

CHAPTER 7

Analysis of size and complexity of randomly constructed food webs by information theoretic metrics

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Introduction

Understanding the interrelationships between properties of ecosystems has been a central theme of ecology for decades (Odum 1969; May 1973). Food webs represent an important feature of ecosystems, and the linkages of food-web properties have been addressed specifically (Pimm 1982; Paine 1988). Food webs consist of species networks, and the effect on ecosystem processes of the imbedded species diversity has become a major focal point for research (Tilman 1997; McGrady-Steed et al. 2001; Chapin et al. 2000). In recent years the properties of food webs have been placed into a network perspective, but a major limitation to addressing these properties is simplification associated with data availability and software limitations (Paine 1988; Cohen et al. 1993). One major simplification involves aggregation of species into guilds or trophic species to reduce the number of taxa to be considered (Ulanowicz 1986a). Sizes of published food-web networks are less than 200 taxa (Martinez 1991) when binary feeding relationships (i.e. diet item or not) are considered, and no more than 125 taxa (Ulanowicz et al. 1998) when feeding relationships are quantified (i.e. as fraction of total diet). We have constructed hypothetical food webs with weighted feeding relationships that overcome the limitation of aggregation. Food webs ranged in size up to 2,426 taxa.

Ulanowicz has developed several metrics of system growth and development based on information theory (Ulanowicz 1986, 1997). They are

predicated on the importance of autocatalysis (i.e. positive feedback loops) during growth and development. Autocatalysis has both extensive and intensive properties. The extensive metric (characteristic of size) is the total amount of flow within the system, that is total system throughput (TST). When the intensive metric (characteristic of complexity) of flow diversity is scaled by TST, the result is called the system's developmental capacity. Flow patterns become increasingly constrained as a system develops and matures, a characteristic represented by average mutual information (AMI). When AMI has been scaled by TST, the ensuing quantity is called the system ascendancy. These metrics, and related ones, provide ways to gauge and characterize systems and changes within systems. For example, eutrophication appears to increase system ascendancy via an increase in TST that more than compensates for a drop in AMI (Ulanowicz 1986b). This quantitative definition distinguishes simple enrichment (which does not induce a drop in AMI) from eutrophication (which does).

The objectives of this study were twofold. One objective was to assess the effects of different assumptions used to construct the hypothetical webs. A second objective was to evaluate how recent theoretical metrics of food-web organization and complexity (Ulanowicz 1986a, 1997) respond to two key variables that vary with ecosystem development, namely web size and function. Size was examined in terms of the number of taxa and amount of processing (i.e. TST). Function

was evaluated on the basis of the number and distribution of connections among taxa. We evaluated the interrelationships among size, connectivity, and network metrics of both hypothetical and empirical webs.

Methods

Food-web construction

We generated a large diversity of food webs for analysis by creating thousands of randomly constructed networks varying in size (number of taxa) and distribution of connections. Random, donor-controlled food webs were generated by populating a transfer matrix (A) with random coefficients that were drawn from realistic probability sets, randomly partitioning exogenous inputs (f) among primary producers (gross production), and solving for the biomass vector (x) for the steady-state condition:

$$dx/dt = 0 = f + Ax, \quad (7.1)$$

$$x = -A^{-1}f, \quad (7.2)$$

where f represents a vector of inputs (gross primary production, autochthonous inputs). Inputs to all structured webs (Figure 7.1) were divided into gross primary production (GPP) and

allochthonous import of organic matter. GPP was set at $1,000 \text{ kcal m}^{-2}$ per year. Allochthonous import was 100 kcal m^{-2} per year. Total input to unstructured webs was fixed at $1,100 \text{ kcal m}^{-2}$ per year. These standard conditions facilitated comparison of networks.

The food webs were donor-controlled in the sense that the flow from one taxon to the next was proportional to the biomass of the donor taxon. The model structure was purely descriptive and not meant to have any predictive capability of temporal dynamics. Rather, every feasible food web generated is a description of possible energy flows within a hypothetical network constructed from realistic principles. We posit that real food webs lie within the state space of these randomly generated food webs, provided that the sample size of hypothetical webs is sufficiently large.

Solving for the steady state (equation 7.2) from a randomly generated transfer matrix can result in negative biomass numbers for any number of taxa. Such webs were identified as being nonfeasible and were discarded. Hypothetical food webs were generated until a sufficiently large population of feasible (positive biomass for all taxa) webs were obtained to make a convincing analysis of their properties and trends. Four kinds of networks are considered here (Figure 7.1) and the rules are described below.

We constructed networks using different sets of rules concerning the nature of connections. Every structured food web consisted of "taxa" that were each defined as belonging to a group of primary producers, primary, secondary, and tertiary consumers, or detritivores, plus an organic matter or detritus compartment (Figure 7.2; plate 2). For each web that was generated, the number of taxa within each group was determined randomly. By this method we generated feasible webs that consisted of as few as 7 or as many as about 2,200 taxa.

For each structured web we generated three types of connections among food-web members (Figure 7.2). These included mandatory flows from all taxa to organic matter or detritus, mandatory flows from lower to higher trophic levels, and nonobligatory flows among taxa, such as a flow from a secondary consumer to a primary

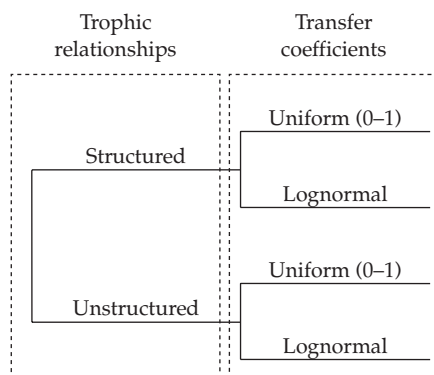


Figure 7.1 Terminology and classification of hypothetical food web construction. Realistic trophic structure was imposed on structured webs (Figure 7.2), while the taxa in unstructured webs were randomly connected without regard to trophic identity. Structured webs had no constraints on the relative numbers of taxa within each trophic level. Transfer coefficients were drawn either from lognormal or uniform distributions.

