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WHERE DO THEY GO WHEN THEY DIE?

by

Meridith L. Bartley

2009

A Capstone Experience/Thesis

Submitted in partial fulfillment of the requirements of

University Honors College at

Western Kentucky University

Approved by:

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Albert Meier

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Ouida Meier

ABSTRACT

Food webs and matrices are vital to understanding feeding relationships and ecology. Adjacency matrices can be employed to present the direct relationships between predators and prey; these binary matrices utilize 0's to denote no direct link and 1's to denote a direct link. We analyzed a variety of published food webs ranging from pine forests in the United States to tussock grasslands in New Zealand. The food webs varied in number of distinguishable taxa present, functional diversity, climates and habitats. Consequently, we expect that our results are not specific to a given system. The published food webs lack flows from organisms to detritus despite the fact that organisms in these webs consume detritus. This discrepancy leads us to question how the inclusion of flows to detritus influences indirect connectance within large food webs. By including the flows to detritus, the number of indirect paths of length n as well as indirect relationships throughout the systems increased. Null model simulations were compared to detrital models in power series and eigen analysis. Pathway proliferation was found in all simulations with detrital models exhibiting greater potential indirect paths and detritus contributing greatly to energetic cycling by serving as energy storage to dead and decaying organic matter in ecosystems.

Index words: food web, mathematical modeling, detritus, indirect links.

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Committee Chair: Albert Meier

Committee: Ouida Meier

Electronic Version Approved:

Honors College
Western Kentucky University
December 2009

DEDICATION

I would like to dedicate this Capstone Experience and Thesis to my parents who taught me the importance of an education. I will always love and appreciate you guys even when you were scared I would not finish!

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My unending gratitude for my Thesis Partner in Crime, Jonathan Bowers, must be acknowledged as completion would not have been possible without him. I would like to thank Stuart Borrett and his family for the MATLAB coding and true southern hospitality they showed us. This trip to UNC Wilmington would not have been possible without an Honors Development Grant from the Honors College. Thanks also to my Thesis Advisement Board whose patience and never ending faith in me deserves the highest sort of gratitude. My remaining sanity is due in no small part to the other women who comprise the Tribal Trio, Rachel Wigginton and Cabrina Hamilton. A final salute to all of my fellow students who asked for thesis updates even when they knew I'd cringe at the thought.

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INTRODUCTION

The overall health and stability of a biological system is a function of the organismal components and organic matter that make up its network. All components must be considered when studying an entire system. Food webs employed to represent these systems are vital to understanding the feeding relations among all organisms found within a defined habitat. Food webs based upon ecological observations of predator-prey relationships map direct interactions of species and with later evaluation, the subsequent indirect paths between species (Polis, 1996). Each of these links generally occur between a consumer taxon and the consumed resource taxon (Williams et al., 2002). Direct links reflect energy or matter passed directly from prey to predator. Indirect paths appear when the abundance of one species is altered and affects the abundances of subsequent species down a chain of direct links, a phenomenon known as 'trophic cascade' (Schmitz, 1998).

It is important to include all nodes in a system as well as all possible links. For example, in a three-component chain with a flow i - j - k, with energy flowing through ascending letters, the direct flows are i - j and j - k (see Fig. 1) The flow i - k is an indirect link with one node of separation, thus making it a second order flow with a path length of 2. Analyzed separately, nodes i and k would have seemed unrelated; only with all three components can they be analyzed as one system (Fath and Patten, 1999). Ecologists often use these links to predict patterns within food webs. From a trophic-dynamic viewpoint, these linkages reveal the potential flow of energy throughout a web (Lindeman, 1942). A stable biological network will persist when energy remains continuously available to the taxa. To accurately portray a stable network, the respective

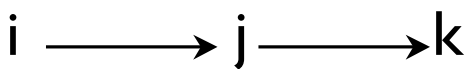
food web must contain all components of the system that connect the taxa, or nodes, so that energy continues to cycle around the network. Much research has been conducted in the field of Environ Analysis (Fath and Patten, 1999; Higashi and Patten, 1986), resulting in the isolation of several key characteristics of networks that confirm the validity of using these mathematical representations for biological systems. Methods of Environ Analysis and similar analytic techniques seek to find metrics that summarize a network's structure and function based on various complexity and stability measures (May, 1972; May, 1973).

$$i \longrightarrow j \longrightarrow k$$

Figure 1. Three-compartment chain with energy flowing through ascending letters. Direct flows are represented by i - j and j - k. An indirect flow of path two occurs between i and k.

Network models arise from any mathematical graph that is composed of nodes (*vertices*), and edges (*links)* that connect the nodes (Borrett et al., 2007). Biological systems are simplified into networked food webs in either graph or matrix form. Each taxon, often representative of species but sometimes of feeding guilds or life history stages, involved in the transfer of energy within a biological system becomes a *node* in the network. The connections representing immediate flow of energy between these nodes are referred to as *edges* of the network (Newman, 2003). These graphs are used with vast systems such as social networking and the World Wide Web and can be transferred into mathematical matrices. Food webs that represent the presence or absence of energy flows are compiled into binary adjacency matrices $\mathbf{A = (a_{ij}), [i = j]}$. Numerical values of one represent an observable transfer of energy between nodes from the consuming taxon along row *i* to the consumed taxon in the *j* column. Values of zero denote no direct transfer of energy (see Fig. 2). While trophic relations show that *i* eats j, the flow of energy is from *j* to *i*

and it is this flow that most interests ecologists. The majority of these flows result from trophic (feeding) interactions; however, non-consumptive flows, such as flows to detritus, can also be represented in network models because this pathway allows material to travel realistically in the network. By representing biological systems in this manner, techniques of analysis and properties of both graph theory and linear algebra can be used to analyze the data.

