B.D. Fath, International Journal of Ecodynamics. Vol. 1, No. 1 (2006) 28–43

A NONTHERMODYNAMIC CONSTRAINT TO TROPHIC TRANSFER EFFICIENCY BASED ON NETWORK UTILITY ANALYSIS

B.D. FATH
Biology Department, Towson University, Towson, MD 21252, USA.

ABSTRACT

In this paper, network utility analysis is used to investigate the efficiency of flow between two ecological components. Empirical studies have shown that the efficiency of resource transfer between trophic levels in an ecosystem tends to be relatively low in spite of the considerable amount of time organisms have had to evolve efficient uptake and assimilation processes. In fact, a general rule of thumb in ecology is that only about 10% of the total energy intake into an organism is transferred to the next trophic level. In addition to the possible thermodynamic, physical, chemical, and biological limitations, this research indicates another possible limitation to trophic transfer efficiency. Utility analysis, a resource-based input–output measure of the overall usefulness a compartmental flow has on the entire system, is used to identify the qualitative and quantitative relations in a model. However, when the transfer efficiencies are too large the utility metric is not calculable. This is interpreted to mean that utility, which is inherently positive, is not conveyed within these systems. This research shows for simple food chain models where the breakdown in utility analysis occurs and what patterns exist as systems approach this threshold. Although computable utility may not be a necessary condition for low trophic efficiency, it may be sufficient to explain low transfer efficiencies in ecosystems.

Keywords: ecological efficiency, mathematical ecology, network analysis, trophic transfer efficiency, utility analysis.

1 INTRODUCTION

Energy is the ultimate limiting factor for all processes. In a homogenous environment lacking an energy gradient, no work can be performed and no life can exist. Life on earth is possible because of the thermal gradient established by the temperature difference between solar (6000 K) and terrestrial (300 K) surfaces. Ecological webs, of which organisms are a part, capture and concentrate this energy. Once captured, this energy establishes ecosystems as 'far from equilibrium' such that the ecosystem's exergy storage and energy throughflow increase [1, 2]. Living organisms continually work against entropic processes to build and sustain their own life. It has also been proposed that ecosystem development is a response to degrade the energy gradient particularly early in the development stage [3]. Here, a new perspective, using network utility analysis, is proposed as another possible limitation to the efficiency of energy transfer between components of an ecosystem.

There are many physical, chemical, and biological limitations to the effectiveness and efficiency of energy transfer in nature. The primary constraints are supplied by the two laws of thermodynamics. The first law of thermodynamics states that energy cannot be created or destroyed. Ecologically this means the sum of all energy that enters into a component must equal the sum of all the energy leaving. This law does not implicate a specific form of the energy but rather refers to energy of all forms passing through the system. Therefore, the efficiency of any energy transfer must range between 0 and 100%. The second law of thermodynamics takes into account the form of energy and states that not all the energy in the system can be converted to useful work (exergy). Some energy must be lost as waste heat as the overall entropy of the system increases. Ecologically this means that not all energy in one species can be passed to the next species without some loss of useful energy, and the transfer efficiency must be less than 100%. Unusable energy is represented in the flow exiting the components

ISSN: 1743-5242 (paper format), ISSN: 1743-5250 (online), http://journals.witpress.com

that leaves the system boundaries to the external environment. The second law also requires system openness because compartments are energetically open to their environments.

In addition to thermodynamic constraints to trophic transfer efficiency, there are also ecological constraints. Empirical evidence has shown that trophic transfer efficiencies are relatively low compared to the limit imposed by thermodynamics. ‘It may be expected that future field estimates [of trophic transfer efficiency] will tend to converge on some relatively narrow range of values around 10 percent’ [4]. This empirical value, which is an order of magnitude less than the theoretical limit imposed by thermodynamics, may indicate that there are other processes limiting the efficiency. One possibility, based on network utility analysis, is investigated here.

2 METHODS

2.1 Network analysis

In network ecology, the structure and function of an ecological network is analyzed using mathematical models based on the flows and storages in a system. The techniques used in network ecology originated in input–output economics as a way to identify the relationships between the many sectors of an integrated economic system [5]. Hannon [6] applied economic input–output analysis to ecological systems, and Finn [7], Barber [8], Patten [9], Ulanowicz [10, 11], and others further extended this methodology (see [12] for more details). Path analysis can be used to identify the path structure in the network. The three main lines of research in functional network analysis are *flow analysis*, *storage analysis*, and *utility analysis*. Each of the functional analyses is based on a different nondimensional normalization of the flow properties of the network. In the flow analysis, the flows from component j to i, f_{ij}, are normalized by the total steady-state throughflow at component j, $T_j = \sum_{i=0}^{n} f_{ji} = \sum_{i=0}^{n} f_{ij}$, where f_{j0} is the inflow to j from the environment and f_{0j} is the flow from j to the environment. In storage analysis, the flows are normalized by the steady-state storage at the originating component j (a time step is needed to make this quantity dimensionless). And, in utility analysis, the *net* flow between i and j is normalized by the steady-state throughflow at i. Note that the three analyses described above are the output oriented analysis. Analogous analyses exist for the input orientation such that the flow and storage are normalized by the receiving component, not the originating one.

Flow analysis is used to identify system-wide properties of networks such as retention time, turnover rates, and indirect effects. Storage analysis is used in evaluating the stability of the system. Utility analysis is used to identify direct and indirect qualitative relations (such as mutualism, predation, competition) in a network. Utility analysis incorporates the relative net flow between pairs of components and has application to trophic transfer efficiency.

