

## TROPHIC NETWORK ASSESSMENT OF GRASSLAND ECOSYSTEM STATUS

O. Y. BUZHDIYGAN, S. S. RUDENKO

*Department of Ecology and Biomonitoring, Institute of Biology, Chemistry and Bioresources,  
Chernivtsi National University, Chernivtsi 58012, Ukraine  
e-mail: oksana.buzh@gmail.com  
s.rudenko@chnu.edu.ua*

*Ecological networks capture the organisms (identities) within the system and multiple interactions between them. Such interactions serve for the exchange of the conservative substances, such as energy and matter, creating the complex structure and behavior of ecological systems. Network organization can be considered as the reflection of ecosystem structure and functions. Network view of systems, as a fundamentally different way of system assess, gave rise to a fast development and acceptance of a new powerful analytical tool named "Network Analysis". Series of network measures have grown up around the Network Analysis. However the linking of network properties to the ecosystem status is limited because of the gaps concerning the levels and directions of network measures interrelations with empirical ecosystem parameters. Network indicator-based reference values (warning thresholds, standards) are also needed in order to transfer Network Analysis results into the ecosystem decision-making. The aim of current paper is to incorporate Network Analysis tools and empirical comparative analysis of grasslands in Chernivtsi Region in order to assess their ecosystem status. Our results show that most of the network indices demonstrate positive associations with each other, but negative relations with network synergism. It shows that the objective measures of system-wide properties express in different ways a general intuition about the nature of network organization. Our results also shows the contribution of each network property under the study to the ecosystem status by assessing of the interrelations between trophic network measures and the empirically derived parameters of the study grasslands, such as: plant biomass, insect species biodiversity, cattle density, soil microbial groups, soil acidity, and geographical location. In the framework of the current paper we also establish the network indicator-based reference values for grassland ecosystems, linked to the physic-geographic area of Carpathian Mountains, Ukraine. Eventually, we assessed the deviations of the network properties from their reference values and showed the warning status of grassland ecosystems to invoke consequently further precaution.*

*Keywords: trophic networks, grassland ecosystem, ecosystem status, reference value, Ecological Network Analysis.*

**Introduction.** The concept of system emergence has been in use in Science, Philosophy, and Art since the time of Aristotel. It says that whole is incommensurable and greater than the sum or difference of its parts (Lewes, 1875). But Ecology so far has trying to understand ecosystems mostly by studying some of their components or certain specific processes that leads to reduction of whole to the sum of its parts. Such a reducing of natural systems and selective study of their components can distort our understanding of the world and make it unpredictable and unknown. To understand ecosystem's behavior we need holistic view and system thinking which can meld together multidisciplinary knowledge and perspectives on complex problems.

System theory has been heightened by the renowned discovery of atoms and subatomic particles in Quantum Mechanics that argued the absence of isolated compartments in nature. Any objects in nature represent the network of interactions. Such interactions are basic in

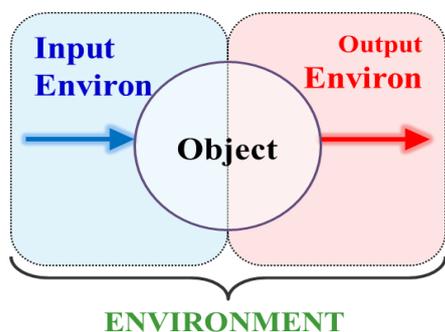
understanding of system. Thus, the paradigm shift from the parts to the whole and the interpretation of life in the way of networks within bigger networks became the Network view of study and one of the key characteristic of System Thinking (Capra, 2002). Networks are everywhere and have implications for science, philosophy, business, politics, health care, education, society, and life (Fath, 2006).

Elton's conception of ecological niche (1927) has become the driver of System Thinking in Ecology. Elton defined niche as the fundamental role of organism in the community, as the interactions of individual with other species.

System Ecology and modeling approaches indicate the network organization as equal to, or even more important than genetic information in ecosystem capacity supply for vital activity (Fath and Patten, 1999). Ecological networks capture the organisms (identities) within the system and multiple interactions between them. Such interactions serve for the exchange of the

conservative substances, such as energy and matter, creating the complex structure and behavior of ecological systems. Network organization can be considered as the reflection of ecosystem structure and functions. Network view of systems, as a fundamentally different way of system assess, gave rise to a fast development and acceptance of a new powerful analytical tool named “Network Analysis”. It is growing interdisciplinary area that makes it possible to study objects as part of whole interconnected system (Fath and Patten, 1999). In Ecology Network Analysis is an environmental application of Leontief’s economic input-output analysis (1936, 966). It has been developed as the way to bring multi-compartment modeling (Matis et al., 1979) into ecological system analysis and theory.

Classic Thermodynamics define an isolated system as one moving toward thermodynamic equilibrium with increasing of entropy in it. The result of such a process is a death of system. Ecosystems cannot be isolated as they are moving away from thermodynamic equilibrium. Also ecosystems cannot be closed as they receive energy, matter and information from outside of system boundaries. Openness of real ecological systems requires the proper theory and applicable modeling methods to be able to capture the holistic nature and complexity of the real world. Such a system analysis methodology is drawn on Patten’s Environ Theory (1976) and implemented quantitatively into Network Environ Analysis. Patten (1976, 1978) considers a system object at any level in a system hierarchy to be an input-state-output entity, as follows: looking backward in time defines the environment that produces the input, or the input environ; and looking forward in time defines the environment that is affected by the system’s output, or output environ (Fig. 1).



**Fig. 1. Input and output enviros as two environments of an object within the system boundaries (Patten’s concept of enviros, 1978, 1982).**

Patten (1978, 1982) evolved the concept of enviros in Ecology as a branch of Network Analysis and established the following key ideas

toward an environmental system theory (Patten,1978):

- every object within a system has two environments which are specified as enviros within the system boundaries (Fig. 1.2), and they can be quantified;
- external reference state is needed for quantifying of the internal causation of a system;
- the propagation of flow along each pathway is uniquely targeted for and derived from a particular compartment.

