



Structure of pathways in ecological networks: relationships between length and number

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Abstract

In ecosystems network, structure determines adjacent (direct) and non-adjacent (indirect) pathways over which energy, matter, and information can flow. The more pathways, the more possible ways the conservative substance can move in zero-sum transactions between network nodes that the pathways interconnect, and the more possible non-conservative, nonzero-sum relations can be secondarily derived from these. Structural analysis is a tool we employ, from a family of input–output methods for exploring zero- and nonzero-sum attributes of environmental networks, to count pathways of varying length between network nodes. In this paper, we examine the relationship between pathway length (k) and number (P_k) as determined by system size (n , number of nodes) and extent and pattern of connectance (C). We develop a measure (m_a) of pathway growth in numbers with increasing length, and then normalize this to the maximum rate possible (m_a/m_c) for a given system size. These measures apply to two pathway types—*paths*, $m_a(0)$ and $m_a(0)/m_c(0)$, which forbid adjacent node repetitions, and *walks*, $m_a(1)$ and $m_a(1)/m_c(1)$, which allow them. We find that network size has a curvilinear effect on the pathway number versus length relationship, and extent and pattern of connectance are convolved. Values computed for the paths and walks of three ecosystem models (oyster reef, freshwater marsh, and reservoir cove) are used to compare their pathway structure.

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1. Introduction

Environ analysis (Patten, 1978a, 1982; Matis and Patten, 1981) is a family of input–output methods of network analysis descended from Leontief (1965, 1966) and introduced into ecology by Hannon (1973). Environ methodology is employed in the holistic study of ecological networks to describe, quantify, and analyze component-level environments (environs) within systems. These environments are of two types, affer-

ent (input environs) which are generated by history, and efferent (output environs) which are propagated to the future. Environ methods include analyses for structure, flows, utilities, and control within systems, and are a form of complex-systems analysis as described by Allen and Hoekstra (1992, p. xiv). In this paper, we elucidate several attributes of environ network structure, which underlies much of the environ analysis methodology.

Network *structure* establishes the pathways (direct and indirect) over which conserved material can flow between entities in connected systems (Fath and Patten, 1999). The relationship between pathway numbers and length is a significant component of this

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structure because it describes how quickly indirect pathways increase, and with this also, proportional opportunities for substance to move and for positive “nonzero-sumness” (Wright, 2000) to be realized. In a well-connected system, the number of pathways in a network increases without bound as pathway length increases (Fath, 1998; Patten, 1985). The rate of this increase, however, varies (Borrett, 2001; Fath, 1998). Here, we investigate the cause of this variation by developing measures to examine the proposition that the relationship between pathway length and number is determined by three variables: system size, connectance degree, and connectance pattern. We apply our measures to three ecosystem models and then consider the results.

1.1. Transactions and relations

The network perspective (Margalef, 1963; Higashi and Burns, 1991) conceptualizes an ecosystem as a reticulum of interactions. These are of two types, transactions and relations (Fath and Patten, 1998).

Transactions are physical (ontic, electromagnetic) and have primacy. They are zero-sum exchanges of conservative substances between adjacent network nodes representing processes and storages (slow processes). Zero-sumness means what is gained (+) by one member of an interacting node pair identically equals what is lost (−) by the other. The quantities being equal, their signs opposite, and the substance transferred conservative means the interactive sum is zero.

Relations are phenomenal (epistemic, semiotic) interactions as experienced and interpreted by participants and observers. What is transferred between non-adjacent nodes is conservative but nonzero-sum (Wright, 2000), and in the latter property begins to have attributes of non-conservative information. Competition, predation, and mutualism are classic examples of relations in ecology. In general, relations have their basis in transactions but need not in themselves involve direct energy or matter interchange, e.g. predation does, but competition and mutualism do not.

By conceptualizing complex systems like ecosystems as networks, we can analyze them holistically for properties arising from the transactions and relations interconnecting component parts.

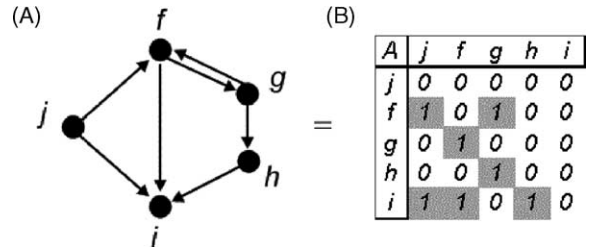


Fig. 1. Example network. Two isomorphic representations of an example network with $n = 5$ and $C = 0.28$: (A) digraph and (B) adjacency matrix. Note how the pattern of connections in the digraph is represented in the matrix.

1.2. Pathways and cycles

Network structure can be represented by digraphs (directed graphs) or isomorphic matrices (Margalef, 1963; Hannon, 1973; Patten, 1985). In digraphs a *node* is a point representing a system component and an *arc* is an arrow denoting a directed transaction (energy or matter flow) or relation (Fig. 1A). A *pathway* is a sequence of nodes and arcs over which a substance flows (in transactions) or relationships emerge (in relations) from node j to node i . *Pathway length* (k) is the number of arcs from an initial to a terminal node. A *direct pathway* between two nodes has only one arc, $k = 1$; an *indirect pathway* has $k > 1$ arcs. Pathways can be *simple*, where there are no repeated nodes, or *compound*, with repeated nodes. In the Fig. 1, network $j \rightarrow f \rightarrow g \rightarrow h \rightarrow i$ is a simple pathway from j to i while $j \rightarrow f \rightarrow g \rightarrow f \rightarrow i$ is a compound pathway. Both are indirect and of length $k = 4$.

Cycles are an important type of pathway in network structures (Patten et al., 1990). A *cycle* is a pathway starting and ending at the same node, as in the embedded pathway segment $\dots \rightarrow f \rightarrow g \rightarrow f \rightarrow \dots$ in our example (Fig. 1A). Like other pathways, cycles can be simple (first time around) or compound. A cycle of length $k = 1$ is a *self-loop*; this can be used to represent node storage in a network (e.g. $\dots \rightarrow i \rightarrow i \rightarrow \dots$).

