(d+g).$$

If $2b+e\geq f$, this will be positive, along with the overall element (3, 2). If $2b+e<f$, this and the overall element may be positive, negative, or zero, based on the relative values of all flows in the model. To summarize, Model 9 produces two parametrically determined elements in its relational matrix:

$$sign(\mathbf{U}_9)=\begin{bmatrix}+ & - & (b,e,f)?\\ + & + & -\\ + & (a,b,c,d,e,f,g)? & +\end{bmatrix}.$$

One of the parametrically determined elements depends on three flow values, while the other depends on all seven in the model. We can also narrow down the outcomes based on the relationships among *b*, *e*, and *f*, so that:

$$sign(\mathbf{U}_9)=\begin{bmatrix}+ & - & +\\ + & + & -\\ + & + & +\end{bmatrix},\quad sign(\mathbf{U}_9)=\begin{bmatrix}+ & - & 0\\ + & + & -\\ + & + & +\end{bmatrix},\quad \text{and}\quad sign(\mathbf{U}_9)=\begin{bmatrix}+ & - & -\\ + & + & -\\ + & (a,b,c,d,e,f,g)? & +\end{bmatrix}$$

when $2b+e>f$, $2b+e=f$, and $2b+e<f$, respectively. The parametric determination of Model 9 contrasts with the structural determination of Model 7, raising the possibility that the presence of multiple cycles does contribute to parametric determination of $sign(\mathbf{U}_m)$, similarly to the presence of multiple inputs. To our knowledge, such a topology has not previously been considered for analysis of $\mathbf{U}_m$ or $sign(\mathbf{U}_m)$.

Overall, it is evident that all models for which $\mathbf{U}_m$ was throughflow reducible (i.e., Models 1, 3, and 4) exhibited topological determination. Although throughflow reducibility appears to be a sufficient condition for topological determination, it was not necessary; only models for which $\mathbf{U}_m$ was not throughflow reducible exhibited parametric determination in $sign(\mathbf{U}_m)$, in particular Models 6, 8, and 9. However, $sign(\mathbf{U}_2)$, $sign(\mathbf{U}_5)$, and $sign(\mathbf{U}_7)$ were topologically determined. It is further noteworthy that, for all nine models examined here, the overall greater presence of positive elements than negative or zero elements is topologically guaranteed, a finding that is described further in the Janus Hypothesis (Patten, 2014). Although the number of parametrically determined elements in $sign(\mathbf{U}_m)$ varied from zero to two, at least five of the nine matrix elements are topologically determined as positive in each of the three-compartment models. This pattern was consistent regardless of whether or not parametric determination arose from the overall model topology. This finding extends the identification of network mutualism in all possible three-compartment model topologies for a universally fixed transfer efficiency of $g_{ij}=0.1$ (Fath, 2007) and previous descriptions of network mutualism in particular model topologies (Fath, 2007; Lobanova et al., 2009) to include $sign(\mathbf{U})$ for models not previously considered in their generalized form.

An interesting pattern seen for models having parametrically determined elements in $sign(\mathbf{U}_m)$ was the large number of flow components involved in determining these elements. Particular parametrically determined matrix elements could be determined using small numbers of components, e.g., (1, 3) in $sign(\mathbf{U}_6)$. However, parametric determination of $sign(\mathbf{U}_6)$ and $sign(\mathbf{U}_9)$ as a whole did not allow the dismissal of any components, and $sign(\mathbf{U}_8)$ allowed the dismissal of only *a*, which made up part of the input and output for Compartment 1 therein. Algebraically analyzing the flows involved in parametrically determining the sign of a given element in $\mathbf{U}_m$, also allows the identification of conditions under which a model with numerical flows will generate positive, zero, or negative parametrically-determined elements. Lobanova et al. (2009) previously carried out similar work in identifying possible values of $sign(\mathbf{U}_m)$, although the approach for that work was centered more strongly around individual flows rather than throughflows and flow components, as we have done here. We did not exhaustively carry out such work here due to the high number of flow components for some matrix elements, but we have attempted to identify restrictions on $sign(\mathbf{U}_m)$ based on combinations of two or three components. In keeping with previous work, elements with signs parametrically determined by n flows may ultimately have their boundary conditions (i.e., conditions under which the sign of the element is zero) graphed in n-dimensional space, somewhat similar to the plot in Lobanova et al. (2009) of Model 6s possible goal functions.