The study of objects separately from their environment represents the reductionist science (Fath & Patten, 1999) that is traditional view in ecology. In contrast with this, above Patten’s ideas reflect holistic view on ecological system.

Series of network measures have grown up around the Network Analysis. However the linking of network properties to the ecosystem status is limited because of the gaps concerning the levels and directions of network measures interrelations with empirical ecosystem parameters. Network indicator-based reference values (warning thresholds, standards) are also needed in order to transfer Network Analysis results into the ecosystem decision-making.

The main idea of this paper is to incorporate Network Analysis tools and empirical comparative analysis of grasslands in Chernivtsi Region in order to assess holistically their ecosystem status.

#### **Materials and methods.**

**Pastoral ecosystems sampling.** We studied grassland ecosystems located at Carpathian Mountains of Chernivtsi Region, Ukraine. The soils are sod-brown and leached, with low humus content, and high acidity (pH = 3.6 – 5.0) due to high Al+3 concentration in the soil solution. Mean annual rainfall is 700 – 1200 mm and mean annual temperature is 4.6° C. The Chernivtsi Region has a humid Temperate Continental Climate, highly influenced by humid Atlantic air masses. The Carpathian Mountain climate is severe due to cold and short summers.

There are no significant differences in elevation or climate between the study plots. All the 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.

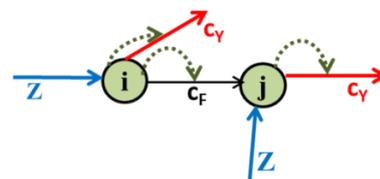
Sampling and analysis were performed identically for each of the compared ecosystems. Biological samples for food-web analysis were gathered during peak growing seasons (June – July) in years 2005, 2006, and 2007. Study plots were 10m × 10m. Sampling of each pasture included four plots, each with four replicates. Species of plants

and insects were identified. Plant standing stocks were assessed as oven-dried biomass of plants / m<sup>2</sup> using a quadrat with 1 m sides. Earthworms (Oligochaeta) were separated from the 1 m<sup>3</sup> plots by a standard Quantitative Hand Sorting method. Microbiological soil surface 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 < 30oC; Fungi (Micromycetes): modified Czapek-Dox substrate with streptomycin, 20 < T < 25oC; Ray Fungi (Actinomycetes): starch-ammonium agar, 28 < T < 30oC. Cattle density was determined and converted to number of animals per 100 m<sup>2</sup>. It is considered as the measure of grazing intensity of the study pastures. Plant and insect specimens were identified as much as possible to species. Plant standing stocks were assessed as oven-dried biomass of plants / m<sup>2</sup>.

**Food-web construction.** We defined trophic compartments based on distinct feeding roles 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 construct and portray our food webs we used software Pajek (Batagelj & Mrvar, 2010) for Large Network Analysis, and *Ucinet 6* (Borgatti, et al., 2002) for Social Network Analysis. 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 ( $f_{ij} = 0$ ). We use Network Environ Theory (Patten, 1981, 1982) to construct the food-web networks. Thus each compartment  $i$  has a boundary input  $z_i$  [ $ML^{-2}T^{-1}$ ], and output  $y_i$  [ $ML^{-2}T^{-1}$ ]. We defined trophic compartments based upon distinct feeding roles 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 quantify adjacency-based relations from qualitative digraphs, we transformed the adjacency matrix,  $A_{n \times n}$  in a 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's 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 ( $1, \dots, n$ ) including a boundary output  $y_i$ . Boundary inputs  $z_i$  and standing stocks  $x_i$  equal to 1. To investigate the number of trophic classes ( $CI$ ) in our food-webs we used the regular equivalence method drawn from Social Network Theory (Borgatti & Everett, 1993) and applied as a tool in *Ucinet 6* (Borgatti, et al., 2002). Regular equivalence algorithm assesses similarity of the trophic roles of compartments using the binary presence-absence feeding relations (adjacency matrix  $A_{n \times n}$ ) between them. Johnson's Hierarchical Clustering (Johnson, 1967) of equivalence similarity values allows us to define the separate trophic classes. For more details of regular equivalence algorithm and current aggregation methods see Borgatti & Everett (1993), and Luczkovich et al. (2003). Based on the trophic role species play in pastoral ecosystems the 15 trophic classes were derived from the above-stated method.

**Food-web simulation.** For simulation of study networks we used a dynamic web-based simulation and network analysis software, *EcoNet 2.1 Beta*. Network analysis was performed based on the final state of the solution when systems reached a static steady state ( $dx_i/dt=0$ , as the system inputs and outputs are equal at steady state). 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 rate of the flow from  $i$  to  $j = c_{Fij} \times x_i$  as follows:



A differential mass-energy balance equation for donor-controlled flow type is as follows:

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

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 Kazanci (2007), and Schramski et al. (2010).

**System-wide properties.** As stated above *EcoNet* drives the system from the given initial conditions to steady state and outputs the system-

wide organizational properties based on the final state of the solution.

Ten system-level indices assessed are fully documented in literature, but brief descriptions and abbreviations are provided below. While our focus is on these whole system variables, we incorporate the **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 properties appropriate to comparative interpretations.

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

$$LD = L / N.$$

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

$$C = L / N^2.$$

**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):

$$TST = \sum T_i,$$

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):

$$FCI = TST_c / TST,$$

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

$$TST_c = C_1 T_1 + C_2 T_2 + \dots + C_n T_n.$$

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; Fath and Borrett, 2006).

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

$$IEI = \sum (N - I - G)z / \sum Gz,$$

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

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

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

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

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,

$G^2 \dots G^m$  are the indirect flow intensity matrices (fractions of boundary flow that travels from node  $i$

to  $j$  over all pathways of length  $m$ , where  $m$  shows the orders given by the divergent power series ( $m=2, \dots, \infty$ ). The integral matrix  $N$  multiplied by boundary input vector  $z$  returns the throughflow vector  $T$ :  $T=Nz$ .