1.3. Network structural measures

The *size* (n) of a network equals its number of nodes. *Connectance* (C) is the proportion of realized direct ($k = 1$) pathways, often termed *links* (L) in food-web literature (Cohen et al., 1990; Martinez, 1994; Bersier

et al., 1999; Williams and Martinez, 2000), divided by the number of possible links, n^2 : $C = L/n^2$ (see Margalef, 1991; Newman, 2002 for alternative formulations).

Digraphs have isomorphic representations as adjacency matrices, $A_{n \times n} = (a_{ij})_{n \times n}$ (Fig. 1B). An *adjacency matrix* is a square matrix whose rows and columns are indexed by the node vector ($i, j = 1, 2, \dots, n$) and whose elements take values $a_{ij} = 1$ if and only if a link directed from column j to row i exists, otherwise $a_{ij} = 0$.

Each column denotes the presence (ones) or absence (zeros) of links directed from node j to node i in the corresponding digraph, that is, links in the j 'th output environ of the system. In Fig. 1B, for example, column j has ones at rows f and i denoting links $j \rightarrow f$ and $j \rightarrow i$ in Fig. 1A. The orientation from columns (initial nodes) to rows (terminal nodes) is the same as that of the digraph arrows, reflecting the fact that output environs extend forward through the system from starting to ending nodes.

Each row of A denotes the presence or absence of links directed to node i from row j in the system's i 'th input environ. Thus, in Fig. 1B row i has ones at columns j, f and h denoting links $i \leftarrow j, i \leftarrow f$, and $i \leftarrow h$ in Fig. 1A. The orientation to rows (terminal nodes) from columns (initial nodes) is opposite that of the digraph arrows, reflecting the fact that input environs extend backward through the system from ending to starting nodes.

This reverse orientation can be treated separately in the columns-to-rows format of A matrices by performing the operations of this paper on corresponding transposes $A_{n \times n}^T = (a_{ji})_{n \times n}$, mentally reversing the arrow directions. Numerical results would differ since the pathway structure directed from initial to terminal nodes differs from that in the reverse direction, but the principles elaborated would be the same. Therefore, for present purposes we will limit further attention to output environs whose structure is generated by matrices A , not their transposes.

We will employ two forms of the adjacency matrix. $A(0)$ will denote a matrix with zero principal diagonal entries, $a_{jj} = 0$, signifying no node storage, and $A(1)$ will be a matrix with diagonal ones, $a_{jj} = 1$, representing digraph self-loops denoting storage. The former pathways are termed *paths* and the latter *walks* in subsequent usage. *Connectance pattern* is the network

geometry (topology) of nodes and arcs as reflected in a digraph or its corresponding adjacency matrix.

A power matrix, A^k can be used to compute the number of pathways of length $k \geq 0$ directed from j to i in a network (Harary, 1969; Hill, 1981); $k = 0$ denotes self-loops. The total number of pathways (P_k) of different lengths (k) from all nodes to all other nodes is given by the scalar measure:

$$P_k = \sum_{j=1}^n \sum_{i=1}^n (a_{ij})^k.$$

The number of pathways of all lengths from each j to each i is generated by the matrix power series:

$$I + A + A^2 + A^3 + \dots + A^k + \dots$$

The first term $A^0 = I_{n \times n}$ corresponding to $k = 0$ signifies the network's n nodes as initial in pathway propagation. The next term A denotes adjacency—direct links ($k = 1$) defined by zero-sum transactions directed from j 's to i 's. The remaining terms A^k , $k > 1$, denote pathways that are non-adjacent, indirect, relational, and carry nonzero-sum flows. In a well-connected system, one with cyclic feedback and a maximum real eigenvalue greater than one, the series diverges because sums of powers of the A -matrix entries grow as k increases (Fath, 1998). This is consistent with the fact that ecological systems are dissipative; energy and matter pass through them and ultimately exit as a limit process. This implies $k \rightarrow \infty$ and therefore $A^k \rightarrow \infty$. Also, as k increases, P_k increases approximately geometrically. By log-transforming P_k we generate a line of slope m_a (index a referring to the digraph corresponding to A) that can be used to describe the rate of growth of P_k with k .

1.4. Network structure in environ analysis

The methods of environ analysis (Patten, 2003, Chapter 4) can be grouped in pairs:

- (1 and 2) Input and output environ *structure*, which is our focus in this paper.
- (3 and 4) Input and output environ *flows to throughflows*. Throughflows (T_i) are sums of flows at nodes ($i = 1, \dots, n$) in storage-and-flow networks. The input environ case corresponds to original Leontief (1965, 1966) input–output analysis.

- (5 and 6) Input and output environ flows to node storage (x_i , $i = 1, \dots, n$). From the network perspective, storage is interpreted as flow impedance, like capacitance in electrical networks.
- (7 and 8) Throughflow- and storage-based utilities, $u(T_i)$ and $u(x_i)$ respectively, generated by net input- and output-environ direct flows between node pairs (Patten, 1991). Utility measures direct and indirect values of throughflow and storage conferred by the particulars of network organization.
- (9 and 10) Throughflow-based control (Patten, 1978b) and storage-based control (Patten, 2003), $c(T_i)$ and $c(x_i)$, respectively, exerted over network distances, k . Direct and indirect control are assessed and quantified between each node pair in a system.

