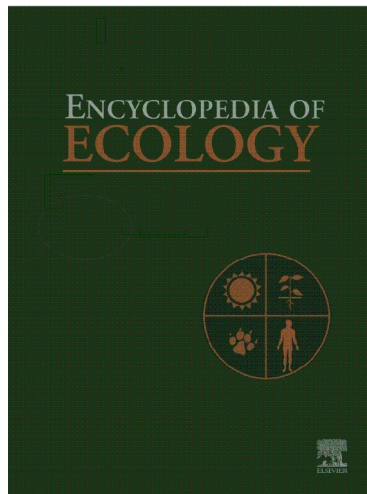


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animals that appear on and in dung and the processes they initiate are highly predictable, but in detail depend on the habitat and climate under investigation. Specialized coprophilous fungi, similarly, exhibit a clear sequence of utilization of their habitat, spores of early stages already being present in the dung when it is deposited by the herbivore. Apparently, users of dung are highly specialized, and their community is significantly different from what usually is referred to as decomposers or detritivores. Depending on climate, dung patches may become completely decomposed in less than 2 months but may also last for more than 2 years. Thus, as for most types of detritus, nutrient release is not sudden but extended over a longer time interval, so that detritus provides a long-term store and source of nutrients at the basis of ecosystems.

See also: Decomposition and Mineralization; Freshwater Lakes; Freshwater Marshes; Habitat.

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Development Capacity

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Introduction
Ecosystem Network Analysis
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Introduction

The ever-increasing interest toward ecosystem status and performance stimulates the application of tools for whole-system assessment; a prominent collection of quantitative methods to achieve this aim consists of ecosystem network analysis (ENA).

The apparatus of ENA comprises indices, derived from information theory, that quantify global attributes, and, in particular, ascendency (A) measures growth (size) and development (organization of flows) of ecosystems.

Ascendency is estimated as the product of average mutual information (AMI) by total system throughput (TST). It measures the ability of a system to prevail over alternative configurations. AMI evaluates how the system is developed, defining flow articulation, and TST expresses the size of an ecosystem as the sum of all the flows.

Since growth and development are natural processes, they possess finite limits: the minimum value for ascendency is 0, while its upper boundary, defined as development capacity (C), is affected by system topology.

Total System Throughput and Average Mutual Information

Besides the graphical and mathematical representation of 'who eats whom' and 'at what rate', ENA performs calculus focusing both on single-compartment and whole-system levels.

TST and AMI are basal indices advocating a systemic approach.

The total amount of flows occurring in the system is called TST, and for Cone Spring is equal to 42 445 kcal m⁻² yr⁻¹:

$$TST = \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} t_{ij} \quad [2]$$

TST defines ecosystem activity (size) and it conceptually corresponds to what in economy is known as gross national product (GDP), an indicator of economic community size.

Ecosystem development is connected to flow organization and it increases when uncertainty is diminishing. Mathematically, uncertainty (H), related to a distribution of probability over n categories (with scalar constant K), is equivalent to

$$H = -K \sum_{i=1}^n p_i \log p_i \quad [3]$$

System flow disorganization is measured by uncertainty and its amount can be distinguished into output $H(a)$ and input $H(b)$ contributions:

$$H(a) = -K \sum_{i=0}^{n+2} p(a_i) \log p(a_i) \quad [4]$$

$$H(b) = -K \sum_{j=0}^{n+2} p(b_j) \log p(b_j) \quad [5]$$

With completely independent events, total system uncertainty becomes $H(a) + H(b)$. However, inputs and outputs in ecosystems are not always independent and the associated uncertainty can be computed adopting joint probabilities $p(a_i, b_j)$:

$$H(a, b) = -K \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} p(a_i, b_j) \log p(a_i, b_j) \quad [6]$$

Therefore, with inputs and outputs that are not completely independent,

$$H(a, b) < H(a) + H(b) \quad [7]$$

and, in this case, the degree of system organization is defined as

$$A(a; b) = H(a) + H(b) - H(a, b) \quad [8]$$

yielding to

$$A(a; b) = K \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} p(a_i, b_j) \log \frac{p(a_i, b_j)}{p(a_i)p(b_j)} \quad [9]$$

since

$$p(a_i) = \sum_{j=0}^{n+2} p(a_i, b_j) \quad [10]$$

$$p(b_j) = \sum_{i=0}^{n+2} p(a_i, b_j) \quad [11]$$

To measure transfer uncertainty with network analysis notation, the probability that a quantum of matter (or energy) would flow from compartment i to j is computed as

$$p(a_i, b_j) \cong \frac{t_{ij}}{TST} \quad [12]$$

with output and input probabilities that can be written as marginal sums of joint probabilities:

$$p(a_i) \cong \sum_{j=0}^{n+2} \frac{t_{ij}}{TST} \quad [13]$$

$$p(b_j) \cong \sum_{i=0}^{n+2} \frac{t_{ij}}{TST} \quad [14]$$

AMI is the index measuring system organization (ecosystem development intended as flow articulation). Using the expressions provided by formulas [12]–[14] into [9], and simplifying, one obtains for this quantity the following representation:

$$AMI = \frac{K}{TST} \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} t_{ij} \cdot \log \left[\frac{t_{ij} \cdot TST}{\sum_{q=0}^{n+2} t_{qj} \sum_{v=0}^{n+2} t_{iv}} \right] \quad [15]$$

