International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report **IR-07-021**

Exploring Simple Structural Configurations for Optimal Network Mutualism

Galina Lobanova (galo4ka1985@list.ru)
Brian D. Fath (bfath@towson.edu, fath@iiasa.ac.at)

Approved by

Arkady Kryazhimskiy
Leader, DYN

August, 2007

Contents

Abstract

Energy flow is a primary organizing principle in ecological systems, and therefore various aspects of this have been proposed as ecological goal functions [8, 5]. One such goal function considers that the integral utility (direct + indirect) will tend to be positive in well-developed systems [3, 4, 10]. In this research, we investigate several basic network structures to determine the specific relationship types between compartments and identify those structures that lead to greater quantitative and qualitative utility. This research contributes to the overall discipline of ecological network analysis.

Acknowledgments

The authors would like to thank Arkady Kryazhimskiy and Elena Rovenskaya for their valuable comments and encouragement on the manuscript.

About the Authors

Galina Lobanova
Faculty of Computational Mathematics
and Cybernetics
Department of Optimal Control
Moscow State University
Moscow
Russia

Brian D. Fath
Biology Department
Towson University
Towson, MD 21252
U.S.A.

and

International Institute for Applied Systems Analysis
Dynamic Systems Program
A-2361 Laxenburg
Austria

Exploring Simple Structural Configurations for Optimal Network Mutualism

Galina Lobanova (galo4ka1985@list.ru)
Brian D. Fath (bfath@towson.edu)

1 Introduction

Ecologists have long been concerned about the relations between organisms in an ecological food web. The web itself represents the active and passive (if flows to detritus are included) energy transfers in the ecosystem, which together comprise a richly connected network. First, energy enters a system from the external environment (for example, solar radiation, energy of ocean, river inputs, organic matter, etc.). The system compartments transfer energy between each other. The initial energy input diminishes after each step until all energy has been dissipated back to the external environment. When the system inputs and outputs are balanced, the steady-state total energy throughflow is constant. Using the foundations of ecological network analysis, Patten [9, 10] introduced utility analysis, which considers the quantitative and qualitative relations between systems compartments. Network utility analysis uses the net flow between compartments normalized by the total system throughflow of one of the compartments to determine the direct and indirect relations in the network [9, 10]. If an energy flow transaction originates from compartment j to compartment i, then the relation j to i is characterized as negative relation, from j's perspective, and the relation i to j as positive result on i. Two ecological goal functions based on network utility analysis can be considered, one accounting for the quantity of utility (synergism – see [3]) and the other the utility quality (mutualism) as measured by the number of positive or negative relations. For example, the second measure is a ratio between the overall number of positive relations and the number negative relations in the system. In other words it takes into account the sign of the relation only. It has been shown that synergism always occurs [4], therefore quantitative positive utility is always greater than negative utility. However, mutualism occurrence depends on the flow configurations and values [2].

The goal of this research is to:

- study possible network configurations that exhibit various goal function values under constraints on the ecosystems' structure and
- describe configurations on which the qualitative goal function takes its maximal value (*optimal configurations*).

The present paper contributes to IIASA's cross-program feasibility study, The Fragility of Critical Infrastructures and also to the Network on Environmental Applications developed within IIASA's DYN Program.

2 Model and Method

Patten [9, 10] was the first to introduce ecological network utility analysis. An ecosystem's network model is described by *the direct flow matrix*, F, that includes all flows between the compartments inside the system but does not include the relations between compartments and the environment. We call *a direct relation* the interaction proceeding directly between two compartments. We denote flows between compartments via f_{ij} (oriented from columns to rows such that f_{ij} is the flow from j to i), where $f_{ij} \geq 0$ for all $j, i = 1, \ldots, n$. Flows with zero indexes, f_{0j} and f_{i0} are ones to and from the external environment correspondingly. If $f_{ij} = 0$ then there is no flow from j to i.

Total flow into each compartment is given by $T_i = \sum_{j=0}^{n} f_{ij}$. Analogously, total flow out of each compartment is given by $T_i = \sum_{j=0}^{n} f_{ji}$. At steady state they are equal and we get a single throughflow value T_i. Network utility analysis is based on the net flows between compartments normalized by the compartmental throughflow such that $d_{ij} = \frac{f_{ij} - f_{ji}}{T_i}$ $(j, i = 1 \ldots n)$. Normalization gives us *a net flow matrix* $D = D(F)$. In addition to the direct relations, the numerous pathways in the network lead to many indirect relations as well. *Indirect relations* are interactions that do not proceed directly between two components. Therefore, the indirect relations between compartments are determined by the entire ecological network organization. We investigate both direct and indirect ecological relations.

We can identify indirect utilities associated with path sequences of length m by calculating D^m. The length of the path sequence is equal in value to the power of D. An integral utility matrix, which describes the contribution of all direct and indirect relations, could be found by summing all powers of D. Therefore, U is *an integral utility matrix* because its elements represent the total non-dimensional utility associated with transactions of the same order expressed between the compartments by powers of D [9, 10]. An analytic representation of U is

$$U = \sum_{m=0}^{\infty} D^m.$$

Let us introduce *a class* Φ *of admissible direct flow matrix* F. Let us give a set of conditions defining the class Φ.

(*i*) Structural stationarity condition: this condition treats the number of compartments and direct flow signs in the matrix F to be constant.

(*ii*) Flow stationarity condition: for all

$$F = (f_{ij}) \in \Phi$$
$$T_i = \sum_{j=0}^{n} f_{ij} = \sum_{j=0}^{n} f_{ji} \quad i = 1, \ldots, n.$$

(*iii*) Convergence condition: it holds that

$$U(F) = \sum_{m=0}^{\infty} D(F)^m = (I - D(F))^{-1}.$$

The above infinite power series converges if and only if all eigenvalues of D are strictly less than one in magnitude [9]. Therefore, we treat the convergence condition as follows: for all

$$F \in \Phi$$
$$\max_{k=\overline{1 \ldots n}} |\lambda_k(F)| < 1,$$

where $\lambda_1(F), \ldots, \lambda_k(F)$ are all the eigenvalues of D.

The class, Φ, of admissible matrices is described. Here and what follows we consider direct flow matrix F from class Φ.

Let us introduce function $J(\cdot)$ defined on Φ by letting:

$$J(F) = \frac{S_+(F)}{S_-(F)};$$

here
$S_+(F) = \sum_{i,j} \max(sign(u_{ij}(F)), 0)$,
$S_-(F) = \sum_{i,j} (-\min(sign(u_{ij}(F)), 0))$.
Thus $S_+(F)$ is the number of all positive relations, and $S_-(F)$ is that of all negative relations in matrix $U(F)$.

Thus, $J(F)$ characterizes the ratio between the numbers of all positive and all negative relations. In networks given by flow matrix F consider as *a goal function* related to the network mutualism in the ecosystem. When $J(F) > 1$ mutualism occurs, indicating that the system overall has more positive relations than negative ones. Keep in mind that this ratio for the direct sign matrices is always 1 (number of positive relations equals number of negative relations).

2.1 Optimization and Classification

Optimization problem

We aim to find a matrix $F \in \Phi$, for which the goal function $J(F)$ takes the greatest value:

$J(F) \to \max$
$F \in \Phi$.

Classification problem

We aim to divide all matrices from class Φ into level subclasses, $\Phi_1, \ldots, \Phi_m$, so that each subclass contains matrices which have the same value of the goal function. For all

$F_1 \in \Phi_j,\ F_2 \in \Phi_k\ (j, k = 1, ..., m)$
$j = k\ J(F_1) = J(F_2)$
$j \neq k\ J(F_1) \neq J(F_2)$.

For finite networks the number of values taken by the goal function values is finite.

3 Three-component ecological models

Example 1: a consequent interaction

First, we consider a three-component chain (Fig. 1).

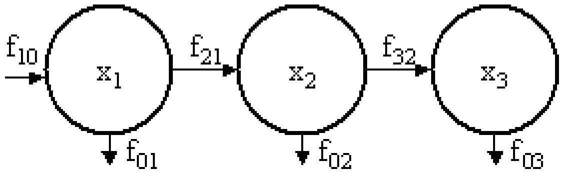

Fig. 1. Sequential chain.

Let us describe class Φ of admissible flow matrix F. The direct flow matrix F for this network is

$$F = \begin{bmatrix} 0 & 0 & 0 \\ f_{21} & 0 & 0 \\ 0 & f_{32} & 0 \end{bmatrix}, \tag{1}$$

where due to *(ii)* the total throughflows for each component are

$$T_1 = f_{10} = f_{21} + f_{01}, \quad T_2 = f_{21} = f_{32} + f_{02}, \quad T_3 = f_{32} = f_{03}.$$

Structural constraints *(i)* on elements of the matrix F are:

$$0 < f_{21} < f_{10}, \quad 0 < f_{32} < f_{21}. \tag{2}$$

The direct utility flow matrix D corresponding to the given matrix F (1) is

$$D = D(F) = \begin{bmatrix} 0 & -\frac{f_{21}}{T_1} & 0 \\ \frac{f_{21}}{T_2} & 0 & -\frac{f_{32}}{T_2} \\ 0 & \frac{f_{32}}{T_3} & 0 \end{bmatrix} = \begin{bmatrix} 0 & -\frac{f_{21}}{f_{10}} & 0 \\ 1 & 0 & -\frac{f_{32}}{f_{21}} \\ 0 & 1 & 0 \end{bmatrix}.$$

Let

$a = \frac{f_{21}}{f_{10}}, \quad b = \frac{f_{32}}{f_{21}}.$

Then (2) turn into $a, b \in (0,1)$, and we get

$$D = \begin{bmatrix} 0 & -a & 0 \\ 1 & 0 & -b \\ 0 & 1 & 0 \end{bmatrix}, \quad \text{sign}D = \begin{bmatrix} 0 & - & 0 \\ + & 0 & - \\ 0 & + & 0 \end{bmatrix}.$$

In order to find an integral utility matrix $U = U(F)$ we construct a characteristic polynomial for the matrix $D = D(F)$ and estimate magnitude of its eigenvalues. Namely, we have

$$\det(U - \lambda I) = \det \begin{bmatrix} -\lambda & -a & 0 \\ 1 & -\lambda & -b \\ 0 & 1 & -\lambda \end{bmatrix} = 0,$$

hence,

$\lambda^3 + \lambda(a+b) = 0$, $\lambda_1 = 0$, $\lambda_2 = i\sqrt{a+b}$, $\lambda_3 = -i\sqrt{a+b}$.

