
ECOSYSTEM ANALYSIS



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MULTIVARIATE COMPARISON OF TROPHIC NETWORKS OF GRASSLAND ECOSYSTEMS

Abstract. This article compares 13 network properties of food webs of 31 Ukrainian grasslands. The properties are: network size N , trophic link number L , trophic classes CI , system connectance C , link density LD , total system throughflow TST , network cycling FCI , ascendancy AS , developmental capacity DC , indirect effects dominance IE , system aggradation AI , system synergism SI , and mutualism MI . Our results show these properties are highly correlated and can be aggregated into the three latent factors. The first factor includes N , TST , AS , DC , SI , L , and LD , where network size N appears to be a central defining variable. The second latent factor includes FCI , AI , and CI , and is driven by indirect effects dominance IE . The third factor includes mutualism MI and connectance C , the last being the driving variable. Network Synergism SI is negatively correlated with the other network properties, while all others are positively intercorrelated. Network connectance appears to be a scale invariant property, while link density is highly sensitive to network size. Our data also show that network mutualism MI is more tied to the network complexity than simply to system scale or number of feeding links.

Keywords: ecological network analysis, trophic networks, multivariate analysis, grassland ecosystems, system-wide network properties.

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БАГАТОФАКТОРНИЙ ПОРІВНЯЛЬНИЙ АНАЛІЗ ТРОФІЧНИХ МЕРЕЖ ЛУЧНИХ ЕКОСИСТЕМ

Анотація. Екологічний мережевий аналіз (ЕНА) – міждисциплінарний аналітичний підхід в екології, який дозволяє вивчати, а також кількісно та якісно оцінювати різні типи

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екологічних мереж, а саме трофічні мережі, біогеохімічні колообіги, мутуалістичні мережі та мережі взаємозв'язків господар – паразит. Кількісні та якісні індекси екологічного мережевого аналізу є емерджентними показниками екосистеми, які виникають внаслідок прямих та опосередкованих зв'язків між біотичними (організмами) та абіотичними (грунт, детрит) компонентами екосистеми. Однак ряд науковців доводять, що деякі емерджентні показники екосистеми корелюють та мають схожу структуру та динаміку. Більшість досліджень емерджентних властивостей екосистеми визнають необхідність в порівнянні ENA індексів на основі емпіричних даних для розуміння їх поведінки та якісного вкладу в характеристику структурно-функціональної організації екосистеми. Метою роботи було порівняння динаміки та поведінки 13 емерджентних показників, використовуючи трофічні мережі екосистем лучного типу, а саме: розмір мережі N , кількість трофічних зв'язків L , трофічних класів CI , складність трофічної мережі C , щільність трофічних зв'язків LD , загальний потік енергії TST , колообіг FCI , ступінь розвитку трофічної мережі AS , ємність трофічної мережі DC , домінування непрямих зв'язків у системі IE , середня довжина потоків у системі AI , ступінь синергізму SI та мутуалізму MI . Відповідно до мети побудовано трофічні мережі для 31 лучних екосистем Чернівецької області та оцінено емерджентні показники для кожної трофічної мережі. Визначено силу і напрям попарних взаємозв'язків між ENA індексами та встановлено їх поведінку відносно один до одного. Порівнюючи 31 трофічну мережу та використовуючи багатофакторний порівняльний аналіз, виділено індекси, які мають подібну динаміку та поведінку.

Результати показують, що досліджувані показники мають високу статистично достовірну кореляцію і складають групу з трьох латентних факторів. Перший фактор включає N , TST , AS , DC , SI , L та LD , де центральним показником є розмір мережі N . Розмір мережі вимірюється як кількість компонентів в екосистемі і відіграє фундаментальне значення в структурно-функціональній організації мережі, оскільки компоненти екосистеми та взаємозв'язки між ними визначають структуру мережі. З результатів досліджень видно, що загальний потік енергії TST , ступінь розвитку трофічної мережі AS , ємність трофічної мережі DC , ступінь синергізму SI , кількість L та щільність LD трофічних зв'язків мають однаково поведінку щодо характеристики організації мережі і залежать в основному від розміру трофічної мережі. Другий латентний фактор базується в основному на показнику домінування непрямих зв'язків IE , а також включає такі показники як FCI , AI та CI . Домінування непрямих зв'язків зростає при збільшенні колообігу речовини в трофічній мережі FCI . Однак результати свідчать, що непрямі зв'язки відіграють основну роль в динаміці поведінки FCI , AI та CI . Третій фактор включає MI та C , де складність трофічної мережі є домінуючим показником. Синергізм трофічної мережі SI негативно корелює з усіма іншими показниками, в той час як усі інші показники позитивно корелюють один з одним. Складність мережі C виявився інваріантним показником щодо змін розміру трофічної мережі, в той час як показник щільності трофічних зв'язків LD виявив високу чутливість до варіації в розмірі трофічних сіток. Результати наших досліджень також підтверджують, що мутуалізм трофічної мережі MI є залежним не від розміру мережі, а від складності її структури.

Ключові слова: екологічний мережевий аналіз, трофічна мережа, багатофакторний аналіз, лучна екосистема, системні показники трофічної мережі.

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МНОГОФАКТОРНЫЙ СРАВНИТЕЛЬНЫЙ АНАЛИЗ ТРОФИЧЕСКИХ СЕТЕЙ ЛУГОВЫХ ЭКОСИСТЕМ

Аннотация. Выполнено сравнение 13 показателей трофических сетей 31 луговых экосистем Украины, а именно: размер сети N , количество трофических связей L , трофических классов CI , сложность трофической сети C , плотность трофических связей LD , общий поток

энергии *TST*, круговорот *FCI*, степень развития трофической сети *AS*, емкость трофической сети *DC*, доминирование не прямых связей в системе *IE*, средняя длина потоков в системе *AI*, степень синергизма *SI* и мутуализма *MI*. Результаты показали, что исследуемые показатели имеют высокую статистически достоверную корреляцию и составляют группу из трех латентных факторов. Первый фактор включает *N*, *TST*, *AS*, *DC*, *SI*, *L* и *LD*, где центральным показателем является размер сети *N*. Второй латентный фактор базируется в основном на показателе доминирование не прямых связей, а также включает такие показатели как *IE*, *FCI*, *AI* и *CI*. Третий фактор включает *MI* и *C*, где сложность трофической сети является доминирующим показателем. Синергизм трофической сети *SI* коррелирует отрицательно со всеми показателями, в то время как все остальные показатели положительно коррелируют друг с другом. Сложность сети *C* оказалась инвариантным показателем к изменению размера трофической сети, в то время как показатель плотности трофических связей *LD* показал высокую чувствительность к вариации размеров трофических сетей. Результаты наших исследований также подтверждают, что мутуализм трофической сети *MI* является зависимым не от размера сети, а от сложности ее структуры.

Ключевые слова экологический сетевой анализ, трофическая сеть, многофакторный анализ, луговая экосистема, системные показатели трофической сети.

INTRODUCTION

Ecological Network Analysis (ENA) is a growing multidisciplinary analytical tool that makes it possible to study different types of ecological networks, such as food webs, biogeochemical nutrient cycles, mutualistic networks and host-parasitoid webs. Systems ecologists name three main advantages of ENA in the study of ecological systems.

First, ENA is a way of investigating ecological holism (Patten, 1978, 1981, 1982, 1985, Ulanowicz, 1980, 1983, 1986, 1997, 2004; Fath and Patten, 1999; Fath et al., 2007). It considers organisms and their multiple interactions (links, flows) as a whole interconnected system expressed by the network. Moreover, several ENA approaches provide the possibility to study ecosystems as thermodynamically open to energy and matter, for example, Network Environ Analysis (Patten, 1978, 1981, 1982, 1985) and Ascendency Analysis (Ulanowicz, 1980, 1986, 1997). ENA is a core methodology of Holocology (Patten et al., 1976; Fath and Patten, 1999).

Second, ENA applications make it possible to study networks quantitatively by evaluating a set the system-wide network properties (Fath et al., 2007; Fath and Patten, 1999). Several advanced quantitative approaches have arisen in order to perform ENA, such as: Network Environ Analysis (Patten, 1978, 1981, 1982, 1985); Input-Output Analysis (Hannon, 1973); Ascendency Analysis (Ulanowicz, 1980, 1986, 1997); and Embodied Energy Analysis (Odum, 1983; Herendeen, 1981, 1989). Borrett's (2013) review of ENA literature indicates more than 15000 published scientific papers have addressed assessment of network measures.

Finally, ENA measures represent system-level properties not evident from direct empirical observations (Fath et al., 2007). These properties are hidden because the complex structure and behavior of ecological systems are driven by a multiplicity of invisible interactions among living organisms and non-living matter.