Ascendency and Development Capacity

Ascendency, being the product of TST and AMI, takes the following mathematical form:

$$A = AMI \cdot TST = \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} t_{ij} \cdot \log \left[\frac{t_{ij} \cdot TST}{\sum_{q=0}^{n+2} t_{qj} \sum_{v=0}^{n+2} t_{iv}} \right] \quad [16]$$

Assessing ecosystem growth and development can be done comparing ascendency with its maximum and minimum limits. Ascendency, deriving from TST and AMI, shows a minimum value of 0 (when output and input flow probabilities are completely independent; see **Figure 3a**), while the upper boundary is defined as development capacity.

For each ecosystem, the development capacity depends on the constraints established by real network topology. When number of compartments (n) and TST are assigned, the highest development capacity is associated to a wholly connected and balanced network, decreasing when flows

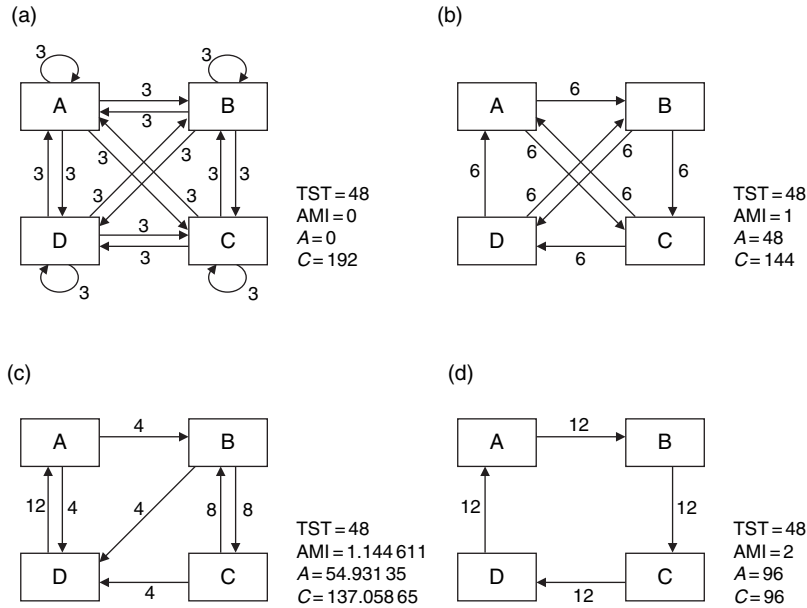


Figure 3 Hypothetical networks with four compartments and TST = 48 energy units: (a) the more unarticulated topology with minimum AMI and ascendency values (both equal to 0) and maximum development capacity (192); (b) and (c) intermediate configurations showing increasing AMI and A; C is lower than that observed for the first network; (d) a closed and linear chain (maximally articulated flows) with highest AMI (2) and ascendency equal to development capacity (96).

Table 1 Development capacity calculated for the hypothetical networks depicted in Figure 3; the values of C decrease when the network topology becomes more articulated

Network topology	Development capacity (C)
Fully connected (A)	192
Intermediate I (B)	144
Intermediate II (C)	137
Linear and closed chain (D)	96

become more articulated (its minimum value is achieved with closed linear chain topology, when it corresponds to system ascendency) (see Figure 3 and Table 1).

In what follows, minimum and maximum ascendency limits are explained through a probabilistic approach.