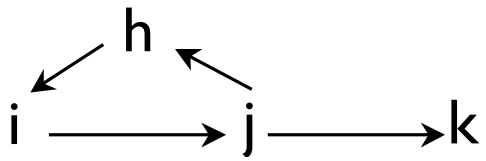


	i	j	k
i	0	1	0
j	0	0	1
k	0	0	0

Figure 2. A simple three-component chain represented by both graph and binary adjacency matrix form. Energy flows through *nodes* in the graph and from row to columns where 1's are present in the matrix.

Network properties have previously been derived using an environ approach, which includes several cardinal hypotheses of holoecology (Borrett and Patten, 2003). Constructed and published food webs can be tested for stability using these properties; however the networks often fail to meet these standards. An overwhelming fraction of these webs have drawn criticism due to the lack of species diversity, accountability, and general incompleteness even at the ecosystem level (Williams et al., 2002). There is a tendency in published food web networks to construct a pyramid of chains resulting in an energy leak at the top trophic level of the system. Though this "trophic cascade" representation of energy flow in systems is a simple and effective tool, it lacks the practicality of complex cycling of energy required for network function and

sustainability. A *cycle* in the system results when energy in the system travels from one node along a pathway so that it eventually returns to the original node (see Fig. 3). Cycling makes possible the proliferation of indirect pathways; further research suggests that indirect paths account for more than 80% of total system throughflow (TST), supporting one of Patten's cardinal hypotheses (Borrett et al., 2006; Borrett and Patten, 2003).



	h	i	j	k
h	0	1	0	0
i	0	0	1	0
j	1	0	0	1
k	0	0	0	0

Figure 3. A four-compartment system containing a three-compartment *cycle* represented by both graph and binary adjacency matrix. Nodes h, i, and j create the cycle involved.

Throughout the majority of published food webs, a link back to detritus has been omitted, despite the many organisms that consume detritus within the webs. This omission could be due in part to the predator-prey specific interactions commonly documented in food webs. A consequence of this restriction is the failure to acknowledge the true nature of energy transfer in biological systems. Lindeman's trophic-dynamic viewpoint (1942) emphasizes the importance of the nonliving 'ooze' through which nutrients are reincorporated back into the community. Once an organism dies, it becomes a vital source of energy for saprophagous organisms, which feed directly on dead tissue. In the aforementioned criticized networks energy is leaked out; however in a true biological system, as organisms of all trophic levels die the energy that they once stored, direct or indirectly, returns to the detrital trophic level. Proliferation of indirect links due to the

inclusion of detritus would indicate that this node has a much larger effect on the community than previously thought.

As previously mentioned, most currently published food webs focus on predator-prey interactions that fail to incorporate detritus as an energy or biomass sink. Previous models show that reducing detritus in a system by 10% can cause a 50% reduction of plant biomass (DeAngelis, 1992). These results are due to indirect effects in the system, and may reinforce the importance of energy cycling for ecosystem health and function. Fath and Patten (1999) introduced methods that provide insight into the behaviors of holistic network interactions. *Network analysis* is a tool that can be employed to further our understanding of objects as part of a connected system, and identify and quantify the indirect effects within. This analysis is an environmental application of input-output analysis, which has been used in ecology for various topics of research, including the exploration of organism interdependence within an ecosystem to determine the energy flows that link the component directly and indirectly to its ecosystem. As network analysis employs matrix algebra, eigen analysis has been conducted in other disciplines as well, such an example being the internet network and search engines such as Google (Bryan and Leise, 2006).

Three key ideas have previously been established for environmental system theory (Patten, 1978). First, every object, or organism, within a system has two specified and quantified *environs* where one acts on the organism, and the other is acted upon by the organism. Second, any node within a system is linked to its surroundings and depends on these surroundings for its internal identity and structural and functional completeness. Third, the continuing flow of energy

along each pathway is targeted for and derived from a particular component. Network analysis provides insight into a system and the relationships between its components without having to remove them from the system.

Network analysis includes ability to identify where the direct and more importantly, the indirect pathways in a network are located. *Connectance* represents a standard measure of food web complexity that allows researchers to observe the fraction of experienced links (Williams et al., 2002). Connectance is quantified by the ratio of total links to the number of links possible in the system. Because connectance (C) is independent of total species diversity, it is a good indicator for observing these experienced links:

C = (links observed) / (links possible)

Pathway analysis reveals indirect pathways of length *n* when the adjacency matrix is raised to a power, *n (*Fath and Patten, 1999). When a matrix is raised to the second power, $\mathbf{A}^2$, the values at intersecting nodes reflect the number of possible indirect pathway through two links. In a healthy system, the total number of possible pathways should increase as path lengths increase. A decrease in path lengths indicate that energy is either leaking or being transported out of the system and collapse is possible. Pathway lengths (k) and numbers are significant components of network analysis as they describe how quickly indirect pathways increase (Borrett and Patten, 2003).