**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 & Patten, 1998; Fath & Borrett, 2006):

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

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

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

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

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

where  $d_{ij}$  can be positive or negative ( $-1 \leq d_{ij} < 1$ ) 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;

$D^2 \dots D^m$  are the indirect utilities corresponding to the flows of the same power  $m = 2, \dots, \infty$ .

**Mutualism Index (MI)** – ratio of number of positive (+) to negative (–) signs in network utility analysis matrices specifying kinds of pairwise interactions (Patten, 1991, 1992; Fath & Patten, 1998, 1999; Fath & Borrett, 2006; Fath, 2007):

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

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; Patrício et al., 2004; Ulanowicz et al., 2006; Morris et al., 2005):

$$AS = TST \times AMI,$$

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

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

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

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

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

**Full Development Capacity (DC)** – network flow organization, the upper bound of ascendency. 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; Christian et al., 2005):

$$DC = TST \times H_f,$$

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

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

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 & Fath, 1998; Fath & Patten, 2001; Ulanowicz et al., 2006):

$$AI = TST / \sum z_i,$$

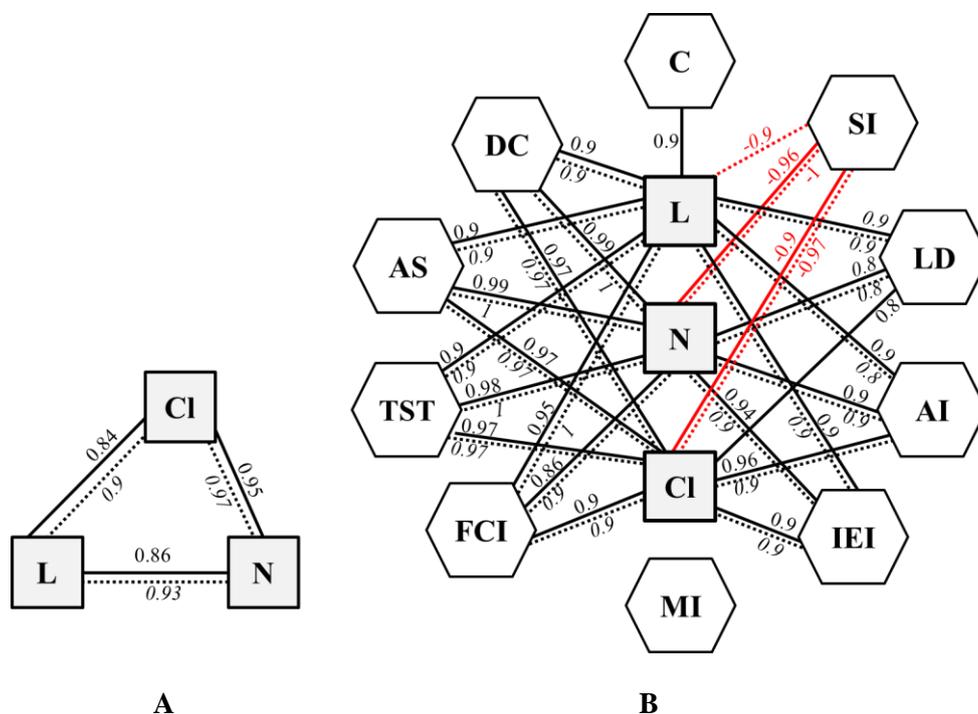
where  $z_i$  is a boundary input of compartment  $i = 1, \dots, n$ ;  $TST$  is total system throughflow.

### Results and Discussion:

**Network Properties Interrelations.** The analysis of relationships between the network properties all across the 7 pastoral ecosystems within the study Mountain area of Chernivtsi Region demonstrates few different behavioral patterns. Most of the network analysis variables (specifically  $N$ ,  $L$ ,  $CI$ ,  $LD$ ,  $C$ ,  $TST$ ,  $FCI$ ,  $IEI$ ,  $AS$ ,  $DC$ ,  $AI$ , and  $MI$ ) are positively related to each other, and negatively related to  $SI$ . Consequently,  $SI$  (network synergism) runs counter to other trends in our analyses.

Fig. 2-3 demonstrate the presence and degree of statistically significant relations between the whole-system properties assessed within the study area. Each of these properties varies in a number of interrelations with others. This shows their Particularly, number of links  $L$ , classes  $CI$ , link density  $LD$  and indirect effects measure  $IEI$  show the highest number of interrelations with other network properties pairwise significant relations (11 from 12 possible interrelations). They are followed by total system throughflow  $TST$ , cycling  $FCI$ , ascendancy  $AS$ , development capacity  $DC$ , and network aggradation  $AI$ . Each of them has 10 from 12 possible interrelations. System size  $N$  shows relations with 9 network properties. Degree of connectance  $C$  is significantly correlated with only 3 of 12 indices, while network mutualism  $MI$  has only 1 statistically significant association.

Increase in species (nodes) number  $N$  in a food web drives the multiplicity of relations (links)  $L$  between them. From other side higher number of species leads to a higher number in trophic roles they play in community that is a number of trophic classes  $CI$ . Our analysis of interrelations between network properties shows the high significant linear as well as non-linear correlations between  $N$ ,  $L$ , and  $CI$  pairwise (Fig. 2.A).



**Fig. 2. Interrelationships between the number of nodes  $N$ , number of links  $L$ , and number of trophic classes  $CI$  pairwise (A) and between them and the other network properties assessed (B) all across the 7 pastoral ecosystems within the study Mountain area of Chernivtsi Region. The solid and dotted lines illustrate the presence of statistically significant ( $P \leq 0.05$ ) linear Pearson and non-linear Spearman correlations respectively. Numbers near the lines show the degree of correlations. Red lines and numbers illustrate the negative relations.**

Some theoretical studies report a hyperbolic decline in a connectance  $C$  with increasing number of compartments  $N$  (reviewed by Fonseca & John, 1996). By contrast, Martinez (1992) found that connectance of different-sized food webs was almost constant. Our results show no clear interrelations between  $C$  and  $N$  (Fig. 2.B). Connectance appears to be a scale-invariant property. However, our observed significant strong associations of connectance  $C$  versus indirect effects dominance  $IEI$  and network mutualism  $MI$  (Fig. 3) demonstrate the complex nature of this topological property in food webs.