The lower ascendency value rises with fully connected topology, that is when input and output flow probabilities are completely independent:

$$p(a_i, b_j) = p(a_i) \cdot p(b_j) \quad [17]$$

Substituting this relation into eqn [9] yields

$$\begin{aligned} A(a; b) &= K \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} p(a_i)p(b_j) \log \frac{p(a_i)p(b_j)}{p(a_i)p(b_j)} \\ &= K \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} p(a_i)p(b_j) \log(1) = 0 \end{aligned} \quad [18]$$

Conversely, under minimum uncertainty conditions, ascendency can be inferred setting each inflow and

outflow probabilities as mutually determined (to the output a_i coincides, exclusively, the input b_j):

$$p(a_i, b_j) = p(a_i) = p(b_j) \quad [19]$$

and the consequent development capacity is

$$C = K \sum_{i=0}^{n+2} p(a_i) \log \frac{p(a_i)}{p(a_i)p(a_i)} = -K \sum_{i=0}^{n+2} p(a_i) \log p(a_i) \quad [20]$$

$$C = K \sum_{j=0}^{n+2} p(b_j) \log \frac{p(b_j)}{p(b_j)p(b_j)} = -K \sum_{j=0}^{n+2} p(b_j) \log p(b_j) \quad [21]$$

or, in terms of energy (or matter) transfers (with $K = TST$),

$$C = - \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} t_{ij} \log \frac{t_{ij}}{TST} \quad [22]$$

The more articulated topology (Figure 3d), with receiving node always determined when the compartment from which the flow is exiting is known, implies that $C = A$. In general,

$$C \geq A \geq 0 \quad [23]$$

From the strictly positive difference between development capacity and ascendency is estimated the system overhead (Φ), measuring the degree of freedom in flow organization preserved by an ecosystem:

$$\Phi = C - A \quad [24]$$

Ascendency and system overhead are usually scaled with development capacity to define them as percentage of the theoretical upper bound on organization:

$$A(\%) = \frac{100 \cdot A}{C} \quad [25]$$

$$\Phi(\%) = \frac{100 \cdot \Phi}{C} \quad [26]$$

System Overhead and Its Constitutive Terms

Path multiplicity and low level of flow organization, giving rise to overhead, can be interpreted as system inefficiency in processing material and energy, but, in case of stress and perturbations, they represent an advantage in terms of system adaptability to new threats.

The system overhead can be divided into four separate contributions, each related to a certain form of multiplicity of pathways: input from outside (overhead on imports, Φ_I), exports to other systems (overhead on exports, Φ_E), respirations (dissipative overhead, Φ_D), and internal transfers (redundancy, Φ_R):

$$\Phi = \Phi_I + \Phi_E + \Phi_D + \Phi_R \quad [27]$$

$$\Phi_I = - \sum_{j=1}^n t_{0j} \cdot \log \left[\frac{t_{0j}^2}{\sum_{q=0}^n t_{qj} \sum_{v=1}^n t_{0v}} \right] \quad [28]$$

$$\Phi_E = - \sum_{i=1}^n t_{i,n+1} \cdot \log \left[\frac{t_{i,n+1}^2}{\sum_{q=1}^n t_{q,n+1} \sum_{v=1}^{n+2} t_{iv}} \right] \quad [29]$$

$$\Phi_D = - \sum_{i=1}^n t_{i,n+2} \cdot \log \left[\frac{t_{i,n+2}^2}{\sum_{q=1}^n t_{q,n+2} \sum_{v=1}^{n+2} t_{iv}} \right] \quad [30]$$

$$\Phi_R = - \sum_{i=1}^n \sum_{j=1}^n t_{ij} \cdot \log \left[\frac{t_{ij}^2}{\sum_{q=0}^n t_{qj} \sum_{v=1}^{n+2} t_{iv}} \right] \quad [31]$$

where t_{ij} stands for a transfer from compartment i to j ; t_{0j} depicts imports to j ; $t_{i,n+1}$ and $t_{i,n+2}$ denote, respectively, export and respiration flows from node i .

Overhead on inputs summarize the fraction of 'flow inefficiency' related to the number and magnitude distribution of flows coming from the outside of the studied system. When the number of external inputs enlarges and becomes more evenly distributed, overhead on imports increases, measuring a higher inefficiency in getting medium from the outside; nevertheless, the maintenance of an adequate portion of overhead on imports becomes essential to the system survival. In fact, a system depending only on one input would be extremely efficient (in this case overhead on imports is minimized and equal to 0, regardless of the magnitude of the flow) but too fragile, showing risks of catastrophic extinctions in

case of external source collapse (with all the inputs to the system occurring via one single arrow).

Overhead on exports quantifies pathway multiplicity for medium exiting the system in a usable form. Like the overhead on inputs, it ranges from a minimum of 0, when all the matter (or energy) leaving the system is concentrated on a single node, to a maximum value achieved in case of exports evenly distributed on each single compartment. When the topology of exports and their relative importance are assigned, this overhead component tends to increase with higher amount of matter exported.

The dissipative overhead is related to the fraction of medium that is modified by internal processes (i.e., respiration in ecosystems) and exiting the system in an unusable form (flows that do not connect boxes). It increases with dissipation intensity and because of thermodynamic and ecological constraints must always be greater than 0.