Pathway proliferation is another characteristic of networks that looks at energy and matter transmission between nodes. Pathway proliferation is the tendency for the number of pathways in a network to increase without bound as pathway length increases. The rate of this

proliferation has been shown to be variable among networks (Fath, 1998; Borrett and Patten, 2003; Borrett et al., 2007). This rate characterizes how quickly the number of pathways available for interactions increase. Shorter pathways have been proposed as more significant to the system; however, network analysis results indicate that flows over long, indirect pathways dominate the total system throughflow (Higashi and Patten, 1989; Patten, 1983). A good measure of the pathway proliferation rate is the dominant, or largest, eigenvalue of the network $\boldsymbol{\lambda_1(A)}$ (Borrett et al., 2007).

These eigenpairs exist only if there exists a vector x such that the following equation is satisfied:

$Ax = \lambda x$ (1) where A defines a matrix and λ is the eigenvalue associated with x

In a matrix, there is an eigenvalue for every subset of nodes that both start and end on a single node, referred to as *strongly connected components* (K_i, i = 1, ...,α, where $\alpha \geq n$). These components can be trivial, one node subsets, as in the case of cannibalism or they can span many nodes and create a *non-trivial cycle* that is vital to maintaining energy within a system. While each subset has an individual eigenvalue and subsequent rate of pathway proliferation, only the largest eigenvalues will influence pathway proliferation of the entire system. Pathway proliferation depends on these strongly connected components that induce cycling, thus a system with only trivial single node components will not allow for pathway proliferation. In a well-connected system, the dominant eigenvalue will be at least 1, implying that A has at least one cycle.

To test the true importance of detritus as a cycle inducing element, we employed several methods of environ analysis to explore how the dynamics of systems changed. Twelve published food webs were modified to include direct links carrying energy from all taxa in a food web back to detritus. In a system, all organisms die and any energy sequestered during their life follow this path and is stored as detritus until subsequently consumed by detritivores. The resulting indirect effects from this modification should increase cycling of energy, and thus increase the stability of the food web. We expect that systems containing detrital cycles will show increased overall health when connectance, total pathway length, dominant eigenpairs, and rate of pathway proliferation are compared.

METHODS

Study Areas. Twelve food webs were organized from the literature via the website http://www.nceas.ucsb.edu/interactionweb/, an interaction web database including a series of American and New Zealand food webs developed and analyzed by Thompson and Townsend (Jaarsama et al. 1998; Townsend et al., 1998; Thompson and Townsend, 2003; Thompson and Townsend, 2005). All chosen food webs included a detrital node as consumed taxa, but no energy or biomass shown to return to this node (eg., through death). These food webs vary widely with respect to habitat, climate, and distinguishable taxa. In addition, indices used in the description of biological networks (eg., network size, connectance, and linkage density) were also found to be highly varied. This variation ensures that results are not specific to a particular system, the nodes (taxa) which define its structure, or the size and connectedness of the system

itself. Thompson and Townsend's development of these network models allow for the analysis of highly varied food webs in the form of adjacency matrices.

We selected a variety of food webs ranging from pine forests in the United States to tussock grasslands in New Zealand. One such site, the Martins site on the main stem of Martins Stream in Maine, is composed of predominantly white pine and balsam fir growing in mixed-age stands. In this site, there is a prolific understory of broadleaf species dominated by red maple. This forest is the product of natural regeneration of pastoral land retired 60 yr ago and is minimally managed to encourage good timber species such as fir and pine. Areas immediately next to the stream had not been harvested in the last 60 years and contained large specimens of white pine that form a closed canopy over the stream (Thompson and Townsend, 2003). This food web is composed of 105 species. In contrast to the Martins site, another location's food web are composed of taxa within a tussock grassland in Otago, New Zealand. Tussock defines grasses with a clumping growth form, dominated primarily by plants of the genera *Carex* (true sedges), *Chionochloa* (a tussock genus including red and snow tussock grass), *Festuca* (fescue, perennial tufted grasses), and *Poa* (perennial, cool temperate grasses). The food webs varied in number of distinguishable taxa present, functional diversity, and climates and habitats. Consequently, we expect that our results are not specific to a given system. Should similar results arise among all of these various ecosystems due to the addition of links to detritus one could suggest that the effects had by the detrital node would be present across all ecosystems.