The basis for network analysis is the infinite power series of the direct normalized matrices. This procedure is performed in all three analyses—flow, storage, and utility—to quantify system-wide interactions based on the contributions of all paths of all lengths that arise from the normalized, direct interaction matrices. This procedure takes advantage of the fact that a matrix raised to a particular power gives the influence (expressed nondimensionally) due to all paths of lengths commensurate with the power. Integral interaction matrices are found by summing the infinite power series of the direct interaction matrices. For example, direct utility is a measure of the net flow matrix normalized by the total throughflow, T_i at i: $\mathbf{D}$. The integral utility matrix $\mathbf{U}$ which accounts for the contribution of all direct and indirect interactions is found by summing all powers of $\mathbf{D}$. $\mathbf{U}$ is the integral utility matrix because its elements represent the total nondimensional utility expressed between the components by powers of $\mathbf{D}$ [13–15]. The relations in $\mathbf{U}$ are the basis for the qualitative and quantitative integral utility in the system. The integral flow and storage matrices are similarly derived.

In order for the power series analysis to proceed, it is necessary for the series to converge. The infinite power series converges when $|\lambda_{\max}| < 1$, where $\lambda_{\max}$ is the eigenvalue of the direct matrix with the greatest magnitude. The eigenvalues, λ, are calculated from the characteristic equation of the direct matrix. For example, with utility analysis the characteristic equation is: $|\mathbf{I}\lambda - \mathbf{D}| = 0$, where $\mathbf{I}$ is the $n \times n$ identity matrix. When the series converges a general solution is written as:

$$\mathbf{U} = \sum_{k=0}^{\infty} \mathbf{D}^k = (\mathbf{I} - \mathbf{D})^{-1}. \tag{1}$$

If $|\lambda_{\max}| \geq 1$, then the infinite power series does not converge and the integral utility is not calculable.

The elements of the direct flow intensity matrix, **G**, are calculated so as to ensure openness (i.e. the column sums are less than 1). This guarantees that the convergence criterion is always met for flow analysis. In storage analysis, the direct storage intensity matrix, **C**, is made nondimensional by multiplying with a time step. The time step can be chosen to be small enough so that convergence will always occur [8]. However, convergence of the integral utility power series may or may not occur depending on the flows and connections in the system. It is the only power series in which the convergence criterion must be considered for each model analysis. It has been shown that, when calculable, the integral utility is always positive giving rise to the network synergism property [15]. However, nothing can be said about the utility or the positive relationships in a system if the power series does not converge. Taking this one step further, if we assume that the lack of convergence is interpreted to mean that positive utility is not conferred in these systems, then the convergence criterion can be used as a constraint on the flow pattern in the network since it is assumed that having positive relationships is a beneficial condition. It is shown here that the eigenvalues can be written as a function of the transfer efficiency levels. Since the transfer efficiency between two components determines the flow values, the constraint can be viewed as the efficiency level between the components.

The integral utility matrix, **U**, gives the overall relations between components in the system. Qualitative interaction types are found by comparing the signs of cross diagonal elements (u_{ji}, u_{ij}) [13]. The numerical value quantifies the strength of those interactions. For the quantitative analysis it is necessary, first, to redimensionalize the integral utility matrix **U** by multiplying it by $\check{\mathbf{T}}$, where $\check{}$ indicates a diagonalized vector. This quantifies the synergism based on the throughflow values specific to that system giving a dimensionalized integral utility matrix $\boldsymbol{\Upsilon} = \check{\mathbf{T}}\mathbf{U}$. Similarly the direct utility matrix can be redimensionalized: $\boldsymbol{\Delta} = \check{\mathbf{T}}\mathbf{D}$, which gives back the original flow values. The integral utility values found in $\boldsymbol{\Upsilon}$ are always greater than the direct utility values of $\boldsymbol{\Delta}$. The elements in $\boldsymbol{\Upsilon}$ that are greater than 0 confer positive utility, whereas the elements less than 0 confer negative utility. (Across diagonal sign pairings of $\boldsymbol{\Upsilon}$ are used to determine the qualitative relations between components [13–15]). Since the integral utility is more positive than the direct utility, this implies that the individual components receive positive utility by being part of the system through the network interactions. In addition, the sum of positive utility in $\boldsymbol{\Upsilon}$ is greater than the negative utility. A benefit–cost (b/c) ratio, where the positive utility is a benefit and the negative utility a cost, in the dimensional, integral utility matrix $\boldsymbol{\Upsilon}$, measures the relative strength of synergism in the network:

$$\frac{b}{c} = \frac{\sum \text{Utility}_+}{\sum \text{Utility}_-}. \tag{2}$$

Network synergism occurs when b/c is greater than 1 [13, 15]. An equivalent test for synergism is to sum the elements of $\boldsymbol{\Upsilon}$. If the sum is greater than 0, then the positive utility is greater than the negative utility and network synergism occurs.

2.2 Utilities as transfer efficiencies

Patten [13, 14] originally derived the nondimensional direct utility matrix, **D**, from the input and output transfer efficiencies in the system; the net flow interpretation came later [15]. The elements of the output transfer efficiency matrix, **G**, give the percentage of flow through component j that directly flows to component $i, g_{ij} = f_{ij}/T_j$. The elements of the input transfer efficiency matrix, $\mathbf{G}'$, give the percentage of flow into component i that comes directly from component $j, g'_{ij} = f_{ij}/T_i$. We can write the direct utility matrix as $\mathbf{D} = \mathbf{G}' - \mathbf{G}^{\mathrm{T}}$ (where $\mathbf{G}^{\mathrm{T}}$ is the transpose of **G**). Using this formulation, the direct utility matrix is based on the input and output transfer efficiencies. Equation (1) can be rewritten such that the integral utility matrix is a function of the transfer efficiencies:

$$\mathbf{U} = \sum_{k=0}^{\infty} (\mathbf{G}' - \mathbf{G}^{\mathrm{T}})^k = (\mathbf{I} - \mathbf{G}' - \mathbf{G}^{\mathrm{T}})^{-1}. \tag{3}$$

In this form, it is clear that the convergence criterion is also a function of the inflow and outflow transfer efficiencies, g_{ij} and g'_{ij}, respectively. For simple chain systems, the input efficiencies are equal to 1 because $f_{ij} = T_i$, so $g'_{ij} = 1$. Therefore, the utility parameter is determined completely from the values of the transfer efficiencies of the output environ, g_{ij}. In more complex models with feedback, cycling, and external inputs, both forward and backward exchange efficiencies play a role.