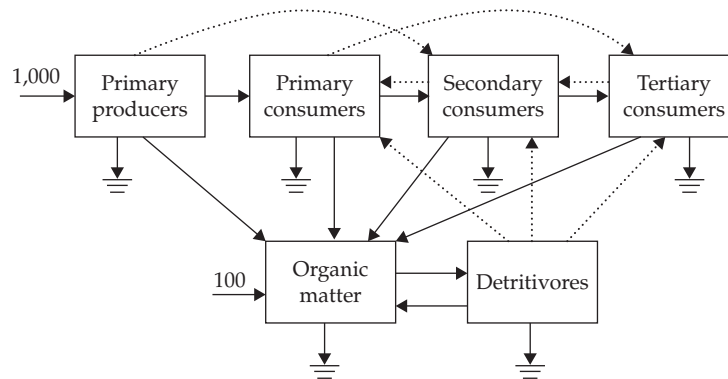


Figure 7.2 This figure shows the basic architecture of structured food-webs constructed with realistic trophic relationships. The energy input to every randomly constructed food web was standardized at $1,000 \text{ kcal m}^{-2} \text{ yr}^{-1}$ of GPP and $100 \text{ kcal m}^{-2} \text{ yr}^{-1}$ of exogenous organic matter input. Solid arrows (\longrightarrow) denote mandatory flows of energy and their direction. For example, every primary consumer in the web is made to consume at least one primary producer. Dotted arrows ($\cdots\rightarrow$) denote flows that are possible, but not mandatory. The rules for making these connections are discussed in the text.

consumer. Consumer taxa belonging to the same trophic group were not connected. With flows of the second and third kind, a random number generator was used to determine the presence of a flow between two specific nodes. Mandatory flows from lower to higher trophic levels defined the trophic positions of taxa. For mandatory flows from lower to higher trophic levels, such as flow from primary producers to herbivores, the probability of flow from a lower to a higher-level taxon was assumed to be inversely proportional to the number of taxa within the lower trophic level. For example, with four primary producers in the food web, there was a 25% probability that any one of them flowed to any one of the herbivores. Unit random numbers were drawn for each pair of donor and recipient taxa to make the connections, subject to the requirement that every higher-level taxon had to feed on at least one lower level taxon. Connections of the third kind, or non-obligatory flows as from a tertiary to a secondary consumer, were made using a unit random number drawn for each possible pair of taxa after first drawing a unit random number that set the overall connectivity of the web. For each one of these possible connections, a connection or flow was made if the value of a unit random number was less than the overall connectivity. This procedure generated food webs that ranged from sparsely to densely connected.

The structure we have described above is general, and definitions of trophic components and flows are flexible. For example, loss from the organic matter compartment can be defined as either a respiratory flow and/or an export from the system depending on how the microbial community is defined. If detritivores include microbes, then export from organic matter is best defined as a loss from the system rather than a respiratory loss. At the level of the whole web, the entirety of living components can be thought of as including microbes that are parasitic or saprophytic on multicellular organisms from neighboring trophic levels.

A second type of web architecture, termed unstructured (Figure 7.1), was purely random in construction. There were no rules of trophic structure of any kind to govern the presence or absence of flows, except that the distribution of GPP was restricted to a group of taxa representing between 5% and 75% of total taxa in the web as determined by random number. Every taxon, including “primary producers,” had an equal probability of feeding on any other taxon as determined by the overall connectivity of the web, which was determined by a uniformly distributed random variable ranging from 0.2 to 0.7. In addition, these unstructured networks had no detritus component to accumulate and degrade the products of mortality. These networks were simply

random distributions of respirations and of exogenous inputs (gross production) and feeding among nodes.

Respiration rates

Weight-specific respiration rate coefficients were randomly chosen from uniform distributions spanning ranges representing realistic rates taken from the literature. The respiration of primary producers consisted of two parts: dark respiration and photorespiration. Photorespiration was accounted for by subtracting a fraction equivalent to 25–50% of the rate of GPP. The rate of photorespiration was randomly chosen for each primary producer. A weight-specific rate of dark respiration ranging from 40% to 70% of plant weight per year was also randomly chosen for each primary producer (Lambers 1985; Landsberg 1986). Heterotrophs (consumers and detritivores) had specific respiration rates ranging from 19% to 3,400% per year of their biomass, which is a range that spans a wide spectrum of body size (Gordon et al. 1972). For each heterotroph, a unit random number was drawn to assign a respiration rate within the appropriate range. Based on numerous sources (Morris and Lajtha 1986; Schomberg and Steiner 1997; Asaeda and Nam 2002; Van Santvoort et al. 2002; Qualls and Richardson 2003; Salovius and Bonsdorff 2004), detritus was given an annual decay rate ranging from 6.6% to 164%. In the case of the unstructured networks, the specific respiration rate assigned to each taxon was like that of the heterotrophs.

Transfer coefficients

Transfer coefficients representing energy flow among taxa were either drawn from a population of unit random numbers (0–1) or from a lognormal with $\mu = -2.3$ and $\delta = 2$, where the mean of the distribution is given by $\exp(\mu + \delta^2/2)$. The lognormal distribution allows for coefficients greater than one as would be the case for biomass turnover rates greater than once annually. The two alternative methods of generating transfer coefficients were applied to the structured webs as well as to the unstructured webs.

Network analysis

For every feasible food web generated, we computed total system biomass, the number taxa within each trophic group, the net production, and total respiration within each trophic group, the number of connections, total system throughput, and various metrics derived from information theory (Ulanowicz 1986, 1997). These included average mutual information or AMI, flow diversity (SI), total system throughput (TST), full development capacity ($Cd = TST \times SI$), and ascendancy ($TST \times AMI$).

