Dynamical and system-wide properties of linear flow-quantified food webs

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ABSTRACT

This paper analyses the transient dynamics, steady states, and a set of diagnostic system-wide properties of a linear flow-quantified pastoral food web from the Chernivtsi Region of Ukraine. The web in question is one of 31 so-described; it contains 86 nodes and 496 links. On-line simulation and network analysis software EcoNet was used to quantify transient dynamics, steady states, and eleven system-wide index parameters. Food-web flows were classified into inputs, interior flows, and outputs. The last two (endogenous) were represented by linear, mass-balance, flow coefficients. The three sets, inputs plus these coefficients, were systematically manipulated in their entirety in different combinations over seven orders of magnitude to determine their effects on system properties. The results of these trials are described and interpreted. They show that linear descriptions of empirical food webs harbor considerable dynamic and relational complexity.

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1. Introduction

Ecologists speak freely of "linear" and "nonlinear" ecological systems, but few realize these terms mean more than linear or curvilinear regressions of empirical data. The defining property of a linear dynamical system is input–output *superposition*, meaning a linear combination of inputs generates the same linear combination of outputs. Inputs and outputs can be constants or time varying; superposition holds or not in either case (Oppenheim, 1965; Oppenheim et al., 1997; Worden and Tomlinson, 2001). A system without this is nonlinear. Linearity is an important property because systems that have it tend to be well-behaved, reliable, and stable whereas those lacking it express erratic dynamics, unreliability, and instability. Using "stability" here we mean resistance/resilience expressed in the original Lyapunov (1992) bounded/asymptotic stability concepts. One analytical consequence of superposition is the *decomposition property*. Linear dynamics are decomposable into a component due to internal state, and another generated by external inputs. The two components together sum to give observed dynamics. Inside and outside components operate also in nonlinear dynamics, but these cannot be separated into distinct behavioral elements.

In ecological literature the adjective "simple" frequently modifies the term "linear system" in the mistaken belief that linear systems are necessarily simple, therefore inappropriate for description of "complex" ecological systems. Because of expected simplicity, it can be surprising when linear systems behavior proves non-simple (Patten, 1975, 1983). This is what we confronted in the preliminaries to this study when we parameterized linearly formulated food-web models differently and examined their steady-state characteristics. Variation of internal flows and external inputs over several orders of magnitude gave identical steady states. We knew from theory that initial conditions make no contribution to steady states of linear systems, only to the rates at which these are approached. But this was different because it was not initial conditions we changed, but rather the rate coefficients that determine dynamics. We first thought, based on our knowledge of dominant network indirect effects associated with higher order (longer) pathways (Patten, 1984; Higashi and Patten, 1989), that the relatively large sizes of our webs caused a high degree of network homogenization such that integral energy-matter propagations equaled out. It appeared the systems absorbed all perturbations induced by external influences and came to the same (numerically identical) final states. We set out to explore the reasons for our observations by systematically manipulating our systems' parameters over a wide range of values.

Two ecological questions can be asked by way of motivating the current study. First, ecologists are interested in how their systems operate and respond to changes in network flows? Systematic study of inputs, interior flows, and outputs in controlled situations that modeling allows can lend understanding to such questions. Second, ecologists widely believe that linear systems are simple in their organization and dynamics. This study will show quite the contrary—that linear systems can be quite complex in their