Each of these methods generates a unique perspective on relationships inherent in ecological networks. These derive from one overarching result from analyses 3–6 above: flows $f(A^k)$ over pathways A^k of lengths $k > 1$ in the adjacency matrix power series often exceed in aggregate those associated with the direct links in the adjacency matrix A itself. That is, $\sum_{k>1} f(A^k) > f(A)$. The reason is because although conservative quantities dissipate with transfers and transformations in networks, this happens more slowly than the rates at which pathways are generated in well-connected networks (Patten, 1985). Each pathway of whatever length carries some quantity of transferred substance until lengths k_d are reached where materials have been effectively dissipated (dissipation is a limit process) such that flows over those pathways are zero. This fact allows power series of non-dimensional flows to converge, which is what enables input–output methods to calculate integral flows carried by all pathways P_k of all lengths $k = 0$ in a system. Small, even infinitesimal, flows over large, approaching astronomical, numbers of pathways generated before lengths k_d are reached can add up to significant total flow over paths P_k of lengths $k > 1$. This is in fact the essential input–output network dynamic. Its consequence is that indirect effects dominate (Patten, 1984; Higashi and Patten, 1989) and make holistic determination (Patten et al., 1976) the principal mode of causality in nature (Patten, 2003).

Higashi (see Patten, 1991) developed algebraic formulations to show that certain network properties increase the dominance of indirect over direct effects. These are system size (n), connectivity (C), network looping (storage), network cycling, feedback cycling (return to initial nodes), and strength of direct arc flows. All but the last are structural properties, as considered here. In this paper, we investigate the relationship between pathway length (k) and number (P_k) as determined by the first two of Higashi's properties, n and C .

As pathway structure defines how conserved substances can flow in connected networks, the more pathways there are the more possible ways exist for energy and matter to move between nodes. Structural analysis, however, does not consider how much substance actually flows along each pathway, it only enumerates the pathways. To determine flow relationships requires other analyses such as those in the environ set of methods. As stated previously, here our topic is structural analysis.

2. Materials and methods

We will investigate how three properties of networks—(1) system size, (2) connectance degree, and (3) connectance pattern—contribute to the rate of pathway proliferation. Below we describe methods to test each, and introduce model ecosystems we will analyze as examples.

2.1. System size

To determine if there is a relationship between system size and pathway length and number, we analyzed digraphs of varying sizes ($n = 1$ to $n = 200$). Both arbitrary digraphs (a) and their complete counterparts (c) were studied. Complete digraphs have a link to and from every node ($a_{ij} = 1, \forall i, j$); their analyses quantify walks due to principal diagonal values of one, $a_{ij} = 1$. For paths, the same digraphs with self-loops excluded ($a_{ij} = 1 \forall i \neq j$, and $a_{ij} = 0$) were analyzed. For a given network a (or c) we determined m_a (or m_c), the slope of a line describing the relationship between pathway length and the logarithm of pathway number. Slopes were calculated as differences between an arbitrarily selected pair of

adjacent P_k values; the values used were $k = 50$ and 51 : m_a (or m_c) = $\log_{10}(P_{51}) - \log_{10}(P_{50})$. If size does not affect the relationship slopes should be roughly equivalent between networks. Use of complete graphs neutralized the effects of degree and pattern of connectance, and also generated the maximum number of possible pathways.

2.2. Extent of connectance

If there were a relationship between system size and pathway length and number, the size effect would have to be removed in order to examine the connectance of systems of different sizes. To accommodate this, we created a normalized response variable by taking ratios of slopes generated by actual digraphs, m_a , to those for complete graphs, m_c , of the same size. For paths this measure is $m_a(0)/m_c(0)$ and for walks $m_a(1)/m_c(1)$. The second part of our investigation was to determine if degree of connectance in adjacency matrices altered m_a/m_c ratios. We held system size constant and then systematically added connections (Fig. 2, networks A1–A4). If connectivity does not affect the relationship, then m_a/m_c should remain constant. It became clear that augmenting connectivity typically alters the pattern of connectance as well (Section 2.3). The two attributes are convolved, such that if varying the pattern changes m_a/m_c , the effects of degree cannot be distinguished from pattern.

2.3. Pattern of connectance

To investigate the effects of connectivity pattern we held network size and degree of connectance constant while varying the pattern (Fig. 2, networks A5–A8). Changes were made so as to maintain cyclic feedback. Each test network had $n = 9$ and $C = 0.12$. In A5 there is a chain of links spanning the network, with two links in the upper right corner providing the possibility for cycle development. Matrix A6 is similar to A5 but the chain is slightly altered. In A7, the chain is replaced with a block of connections in the lower left corner. The final manipulation (A8) was to aggregate the links in the top right and bottom left corners. Structural analysis was performed on each of these networks to determine m_a/m_c for paths and walks. We would consider connectance pattern as having no ef-

fect if these measures remained constant as topology changed.

In addition to actually changing connections (Fig. 2, A5–A8) it is also possible to change the perceived linkage pattern. For example, renumbering nodes in a digraph would leave the pattern of connections unchanged, but the display in the corresponding adjacency matrix would (typically) be altered. To test if this kind of change would be reflected in our measures we analyzed alternative representations of the same network created by interchanging two or more columns and then making an identical change in the corresponding rows (Fig. 2, networks A9–A12; the A9 matrix functions as a control). In A10 column (row) 5 (of A9) was placed between columns (rows) 1 and 2, column (row) 7 between columns (rows) 2 and 3, and column (row) 8 between columns (rows) 3 and 4. Matrix A11 was created by moving column (row) 4 into the first column (row) position and column (row) 9 between columns (rows) 6 and 7. Matrix A12 was generated by moving columns (rows) 5 and 6 into the first two positions. These row and column interchanges clearly changed perceived patterns in the adjacency matrices, but without altering actual network topology. These manipulations are equivalent to symmetric permutations of the adjacency matrix. If m_a/m_c ratios changed under this kind of manipulation we would conclude that the measure is invalid for network structural analysis. A proper measure would yield unique m_a/m_c ratios for a network irrespective of its representation.