Average mutual information is inversely proportional to the degree of randomness in a system and is a measure of the predictability of flow. Adopting the convention that flows can be represented by a matrix T_{ij} (row-column order) in which flow moves from a species in column j to a species on row i , then AMI (bits) was computed as:

$$AMI = \sum_i \sum_j p(T_{ij}) \log_2 [\{p(T_{ij})/p(T_j)\}/p(T_i)], \quad (7.3)$$

where T_{ij} is the flow from species j to species i , $p(T_{ij})$ is the joint probability given by:

$$p(T_{ij}) = T_{ij}/TST, \quad (7.4)$$

$$p(T_i) = \sum_j p(T_{ij}), \text{ and } p(T_j) = \sum_i p(T_{ij}),$$

and where TST is total system throughput:

$$TST = \sum_i \sum_j |T_{ij}| \quad (7.5)$$

The Shannon flow diversity (SI) is based on the individual joint probabilities of flows from each species j to each species i :

$$SI = \sum_i \sum_j [-p(T_{ij}) \log_2(p(T_{ij}))]. \quad (7.6)$$

Empirical food webs

The hypothetical data were compared against data consisting of biomass and flow distributions of 31 empirically derived food webs from various

ecosystems. The empirical webs were analyzed using the same suite of metrics as described above. However, the biomass and flows of the empirical food webs were first scaled so as to transform the total GPP of the empirical webs to a constant 1,000 units across all webs in order that they would be consistent with the GPP of hypothetical webs and to remove GPP as a variable. The procedure was to scale the input vector f and absolute flows by the quotient $1000/\Sigma f$.

Results

Food-web dimensions

Food webs that have been described empirically are necessarily aggregated to various degrees and typically overlook connections or flows that are minor. The average number of taxa in the set of empirical food webs was 39 ± 36 (± 1 SD). The largest empirical food web contained 125 taxa; the smallest contained 4. Empirical food webs averaged 350 ± 563 (± 1 SD) total connections and 5 ± 5 connections per taxon (Table 7.1). The minimum and maximum numbers of connections per web were 4 and 1,969. Minimum and maximum connections per taxon were 1 and 15.7.

The accounting of flows or connections among the taxa that comprise empirical food webs is likely to miss rare items in an organism's diet, and we arbitrarily defined rarity as any flow that constitutes 5% or less of an organism's diet. Thus, major flows were greater than 5% of an organism's diet. Using this definition of a major flow, the theoretical maximum number of major flows per taxon approaches 20, provided the flows into a taxon are equal in magnitude. The theoretical minimum number of major flows is zero as, for example, when there are greater than 20 uniform flows. Among empirical food webs the number of major flows per taxon averaged 2.3 ± 1 , and ranged from 1 to 4.5.

Hypothetical webs had a mean size of 827 ± 444 taxa per web, with a maximum size of 2,426 and a minimum of 7. The probability of generating a feasible (biomass of all taxa must be positive), structured web declined precipitously at sizes exceeding 500 taxa (Figure 7.3) and was independent

of the means of generating transfer coefficients (uniform or lognormal). The probability distribution was described by a sigmoid: $Y = 1/(1 + \exp(.02X - 11))$, where Y is the probability and X is the number of taxa. For webs with 500 taxa the probability of successfully generating a feasible random web was 0.5. For webs with 1,000 taxa the probability declined to 0.0001.

For each web generated, we calculated the actual number of connections as well as the maximum possible number of connections, which depends on size as well as the specific distribution of taxa among trophic groups (Figure 7.4). Among structured webs, the total number of connections per web averaged $280,763 \pm 324,086$, with a maximum of 1,885,606 and a minimum of 23. The number of connections per taxon averaged 263 ± 220 , with a maximum of 1050 and a minimum of 2. The set of hypothetical webs varied greatly in the total number of connections and connections per taxon, irrespective of size (number of taxa) (Figure 7.4). Both sparsely and densely connected webs were generated, even among the largest sizes. The average number of major (flows greater than 5% of the total input flows) flows per taxon in the set of hypothetical webs was similar to the empirical webs and averaged 2.1 ± 1.2 per taxon. This may be an artifact of a process that produces a distribution like that of the broken stick model (MacArthur 1957), but the distribution of flow stems ultimately from the transfer coefficients in a donor-controlled fashion, and their distribution does not resemble a broken stick distribution (Figure 7.5). On the other hand, GPP imposes a limit on flow in a manner similar to the resource space that MacArthur (1957) argued should set a limit on the distribution of species. Ulanowicz (2002) used an information-theoretic homolog of the May-Wigner stability criterion to posit a maximal connection per taxon of about 3.01 (which accords with these results).

The values of individual fractional flows into each taxon as a percentage of the total flow into each taxon were computed for each food web generated, excluding gross photosynthesis, by type of web construction. For each food web generated, a frequency distribution of these fractional flows was computed, and then the global average

Table 7.1 Summary statistics from empirical ($n=31$) and hypothetical food-webs. Statistics were computed from 800 samples each of the lognormal and uniform variety of unstructured webs and 641 and 1006 samples of structured lognormal and uniform webs, respectively

Variable	Web type	Mean	Standard deviation	Minimum	Maximum
Number of connections per taxon	Empirical	5.1	4.8	1.0	15.8
	Unstructured lognormal	349.7	242.6	1.3	1025.3
	Unstructured uniform	358.8	247.2	2.0	1049.7
	Structured lognormal	179.7	156.5	3.2	849.0
	Structured uniform	172.6	138.6	4.2	829.6
Number of major connections per taxon	Empirical	2.3	1.0	1.0	4.5
	Unstructured lognormal	3.1	0.8	1.5	4.9
	Unstructured uniform	0.8	0.9	0.0	5.1
	Structured lognormal	2.9	0.5	1.0	4.0
	Structured uniform	1.7	0.8	0.5	5.4
TST ($\text{kcal m}^{-2} \text{yr}^{-1}$)	Empirical	3,412	662	2,175	4,684
	Unstructured lognormal	18,120	11,311	2,209	50,934
	Unstructured uniform	14,051	7,992	2,299	36,381
	Structured lognormal	4,117	801	2,382	11,250
	Structured uniform	4,052	637	2,912	9,133
AMI	Empirical	1.6	0.3	1.0	2.0
	Unstructured lognormal	3.3	0.6	1.0	4.5
	Unstructured uniform	1.6	0.4	0.9	2.5
	Structured lognormal	2.7	0.4	1.2	4.0
	Structured uniform	2.0	0.3	1.2	2.9
Flow diversity (bits)	Empirical	4.0	1.0	1.8	5.7
	Unstructured lognormal	13.4	3.2	1.3	17.5
	Unstructured uniform	15.0	3.7	2.0	19.8
	Structured lognormal	9.2	1.7	3.2	14.7
	Structured uniform	10.5	1.7	4.2	16.5
Full capacity	Empirical	13,905	5,001	3,935	25,104
	Unstructured lognormal	273,323	205,619	2,892	889,544
	Unstructured uniform	236,335	167,057	4,824	720,361
	Structured lognormal	39,146	15,008	7,736	165,117
	Structured uniform	43,379	13,731	13,059	143,630
Ascendency as a fraction of full capacity	Empirical	0.41	0.07	0.31	0.64
	Unstructured lognormal	0.26	0.04	0.19	0.76
	Unstructured uniform	0.12	0.05	0.05	0.52
	Structured lognormal	0.30	0.03	0.23	0.38
	Structured uniform	0.20	0.04	0.11	0.29