A number of authors have demonstrated that certain measures of systemic network organization are related. Jørgensen (1994) showed high correlations between the system goal functions *exergy* (Jørgensen (1992), *emergy* (Odum, 1988), *ascendency* (Ulanowicz, 1997), and *indirect effects* (Patten, 1984)) in a set of lake models. Patten (1995) showed that these and also *maximum power* (Lotka, 1922) had a common basis in network structure and dynamics. Fath et al. (2001) demonstrated mutual consistency of the following ten system properties: *maximum power* (Lotka, 1922), *maximum storage* (Jørgensen and Mejer, 1979), *maximum empower and emergy* (Odum, 1988), *maximum ascendency* (Ulanowicz, 1997), *maximum dissipation* (Schneider and Kay, 1990), *maximum cycling* (Morowitz, 1968), *maximum residence time* (Cheslak and Lamarra, 1981), *minimum dissipation* (Onsager, 1931; Prigogine, 1995), and *minimum empower to exergy ratio* (Bastianoni and

Marchettini, 1997), suggesting a common pattern for ecosystem development. Borrett (2010), comparing 50 trophic networks, demonstrated interrelatedness of network *homogenization* (Patten et al., 1990) with *network size*, *connectance* and *cycling* (Finn, 1976). Fath (2004, 2007) investigated the behavior of network *synergism* and *mutualism* measures (Patten, 1991, 1992) with increasing system size. Most of these studies acknowledge that further multi-property comparisons based on empirical data are needed to understand the network measures' contributions to ecosystem structure and function (Jørgensen, 2002). Moreover, ENA literature acknowledges limitations associated with network data availability, making direct comparisons of network properties and their interrelations difficult (Borrett et al., 2007; Fath et al., 2007; Finn, 1976; Ulanowicz, 1986). Examples:

(1) Widely used randomly generated networks (Gardner and Ashby, 1970; May, 1972) or hypothetically structured systems do not adequately represent the common structure of ecosystems, unlike empirically based networks (McCann, 2000). Systems ecologists suggest that ecological systems are constrained due to thermodynamic laws as well as by natural history (Lawler, 1978; Jørgensen et al., 1992) as opposed to being pure random structures.

(2) Network simplification by employing subsets that capture too few selected compartments and their interactions (e.g., competition and predator-prey subnetworks) give incomplete and potentially misleading results. Fath et al. (2007) showed that excluding a majority of species and abiotic subsets makes it impossible to quantify the wholeness and consequent indirectness in the ecological system.

(3) Differences in network construction and aggregation make it difficult to directly compare systems, even of the same type and organizational level (Ulanowicz, 1986).

(4) Differences in flow currency and time scales limit comparative conclusions. The actual meaning of compartments (e.g., individuals, species, trophic levels, abiotic categories) makes a difference in interpreting results (Finn, 1976).

(5) Most ENA approaches compare a few particular indices. Repetitions of such quantitative studies remain necessary. Jørgensen (2002) stressed it is important to integrate multiple contributions of different system ecologists in order to understand network organization and formulate a consistent network theory.

(6) Because of limitations in data availability, most approaches do not apply network measures to empirically observed ecological processes and empirically assessed parameters of ecological systems. Numerous authors strongly advocate the use of ENA and network science generally to explain ecological observations (Pimm, 1991; Patten et al., 1997; Jørgensen et al., 1992; Jørgensen, 2002;). Jørgensen (2002) holds that such applications are required to assess how and where theory needs improvement.

In this paper we speak to the above limitations by comparing system-wide properties of 31 empirically described pastoral food webs from nearby geographic locations (Chernivtsi Region, Ukraine). Each web is based on field and laboratory data collected at the same level of organization, with similar details of construction, aggregation, currency, and time scale. Our goals are to compare thirteen ENA measures across these webs and consider how the findings reflect on the structure and function of the 31 ecosystems as operating pasture lands. To achieve them the following specific objectives are considered:

(1) Assess the strength and direction of interrelations between ENA measures pairwise in order to investigate their behavior in relation to each other.

(2) Distinguish network measures which have the similar behavioral patterns while comparing the set of 31 food webs. For this we use multivariate factor analysis techniques, namely Principal Component Analysis (PCA).

MATERIALS AND METHODS

Study Area

The 31 pastoral ecosystems under study are distributed throughout the Chernivtsi Region (47°43' – 48°41' N × 24°55' – 27°30' E) which is located in south western Ukraine (Fig. 1).

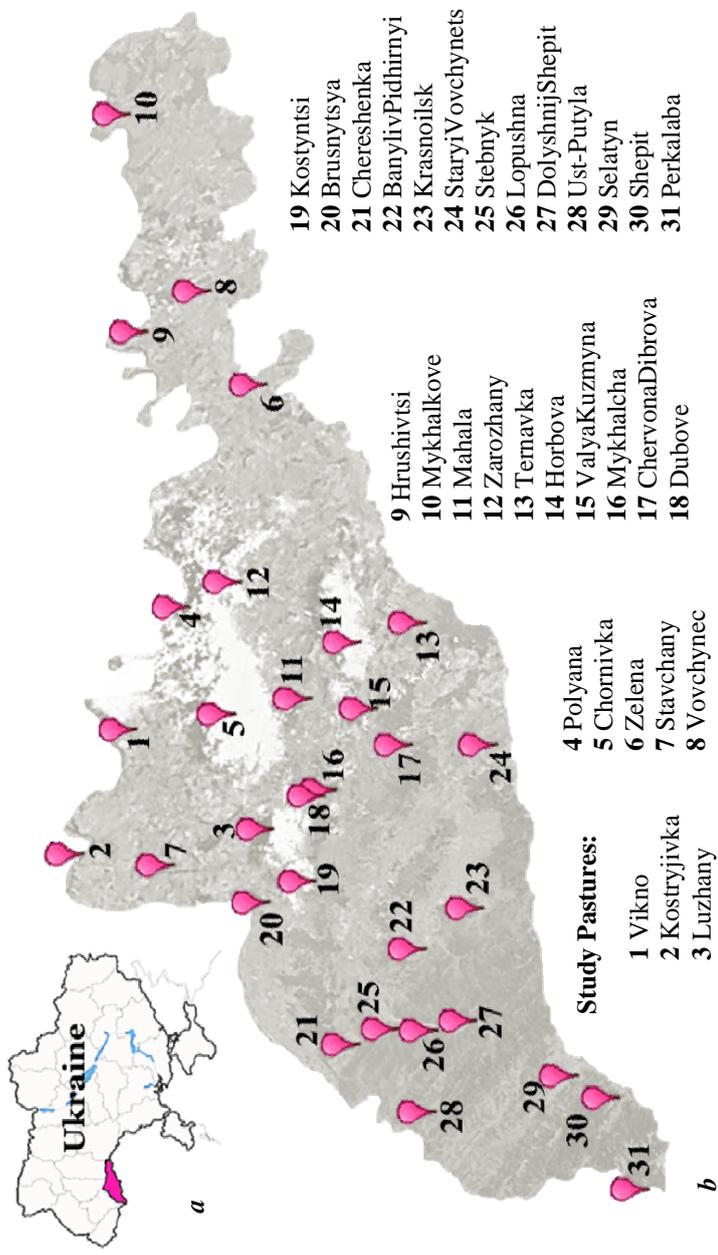


Fig. 1. Map of the study area:
a – shows a map of Ukraine, where the highlighted is the study area (Chernivtsi Region);
b – shows the locations and list of the study plots (pastures)

The study area experiences Temperate Continental Climate highly influenced by humid air masses from the Atlantic. Precipitation is highly variable seasonally, with an annual mean of 650–750 mm/year. Complex terrain causes climatic variations in the different physical-geographic zones. In the east it is more continental, and moving from the central foothills toward the southwestern mountains it becomes more severe due to cold and short summers. Physiography includes a wide range of relief types, including flat plains, hills, and mountains with respective mean elevations of 230 m, 350 m and 900 m above sea level.

All the study grasslands, unmanaged since 1992, are used as commons for cattle pasturing by private household farms, which typically have two to three head of cattle per farm. For comparisons between pastures to be valid, sampling and analysis methods were identical for each study pasture.

Sampling

Biological samples for food-web analysis were gathered during peak growing seasons (June – July) in years 2005, 2006, and 2007. Study plots for each of the compared pastures were 10m × 10m.

Plant and insect specimens were identified to species. Earthworms (subclass Oligochaeta) were separated from the 1 m³ plots by a standard method, Quantitative Hand Sorting. Microbiological soil analysis was based on cell counts of three microbial groups: Heterotrophic Bacteria, Fungi (Micromycetes), and Ray Fungi (Actinomycetes). Cells were cultured on specific substrates under controlled temperature (T) conditions – Heterotrophic Bacteria: meat-peptone agar, 28 < T < 30 °C; Fungi (Micromycetes): modified Czapek-Dox substrate with streptomycin, 20 < T < 25 °C; Ray Fungi (Actinomycetes): starch-ammonium agar, 28 < T < 30 °C. Cattle density was counted as number of animals/100 m².

Several faunal groups were omitted because of available resource limitations. This impacts our food webs as descriptions, but still allows their valid comparative study as our sampling and analysis methods were standardized.

Construction of Trophic Networks

Trophic compartments were defined based on distinct feeding roles they play in the studied pastures. Our basic categories for compartments were plant species, their pollen and nectar, cattle, ontogenetic stages and sexes of insects reflecting distinct trophic roles, earthworms, heterotrophic bacteria, fungi, ray fungi, plant litter, animal litter, detritus, and cattle excrement. To build and visualize our food webs we used Large Network Analysis software *Pajek* (Batagelj and Mrvar, 2010) and Social Network Analysis software *Ucinet 6* (Borgatti, et al., 2002).

Supplementary data associated with this article can be found, in the online version, at Buzhdygan et al. (2012a): at doi:10.1016/j.ecolmodel.2012.02.024.

To construct our trophic networks we formed a square adjacency matrix, $A_{n \times n} = (a_{ij})$, where $i, j = 1, \dots, n$ compartments, oriented from rows (i) to columns (j). A matrix entry $a_{ij} = 1$ signifies a biomass [M(mass)-L(length)-T(time) dimensions = M] feeding flow, f_{ij} [$ML^{-2}T^{-1}$ (mass /unit area•time)], directed from row compartment i to column compartment j ; $a_{ij} = 0$ indicates no i to j food transfer ($f_{ij} = 0$).

Each compartment i has a boundary input z_i [$ML^{-2}T^{-1}$], and output y_i [$ML^{-2}T^{-1}$] in accordance to the Network Environ Theory (Patten, 1981, 1982).