The fourth component of overhead is related to the redundancy of pathways within the system. It is a contribution to disorder (inefficiency – disorganization) because sending medium over diverse routes costs more in terms of dissipation than channeling it over few efficient pathways; nevertheless, it becomes absolutely essential to system survival whenever an unexpected perturbation occurs. Under these circumstances, redundancy reflects 'strength in reserve' from which the system can draw to adapt to the new conditions.

The lower limit for redundancy is 0 when no uncertainty is preserved by internal flow structure (this is the unlikely case of a linear chain; see **Figure 3d**), while the value of its upper bound depends on TST and is associated to a wholly connected topology (maximum of flow uncertainty; see **Figure 3a**).

Table 2 summarizes, for 14 real ecosystems, the values of development capacity, ascendency, and overhead, with this latter split into its four constitutive components. Values are also given as percentage of the development capacity.

Additionally, one can also compute an internal development capacity (IC), considering only intercompartmental exchanges. This form finds its counterparts in other internal indices such as internal ascendency (IA) and internal redundancy (IR). Final results will be measured as percentage of the maximum upper bound (internal capacity) (see **Table 3**):

$$IC = - \sum_{i=1}^n \sum_{j=1}^n t_{ij} \log \frac{t_{ij}}{TST} \quad [32]$$

$$IA = \sum_{i=1}^n \sum_{j=1}^n t_{ij} \cdot \log \left[\frac{t_{ij} \cdot TST}{\sum_{q=0}^{n+2} t_{qj} \sum_{v=0}^{n+2} t_{iv}} \right] \quad [33]$$

$$IR = IC - IA \quad [34]$$

$$IA (\%) = \frac{100 \cdot IA}{IC} \quad [35]$$

$$IR (\%) = \frac{100 \cdot IR}{IC} \quad [36]$$

Internal capacity aims to define the upper limit to intercompartmental flow organization. While IR and redundancy (Φ_r) coincide, we get a further detail estimating IA, that is, the fraction of rigidly linked flows between system nodes with respect to the whole ascendancy (A).

Table 2 Fourteen real ecosystems are listed with their values of development capacity (C), ascendancy (A), and overhead (Φ_i , Φ_E , Φ_D , Φ_R). Data are obtained from Dr. Ulanowicz' database (datall.dat) and processed with NETWRK 4.2b software (<http://www.cbl.umces.edu/~ulan/>). Flows are measured in $mg\ C\ m^{-2}\ d^{-1}$ (Charca de Maspalomas, Crystal River Creek control and delta temp., St. Marks River, and Lake Michigan), $mg\ C\ m^{-2}\ sum^{-1}$ (Chesapeake Bay Mesohaline, Lower, Middle, and Upper Chesapeake Bay), $g\ C\ m^{-2}\ yr^{-1}$ (Everglades graminoids – wet season, Florida Bay – wet season, and Ythan Estuary), $mg\ C\ m^{-2}\ yr^{-1}$ (Final Narragansett) and $g\ AFDW\ m^{-2}\ yr^{-1}$ (Mondego Estuary)

	C	A	Φ_i	Φ_E	Φ_D	Φ_R
Charca de Maspalomas	39 886 000	16 871 000	2 755 700	906 760	5 538 700	13 814 000
		42.30%	6.91%	2.27%	13.89%	34.63%
Chesapeake Bay Mesohaline	19 655 000	8 593 800	1 702 300	79 705	3 565 200	5 714 500
		43.72%	8.66%	0.41%	18.14%	29.07%
Crystal River Creek (control)	70 712	28 340	3 205	6 193	18 408	14 566
		40.08%	4.53%	8.76%	26.03%	20.60%
Crystal River Creek (delta temp.)	56 315	22 434	2 588	3 892	15 030	12 372
		39.84%	4.60%	6.91%	26.69%	21.97%
Everglades graminoids (wet season)	79 572	38 643	11 391	675	10 181	18 682
		48.56%	14.32%	0.85%	12.79%	23.48%
Florida Bay (wet season)	18 540	7 004	2 064	53	2 629	6 791
		37.78%	11.13%	0.29%	14.18%	36.63%
Lower Chesapeake Bay	7 713 700	2 966 500	633 140	81 527	1 271 200	2 761 400
		38.46%	8.21%	1.06%	16.48%	35.80%
Middle Chesapeake Bay	9 328 300	3 872 600	634 340	37 609	1 548 700	3 235 000
		41.51%	6.80%	0.40%	16.60%	34.68%
Upper Chesapeake Bay	4 583 700	1 822 300	387 190	15 984	791 020	1 567 200
		39.76%	8.45%	0.35%	17.26%	34.19%
St. Marks River	11 264	3 726	1 488	353	2 267	3 432
		33.08%	13.21%	3.13%	20.12%	30.47%
Lake Michigan	140 690	65 649	10 409	1 814	12 013	50 805
		46.66%	7.40%	1.29%	8.54%	36.11%
Mondego Estuary	39 126	16 547	4 799	500	6 932	10 347
		42.29%	12.27%	1.28%	17.72%	26.45%
Final Narragansett	20 464 000	7 506 700	586 940	360 110	2 742 100	9 268 300
		36.68%	2.87%	1.76%	13.40%	45.29%
Ythan Estuary	23 397	8 663	1 845	1 363	4 158	7 368
		37.02%	7.89%	5.82%	17.77%	31.49%