Looking at this problem from another point of view, there is only a certain range of values for the transfer efficiencies for which the convergence criterion is met. If we assume that convergence must be met for the positive utility to be realized, then the transfer efficiencies are limited to values for which this occurs. Therefore, network utility analysis can be used to determine the range of possible values for the transfer efficiencies based on the convergence criterion. In Section 3, the range in which the transfer efficiencies are constrained in order for the utility metric to be calculable is determined, and how this range changes for various structure and flow combinations is shown. In particular, we identify a general pattern regarding the effect of transfer efficiency on utility analysis for simple food chain models and extend the analysis to a complete three-component system.

3 RESULTS

3.1 Food chain

The simplest model in ecology is a sequential food chain. A generalized flow matrix for a food chain can be written as:

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & \dots & 0 & 0 \\ f_{21} & 0 & \dots & 0 & 0 \\ 0 & f_{32} & \ddots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & \dots & f_{n,n-1} & 0 \end{bmatrix}. \tag{4}$$

In the unidirectional food chain, all flow comes from the component immediately preceding it ($f_{i,i-1} = T_i$ for $i = 2, \dots, n$). Therefore, the elements of the input flow efficiency matrix, $\mathbf{G}'$, are equal to 1. The elements of **G** are the output transfer efficiencies along each step of the chain. The integral utility matrix, **U**, is calculable when eqn (1) converges. This occurs when the eigenvalues of **D** are strictly less than 1. The characteristic equation associated with $\mathbf{D} = \mathbf{G}' - \mathbf{G}^{\mathrm{T}}$ for a food chain has the general form:

$$|\mathbf{I}\lambda - \mathbf{D}| = \begin{vmatrix} \lambda & \frac{f_{21}}{T_1} & 0 & 0 & \cdots & 0 \\ \frac{-f_{21}}{T_2} & \lambda & \frac{f_{32}}{T_2} & 0 & \ddots & 0 \\ 0 & \frac{-f_{32}}{T_3} & \lambda & \frac{f_{43}}{T_3} & \ddots & 0 \\ 0 & 0 & \frac{-f_{43}}{T_4} & \lambda & \ddots & 0 \\ \vdots & \ddots & \ddots & \ddots & \ddots & \frac{f_{n,n-1}}{T_{n-1}} \\ 0 & 0 & 0 & 0 & \frac{-f_{n,n-1}}{T_n} & \lambda \end{vmatrix} = 0. \tag{5}$$

Simplifying, using the fact that in the food chain $f_{ij}/T_i = 1$ and $f_{ij}/T_j = g_{ij}$, gives the following:

$$|\mathbf{I}\lambda - \mathbf{D}| = \begin{vmatrix} \lambda & g_{21} & 0 & 0 & \cdots & 0 \\ -1 & \lambda & g_{32} & 0 & \ddots & 0 \\ 0 & -1 & \lambda & g_{43} & \ddots & 0 \\ 0 & 0 & -1 & \lambda & \ddots & 0 \\ \vdots & \ddots & \ddots & \ddots & \ddots & g_{n,n-1} \\ 0 & 0 & 0 & 0 & -1 & \lambda \end{vmatrix} = 0. \tag{6}$$

In a food chain, the convergence test is dependent only on the forward transfer efficiencies in the output orientation. Equation (6) is a variation of a commonly studied class of matrices called continuants [16–18]. A continuant is a matrix in which the elements lying outside the principle diagonal and the two minor subdiagonals are equal to 0, and the elements of one of the minor subdiagonals are each equal to -1. Analyses of these ecological network models were aided by the previous work done on these types of matrices.

3.1.1 Three-component food chain

The three-component food chain model is ubiquitous in ecology. Slobodkin [4] introduced a hypothetical model, in which grain flowing down a chute is eaten by mice as it goes by, and a cat in turn is snatching an occasional mouse, to define ecological efficiency as:

$$\text{Ecological efficiency} = \frac{\text{Calories of mice consumed by the cat per unit time}}{\text{Calories of grain consumed by mice per unit time}}.$$

Ecological efficiency is the ratio of flow from j to i, to the total throughflow at j. This is conceptually and mathematically identical to both g_{ij} in network analysis [7] and Lindeman [19] efficiency. Therefore, a consistency of terminology exists among the different approaches. Equation (6) for a three-component food chain gives:

$$|\mathbf{I}\lambda - \mathbf{D}| = \begin{vmatrix} \lambda & g_{21} & 0 \\ -1 & \lambda & g_{32} \\ 0 & -1 & \lambda \end{vmatrix} = 0. \tag{7}$$

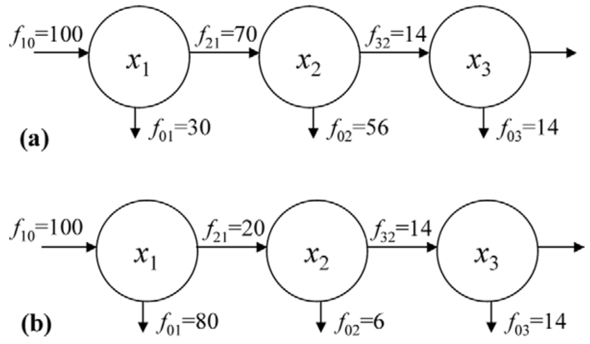

Figure 1: Comparison of two three-component food chains with different transfer efficiencies.

The three eigenvalues associated with the direct utility matrix, **D**, are:

$$\lambda = 0, \pm\sqrt{-g_{21} - g_{32}}. \tag{8}$$

For the convergence test to be met, the absolute value of the sum of the two transfer efficiencies, g_{21} and g_{32}, must be less than 1. Clearly, since each g_{ij} is a probability ($0 \leq g_{ij} < 1$), there are cases even for the simple three-component model in which the integral utility is not calculable. Network utility analysis places a limitation on the transfer efficiencies of a three-component linear model that they must sum to less than 1.