Several studies generalized the idea that link density  $LD$  tends to remain constant across networks of varying size (Yodzis, 1980; Cohen & Briand, 1984). But other researches do not confirm this (Winemiller, 1990; Havens, 1992). Our analyses do not support scale invariance of  $LD$  across the studied food webs (Fig. 2.B). Despite the fact that  $C$  and  $LD$  are both measures of system complexity, we found link density  $LD$  to be much more sensitive to variations in other network properties (Fig. 3).

Several investigations show the effect of network size  $N$  on the behavior of other network properties (Fath, 2004) assessed here. Finn (1976) suggests that total system throughflow  $TST$  is sensitive to the number of compartments  $N$ . Our results give strong evidence for the increasing monotonic association between  $TST$  and  $N$  (Fig. 2.B). Also, the measures of network ascendancy  $ASC$  and developmental capacity  $DC$  demonstrate the same tendency (Fig. 2.B). Recalling the definitions of the last two variables, it is

clear they both are driven by  $TST$  and limited by  $N$ , as  $TST$  increases with  $N$ . Higashi and Patten (1989) also gives an algebraic proof that indirect effects  $IEI$  also increase with  $N$ . Using synthesized large-scale "cyber-networks" Fath (2004) supports these results and demonstrates also a strong direct association between cycling index  $FCI$  and network size  $N$ . This author also indicates that the indirect effects ratio  $IEI$  is more strongly related with  $N$  than is the cycling index  $FCI$ . Our data confirm this in the case of linear relations between the assessed indices (Fig. 2.B).

Network synergism  $SI$  occurs in all models regardless of the system size  $N$  (Fath and Patten, 1998). However, Fath (2004) illustrates that synergism  $SI$  decreases with increased network size  $N$ . These results agree with our investigations as well (Fig. 2.B). Moreover, we observe decreasing  $SI$  in relation to the other system-wide properties assessed (Fig. 3).

There is the evidence that network properties are strongly dependent on degree of cycling (Fath, 2004). Comparative study of aquatic ecosystems by Christensen (1995) shows strong increasing correlation of cycling index  $FCI$  with network aggradation  $AI$ , but not with total system throughflow  $TST$ . However, Borrett & Osidele (2007) observe strong correlations between  $FCI$ ,  $AI$ , and  $TST$ . Our comparative study confirms strong correlations between  $FCI$ ,  $AI$ , and  $TST$  pairwise. We also found that network aggradation  $AI$  tends to increase with increasing network size  $N$  (Fig. 2.B).

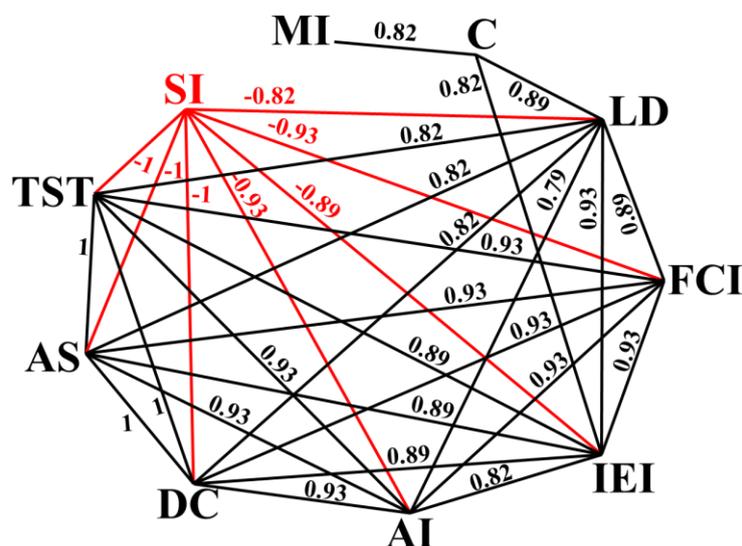


Fig. 3. Interrelationships between the network properties assessed all across the 7 pastoral ecosystems within the study Mountain area of Chernivtsi Region. Lines illustrate the presence of statistically significant ( $P \leq 0.05$ ) non-linear Spearman correlations. Numbers near the lines show the degree of correlations. Red lines and numbers illustrate the negative interrelations.

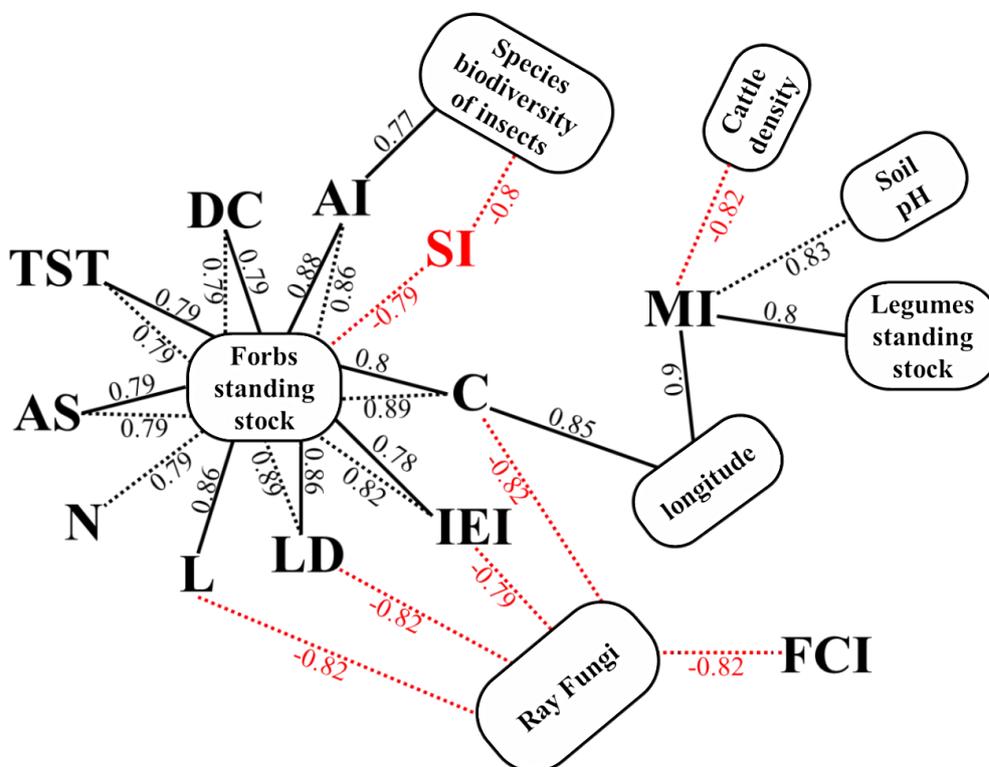
Patten and Higashi (1986) show that network connectance  $C$ , cycling index  $FCI$ , and total system throughflow  $TST$  increase the dominance of indirect effects  $IEI$ . Fath (2004) provides strong evidence for the increasing relations between indirect effects index  $IEI$  and cycling  $FCI$ . Our results support all these findings and additionally show strong increasing relations of  $IEI$  with link density  $LD$ , network ascendancy  $AS$ , development capacity  $DC$ , and decreasing association with network synergism  $SI$  (Fig. 3).