Modification. Each food web was already in the form of an adjacency matrix when acquired from the interaction web database. It is important to note the matrix model's representation of energy flow being from row to column vectors. As such, a modification

returning energy flows to detritus can be simulated by entries of 1 throughout the column representing detritus. One would expect an increased connectance and linkage density associated with this modification will result in increases in path lengths $n > 2$. To focus on the effects of these modifications directly resulting from detritus as the selected node, a series of null models can be used to test the effects of the distribution of these connections (rather than their number) in the network structure

Network Analysis. Analysis begins with the calculation of some "vital stats" of the network such as network size (n), connectance (c), and linkage density (l). These properties will aid in comparative analyses of networks as well as the appropriate construction of null models to test detritus directly. Connectance (C), which represents the ratio of observed versus potential links of a binary adjacency matrix can easily be calculated through:

$$\mathbf{C = \Sigma A_{ij}/n^2 \text{ where } n = i = j}$$

Linkage density, or the average number of direct links per species, is calculated by the convention:

$$\mathbf{L = \Sigma A_{ij} /n}$$

Analysis was performed on original, modified and null modified food web matrices in MatLab using coding written by Stuart Borrett (Appendices 3, 4). An initial Power Series is performed on the original and modified food web matrices to reveal whether energy in the systems is leaking or cycling. When adjacency matrices are raised to a particular power *n*, the elements of the resulting matrix are equal to the number of potential pathways of length *n* from row *i* to column *j*. Power Series were found for original and modified food webs as well as for a null modified web at lengths of two, three, and ten. Totaling the values of the elements in a matrix, $\mathbf{A^n}$ will

provide the total number of paths of length *n* which can be compared between the original, modified, and modified null matrices. Random null models for each modified matrix are designed so that they have comparable connectance values as well as the presence of a cycle (Appendix 1). Both random null models and their respective power series were generated using R open source programming language (Appendix 2). This analysis method, however, reports merely the presence or absence of energy cycling. To fully comprehend the role of *detrital* cycling, further analysis is required. It has previously been stated that the rate at which these pathways increase over subsequent path lengths is quantified by Pathway Proliferation (Patten, 1985; Borrett et al., 2007), which employs the eigenvalues of a system.

MATLAB functions were also used to calculate the dominant eigenvalue (λ_{max}), normalized dominant eigenvector, and the number of nodes in any strongly connected components. As the Perron-Frobenius theorem guarantees, there will be one real eigenvalue that is equal to or larger than all other eigenvalues ($\lambda_1 \geq \lambda_i$, i =2,...,*n*). The exponential rate of increase of paths can be estimated through the use of this largest, or dominant eigenvalue, λ_{max} (Borrett et al., 2006). Dominant eigenvalues are associated with a cycling subunit of the network referred to as a strongly connected component (K) (Bang-Jensen and Gutin, 2001). K represents a subunit of the network in which direct interactive paths begin and terminate at the same node. This value is closely related to the cycling capacity of a network; one problem encountered in food web interaction models is the potential of acyclic networks (Cohen et al., 1990). When cycling does not exist in a biological network model, the power series terminates; as a result, $\lambda_{max} = 0$ (Borrett et al., 2006). As this dominant eigenvalue describes cycling, the dominant eigenvector (together: dominant eigenpair) satisfying $Ax = \lambda x$ describes cycling contributions of nodes in the SCC. Average cycling contribution, **(# nodes in SCC)$^{-1}$**, is calculated to represent the minimum

dominant eigenvector that would exist within a SCC whose nodes all have the same participation and contribution to a cycle. This value can be useful when comparing dominant eigenvectors of networks with strongly connected components of varying sizes. Greater deviation from this value could suggest a greater relative contribution to cycling.

RESULTS

Statistical properties of the networks (network size {n}, connectance {c}, and linkage density {l}) were first obtained through the use of R programming language (Table 1 a-b). Each food web and its set of corresponding null models will report the same values for *n* (size), *C* (L/n^2), and *l* (L/n) to observe the roll of structure in the distribution of indirect pathways. The number of nodes in the original, modified, and null webs will never differ, as these webs contained detrital nodes initially and no further nodes were required. Modified food webs showed the expected increase in number of links and connectance; they also subsequently exhibited increases in linkage density. The modified and null models will show no differences in these initial calculations.

Table 1a. Network analysis results for the original 12 matrices representing food webs.

Unmodified	# Nodes in Matrix	# of Links	Connectance	Linkage Density
AkatoreA	85	227	0.0314	2.6706
AkatoreB	58	117	0.0348	2.0172
Blackrock	87	375	0.0495	4.3103
Broad	95	565	0.0626	5.9474
Coweeta	71	148	0.0294	2.0845
Coweeta2	58	126	0.0375	2.1724
Kyeburn	98	638	0.0664	6.4102
Martins	105	343	0.0311	3.2667
NCol	78	241	0.0396	3.0897
Powder	78	268	0.0440	3.4359
Stony	113	832	0.0652	7.3628
Troy	78	181	0.0298	2.3205

Table 1b. Network analysis results for the modified and null modified 12 matrices representing food webs.