The benefit–cost ratio [eqn (2)] measures the level of synergism that occurs in the model. By looking only at cases in which convergence is guaranteed we can investigate how the utility analysis metric is affected by the different transfer efficiencies along each link of the three-component food chain. Comparing the two cases with similar eigenvalues (determined by $g_{21} + g_{32} =$ constant), shows that b/c is greater for the system in which g_{21} is smaller than g_{32} (Fig. 1). In Fig. 1a $g_{21} = 0.7$ and $g_{32} = 0.2$, whereas in Fig. 1b $g_{21} = 0.2$ and $g_{32} = 0.7$. In both cases the eigenvalues of **D** are identical, $\lambda_{\max} = 0.96i$, yet the flows and benefit-to-cost ratios are different. In Fig. 1a, $b/c = 3.88$, whereas in Fig. 1b $b/c = 7.91$. A lower g_{21} corresponds to greater energy dissipation from the system in the first step and the energy gradient degrades more rapidly. More generally, we see from Fig. 2 that if $g_{21} =$ constant and g_{32} increases, then b/c increases slightly, and if g_{32} is constant and g_{21} increases, then b/c decreases exponentially. If we assume that both transfer efficiencies along each link are equal ($g_{21} = g_{32}$) then the efficiencies must be just less than 0.50 to meet the convergence criterion. The assumption of equal efficiencies is used later to investigate longer chain models.

3.1.2 Three-component predator–prey model

Before leaving the three-component system, we also look at the two-predator–one-prey competition model (Fig. 3). In this example, $f_{12} = f_{13} = f_{32} = f_{23} = 0$, and the eigenvalues are:

$$\lambda = 0, \pm\sqrt{-g_{21} - g_{31}}. \tag{9}$$

The total flow through component 1 is $T_1 = f_{01} + f_{21} + f_{31}$, and all the transfer efficiencies out of component 1 sum to unity, $g_{01} + g_{21} + g_{31} = 1$. Since the network is an open dissipating system, $f_{01} > 0$ and $g_{01} > 0$. Therefore, $g_{21} + g_{31} < 1$ and the eigenvalues always converge. The integral utility for this model structure is always calculable regardless of the flow through the system. In fact, the benefit–cost ratio is at a minimum as g_{21} and g_{31} both approach 0.50 and is a maximum when they both simultaneously approach 0.

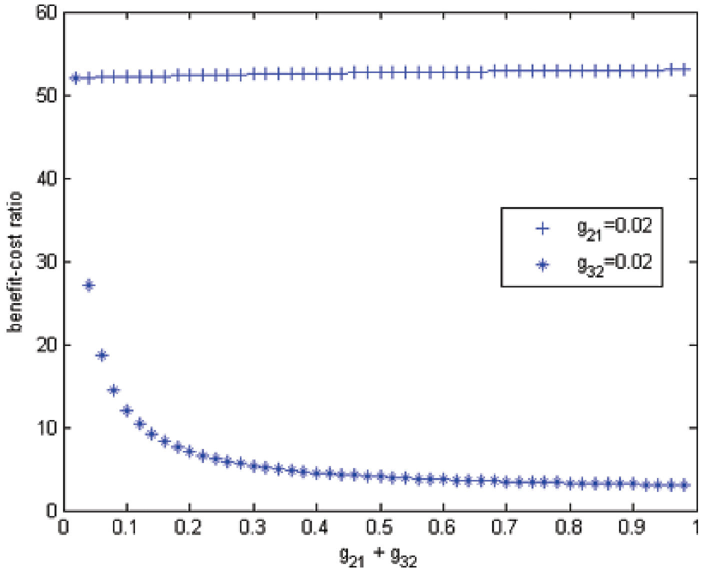

Figure 2: Effect of changing transfer efficiency for the three-component food chain. b/c decreases when g_{21} increases with g_{32} constant. The ratio increases slightly when g_{32} increases with g_{21} constant.

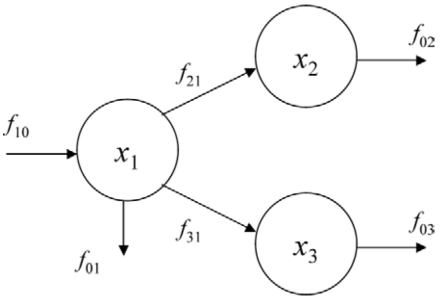

Figure 3: Two-predator–one-prey model.

3.1.3 Four-component food chain

In the three-component food chain, the sum of the two transfer efficiencies, g_{21} and g_{32}, must be less than 1 for the convergence test to be met and the integral utility calculated. As we increase the number of components in the food chain to four, we see that this simple pattern does not continue. The eigenvalues associated with the four-component food chain are:

$$\lambda = \pm\frac{\sqrt{2}}{2}\sqrt{-g_{21} - g_{32} - g_{43} + \sqrt{(g_{21} - g_{43})^2 + g_{32}^2 + 2g_{43}g_{32} + 2g_{21}g_{32}}}$$
$$\pm\frac{\sqrt{2}}{2}\sqrt{-g_{21} - g_{32} - g_{43} - \sqrt{(g_{21} - g_{43})^2 + g_{32}^2 + 2g_{43}g_{32} + 2g_{21}g_{32}}}. \tag{10}$$

The role of the transfer efficiencies in determining the eigenvalues is still present, but has become algebraically more complicated. The convergence criterion is no longer dependent solely on the sum of the individual transfer efficiencies, but on the sum plus several higher-order interaction terms.