Table 3 Internal capacity (IC), internal ascendancy (IA), and internal redundancy (IR) for the 14 ecosystems extracted from Dr. Ulanowicz' database. The last two columns show the percentage of IA and IR with respect to IC

	IC	IA	IR	$IA (\%)$	$IR (\%)$
Charca de Maspalomas	25 147 000	11 333 000	13 814 000	45.07	54.93
Chesapeake Bay mesohaline	11 584 000	5 869 700	5 714 500	50.67	49.33
Crystal River Creek (control)	26 223	11 657	14 566	44.45	55.55
Crystal River Creek (delta temp.)	21 267	8 895	12 372	41.83	58.17
Everglades graminoids (wet season)	34 090	15 407	18 682	45.20	54.80
Florida Bay (wet season)	11 291	4 500	6 791	39.85	60.14
Lower Chesapeake Bay	4 782 000	2 020 500	2 761 400	42.25	57.75
Middle Chesapeake Bay	5 867 500	2 632 500	3 235 000	44.87	55.13
Upper Chesapeake Bay	2 862 600	1 295 400	1 567 200	45.25	54.75
St. Marks River	5 507	2 075	3 432	37.68	62.32
Lake Michigan	71 540	20 735	50 805	28.98	71.02
Mondego Estuary	14 285	3 938	10 347	27.57	72.43
Final Narragansett	13 929 000	4 661 100	9 268 300	33.46	66.54
Ythan Estuary	12 805	5 437	7 368	42.46	57.54

Number of Roles and Development Capacity

Number of nodes, flow organization, and transfer intensities are strongly affected by the level of network detail. Therefore, indices such as TST, AMI, A , Φ , and C depend on arbitrary choices taken when an ecosystem network is built. For instance, if we are interested in decomposition activities, we will emphasize resolution of microbial and nonliving nodes, whereas to evaluate the susceptibility to environmental conditions (water and nutrient availability, solar radiation, temperature, wind intensity, salinity levels, etc.), each compartment will group species showing the same behavior.

To define development capacity variations as a function of the network framework, the connectivity (χ), calculated as flows per node, and the number of roles (ρ) are introduced:

$$\chi = \frac{f}{n} \tag{37}$$

$$\rho = \frac{n}{\chi} = \frac{n^2}{f} = \frac{f}{\chi^2} \tag{38}$$

with n = number of nodes and f = total number of flows.

It appears evident how connectivity and number of flows are directly affected by network topology and, in what follows, are proposed as an alternative way to define whole-system indices.

Although the concept of role has been fundamental to develop ecological niche idea and food web research, it has never been formally defined. Trophic position (TP; computed as the sum of the fractions of trophic activity that each species performs at different trophic levels), trophic niche (the 'ecological function' carried out by species in a given ecosystem), ecological guild (two species belong to the same ecological guild when they exploit the same class of environmental resources and in a similar way), and trophospecies (recently interpreted as a set of species with similar diet or predators) describe, in a slightly different way, the trophic role in an ecosystem, but none is completely satisfactory in wholly capturing relation with respect to food and enemies.

An effective definition can be obtained adopting concepts from social network analysis, where the role is seen as a specialized function joining structurally equivalent nodes. In the framework of ecological flow networks, this means that species belonging to the same role take input from one source and show outflows to a single destination. Then, in a recursive definition, two species (or group of species) are regular equivalent, exhibiting the same role, when eaten by and feeding on equivalent species.

Nevertheless, when role is calculated as a function of connectivity and number of flows, eqn [38] remains a different concept with respect to regular equivalence.

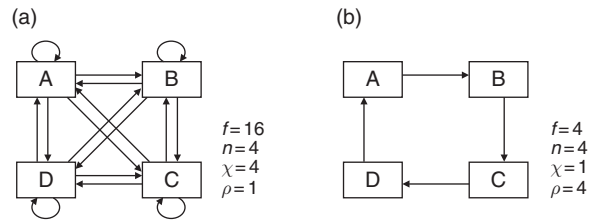


Figure 4 (a) The fully connected topology with four compartments ($n=4$) and 16 flows ($f=16$). In this case, an average number of four flows per node ($\chi=4$) was calculated, with only one role ($\rho=1$). (b) The more articulated network with $n=4$ nodes, $f=4$ flows, connectivity $\chi=1$ flow per node, number of roles $\rho=n=4$.