4.3. Ecological interpretation of integral network utility from a throughflow perspective

The above work demonstrates the ways in which a throughflow perspective can assist in identifying topological vs. parametric determination of overall relational types between compartments within an ecosystem. First, throughflow reducibility appears to be a sufficient condition for topological determination of $sign(\mathbf{U}_m)$. Second, that individual throughflows are invariably positive when defined as sums of algebraic, positive inputs and inflows (or outputs and outflows) considerably facilitates the analysis of $\mathbf{U}_m$ element signs and the identification of critical flows that may change the sign of a parametrically-determined flow. The positive nature of throughflows also contributes to overall positive relationships emergent in transactional (energy–matter storage and flow) networks, as reflected in two Network Environ Analysis properties: *network synergism* ($\mathbf{U}$ matrix |+benefit/−cost| ratio > 1; Fath and Patten, 1998; Patten, 1991, 1992) and *network mutualism* ($\mathbf{U}$ matrix +/– sign ratio > 1; Patten, 1991, 1992).

The throughflow perspective helps to reveal a mathematical basis for network synergism within particular model topologies that, to our knowledge, has not previously been shown. We begin by considering how relative measures of throughflow centrality within each of our nine models as recently described by Borrett (2013). *Throughflow centrality* is an indicator of a compartment's network centrality and defined as that compartment's quantitative throughflow (Borrett, 2013). Among the models used in the current study, only two (Models 5 and 8) have any ambiguity about their relative throughflow centrality; in all other cases, Compartment 1 is both the lone compartment with an input and has the greatest throughflow centrality in the model. Consistent with Borrett's empirically-supported hypothesis that primary producers, decomposers, and nonliving compartments tend to have the greatest throughflow centrality in ecosystems (Borrett, 2013), inputs are often used to represent primary production or influx of organic matter (e.g., Dame and Patten, 1981), although it is theoretically possible to generate a model in which the input is based on, for example, migration. While Models 5 and 8 are at least partially indeterminate in the relative throughflow centrality values for their respective compartments, this is nevertheless associated with the presence of two inputs for each model.

Next, considering the relative values of T_{mi} within $\mathbf{U}_m$ makes it possible to relate throughflow centrality to network synergism. As an example, consider Model 4, in which the first compartment has greater throughflow centrality than the second and third compartments: $T_{41} > T_{42}, T_{43}$. We also know that:

$$\mathbf{U}_4 = \frac{1}{T_{41}+T_{42}+T_{43}}\begin{bmatrix} T_{41} & -T_{42} & -T_{43} \\ T_{41} & T_{41}+T_{43} & -T_{43} \\ T_{41} & -T_{42} & T_{41}+T_{42} \end{bmatrix}.$$

Based on the relative throughflow centralities of each compartment, then, we can quantitatively rank the absolute values of each element (u_{4ij}):

$$(2,2)\&(3,3) > (1,1) = (2,1) = (3,1) > |(1,2)|, |(3,2)|, |(1,3)|, \&|(2,3)|.$$

Since the total number of positive elements is greater than the total number of negative elements, and since each negative element is by definition smaller than the smallest of the positive elements, we know that:

$$\sum_{i=1,j=1}^{(3,3)} u_{4ij} > 0.$$

Thus, network synergism holds for all valid flow quantities of Model 4. Similar demonstrations can be carried out for at least Models 1–3 and 5–7 (data not shown). Fath and Patten (1998) have previously demonstrated the generality of network synergism, so the current results, while not comprehensive, are both consistent with previous work and highlight the role of model-specific throughflows in generating network synergism.

Finally, the throughflow perspective of network integral utility allows the identification of key transactional flows within the network that generate throughflow non-reducibility. This is particularly relevant to understanding the complexity of natural ecosystems and the ways in which they differ from conventional designed systems. It may be possible to challenge the idea that "sustainability is unsustainable" (Patten, 2014, Section 6.1.8) by identifying particular ways in which we may use "dynamical systems principles to both minimize change and match human dynamics to global dynamics" (Patten, 2014, Section 6.1.9) or create human-designed systems that more closely approximate natural ecosystems. Regarding the former, the "assembly-line" tradition of the industrial economic model is strongly associated with the construction of simple input niches, a pattern that began within conventional manufacturing environments but was soon extended to agricultural systems. While networks consisting only of simple input niches generate throughflow reducibility, and therefore are more tractable both mathematically and conceptually, it is evident that even in three-compartment networks the number of possible throughflow non-reducible models outweighs the number of throughflow reducible ones (see also Patten and Whipple, 2007). Furthermore, although specialist species are well known, it is common for heterotrophs to have complex input niches, thus producing ecological networks likely to be nonreducible. The throughflow perspective allows us to move beyond the view of ecosystems as "irreducibly complex" by allowing both easier identification and quantification of "extra" non-throughflow components that arise in the associated $\mathbf{U}$. This feature allows us to quantitatively understand the nature of ecological complexity in particular systems. For example, the importance of the relative values of $2b+e$ and f in Model 9's relations between Compartments 1 and 3 translates into a consideration of the relative strengths of two different pathways: one from the input to Compartment 1, flow to Compartment 3, and finally output (represented by f), and the other from Compartment 2 to Compartment 3 ($b+e$), which then bifurcates to output (e) and Compartment 1 (b) (Fig. 3). Such analyses may