frequency distribution of fractional flows was computed by the type of web (Figure 7.5). Regardless of the type of web construction, the overwhelming majority of flows were less than 5% of the total flow into each taxon. Random webs without realistic structures had the highest percentage of these small flows; $98\% \pm 6$ (± 1 SD) of flows were less than 5% of the total. Among webs with structure, $95\% \pm 9$ of flows were of a magnitude less than 5% of the total.

The distributions of transfer coefficients were also computed and averaged over all webs within each class of web construction to determine if they differed from the distributions expected on the basis of the random number generator. If the distributions differed from the expected, then the web structures must be selecting the distribution. Webs constructed of transfer coefficients drawn from the uniform, unit distribution had frequencies exactly as expected (Figure 7.5). Webs constructed

of transfer coefficients drawn from lognormal distributions also did not differ from the expected. Note that transfer coefficient values greater than 1 were grouped into one category for analysis, which accounts for the upturn in frequency on the tail of the distribution. Among webs constructed of lognormally distributed transfer coefficients, 12.5% ± 0.3 of coefficient values were greater than one.

Total system throughput

Total system throughput, which is simply the sum of all flows among the taxa, including respirations and exogenous flows (i.e. GPP, losses and allochthonous inputs), was bounded within the structured webs. Among the unstructured webs, TST increased with web size without limit, at least within the range of the food-web sizes generated (Figure 7.6; Plate 3). This increase in TST, seemingly without limit and in defiance of the laws of physics, was a consequence of the high degree of flow reciprocity that occurs among unstructured webs constructed without realistic trophic relationships. TST increased by approximately 15 and 21 kcal m⁻² per year per taxon in unstructured uniform and unstructured log-normal webs, respectively. TST was limited among structured webs, as finite inputs dictate a finite TST (Ulanowicz 1997), at least when food webs have realistic structures and thermodynamic

constraints. TST among structured webs was bounded by upper and lower asymptotes. These asymptotes were sensitive to GPP (not shown), which in these examples was always set to 1,000 kcal m⁻² per year. Mean TST among structured webs was about 4,000 kcal m⁻² per year (Table 7.1) or four times GPP. That this mean is very near to four times GPP tells us that the mean effective number of trophic levels (= TST/GPP) is about 4, which is consistent with real food-webs. Of course, the structured webs were designed with 4 trophic levels (Figure 7.2), but it does

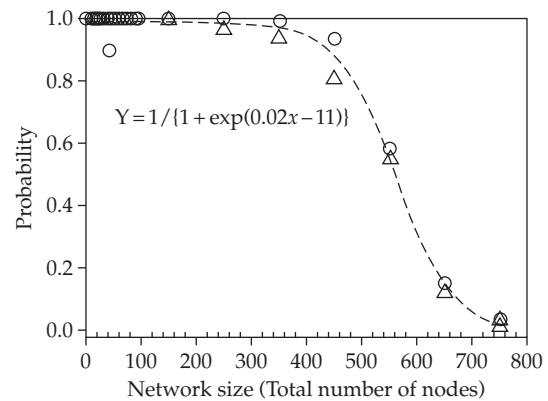


Figure 7.3 Probability of generating a feasible, random network with realistic structure using transfer coefficients drawn from either uniform (Δ) or lognormal (\circ) distributions.

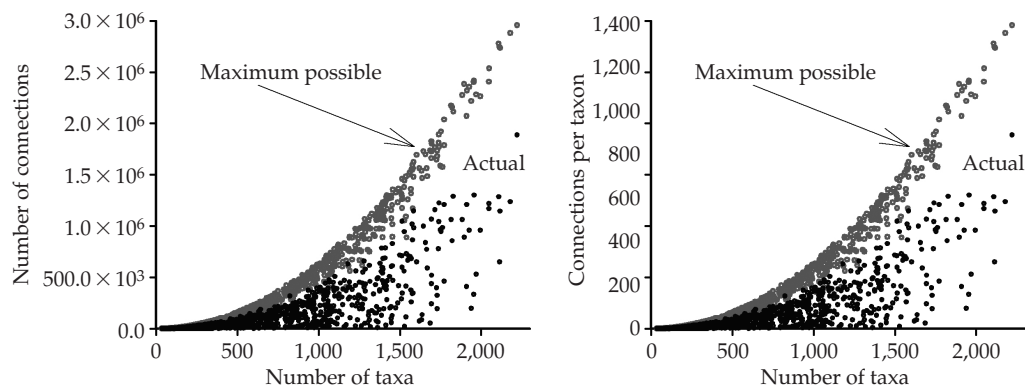


Figure 7.4 Density of connections of structured, hypothetical food webs as a function of the number of taxa. Shown are the maximum possible number of connections (\circ), determined by the greatest number of feasible connections for a particular distribution of taxa, and the corresponding actual number of connections (\bullet) for approximately 6,800 networks (see also Plate 2).

support the choice of coefficients used to construct the hypothetical webs. The mean TST (normalized to $GPP = 1,000 \text{ kcal m}^{-2}$ per year) of the empirical webs was $3,400 \pm 662 \text{ kcal m}^{-2}$ per year (Table 7.1).