Network mutualism  $MI$  (Patten, 1991; Fath, 2007) has received little attention and comparisons of its relationships with the other whole-system properties are quite rare. Our results reveal there are no significant relations of  $MI$  with any other network measures assessed, except degree of connectance  $C$  (Fig. 2-3).

All of above network statistics show the network measures to express in different ways a general intuition about the nature of network organization.

**Contribution of Trophic Network Measures to Ecosystem Status.** There is currently a lack of data about the interrelations between network properties we focus on and the empirical parameters of pastoral ecosystem, such as: species biodiversity, plant biomass, or grazing rate. The understanding of such

interrelationships will clarify the contribution of network indices to pastoral ecosystem status. In order to achieve these goals we use linear and non-linear correlation analysis between food web measures of ecosystems and following empirical parameters of these pastures (fig. 4): (1) Geographical coordinates of explored pastoral ecosystems (Longitude and Latitude); (2) Cattle density; (3) Plant standing stocks (biomass of plants  $g / m^2$ ) that includes the following groups: Legumes, Graminoids, and Forbs; (4) Species biodiversity of insects; (5) The following soil microbial groups (number of cells / 1 g of oven-dried soil): Heterotrophic Bacteria, Fungi, and Ray Fungi (Actinomycetes); and (6) Soil acidity. Our study reveals that degree of network connectance  $C$  and mutualism  $MI$  demonstrate high linear correlation with the Geographical Longitude of explored pastures (fig. 4). It can be interpreted that within the study area more southern pastures have comparatively higher network connectance and mutualism degrees. But further work in confirming of these results is still needed. Furthermore, correlation analysis shows no clear significant associations between the network properties and Geographical Latitude of explored ecosystems. Cattle density shows the decreasing relations with network mutualism degree  $MI$ .



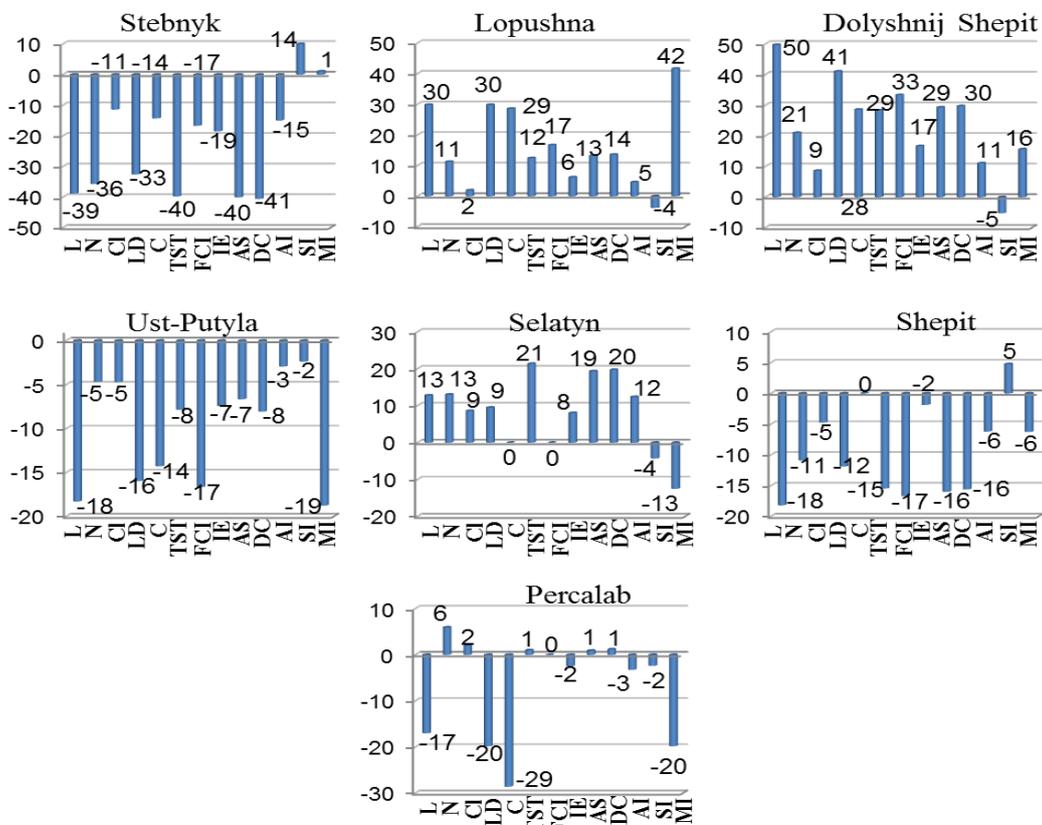
**Fig. 4.** Interrelations between empirical parameters of 7 pastures and their food web properties assessed within the study Mountain area of Chernivtsi Region. The solid and dotted lines illustrate the presence of statistically significant ( $P \leq 0.05$ ) linear Pearson and non-linear Spearman correlations respectively. Numbers near the lines show the degree of correlations. Red lines and numbers illustrate the negative relations.