Due to *(iii)*:

$$\left| \frac{f_{21}}{f_{10}} + \frac{f_{32}}{f_{21}} \right| < 1. \tag{3}$$

Constraints (2), (3) describe a class Φ of matrices F of form (1).

Theorem 1. For all matrixes F (1), which satisfy conditions (2), (3), it holds that

$$J(F) = \frac{7}{2}.$$

Proof. Let us construct an integral utility matrix $U = U(F)$. Due to (3) :
$U = \sum_{m=0}^{\infty} D^m = (I - D)^{-1}$.

We have $(I-D)^{-1} = \dfrac{\widehat{(I-D)}}{\det(I-D)}$, where $\widehat{(I-D)}$ is the adjoint matrix to the matrix $(I-D)$.

Then

$$\det(I-D) = 1+a+b, \quad \widehat{(I-D)} = \begin{bmatrix} 1+b & -a & ab \\ 1 & 1 & -b \\ 1 & 1 & 1+a \end{bmatrix}.$$

Thus

$$U = \frac{1}{(1+a+b)} \begin{bmatrix} 1+b & -a & ab \\ 1 & 1 & -b \\ 1 & 1 & 1+a \end{bmatrix}, \ \text{sign}U = \begin{bmatrix} + & - & + \\ + & + & - \\ + & + & + \end{bmatrix}, \ J(F) = \frac{S_+(F)}{S_-(F)} = \frac{7}{2}.$$

◇ The theorem is proved.

Remark 1. A comparison of sign(D) and sign(U) shows that influence the relation of each component to itself and all relations that are neutral in the original flow matrix become positive in the integral utility matrix U :

$$\text{sign}D = \begin{bmatrix} 0 & - & 0 \\ + & 0 & - \\ 0 & + & 0 \end{bmatrix}, \quad \text{sign}U = \begin{bmatrix} + & - & + \\ + & + & - \\ + & + & + \end{bmatrix}.$$

Example 2: a parallel interaction (competition for a single prey)

In this example we consider a model with two predators feeding on a common prey (Fig. 2).

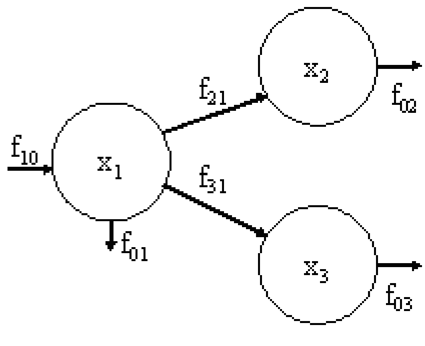

Fig. 2. Competition for a single prey

The direct flow matrix F for a given network is

$$F = \begin{bmatrix} 0 & 0 & 0 \\ f_{21} & 0 & 0 \\ f_{31} & 0 & 0 \end{bmatrix}, \tag{4}$$

where due to *(ii)* the total throughflows for each component are

$$T_1 = f_{10} = f_{21} + f_{01} + f_{31}, \quad T_2 = f_{21} = f_{02}, \quad T_3 = f_{31} = f_{03}.$$

Structural constraint *(i)* on elements of the matrix F is:

$$0 < f_{21} + f_{31} < f_{10}. \tag{5}$$

The direct utility flow matrix D corresponding to the matrix F (4) is

$$D = D(F) = \begin{bmatrix} 0 & -\frac{f_{21}}{T_1} & -\frac{f_{31}}{T_1} \\ \frac{f_{21}}{T_2} & 0 & 0 \\ \frac{f_{31}}{T_3} & 0 & 0 \end{bmatrix} = \begin{bmatrix} 0 & -\frac{f_{21}}{f_{10}} & -\frac{f_{31}}{f_{10}} \\ 1 & 0 & 0 \\ 1 & 0 & 0 \end{bmatrix}.$$

Let

$a = \frac{f_{21}}{f_{10}}$, $b = \frac{f_{31}}{f_{10}}$.

Then structural constraint (5) turns into $a, b, (a+b) \in (0,1)$.

Hence,

$$D = \begin{bmatrix} 0 & -a & -b \\ 1 & 0 & 0 \\ 1 & 0 & 0 \end{bmatrix}, \quad \text{sign}D = \begin{bmatrix} 0 & - & - \\ + & 0 & 0 \\ + & 0 & 0 \end{bmatrix}.$$

A characteristic polynomial for this matrix $D = D(F)$ is

$$\det(U - \lambda I) = \det \begin{bmatrix} -\lambda & -a & -b \\ 1 & -\lambda & 0 \\ 1 & 0 & -\lambda \end{bmatrix} = 0.$$

Therefore,

$\lambda^3 + \lambda(a+b) = 0$, $\lambda_1 = 0$, $\lambda_2 = \sqrt{a+b}$, $\lambda_3 = -\sqrt{a+b}$.

Due to (5) we have that condition *(iii)* is satisfied for all admissible a, b.

Constraint (5) describes a class Φ of matrices F of form (4).

Theorem 2. For all matrixes F (4), which satisfy condition (5), it holds that

$$J(F) = \frac{5}{4}.$$

Proof. Let us construct an integral utility matrix $U = U(F)$. We have

$$\det(I - D) = 1 + a + b, \quad (\widehat{I - D}) = \begin{bmatrix} 1 & -a & -b \\ 1 & 1+b & -b \\ 1 & -a & 1+a \end{bmatrix}.$$

Thus

$$U = \frac{1}{(1+a+b)} \begin{bmatrix} 1 & -a & -b \\ 1 & 1+b & -b \\ 1 & -a & 1+a \end{bmatrix}, \text{sign}U = \begin{bmatrix} + & - & - \\ + & + & - \\ + & - & + \end{bmatrix}, J(F) = \frac{S_+(F)}{S_-(F)} = \frac{5}{4}.$$

⋄ The theorem is proved.

Remark 2. In the above example a comparison of sign(D) and sign(U) shows the self-relations of the components and all initially neutral relations become positive, whereas competition between two predators for one prey remains negative in the integral utility matrix U. Therefore, the value of the goal function is smaller than that in *Example 1.*

$$\text{sign}D = \begin{bmatrix} 0 & - & - \\ + & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, \quad \text{sign}U = \begin{bmatrix} + & - & - \\ + & + & - \\ + & - & + \end{bmatrix}.$$

Example 3: a parallel interaction (apparent competition)

Here we consider a model with one predator feeding on two prey (Fig. 3).

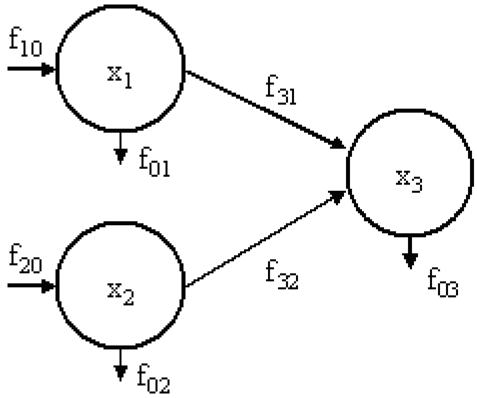

Fig. 3. Apparent competition.

The direct flow matrix F is

$$F = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ f_{31} & f_{32} & 0 \end{bmatrix}, \tag{6}$$

where due to *(ii)* the total throughflows are

$$T_1 = f_{10} = f_{31} + f_{01}, \quad T_2 = f_{20} = f_{32} + f_{02}, \quad T = f_{31} + f_{32} = f_{03}.$$

Structural constraints *(i)* on elements of the matrix F are:

$$0 < f_{31} < f_{10}, \quad 0 < f_{32} < f_{20}. \tag{7}$$

The direct utility flow matrix D corresponding to the matrix F (6) is

$$D = D(F) = \begin{bmatrix} 0 & 0 & -\frac{f_{31}}{T_1} \\ 0 & 0 & -\frac{f_{32}}{T_2} \\ \frac{f_{31}}{T_3} & \frac{f_{32}}{T_3} & 0 \end{bmatrix} = \begin{bmatrix} 0 & 0 & -\frac{f_{31}}{f_{10}} \\ 0 & 0 & -\frac{f_{32}}{f_{20}} \\ \frac{f_{31}}{f_{31}+f_{32}} & \frac{f_{32}}{f_{31}+f_{32}} & 0 \end{bmatrix}.$$

Let

$a = \frac{f_{31}}{f_{10}}, \quad b = \frac{f_{32}}{f_{20}}, \quad c = \frac{f_{31}}{f_{31}+f_{32}}, \quad 1 - c = \frac{f_{32}}{f_{31}+f_{32}}.$

Then structural constraints (7) turn into $a, b, c \in (0, 1)$. Then

$$D = \begin{bmatrix} 0 & 0 & -a \\ 0 & 0 & -b \\ c & 1-c & 0 \end{bmatrix}, \quad \mathrm{sign}D = \begin{bmatrix} 0 & 0 & - \\ 0 & 0 & - \\ + & + & 0 \end{bmatrix}.$$