Null and Modified Food Webs	# Nodes in Matrix	# of Links	Connectance	Linkage Density
AkatoreA	85	312	0.0432	3.6706
AkatoreB	58	175	0.0520	3.0172
Blackrock	87	462	0.0610	5.3103
Broad	95	660	0.0731	6.9474
Coweeta	71	219	0.0434	3.0845
Coweeta2	58	184	0.0547	3.1724
Kyeburn	98	736	0.0766	7.5102
Martins	105	448	0.0406	4.2667
NCol	78	319	0.0524	4.0897
Powder	78	346	0.0569	4.4359
Stony	113	945	0.0740	8.3628
Troy	78	259	0.0426	3.3205

The power series analysis of original and null models shows remarkably different trends. All but two of the original food webs (Broad and Stony, namely) yield the zero matrix of interaction by length 10 (see Table 2a). Broad and Stony show decreasing numbers of paths, resulting in the number of paths reaching an asymptote with increased path length. In the case of the Broad food web, path number remains constant at 222 indirect pathways after length four; Stony asymptotes at 653 indirect paths, also at path length of four. Observation of the properties of the network showed that Broad and Stony are two of the larger systems in terms of *n*. These networks also had two of the highest connectance and linkage density values (Broad → C = 0.0626, L = 5.95; Stony → 0.0652, L = 7.36). It is apparent that a fundamental flaw in network structure exists; the reporting of a dominant eigenvalues, $\lambda_{max}(A)$, equal to zero in ten of twelve food webs in their original form indicates the lack of cycling in the form of a strongly connected component (K). Even Broad and Stony, systems with a dominant eigenvalue of one, can trace

this limited and trivial cycling to a one-loop interaction represented by a one along the diagonal of the matrix (i.e., cannibalism, storage).

Table 2a. Power series analysis of indirect path number as a function of path lengths 2, 3, and 10 in original food webs. Only two of these food webs reached a constant number of paths (Stony, Broad); the remaining ten experienced no pathway proliferation, resulting in a zero interaction matrix.

Original Food Webs	# of Direct Links	# of Paths of Length 2	# of Paths of Length 3	# of Paths of Length 10
AkatoreA	227	129	48	0
AkatoreB	117	81	8	0
Blackrock	375	214	0	0
Broad	565	663	469	222
Coweeta	148	112	0	0
Coweeta2	126	104	68	0
Kyeburn	638	870	447	0
Martins	343	612	679	0
NCol	241	328	184	0
Powder	268	308	200	0
Stony	832	1173	889	653
Troy	181	206	52	0

Both the modified and random null model food web's power series analyses showed exponential pathway increase as pathway length increased. Each modified food web at a path length of ten exhibited a ninth order magnitude increase in the number of pathways (See Table 2b). The null model's power series exhibits similar increase in the number of pathways and even exceeds those within the Broad, Kyeburn, and Stony modified webs (See Table 2c). These three food web networks exhibit relatively large Linkage Densities (see Table 1b). The Broad and Stony original networks had trivial cycles, (Dominant Eigenvalue = 1) products of cannibalism, which could cause more rapid pathway rate increase. Through these Power Series we can determine that both the modified and null model food web networks contain a strongly connected component that allow the network to persist without losses of energy flow. However, to determine the importance of detritus within these cycles further eigen analysis is needed.

Table 2b. Power series analysis of indirect path number as a function of path lengths 2, 3, and 10 in the 12 modified documented food webs. All modified webs show exponential pathway increase as path length increases.

Modified Food Webs	# of Direct Links	# of Paths of Length 2	# of Paths of Length 3	# of Paths of Length 10
AkatoreA	312	3076	12901	6442470381
AkatoreB	175	1764	7598	2431942220
Blackrock	462	3985	23501	18662923102
Broad	660	3983	25592	9635295194
Coweeta	219	2603	11031	6378673803
Coweeta2	184	1796	7982	2683069313
Kyeburn	736	4751	32709	19991218152
Martins	448	6310	37159	119629570434
NCol	319	3221	16506	11489287727
Powder	346	3072	16728	9885405614
Stony	945	7203	56945	98738728284
Troy	259	2805	13513	7643751126

Table 2c. Power series analysis of indirect path number as a function of path lengths 2, 3, and 10 in the 12 null models. All null model webs show exponential pathway increase as path length increases and three webs exceeded the pathway numbers of the modified food webs.

Null Models	# of Direct Links	# of Paths of Length 2	# of Paths of Length 3	# of Paths of Length 10
AkatoreA	312	1209	4707	61356765
AkatoreB	175	553	1727	4395812
Blackrock	462	2449	13064	1642523062
Broad	**660**	**4499**	**30793**	**21833842094**
Coweeta	219	691	2162	6351177
Coweeta2	184	564	1730	5465674
Kyeburn	**736**	**5516**	**41434**	**55438647415**
Martins	448	1973	8544	248407628
NCol	319	1425	6199	187183879
Powder	346	1521	6667	205252164
Stony	**945**	**8063**	**68213**	**213706281677**
Troy	259	798	2425	5139378

Further eigen analysis shows that all food web networks that had been modified to include paths from all nodes back to detritus and their associated null models had dominant eigenvalues greater than one, indicating the presence of a non-trivial cycle (see Tables 3 a-b). Modified food webs exhibited dominant eigenvalues ranging between 5.9809 and 8.3026

(Akatore B and Martins, respectively). The mean dominant eigenvalues of five null models for each food web have a wider range from 3.1068 to 8.4038. The same three null model networks who's pathway number at length 10 exceeded those of the modified networks have greater dominant eigenvalues. The normalized dominant eigenvectors, which represent each node's individual contribution to the dominant eigenvalue, were associated with the detrital node for eleven of the twelve modified food webs. The Powder food web network's dominant eigenvector was *R. curvata;* however, the next greatest eigenvector beyond that was associated with detritus. Randomized null models by nature have no persisting associated nodes: as such, the nodes within the strongly connected component and comprising the dominant eigenvector have no biological interpretation. The strongly connected components within the modified food webs each had a greater number of nodes (29-56 nodes) than those within the null model food webs (11-27 nodes). As seen in Tables 3a and 3b, fewer nodes in a strongly connected component tend to result in larger average cycling contribution (i.e., average throughflow potential). Additionally, greater deviation of the normalized dominant eigenvectors from these average throughflow potentials suggests a greater relative contribution of that vector to cycling. The normalized dominant eigenvectors of the detritus modified networks are consistently much larger than the average cycling contributions than the null model counterparts.