3.2 n-Component food chain

To observe a pattern of convergence, for the four-component and higher food chains, we assume that the transfer efficiencies along each link of the food chain are equal ($g_{ij} = x$, where $0 \leq x < 1$). The eigenvalues for an n-component food chain of this form are derived from the general form:

$$|\mathbf{I}\lambda - \mathbf{D}| = \begin{vmatrix} \lambda & x & 0 & 0 & \dots & 0 \\ -1 & \lambda & x & 0 & \ddots & 0 \\ 0 & -1 & \lambda & x & \ddots & 0 \\ 0 & 0 & -1 & \lambda & \ddots & 0 \\ \vdots & \ddots & \ddots & \ddots & \ddots & x \\ 0 & 0 & 0 & 0 & -1 & \lambda \end{vmatrix} = 0. \tag{11}$$

If P_n is the polynomial for an nth-order food chain, we can write a general expression for P_n as:

$$P_n = \lambda |P_{n-1}| + x|P_{n-2}|. \tag{12}$$

Since we are interested in cases when $|\lambda| < 1$, the greatest value for x, corresponding to the largest possible transfer efficiency, will occur at the limit as $|\lambda| \to 1$. As stated earlier, the nonzero eigenvalues of $\mathbf{D}$ always have imaginary terms. If we let $|\lambda| \to 1$ in eqn (12), then all roots of the polynomial are negative. Therefore, we are only interested in the modulus of x, not the sign. Clearly, x must always be positive because it is the transfer efficiency or probability of transfer. Positive roots (with the same value) of the polynomials can be obtained by changing the sign of the recursion relation so that we get:

$$P_n = |P_{n-1}| + x|P_{n-2}|. \tag{13}$$

The closed-form solution to the recursion relation in eqn (13) is given by (see Appendix):

$$P_n(x) = \frac{\left(1 + \sqrt{1-4x}\right)^{n+1} - \left(1 - \sqrt{1-4x}\right)^{n+1}}{2^{n+1}\sqrt{1-4x}}. \tag{14}$$

Equation (14) is used to generate the polynomial equation for any n-component food chain. The first seven polynomials are:

$$\begin{aligned} P_0 &= & & & +1, \\ P_1 &= & & & +1, \\ P_2 &= & & -x & +1, \\ P_3 &= & & -2x & +1, \\ P_4 &= & +x^2 & -3x & +1, \\ P_5 &= & +3x^2 & -4x & +1, \\ P_6 &= -x^3 & +6x^2 & -5x & +1. \end{aligned} \tag{15}$$

A kth-order polynomial has k roots, however, it is the smallest root, $r_{\min}$, which ensures that $|\lambda_{\max}| < 1$. The smallest roots form an upper bound on the maximum transfer efficiencies admissible

Table 1: Diagonals of Pascal's triangle used for the coefficients in polynomial equations to find the maximum transfer efficiency in a chain with equal efficiencies across each link.

$$\text{Pascal's triangle} = \begin{array}{ccccccccccccccc}
 & & & & & & & & & & & & & & 1 \\
 & & & & & & & & & & & & 1 & & 1 \\
 & & & & & & & & & & & & & \ddots & \\
 & & & & & & & & & & 1 & & 2 & & 1 \\
 & & & & & & & & & & & \ddots & & \ddots & \\
 & & & & & & & & 1 & & 3 & & 3 & & 1 \\
 & & & & & & & & & \ddots & & \ddots & & \ddots & \\
 & & & & & & 1 & & 4 & & 6 & & 4 & & 1 \\
 & & & & & & & \ddots & & \ddots & & \ddots & & \ddots & \\
 & & & & 1 & & 5 & & 10 & & 10 & & 5 & & 1 \\
 & & & & & \ddots & & \ddots & & \ddots & & \ddots & & \ddots & \\
 & & 1 & & 6 & & 15 & & 20 & & 15 & & 6 & & 1 \\
 & & & \ddots & & \ddots & & \ddots & & \ddots & & \ddots & & \ddots & \\
1 & & 7 & & 21 & & 35 & & 35 & & 21 & & 7 & & 1 \\
\text{—} & \text{—} & \text{—} & \text{—} & \text{—} & \text{—} & \text{—} & \text{—} & \text{—} & \text{—} & \text{—} & \text{—} & \text{—} & \text{—} & \text{—} \\
-x^7 & & x^6 & & -x^5 & & x^4 & & -x^3 & & x^2 & & -x^1 & & x^0
\end{array}$$

Table 2: The maximum transfer efficiencies for 2, 3, 4, 5, and 6-component food chains.

No. of components	Maximum transfer efficiency
2	0.500
3	0.382
4	0.333
5	0.308
6	0.293
7	0.283
8	0.276
9	0.272
10	0.268

that will allow calculation of the integral utilities. If this series of equations were continued, it would become evident that the coefficients of the equations are equivalent to those found along the diagonals in Pascal's triangle where the rightmost column contains the x^0 terms and the columns moving to the left represent successive powers of x (Table 1). (Note also that the sum of the coefficients for P_n gives the Fibonacci number, F_n, where $F_n = F_{n-1} + F_{n-2}$.)

Using Pascal's triangle to obtain the coefficients for P_n, we numerically find the roots associated with different size food chains. The magnitude of the roots decreases as the number of links increases. The maximum transfer efficiencies for the 2, 3, 4, 5, and 6-component chains are shown in Table 2.

As the number of components in the chain continues to increase, the smallest root of the equation asymptotically approaches 0.25 (Fig. 4) (see Appendix). Figure 4 shows the largest possible transfer efficiency value for an *n*-component food chain with equal transfer along each *n* – 1 links. The utility feasible efficiency values are constrained to lie within the area below this curve. The integral utility of a chain of any length is calculable provided the transfer efficiencies are below 0.25 in value. Importantly, there is no theoretical limit to the length of a chain based on the convergence constraint.