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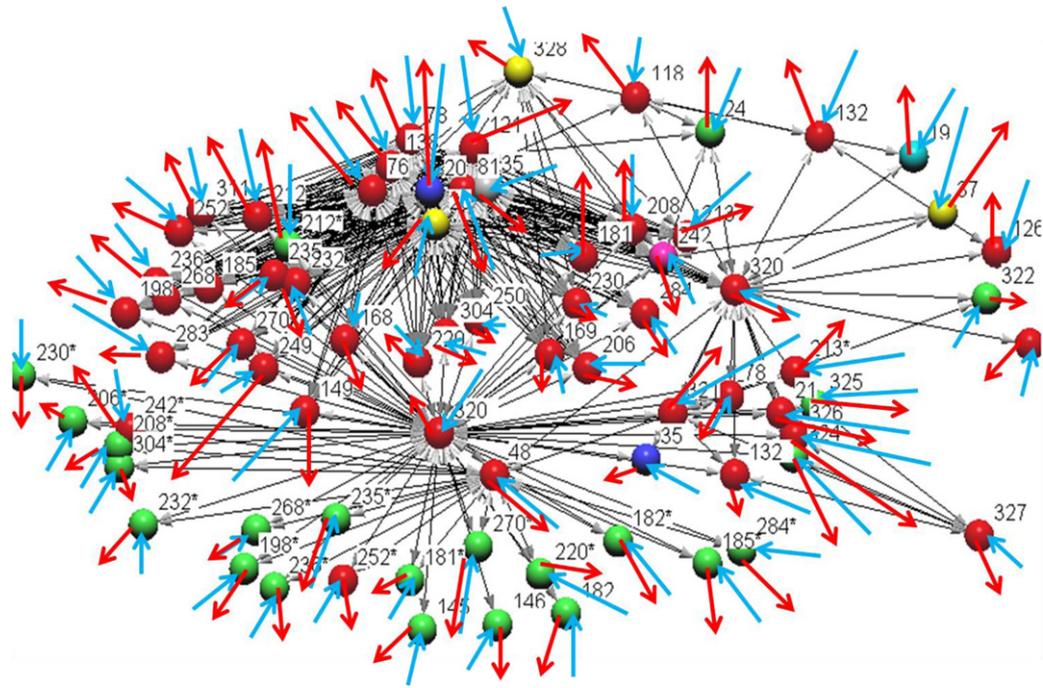
Fig. 1. Qualitative node-link digraph of the food web of the Vikno (Chernivtsi Region, Ukraine) pastoral ecosystem. Nodes represent trophic compartments (86). Directed links represent trophic flows between compartments (496), and inputs and outputs to and from the environment (86 each). Appendix 1 (on-line supplement) lists numerical codes for each node and gives compartmental descriptions.

dynamic properties. Their defining property of superposition is not a prescription for simplicity, only for well-behavedness. We show distinctly complex well-behavedness in this investigation. Our results demonstrate how complex linear dynamics can emerge under superposition through a combination of variations in parameter values expressed over high numbers of indirect pathways that typify real food webs.

The current paper is the first of a planned series of mathematical exercises designed to reveal the sources of dynamic and complexity properties hidden within connected ecological networks.

2. Materials and methods

2.1. Study area

We studied food webs of 31 public pastoral ecosystems distributed throughout the Chernivtsi Region of Western Ukraine ($47°43'$–$48°41'$ N × $24°55'$–$27°30'$ E). These grasslands, unmanaged since 1992, are used as commons for cattle pasturing.

2.2. Sampling

Biological samples for food-web analysis were gathered during peak growing seasons (June–July) in years 2005, 2006, and 2007. Plant and insect specimens were identified as much as possible to species. Earthworms (subclass Oligochaeta) were separated by a standard method, Quantitative Hand Sorting (Fasulaty, 1971). Microbiological soil analysis was based on cell counts of three microbial groups: Heterotrophic Bacteria, Fungi (Micromycetes), and Ray Fungi (Actinomycetes). Cattle density was counted as number of animals/100 m^2. Several faunal groups were omitted because they were too difficult to measure with available resources. This impacts our food webs as descriptions, but still allows their comparative study as our sampling and analysis methods were standardized.

2.3. 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 analyze our food webs we used software Pajek (Batagelj and 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, $j = 1, \ldots, n$ 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 ($f_{ij} = 0$).

In general we found 494 compartments and 14,525 feeding links between them throughout 31 researched pastoral food webs within a study area of Chernivtsi Region. Identification numbers and taxonomic names of compartments are listed in Appendix 1 (on-line data supplement).

We consider it important to include non-living compartments in our food webs as these represent process of energy and matter cycling in ecosystems. Investigation of the feeding history of pastoral species shows that such non-living compartments as **Cattle Excrement**, **Plant Litter**, **Animal Litter**, and **Detritus** are important sources for different colonies of decomposers. Each of these four distinct stages of the decomposition process plays a separate feeding role in pastures and has its specific consumers.