A characteristic polynomial for $D = D(F)$ is

$$\det(U - \lambda I) = \det \begin{bmatrix} -\lambda & 0 & -a \\ 0 & -\lambda & -b \\ c & 1-c & -\lambda \end{bmatrix} = 0.$$

Hence
$\lambda^3+\lambda(b-a)=0$ $\lambda_1=0$, $\lambda_2=i\sqrt{ca+b(1-c)}$, $\lambda_3=-i\sqrt{ca+b(1-c)}$.
Let us prove, that $ca+b(1-c)<1$, or equivalently:

$$\frac{{f_{31}}^2}{f_{10}(f_{31}+f_{32})}+\frac{f_{32}}{f_{20}}\cdot\frac{f_{32}}{(f_{31}+f_{32})}<1, \quad \Rightarrow f_{20}{f_{31}}^2+f_{10}{f_{32}}^2<f_{10}f_{20}(f_{31}+f_{32}), \quad \Rightarrow$$

$$f_{31}f_{20}(f_{31}-f_{10})+f_{10}f_{32}(f_{32}-f_{20})<0, \quad \begin{cases} f_{31}-f_{10}<0 \\ f_{32}-f_{20}<0 \end{cases}.$$

Due to (7) the latter inequality is true. Therefore *(iii)* is satisfied for all admissible a,b.
Constraint (7) describes a class Φ of matrices F of form (6).
Theorem 3. For all matrixes F (6), which satisfy condition (7), it holds that

$$J(F)=\frac{5}{4}.$$

Proof. Let us construct an integral utility matrix $U=U(F)$. We have

$$\det(I-D)=1+ca-b(c-1)>0, \quad (\widehat{I-D})=\begin{bmatrix} 1-b(c-1) & a(1-c) & -a \\ -cb & 1+ac & -b \\ c & 1-c & 1 \end{bmatrix}.$$

Thus

$$U=\frac{1}{(1+ca-b(c-1))}\begin{bmatrix} 1-b(c-1) & a(1-c) & -a \\ -cb & 1+ac & -b \\ c & 1-c & 1 \end{bmatrix}, \text{sign}U=\begin{bmatrix} + & - & - \\ - & + & - \\ + & + & + \end{bmatrix},$$

$$J(F)=\frac{S_+(F)}{S_-(F)}=\frac{5}{4}.$$

◇ The theorem is proved.

Remark 3. This example differs from *Example 2* by the type of competition only. As a consequence, the value of the goal function is equal to that in *Example 2*.

$$\text{sign}D=\begin{bmatrix} 0 & - & - \\ + & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}, \quad \text{sign}U=\begin{bmatrix} + & - & - \\ + & + & - \\ + & - & + \end{bmatrix}.$$

Example 4: a complex interaction

A network's compartments can interact in both consecutive and parallel ways. Let us consider an example of such interaction for a three-compartment model (Fig. 4).

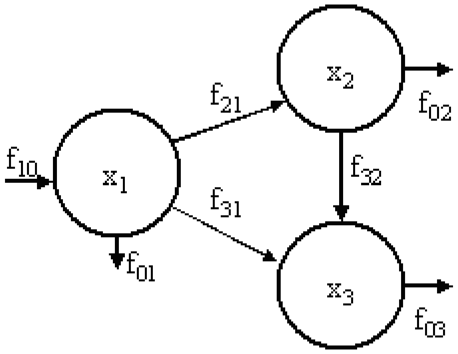

Fig. 4. Complex interaction.

The direct flow matrix F for this structure is

$$F = \begin{bmatrix} 0 & 0 & 0 \\ f_{21} & 0 & 0 \\ f_{31} & f_{32} & 0 \end{bmatrix}, \tag{8}$$

where due to *(ii)* the total throughflows are

$$T_1 = f_{10} = f_{21} + f_{31} + f_{01}, \quad T_2 = f_{21} = f_{02} + f_{32}, \quad T_3 = f_{31} + f_{32} = f_{03}.$$

Structural constraints *(i)* are:

$$0 < f_{21} + f_{31} < f_{10}, \quad 0 < f_{32} < f_{21}. \tag{9}$$

The direct utility flow matrix D corresponding to the matrix F (8) is

$$D = D(F) = \begin{bmatrix} 0 & -\frac{f_{21}}{T_1} & -\frac{f_{31}}{T_1} \\ \frac{f_{21}}{T_2} & 0 & -\frac{f_{32}}{T_2} \\ \frac{f_{31}}{T_3} & \frac{f_{32}}{T_3} & 0 \end{bmatrix} = \begin{bmatrix} 0 & -\frac{f_{21}}{f_{10}} & -\frac{f_{31}}{f_{10}} \\ 1 & 0 & -\frac{f_{32}}{f_{21}} \\ \frac{f_{31}}{f_{31}+f_{32}} & \frac{f_{32}}{f_{31}+f_{32}} & 0 \end{bmatrix}.$$

Let

$a = \frac{f_{21}}{f_{10}}$, $b = \frac{f_{31}}{f_{10}}$, $c = \frac{f_{32}}{f_{21}}$, $d = \frac{f_{31}}{f_{31}+f_{32}}$, $(1-d) = \frac{f_{32}}{f_{31}+f_{32}}$.

Structural constraints (9) turn into $a, b, c, d, (a+b) \in (0,1)$. Then

$$D = \begin{bmatrix} 0 & -a & -b \\ 1 & 0 & -c \\ d & 1-d & 0 \end{bmatrix}, \quad \text{sign}D = \begin{bmatrix} 0 & - & - \\ + & 0 & - \\ + & + & 0 \end{bmatrix}.$$

A characteristic polynomial for $D = D(F)$ is

$$\det(U - \lambda I) = \det \begin{bmatrix} -\lambda & -a & -b \\ 1 & -\lambda & -c \\ d & 1-d & -\lambda \end{bmatrix} = 0.$$

Hence

$$\lambda^3 + \lambda(a + c(1-d) + bd) - acd + b(1-d) = 0. \tag{10}$$

Let us note, that

$$f_{31} = bf_{10}, \quad f_{32} = cf_{21}, \quad \text{therefore,} \quad a = \frac{f_{32}/c}{f_{31}/b} = \frac{f_{32}}{f_{31}}\frac{b}{c}, \quad \frac{f_{32}}{f_{31}} = \frac{ac}{b}.$$

Thus we come to

$$d = \frac{f_{31}}{f_{31} + f_{32}} = \frac{1}{1 + f_{32}/f_{31}} = \frac{1}{1 + ac/b} = \frac{b}{\pm ac} \quad \text{and} \quad 1 - d = \frac{ac}{b + ac}. \tag{11}$$

Applying (11) to (10) we get

$$\lambda^3 + \lambda \left(a + c\frac{ac}{b + ac} + b\frac{b}{b + ac} \right) - ac\frac{b}{b + ac} + b\frac{ac}{b + ac} = 0$$

or

$$\lambda^3 + \lambda \left(a + \frac{ac^2 + b^2}{b + ac} \right) = 0,\ \lambda_1 = 0,\ \lambda_2 = i\sqrt{a + \frac{ac^2 + b^2}{b + ac}},\ \lambda_3 = -i\sqrt{a + \frac{c^2 + b^2}{b + ac}}.$$

Condition (9) leads to

$$a,\ b,\ c,\ (a + b),\ a + \frac{ac^2 + b^2}{b + ac} < 1. \tag{12}$$

Remark 4. The set of parameters $a,\ b,\ c$ that satisfy (12) is nonempty. Indeed, for all $b, c \in (0, 1)$ and small enough $a > 0$ we have

$$a,\ a + b \in (0, 1) \quad \text{and} \quad a + \frac{ac^2 + b^2}{b + ac} \approx 0 + \frac{0 \cdot c^2 + b^2}{b + 0 \cdot c} = b \in (0, 1).$$

However, not all $a,\ b,\ c$ that satisfy $a,\ b,\ c,\ (a{+}b) \in (0, 1)$ satisfy $a{+}\frac{ac^2 + b^2}{b + ac} \in (0, 1)$. Indeed let us take b close to 0 and a close to 1. Then

$$a + \frac{ac^2 + b^2}{b + ac} \approx 1 + \frac{1 \cdot c^2 + 0}{0 + 1 \cdot c} = 1 + c > 1 \quad \text{for all} \quad c \in (0, 1).$$

Constraints (12) describe a class Φ of matrices F (8). Let us prove a theorem resolving the optimization and classification problems for models of given class.

Theorem 4. The class Φ of matrices F of form (8), that satisfy the conditions (12) in the union of three non-intersecting subclasses. All matrices in each subclass have the same value of the goal function. Namely,

$$J(F) = \begin{cases} \frac{7}{2} & \text{if} \quad c > b,\ ac > b, \\ \frac{5}{4} & \text{if} \quad c < b,\ ac > b, \\ 2 & \text{if} \quad c > b,\ ac < b, \end{cases}$$

where

$$a = \frac{f_{21}}{f_{10}}, \quad b = \frac{f_{31}}{f_{10}}, \quad c = \frac{f_{32}}{f_{21}}.$$

Proof. As earlier, we construct an integral utility matrix $U = U(F)$. We have

$$(I - D) = \begin{bmatrix} 1 & a & b \\ -1 & 1 & c \\ -d & d - 1 & 1 \end{bmatrix} = 0, \quad \det(I - D) = (1 - a)(1 - cd) + b + c > 0,$$

$$\widehat{(I - D)} = \begin{bmatrix} 1 - c(d - 1) & b(d - 1) - a & ac - b \\ 1 - cb & 1 + bd & -c - b \\ 1 & 1 - d(1 + a) & 1 + a \end{bmatrix},$$

therefore,

$$U = U(F) = \frac{1}{(1-a)(1-cd)+b+c}\begin{bmatrix} 1-c(d-1) & b(d-1)-a & ac-b \\ 1-cb & 1+bd & -c-b \\ 1 & 1-d(1+a) & 1+a \end{bmatrix},$$

$$\text{sign}U = \begin{bmatrix} + & - & ? \\ + & + & - \\ + & ? & + \end{bmatrix}.$$

The signs of elements u_{13} and u_{32} are not certain yet. The sign of u_{13} is defined by the sign of $(ac-b)$. The sign of u_{32} is defined by the sign of

$$1-d(1+a) = 1 - \frac{b(1+a)}{b+ac} = \frac{a(c-b)}{b+ac}$$

that is the sign of $(c-b)$.