To quantify adjacency-based relations from qualitative digraphs, we transformed the adjacency matrix, $A_{n \times n}$ into an isomorphic flow matrix $F_{n \times n} = (f_{ij})$, where $i, j = 1, \dots, n$ compartments, oriented from rows (i) to columns (j), using the equiprobability concept from probability theory. According to the Laplace principle of indifference a matrix entry f_{ij} (a biomass feeding flow [$ML^{-2}T^{-1}$]) as well as the boundary output y_i are assigned the probability $1/N_i$, where N_i signifies a number of mutually exclusive feeding flows directed from row compartment i to column compartments ($j = 1, \dots, n$) including a boundary output y_i . Boundary inputs z_i and standing stocks x_i are set equal to 1.

Definition of Trophic Classes

Trophic classes (CI) refers to the functional groups of taxa that share the equivalent predators and prey in term of the trophic roles and positions they occupy. To investigate

the number of trophic classes in our food webs we used the regular equivalence approach drawn from Social Network Theory (Borgatti and Everett, 1993) and applied as a tool in *Ucinet 6* (Borgatti, et al., 2002). The Regular Equivalence algorithm assesses similarity of trophic roles of compartments using binary presence–absence feeding relations (adjacency matrix $A_{n \times n}$) between them. Johnson’s Hierarchical Clustering (Johnson, 1967) of equivalence similarity was used to define the separate trophic classes. For more details of the Regular Equivalence algorithm and current aggregation methods see Borgatti and Everett (1993) and Luczkovich et al. (2003).

Simulation of Trophic Networks

For trophic networks the inputs, and interior flows and outputs, they generate are conservative energy and matter. Input vectors, $z_{n \times 1} = (z_i)$, characteristically drive state vectors, $x_{n \times 1} = (x_i)$, from initial conditions, x_0 , through a sequence of changing transient states, $\frac{dx}{dt} \neq 0$, where \bar{x} is expected value, to a sequence of unchanging steady states, where $\frac{dx}{dt} = 0$. The states in compartment models represent storages (standing stocks) of the transferred substance. In these expressions, t is time and dt its differential. Outputs, $y_{n \times 1} = (y_i)$, are generated by dissipative processes that ultimately return the system to equilibrium, $dx/dt = 0$, if inputs are zeroed, $z = 0$.

A matrix differential equation describing system dynamics can be formulated in terms of the three flow categories: inputs (z), outputs (y), and interior flows (F):

$$\frac{dx}{dt} = F \cdot 1 + z. \quad (1)$$

Here, $F_{n \times n} = (f_{ij})$, and $1_{n \times 1}$ is a vector of ones. In F , $f_{ij} \geq 0$ is the flow from compartment i to j for $i \neq j$, and when $i = j$, $f_{ii} = -T_i$, the throughflow, or total flow, at i . If a link, $a_{ij} = 1$, exists in a qualitative food web, then corresponding flow in a quantitative counterpart model is positive, $f_{ij} > 0$; if $a_{ij} = 0$ then $f_{ij} = 0$ also. A term in each T_i is that compartment’s dissipating output, y_i , which thus becomes incorporated in the principal diagonal elements, f_{ii} , of F . Therefore, in effect the term $F \cdot 1$ of equation (1) is dissipative, and offset by the input term, $z \geq 0$, which provides the impetus for change. In general, F is considered empirical; it becomes a linear dynamical process when all the flows are formulated as fractions (c_{ij}) of the donating member of each interacting compartment pair: $f_{ij} = c_{ij} \cdot x_i$. Then, equation (1) becomes:

$$\frac{dx}{dt} = C \cdot x + z, \quad (2)$$

where $C_{n \times n} = (c_{ij})$ is the well-known Jacobian matrix of population and community ecology. By the linear system decomposition property, the solution of this equation can be partitioned into a *zero-input (free) response*, and a *zero-state (forced) response*. In simulations for this investigation we will begin our study systems always at $x_0 = 0$ and generate forced responses for comparative purposes.

For simulation of study networks we used a dynamic web-based simulation and network analysis software, *EcoNet 2.1 Beta*, available at <http://eco.engr.uga.edu/> (Kazanci, 2007).

Network analysis was performed based on the final state of the simulation solution when systems reached a static steady state ($dx/dt=0$, when inputs and outputs become equal).

The simulation flow type was based on donor-controlled mass-action kinetics. Thus, the rate of the flow f_{ij} is computed by *EcoNet* as the product of the flow coefficient c_{ij} and the stock value x_i of the originating compartment i . The flow from i to j is $f_{ij} = c_{ij} \times x_i$. A differential mass-energy balance equation for donor-controlled flow type is as follows:

$$\frac{dx_i}{dt} = z_i + \sum_{j(\neq i)} c_{ji} \times x_j - \sum_{i(\neq j)} c_{ij} \times x_i - y_i, \quad (3)$$

where z_i and y_i are boundary inputs and outputs, respectively.

For a more comprehensive introduction to simulation and network analysis in *EcoNet* refer to <http://eco.engr.uga.edu/DOC/econet1.html>, Kazanci (2007), and Schramski et al. (2010).

Assessment of Network Measures

As stated above *EcoNet* drives the system from the given initial conditions to steady state and outputs the ENA measures based on the final state of the solution. The assessed indices are fully documented in literature, but brief descriptions and abbreviations are provided below.

Link Density (LD) is the ratio of the number of links (L) to network size (number of nodes N) (Gardner and Ashby, 1970; May, 1972, 1973; Cohen et al., 1990; Bersier and Sugihara, 1997):

$$LD = L / N. \quad (4)$$

Connectance (C) is the ratio of actual to possible links (Gardner and Ashby, 1970; May, 1972, 1973; Cohen, 1978; Cohen and Briand, 1984; Cohen et al., 1990):

$$C = L / N^2. \quad (5)$$

Total System Throughflow (TST) – sum of compartment throughflows (total amount of flows within a network); dependent on ecosystem structure (Hannon, 1973; Finn, 1976; Han, 1997):

$$TST = \sum T_i, \quad (6)$$

where T_i is the total amount of flow through compartment $i=1, \dots, n$.

Finn Cycling Index (FCI) – fraction of total system throughflow that cycles (Finn, 1976; 1980):

$$FCI = TST_c / TST, \quad (7)$$

where TST_c , the cycled portion, is the weighted sum of cycling efficiencies of all compartments (Kazanci et al., 2009):

$$TST_c = C_1 T_1 + C_2 T_2 + \dots + C_n T_n. \quad (8)$$

Cycling efficiency is $C_i = n_{ii} - 1/n_{ii}$, where n_{ii} is the number of times a flow quantity will return to i before being lost from the system (Finn, 1976).

Indirect Effects Index (IE) – amount of flow that occurs over indirect versus direct connections (Higashi and Patten, 1986, 1989).

$$IE = \sum (N - I - G)z / \sum Gz, \quad (9)$$

N is the dimensionless integral (boundary + direct + indirect) flow matrix:

$$N = I + G^1 + G^2 + \dots + G^m + \dots = (I - G)^{-1} \quad (10)$$

G is the matrix of dimensionless direct flow intensities from i to j :

$$G = (g_{ij}) = (f_{ij}/T_i), \quad (11)$$

where T_i is the total amount of flow through compartment i ,

$I = G^0$ is the boundary input flow intensity; as stated above G^1 is the direct flow intensity matrix, and G^m ($m=2, \dots, \infty$) are the indirect flow intensity matrices (fractions of boundary flows that travel from node i to j over all pathways of lengths m).

The integral matrix N multiplied by boundary input vector z returns the throughflow vector: $T=Nz$.

Synergism Index (SI) – benefit–cost ratio (b/c) (Patten, 1991, 1992) of total positive utility $\sum(+U)$ to total negative utility $\sum(-U)$ in the system specifying pairwise compartment relations (Patten, 1991, 1992; Fath and Patten, 1998):

$$SI = |b/c| = |\sum(U^+) / \sum(U^-)|, \quad (12)$$

where U^+ and U^- are positive and negative partition matrices of the dimensionless integral (boundary + direct + indirect) utility matrix U (Patten, 1991, 1992):

$$U = I + D^1 + D^2 + \dots + D^m + \dots = (I - D)^{-1} \quad (13)$$

D is a direct utility matrix (net-flow intensity matrix) where:

$$D = (d_{ij}) = ((f_{ij} - f_{ji}) / T_i), \quad (14)$$

where d_{ij} can be positive or negative ($-1 \leq d_{ij} \leq 1$) as it represents the direct utility between compartments j and i (net-flow between j and i is expressed relative to the total amount of flow through compartment i (T_i)); $I = D^0$ is the initial intensive utility input matrix; and D^m ($m = 2, \dots, \infty$) are the indirect utilities corresponding to the flows of the same power.

Mutualism Index (MI) – ratio of number of positive (+) to negative (–) signs in network utility analysis matrices specifying kinds of pairwise interactions (Patten, 1991, 1992):

$$MI = \sum \text{sign}(U^+) / \sum \text{sign}(U^-), \quad (15)$$

where U , U^+ and U^- are as described above (Patten, 1991, 1992).