3.3 Three-component complete system

If we relax the assumption that the system must be a chain, we get a general expression for the characteristic equation for the complete three-component system (Fig. 5):

$$\lambda\left[\lambda^2 + \frac{(f_{12} - f_{21})^2}{T_1 T_2} + \frac{(f_{13} - f_{31})^2}{T_1 T_3} + \frac{(f_{23} - f_{32})^2}{T_2 T_3}\right] = 0. \tag{16}$$

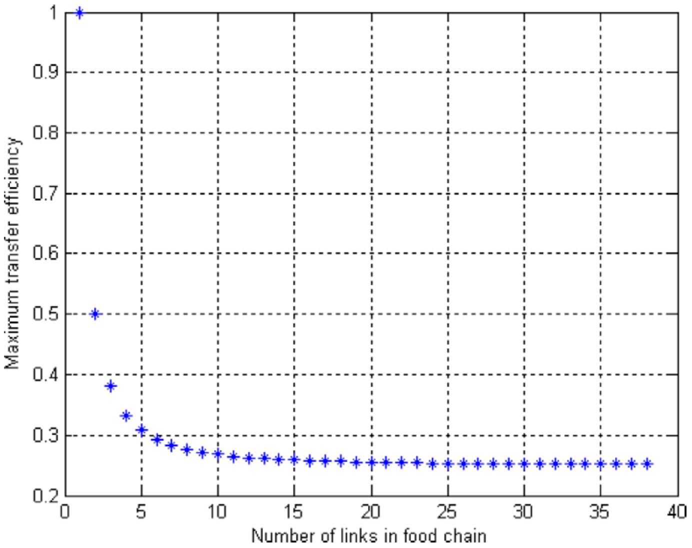

Figure 4: The maximum transfer efficiency for a food chain with equal transfer efficiencies.

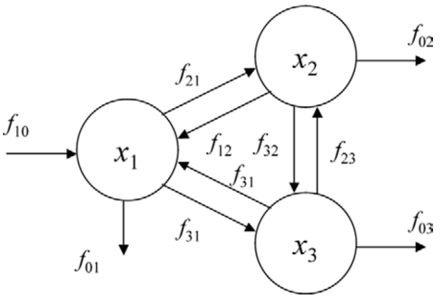

Figure 5: Three-component complete digraph.

Written in terms of the input and output transfer efficiencies, g_{ij} and g'_{ij}, the characteristic equation is:

$$\lambda[\lambda^2 + (g_{12}g'_{12} - 2g_{12}g_{21} + g_{21}g'_{21} + g_{13}g'_{13} - 2g_{13}g_{31} + g_{31}g'_{31}) \\ + (g_{22}g'_{23} - 2g_{23}g_{32} + g_{32}g'_{32})] = 0. \tag{17}$$

Now, the eigenvalues of the matrix **D** depend not only on the output transfer efficiencies, **G**, but also on the input efficiencies, **G**′. Solving for the eigenvalues in terms of the flows gives:

$$\lambda = 0, \pm\sqrt{-\frac{(f_{12}-f_{21})^2}{T_1T_2} - \frac{(f_{13}-f_{31})^2}{T_1T_3} - \frac{(f_{23}-f_{32})^2}{T_2T_3}}. \tag{18}$$

For this model, the systems that do not meet the convergence criterion (i.e. $\lambda \geq 1$) have a large net flow exchange between compartments. This can be minimized by either low transfer efficiencies or by even flow of energy.

4 EMPIRICAL EVIDENCE

The theoretical limit to transfer efficiency based on the utility analysis measure states that the trophic transfer efficiency of a food chain must decrease as the number of components in the chain increases. In an earlier work Patten [20] compared the flow of energy and the transfer efficiencies in four classic ecosystem projects: Lake Mendota [21], Cedar Bog Lake [19], Root Spring [22], and Silver Springs [23] (Table 3). The efficiency is calculated by dividing the flow to the *n*th trophic level by the flow to the previous trophic level. He found that, in general, the ecological efficiency within the systems ranged between 5 and 20%. The one exception, flow to herbivores in the Root Spring system, occurs because there is a large supply of allochthonous input, making the efficiency appear greater when in fact much of the energy in the herbivore compartment did not pass through the producer compartment. In fact, it was this comparison of the classic studies by Patten [20] that Slobodkin [4] references as his source for the '10 percent' transfer efficiency rule mentioned in the Introduction. These values are in line with the limitations provided by utility analysis.

Table 3: Flow and transfer efficiency for four classic ecosystem studies (production is expressed in terms of gcal/cm^2/year).

	Lake Mendota [21]	Cedar Bog Lake [19]	Root Spring [22]	Silver Springs [23]
Flow to				
Producers	480.0	111.3	306.0	2129.6
Herbivores	42.0	14.8	231.8	336.8
Carnivores	2.3	3.1	20.8	38.3
Top carnivores	0.3	0.0	0.0	2.1
Flow efficiency to (%)				
Herbivores	8.8	13.3	75.8	15.8
Carnivores	5.5	20.9	9.0	11.4
Top carnivores	13.0	0.0	0.0	5.5

5 CONCLUSIONS

Network utility analysis has been used to investigate limitations to trophic transfer efficiency. The integral utility metric, when calculable, is always positive giving rise to the property of network synergism [15]. It is not calculable when the eigenvalues associated with the direct utility matrix are too large, and in a food chain the eigenvalues are dependent solely on the transfer efficiencies between components. By setting the transfer across each link to be equal, we see that a general pattern emerges. In particular, we have found that in short chains tradeoffs between the various efficiencies are important—if one goes up the others must come down. For a three-component system a chain with greater dissipation along the first path has a higher b/c ratio (greater utility). This is unexpected if we assume the system is operating to maximize its efficiency. It contrasts with the generally held concepts of maximum power [24, 25] and maximum efficiency [26]. However, it may fit well with the maximum exergy degradation principle which states that 'as ecosystems grow and develop, they should increase their total dissipation by developing structures and processes to assist energy degradation' [3], which has been observed in the early development of ecosystems.