Table 3a. Eigen analysis of modified food web networks. The dominant eigenvalue describes the rate of pathway proliferation due to energy cycling of a strongly connected component (SCC). The elements of the eigenvector explains a node's contribution to cycling within the SCC.

Modified Food Webs	Dominant Eigenvalue	Normalized Dominant Eigenvector	Average Throughflow Potential	# Nodes in SCC	Node associated with DEvector
AkatoreA	6.2832	0.0504	0.0294	34	Detritus
AkatoreB	5.9809	0.0749	0.0345	29	Detritus
Blackrock	6.8916	0.0453	0.0263	38	Detritus
Broad	6.2692	0.0307	0.0270	37	Detritus
Coweeta	6.4458	0.0667	0.0263	38	Detritus
Coweeta2	6.0032	0.0735	0.0345	29	Detritus
Kyeburn	6.7178	0.0314	0.0250	40	Detritus
Martins	8.3026	0.0531	0.0179	56	Detritus
NCol	6.7091	0.0551	0.0217	46	Detritus
Powder	6.5937	0.0554	0.0250	40	*R. curvata* (diatom)
Stony	7.7927	0.0323	0.0200	50	Detritus
Troy	6.5083	0.0587	0.0270	37	Detritus

Table 3b. Eigen analysis of null model food web networks. Mean values of dominant eigenvalues and eigenvectors were obtained from five randomly generated null models for each independent food web.

Null Models	Mean Dominant Eigenvalue	Normalized Dominant Eigenvector	Average Throughflow Potential	# Nodes in SCC
AkatoreA	3.7349	0.0714	0.0625	16
AkatoreB	3.1068	0.0912	0.0833	12
Blackrock	5.3160	0.0440	0.0476	21
Broad	**6.8919**	0.1071	0.0909	11
Coweeta	3.1213	0.0581	0.0476	21
Coweeta2	3.0921	0.0694	0.0556	18
Kyeburn	**7.5190**	0.0411	0.0370	27
Martins	4.3165	0.0461	0.0370	27
NCol	4.0787	0.0539	0.0323	31
Powder	4.3685	0.0583	0.0370	27
Stony	**8.4038**	0.0397	0.0345	29
Troy	3.2964	0.0625	0.0588	17

DISCUSSION

A series of studies looking into the importance of cycling in ecosystems suggest that it is a principal feature of an ecosystem, allowing for tolerance to energy flux perturbations and affecting ecosystem stability and overall function (Loreau 1994; DeAngelis et al. 1989). The Power Series indicated a lack of cycling within the twelve original food web networks. These lack of strongly connected components can perhaps be due to the restrictive nature of representing energy flow that food web research can bring. In predator-prey food webs, energy cycling through means other than feeding relationships may be overlooked. There are two important components to future trophic network analysis which may reveal energetic cycling absent in the original food webs. First, as has oft been the contentious matter in previous literature (Cohen et al., 1990; Pimm et al., 1991; Pimm, 2002), the incompleteness of food webs limit both their size (n) as well as their connectance (C) and linkage density (l). These limitations lower the probability of observing strongly connected components within ecological networks; as a result, methods of eigen analysis cannot be implemented in ecosystem evaluation or network modeling. False negatives of interaction and underestimation of storage, cycling, and cannibalism can also contribute to a network lacking the necessary energy "engine" in the form of at least one strongly connected component, K.

Indirect paths of unmodified food webs often decline in number until no such paths exist, representing a linear progression of energy through a system. This seems an impractical model as randomly generated networks of identical size and connectedness resulted in the presence of at

least one strongly connected component in each of 60 simulations. There are exponential increases in paths along various lengths and the presence of dominant eigenvalues greater than one in all 60 null model simulations. When paths to detritus are included in published food webs, it results in an increased number of direct and indirect paths between predator and prey organisms. The Power Series of the modified food web networks reveal an infinitesimal number of potential pathways which continue to proliferate across ever increasing path lengths. Both the number of indirect paths and the magnitude of the dominant eigenvalues are greater in detrital simulations, suggesting greater pathway proliferation and indirect connectedness as a function of detrital cycling over other forms of random cycling in networks.

It is through the investigation of this eigen analysis which brought interesting aspects of cycling and pathway proliferation. Detritus, through its function as a universal energy sink, incorporated a larger number of nodes into cycling, thus increasing the size of the strongly connected component, K. As such, it may be inferred that there is increased stability in the flow of energy through this trophic network; a larger SCC leaves a system less reliant on any given node for energy cycling. This inference, though, would need a more robust and weighted model to understand and quantify the effects of detritus on ecosystem health and stability through promotion of energy flow.