Ascendency (AS) – degree of network development that includes average mutual information (AMI) and total system throughflow (TST) (Ulanowicz, 1986, 1997):

$$AS = TST \times AMI, \quad (16)$$

where AMI (bits) is the degree of organization with which the exchanges between compartments are processed:

$$AMI = \sum p(T_{ij}) \times \log_2[\{p(T_{ij}) / p(T_j)\} / p(T_i)], \quad (17)$$

where T_{ij} is the flow from j to i ;

$p(T_{ij})$ is the joint probability given by:

$$p(T_{ij}) = T_{ij} / TST, p(T_i) = \sum_j p(T_{ij}), \text{ and } p(T_j) = \sum_i p(T_{ij}). \quad (18)$$

Full Development Capacity (DC) – network flow organization, the upper bound of ascendancy. It is calculated as the product of total system throughflow (TST) by diversity of flow structure (H_f) estimated using the Shannon (1948) information formula (Ulanowicz, 1986):

$$DC = TST \times H_f, \quad (19)$$

where Shannon flow diversity H_f is based on the individual joint probabilities of flows from each species j to each species i :

$$H_f = \sum (-p(T_{ij}) \times \log_2(p(T_{ij}))), \quad (20)$$

where T_{ij} is the flow from j to i ; and $p(T_{ij})$ is as stated above.

Network Aggradation Index (AI) – the multiplier effect (Samuelson, 1948); the average path length (Finn, 1976), the flow multiplying ability (Han, 1997), the average number of times a unit of input flow passes through the system before exiting (Patten and Fath, 1998; Fath and Patten, 2001; Ulanowicz et al., 2006):

$$AI = TST / \sum z_i, \quad (21)$$

where z_i is a boundary input of compartment $i = 1, \dots, n$, and TST is total system throughflow.

While our focus is on the whole network variables summarized above, we incorporate **system size N** (number of nodes), **number of links L** ($\sum_{i \text{ or } j} a_{ij}$), and **number of trophic classes CI** as additional network measures appropriate to comparative interpretations.

Statistical data-analysis

We use the Spearman Rank Order Correlation test in order to assess interrelationships among the network properties under investigation. Spearman correlation coefficients among variables have been used as input in Principal Component (PC) Analysis in order to achieve more interpretable simple structure underlying our dataset. The PC analysis reduces our data into a number of factors (principal components). Each consecutive factor is defined to maximize the variability that is not captured by the preceding factor and all consecutive factors are independent of each other (orthogonal). The decision of when to stop extracting factors basically depends on when there is only very little "random" variability left. To extract number of factors we use the Kaiser (1960) criterion, which is based on retaining only factors with eigenvalues greater than 1. According to confirmatory factor analysis, loadings equal or above 0.7 confirm that independent variables identified are represented by a particular PC factor on the rationale that the 0.7 level corresponds to about half the variance in the indicator being explained by the factor.

Table of Notations

The following abbreviations and statistical notations will be employed in subsequent sections:

Symbol	Description
1	2
General:	
CA	Comparative Analysis
Ecological Network Analysis:	
ENA	Ecological Network Analysis
N	Network size
L	Number of links
CI	Number of trophic classes
LD	Link density

1	2
C	Connectance
TST	Total System Throughflow
FCI	Finn Cycling Index
IE	Indirect Effects Index
SI	Synergism Index
MI	Mutualism Index
AS	Ascendency
DC	Development Capacity
AI	Aggradation Index
Statistical:	
CV	Coefficient of Variation
SD	Standard Deviation
m	Mean Value of a Variable under Investigation
r_s	Spearman's Rank-Order Correlation Coefficient
PCA	Principal Component Analysis
PC	Principal Component (latent factor)
<i>l</i>	Factor (principal component) Loadings (coefficients)

RESULTS

Network Measures: Descriptive Statistics

The 31 empirical pastoral food webs of our study exhibit a range of *sizes* $41 \leq N \leq 135$ ($m = 82$; $SD = 19$; $CV = 24$) and *link numbers* $98 \leq L \leq 977$ ($m = 419$; $SD = 207$; $CV = 49$ %). In general we found 494 compartments and 14525 feeding links between them throughout 31 researched pastoral food webs within the whole study area of Chernivtsi Region.

Link density values vary ($CV = 28$ %) between a low of 2.00 and a high of 7.58 with the mean $m = 4.9$ ($SD = 1.38$) throughout the study 31 food webs. The minimum, maximum and mean values of the network *connectance* **C** within the assessed food webs are $0.03 \leq C \leq 0.09$, $m = 0.06$ ($SD = 0.01$), and $CV = 20$ %.

The range of values of *Finn cycling index* tends to be small all over the 31 food webs ($0.03 \leq FCI \leq 0.1$; $m = 0.05$, $SD = 0.02$; $CV = 37$ %). The *aggradation* measure shows small variability ($CV = 9$ %) and the following descriptive statistics: $2.23 \leq AI \leq 3.38$; $m = 2.82$ ($SD = 0.26$).

All the pastoral food webs show that indirect flows are greater than direct flows by *indirect effects indexes* being greater than one ($1.05 \leq IEI \leq 2.12$) with the mean $m = 1.47$ ($SD = 0.25$) and variability $CV = 18$ %.

Across the Chernivtsi Region study area *total system throughflow* changes in values from 109 to 426 with the mean $m = 232$ ($SD = 67$; $CV = 29$ %). *Ascendency* and *development capacity* vary ($CV = 31$ % for both) in their values all over the study area as follows: $158 \leq AS \leq 728$; $m = 377$, ($SD = 117$) and $441 \leq DC \leq 2017$; $m = 1046$, ($SD = 326$), respectively.

Network *synergism* values show small variability ($CV = 6$ %), ranging $1.6 \leq SI \leq 2.1$, mean $m = 1.8$, ($SD = 0.1$). However, network *mutualism* varies $CV = 25$ % with values ranging from 0.37 to 0.98 ($m = 0.73$; $SD = 0.18$).

The range and variability of network properties of the study area (Chernivtsi Region) are summarized in Tables 1 and 2.

Based on the method of regular equivalence, the trophic compartments in our study food webs are aggregated into the following 15 trophic classes: (1) Gazing Plants; (2) Grazing-Tolerant Plants; (3) Pollen and Nectar; (4) Cattle; (5) Herbivorous Insects; (6) Pollinators; (7) Bloodsucking Parasites of Cattle; (8) Carnivorous Insects; (9) Omnivorous Insects; (10) Nonspecific Insects (consumed in other ecosystems);

(11) Decomposers; (12) Plant Litter; (13) Animal Litter; (14) Cattle Excrement; and (15) Detritus. The variation in number of trophic classes *CI* within the study networks is summarized in Tables 1 and 2.

Table 1

Network properties of the 31 pastoral food webs of this study													
Study pastures	Network Measures												
	N	L	CI	LD	C	TST	FCI	IE	AS	DC	AI	SI	MI
Vikno	86	496	15	5.77	0.07	287.4	0.09	1.86	432.1	1251.7	3.34	1.80	0.81
Kostrzyzhivka	41	147	15	3.59	0.09	108.6	0.05	1.30	157.8	441.4	2.65	2.02	0.87
Luzhany	69	300	13	4.35	0.06	178.8	0.05	1.31	283.8	794.8	2.59	1.80	0.62
Polyana	80	396	13	4.95	0.06	202.3	0.03	1.18	337.3	930.5	2.53	1.74	0.86
Chornyvka	69	362	15	5.25	0.08	202.1	0.06	1.47	310.1	877.4	2.93	1.79	0.70
Zelena	66	295	14	4.47	0.07	176.8	0.06	1.45	279.7	780.5	2.68	1.88	0.81
Vovchynec	66	299	15	4.83	0.07	202.5	0.10	2.03	284.9	854.5	3.07	1.91	0.74
Stavchany	66	319	15	4.53	0.07	187.3	0.08	1.51	271.2	801.0	2.84	1.94	0.85
Grushivcy	83	286	13	3.45	0.04	229.8	0.04	1.47	399.9	1051.2	2.77	1.80	0.50
Myhalkove	68	255	14	3.75	0.06	197.2	0.07	1.70	318.9	867.5	2.90	1.83	0.81
Magala	69	310	14	4.49	0.07	200.7	0.05	1.35	309.9	867.1	2.91	1.78	0.59
Zarozhany	63	250	12	3.97	0.06	163.4	0.03	1.24	272.1	730.0	2.59	1.81	0.66
Temavka	75	399	15	5.32	0.07	209.9	0.05	1.43	345.1	944.3	2.80	1.75	0.98
Gorbovo	135	977	14	7.24	0.05	425.7	0.07	1.75	728.3	2017.1	3.15	1.65	0.98
Valya Kuzmyna	107	773	13	7.22	0.07	299.3	0.05	1.41	500.6	1404.8	2.80	1.69	0.94
Myhalcha	84	512	15	6.10	0.07	284.2	0.09	2.12	431.0	1251.0	3.38	1.83	0.88
Chervona-Dibrova	102	665	15	6.52	0.06	295.9	0.04	1.32	485.2	1358.5	2.90	1.64	0.81
Dubovo	75	311	15	4.15	0.06	239.8	0.07	1.71	374.7	1036.9	3.20	1.80	0.70
Kostynsy	97	641	15	6.61	0.07	293.7	0.06	1.47	463.2	1320.0	3.03	1.72	0.97
Brusnyca	88	475	14	5.40	0.06	240.8	0.06	1.45	383.1	1093.7	2.74	1.76	0.86
Chereshenka	80	460	14	5.75	0.07	243.1	0.07	1.74	391.6	1085.1	3.04	1.83	0.97
Banyliv Pidgimyj	75	297	14	3.96	0.05	190.8	0.03	1.26	316.0	864.8	2.54	1.82	0.59
Krasnoyiisk	66	242	14	3.67	0.06	170.4	0.03	1.21	284.7	760.3	2.58	1.74	0.54
Staryj Vovchynec	93	496	14	5.33	0.06	252.3	0.03	1.27	434.0	1173.6	2.71	1.69	0.71
Stebnyk	49	98	12	2.00	0.04	109.4	0.03	1.05	178.6	476.8	2.23	2.10	0.57
Lopushna	102	686	14	6.73	0.07	288.2	0.05	1.45	489.1	1345.4	2.83	1.72	0.96
Dolyshnij Shepit	113	856	15	7.58	0.07	342.6	0.06	1.62	582.9	1604.6	3.03	1.69	0.71
Ust-Putyla	84	274	13	3.26	0.04	218.7	0.03	1.23	373.3	998.1	2.60	1.75	0.38
Selatyn	104	540	15	5.19	0.05	318.8	0.04	1.48	524.9	1444.2	3.07	1.71	0.44
Shepit	77	275	13	3.57	0.05	192.7	0.03	1.32	319.0	877.4	2.50	1.90	0.50
Percalab	96	285	14	2.97	0.03	249.0	0.04	1.31	417.4	1146.5	2.59	1.75	0.37