The pattern of TST when plotted against the average number of major (>5% flow) connections per web was quite different between the two types of unstructured webs and between the unstructured and structured webs (Figure 7.6). Among unstructured normal webs, TST was greatest at low connectivity and declined toward a lower asymptote as connectivity increased. In contrast, the TST of unstructured, lognormal webs was bifurcated (Figure 7.6). For example, for webs with

2 connections per taxon, TST was either greater than 40,000 or less than $10,000 \text{ kcal m}^{-2}$ per year, while at the highest connectivity, TST focused on a single cluster less than $10,000 \text{ kcal m}^{-2}$ per year. This suggests a strong and peculiar control by the structure of the web over its function. TST of structured and empirical webs was independent of the connectivity.

Flow diversity

Flow diversity (SI) among empirical and hypothetical webs increased with size (taxa) (Figure 7.7; Plate 4). Unstructured, uniform webs had the highest SI, averaging 15 ± 3.7 bits, empirical webs

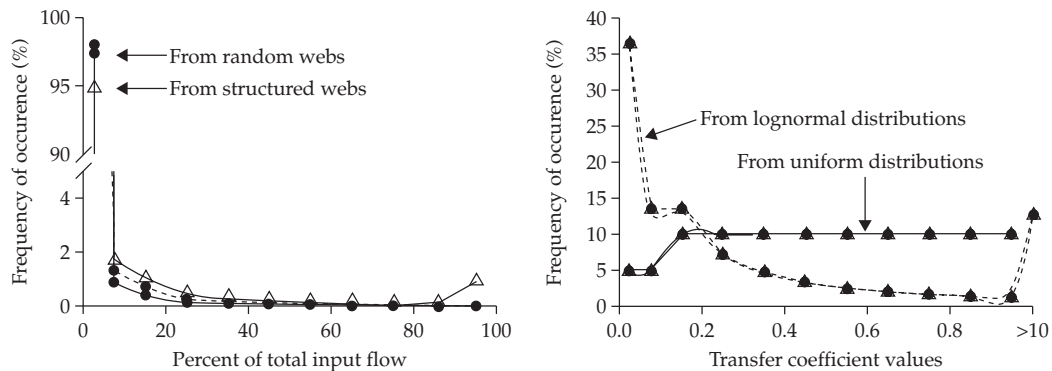


Figure 7.5 Average frequency distribution of flow strengths into taxa expressed as fractions of the total flow into each taxon (left). Average frequency distribution of transfer coefficients (right). Note that the transfer coefficient is equivalent to the fraction of the standing stock of a donor taxon that flows into a recipient taxon in a unit of time in steady state.

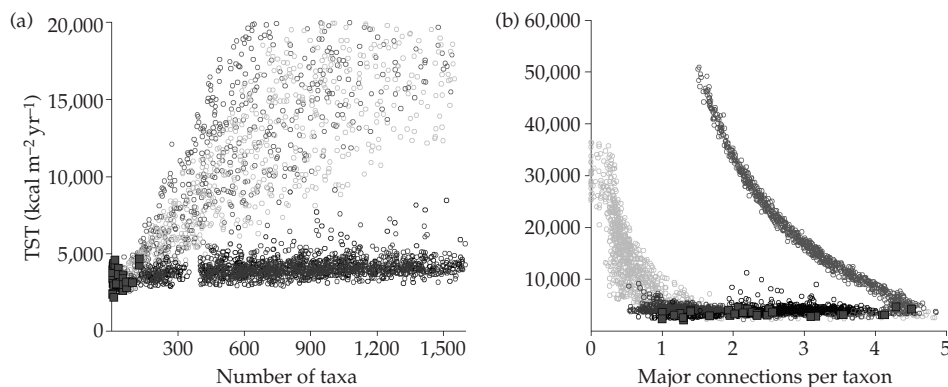


Figure 7.6 TST of different types of hypothetical food-webs as a function of (a) the number of taxa and (b) of the average number of major connections (flows >5% of inputs) per taxon. Hypothetical webs were either unstructured in design with uniformly \circ or lognormally \circ distributed transfer coefficients, or structured in design with uniformly \bullet or lognormally \circ distributed transfer coefficients. Empirical webs are denoted by \blacksquare (see also Plate 3).

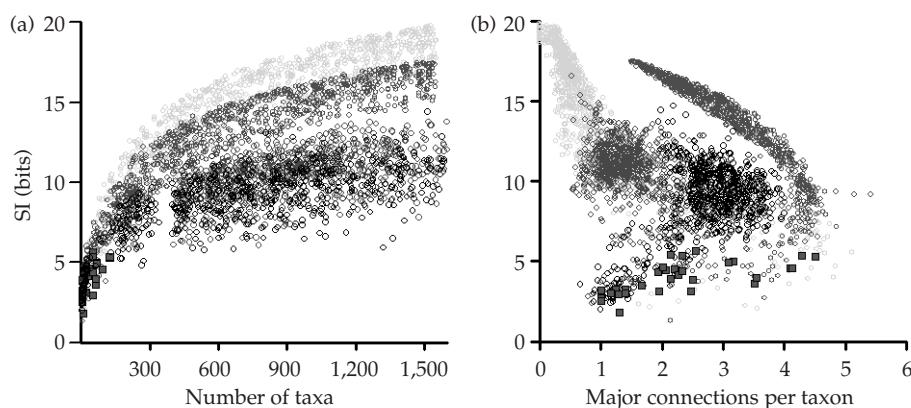


Figure 7.7 Flow diversity (SI) of different types of hypothetical food webs as a function (a) of the number of taxa and (b) of the average number of major connections (flows >5% of inputs) per taxon. Hypothetical webs were either unstructured in design with uniformly \circ or lognormally \circ distributed transfer coefficients, or structured in design with uniformly \bullet or lognormally \circ distributed transfer coefficients. Empirical webs are denoted by \blacksquare (see also Plate 4).

had the lowest (4 ± 1 bits). The SIs of empirical and hypothetical webs were equivalent among webs of comparable size, while structured webs had lower flow diversities for a given size than unstructured webs (Figure 7.7, Table 7.1). For a web with m taxa and m^2 flow paths, the SI reaches an upper limit of $-\log_2(1/m^2)$, provided the flows are uniform in size. Alternatively, if the flows among taxa are dominated by n major flows per taxon, then the SI of structured webs reduces to $-\log_2(1/nm)$, which gives a limit for SI of about 12.1 for a large web of size $m=1500$ and $n=3$. The latter calculation is consistent with the results obtained from the structured webs (Figure 7.7). Note that the mean number of major connections per taxon for this web type was about 3 (Table 7.1). Hence, the imposition of a realistic structure seems to be selecting for webs with a flow diversity that is dominated by a few major flows among taxa, whereas the unstructured webs are more fully connected and have greater uniformity of flow (Figure 7.5).