2.4. Example networks

We applied structural network analysis to three static, steady state, ecosystem models to compare their direct and indirect pathway structure. The models differ in size, connectivity, connectance pattern, and type of ecosystem represented. Our goal was to determine the degree of similarity in these models' network structures. The models were for (1) an intertidal oyster reef in coastal South Carolina (Dame and Patten, 1981), (2) a marsh called Little Cooter Prairie in Okefenokee Swamp (Whipple, 1995), and (3) a reservoir cove in Lake Texoma (Patten et al., 1975). We will refer to these as oyster, marsh, and cove models, respectively. The oyster model has six compartments and connectivity $C = 0.50$. Patten (1985) described the direct

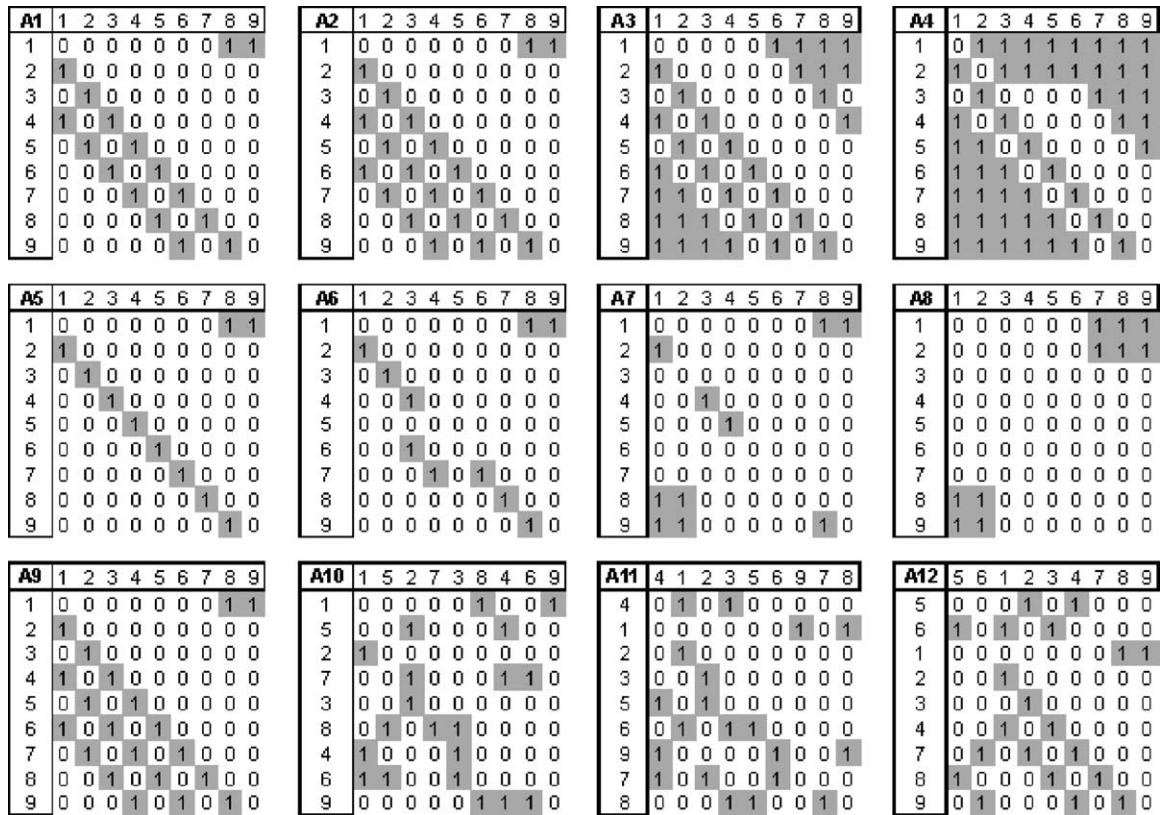


Fig. 2. Experimental networks. Twelve experimental networks were used to investigate degree and pattern of connectance. A1–A4 are the same size and have increasing connectivity. A5–A8 have the same size and connectance, but the pattern of linkage is altered. In A9–A12 size, connectance, and pattern of connection remain constant but reordering the node vector alters the adjacency matrix representation.

and indirect pathway structure of this network, and the model has been used further to develop ecological network theory (e.g. Patten et al., 1990; Higashi and Burns, 1991). The marsh model has 42 compartments and a connectivity of $C = 0.20$. The cove model has 33 compartments and connectivity $C = 0.30$. Like the oyster model, the cove model has been used before in theory development and many of its specific pathways have been identified (e.g. Patten et al., 1982b).

3. Results

Experimental results showed network size, and extent and pattern of connectance all affect the relationship between path numbers (P_k) and length (k).

The effect of connectance degree was inconclusive because this is convolved with pattern. Relabeling digraph nodes without altering real topology changed the adjacency matrix pattern, but did not alter m_a/m_c ratios.

3.1. System size

Fig. 3 shows results of determining if size (n) of fully connected networks increases the rate (m_c) at which higher order pathways are generated. As network size increases the rate of growth of pathway numbers increases and the difference between m_c values for corresponding paths and walks decreases (Fig. 3A). The reason is that the proportion of self-loops (n) in a fully connected network relative to all arcs (n^2) decreases by the factor $n/n^2 = 1/n$. This causes the