Table 2

Range and variability of network properties of the 31 pastoral food webs of this study					
Network Measures	Descriptive Statistics, n = 31				
	<i>m</i>	<i>minimum</i>	<i>maximum</i>	<i>SD</i>	<i>CV, %</i>
N	81.5	41	135	19.4	24
L	418.6	98	977	207.1	49
CI	14.1	12	15	0.93	7
LD	4.90	2.00	7.58	1.38	28
C	0.06	0.03	0.09	0.01	20
TST	232.3	108.6	425.7	67.1	29
FCI	0.05	0.03	0.10	0.02	38
IE	1.47	1.05	2.12	0.25	17
AS	376.8	157.8	728.3	117.3	31
DC	1046.8	441.4	2017.1	326.6	31
AI	2.82	2.23	3.38	0.26	9
SI	1.79	1.64	2.10	0.10	6
MI	0.73	0.37	0.98	0.18	25

Network Measures: Correlations among Variables

Table 3 captures the statistically significant pairwise Spearman (r_s) correlations among system-wide properties that are in interest here. In general, almost all pairwise comparisons among network properties are significantly correlated ($P < 0.05$), with an overall distribution of correlation coefficients $0.37 \leq r_s \leq 0.99$. Pairwise relations among **TST** and **DC**, and also among **DC** and **AS**, approach the perfect Spearman correlation ($r_s = 0.99$). Recalling the definitions of **DC** and **AS** variables, it is clear they both are driven by **TST**, in fact they are scaled **TST**'s, and that explains the near-perfect monotonically increasing relation between them.

Our study shows that 12 of the 13 study network indices are positively correlated to each other and negatively correlated to the network synergism index **SI**, which is a benefit/cost ratio measure in a network. This reveals that **SI** goes counter to other network properties in expressing the nature of network organization.

The sensitivity of system-wide properties to each other can be expressed quantitatively by the number of statistically significant pairwise interrelations (n_k) and qualitatively by the average correlation coefficient (ave_k) of the statistically significant pairwise interrelations (Table 4).

Link density has the largest number of statistically significant relations (it is correlated with each of the studied network indices). It is followed by the network **aggradation** measure, **number of links**, and **indirect effects** index. Less sensitive are the following network measures: **connectance**, **synergism**, **mutualism**, and number of **trophic classes** (each of them correlated with 6 of 13 possible network measures) (Table 4).

Qualitatively the network properties' sensitivity (ave) in the pairwise interrelations to each other is in the following descending order (Table 4):

$$N > TST > DC > AS > SI > L > LD > FCI > AI > MI > CI > IE > C$$

Clustering of the results of non-parametric correlation shows the degrees of similarity among the study network measures based on their pairwise interrelations (Fig. 2). In both cases **TST**, **AS**, and **DC** are joined as the most similar of the network measures assessed. As stated previously, they have almost perfect monotonically increasing correlations among each other. Thus, they form the smallest distance subcluster, which is chained by the **network size** measure. The next closest distance subcluster is formed by the number of **trophic links** and **link density** measure and it is joining the previous subclusters. Separate subclusters are formed by the **indirect effects** measure, **network aggradation** and **Finn's cycling index**. They are chained by a subcluster of **trophic classes' number**, which, in particular, is joined by the network **mutualism index** and **connectance** measure with the larger clustering distance. Network **synergism** demonstrates the longest distance (the smallest similarity) in a linkage hierarchy of the clustering dendrograms.

Table 4

Sensitivity of each network property to the others under study based on the statistically significant pairwise non-parametric (r_s) correlations among them

Network property k	Sensitivity of each network property k to the others under study ($n = 13$) based on the statistically significant pairwise correlations among them	
	<i>quantitative sensitivity</i> (n_k)*	<i>qualitative sensitivity</i> (ave_k)**
LD	12	0.63
AI	11	0.6
L	11	0.68
IE	10	0.54
TST	8	0.79
DC	8	0.78
AS	8	0.76
N	7	0.79
FCI	7	0.62
C	6	0.53
SI	6	0.7
MI	6	0.55
CI	6	0.55

* *quantitative sensitivity* (n_k) of a k^{th} network property expresses the total number of the pairwise statistically significant correlations of k with the other study network measures ($n = 13$).

** *qualitative sensitivity* (ave_k) of the k^{th} network property shows an average correlation coefficient of the pairwise statistically significant interrelations of k with the other study network measures ($n = 13$).

Principal Component Analysis of nonparametric correlations among the study network properties results in a three-factor solution which explains 91 % of the variation in our data (Figure 3, *a*). The outputs of PCA are factor loadings (Figure 3, *b*), which represent the weights and correlations between each ENA variable and the extracted principal components. Loading-plot projection of the ENA variables on the factor-plane shows the extracted factors' dimensionalities and associated with them network measures (Figure 3, *c*).

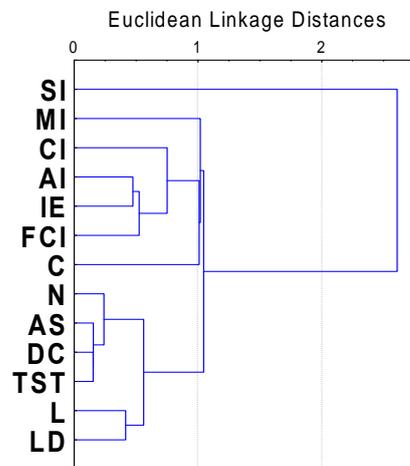
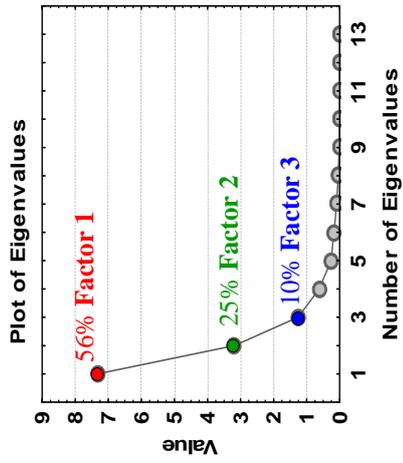
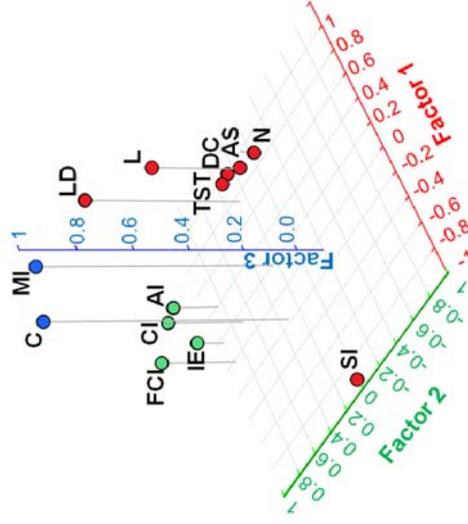


Fig. 2. Clustering dendrogram showing clusters of network measures according to the degree of their pairwise non-parametric correlation

The main principal component (Factor 1) accounts for 56 % of the total variance and is driven by network parameters whose behaviors are highly affected by the structural patterns of the networks. This is because the principal variable defining dimensionality of



Factor Loadings (I)			
(Rotation: Varimax normalized)			
Extraction: Principal components			
Variables:	Factor 1	Factor 2	Factor 3
<i>Network Measures</i>			
L	0.81	0.29	0.44
N	0.98	0.07	-0.02
LD	0.66	0.31	0.65
C	-0.21	0.41	0.82
TST	0.93	0.33	0.06
FCI	-0.01	0.88	0.36
IE	0.19	0.94	0.11
AS	0.97	0.20	-0.01
DC	0.96	0.26	0.03
AI	0.36	0.87	0.18
SI	-0.87	0.24	-0.10
MI	0.20	0.23	0.86
CI	0.10	0.71	0.29



a

b

c

Fig. 3. **Outputs of Principal Component Analysis of the network measures:**

a – plot of eigenvalues with the proportion of total variance (%) extracted by the factor. Number of factors extracted successively and account for less variance overall;

b – factor loadings, which are the weights and correlations between each variable and the factor underlying the data set;

c – loading plot projection of the variables on the factor plane

Factor 1 is network size N which has the highest Factor 1 loading ($l_N = 0.98$). More clearly it can be tracked from loading-plot projections of the ENA variables onto the correlation cycle on the factor plane with the axes of the extracted factor pairwise (Figure 4). The further a point is from the origin of the correlation circle, the greater the correlation of the corresponding variable with the factor axes.

Interrelations between Network Measures: Multivariate Analysis

Ascendency AS , development capacity DC and total system throughflow TST join network size N in reflecting mainly the variations in the latent (unobserved) first principal component (factor loadings are respectively: $l_{AC} = 0.97$, $l_{DC} = 0.96$ and $l_{TST} = 0.93$). All of these three measures are extensive, that is dimensional, network properties, and they are directly dependent on network size (Table 3).