Full development capacity

The total potential order or complexity (kcal bits m^{-2} per year) is termed full developmental capacity (Cd) and is the product of TST and the flow diversity (SI) (Ulanowicz 1986; Ulanowicz and Norden 1990). Based on the above generalizations about the limits

to flow diversity and total system throughput, we can place limits on Cd. For fully connected, unstructured webs of uniform flow and $m^2 - m$ flow paths, $\text{Cd}_{\max} = -\text{TST} \cdot \log_2[1/(m^2 - m)] = -\alpha m \log_2[1/(m^2 - m)]$, where α is a proportionality constant, equivalent to 15 and 21 kcal m^{-2} per year per taxon in unstructured uniform and unstructured lognormal webs, respectively. For an arbitrary range of sizes starting with $m=100$, this gives $20 \cdot 10^3$ to $28 \cdot 10^3$ kcal bits m^{-2} per year and $166 \cdot 10^3$ to $232 \cdot 10^3$ kcal bits m^{-2} per year for $m=600$, depending on α , and these values are consistent with the Cd observed for the unstructured webs without realistic trophic structure (Figure 7.8; Plate 5).

For webs with realistic structure or webs with limited TST, a fully connected web also would have $\text{Cd} = -\text{TST} \cdot \log_2[1/(m^2 - m)]$, which for the hypothetical webs here, where $\text{TST} \approx 4\text{GPP}$, we estimate that Cd_{\max} would be about $84 \cdot 10^3$ kcal bits m^{-2} per year when $m=1,500$. This is near the upper range of Cd observed among the hypothetical webs with realistic structure (Figure 7.8). When a web is dominated by a few flows per taxon, a more realistic example, the Cd_{\max} is approximated by $-\text{TST} \cdot \log_2(1/3m)$, which gives $\text{Cd}_{\max} \approx 4 \cdot \text{GPP} \cdot \log_2(1/3m)$ or $35 \cdot 10^3$ kcal bits m^{-2} per year. This value is in the middle of the observed Cd for structured webs (Figure 7.8) and close to the mean Cd of the structured, lognormal webs (Table 7.1).

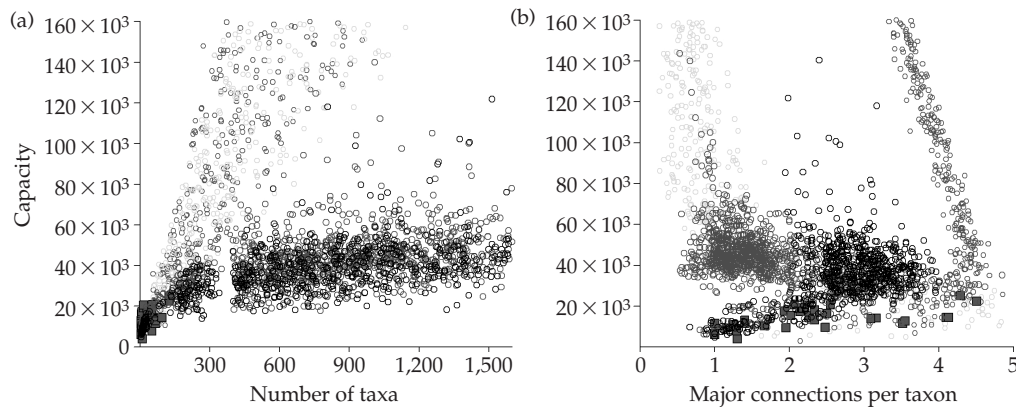


Figure 7.8 Full development capacity of different types of hypothetical food-webs as a function (a) of the number of taxa and (b) of the average number of major connections (flows $>5\%$ of total inputs) per taxon. Hypothetical webs were either unstructured in design with uniformly \circ or lognormally \circ distributed transfer coefficients, or structured in design with uniformly \bullet or lognormally \circ distributed transfer coefficients. Empirical webs are denoted by \blacksquare (see also Plate 5).

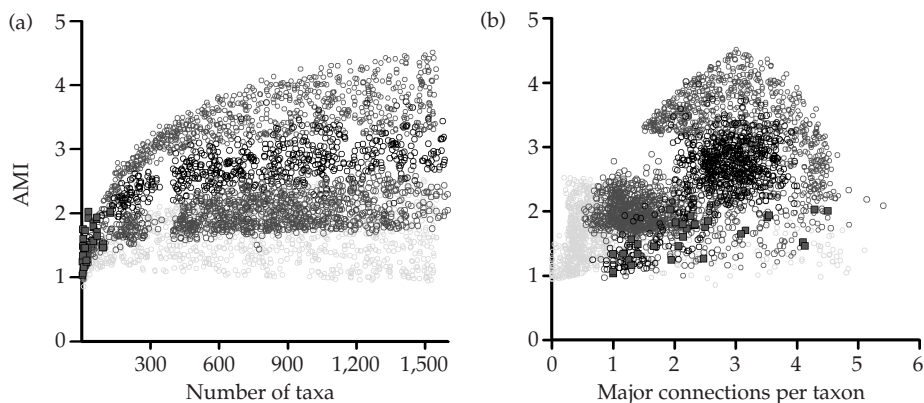


Figure 7.9 AMI content of different types of hypothetical food webs as (a) a function of the number of taxa and (b) of the average number of major connections ($>5\%$ of input flows) per taxon. Hypothetical webs were either unstructured in design with uniformly \circ or lognormally \circ distributed transfer coefficients, or structured in design with uniformly \bullet or lognormally \circ distributed transfer coefficients. Empirical webs are denoted by \blacksquare (see also Plate 6).