Four cases are possible:

1) $\begin{cases} c > b \\ ac > b \end{cases}$ if $u_{13} > 0, \quad u_{32} > 0,$

2) $\begin{cases} c < b \\ ac < b \end{cases}$ if $u_{13} < 0, \quad u_{32} < 0,$

3) $\begin{cases} c > b \\ ac < b \end{cases}$ if $u_{13} < 0, \quad u_{32} > 0,$

4) $\begin{cases} c < b \\ ac > b \end{cases}$ if $u_{13} > 0, \quad u_{32} < 0.$

It is clear that one can find (a, b, c) from the set described by (12) for which cases 1), 2) and 3) hold. System 4) is obviously not compatible.

◇ Theorem is proved.

Remark 5. Let us compare the net flow matrix D and the integral utility matrix $U = U(F)$ in cases $1, 2$ and 3.

In case 1, consecutive interaction prevails:

$$signD(F) = \begin{bmatrix} 0 & - & - \\ + & 0 & - \\ + & + & 0 \end{bmatrix}, \quad signU(F) = \begin{bmatrix} + & - & + \\ + & + & - \\ + & + & + \end{bmatrix}.$$

In case 2, parallel interaction prevails:

$$signD(F) = \begin{bmatrix} 0 & - & - \\ + & 0 & - \\ + & + & 0 \end{bmatrix}, \quad signU(F) = \begin{bmatrix} + & - & - \\ + & + & - \\ + & - & + \end{bmatrix}.$$

Case 3 describes a system state in which all relations are equal:

$$signD(F) = \begin{bmatrix} 0 & - & - \\ + & 0 & - \\ + & + & 0 \end{bmatrix}, \quad signU(F) = \begin{bmatrix} + & - & - \\ + & + & - \\ + & + & + \end{bmatrix}.$$

We see that the goal function J takes its maximum value when consecutive interaction prevails in the system. Thus, consecutive interaction is preferable from the viewpoint of the goal function J.

Figure 5 illustrates these qualitative conclusions about the structure of the system at which different values of the goal function J are realized. Three areas in three-dimensional space where the axes correspond to $x = \dfrac{f_{21}}{f_{10}}, \quad y = \dfrac{f_{31}}{f_{10}}, \quad x = \dfrac{f_{32}}{f_{21}}$.

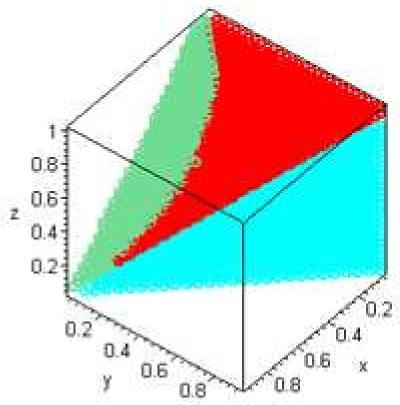

Fig. 5. The domains three-compartment complex.

Three areas colored in red, blue, and green correspond to areas described in *Theorem 4*. Namely, the red central area corresponds to systems with value of goal function equal 2. The blue area corresponds to systems with the goal function value equal to 7/2 and the green equal to 5/4. Supposing that the probability of a system to exhibit concrete values is proportional to the volume of the corresponding area, we can notice that position with $J(F) = 7/2$ (blue) is the most probable position for the system, and position with $J(F) = 5/4$ (green) is the least probable. Therefore, the highest mutualism value is most likely to occur and the lowest, the least likely to occur.

Example 5: a cyclic interaction

Let us consider an example of an interaction for a three-compartment cyclic model assuming each compartment receives an inflow from the system and produces an outflow to the system (Fig. 6).

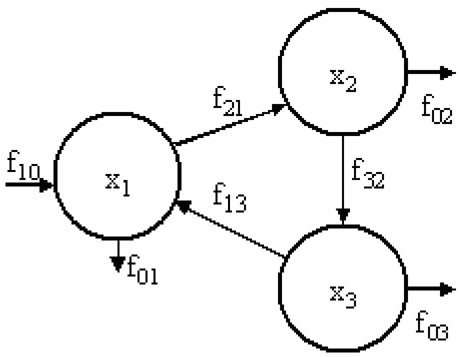

Fig. 6. Cyclic interaction.

Remark 6. First, let us consider the case where $f_{10} = 0$ (Fig. 7).

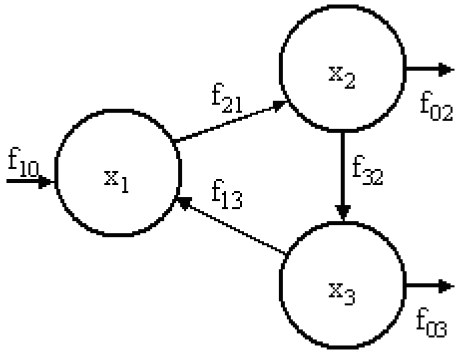

Fig. 7. Cyclic interaction without the outflow f_{10} .

The direct flow matrix F for this network is

$$F = \begin{bmatrix} 0 & 0 & f_{13} \\ f_{21} & 0 & 0 \\ 0 & f_{32} & 0 \end{bmatrix}, \tag{13}$$

where due to *(ii)* the total throughflow for each component are

$$T_1 = f_{10} + f_{13} = f_{21}, \quad T_2 = f_{21} = f_{32} + f_{02}, \quad T_3 = f_{32} = f_{13} + f_{03}.$$

Structural constraints *(i)* on elements of the matrix F are:

$$0 < f_{21} < f_{10}, \quad 0 < f_{32} < f_{21}, \quad 0 < f_{13} < f_{32}. \tag{14}$$

The direct utility flow matrix D corresponding to the given matrix F (13) is

$$D = D(F) = \begin{bmatrix} 0 & -\frac{f_{21}}{T_1} & \frac{f_{13}}{T_1} \\ \frac{f_{21}}{T_2} & 0 & -\frac{f_{32}}{T_2} \\ -\frac{f_{13}}{T_3} & \frac{f_{32}}{T_3} & 0 \end{bmatrix} = \begin{bmatrix} 0 & -1 & \frac{f_{13}}{f_{21}} \\ 1 & 0 & -\frac{f_{32}}{f_{21}} \\ -\frac{f_{13}}{f_{32}} & 1 & 0 \end{bmatrix}.$$

Let

$a = \frac{f_{32}}{f_{21}}, \quad b = \frac{f_{13}}{f_{32}}.$

Then the structural constraints (14) become $a, b \in (0, 1)$. Then

$$D = \begin{bmatrix} 0 & -1 & ab \\ 1 & 0 & -a \\ -b & 1 & 0 \end{bmatrix}.$$

A characteristic polynomial for this matrix $D = D(F)$ is

$\det(U - \lambda I) = \lambda(\lambda^2 + ab^2 + a + 1)$

and hence eigenvalues become,

$\lambda_1 = 0$, $\lambda_2 = i\sqrt{ab^2 + a + 1}$, $\lambda_3 = -i\sqrt{ab^2 + a + 1}$.

As $ab^2 + a + 1 > 1$ then for model with structure (13) and constraints (14) the condition *(iii)* is never satisfied. Thus, assumption is inappropriate, and we come back to the case where $f_{01} > 0$ (Fig. 6).

The direct flow matrix F is

$$F = \begin{bmatrix} 0 & 0 & f_{13} \\ f_{21} & 0 & 0 \\ 0 & f_{32} & 0 \end{bmatrix}, \tag{15}$$

where due to *(ii)* the total throughflows

$$T_1 = f_{10} + f_{13} = f_{21} + f_{01}, \quad T_2 = f_{21} = f_{32} + f_{02}, \quad T_3 = f_{32} = f_{13} + f_{03}.$$

Structural constraints *(i)* on elements of the matrix F are:

$$0 < f_{21} < f_{10}, \quad 0 < f_{32} < f_{21}, \quad 0 < f_{13} < f_{32}. \tag{16}$$

The direct utility flow matrix D corresponding to the given matrix F (15) is

$$D = D(F) = \begin{bmatrix} 0 & -\frac{f_{21}}{T_1} & \frac{f_{13}}{T_1} \\ \frac{f_{21}}{T_2} & 0 & -\frac{f_{32}}{T_2} \\ -\frac{f_{13}}{T_3} & \frac{f_{32}}{T_3} & 0 \end{bmatrix} = \begin{bmatrix} 0 & -\frac{f_{21}}{f_{01}+f_{21}} & \frac{f_{13}}{f_{01}+f_{21}} \\ 1 & 0 & -\frac{f_{32}}{f_{21}} \\ -\frac{f_{13}}{f_{32}} & 1 & 0 \end{bmatrix}.$$

Let

$a = \frac{f_{32}}{f_{21}}, \quad b = \frac{f_{13}}{f_{32}}, \quad c = \frac{f_{21}}{f_{01}+f_{21}}, \quad d = \frac{f_{13}}{f_{01}+f_{21}}.$