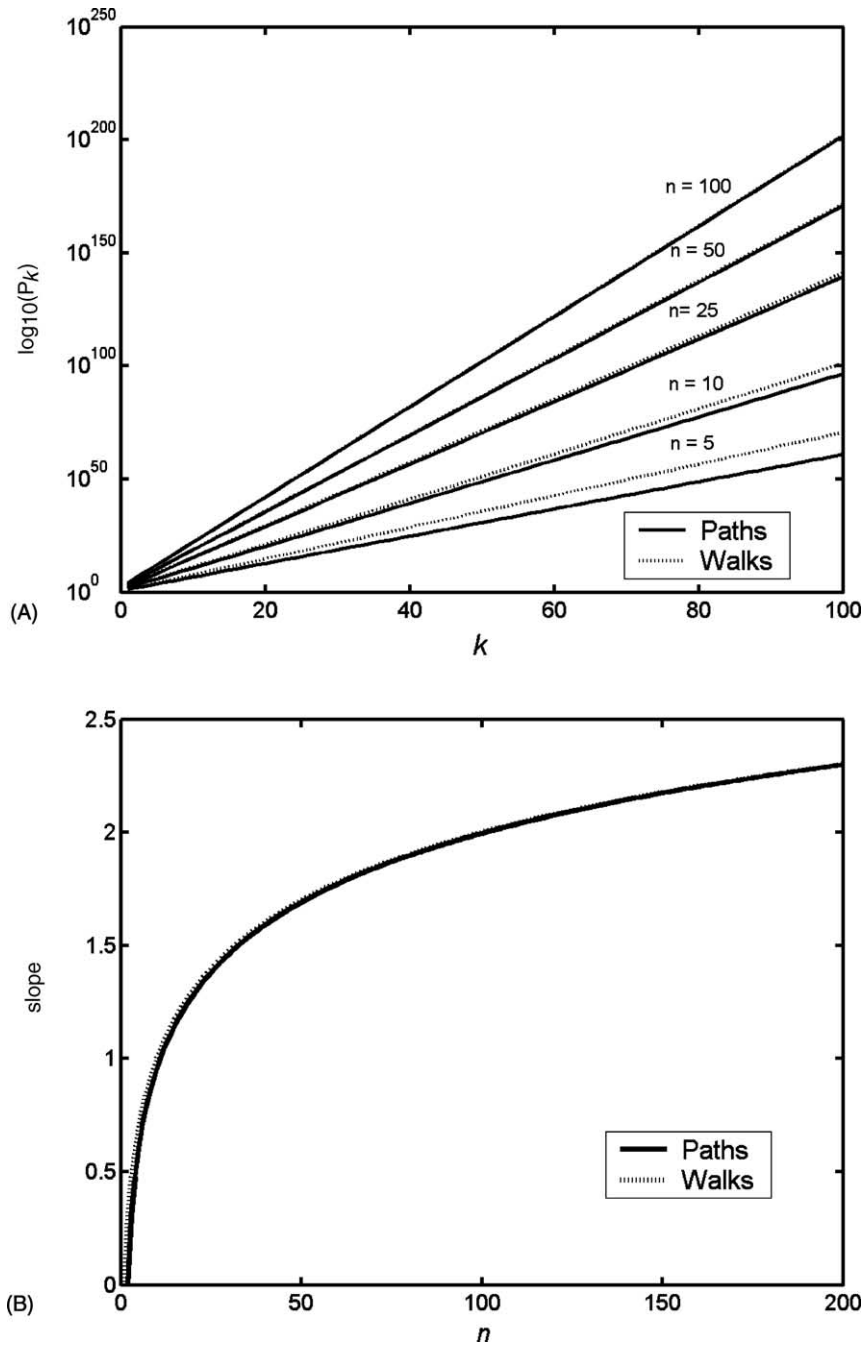


Fig. 3. Relationships between number of pathways (P_k) and pathway length (k) as network size (n) increases from 1 to 200. (A) Selected networks to demonstrate relationships. Note how differences between paths, $A(0)$, and walks, $A(1)$, decrease as size increases. (B) Using the slope (m_a) of the relationship to describe it, we see that size has a curvilinear affect on m_a .

relationship between system size and rate of pathway increase to be curvilinear (Fig. 3B). In fully connected networks size influences the growth of system structure most in smaller networks where the ratio of n to n^2 is greatest.

3.2. Extent of connectance

To evaluate degree of connectance in non-complete digraphs requires use of a normalized metric like m_a/m_c . Given $C < 1$ (incomplete connectance) one can visualize slopes of actual networks (m_a) being less than those of corresponding complete networks (m_c). Then, in Fig. 3A format, m_a values would generate lines of lesser slope than m_c and curve forms like those of Fig. 3B would rise more slowly. Connectance changes made in the experimental networks A1–A4 of Fig. 2 changed the values of m_a/m_c (Table 1). These ratios increased with connectance but not consistently. For example, network A8 in Table 1 has lower connectance than A1, but its m_a/m_c values are larger. This shows that extent and pattern of connectance are interwoven quantities, not easily separated by simple measures.

Table 1
Effect of connectance degree and pattern on measures of the rate of pathway proliferation for walks ($m_a(1)/m_c(1)$), paths ($m_a(0)/m_c(0)$), and the asymptotic rate ($\max|\lambda|$); Fath, 1998; Hill, unpublished manuscript)

Matrix	n	C	$m_a(1)/m_c(1)$	$m_a(0)/m_c(0)$	$\max \lambda $
Connectance					
A1	9	0.20	0.2688	0.4602	1.7489
A2	9	0.25	0.3406	0.5046	2.0306
A3	9	0.41	0.6449	0.7161	3.8229
A4	9	0.62	0.8352	0.8642	5.6786
Pattern of connectance					
A5	9	0.12	0.0413	0.3345	1.0851
A6	9	0.12	0.1024	0.3668	1.2388
A7	9	0.12	0.3211	0.4923	1.9498
A8	9	0.12	0.3333	0.5000	2.0000
Network representation					
A9	9	0.25	0.3406	0.5046	2.0306
A10	9	0.25	0.3406	0.5046	2.0306
A11	9	0.25	0.3406	0.5046	2.0306
A12	9	0.25	0.3406	0.5046	2.0306

Matrix number corresponds to experimental networks shown in Fig. 2.

3.3. Pattern of connectance

Changing the pattern of connectance clearly alters the relationship between number (P_k) and length (k) of pathways. In Table 1, network A5 has $m_a(0)/m_c(0) = 0.0413$ and $m_a(1)/m_c(1) = 0.3345$. The small pattern change in A6 versus A5 causes $m_a(0)/m_c(0)$ to increase to 0.1024 and $m_a(1)/m_c(1)$ to 0.3668. The pattern in A7 generates $m_a(0)/m_c(0) = 0.3211$ and $m_a(1)/m_c(1) = 0.4923$, while A8 has an $m_a(0)/m_c(0)$ ratio of 0.3333 and an $m_a(1)/m_c(1)$ value of 0.5000. As connections become more concentrated in the lower left and top right corners of the matrix, reflecting an increase in the number of cycles, m_a/m_c increases.