Network synergism SI shows high negative association with other elements in the first latent factor, that is, it is negatively correlated with the other Factor 1 variables (Table 3 and Figure 3, *b*).

Feeding link number L is also an attribute of Factor 1 ($l_L = 0.81$). But not uniquely, as it is also represented in Factor 3 as well (Figure 3, *b*), which explains almost 20 % of the variance in the L measure.

Feeding link density LD measure is secondary for both, factor 1 and factor 3, as its variance is almost equally sheared among these two latent factors (44 % of LD 's variance is explained by factor 1 and 42 % – by factor 2).

The uniqueness of the L and LD measures is expressed by the plot of their loadings into the correlation cycle as the points that approach the edge of the axis of the other than first latent factor (Figure 4, *b, c*).

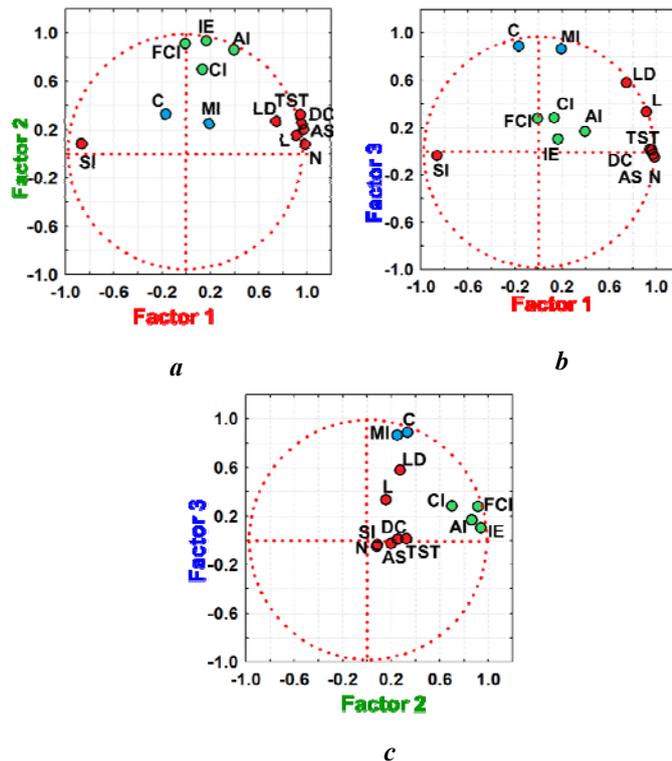


Fig. 4. Loading plot projection of the network measures on the factor-plane onto the correlation cycle, with the pair of factor axes. The further a point is from the origin of the circle, the greater the correlation of the corresponding variable with the factor axes. Loading plot projections are respectively for the pair of factor axes as follows:

a – for Factor 1 and Factor 2; *b* – for Factor 1 and Factor 3; *c* – for Factor 2 and Factor 3

The second principal component (Factor 2) accounts for 25 % of the data variance. It reflects the joint variations of 4 of the 13 studied network measures. The driving variable in defining the dimensionality of Factor 2 is a network measure of indirect effects dominance **IE** ($l_{IE} = 0.94$). Also network cycling measures, such as Finn cycling index **FCI** ($l_{FCI} = 0.88$) and network aggradation index **AI** ($l_{AI} = 0.87$). In addition, number of trophic classes **CI** ($l_{CI} = 0.71$) shows high association with Factor 2.

On the other hand **FCI**, **AI** and **CI** are not highly unique in respect of their variance been explained by second latent factor extracted by PCA from our data (Figure 4, *a*, *c*), namely: almost 13 % of **FCI** value variance and 8 % of **CI** variability is explained by Factor 3, while the 13 % of **AI** data variance is reflected by the first principal component.

Variations in two of the 13 network measures, namely mutualism index **MI** and connectance **C**, are mainly reflected by the third latent factor, which accounts for 10 % of the variability in our data. Both these measures are highly associated with Factor 3 ($l_{MI} = 0.86$; $l_C = 0.82$), but they are also sheared in respect of their variance being explained by other latent factors, as follows: 17 % of connectance variance is explained by Factor 2, while 8 % of network mutualism variance is captured equally by the first and second latent factors (Figure 4, *a*).

DISCUSSION

The above results show that the network measures under investigation are highly intercorrelated amongst each other. Based on this the 13 ENA output variables can be reduced to the three latent factors that account for the main meaningful variability underlying our dataset. In this section we address the explanation of network measure relations within each of extracted factors.

Seven (**N**, **TST**, **AS**, **DC**, **SI**, **L**, and **LD**) of thirteen network measures under study are merged by the main principal component (that is Factor 1), where **network size** shows to be the central defining variable. Network size is measured as the number of compartments. It is fundamental in network organization since compartments and links associated with them explicitly define network topology.

From an ecosystem prospective, the multiplicity of species is considered as a barrier against external stresses (MacArthur, 1955). The diversity–stability concept suggests increasing ecosystem stability with increasing species diversity. The numerous compartments of higher diversity maintain basic ecosystem functions by giving options to replace extinct system elements from the assortment of multiple species.

The next three network measures in defining the first latent factor are **total system throughflow**, **ascendency** and **development capacity**. It shows them to be highly determined by network size. This is consistent with the previous developments, and also the following ones we would like to address.

According to Han (1997) total system throughflow, measured here as the sum of compartment throughflows, is explicitly dependent on ecosystem structure since it counts each flow element each time it passes through a compartment. Finn (1976) also found **TST** to be highly sensitive to the number of compartments in the system model.

From the other side, network **ascendency** measure (**AS**) incorporates aspects of both network size and the constitutive nature of the system. Ulanowicz (1986) indicated that an increase in **AS** is a quantitative sign that the system is growing and developing.

Network **development capacity**, measured here by **DC**, is the upper bound of ascendency and depends on **TST** and the flow structure. According to Ulanowicz (1986), **DC** represents maximal system organization expressed in terms of network flows.

All these three measures (**TST**, **AS** and **DC**) are extensive or dimensional network properties. Therefore it is not surprising that the behaviors of these measures are highly affected by the **structural patterns** of the networks.

Network **synergism**, **SI**, an intensive measure, is also highly represented in Factor 1, showing it to be strongly affected by structural patterns of the study food webs. In our data

intensive synergism decreases with the increase of all other network measures. We previously showed this in a comparison of seven mountain pastoral food webs (Buzhdygan et al., 2012b). Fath (2004), studying large-scale synthetic networks, also found the **SI** measure to be closely tied to structural pattern. In the present study the unit **SI** vector is positioned far away from the other network measures in the loading plot projection of the variables onto the factor plane (Figure 4). This means the influence of **SI** on the positioning of objects is dissimilar from all the other network properties. Moreover, **SI** is negatively correlated with the other properties. It is expected from network theory (Fath and Patten, 1998) that synergism of ecological systems will increase with system development and scale. These authors suggest that the potential for network synergism is especially high in sparsely connected networks since zero elements in the direct transaction matrix fill in with non-zero indirect relations.

Patten (2013), studying a sequence of simple models with 1–10 compartments, of progressively increasing complexity (N and C), showed that *extensive* network synergism (*intensive SI* weighted by *TST*) increases with system size N and connectivity C . **SI** increased early in the complexification sequence, but after mid-size was reached and cycling began it then subsequently decreased, giving diminishing returns. It is the latter that are reflected in the negative correlations of **SI** with the other variables in the present study of fully matured food webs (Table 3, Figure 3, *b*). Using synthesized large-scale «cyber-ecosystem» networks, Fath (2004) also found that **SI** values decrease with system size. These and Patten's (2013) results with synthetic models are consistent with our present findings for real empirically described food web systems.

Feeding link number **L** and link density **LD** are also attributes in the first latent factor. It is not surprising that these variables reflect the structural patterns of the study networks as both are known as network topology properties. On the other hand, both are not unique for Factor 1 as they define also the other latent factors. This is explained by their high sensitivity in interrelations to the other network properties, as follows: **L** is correlated with 11 of 12 network variables, while **LD** is correlated with each of the 12 under study. According to network literature, link number and link density are expected to be positive system stability measures. Number of links, **L**, represents the number of all feeding connections among trophic compartments. Odum (1953) stated the amount of choice energy has when flowing through a trophic network is a driver of system persistence. Number of links can be considered as Odum's number of choices for energy to move within the network. According with Puzachenko (1989), feeding links are the ecosystem tools to resist disturbances. On the other hand link density, **LD**, measured here as the number of links per node, shows how much the species contribute to the distribution of energy, matter and information in the system. It is a degree of connectivity between compartments in the network and one of the system complexity measures. **LD** reflects, potentially, how stable a food web may be (Link, 2002). Link density is one of the key elements in the complexity-stability concept. Furthermore, due to Rossberg et al. (2006), link density can be understood as a measure for the average trophic niche breadth in a community. Our findings show both **L** and **LD** to be negatively related to network synergism, **SI**, and positively correlated to all other network properties.

Several studies generalized the idea that link density **LD** tends to remain constant across networks of varying scale (Yodzis, 1980; Cohen and Briand, 1984; Sugihara et al., 1989). But other researchers do not confirm this (Winemiller, 1990; Martinez, 1992; Havens, 1992). Our analyses do not support scale-invariance of **LD** across the studied food webs.