Once a chain is longer than three components, the overall efficiency is not a sum of parts. The eigenvalues are more complexly dependent on the transfer efficiencies. Since the efficiency value for the n-component chain asymptotically approaches 0.25 as $n \to \infty$, there is no theoretical limit to the number of components in an isolated food chain. The efficiency never drops to 0. If it did, then this would indicate that there is a theoretical limit to the number of components because it is impossible to add another component if the efficiency to get there is 0. This also implies that adding another component has less influence on the efficiency level of the previous ones as the number of components increases.

The transfer of energy within an ecosystem is constrained by many processes. Thermodynamically, the cumulative efficiency must be between 0 and 1. However, empirical results [4, 20] indicate that the transfer efficiency is generally considerably less then the theoretical limit imposed by thermodynamics. This paper shows, using network analysis and food chain models, why in cases where transfer efficiencies are high the convergence criterion is not met. In order for the integral utility to be calculable, efficiencies must be relatively low, and therefore it may also be true that transfer efficiencies observed in nature have to be low for components to receive systemic benefits. This is a system design criterion not inherent in other aspects (physicochemical) of ecosystem energetics. Network utility analysis is a relatively new way of viewing the interactions and relationships between components in a connected system and much work is still needed to understand the nuances and subtleties of this approach.

ACKNOWLEDGEMENTS

I would like to thank Bernard Patten for sharing his insight and encouragement regarding ecological network organization. Special thanks are given to Luis Suarez and Craig Barber for their help with the derivation in the Appendix.

APPENDIX

This appendix presents a closed-form solution to the recursion relation in eqn (13):

$$P_{n+2} = |P_{n+1}| - x|P_n|, \tag{19}$$

and determines the maximum value for the transfer efficiency in which utility is calculable. This case corresponds to a sequential chain in which the efficiency along each connection is the same.

Rewriting eqn (13) using a z transformation gives:

$$z^2P(z) - z^2\sum_{k=0}^{1} P_k z^{-k} = z^1P(z) - z^1\sum_{k=0}^{1} P_k z^{-k} - xP(z), \tag{20}$$

and then simplifying:

$$z^2P(z) - z^2(P_0 + P_1z^{-1}) = zP(z) - zP_0 - xP(z), \tag{21}$$

$$z^2P(z) - z^2P_0 - z^1P_1 = zP(z) - zP_0 - xP(z), \tag{22}$$

$$P(z)(z^2 - z + x) = z^2P_0 + zP_1 - zP_0, \tag{23}$$

$$P(z) = \frac{z^2P_0 + zP_1 - zP_0}{z^2 - z + x}, \tag{24}$$

where $P(z)$ is the transformation of $P(x)$. Given the initial conditions, $P_0 = P_1 = 1$, we get:

$$P(z) = \frac{z^2}{z^2 - z + x}. \tag{25}$$

Now, transform back to the x domain using the inverse transform:

$$P_n(x) = \frac{1}{2\pi i}\int \frac{z^2 z^{n-1}}{z^2 - z + x}\mathrm{d}z, \tag{26}$$

$$P_n(x) = \frac{1}{2\pi i}\int \frac{z^2 z^{n+1}}{z^2 - z + x}\mathrm{d}z. \tag{27}$$

The roots of $z^2 - z + x$ are:

$$\begin{aligned} \lambda_1 &= \frac{1 + \sqrt{1-4x}}{2}, \\ \lambda_2 &= \frac{1 - \sqrt{1-4x}}{2}, \end{aligned} \tag{28}$$

$$P_n(x) = \frac{1}{2\pi i}\int \frac{z^{n-1}}{z^2 - z + x}\mathrm{d}z = \text{Residue}(\lambda_1) + \text{Residue}(\lambda_2), \tag{29}$$

$$\begin{aligned} \text{Residue at } \lambda_1\text{:}\ \left.\frac{z^{n+1}}{z-\lambda_2}\right|_{z=\lambda_1} &= \frac{\lambda_1^{n+1}}{\lambda_1 - \lambda_2}, \\ \text{Residue at } \lambda_2\text{:}\ \left.\frac{z^{n+1}}{z-\lambda_1}\right|_{z=\lambda_2} &= \frac{\lambda_2^{n+1}}{\lambda_2 - \lambda_1}, \end{aligned} \tag{30}$$

$$P_n(x) = \frac{\lambda_1^{n+1} - \lambda_2^{n+1}}{\lambda_1 - \lambda_2}, \tag{31}$$

where

$$\lambda_1 - \lambda_2 = \sqrt{1-4x}. \tag{32}$$

Equation (33) gives one form for $P_n(x)$:

$$P_n(x) = \frac{(1+\sqrt{1-4x})^{n+1} - (1-\sqrt{1-4x})^{n+1}}{2^{n+1}\sqrt{1-4x}}. \tag{33}$$

This is the form of eqn (14). It can be rewritten to see more clearly the relation between x and n. Looking at the numerator first, we let $b = \sqrt{1-4x}$ and expand using the binomial theorem

$$(1+b)^{n+1} = \sum_{i=0}^{n+1} \binom{n+1}{i} b^i 1^{n+1-i}, \tag{34}$$

$$(1-b)^{n+1} = \sum_{i=0}^{n+1} \binom{n+1}{i} b^i (-1)^i, \tag{35}$$

$$(1+b)^{n+1} - (1-b)^{n+1} = \sum_{i=0}^{n+1} \binom{n+1}{i} b^i (1-(-1)^i), \tag{36}$$

$$(1+b)^{n+1} - (1-b)^{n+1} = \sum_{i=0}^{\lceil n/2 \rceil} \binom{n+1}{2i} b^{2i}(1-(-1)^{2i}) + \sum_{i=0}^{\lceil n/2 \rceil} \binom{n+1}{2i+1} b^{2i+1}(1-(-1)^{2i+1}). \tag{37}$$