Reordering network nodes in the adjacency matrix under the constraint that order is consistent for both rows and columns, does not affect m_a/m_c . In all four representations of a fixed topology (A9–A12), the same path and walk ratios were obtained (Table 1): $m_a(0)/m_c(0) = 0.3406$ and $m_a(1)/m_c(1) = 0.5046$. This result is not unexpected and is quite general because symmetric permutations of adjacency matrices generate isomorphic graphs, which have identical structural properties (Logofet, 1993; Bondy and Murty, 1976).

3.4. Comparison of example models

In non-complete networks of the oyster, marsh, and cove models pathway numbers (P_k) increased without bound as length (k) increased (Fig. 4). As in the experimental networks of Fig. 2, walks increased faster than paths and differences in their rates of increase decreased with system size. The rate (m_a) at which number of pathways increases in the oyster model is less than that of the marsh and cove models, which between themselves are very similar. Rates $m_a(0)$ and $m_a(1)$ of, respectively, path and walk generation in the three models indicate that the difference between marsh and cove models is small and that between these two and the oyster model larger (Table 2).

The normalized measure m_a/m_c indicates somewhat different relationships than those based on non-normalized slopes. In Table 2, $m_a(0)/m_c(0)$ is least for the oyster model (0.4750) and greatest for the cove model (0.6826), whereas $m_a(1)/m_c(1)$ is least for the marsh model (0.6321) and greatest (0.7027) for the cove model. The ranking changes between

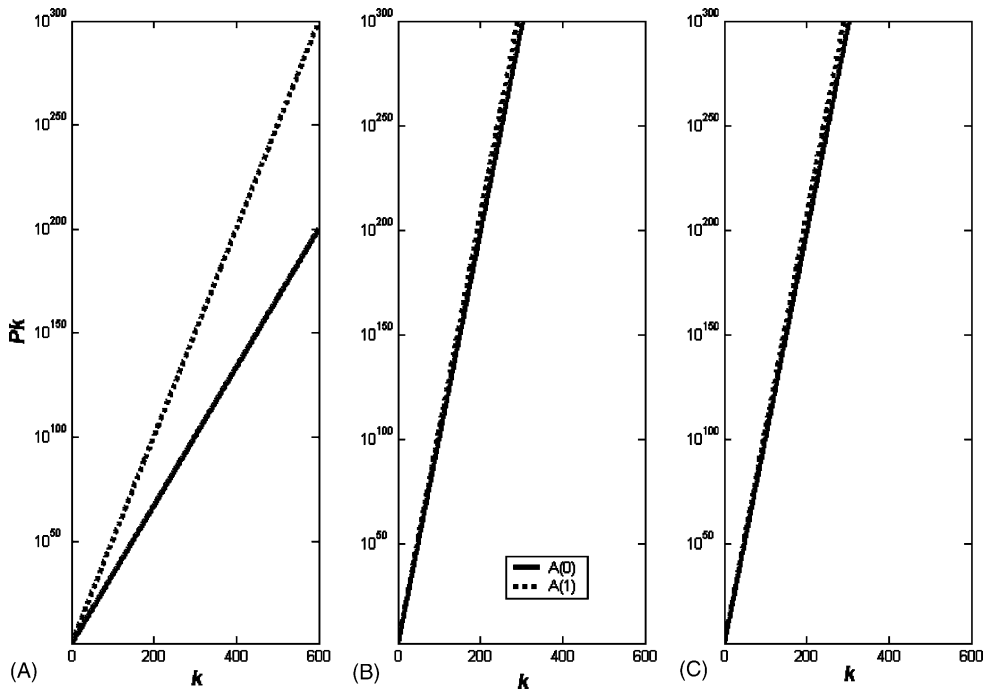


Fig. 4. Structural comparison of three model ecosystems: (A) oyster reef (Dame and Patten, 1981), (B) Okefenokee marsh (Whipple, 1995) and (C) Lake Texoma cove (Patten et al., 1975).

Table 2
Comparison of pathway proliferation rates in three ecosystem models

Model	n	C	$m_a(0)$	$m_c(1)$	$m_a(0)/m_c(0)$	$m_a(1)/m_c(1)$	$\max \lambda $
Oyster	6	0.50	0.33	0.50	0.4750	0.6400	2.1479
Marsh	42	0.20	0.98	1.03	0.6095	0.6321	9.6170
Cove	33	0.30	1.02	1.06	0.6826	0.7027	10.4217

paths and walks. Faster walk than path development in the oyster versus the other two models is a size ($n/n^2 = 1/n$) effect, as previously described. Adding n self-loops to $<n^2$ arcs (in incomplete graphs) has a greater effect when n is small. It is also evident from higher values of $m_a(0)/m_c(0)$ and $m_a(1)/m_c(1)$ for the cove model (Table 2) that more of the potential ways to move energy and matter are realized in this model than in the oyster and marsh models.

4. Discussion

In ecosystems virtual structure is defined by direct (adjacent) zero-sum transactions of conservative en-

ergy and matter exchanged between organisms and their environments. The transactions set up more diverse and wide-ranging informational relations that are indirect (non-adjacent) and nonzero-sum. Relations make life in the ecosphere infinitely varied and for the most part positively experienced by organisms (Patten, 1991) over their time-lines (Jørgensen et al., 1992).