Then the structural constraints (16) turn into $a,\ b,\ c,\ d \in (0,1)$. Seeing that $ab = \dfrac{d}{c} = \dfrac{f_{31}}{f_{21}}$, we concluded that $d = abc$. Then

$$D = \begin{bmatrix} 0 & -c & abc \\ 1 & 0 & -a \\ -b & 1 & 0 \end{bmatrix}, \quad \text{sign}D = \begin{bmatrix} 0 & - & + \\ + & 0 & - \\ - & + & 0 \end{bmatrix}.$$

A characteristic polynomial for $D = D(F)$ is

$\det(D - \lambda I) = \lambda(\lambda^2 + ab^2c + a + c) = 0.$

Hence,

$\lambda_1 = 0,\ \lambda_2 = i\sqrt{ab^2c + a + c},\ \lambda_3 = -i\sqrt{ab^2c + a + c}.$

Coming back to our initial notations, we write a condition guaranteeing *(iii)* as follows:

$$\left| \frac{f_{13}^2}{f_{32}(f_{21} + f_{01})} + \frac{f_{32}}{f_{21}} + \frac{f_{21}}{f_{21} + f_{01}} \right| < 1. \tag{17}$$

Remark 7. Let us show that there exist networks whose flow matrices F satisfy (17). Let us consider the case of constant compartments' efficiency. In other words let us assume that each compartment transports a constant fraction of its inflow, $p \in (0,1)$, to the next compartment. Then we have

$\dfrac{f_{21}}{f_{21} + f_{01}} = \dfrac{f_{32}}{f_{21}} = \dfrac{f_{13}}{f_{32}} = p.$

In this case (17) turns into $p^4 + 2p - 1 < 0$. Let us notice that $y(p) = p^4 + 2p - 1$ increases on the interval (0,1), $y(0) = -1 < 0,\ y(1) = 2 > 0$. Hence, there exists a $\widehat{p} \in (0,1)$ such that for all $p \in (0, \widehat{p})$ (17) holds.

Constraints (16), (17) describe a class Φ of matrices F of form (15).

Theorem 5. Let the class Φ of admissible matrices F of form (15) be defined by (16), (17). Then for all $F \in \Phi$

$$J(F) = \frac{7}{2}.$$

Proof. As earlier, we construct an integral utility matrix $U = U(F)$. We have

$$\det(I-D) = 1 + a + c + ab^2c > 0, \quad \widehat{(I-D)} = \begin{bmatrix} 1+a & abc-c & abc+ac \\ 1+ab & 1+ab^2c & abc-a \\ 1-b & 1+cb & 1+c \end{bmatrix}.$$

Consequently,

$$U = \frac{1}{(1+a+c+ab^2cb)} \begin{bmatrix} 1+a & abc-c & abc+ac \\ 1+ab & 1+ab^2c & abc-a \\ 1-b & 1+cb & 1+c \end{bmatrix}, \ \mathrm{sign}U = \begin{bmatrix} + & - & + \\ + & + & - \\ + & + & + \end{bmatrix},$$

$$J(F) = \frac{S_+(F)}{S_-(F)} = \frac{7}{2}.$$

◇ The theorem is proved.

Remark 8. Let us compare the net flow matrix D and the integral utility matrix U. We see that the link that completes the cycle (a flow from X_3 to X_1) and represents competition in matrix D, turns into mutualism in matrix U. Note that the value of the goal function J is the same as in the case of consequent interaction (*Example 1*).

$$\mathrm{sign}D = \begin{bmatrix} 0 & - & + \\ + & 0 & - \\ - & + & 0 \end{bmatrix}, \quad \mathrm{sign}U = \begin{bmatrix} + & - & + \\ + & + & - \\ + & + & + \end{bmatrix}.$$

4 Ecological models with arbitrary number of components

Example 6: consecutive n-component chains

Earlier we showed that for three-compartment systems a chain assuming consecutive interactions only provides a maximal value to the goal function.

Let us consider a system with an arbitrary number of n compartments $(n \geq 3)$, in which all interactions are consecutive (see Fig. 8).

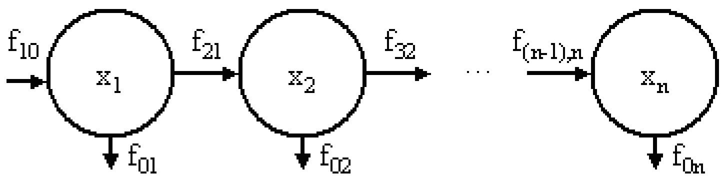

Fig. 8. Consecutive interaction in an n-component chain.

The direct flow matrix F for this network is:

$$F = \begin{bmatrix} 0 & 0 & 0 & \dots & 0 \\ f_{21} & 0 & 0 & \dots & 0 \\ 0 & f_{32} & 0 & \dots & \dots \\ \dots & \dots & \dots & \dots & 0 \\ 0 & 0 & \dots & f_{n,(n-1)} & 0 \end{bmatrix}. \tag{18}$$

Due to *(ii)* the total throughflows are:

$$T_1 = f_{10}, \quad \dots, \quad T_n = f_{n,(n-1)}.$$

Structural constraints *(i)* are:

$$0 < f_{21} < f_{10}, \quad \dots, \quad 0 < f_{n,(n-1)} < f_{(n-1),(n-2)}. \tag{19}$$

The direct utility flow matrix D corresponding to the given matrix F (18) is

$$D = \begin{bmatrix} 0 & -\frac{f_{21}}{T_1} & 0 & \dots & 0 \\ \frac{f_{21}}{T_2} & 0 & -\frac{f_{32}}{T_2} & \dots & 0 \\ 0 & \frac{f_{32}}{T_3} & 0 & \dots & \dots \\ \dots & \dots & \dots & \dots & -\frac{f_{n,(n-1)}}{T_{n-1}} \\ 0 & 0 & \dots & \frac{f_{n,(n-1)}}{T_n} & 0 \end{bmatrix} = \begin{bmatrix} 0 & -\frac{f_{21}}{T_1} & 0 & \dots & 0 \\ 1 & 0 & -\frac{f_{32}}{T_2} & \dots & 0 \\ 0 & 1 & 0 & \dots & \dots \\ \dots & \dots & \dots & \dots & -\frac{f_{n,(n-1)}}{T_{(n-1)}} \\ 0 & 0 & \dots & 1 & 0 \end{bmatrix}.$$

Let

$a_i = \frac{f_{(i+1),i}}{T_i}, \quad (i = 1, \dots, n-1).$

Then structural constraints (19) turn into $a_i \in (0,\, 1)\, (i = 1, \dots, n-1)$. We have

$$D = \begin{bmatrix} 0 & -a_1 & 0 & \dots & 0 \\ 1 & 0 & -a_2 & \dots & 0 \\ 0 & 1 & 0 & \dots & \dots \\ \dots & \dots & \dots & \dots & -a_{n-1} \\ 0 & 0 & \dots & 1 & 0 \end{bmatrix}.$$

Assumption 1. Convergence conditions for infinite chains have been explored in [1] with the conclusion that for equal transfer ratios less than 0.25, convergence is met. We assume that the convergence condition is satisfied for the direct flow matrix (18). Constraints (19) and the assumption describe a class of matrices (18).

Our result for systems under consideration is the following.

Theorem 6. For all matrixes F (18), which satisfy to the conditions (19) and the Assumption, it holds that

$$J(F) = \begin{cases} 3 & \text{if} \quad \text{n is even,} \\ \dfrac{3n^2+1}{n^2-1} & \text{if} \quad \text{n is odd.} \end{cases}$$

Proof. First, let us prove a lemma.

Lemma 1. Let $a_i \in (0,\, 1)\, (i = 1, \dots, n-1)$. Then for any $n \times n$ matrix of the form

$$A_n = \begin{bmatrix} 0 & a_1 & 0 & \dots & 0 \\ -1 & 0 & a_2 & \dots & 0 \\ 0 & -1 & 0 & \dots & \dots \\ \dots & \dots & \dots & \dots & a_{n-1} \\ 0 & 0 & \dots & -1 & 0 \end{bmatrix}$$

it holds that

$D_n = \det A_n > 1.$

Proof. Let us prove by induction that for any n we have an increasing sequence of determinants

$D_n > D_{n-1} > \cdots > D_1 = 1.$

First, we prove this for $n = 2$. From direct calculations we get

$D_1 = 1, \quad D_2 = 1 + a_1 = D_1 + a_1.$ As $a_1 \in (0,1)$ we have $D_2 > D_1$.

Now let the statement of Lemma 1 hold for some $n = k$,

$D_k > D_{k-1} > \ldots > D_1.$

We will show that it holds for $n = k+1$. The next recursive equation holds [6]:

$D_{k+1} = D_k + a_k D_{k-1}, \quad k \geq 3.$

By assumption 1 $a_k \in (0,1)$. Thus we get

$D_{k+1} > D_k > \ldots > D_1 = 1.$

⋄ *Lemma is proved.*

Proof of Theorem 6. By assumption

$U = \sum_{m=0}^{\infty} D^m = (I - D)^{-1}.$

We have

$$I - D = \begin{bmatrix} 1 & a_1 & 0 & \ldots & 0 \\ -1 & 1 & a_2 & \ldots & 0 \\ 0 & -1 & 1 & \ldots & \ldots \\ \ldots & \ldots & \ldots & \ldots & a_{n-1} \\ 0 & 0 & \ldots & -1 & 1 \end{bmatrix}, \tag{20}$$

$$(I - D)^{-1} = \frac{(\widehat{I - D})}{\det(I - D)},$$

where $(\widehat{I - D})$ is the adjoint matrix to the matrix $(I - D)$ [6].