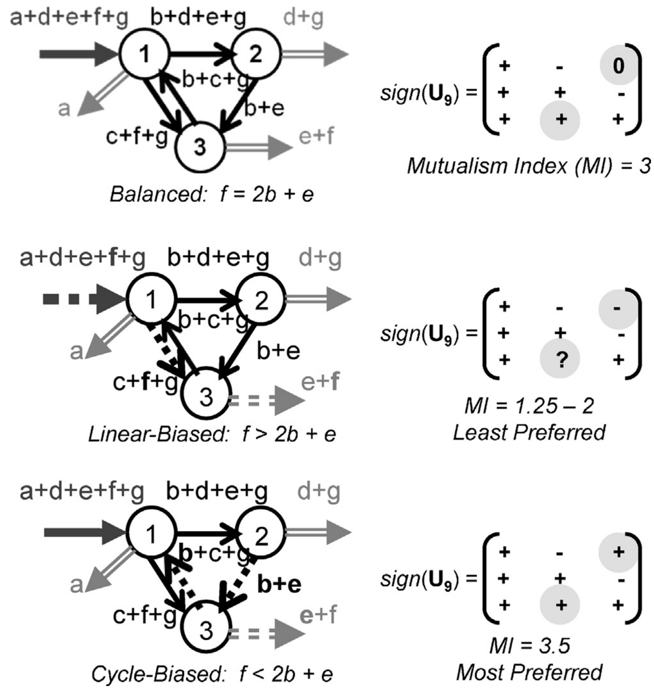

Fig. 3. Assessing Model 9 sustainability based on flow components *b*, *e*, and *f*. Depending on the relative values of *f* and $2b+e$, the mutualism index of Model 9 may be increased up to 3.5 or decreased down to 1.25. Designing or altering systems to produce higher mutualism indices may be one approach to improve sustainability; here, maintaining $f<2b+e$ would be the most preferred outcome.

contribute to greater sustainability in human-designed or human-dominated systems by clarifying focal transactions for environmental management and mitigation scenarios. This novel approach would benefit from further formalization beyond the scope of this paper, but like NEA-based ecological risk assessments (Chen et al., 2011) and NEA-based functional ecosystem assessments (Christian et al., 2009), it represents a new way in which systems ecology can be applied to prevent or mitigate negative environmental changes.

5. Conclusions

Here, we have used a symbolic algebra approach to analyze integral utility matrices for nine small ecosystem models. In particular, the use of algebraic sums of flow components allowed us to analyze nine $\mathbf{U}_m$ at a finer scale than the use of "complete" flows f_{ij} allows. By reducing the elements of $\mathbf{U}_m$ for each model m to compartment throughflows to the greatest extent possible, we have identified model topologies producing throughflow reducible and non-reducible $\mathbf{U}_m$, linked throughflow reducibility to the presence of only simple input niches, and identified throughflow reducibility as a sufficient, but not necessary, condition for topological determination of $sign(\mathbf{U}_m)$. The throughflow perspective also facilitated the analysis of parametrically-determined elements within $sign(\mathbf{U}_m)$ by allowing a focus on negatively-signed or subtracted throughflow and flow components. We demonstrated that simple cycles can produce topologically-determined $sign(\mathbf{U}_m)$, although additional inputs to a cycle will generate parametric determination. Beyond this novel finding, our results are broadly consistent with previous work on network mutualism and synergism while focusing on specific model topologies to analyze the mathematical, topology-specific basis for these phenomena more closely. For instance, we provided an example showing how comparisons of throughflow centrality among compartments for a given model topology can help to reveal the quantitative basis of its network synergism. We note finally that the throughflow perspective of integral network utility allows us to identify specific transactional flows that contribute to ecological complexity, helping to qualitatively distinguish between natural ecosystems and most human-designed systems.

The current work lays a foundation to further generalize two and three-compartment models. The development of a universal three-compartment model in particular, with algebraic inputs, flows, and outputs, is nontrivial and would allow the calculation of algebraic **F**, **T**, **D**, and **U** matrices for all possible network topologies by setting to zero any algebraic components lacking a positive value, rather than adding new ones. The resulting matrices could be considered as systemic utility "building blocks" facilitating numerical or algebraic work in applied or basic NEA and may be able to provide more general insights into the role of throughflow in integral network utility.

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