Higashi and Patten (1986, 1989) and Patten (1984) postulated that indirect effects, **IE**, are dominant as a general property of all well connected ecological networks. Cycling is one of the network properties that contribute to this. Our present findings are consistent with this. **IE** is the defining property of the second latent factor, which also network cycling, **FCI** and aggradation, **AI**. Higashi and Patten (1989) and Patten (1991) showed that system cycling (measured by **FCI**) increases the indirect effects dominance (**IE**). The

Finn cycling index quantifies the importance of cycling (Finn, 1976). It measures the fraction of total system throughflow that cycles and is affected by lumping of compartments that exchange flows. The aggradation *AI*, also known as average path length, distinguishes differences between flows in various ecosystems and, because cycles have infinite length, reflects cycling. Han (1997) as well suggested an aggradation index to express flow multiplying ability and cycling. Borrett and Osidele (2007) concluded that cycling plays a central role in the Finn cycling index, ratio of indirect-to-direct flows, and network aggradation. Therefore, it makes sense that dominant indirect effects *IE*, cycling *FCI*, and network aggradation *AI*, are all attributable to a single PCA factor, Factor 2.

From the other side, Finn (1976) suggests that the aggradation measure might also express the difference in number of trophic groups while comparing the ecosystems of similar structure and on the same level of organization, which our networks are. This may explain the high positive correlation of number of trophic classes *CI* with the aggradation measure and also its strong association with Factor 2. Finn (1980) indicates that separating out similar species in a model should have no effect on cycling measures. We consider that the loss of trophic classes, representing distinct feeding roles, might intensively effect cycling properties as well as related indirect effects. We pointed out above that multiplicity of compartments (system size *N*) serves to provide options system needs to survive disturbances by replacing extinct species with others. In pastoral food webs commonly grazed plants cannot be replaced by grazing-tolerant ones because cattle would not feed on them. Then, the community would lose its main consumers (cattle) that determine the system to be a pasture. Thus, besides compartment number, the number of trophic classes also reflects the community ability to maintain basic ecosystem functions.

Some theoretical studies report a hyperbolic decline in network connectance *C* with increasing number of compartments *N* (reviewed by Fonseca and John, 1996). By contrast, Martinez (1992) found that connectance of different-sized food webs was almost constant. Several comparative analyses of empirical food webs show no clear association between *C* and network size (Martinez, 1991; Christian and Luczkovich, 1999; Garlaschelli, 2004). Our results confirm this «constant connectance hypothesis», showing no clear interrelations between network connectance and network size, as it appears to be a scale-invariant property. Despite the fact that connectance *C* and link density *LD* are both measures of system complexity, we found that the last measure is much more sensitive in relation to the other network properties. Recalling the definitions of link density ($LD = L/N$) and connectance ($C = L/N^2$) it is clear that the resolution of *N* causes the smaller range of connectance values across the study food webs, which may be the reason for the small sensitivity of *C*. Such a scale invariance of network connectance measure and low sensitivity to the behavior of other network properties probably causes in the principal component analysis the formation of the separate latent Factor 3, which is driven by *C* and also defined by network mutualism *MI*. Network mutualism (Patten, 1991; Fath, 2007) has received little attention and comparisons of its relationships with the other whole-system properties are quite rare. While comparing the seven mountain pastoral food webs Buzhdygan et al. (2012b) show there are no significant correlations of *MI* with other network measures, except degree of connectance *C*. The present comparison of a larger number and wider range of trophic networks reveals that network mutualism is significantly positively correlated with number *L* and density *LD* of links, and also with the cycling measures, *FCI* and *AI*. Our data show that network mutualism is related to other aspects of network complexity than just simply size and number of feeding links, as the contribution of species to the distribution of network currency (energy, matter, information) reveals to be the most effective on the behavior of network mutualism measure.

SUMMARY AND CONCLUSIONS

Our results show that the 13 network measures under investigation are highly intercorrelated amongst each other, which suggests they express in different ways a general

intuition about the nature of network organization as revealed by their PCA aggregate into three latent factors.

The first latent factor, for which network size appears to be the central defining variable, includes seven of the 13 measures – *N*, *L*, *LD*, *TST*, *AS*, *DC*, and *SI*. Network synergism *SI* is an anomalous variable in being negatively correlated to most of the other network properties which are positively correlated among themselves. The second latent factor is driven by dominant indirect effects *IE*, and also includes cycling measures *FCI* and *AI* and number of trophic classes *CI*.

The third factor includes mutualism *MI* and connectance *C*, the last appearing to be the driving variable. Our data also show that *MI* is more tied to the network complexity than simply to system scale or number of feeding links.

Finally, we conclude with the observation that ecological network analysis methods (NA) appear to have promise for providing new understanding of Complex Adaptive Hierarchical Systems (Patten et al., 2002a, b) of landscape scale, such as the widespread pastoral ecosystems of Ukraine, and giving a quantitative and qualitative basis for their monitoring, prediction and management.

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REFERENCES

- Bastianoni, S., Marchettini, N., 1997. Emergy/exergy ratio as a measure of the level of organization of systems. *Ecological Modelling* 99, 33–40.
- Batagelj, V., Mrvar, A., 2010. Pajek. <http://vlado.fmf.uni-lj.si/pub/networks/pajek/>
- Bersier, L.-F., Sugihara, G., 1997. Scaling regions for food web properties. *Proc. Natl Acad. Sci. USA* 94, 1247–1251.
- Borgatti, S. P., Everett, M. G., 1993. Two algorithms for computing regular equivalence. *Social Networks* 15, 361–376.
- Borgatti, S. P., Everett, M. G., Freeman, L. C., 2002. UCINET VI. Software for Social Network Analysis. Natick, Analytic Technologies.
- Borrett, S. R., 2013. Characterization of Topics in Network Ecology and the Community that Studies Them. Symposium in Honor of Bernard C. Patten «Systems Ecology: A Network Perspective & Retrospective». April 12–15, 2013. Athens, Georgia, USA.
- Borrett, S. R., Fath, B. D., Patten, B. C., 2007. Functional integration of ecological networks through pathway proliferation. *Journal of theoretical biology* 245, 98–111.
- Borrett, S. R., Osidele, O. O., 2007. Environ indicator sensitivity to flux uncertainty in a phosphorus model of Lake Sidney Lanier, USA. *Ecological Modelling* 200, 371–383.
- Borrett, S. R., Salas, A. K., 2010. Evidence for resource homogenization in 50 trophic ecosystem networks. *Ecological Modelling* 221, 1710–1716.
- Buzhdygan, O. Y., Patten, B. C., Kazanci, C., Ma, Q., Rudenko, S. S., 2012 (a). Dynamical and system-wide properties of linear flow-quantified food webs. *Ecological Modelling* 245, 176–184.
- Buzhdygan, O. Y., Patten, B. C., Rudenko, S. S., 2012 (b). Trophic Network Analysis: Comparison of System-Wide Properties. In: Jordan, F., Jørgensen, S. E. (Eds.), *Models of the Ecological Hierarchy*. Elsevier, Oxford, UK, 181–199.
- Cheslak, E. F., Lamarra, V. A., 1981. The residence time of energy as a measure of ecological organization. In: Mitsch, W. J., Bossermann, R. W., Klopatek, J. M. (Eds.), *Energy and Ecological Modelling*. Amsterdam. Elsevier, 591–600.
- Christian, R. R., Luczkovich, J. J., 1999. Organizing and understanding a winter's seagrass food web network through effective trophic levels. *Ecological Modelling* 117, 99–124.
- Christian, R. R., Baird, D., Luczkovich, J., Johnson, J. C., Scharler, U. M., Ulanowicz, R. E., 2005. Role of network analysis in comparative ecosystem ecology of estuaries. In: Belgrano, A., Scharler, U. M., Dunne, J., Ulanowicz, R. E. (Eds.), *Aquatic Food Webs, An Ecosystem Approach*. Oxford University Press Inc., New York, pp. 25–40.
- Cohen, J. E., Briand, F., Newman, C. M., 1990. *Community food webs: data and theory*. Springer-Verlag, Berlin, Germany.