The first summation includes the even terms and the second, the odd terms. However, all the even terms are 0 because $1-(-1)^{2i}$ is 0. Therefore, all we are left with is:

$$(1+b)^{n+1} - (1-b)^{n+1} = \sum_{i=0}^{\lceil n/2 \rceil} \binom{n+1}{2i+1} b^{2i+1}(1-(-1)). \tag{38}$$

Substituting back in for b gives:

$$(1+\sqrt{1-4x})^{n+1} - (1-\sqrt{1-4x})^{n+1} = 2\sum_{i=0}^{\lceil n/2 \rceil} \binom{n+1}{2i+1} \left(\sqrt{1-4x}\right)^{2i+1}. \tag{39}$$

Substituting this back in for $P_n(x)$ gives:

$$P_n(x) = \frac{2}{2^{n+1}\sqrt{1-4x}} \sum_{i=0}^{\lceil n/2 \rceil} \binom{n+1}{2i+1} \left(\sqrt{1-4x}\right)^{2i+1}. \tag{40}$$

Equation (41) gives a second form for $P_n(x)$:

$$P_n(x) = \frac{1}{2^n} \sum_{i=0}^{\lceil n/2 \rceil} \binom{n+1}{2i+1} \left(\sqrt{1-4x}\right)^{i}. \tag{41}$$

Using eqn (41), we see that around the point $x = 1/4$ the higher-order terms of i become negligible. Solving $P_n(x)$ looking at the terms only when $i = 0$ and $i = 1$ we get:

$$P_n(x) = \frac{1}{2^n}\left[n+1+\binom{n+1}{3}(1-4x)\right]. \tag{42}$$

Since we are looking for the root, we set eqn (42) equal to 0 and solve for x

$$n + 1 + \frac{(n+1)n(n-1)(n-2)!}{3!(n-2)!}(1-4x) = 0, \tag{43}$$

$$n + 1 + \frac{(n+1)n(n-1)}{6}(1-4x) = 0, \tag{44}$$

$$n(n-1)(1-4x) = -6, \tag{45}$$

$$x = \frac{1}{4} + \frac{3}{2n(n-1)}. \tag{46}$$

Now, it is clear that as $n \to \infty,\ x \to 1/4$.

REFERENCES

[1] Jørgensen, S.E., Patten, B.C. & Straškraba, M., Ecosystems emerging: 4. Growth. *Ecological Modelling*, **126**, pp. 249–284, 2000.

[2] Fath, B.D., Jørgensen, S.E., Patten, B.C. & Straškraba, M., Ecosystem growth and development. *Biosystems*, **77**, pp. 213–218, 2004.

[3] Schneider, E. & Kay, J., Complexity and thermodynamics: towards a new ecology. *Futures*, **26**, pp. 626–648, 1994.

[4] Slobodkin, L.B., *Growth and Regulation of Animal Populations*, Holt, Rinehart and Winston: New York, p. 138, 1961.

[5] Leontief, W.W., *Input-Output Economics*, Oxford University Press: New York, 1966.

[6] Hannon, B., The structure of ecosystems. *Journal of Theoretical Biology*, **41**, pp. 535–546, 1973.

[7] Finn, J.T., Measures of ecosystem structure and function derived from analysis of flows. *Journal of Theoretical Biology*, **56**, pp. 363–380, 1976.

[8] Barber, M.C., A note concerning time parameterization of Markovian models of ecosystem flow analysis. *Ecological Modelling*, **6**, pp. 323–328, 1979.

[9] Patten, B.C., Systems approach to the concept of environment. *The Ohio Journal of Science*, **78**, pp. 206–222, 1978.

[10] Ulanowicz, R.E., *Growth and Development: Ecosystem Phenomenology*, Springer-Verlag: New York, 1986.

[11] Ulanowicz, R.E., *Ecology, The Ascendant Perspective*, Columbia University Press: New York, 1997.

[12] Fath, B.D. & Patten, B.C., Review of the foundations of network environ analysis. *Ecosystems*, **2**, pp. 167–179, 1999.

[13] Patten, B.C., Network ecology: indirect determination of the life-environment relationship in ecosystems. *Theoretical Studies of Ecosystems: The Network Perspective*, eds M. Higashi & T. Burns, Cambridge University Press: New York, pp. 288–351, 1991.

[14] Patten, B.C., Energy, emergy and environs. *Ecological Modelling*, **62**, pp. 29–69, 1992.

[15] Fath, B.D. & Patten, B.C., Network synergism: emergence of positive relations in ecological systems. *Ecological Modelling*, **107**, pp. 127–143, 1998.

[16] Scott, R.F., *Treatise on the Theory of Determinants and their Applications in Analysis and Geometry*, Cambridge University Press: Cambridge, 1880.

[17] Muir, T., *A Treatise on the Theory of Determinants*, Macmillan and Co.: London, 1882.

[18] Turnbull, H.W., *The Theory of Determinants, Matrices, and Invariants*, Blackie Press: London, 1945.

[19] Lindeman, R.L., The trophic dynamic aspect of ecology. *Ecology*, **23**, pp. 399–418, 1942.

[20] Patten, B.C., An introduction to the cybernetics of the ecosystem: the trophic dynamic aspect. *Ecology*, **40**, pp. 221–231, 1959.

[21] Juday, C., The annual energy budget of an inland lake. *Ecology*, **21**, pp. 438–450, 1940.

[22] Teal, J.M., Community metabolism in a temperate cold spring. *Ecological Monographs*, **27**, pp. 283–302, 1957.

[23] Odum, H.T., Trophic structure and productivity of Silver Springs, Florida. *Ecological Monographs*, **27**, pp. 55–112, 1957.

[24] Lotka, A., Contributions to the energetics of evolution. *Proceedings of the National Academy Sciences*, **8**, pp. 147–151, 1922.

[25] Odum, H.T. & Pinketon, R.C., Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. *American Scientist*, **43**, pp. 331–343, 1955.

[26] Odum, E.P., The strategy of ecosystem development. *Science*, **164**, pp. 262–270, 1969.