All other food web measures appear to be invariant with cattle density variations. Forbs standing stock demonstrates high increasing interrelations with *N*, *L*, *LD*, *C*, *TST*, *IEI*, *AS*, *DC*, *AI*, and decreasing relations with network synergism *SI*. On the other hand Legumes standing stock is positively correlated with only one (*MI*) of network properties assessed. The shape of relationship between the Graminoids standing stock and food web measures is not determined by our research as the both linear and non-linear correlations between them show not statistical significance. Species biodiversity of insects shows increasing association with network aggradation *AI* and decreasing relations with network synergism *SI*. Our study of Heterotrophic Bacteria and Fungi soil microbial groups shows no significant associations between them and network properties under assess. However, the cell number of Ray Fungi demonstrates decreasing non-parametric associations with *L*, *LD*, *IEI*, *C*, and *FCI*. Mountain soils of study area are acidic, that is a limiting factor for many plants. Network mutualism *MI* tends to decrease with the increasing soil acidity (pH decreasing).

**Trophic Network Assessment of Grassland Degradation (Ecosystem Status).** Environmental decision-making is usually based upon theoretical and

empirical reference values (thresholds, standards), which are the indicator-based points where we want our system to be. The challenge is to define appropriate decision criteria for our study ecosystems because there are currently no reference values for network properties we focus on. On the other hand our empirical dataset of network properties assessed across the study Mountain area forms the basis, both empirical and theoretical, for the development of reference values. Link (2005) points out that the reference values are linked to a particular process, and their choice is ultimately arbitrary.

We suggest linking the reference value to a specific physic-geographic area. This approach was chosen because each physic-geographical zone is determined by specific homogeneous characteristics of landscapes, climate, age and type of rocks in the area. It gives us opportunity to avoid the significant influences of environmental physical conditions on our comparative analysis of pastures degradation. Consequently, we link the reference value for each network property to its mean (*m*) assessed across all pastures within the study Carpathian Mountain physic-geographical zone of Chernivtsi Region.



**Fig. 5. Relative deviation *r* (%) of network properties from their reference values for each of researched ecosystems within the study area.**

Realizing the indicator-based reference values raises a question: where is each system relative to these reference points and what are the statuses of systems? To answer this question we suggest assessing a relative deviation  $r_k$  (%) of each network property  $k$  from its reference value  $\mathbf{m}_k$  for each of researched ecosystems as follows:

$$r_k = (a_k - \mathbf{m}_k) / \max_k \times 100,$$

$r_k$  is a relative deviation of network property  $k$  in a specific ecosystem from the reference value  $\mathbf{m}_k$ ;

$\mathbf{m}_k$  is a mean value ( $\mathbf{m}$ ) of network property  $k$  assessed across all pastures within the study physic-geographical zone;

$a_k$  is a value of a network property  $k$  for a specific ecosystem;

$\max_k$  is a maximum value of network property  $k$  assessed throughout all researched food webs within the ecosystems of the study physic-geographic zone.

For example a relative deviation of link density  $L$  of a food web *Stebnyk* from the reference value is equal as follows:

$$r_L = (98 - 430.6) / 856 \times 100 = -39.$$

Therefore, link density  $L$  of a food web *Stebnyk* shows a 39% below reference value. Relative deviations of studied network properties from its reference values are assessed for each of 7 pastures under research and are presented on a fig. 5.

For the reason that network synergism  $SI$  runs counter in interrelations with the other food web properties we suggest to consider a relative deviation of  $SI$  from its reference value to be with a negative sign ( $-r_{SI}$ ).

No currently warning limits for studied network properties concerning their reference value exceeding or declining are developed in literature. However Link (2005) recommends for water food webs that a decline in link density  $LD$  of 10% below the maximum observed in a community across the time-series represents a warning threshold. We suggest that a value of approximately 10% below the reference point for the properties  $N$ ,  $L$ ,  $CI$ ,  $LD$ ,  $C$ ,  $TST$ ,  $FCI$ ,  $IEI$ ,  $AS$ ,  $DC$ ,  $AI$ , and  $MI$  and 10% above the reference point for  $SI$  might be considered as the warning results for ecosystem status to invoke further precaution.

To assess the food web status of each pasture expressed relative to the reference point of physic-geographic zone we quantify an overall deviation  $R$  of network properties for each of studied ecosystems as follows:

$$R = \sum r_k / n,$$

where  $\sum r_k$  is a sum of relative deviation values for all of the network properties under assess;  $r_k$  for network synergism  $SI$  is considered with a negative sign ( $-r_{SI}$ ) as it runs counter in interrelations with the other network properties (fig. 2-3):

$$\sum r_k = r_L + r_N + r_{CI} + r_{LD} + r_C + r_{TST} + r_{FCI} + r_{IE} + r_{AS} + r_{DC} + r_{AI} + r_{MI} - r_{SI};$$

$n$  is a number of network properties ( $n = 13$  for current study).

Fig. 6. captures the results of network properties deviation ( $R$ ) for each of studied ecosystems.