It follows from the Lemma 1, $\det(I - D) > 1$. Hence the latter determinant does not influence the signs of the elements of the integral utility matrix U. Therefore, to prove the theorem it is sufficient to specify the signs of the elements of the matrix $(\widehat{I - D})$. We have

$$(\widehat{I - D}) = \begin{bmatrix} (\widehat{I - D})_{11} & (\widehat{I - D})_{21} & \ldots & (\widehat{I - D})_{n1} \\ (\widehat{I - D})_{12} & (\widehat{I - D})_{22} & \ldots & (\widehat{I - D})_{n2} \\ \ldots & \ldots & \ldots & \ldots \\ (\widehat{I - D})_{1n} & (\widehat{I - D})_{2n} & \ldots & (\widehat{I - D})_{nn} \end{bmatrix}$$

where $(\widehat{I - D})_{ij}$ is the algebraic complement to the elements $(I - D)_{ji}$ of the matrix $(I - D)$.

We divide the rest of the proof in three parts.

1. Let us find the signs of the diagonal elements $(\widehat{I - D})_{ii}$ $(i = 1, \ldots, n)$. By direct

calculations from (20) we get that for any $i = 1, \dots, n$

$$(\widehat{I-D})_{ii} = \det \begin{pmatrix} A_{i-1} & 0 \\ 0 & A_{n-i} \end{pmatrix} = \det A_{i-1} \cdot \det A_{n-i},\ \det A_0 = 1$$

where

$$A_{i-1} = \begin{bmatrix} 1 & a_1 & 0 & \dots & 0 \\ -1 & 1 & a_2 & \dots & 0 \\ 0 & -1 & 1 & \dots & \dots \\ \dots & \dots & \dots & \dots & a_{i-2} \\ 0 & 0 & \dots & -1 & 1 \end{bmatrix}, A_{n-i} = \begin{bmatrix} 1 & a_{i+1} & 0 & \dots & 0 \\ -1 & 1 & a_{i+2} & \dots & 0 \\ 0 & -1 & 1 & \dots & \dots \\ \dots & \dots & \dots & \dots & a_{n-1} \\ 0 & 0 & \dots & -1 & 1 \end{bmatrix}.$$

According to Lemma 1 $\det A_{i-1} > 0$, $\det A_{n-i} > 0$, and hence, $(\widehat{I-D})_{ii} > 0$ $(i = 1, \dots, n)$.

2. Let us find the signs of the elements $(\widehat{I-D})_{ij}$ $(i < j,\ \ i = 1, \dots, n,\ j = 2, \dots, n-1)$. Located below the main diagonal by direct calculations we get that for every $i < j$

$(\widehat{I-D})_{ij} = \det A_{i-1} \cdot \det A_{n-j}, \quad \det A_0 = 1,$

where A_{i-1}, A_{n-j} are given by (20). By lemma 1 $\det A_{i-1} > 0$, $\det A_{n-j} > 0$, therefore, $(\widehat{I-D})_{ij} > 0$ $(i < j,\ \ i = 1, \dots, n,\ \ j = 2, \dots, n-1)$.

3. Let us find the signs of the elements located above the main diagonal $(\widehat{I-D})_{ij}$ $(i > j,\ \ i = 2, \dots, n-1,\ \ j = 1, \dots, n)$. By direct calculations we get that for every $i > j$

$(\widehat{I-D})_{ij} = (-1)^{i+j} \cdot \prod_{k=j}^{i-1} a_k \cdot \det A_{j-1} \cdot \det A_{n-i}, \quad \det A_0 = 1,$

The inclusion $a_k \in (0,1)$ and Lemma 1 imply that $\det A_{j-1} > 0$, $\det A_{n-i} > 0$. Therefore, $\prod_{k=j}^{i-1} a_k \cdot \det A_{j-1} \cdot \det A_{n-i} > 0$. Thus every element of either the matrix $(\widehat{I-D})$ or the matrix U which is located above the main diagonal, is positive if $i + j$ is even, and is negative if $i + j$ is odd.

Consequently,

if n is even, then:

$$\text{sign}U = \begin{bmatrix} + & - & + & \dots & - & + & - \\ + & + & - & \dots & + & - & + \\ + & + & + & \dots & - & + & - \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ + & + & + & \dots & + & + & + \end{bmatrix},$$

and if n is odd, then:

$$\text{sign}U = \begin{bmatrix} + & - & + & \dots & + & - & + \\ + & + & - & \dots & - & + & - \\ + & + & + & \dots & + & - & + \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ + & + & + & \dots & + & + & + \end{bmatrix}.$$

In both cases above the main diagonal the “sub-diagonals” consisting of minuses alternate with the “sub-diagonals” consisting of pluses. A difference between these two cases consists in the following for an even n the element of the top is a minus, and for an odd n it is a plus.

Thus,

if n is even, then:

$$S_-(F) = \underbrace{1 + 3 + 5 + \ldots + (n-1)}_{\frac{n}{2}} = \frac{1 + (n-1)}{2} \cdot \frac{n}{2} = \frac{n^2}{4},$$

$$S_+(F) = n^2 - S_-(F) = \frac{3n^2}{4}, \quad J(F) = 3;$$

if n is odd,then:

$$S_-(F) = \underbrace{2 + 4 + 6 + \ldots + (n-1)}_{\frac{(n-1)}{2}} = \frac{2 + (n-1)}{2} \cdot \frac{(n-1)}{2} = \frac{n^2 - 1}{4},$$

$$S_+(F) = \frac{3n^2 + 1}{4}, \quad J(F) = \frac{3n^2 + 1}{n^2 - 1}.$$

⋄ The theorem is proved.

Remark 9. Therefore for infinite chains with consecutive interactions the integral flow matrix can be constructed for an arbitrary number of compartments. We see that any compartment of a network distant from the first element at an even length of the chain gets a plus in the integral flow matrix, i.e. this element interacts with the first one positively. On the other hand, an element distant from the first one at an odd distant is negatively related to the latter. *Example 1* illustrates this statement for $n = 3$.

Remark 10. One can prove that the value of the goal function tends to 3 (from above) as the length of the chain tends to infinity:

$$\lim_{n \to \infty} J(F) = 3.$$

Example 7: parallel interaction in n–component networks

As a second n–compartment example let us consider a system $(n \geq 3)$, in which one component, X_n, acts as a sink for flows coming from all other components (X_n is a top-down controller) (Fig. 9). All components, except for the consumer X_n compete for a common resource. The logic suggested in section 3, implies that this structure is worst for maximizing the goal function. It is natural to assume that in the considered case the value of the goal function should approach zero as n increases to infinity. Let us prove it.

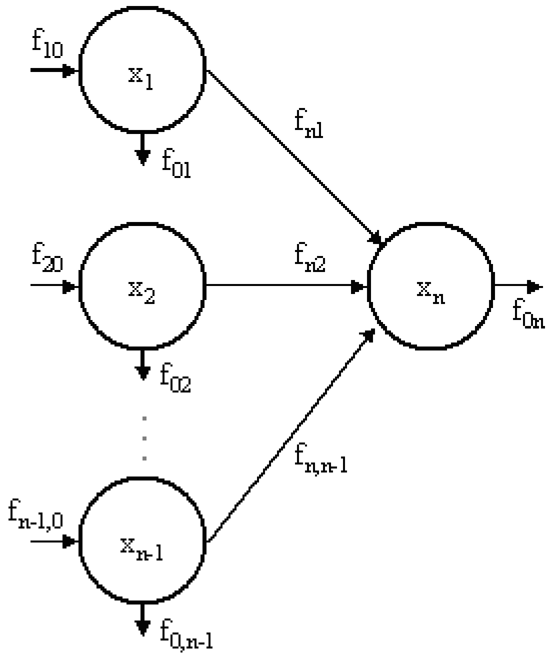

Fig. 9. Parallel interaction in an n-component network with one predator.

Introduce the relevant class Φ of admissible matrices F. The direct flow matrix is

$$F = \begin{bmatrix} 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & 0 \\ f_{n,1} & f_{n,2} & \dots & f_{n,(n-1)} & 0 \end{bmatrix}, \qquad (21)$$

where due to *(ii)* the throughflows for each component are:

$$T_1 = f_{10} = f_{n1} + f_{01}, \dots, T_{n-1} = f_{(n-1),0} = f_{n,(n-1)} + f_{0,(n-1)}, T_n = f_{0n} = \sum_{i=1}^{n-1} f_{ni}.$$

Structural constraints *(i)* on elements of F are the following:

$$0 < f_{n1} < f_{10}, \quad \dots, \quad 0 < f_{n,(n-1)} < f_{(n-1),0}. \qquad (22)$$

The direct utility flow matrix D corresponding to F (21) has the form

$$D = \begin{bmatrix} 0 & 0 & \dots & 0 & -\frac{f_{n1}}{T_1} \\ 0 & 0 & \dots & 0 & -\frac{f_{n2}}{T_2} \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & -\frac{f_{n,(n-1)}}{T_{(n-1)}} \\ \frac{f_{n1}}{T_n} & \frac{f_{n2}}{T_n} & \dots & \frac{f_{n,(n-1)}}{T_n} & 0 \end{bmatrix} = \begin{bmatrix} 0 & 0 & \dots & 0 & -\frac{f_{n1}}{f_{10}} \\ 0 & 0 & \dots & 0 & -\frac{f_{n2}}{f_{20}} \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & -\frac{f_{n,(n-1)}}{f_{(n-1),0}} \\ \frac{f_{n1}}{\sum_{i=1}^{n-1} f_{ni}} & \frac{f_{n2}}{\sum_{i=1}^{n-1} f_{ni}} & \dots & \frac{f_{n,(n-1)}}{\sum_{i=1}^{n-1} f_{ni}} & 0 \end{bmatrix}.$$

Let

$a_i = \frac{f_{ni}}{T_i}$, $\quad b_i = \frac{f_{ni}}{T_n} \quad (i = 1, \dots, n-1)$.