There seems to be much promise in the use of eigen decomposition in the analysis of the structure, stability, and function of biological networks with much work currently being conducted in various studies (See Fath and Patten, Borrett et al. 2006, Borrett et al. 2007, Allesina and Pascual, 2008). As the dominant eigenvalue is an estimate of proliferation rate it can subsequently be used as a metric of indirect connectedness of a trophic network. To satisfy equation (1), there must exist a dominant eigenvector associated with λ_{max} which can be seen as

breaking down each the magnitude of nodes contributing to the dominant eigenvalue. This eigenvector has *n* elements corresponding to the *n* nodes of the network. The values of each element thus explain a node's contribution to the scalar magnitude of the eigenvalue. If λ_{max} is defining the proliferation rate of a network through an SCC, the dominant eigenvector identifies the nodes participating in this cycling as well as quantifying their relative contribution to this cycling.

In ecosystem ecology and network analysis, we seek general trends and patterns which help us in management and assessment by serving as a metric for ecosystem function. Trophic interactions and energy cycling are no exception; the changes in dominant eigenvalues and projected proliferation rates between random and detrital models signifies the importance of structure in ecosystems while indicating the precedence of structural form over ecosystem function. Eigenvector analyses of the modified and null networks reveal that detritus did not seem to be any more heavy a contributor to energy cycling than nodes associated with dominant eigenvectors in null models. It should be pointed out, however, that there is a significant difference in strongly connected component size between model types. As such, the average contribution possible in null networks is higher. Detritus did show a greater contribution to throughflow *relative* to the average contribution expected. All of these collective findings show potential of eigenvalues and eigenvectors as metrics of energy cycling in ecosystems, especially when used in conjunction with weighted trophic networks; results of eigen analysis of detrital models indicated significantly more pathway proliferation and cycling contribution as a function of detritus than found in random networks. Quantifying this energetic value of detritus within weighted food web networks would be next.

These networks and adjacency matrices function as models of trophic interactions in ecosystems. To better understand ecosystem function and health, models better representing real-world processes and variation will help to give more analytical power to these metrics. Understanding the process of energy throughflow in ecosystems is more realistic when modeling systems with weighted energetic data across dynamically variable temporal scales. Mesocosm and field research which attempt to quantify energy flow while incorporating seasonal variation in throughflow will serve to weight the networks; eigen analysis would then quantify indirect effects rather than suggesting potential paths of these flows. With energy serving as the currency of trophic networks, tracking and understanding its flow can be potentially beneficial in conservation and management. The dominant eigenvalue can serve to identify nodes (species) participating in cycling through the means of an SCC while the dominant eigenvector of a weighted digraph can truly quantify a species' role in energy cycling.

In conservation and management practices it would be key to quantify and identify a compartment within an ecosystem vital to its energetic function. The dominant eigenpair points to that energy compartment; this analysis conducted on weighted, dynamic models may serve to explain cycling, pathway proliferation, and the major participants in ecosystem maintenance and health through their energy throughflow.

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Appendix

1. R open source programming code to create null model matrices for each modified matrix.

```
 n<-$Size of the Matrix$
## This assigns a vector of a particular length n ##
Martins<-rbinom(n^2,1,$C=Connectance$)
## This forces an string of numbers of binary form with given connectance##
## Connectance can be viewed as an assigned probability of a "1" entry##
MartinNullOne<-matrix(rbinom(n^2,1,$C=Connectance),ncol=n)
## This forces the string of n^2 length into a matrix of n x n size##
MartinNullOne
sum(MartinNullOne)/n^2
## A test of the random generator for accuracy with connectance##
eigen(MartinNullOne)
## A test of the random generator in forming a cycle such that the dominant eigenvalue > 1##
write.table(MartinsNullOne,file="MartinsNullOne.csv",sep=",",col.names=F,row.names=F)
## Output null model into comma separated values Excel file##
```

2. R open source programming code to calculate the Power Series for powers of two, three, and ten.

```
x<-read.csv("$ENTER FILE NAME HERE$.csv",header=FALSE)
## Reads comma separated values files created in Excel in the working directory##
x<-as.matrix(x)
## Forces square matrix assignment of .csv file##
length2<-sum(x%*%x)
length2 ## Reports sum of all indirect paths of length 2 ##
length3<-sum(x%*%x%*%x)
length3 ## Reports sum of length 3 ##
length10<-sum(x%*%x%*%x%*%x%*%x%*%x%*%x%*%x%*%x%*%x%*%x)
length10 ## Reports sum of length 10 ##
```