Network structure establishes pathways over which conserved material can flow between entities in connected systems. The relationship between pathway numbers and length is a significant network attribute because it describes how quickly indirect pathways increase, and thus, the volume of pathways available for transactions and relations. In this paper we

have demonstrated, consistent with other findings from environ analysis, that network size (n) and connectance degree (C) and pattern contribute to shaping of the pathway length (k) and number (P_k) relationship. System size was shown to have a curvilinear effect. Connectance extent and pattern were found to jointly influence this relationship, though in ways not easily separated. Our main conclusions are the following:

1. in well-connected networks, pathways increase geometrically with length regardless of system size, as measured by m_a ;
2. system size has a curvilinear effect on the relationship between pathway length and number;
3. irrespective of system size, connectance can be compared utilizing the measure m_a/m_c ; and
4. while connectance degree is entangled with pattern, connectance pattern has a clear role in determining the rate of pathway increase, as measured by m_a .

Our measure of path growth, m_a , indicates an increase rate based on the total number of pathways P_k of selected lengths k . A less empirical (and less heuristic) metric is the dominant eigenvalue of the adjacency matrix, $\max|\lambda|$. This analytically determines the asymptotic growth rate of paths between any node pair (Fath, 1998; Hill, unpublished manuscript). This rate is identical for all node pairs and represents the overall growth rate of pathways for that structure. Experimental trials using the maximum eigenvalue measure (Tables 1 and 2) are consistent with those reflected in m_a .

By eliminating the effect of size, our normalized measures m_a/m_c for paths and walks characterize the combined effect of connectance and topology on the indirect network structure. The measures can be used to compare indirect structure between systems of different sizes, and the next logical step in this research would be to try to establish a relationship between particular connectance patterns and associated variation in m_a/m_c values. Teasing apart the effect of magnitude from the pattern of connectance itself we consider important to making inferences from m_a/m_c back to network structure. Other research questions also present themselves, such as the relationship between m_a and m_a/m_c and network properties such as the cycling index (Finn, 1976), or some of the eleven cardinal properties of “holoecology” (Patten, 2003) derived from

the environ approach:

- #1. *Network proliferation*—increase in pathway numbers (P_k) with length (k), which is geometric increase as described herein.
- #2. *Network nonlocality*—dominance of indirect effects as carried by transactive flows (f), $\sum_{k>1} f(A^k) > f(A)$.
- #3. *Network holocontrol*—dominance of indirect control (c), $\sum_{k>1} c(A^k) > c(A)$.
- #4. *Network homogenization*—tendency to uniformly distribute causality.
- #5. *Network amplification*—obtaining more than face value from boundary inputs $f(a_{ij}^{(0)})$: $\sum_{k>0} f(a_{ij}^{(k)}) > f(a_{ij}^{(0)})$.
- #6. *Network unfolding*—proliferation of transfer levels as a limit process, which in food webs leads to trophic pyramids with an indefinite number of trophic levels.
- #7. *Network synergism*—dominance of indirect over direct utility (u), $\sum_{k>1} u(A^k) > u(A)$.
- #8. *Network mutualism*—indirect utilities becoming more positive than direct.
- #9. *Network aggradation*—internal order exceeding generated disorder.
- #10. *Network enfolding*—recursive incorporation of indirect into direct causes such that $f(A)$ is really $f(A(\sum_{k>1} f(A^k)))$.
- #11. *Network holoevolution*—the coevolution of wholes and parts together.

The classical concept of “pattern and process” in ecology comes to the fore in this list. Pathway notations ($A^k = (a_{ij}^{(k)})$, $k = 0$) introduced into some of the definitions show how central network structure is to the principal results of environ analysis. That network properties reflecting function (“process”) can be depicted (in functional notation) as functions of structure (“pattern”) underscores how closely the two are intertwined. In fact, as previously stated, structure is virtual and follows function (transactions), which is actual. From this it is reasonable to expect that structural measures such as m_a and m_a/m_c can be useful in predicting or bounding measures of function such as the cycling index or some of the eleven above. The logic here is that labyrinthine transactions define and implicate, respectively, the direct and indirect pathway structure within systems, including cycles. In fact the

implication is mutual. Structure and function, or pattern and process, go together and methods like those in the set of environ analyses are going to be required to distinguish one from the other.

Scale and modeling issues will be ever present in this. The oyster reef, swamp marsh, and reservoir cove ecosystems were each modeled at particular scales not necessarily alike. Network size and connectivity in models reflect the resolution at which systems are studied. A network representation of the interior of a cell can be far more intricate than that for an ecosystem (e.g. Guet et al., 2002; Jeong et al., 2000; Maslov and Sneppen, 2002). At their own scales it is true that both can be equally complex, or the smaller perhaps more complex than the larger. In general, finer grain of observation leads to more nodes and links, which by Higashi's algebraic relations translates into greater dominance of indirect effects. However, recalling the definition of connectance ($C = L/n^2$, L the number of links), it is clear that finer resolution of nodes (n) will cause n^2 to grow faster than n , rarefying C . At very large system sizes adjacency matrices can be expected to become extremely sparse though number of links is astronomical. A system with a billion nodes ($n = 10^9$) and a trillion transactions interconnecting them ($L = 10^{12}$) will be only one-millionth connected ($L/n^2 = 10^{-6}$), a sparse universe indeed in the present experience of ecological modeling. How to balance practical needs to describe and predict with the companion need to understand principles in order to better describe and predict, will present a continuing challenge.