Then the structural constraints (22) become $a_i,\ b_i \in (0,1) \quad (i = 1, \dots, n)$, and we have

$$D = \begin{bmatrix} 0 & 0 & \dots & 0 & -a_1 \\ 0 & 0 & \dots & 0 & -a_2 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & -a_{n-1} \\ b_1 & b_2 & \dots & b_{n-1} & 0 \end{bmatrix}, \quad \text{sing}D = \begin{bmatrix} 0 & 0 & \dots & 0 & - \\ 0 & 0 & \dots & 0 & - \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & - \\ + & + & \dots & + & 0 \end{bmatrix}.$$

Lemma 2. For all matrices F of the form (21) satisfying (22) condition *(iii)* holds.

Proof. We construct the characteristic polynomial for the direct utility flow matrix D and estimate the magnitude of its eigenvalues. We have

$$\det(D - \lambda I) = \begin{vmatrix} -\lambda & 0 & \dots & 0 & -a_1 \\ 0 & -\lambda & \dots & 0 & -a_2 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & -\lambda & -a_{n-1} \\ b_1 & b_2 & \dots & b_{n-1} & -\lambda \end{vmatrix}.$$

Multiplying the first row by $\frac{b_1}{\lambda}$, the second row by $\frac{b_2}{\lambda}$ etc, and adding all the rows to the row n row (which does not change the determinant), we get

$$\det(D - \lambda I) = \begin{vmatrix} -\lambda & 0 & \dots & 0 & -a_1 \\ 0 & -\lambda & \dots & 0 & -a_2 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & -\lambda & -a_{n-1} \\ 0 & 0 & \dots & 0 & -\lambda - \frac{1}{\lambda}\sum_{i=1}^{n-1} a_i b_i \end{vmatrix}.$$

The characteristic equation $\det(D - \lambda I) = 0$ turns into

$\lambda^{n-2}\left(\lambda^2 + \sum_{i=1}^{n-1} a_i b_i\right) = 0.$

We see that

$\lambda_1 = \lambda_2 = \ldots = \lambda_{n-2} = 0, \quad \lambda_{n-1} = i\sqrt{\sum_{i=1}^{n-1} a_i b_i}, \quad \lambda_n = -i\sqrt{\sum_{i=1}^{n-1} a_i b_i}.$

Let us prove that $\sum_{i=1}^{n-1} a_i b_i < 1$ which is equivalent to: $\sum_{i=1}^{n-1} \frac{f_{ni}}{T_i}\frac{f_{ni}}{T_n} < 1$ or

$$\frac{f_{n1}^2}{f_{10}(f_{n1} + \cdots + f_{n,(n-1)})} + \cdots + \frac{f_{n,(n-1)}^2}{f_{(n-1),0}(f_{n1} + \cdots + f_{n,(n-1)})} < 1.$$

Multiplying both parts of the last inequality by $f_{10} \dots f_{(n-1),0}(f_{n1} + \cdots + f_{n,(n-1)}) > 0$, we get

$$f_{n1}^2 \dots f_{(n-1),0} + \cdots + f_{n,(n-1)}^2 f_{10} \dots f_{(n-2),0} < f_{10} \dots f_{(n-1),0}\left(f_{n1} + \cdots + f_{n,(n-1)}\right) \Leftrightarrow$$

$$f_{n1} \dots f_{(n-1),0}(f_{n1} - f_{10}) + \cdots + f_{n,(n-1)} f_{10} \dots f_{(n-2),0}(f_{n,(n-1)} - f_{(n-1),0}) < 0.$$

Due to (22) the multipliers in the brackets are negative, and hence $\sum_{i=1}^{n-1} a_i b_i < 1$.

◇ *Lemma 2* is proved.

Thus constraints (22) describe a class Φ of admissible matrices F of form (21). The main result of this section is the following.

Theorem 7. For all matrices F of form (21) whose elements satisfy conditions (22), it holds that

$$J(F) = \frac{2n-1}{(n-1)^2}.$$

Proof. For finding elements of the integral utility matrix we use formula $U = (I-D)^{-1}$ and apply the following algorithm described [6]. We build the tended matrix $[(I-D)|I]$ and transform its rows so that the matrix $I-D$ turns into a unitary matrix I, whereas the inverse matrix replaces $(I-D)^{-1}$. Then the tended matrix is transformed into

$$[(I-D)|I] = \left[\begin{array}{cccc|cccc} 1 & \dots & 0 & a_1 & 1 & \dots & 0 & 0 \\ 0 & \dots & 0 & a_2 & 0 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 1 & a_{n-1} & 0 & \dots & 1 & 0 \\ -b_1 & \dots & -b_{n-1} & 1 & 0 & \dots & 0 & 1 \end{array}\right].$$

Multiplying the first row by b_1, the second row by b_2, and so on, adding rows 1 through n+1 to row n, and then dividing row n by $1+\sum_{i=1}^{n-1} a_i b_i$, we get

$$[(I-D)|I] =$$

$$= \left[\begin{array}{cccc|cccc} 1 & \dots & 0 & a_1 & 1 & \dots & 0 & 0 \\ 0 & \dots & 0 & a_2 & 0 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 1 & a_{n-1} & 0 & \dots & 1 & 0 \\ 0 & \dots & 0 & 1 & \frac{b_1}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \dots & \frac{b_{n-1}}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \frac{1}{(1+\sum_{i=1}^{n-1} a_i b_i)} \end{array}\right].$$

Now we multiply the row n by $(-a_{n-1})$, add it to row (n-1), multiply row n by $(-a_{n-2})$ and add it to row (n-2) and so on, and finally multiply row n by $(-a_1)$ and add it to row 1. We get

$$[(I-D)|I] =$$

$$= \left[\begin{array}{cccc|cccc} 1 & \dots & 0 & 0 & 1-\frac{b_1 a_1}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \dots & -\frac{b_{n-1} a_1}{(1+\sum_{i=1}^{n-1} a_i b_i)} & -\frac{a_1}{(1+\sum_{i=1}^{n-1} a_i b_i)} \\ 0 & \dots & 0 & 0 & -\frac{b_1 a_2}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \dots & -\frac{b_{n-1} a_2}{(1+\sum_{i=1}^{n-1} a_i b_i)} & -\frac{a_2}{(1+\sum_{i=1}^{n-1} a_i b_i)} \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 1 & 0 & -\frac{b_1 a_{n-1}}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \dots & 1-\frac{b_{n-1} a_{n-1}}{(1+\sum_{i=1}^{n-1} a_i b_i)} & -\frac{a_{n-1}}{(1+\sum_{i=1}^{n-1} a_i b_i)} \\ 0 & \dots & 0 & 1 & \frac{b_1}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \dots & \frac{b_{n-1}}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \frac{1}{(1+\sum_{i=1}^{n-1} a_i b_i)} \end{array}\right].$$

Thus,

$$U = (I - D)^{-1} = \begin{bmatrix} 1 - \dfrac{b_1 a_1}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \dots & -\dfrac{b_{n-1} a_1}{(1+\sum_{i=1}^{n-1} a_i b_i)} & -\dfrac{a_1}{(1+\sum_{i=1}^{n-1} a_i b_i)} \\ -\dfrac{b_1 a_2}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \dots & -\dfrac{b_{n-1} a_2}{(1+\sum_{i=1}^{n-1} a_i b_i)} & -\dfrac{a_2}{(1+\sum_{i=1}^{n-1} a_i b_i)} \\ \dots & \dots & \dots & \dots \\ -\dfrac{b_1 a_{n-1}}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \dots & 1 - \dfrac{b_{n-1} a_{n-1}}{(1+\sum_{i=1}^{n-1} a_i b_i)} & -\dfrac{a_{n-1}}{(1+\sum_{i=1}^{n-1} a_i b_i)} \\ \dfrac{b_1}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \dots & \dfrac{b_{n-1}}{(1+\sum_{i=1}^{n-1} a_i b_i)} & \dfrac{1}{(1+\sum_{i=1}^{n-1} a_i b_i)} \end{bmatrix}.$$

Since $a_i, b_i \in (0,\,1)$ $(i = 1, \dots, n-1)$ and $\sum_{i=1}^{n-1} a_i b_i < 1$, we have

$$\text{sign}U = \begin{bmatrix} + & - & \dots & - & - \\ - & + & \dots & - & - \\ \dots & \dots & \dots & \dots & \dots \\ - & - & \dots & + & - \\ + & + & \dots & + & + \end{bmatrix}.$$

Finally, $S_+(F) = 2n - 1$, $S_-(F) = n^2 - (2n-1) = (n-1)^2$, $J(F) = \dfrac{2n-1}{(n-1)^2}$.

◇ The theorem is proved.

Remark 11. We have shown that indeed for the given case the following asymptotic result takes place:

$$\lim_{n \to \infty} J(F) = 0.$$

Remark 12. Our previous analysis of three-component systems shows that a type of competition does not influence the value of goal function (is robust to the type of competition). Accordingly a result similar to (Theorem 7) holds true for networks in which one component is preyed upon by all other components (Fig. 10). We omit the exact formulation.

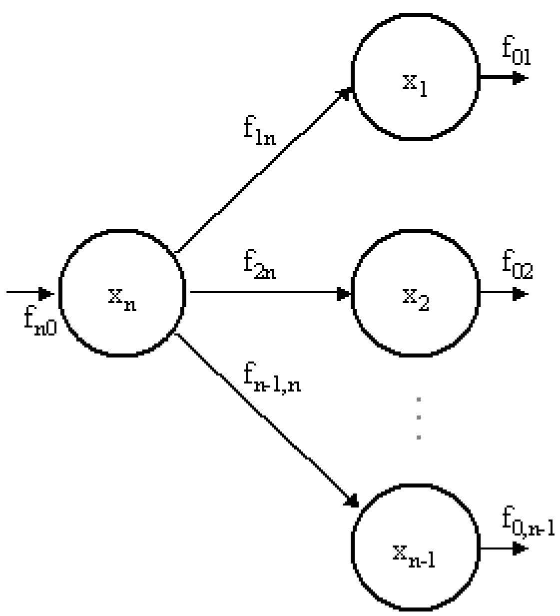

Fig. 10. Parallel interaction in an n-component network with one source.