Average mutual information

The AMI of empirical and hypothetical webs were consistent among webs of comparable size (Figure 7.9(a)). Among the hypothetical webs, the highest AMI was found among large, unstructured lognormal webs, while the lowest AMI was found among unstructured, uniform webs. Unstructured webs had higher total number of connections than structured webs, and unstructured lognormal webs had the greatest average

number of major connections per taxon, but the unstructured uniform webs had the lowest average number of major connections per taxon (Figure 7.9; Plate 6, Table 7.1). Among structured webs, the lognormal variety tended to have higher AMI than the uniform variety (Figure 7.9) and, while the total connectivity was equivalent (Table 7.1), the lognormal webs had the greater number of major connections per taxon (Figure 7.9).

For a food web of size m with nm uniform flows of size TST/nm , the joint probability of flow will be $p(T_{ij}) = (TST/nm)/TST = 1/(nm)$; the row and column sums of the joint probabilities, $p(T_i)$ and $p(T_j)$ respectively, are each equivalent to n/nm . Making these substitutions into equation 7.3 and solving gives the maximum theoretical $AMI = \log_2(m/n)$. Thus, AMI will tend to rise with network size as our results demonstrate (Figure 7.9(a)). A large food web of $m = 1,500$ taxa would have a maximum AMI of about 10.5 bits when there is $n = 1$ uniform connection per taxon. AMI will decline as the connectedness of the food web increases. For example, for a web of size m taxa and $n = m$ connections of uniform flow per taxon, the AMI reduces to $AMI = \log_2(m/m) = 0$. Thus, AMI rises with network size and declines as the uniform number of connections (total and per taxon) rises (as the direction of flow becomes less certain).

The relationship between AMI and SI is complex. For networks of n uniform flows per taxon, $AMI = \log_2(nm)$, and $SI = -\log_2(1/nm)$. SI may be rewritten as $SI = [\log_2(nm) - \log_2(1)] = AMI$. Thus,

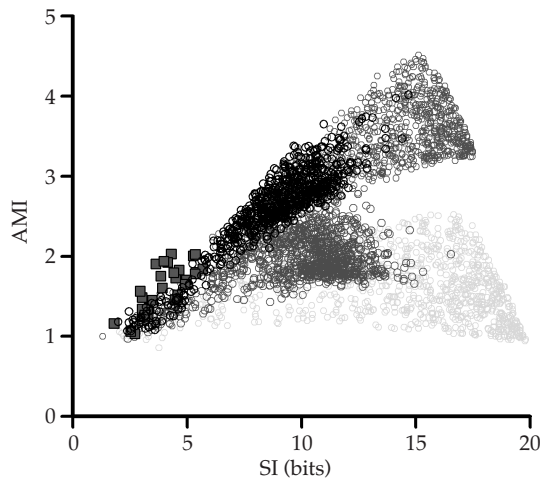


Figure 7.10 AMI as a function of flow diversity (SI) in empirical (■) and hypothetical webs. Hypothetical webs were either unstructured in design with uniformly ○ or lognormally ○ distributed transfer coefficients, or structured in design with uniformly ● or lognormally ● distributed transfer coefficients (see also Plate 7).

AMI is equivalent to SI when flows are uniform and highly predictable. SI and AMI were positively correlated in both empirical and hypothetical webs (Figure 7.10; Plate 7). However, the flows in the empirical and hypothetical webs were neither uniform nor highly predictable, and the AMI was less than the SI (Figure 7.10). For a given flow diversity, the range of possible AMIs increased as flow diversity increased. Thus, as flow diversity increases, the potential AMI also increases. As expected, the hypothetical webs constructed of uniformly distributed transfer coefficients had lower AMI:SI than their log-normal counterparts (Figure 7.10) due to greater uniformity (=greater unpredictability of direction) of flow among the former web types. Empirical webs clustered at the low end of the SI and AMI distributions, but were otherwise consistent with the results of the hypothetical networks.

Ascendency

Interestingly, and importantly, structured webs with realistic trophic structure had greater As/Cd than unstructured webs, within each class of transfer coefficient distribution (Table 7.1, Figure 7.11; Plate 8). Thus, the imposition of a realistic trophic structure, which constrained the flow distribution, raised the As/Cd. Average As/Cd of empirical webs was considerably greater than the average As/Cd of the hypothetical webs (Table 7.1), but at the low end of the size range, empirical webs and hypothetical webs had similar As/Cd (Figure 7.11). Thus, the small size of both empirical and hypothetical webs appears to constrain the flow distribution and raise As/Cd. The As/Cd of hypothetical webs declined rapidly with increasing web size toward a relatively stable average value (depending on web design), with considerable variability around the mean (Table 7.1, Figure 7.11). For a given size of web, the As/Cd of lognormal webs was greater than that of uniform webs (Figure 7.11), which is a consequence of the greater inequality of flow among the lognormal webs.

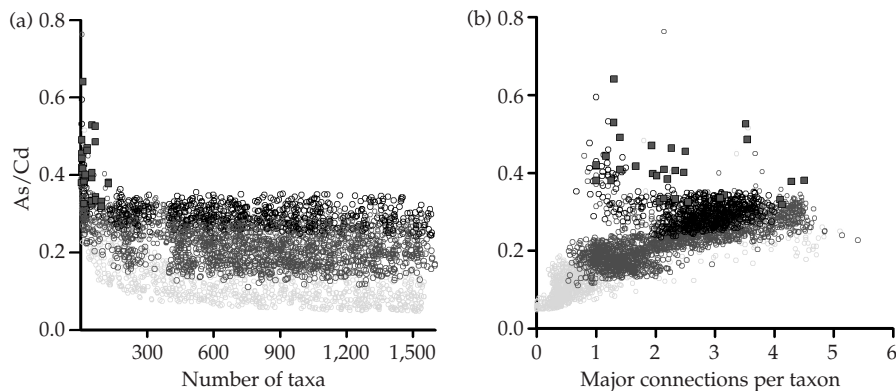


Figure 7.11 Ascendency:capacity as a function of (a) web size and (b) of the average number of major connections (flows >5% of inputs) per taxon (right). Hypothetical webs were either unstructured in design with uniformly \circ or lognormally \circ distributed transfer coefficients, or structured in design with uniformly \bullet or lognormally \circ distributed transfer coefficients. Empirical webs are denoted by \blacksquare (see also Plate 8).