Rather than considering the two approaches in contrast with one another, it is interesting to stress the potential for their integration. The relationship between regular equivalence and number of roles is clearest when the network contains no cycles. In a linear chain with n nodes we identify n roles, while in a fully connected topology of n compartments, there is only one role (see Figure 4).

The example of Figure 4 represents two hypothetical unweighted networks, not really suitable to describe the real world. In what follows, a method to extend the role calculation when dealing with real ecosystems (where flows have unequal size, with sometimes extraordinary differences) is suggested.

In weighted networks, the effective connectivity is estimated accounting for the weights of flows and the portion of TST processed by each node. Applying a weighted geometric mean, connectivity (χ) and total system flows (f) become

$$\chi = \prod_{i=0}^{n+2} \prod_{j=0}^{n+2} \left(\frac{t_{ij}^2}{\sum_{q=0}^{n+2} t_{qj} \sum_{v=0}^{n+2} t_{iv}} \right)^{-(1/2) \cdot (t_{ij}/TST)} \tag{39}$$

$$f = \prod_{i=0}^{n+2} \prod_{j=0}^{n+2} \left(\frac{t_{ij}}{TST} \right)^{-(t_{ij}/TST)} \tag{40}$$

and the derived number of roles (ρ) is

$$\rho = \frac{f}{\chi^2} = \prod_{i=0}^{n+2} \prod_{j=0}^{n+2} \left(\frac{t_{ij} \cdot TST}{\sum_{q=0}^{n+2} t_{qj} \sum_{v=0}^{n+2} t_{iv}} \right)^{(t_{ij}/TST)} \tag{41}$$

The logarithm of ρ can also be a convenient value to measure AMI and ascendency of the system:

$$\log \rho = \frac{K}{TST} \sum_{i=0}^{n+2} \sum_{j=0}^{n+2} t_{ij} \cdot \log \left[\frac{t_{ij} \cdot TST}{\sum_{q=0}^{n+2} t_{qj} \sum_{v=0}^{n+2} t_{iv}} \right] = AMI \tag{42}$$

$$A = TST \cdot \log \rho \tag{43}$$

The concept of role establishes a relationship between number of nodes, connectivity, and information theory indices (AMI, A , and C).

Given the relation [42], when AMI of a system is known, the corresponding number of roles is deduced from the AMI power of e (Nepero number). As a consequence, with assigned ascendency and TST, the number of roles results e raised to the power of A/TST . Moreover, dividing the value of C by TST, it is also possible to infer the logarithm of roles when the maximum development is reached and, accordingly, the associated number of roles (ρ_C):

$$\rho = e^{AMI} \quad [44]$$

$$\rho = e^{\frac{A}{TST}} \quad [45]$$

$$\rho_C = e^{\frac{C}{TST}} \quad [46]$$

In **Table 4**, TST, AMI, ascendency, development capacity, and number of roles (corresponding to A and C) in real ecosystems are summarized.

For the 14 ecosystems of **Table 4**, when the number of roles is computed starting from the ascendency, through formula [45], it ranges between 3.465 583 (Crystal River Creek – delta temp.) and 9.492 356 (Charca de Maspalomas), with an average value of 6.405 319. These data confirm how the concept of role shows several relationships to that of TP, since both these indices are limited by the maximum number of passages that energy can experience from the ultimate source of energy (imports – outside environment).

Values of 10–20% are rather accepted as average living compartment efficiency in processing food, setting six to eight as the maximum number of energy steps (corresponding to TPs) in real networks. While TP is a property depending exclusively on compartment feeding activity, both prey items and predators affect the role that is assigned to each node. In ecosystems, even though

procedures computing TPs and roles slightly differ, they are deeply settled by energy and efficiency constraints.

Therefore, it appears evident how the number of roles computed through the development capacity (eqn [46]) is overestimated (minimum = 22.645 125, maximum = 234.292 711, mean = 119.320 020), being associated to an ecologically unfeasible topology that does not consider constraints to energy-transfer efficiency in natural systems.

Ecological Applications

Development capacity is estimated as the product of the ecosystem size (TST) and the diversity of flow structure, calculated using the Shannon information formula. Though information indices depend on arbitrary choices of what constitute a compartment, ascendency, overhead, and development capacity remain efficient indicators and they are widely applied in ENA.

In case studies, the ascendency measures how network structure and form reflect constraints to potential indeterminacy, while the potential degree of freedom preserved by an ecosystem is defined as overhead. Ascendency and overhead are the constitutive terms of the development capacity.