- Cohen, J. E., 1978. Food webs and niche space. Princeton University Press, Princeton, New Jersey, USA.
- Cohen, J. E., Briand, F., 1984. Trophic links of community food web. Proceedings of the National Academy of Sciences of the USA 81, 4105–4109.
- Fath, B. D., 2004. Network analysis applied to large-scale cyber-ecosystems. Ecological Modelling 171, 329–337.
- Fath, B. D., 2007. Network mutualism, positive community-level relations in ecosystems. Ecological Modelling 208, 56–67.
- Fath, B. D., Borrett, S. R., 2006. A MATLAB function for network environ analysis. Environ. Model. & Soft. 21, 375–405.
- Fath, B. D., Patten, B. C., 1998. Network synergism, emergence of positive relations in ecological systems. Ecological Modelling 107, 127–143.
- Fath, B. D., Patten, B. C., 1999. Review of the foundations of Network Environ Analysis. Ecosystems 2, 167–179.
- Fath, B. D., Patten, B. C., 2001. A progressive definition of network aggradation. In: Ulgiati, S., Brown, M. T., Giampietro, M., Herendeen, R. A., Mayumi, K. (Eds.), Proceedings of the Second International Workshop on Advances in Energy Studies, Exploring Supplies, Constraints and Strategies. May 23–27, 2000, Porto Venere, Italy, 551–562.
- Fath, B. D., Patten, B. C., Choi, J. S., 2001. Complementarity of ecological goal functions. Journal of theoretical biology 208, 493–506.
- Fath, B. D., Scharler, U. M., Ulanowicz, R. E., Hannon, B., 2007. Ecological network analysis: network construction. Ecological Modelling 208, 49–55.
- Finn, J. T., 1976. Measures of ecosystem structure and function derived from analysis of flows. Journal of theoretical biology 56, 363–80.
- Finn, J. T., 1980. Flow Analysis of Models of the Hubbard Brook Ecosystem. Ecology 61, 562–571.
- Fonseca, C. R., John, J. L., 1996. Connectance, a role for community allometry. Oikos 77, 353–358.
- Gardner, M. R., Ashby, W. R., 1970. Connectance of large (cybernetic) systems, critical values for stability. Nature 228, 784.
- Garlaschelli, D., 2004. Universality in food webs. The European Physical Journal B – Condensed Matter 38, 277–285.
- Han, B., 1997. On several measures concerning flow variables in ecosystems. Ecological Modelling 104, 289–302.
- Hannon, B., 1973. Structure of ecosystems. Journal of theoretical biology 41, 535–546.
- Havens, K. E., 1992. Scale and structure in natural food webs. Science 257, 1107–1109.
- Herendeen, R. A., 1981. Energy intensities in ecological and economic systems. Journal of theoretical biology 91, 607–620.
- Herendeen, R. A., 1989. Energy intensity, residence time, exergy, and ascendency in dynamic ecosystems. Ecological Modelling 48 (1–2), 19–44.
- Higashi, M., Patten, B. C., 1989. Dominance of indirect causality in ecosystems. The American Naturalist 133, 288–302.
- Higashi, M., Patten, B. C., 1986. Further aspects of the analysis of indirect effects in ecosystems. Ecological Modelling 31, 69–77.
- Johnson, S. C., 1967. Hierarchical clustering schemes. Psychometrika 32, 241–253.
- Jørgensen, S. E., 1994. Review and comparison of goal functions in systems ecology. Vie Milieu 44, 11–20.
- Jørgensen, S. E., 2002. Integration of Ecosystem Theories: A Pattern, third ed. Kluwer Academic Publishers, Dordrecht.
- Jørgensen, S. E., Mejer, H. F., 1979. A holistic approach to ecological modelling. Ecological Modelling 7, 169–189.
- Jørgensen, S. E., Patten, B. C., Straškraba, M., 1992. Ecosystems emerging: toward an ecology of complex systems in a complex future. Ecological Modelling 62, 1–27.
- Kaiser, H. F., 1960. The application of electronic computers to factor analysis. Educational and Psychological Measurement 20, 141–151.
- Kazanci, C., 2007. EcoNet: A new software for ecological modeling, simulation and network analysis. Ecological Modelling 208, 3–8.
- Kazanci, C., Matamba, L., Tollner, E. W., 2009. Cycling in ecosystems: An individual based approach. Ecological Modelling 220, 2908–2914.
- Lawler, L., 1978. A comment on randomly constructed model ecosystems. The American Naturalist 112, 445–447.
- Link, J. S. 2002. Does food web theory work for marine ecosystems? Marine Ecology Progress Series 230, 1–9.
- Lotka, A. J., 1922. Contribution to the energetics of evolution. Proceedings of the National Academy of Sciences of the United States of America 8, 147–151.
- Luczkovich, J. J., Borgatti, S. P., Johnson, J. C., Everett, M. G., 2003. Defining and Measuring Trophic Role Similarity in Food Webs Using Regular Equivalence. Journal of Theoretical Biology 220, 303–321.

- Martinez, N. D. 1992. Constant connectance in community food webs. *The American Naturalist* 139, 1208–1218.
- Martinez, N. D., 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecological Monographs* 61 (4), 367–392.
- May, R. M., 1972 Will a large complex system be stable? *Nature* 238, 413–414.
- May, R. M., 1973. Stability and complexity in model ecosystems. Princeton Univ. Press.
- McCann, K. S., 2000. The diversity-stability debate. *Nature* 405, 228–33.
- Morowitz, H. J., 1968. Energy Flow in Biology; Biological Organization as a Problem in thermal Physics. New York: Academic Press.
- Morris, J. T., Christian, R. R., Ulanowicz, R. E., 2005. Analysis of size and complexity of randomly constructed food webs by information theoretic metrics. In: Belgrano, A., Scharler, U.M., Dunne, J., Ulanowicz, R. E. (Eds.), *Aquatic Food Webs, An Ecosystem Approach*. Oxford University Press Inc., New York, pp. 73–85.
- Odum, E. P., 1953. *Fundamentals of ecology*. W. B. Saunders Coop., Philadelphia.
- Odum, H. T., 1983. *Systems Ecology: An Introduction*. Wiley, New York.
- Odum, H. T., 1988. Self-organization, transformity, and information. *Science* 242, 1132–1139.
- Onsager, L., 1931. Reciprocal relations in irreversible processes. *Physical Review* 38, 2265–2279.
- Patricio, J., Ulanowicz, R., Pardal, M. A., Marques, J. C., 2004. Ascendency as an ecological indicator: a case study of estuarine pulse eutrophication. *Estuarine, Coastal and Shelf Science* 60, 23–35.
- Patten B. C. 2013. Systems Ecology and Environmentalism – Getting the Science Right: The Janus Hypothesis. Symposium in Honor of Bernard C. Patten «Systems Ecology: A Network Perspective & Retrospective». April 12–15, 2013, Athens, Georgia, USA.
- Patten, B. C., 1978. Systems approach to the concept of environment. *Ohio Journal of Science* 78, 206–222.
- Patten, B. C., 1981. Environs: the super niches of ecosystems. *American Zoology* 21, 845–852.
- Patten, B. C., 1982. Environs: relativistic elementary particles for ecology. *American Naturalist* 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. *Ecological Modelling* 28, 1–71.
- Patten, B. C., 1991. Network ecology, indirect determination of the life-environment relationship in ecosystems. In: Higashi, M., Burns, T. P. (Eds.), *Theoretical Studies of Ecosystems, The Network Perspective*. Cambridge University Press, New York, 288–351.
- Patten, B. C., 1992. Energy, energy and environs. *Ecological Modelling* 62, 29–69.
- Patten, B. C., 1995. Network integration of ecological extremal principles: exergy, energy, power, ascendancy, and indirect effects. *Ecological Modelling* 79, 75–84.
- 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, 457–579.
- Patten, B. C., Fath, B. D., 1998. Environ theory and analysis: relations between aggradation, dissipation, and cycling in energy-matter flow networks at steady state. In: Ulgiati, S., Brown, M. T., Giampietro, M., Herendeen, R. A., Mayumi, K. (Eds.), *Advances in Energy Studies: Energy Flows in Ecology and Economy*. MUSIS Publisher, Rome, Italy, 483–497.
- Patten, B. C., Higashi, M., Burns, T. P., 1990. Trophic dynamics in ecosystem networks: significance of cycles and storage. *Ecological Modelling* 51, 1–28.
- Patten, B. C., in prep., *Holoecology: The Unification of Nature by Network Indirect Effects*.
- Patten, B. C., Straškraba, M., Jørgensen, S. E., 1997. Ecosystems emerging: 1. conservation. *Ecological Modelling* 96, 221–284.
- Patten, B. C., Fath, B. D., Choi, J. S., 2002a. Complex Adaptive Hierarchical Systems – background. In: Costanza, R. and Jørgensen, S. E. (Eds.), *Understanding and Solving Environmental Problems in the 21st Century*. Elsevier Science Ltd., London. 41–94.
- Patten, B. C., Fath, B. D., Choi, J. S., 2002b. Complex Adaptive Hierarchical Systems – consensus. In: Costanza, R. and Jørgensen, S. E. (Eds.), *Understanding and Solving Environmental Problems in the 21st Century*. Elsevier Science Ltd., London. 95–99.
- Pimm, S. L., 1991. Food web patterns and their consequences. *Nature* 350, 669–674.
- Prigogine, I., 1955. *Introduction to the Thermodynamics of Irreversible Processes*. Wiley & Sons, New York.
- Puzachenko, Y. G., 1989. Ecosystems in the critical state. *Nauka, Moskow* (in Russian).

- Rossberg, A. G., Yanagi, K., Amemiya, T., Itoh, K., 2006. Estimating trophic link density from quantitative but incomplete diet data. *Journal of theoretical biology* 243, 261–72.
- Samuelson, P. A., 1948. *Economics: An Introductory Analysis*. McGraw–Hill Book Co., New York.
- Schneider, E. D., Kay, J. J., 1990. Life as a phenomenological manifestation of the second law of thermodynamics. *Environment and Resource Studies*. University of Waterloo, Canada.
- Schramski, J. R., Kazanci, C., Tollner, E. W., 2010. Network environ theory, simulation and EcoNet 2.0. *Environ. Model. Softw.* 26, 419–428.
- Shannon, C. E., 1948. A mathematical theory of communication. *Bell System Technical Journal* 27, 379–423.
- Sugihara, G., Schoenly, K., Trombla, A., 1989. Scale invariance in food web properties. *Science* 245, 48–52.
- Ulanowicz, R. E., 1980. An hypothesis on the development of natural communities. *Journal of theoretical biology* 85, 223–45.
- Ulanowicz, R. E., 1983. Identifying the structure of cycling in ecosystems. *Mathematical Biosciences* 65, 219–237.
- Ulanowicz, R. E., 1986. *Growth and Development: Ecosystem Phenomenology*. Springer-Verlag, New York.
- Ulanowicz, R. E., 1997. *Ecology, the Ascendant Perspective*. Columbia University Press, New York.
- Ulanowicz, R. E., 2004. A synopsis of quantitative methods for Ecological Network Analysis. *Computational Biology and Chemistry*, 28(5–6), 321–339.
- Ulanowicz, R. E., Jorgensen, S. E., Fath, B. D., 2006. Exergy, information and aggradation: An ecosystems reconciliation. *Ecological Modelling* 198, 520–524.
- Winemiller, K. O., 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60, 331–367.
- Yodzis, P., 1980. The connectance of real ecosystems. *Nature* 284, 544–545.

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