Example 8: cyclic interaction in n-component networks

As a third "infinite" network example let us consider a system with arbitrary number n of components $(n \geq 3)$ in which all the components form a cycle (Fig. 11). Let us recall that considering three-component networks we get the following result: the goal function J takes the same value, 7/2, for the consequent chain and a cycle of n components (see Remark 8). It may lead to the conclusion that adding one additional link to close the cycle does not change the value of the goal function. But in this section we show that generally it does not hold - as the number of system's components increases the value of J for a cyclic network tends to infinity. Let us demonstrate this fact.

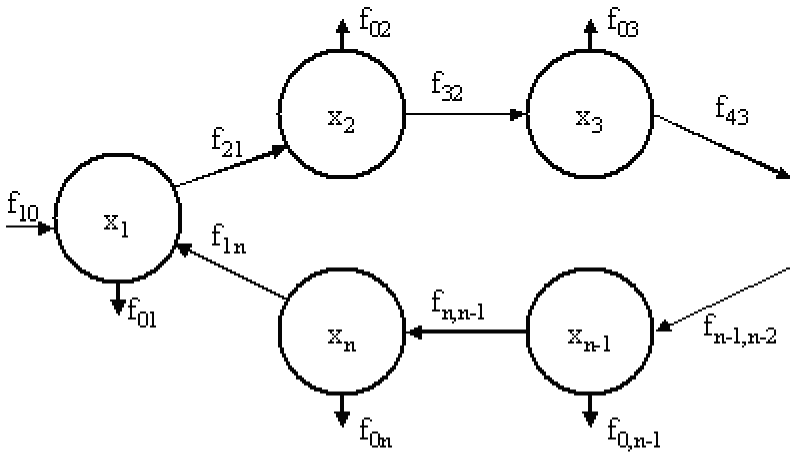

Fig. 11. Cyclic interaction in an n-component chain.

The direct flow matrix F is

$$F = \begin{bmatrix} 0 & 0 & \dots & 0 & f_{1,n} \\ f_{21} & 0 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & f_{n,(n-1)} & 0 \end{bmatrix}, \tag{23}$$

where due to *(ii)* the total throughflow at each component are

$$T_1 = f_{21} + f_{01} = f_{1n} + f_{10},$$

$$T_i = f_{i,(i-1)} = f_{0i} + f_{(i+1),i} \, (i = 2, \dots, n-1),$$

$$T_n = f_{n,(n-1)} = f_{1n} + f_{0n}.$$

The structural constraints *(i)* on elements of the matrix F are

$$0 < f_{21} < f_{10} + f_{1n}, \quad f_{(i+1),i} < f_{i,(i-1)} \, (i = 2, \dots, n-1), \quad f_{1n} < f_{n,(n-1)} \tag{24}$$

The net flow matrix D corresponding to the given matrix F (23) is

$$D = \begin{bmatrix} 0 & -\frac{f_{21}}{T_1} & \dots & 0 & \frac{f_{1n}}{T_1} \\ \frac{f_{21}}{T_2} & 0 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & -\frac{f_{n,(n-1)}}{T_{n-1}} \\ -\frac{f_{1n}}{T_n} & 0 & \dots & \frac{f_{n,(n-1)}}{T_n} & 0 \end{bmatrix} = \begin{bmatrix} 0 & -\frac{f_{21}}{T_1} & \dots & 0 & \frac{f_{1n}}{T_1} \\ 1 & 0 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & -\frac{f_{n,(n-1)}}{T_{n-1}} \\ -\frac{f_{1n}}{T_n} & 0 & \dots & 1 & 0 \end{bmatrix}$$

Let

$a_{ij} = \frac{f_{ji}}{T_i} \quad (i = 1, \dots, n-1,\ j = 2, \dots, n), \quad a_{1n} = \frac{f_{1n}}{T_1}, \quad a_{n1} = \frac{f_{1n}}{T_n},$

Then the structural constraints (24) become $a_{ij} \in (0,1) \quad (i, j = 1, \dots, n)$. Then

$$D = \begin{bmatrix} 0 & -a_{12} & \dots & 0 & a_{1n} \\ 1 & 0 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & -a_{(n-1),n} \\ -a_{n1} & 0 & \dots & 1 & 0 \end{bmatrix}, \quad \text{sign}D = \begin{bmatrix} 0 & - & \dots & 0 & + \\ + & 0 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & - \\ - & 0 & \dots & + & 0 \end{bmatrix}.$$

Assumption 2. We assume that for all matrices F of form (23) satisfying (24) condition *(iii)* holds.

Thus constraints (24) together with Assumption 2 describe a class Φ of admissible matrices F of form (23). An analysis of particular cyclic networks of dimensions 3, 4, etc. shows that regardless of the number of components in a network integral utility matrix U consists of pluses only except for its “above-diagonal diagonal” elements. We summarize it as a conjecture.

Conjecture 1. For all matrices F of form (23) whose elements satisfy (24) and Assumption 2, it holds that

$$J(F) = \frac{n^2 - n + 1}{n - 1},$$

Remark 13. Conjecture 1 implies that the integral utility matrix has the form

$$\text{sign}U = \begin{bmatrix} + & - & + & \dots & + & + & + \\ + & + & - & \dots & + & + & + \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ + & + & + & \dots & + & + & - \\ + & + & + & \dots & + & + & + \end{bmatrix}.$$

We see that the link that completes the cycle in the network (a flow from X_n to X_1) and represents competition in matrix D turns into mutualism in matrix U and all initially neutral relations become positive. Thus, it turns out that for all compartments it is favorable to be included in consecutive interaction if there is a cycle in the network.

5 Conclusions

In this research, we found analytical solutions for the network utility goal function under several structural configurations. For example, the three compartment food chain always resulted in a mutualism ratio of 7/2, and two three-compartment competition models had a ratio of 5/4. In a more complex interaction (*Example 4*) the mutualism ratio is not constant but depends on the parameter values governing flow between the components. Interestingly though, in this example, the solution that exhibited the highest mutualism ratio was the one that had the highest probability of occurring and the lowest ratio the lowest probability.

Furthermore, certain structural configurations result in greater number of positive relationship types than others, which leads one to ask if there is an optimal structure that maximizes the network mutualism ratio. In the last three examples, all dealing with arbitrarily long chains, it was found that the mutualism ratio converges to a value of 3 as n increases and the network with one source and infinite predators converges to a mutualism ratio of zero, meaning that this is not a favorable configuration. Before one can conclude that it is the most unfavorable it would be necessary to show that it converges more rapidly than any other configuration. The most interesting case is the infinite cycle (*Example 8*) since here the mutualism ratio diverges without bound as the number of component in the cycle increase. It is also interesting to note that each component has a positive relation with every other one in the network except the one that is directly feeding on it. This indicates that components benefit greatly by inserting themselves in a cyclic process because they are mutualists with all the other components except one. This result documenting the beneficial nature of cycles is consistent with the work done on cycles and auto-catalysis as a organizing ecosystem principle [8, 11]. This also supports the observation that systems tend to self-organize into these network structures. Ecologically, auto-catalytic cycles with 3 components have been observed, but there may be other factors limiting the development of longer auto-catalytic cycles such as energy limitations or stability, even though they would gain greater network mutualism.

While real ecosystem webs are much more complex than the examples here, these examples represent decompositions of these larger systems into smaller manageable subunits. Analytic solutions of more complex structures are not possible, but the methodology to determine the relationship types and number of beneficial relations can be applied numerically to any system. Further studies of empirical systems are needed to assess the overall trend of network mutualism and whether they are "preferred" configurations in nature, but this research clearly shows that some structures have more beneficial relations than others. The question "Does nature tend to self-organize into structures that exhibit high levels of network mutualism?" is an interesting one that requires additional research.

References

[1] Fath BD. 2006. A non-thermodynamic constraint to trophic transfer efficiency based on network utility analysis. *International Journal of Ecodynamics.* 1, 28-43.

[2] Fath BD. 2007. Community-level Relations and Network Mutualism. Accepted in Ecol. Model.

[3] Fath BD, Patten BC. 1998a. Network orientors: "Utility" as a goal function. In: Muller F, Leupelt M. (eds.) Eco Targets, Goal Functions, and Orientors, Springer-Verlag, New York. 161-176.

[4] Fath BD, Patten BC. 1998b. Network synergism: Emergence of positive relations in ecological systems. Ecol. Model., 107, 127-143.

[5] Fath BD, Patten BC,Choi JS. 2001. Complementarity of ecological goal functions. J. Theor. Biol., 208, 493-506.

[6] Gantmakher FR. 1959. Theory of matrices (translated from the Russian 1954 version). Chelsea Publishing Company.

[7] Morowitz HJ. 1968. Energy Flow in Biology, Academic, New York.

[8] Muller F, Leupelt M. (eds.). 1998. Eco Targets, Goal Functions, and Orientors, Springer-Verlag, New York.

[9] Patten BC. 1991. Network ecology: indirect determination of the life-environment relationship in ecosystems. In Higashi, M. and Burns T.P. (Eds.), Theoretical Ecosystem Ecology: The Network Perspective. London, Cambridge University Press, 288-351.

[10] Patten BC. 1992. Energy, emergy and environs. Ecol. Model. 62, 29-69.

[11] Ulanowicz RE. 1986. Growth and Development: Ecosystems Phenomenology. Springer-Verlag, New York, 203.