Development capacity of a system may rise when the scaling factor TST is augmented or through an increasing number of compartments with unarticulated flows. In presence of few limiting factors, TST tends to augment, but, in real systems, nutrient availability and respiration flows contribute to limit both its rise and a finer partition of transfers.

Level of resolution in building networks, on which ecosystem topology depends, affects both ascendency and development capacity. So, the same network could

Table 4 Total system throughput (TST), average mutual information (AMI), ascendency (A), and development capacity (C) are summarized for 14 ecosystems. Number of roles related to ascendency and development capacity are computed (Roles (A) and Roles (C)) adopting formula [43] as a reference

	TST	AMI	A	C	Roles (A)	Roles (C)
Charca de Maspalomas	7 496 600 mg C m ⁻² d ⁻¹	2.250 487	16 871 000	39 886 000	9.492 356	204.495 366
Chesapeake Bay mesohaline	4 116 200 mg C m ⁻² sum ⁻¹	2.087 799	8 593 800	19 655 000	8.067 143	118.514 489
Crystal River Creek (control)	22 420 mg C m ⁻² d ⁻¹	1.264 050	28 340	70 712	3.539 728	23.428 885
Crystal River Creek (delta temp.)	18 050 mg C m ⁻² d ⁻¹	1.242 881	22 434	56 315	3.465 583	22.645 125
Everglades graminoids	19 949 g C m ⁻² yr ⁻¹	1.937 090	38 643	79 572	6.938 528	53.988 517
Florida Bay	3 459 g C m ⁻² yr ⁻¹	2.024 571	7 004	18 540	7.572 859	212.578 400
Lower Chesapeake Bay	1 451 200 mg C m ⁻² sum ⁻¹	2.044 170	2 966 500	7 713 700	7.722 749	203.444 686
Middle Chesapeake Bay	1 879 000 mg C m ⁻² sum ⁻¹	2.060 990	3 872 600	9 328 300	7.853 740	143.237 257
Upper Chesapeake Bay	854 330 mg C m ⁻² sum ⁻¹	2.133 017	1 822 300	4 583 700	8.440 289	213.846 183
St. Marks River	2 064 mg C m ⁻² d ⁻¹	1.804 825	3 726	11 264	6.078 907	234.292 711
Lake Michigan	36 985 mg C m ⁻² d ⁻¹	1.775 017	65 649	140 690	5.900 381	44.879 207
Mondego Estuary	10 852 g AFDW m ⁻² yr ⁻¹	1.524 788	16 547	39 126	4.594 170	36.797 075
Final Narragansett	4 611 300 mg C m ⁻² yr ⁻¹	1.627 892	7 506 700	20 464 000	5.093 129	84.588 144
Ythan Estuary	5 440 g C m ⁻² yr ⁻¹	1.592 273	8 663	23 397	4.914 906	73.744 240

show a high detailed representation with many compartments and transfers, or it could be depicted with few nodes grouping several species that were separated in the previous case. When TST is assigned, in the first hypothesis, development capacity and ascendency are higher than in the latter since a lot of flows collapse in presence of few bigger nodes including many species, with a consequent reduction of articulation.

This is a sort of scale-resolution sensitivity, reflecting the importance of flow structure on C .

Once we know relationships among system components together with their weight (i.e., in presence of a network at a given level of resolution), development capacity and its constitutive terms, ascendency (indicator of organized flow structure), and overhead (index of potential resiliency) can be estimated. The only requirement is that all measurements have the same currency. In ecological applications, these three indices provide a sort of 'snapshot' of the developmental status of the system and their variations in time can give clues about ecosystem health and integrity.

In what follows, very general and theoretical patterns in information index variations are sketched out, but to test their predictive adequacy sufficient data sets describing ecosystem trophic relations before and after perturbation are required. At present, time series are exceedingly rare.

In general, in presence of novel perturbations, we expect ascendency to decrease, depending on a reduction of system size (TST) and flow articulation (AMI), while for unimpacted ecosystems a trend toward increasing ascendency, in both its constituent terms, would be detected.

Also, development capacity reflects changes occurring to the system status, showing a tendency to decrease in case of impacted conditions.

In contrast to the ascendency falling down in disturbed ecosystems, both overhead related to internal flows (redundancy) and respiration (dissipative overhead) exhibit increasing trends, as one would expect in response to stress. Overhead on imports and overhead on exports may instead change in an apparently not characteristic fashion, with slight drops in their values. This could be caused by the strong influence of TST component that overwhelms, with its falling down in presence of perturbation (lower level of total system activity intended as less medium processed), the effects produced by higher flow disorder and incoherence.