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References

- Allen, T.F.H., Hoekstra, T.W., 1992. *Toward A Unified Ecology*. Columbia University Press, New York.
- Bersier, L.F., Dixon, P., Sugihara, G., 1999. Scale-invariant or scale-dependent behavior of the link density property in food webs: a matter of sampling effort? *Am. Nat.* 153, 676–682.
- Bondy, J.A., Murty, U.S.R., 1976. *Graph Theory with Applications*. North-Holland, New York.
- Borrett, S.R., 2001. Sources of system complexity in the Lake Lanier ecosystem, GA, USA. Paper Presented at Ecological Society of America 86th Annual Meeting, August, Madison, WI.
- Cohen, J.E., Briand, F., Newman, C.M., 1990. *Community Food Webs: Data and Theory*. Springer, New York.
- Dame, R.F., Patten, B.C., 1981. Analysis of energy flows in an intertidal oyster reef. *Mar. Ecol. Prog. Ser.* 5, 115–124.
- Fath, B.D., 1998. *Network analysis: foundations, extensions, and applications of a systems theory of the environment*. Ph.D. Thesis. Institute of Ecology, University of Georgia, Athens, Georgia.
- Fath, B.D., Patten, B.C., 1998. Network synergism: emergence of positive relations in ecological systems. *Ecol. Model.* 107, 127–143.
- Fath, B.D., Patten, B.C., 1999. Review of the foundations of network environ analysis. *Ecosystems* 2, 167–179.
- Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. *J. Theor. Biol.* 56, 363–380.
- Guet, C.C., Elowitz, M.B., Hsing, W., Leibler, S., 2002. Combinatorial synthesis of genetic networks. *Science* 296, 1466–1470.
- Hannon, B., 1973. The structure of ecosystems. *J. Theor. Biol.* 41, 535–546.
- Harary, F., 1969. *Graph Theory*. Addison-Wesley, Reading, MA.
- Higashi, M., Burns, T.P., 1991. *Theoretical Studies of Ecosystems: The Network Perspective*. Cambridge University Press, Cambridge.
- Higashi, M., Patten, B.C., 1989. Dominance of indirect causality in ecosystems. *Am. Nat.* 133, 288–302.
- Hill IV, J., 1981. *Influence: a theory of the structural organization of systems*. Ph.D. Thesis, University of Georgia, Athens, Georgia, USA.
- Hill IV, J., On the Largest Real Root of a Polynomial. Unpublished manuscript.
- Jeong, H., Tomnor, B., Oltvai, Z.N., Barabási, A.-L., 2000. The large-scale organization of metabolic networks. *Nature* 407, 651–654.
- Jørgensen, S.E., Patten, B.C., Straškraba, M., 1992. Ecosystems emerging: toward an ecology of complex systems in a complex future. *Ecol. Model.* 62, 1–27.
- Leontief, W.W., 1965. The structure of the American economy. *Sci. Am.* 212, 25–35.
- Leontief, W.W., 1966. *Input-Output Economics*. Oxford University Press, New York.
- Logofet, D.O., 1993. *Matrices and Graphs: Stability Problems in Mathematical Ecology*. CRC Press, Boca Raton.
- Margalef, R., 1963. Certain unifying principles in ecology. *Am. Nat.* 97, 357–374.
- Margalef, R., 1991. Networks in ecology. In: Higashi, M., Burns, T.P. (Eds.), *Theoretical Studies of Ecosystems: The Network Perspective*. Cambridge University Press, Cambridge, pp. 41–57.
- Martinez, N.D., 1994. Scale-dependent constraints on food-web structure. *Am. Nat.* 144, 935–953.

- Maslov, S., Sneppen, K., 2002. Specificity and stability in topology of protein networks. *Science* 296, 910–913.
- Matis, J.H., Patten, B.C., Environ analysis of linear compartmental systems: the static, time invariant case. In: Proceedings of the 42nd Session of International Statistical Institute, Manila, Philippines, 4–14 December 1979. *Bull. Int. Stat. Inst.* 48, 527–565.
- Newman, M.E.J., 2002. Random graphs as models of networks. In: Bornholdt, S., Schuster, H.G. (Eds.), *Handbook of Graphs and Networks*. Wiley-VCH, Berlin. preprint [online] <http://arxiv.org/abs/cond-mat/0202208>.
- Patten, B.C., 1978a. Systems approach to the concept of environment. *Ohio J. Sci.* 78, 206–222.
- Patten, B.C., 1978b. Energy environments in ecosystems. In: Fazzolare, R.A., Smith, C.B. (Eds.), *Energy Use Management*. Pergamon Press, New York, pp. 853–857.
- Patten, B.C., 1982. Environs: relativistic elementary particles for ecology. *Am. Nat.* 119, 179–219.
- Patten, B.C., 1984. Toward a theory of the quantitative dominance of indirect effects in ecosystems. *Verh. Gesellschaft für Ökologie*. 13, 271–284.
- Patten, B.C., 1985. Energy cycling in the ecosystem. *Ecol. Model.* 28, 1–71.
- Patten, B.C., 2003. Holoecology: The Unification of Nature by Network Indirect Effects. *Complexity in Ecological Systems Series*. Columbia University Press, New York, in preparation.
- Patten, B.C., Bosserman, R.W., Finn, J.T., Cale, W.G., 1976. Propagation of cause in ecosystems. In: Patten, B.C. (Ed.), *Systems Analysis and Simulation in Ecology*, vol. IV. Academic Press, New York, pp. 457–579.
- Patten, B.C., Egloff, D.A., Richardson, T.H., and 38 coauthors, 1975. Total ecosystem model for a cove in Lake Texoma. In: Patten, B.C. (Ed.), *Systems Analysis and Simulation in Ecology*, vol. III. Academic Press, New York, pp. 205–421.
- Patten, B.C., Higashi, M., Burns, T.P., 1990. Trophic dynamics in ecosystem networks: significance of cycles and storage. *Ecol. Model.* 51, 1–28.
- Patten, B.C., Richardson, T.H., Barber, M.C., 1982b. Path analysis of a reservoir ecosystem model. *Can. Water Resour. J.* 7, 252–282.
- Whipple, S.J., 1995. Systems analysis of the path and trophic structure on an ecosystem model of a macrophyte marsh in the Okefenokee Swamp. Ph.D. Thesis. Institute of Ecology, University of Georgia, Athens, Georgia, USA.
- Williams, R.J., Martinez, N.D., 2000. Simple rules yield complex food webs. *Nature* 404, 180–183.
- Wright, R., 2000. *Nonzero: The Logic of Human Destiny*. Pantheon, New York.