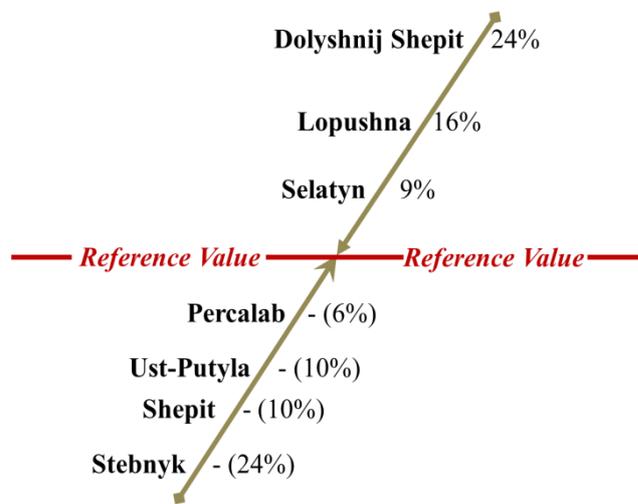


Fig. 6. Food web status of each researched ecosystem expressed relative to the reference point of food web properties within the study area.

**Ecosystem control rules and management actions.** The ecosystem control rule would be to alleviate the perturbation by whichever of the alternate causal processes appears to be the most important for each particular pasture with the deviation of food web properties below the reference point. Food web of pasture *Dolyshnij Shepit* shows the maximum deviation of network properties above reference point. Consequently it may serve as an etalon of food web structure and functions and as a way for improving of other pastures within the *Carpathian Mountain* physic-geographical zone of Chernivtsi Region.

It is important linking ecosystem control rules to each network property due to their interrelations with empirical parameters of pastures. Mechanisms to influence the warning level of each network measure can be addressed to the correlated with it empirical parameters of pastures. No one control method works alone. Ecosystem-based control rules for pastures require to be formulated with respect to the moderate exploitation (proper grazing), weed control, promotion of edible vegetation for cattle, and proper land use practice.

#### Conclusions.

The findings of this research make the following primary contributions to ecosystem network analysis:

- This study determines the levels and directions of interrelations between network properties in

empirically derived ecosystem models. Most of the assessed network indices, such as *LD*, *C*, *TST*, *FCI*, *IEI*, *AS*, *DC*, *AI*, and *MI* demonstrate positive associations with one other, but negative relations with *SI*. It shows that the objective measures of system-wide properties express in different ways a general intuition about the nature of network organization. On the other hand network synergism *SI* appears to run counter in interrelations with the other network properties. Continued research and theoretical developments into network-based indices interrelations are required to bear further examinations.

– Current paper is an attempt to introduce the contribution of network properties to the pastoral ecosystem status by assessing of the interrelations between food web measures and the empirically derived parameters of pastures, such as: plant biomass, insect species biodiversity, cattle density, soil microbial groups, soil acidity, and geographical location. Additional work is necessary to support these results. Also a larger set of the empirically derived ecosystems parameters will let us develop a meaningful base to evaluate ecosystem status.

– Two previous steps unable us to establish the network indicator-based reference values, which are linked to a specific physic-geographic area. More case studies can be addressed in a future in order to develop the food web indicator-based reference values in a time series.

– Eventually, our work introduces the assessment of network properties deviation from their reference value and shows the warning status of ecosystems to invoke consequently further precaution.

**Acknowledgments.** This research was supported by Chernivtsi National University, Ukraine and Freie Universitaet Berlin, Germany. We thank Bernard C. Patten for providing comments. Suggestions from Stuart J. Whipple improved the paper, which also benefited from comments of other University of Georgia, USA scientists at the Odum School of Ecology and Faculty of Engineering. We also thank scientists of the Department of Ecology and Biomonitoring of Chernivtsi National University for many helpful conversations and discussions.

#### References:

- Aristotle 1908-1952. The Works of Aristotle Translated into English Under the Editorship of WD Ross, 12 vols. Oxford: Clarendon Pless.
- 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. Osidele, O.O., 2007. Environ indicator sensitivity to flux uncertainty in a phosphorus model of Lake Sidney Lanier, USA. Ecol. Model. 200, 371–383.
- Borrett, S.R., Whipple, S.J., Patten, B.C., Christian, R.R., 2006. Indirect effects and distributed control in ecosystems. Temporal variability of indirect effects in a seven-compartment model of nitrogen flow in the Neuse River Estuary (USA) – Time series analysis. Ecol. Model. 194, 178–188.
- Capra Fritjof. 1996. The Web of Life: A New Synthesis of Mind and Matter. Hammersmith, London: HarperCollins.
- Christensen, V., 1995. Ecosystem maturity–towards quantification. Ecol. Model. 77, 3–32.
- Christian, R.R., et al., 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., F. Briand, and C. M. Newman. 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.
- Cohen, J.E., F. Briand, 1984. Trophic links of community food webs. Proc. Natl Acad. Sci. 81, 4105–4109.
- Elton, C. S. 1927. Animal Ecology. Sidgwick and Jackson, London.
- Fath, B.D., 2004. Network analysis applied to large-scale cyber-ecosystems. Ecol. Model. 171, 329–337.
- Fath, B.D., 2007. Network mutualism, positive community-level relations in ecosystems. Ecol. Model. 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. Ecol. Model. 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 aggregation, 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, pp. 551–562.
- Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. J. Theor. Biol. 56, 363–380.