Therefore, final values of information indices could be deeply affected by system size (TST), as described above in the case of overhead on imports and on exports, hiding the contribution of system flow organization (AMI). Because of this tendency, a detailed analysis of the flow structure status could be stressed dividing C , A , and Φ by TST. It should be noted, however, that differences in the AMI component of these information indices represent

logarithms of variations in actual probabilities and are, consequently, much-attenuated indicators of change.

Besides theoretical patterns, trends outlined by studies on eutrophication (system overenrichment of nutrients, usually nitrogen and phosphorus) show apparently strange increasing values in ascendency and development capacity.

In fact, information indices exhibit characteristic behaviors in case of eutrophication and the most evident consequence of the ecosystem growth (augmented system activity – TST) is the rise of C and A , in spite of an oversimplified and degraded web structure.

The higher ascendency in presence of eutrophication is due to the exclusive effect of TST that more than compensates for a concomitant fall in the degrees of freedom remaining in the system. It is then obvious that not every increase in system ascendency represents healthy change.

In addition to ecosystem networks, urban systems can also be depicted with compartments and flows connecting them, adopting different currencies: water, energy, metals, wood, and many others. When size of flows is increased, there is a simple growth of TST without any change in network articulation and, accordingly, ascendency and development capacity rise. Often, in urban networks, this growth of system size is confused with system development. A great insight into this misleading idea is supplied scaling ascendency with C . In fact, there are many examples of urban water network with ascendency set around the 40% of development capacity, while this percentage is considerably higher in ecosystems, reaching till 55% and 60% of the maximum capacity (data available from the Florida Bay data set; <http://www.cbl.umces.edu/~atlss/>).

These data contradict the common perception that human systems are well organized, highlighting the need for increasing ascendency through a more efficient transfer organization and use of resources. A more articulated topology could be obtained, for instance, by reducing dissipations, increasing internal recycling, and process efficiencies or limiting exports.

The importance of development capacity as an ascendency and overhead scaling factor is strengthened by its application to assess both system performance and integrity.

Homeostasis, transfer efficiency, opportunity for growth, stability, sustainability, and minimal external support are many attributes commonly grasped into the definition of ecosystem health, that addresses how well the system is functioning, assessing its performance. For example, if the ratio between overhead on imports and development capacity decreases, over a sufficiently wide time lag, the ecosystem under analysis shows a trend toward organization and minimization of its dependence on external supports. This inclination could be confirmed

by a more efficient transfer organization of internal flows (IA scaled with internal capacity) and by an increased amount of recycled matter.

At the same time, another ecosystem health property as transfer efficiency increases when the network becomes more articulated and this is the case when ascendancy exceeds a given threshold (i.e., 50% of the development capacity).

The integrity concept endorses how well a system performs on a temporal scale, being associated to: capability for future developmental options, capacity to withstand stress (i.e., resilience and resistance), and ability for change and development. Integrity preservation can be estimated, for example, by scaling overhead indices with C . When a stabilized and sufficiently high percentage of redundancy is showed, the ecosystem offers a multiplicity of pathways. This aspect may produce a good ability to overcome the perturbations: the more unarticulated is the system, the higher is the number of available pathways that energy can experience to flow through the network. In this way, if a species is no more, the multiplicity of trophic relations (that is variety of routes) reduces risks of indirect extinction of other species. In fact, it is quite unlikely that, in presence of high redundancy percentage, many species exclusively feed on the extinguished node.

Also, the simple calculation of development capacity appears as an appropriate measure of ecological integrity, being the sum of a term describing the tendency to an organized and well-performing behavior (A), with its complement that represents the degrees of freedom remaining in the system for reconfiguration in response to injury (Φ).

Therefore, development capacity cannot be simply seen as an ascendancy and redundancy scaling factor. Rather, its interplay with ascendancy and overhead, giving rise to the percentage of organized complexity (A/C) and not constrained flows (Φ_R/C), is an effective approach to check complex properties as ecosystem health and integrity. As a consequence, the action of ascendancy and overhead might be described as balanced result between two antagonistic tendencies than being explained in a rigorous and algorithmic fashion.

Sufficient amounts of both attributes (A and Φ) should be preserved for the persistence of each system over the long term, and a monitoring process to quantitatively track changes in these two partitions over time should be planned to trace ecological dynamics.

See also: Ascendancy; Biological Integrity; Ecological Network Analysis, Ascendancy; Ecological Network Analysis, Energy Analysis.

Further Reading

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Relevant Website

<http://www.cbl.umces.edu> – Network Analysis of the Trophic Dynamics of South Florida Ecosystems (a component of ATLSS); Robert E. Ulanowicz' Home Page, at Chesapeake Biological Laboratory.