3. Stuart Borrett's MatLab coding to determine STUFF

```
% ************************************************************************
% Network Structural Properties (NSP2)
% ************************************************************************
function [y,lv1,rv1]=nsp2(A);
% calculate basic network statistics of the adjacency matrix A
% This modified version of NSP also finds the dominant eigenvectors (L & R)
% ------------------------------------------------------------------------
n  =length(A);       % number of nodes in A
L  =nnz(A);          % number of direct connections in A
C  =L/n^2;           % connectivity
LD =L/n;             % link density (equivalent to n*C)
```

```
e  =sort(eig(A));     % sorted eigenvalues of A.
aer=round(abs(e)*100000)/100000;    % round the eigenvalue magnitudes
m1A=length(find(aer==aer(n)));      % finds the multiplicativity of SR
SR=abs(e(n));    % dominant eigenvalue of A.  Also termed spectral radius.
                % This is 1) a measure of connectivity,
                % 2) approximately equal to LD, and the rate of pathway
                % proliferation.
d=abs(SR-LD);    % difference between dominant eigenvalue and link density

if (n-m1A)>0
        lam2A=abs(e(n-m1A)); % magnitude of second largest eigenvalue
        rho=SR/abs(lam2A);   % damping ratio, an indicator of how quckly a^(m)/a^(m-1) goes
to lam1(A)
   R=abs(e(n))-abs(e(n-1))/(abs(e(n-1))-abs(e(1)));    % distiance of lam1(A) from the bulk of the
eigen spectrum (Farkas et al 2001)
else
   lam2A=-99; rho=-99; R=-99;    % flag to indicate these do not exist
end

y=[n L C LD SR m1A lam2A rho R d];
nsp_labels= {'n','L','C','LD','SR','mult of lam1(A)','lam2(A)','Damp Ratio', 'lam1(A) dist','d'};


% RIGHT EIGENVECTORS
[v,e]=eig(A);
e = diag(e);
if max(abs(e))>0
        [j]=find(abs(e) == max(abs(e)));
        rv1=v(:,j);   % left hand eigenvector associated with dominant eigenvalue
else
        rv1=-9999;
end

if sum(rv1)>0
        rv1=rv1/sum(rv1);  % normalize lv1 by the sum of the vector
end

% LEFT EIGENVECTORS
[v,e]=eig(A');
e = diag(e);
if max(abs(e)) > 0
        [j]=find(abs(e) == max(abs(e)));
        lv1=v(:,j);   % right hand eigenvector associated with dominant eigenvalue
```

```
else
        lv1=-9999;
end

if min(abs(lv1)) > 0 & lv1~=-9999
        lv1=abs(lv1/min(abs(lv1)));  % normalize rv1 by the sum of the vector
end
```

4. Stuart Borrett's MatLab Coding Awesomeness

```
function [Ap,Kp,LV,RV]=sccw3(A);
% y = sccw3(A) -- strongly connected componets wrapper
%
% This function identifies and characterizes the strongly connected
% componets in the network represented by the adjacency matrix A.
% It returns a vector of the network propoerties of A (Ap) and of any
% embedded strongly connected components (KP).
%
% Stuart Borrett || Oct. 4, 2008
% ***********************************************************************
tic
% PROGRAM PARAMETERS
tol=0.001; cnt1=1;
trials=10;
Ap_labels={'n' 'L' 'C' 'LD' 'SR' 'mult_of_lam1(A)' 'lam2(A)' 'Damp_Ratio' 'lam1(A)_dist' 'd'
'scc_number' 'scc_number_lg' 'nmbr_nds_scc_lg'};
Kp_labels={'K#' 'n' 'L' 'C' 'LD' 'SR' 'rho' 'd' 'p1_SR' 'Z1_SR' 'p1_d' 'Z1_d'};
% ANALYZE WHOLE NETWORK
[y1,lv1,rv1]=nsp2(A);                % calls nsp (network structural properteis) {[n L C LD SR rho
d]}
% stats_nm1_FW=snm1(A,trials);  % determines probability of SR and d in random net

% Identify, Enumerate, and Characterize SCC -------------------
[c,v] = scc(A,tol); % calls function to identify strongly connected components c=reachability,
v=scc lists
[m,n]=size(v);
scc_number=m                 % number of scc
temp1=sign(v);               % convert v into binary matrix
scc_size=sum(temp1');        % vector of sizes of scc
temp2=find(scc_size>1);      % find address of non-trivial scc
scc_number_lg=length(temp2);    % number of large scc (>1 node)
nmbr_nds_scc_lg=sum(scc_size(temp2));   % number of nodes in large scc's
%cnt1=1;
```

```
if nmbr_nds_scc_lg > 0 & length(scc_number) > 0
   for j=1:scc_number_lg
      nn=v(temp2(j),1:scc_size(temp2(j))); % nodes of Component
      K=A(nn,nn);      % adjacency matrix of SCC
      %stats_nm1_scc=snm1(K,trials);    % determines probability of SR and d in random net
      [y,lv,rv]=nsp2(K);
                  Kp(j,:)=[j y];
                  LV{j}=lv;
                  RV{j}=rv;
                  %Kp(cnt1,:)=[i j nsp(K) stats_nm1_scc];    % network statistics of SCC
      %cnt1=cnt1+1;
   end
end


%%%%%%%%%%%%%%%%%%%%%%%%%%
if scc_number == 1
   display('The Graph is one SCC -- A GIANT!');
   Kp= ones(1,max(size(Kp_labels))) * -9999;        % flag non-existance
end

if nmbr_nds_scc_lg ==0
         Kp= ones(1,max(size(Kp_labels))) * -9999;        % flag non-existance
         LV=lv1;
         RV=rv1;
end

size(y1);

Ap=[y1 scc_number scc_number_lg nmbr_nds_scc_lg];
%save pp_05feb02_foodwebTRO FWstats Kstats notes

toc
```