23. Fonseca, C.R., John, J.L., 1996. Connectance, a role for community allometry. *Oikos* 77, 353–358.
24. Gardner, M.R., Ashby, W.R., 1970. Connectance of large (cybernetic) systems, critical values for stability. *Nature* 228, 784.
25. Han, B.P., 1997. On several measures concerning flow variables in ecosystems. *Ecol. Model.* 104, 289–302.
26. Hannon, B., 1973. The structure of ecosystems. *J. Theor. Biol.* 41, 535–546.
27. Havens, K.E., 1992. Scale and structure in natural food webs. *Science* 257, 1107–1109.
28. Higashi, M., Patten, B.C., 1989. Dominance of indirect causality in ecosystems. *American Naturalist* 133, 288–302.
29. Higashi, M., Patten, B.C., 1986. Further aspects of the analysis of indirect effects in ecosystems. *Ecol. Model.* 31, 69–77.
30. Johnson, S.C., 1967. Hierarchical clustering schemes. *Psychometrika* 32, 241–253.
31. Kazanci, C., 2007. EcoNet: A new software for ecological modeling, simulation and network analysis. *Ecol. Model.* 208, 3–8.
32. Kazanci, C., Matamba, L., Tollner, E.W., 2009. Cycling in ecosystems: An individual based approach. *Ecol. Model.* 220, 2908–2914.
33. Leontief, W.W., 1936. Quantitative input-output relations in the economic system of the United States. *Rev. Econ. Stat.* 18, 105–125.
34. Leontief, W.W., 1966. *Input-Output Economics*. Oxford University Press, London / New York.
35. Lewes, G.H. 1875. *Problems of Life and Mind (First Series)*, 2, London: Trübner
36. Link, J.S. 2005. Translating ecosystem indicators into decision criteria. *ICES Journal of Marine Science* 62, 569–576.
37. Luczkovich, J.J. et al., 2003. Defining and Measuring Trophic Role Similarity in Food Webs Using Regular Equivalence. *J. Theor. Biol.* 220(3), 303–321.
38. Martinez, N.D. 1992. Constant connectance in community food webs. *The Amer. Natur.* 139, 1208–1218.
39. Matis, J.H., Patten, B.C., White, G.C. (Eds.), 1979. *Compartmental Analysis of Ecosystems Models*. International Co-operative Publishing House, Fairland, Maryland, USA.
40. May, R.M., 1972. Will a large complex system be stable? *Nature* 238, 413–414.
41. May, R.M., 1973. *Stability and complexity in model ecosystems*. Princeton Univ. Press.
42. 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.
43. Patrício, J. et al., 2004. Ascendency as an ecological indicator: a case study of estuarine pulse eutrophication. *Estuarine, Coastal and Shelf Science* 60, 23–25.
44. Patten, B.C., 1978. Systems approach to the concept of environment. *Ohio Journal of Science* 78, 206–222.
45. Patten, B.C., 1981. Environs: the super niches of ecosystems. *American Zoology* 21, 845–852.
46. Patten, B.C., 1982. Environs: relativistic elementary particles for ecology. *American Naturalist* 119, 179–219.
47. Patten, B.C., 1991. Network ecology, indirect determination of the life-environment relationship in ecosystems, in: Higashi, M., Burns, T. (Eds.), *Theoretical Studies of Ecosystems, The Network Perspective*. Cambridge University Press, New York, pp. 288–351.
48. Patten, B.C., 1992. Energy, emergy and environs. *Ecol. Modell.* 62, 29–69.
49. Samuelson, P.A., 1948. *Economics: An Introductory Analysis*. McGraw-Hill Book Co., New York.
50. Schramski, J.R., Kazanci, C., Tollner, E.W., 2010. Network environ theory, simulation and EcoNet 2.0. *Environ. Model. Softw.* 26, 419–428.
51. Shannon, C.E., 1948. A mathematical theory of communication. *Bell System Tech. J.* 27, 379–423.
52. Ulanowicz, R.E., 1986. *Growth and Development, Ecosystems Phenomenology*. Springer-Verlag, NY.
53. Ulanowicz, R.E., 1997. *Ecology, the Ascendant Perspective*. Columbia University Press, NY.
54. Ulanowicz, R.E., Jorgensen, S.E., Fath, B.D., 2006. Exergy, information and aggradation: An ecosystems reconciliation. *Ecol. Model.* 198, 520–524.
55. Winemiller, K.O., 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monog.* 60, 331–367.
56. Yodzis, P., 1980. The connectance of real ecosystems. *Nature* 284, 544–545.
57. Zvagyncev, D. G., Kurakov, A. B., Fylyp, Z. 2000. The changes of heterotrophic microorganism complex in case of Pb contamination of soddy podzolic soil. *Pedology* 12: 1448–1456.

## **ОЦІНКА ЕКОЛОГІЧНОГО СТАНУ ЛУЧНИХ ЕКОСИСТЕМ НА ОСНОВІ ТРОФІЧНИХ МЕРЕЖ**

**О. Я. Буждиган, С. С. Руденко**

*Екологічні мережі включають компоненти екосистеми (організми та неживі елементи середовища) та множинні взаємодії між ними, що служать для обміну речовин, енергії та інформації, створюючи складну структуру і поведінку екологічних систем. Організація трофічної мережі відображає структуру екосистеми і її функції. Вивчення екологічних систем у вигляді мереж дало поштовх до швидкого розвитку нового аналітичного підходу в екологічній науці під назвою "Мережевий аналіз", що призвело до розвитку значної кількості індексів щодо оцінки стану трофічних мереж. Однак, залишаються прогалини щодо взаємозв'язків між показниками трофічної мережі та станом екосистеми. Крім того необхідно визначити фонові значення*

*(порогові, еталонні значення та стандарти) для даних індикаторів для того щоб застосувати результати Екологічного Мережевого Аналізу для менеджменту екосистем. Мета даної роботи – інтегрувати Екологічний Мережевий Аналіз та емпіричний порівняльний аналіз для оцінки стану лучних екосистем Чернівецької області. Результати наших досліджень показують, що більшість показників трофічних мереж позитивно корелюють один з одним та негативно корелюють з індексом синергізму трофічної мережі. Це доводить що дані показники різними методами відображають стан структурно-функціональної організації трофічної мережі. Визначивши взаємозалежності між показниками трофічних мереж та емпіричними параметрами екосистеми (а саме біомаса рослин, різноманіття комах, щільність великої рогатої худоби на луці, різноманіття угруповання ґрунтових мікроорганізмів, кислотність ґрунту та географічна локалізація екосистеми), продемонстровано роль кожного індексу трофічної мережі щодо стану екосистеми. Визначено фонові значення для кожного показника трофічних мереж досліджуваних лучних екосистем та оцінено відхилення даних показників від їх фонових значень. На основі цього для кожної з досліджуваних лучних екосистем встановлено її стан в порівнянні з фоновим значенням.*

*Ключові слова: трофічна мережа лучна екосистема, стан екосистеми, фонове значення, Екологічний Мережевий Аналіз.*

*Отримано реколегією 24.06.2016*