Discussion

The rules of organization of the random webs had significant effects on the various information indices. These rules of organization defined both the size of the networks (i.e. number of taxa and TST) and function (i.e. number and distribution of connections). Some of the responses of these information metrics to the rules were quite predictable, at least qualitatively, while others were not. It was shown that that flow diversity (SI) increased with network size (Figure 7.7), and with uniformity of flow and connectedness. Average mutual information also increased with network size (Figure 7.9), but the distribution of flows had greater impact on AMI than did network size. The SI had an upper bound depending on the size of the network. For example, if flows are uniformly distributed, then a fully connected web of size m with $m^2 - m$ connections, excluding losses and inputs, will have joint flow probabilities that are determined by the species diversity m . The flows T_{ij} are given by $TST/(m^2 - m)$, and the joint probabilities (from equation 7.4) by $1/(m^2 - m)$. From equation 7.6, the flow diversity would be equal to $-\log_2[1/(m^2 - m)]$, which gives an SI for a large web ($m = 1,500$) of about 21 bits, and this is consistent with the results for the unstructured webs with uniformly distributed transfer coefficients (Figure 7.7). Unevenness in flow reduces SI, and unstructured lognormal webs

had lower SI than unstructured uniform webs (Figure 7.7, Table 7.1).

Average mutual information is a measure of the average constraint or probability of flow from one taxon to the next (Ulanowicz 1997). It is not easily decomposed like flow diversity (SI) and has a behavior that is far more complex. AMI has a minimum value of zero when a network is maximally connected with uniform flows, or when there is an equal probability of flow moving from one taxon to any other taxon and the uncertainty in the direction of flow is greatest. Conversely, AMI is maximized when a web is minimally connected and flows are uniform. In other words, there is no uncertainty about direction of movement.

Zorach and Ulanowicz (2003) provided an extension of AMI by relating it to the number of roles in a network, where a role is a unique flow pattern within a food web that is common to one or more species. The number of roles is a measure of the diversity of functions that are occurring within a network. The empirical food webs analyzed here had about 2–5 roles per food web, and occupied a graphical area termed the window of vitality (Zorach and Ulanowicz 2003), similar to the clustering we observed between AMI and the density of major connections (Figure 7.9(B)). This is an idea similar to the network motifs or recurring circuit elements described by Milo et al. (2004), and seems to be a powerful way of characterizing

and classifying webs. However, the application of these metrics to real webs suffers from the same problems of aggregation as the information theoretic metrics.

Interestingly, unstructured uniform and structured uniform networks gave the lowest range of AMI (Table 7.1) and, therefore, the lowest number of roles. Conversely, the lognormal networks gave the greatest range of AMI and highest number of roles. Intuitively, a greater number of roles is consistent with the greater variation in flow strength afforded by the lognormal distribution, and on a mechanistic level this is most likely a consequence of the differences in the distributions of transfer coefficients. However, the actual flow distributions expressed as a percent of total inflow hardly differed among the different web types (Figure 7.5).

Ascendency (As) is given by the product of AMI times TST and is a measure of the absolute order in a system times the power generated, also described as the performance of the system (Ulanowicz 1986, 1997). The quotient As/Cd is a measure of the degree of organization of the system. We had hypothesized that As/Cd would be higher for structured webs than for unstructured webs and this was confirmed by our hypothetical data. Recall that Cd (full capacity) is a measure of the total potential order or complexity, and As is the realized complexity. All web types had a moderate range of As/Cd for webs of constant size, and for large webs the As/Cd appeared to be insensitive to web size, which is consistent with the calculations made above. Thus, As/Cd was most sensitive to flow distribution and insensitive to size, except among the smallest size classes where size apparently constrains the flow distributions and raises As/Cd. This raises the unsettling possibility that the aggregation of species that is characteristic of the relatively small empirical webs artificially raises As/Cd. This may be associated with the general inability to define minor flows in highly aggregated, small food webs. Even larger empirical webs lack resolution of flows of less than a few percent, and no current empirical web has species-level resolution for smaller organisms (Christian and Luczkovich 1999).

We can make some generalizations about the behavior of As/Cd by making the simplifying assumption that there are nm uniform flows in a web of size m . With this assumption, As/Cd reduces to $-\log_2(m/n)/\log(1/nm)$. For one uniform connection per taxon ($n=1$), the quotient As/Cd = 1 and is independent of size m . A network of $n=1$ is fully specialized. At the opposite extreme ($n=m$), the quotient As/Cd = 0, and the network is maximally disorganized. Among hypothetical and empirical webs, the average As/Cd were less than 0.5 (Table 7.1), which affirms a large diversity of flows. Like the hypothetical webs, data on interaction strengths in natural food webs indicate that interaction strengths are characterized by many weak interactions and a few strong interactions, which is thought to increase stability by dampening oscillations between consumers and resources (McCann et al. 1998).

Do empirical food webs reflect real webs? This has been a major source of concern in ecology for the past quarter century (Pimm 1982; Paine 1988; Martinez 1991; Cohen et al. 1993; others). We contend that networks of fully articulated food webs fall within the universe of our random networks. The structured webs (both uniform and lognormal) are a subset that should more closely contain organized, real food webs. Of the metrics considered, the highly aggregated empirical food webs have characteristics that fall within at least the smaller examples of the reference universe of structured webs. Reasonable similarities occur for total system throughput (normalized for inputs), number of major connections per taxon, SI, and Cd. However, AMI and As/Cd tend to be higher for empirical webs than their hypothetical counterparts of similar size. This may be a matter of resolution of flows. Major flows (>5%) are dominant in empirical webs because (1) the number of interaction possibilities is low and (2) the ability to identify rare diet items is low (Cohen et al. 1993). Major flows in these webs may constitute all flow, whereas major flows in the hypothetical webs do not necessarily constitute all flows. These minor flows affect the AMI and thus As and As/Cd. Thus, the true significance of these metrics may not be realized within our current means of characterizing food webs.

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