In this paper we focus on one of the 31 food webs, for the pastoral ecosystem Vikno located in the northern part of the Chernivtsi Region ($48°34'$ N–$25°58'$ E). This web (Fig. 1) has $n = 86$ compartments, each with a boundary input, z_i [$ML^{-2} T^{-1}$], and output y_i [$ML^{-2} T^{-1}$], and $\sum a_{ij} = 496$ interior links. The basic network statistics for the food web under investigation are summarized

in Appendix 2. The food web for Vikno has 47% basal compartments, which are represented by pastoral plant species. The top consumers (23%) are mostly represented by cattle, carnivorous insects, and decomposers. Intermediate species represent 30% of compartments.

The pasture web in its essential properties could represent any system. What is important is these essential web properties captured in actual extensive empirical data.

3. Food webs as linear systems

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

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

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

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

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

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

For simulations, we used the simulation and network analysis software EcoNet 2.1 Beta (Kazanci, 2007). EcoNet features the donor-controlled flow type of Eq. (2) that enables us to accomplish linear analysis of flow-quantified food webs. As shown in the diagram below, we performed three kinds of parameter manipulations and use the following notations to indicate these: *inter-compartmental flow coefficients*, c_F; *output flow coefficients*,

c_Y; and *input flows*, Z; c_F, c_Y, and Z denote parameter sets.
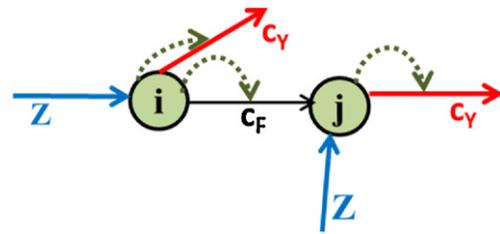
4. System-wide properties

For comparisons of system responses to parameter manipulations, we used the set of system-wide index properties employed in EcoNet. These are fully described in the EcoNet documentation but brief descriptions and abbreviations are provided below, ordered by how parameter changes pattern their responses. The topology of the studied food web remains unchanged through different model parameterizations. Thus, the first two properties (Connectance and Link Density) do not change their values as they are graph-structured and the graph is fixed. The second set of properties (five) is based on ratios that make them intensive or non-dimensional. The third set (three) is extensive or dimensional.

4.1. Structural properties

1. *Link Density* (**LD**) – number of links (L) per node (N) (Gardner and Ashby, 1970; May, 1972, 1973; Cohen et al., 1990; Bersier and Sugihara, 1997):

$$\mathbf{LD} = \frac{L}{N}.$$

2. *Connectance* (**C**) – quotient of number of actual and possible links (Gardner and Ashby, 1970; May, 1972, 1973; Cohen, 1978; Cohen and Briand, 1984; Cohen et al., 1990):

$$\mathbf{C} = \frac{L}{N^2}.$$

4.2. Intensive/nondimensional properties

3. *Finn Cycling Index* (**FCI**) – fraction of total system throughflow that cycles (Finn, 1976):

$$\mathbf{FCI} = \frac{TST_c}{TST}$$

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

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

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).

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

5. *Aggradation Index* (**AI**) – average path length, the average number of compartments a unit of introduced flow passes through before exiting the system (Patten and Fath, 1998; Ulanowicz et al., 2006):

$$\mathbf{AI} = \frac{TST}{z_1 + z_2 + \cdots + z_n}.$$

6. *Synergism Index* (**SI**) – ratio of sums of positive (benefit) to negative (cost) entries in network utility analysis matrices specifying pairwise compartment relations (Fath and Patten, 1999; Fath and Borrett, 2006).

7. *Mutualism Index* (**MI**) – ratio of number of positive (+) to negative (−) signs in network utility analysis matrices specifying kinds of pairwise interactions (Fath and Patten, 1999; Fath and Borrett, 2006).

8. *Homogenization Index* (**HI**) – measures uniformity of network flows (Fath and Patten, 1999).

4.3. Extensive/dimensional properties

9. *Total System Throughflow* (**TST**) – sum of compartment through-flows (Dame, 1996); dependent on ecosystem structure (Hannon, 1973; Finn, 1976; Han, 1997):

$$\mathbf{TST} = T_1 + T_2 + \cdots + T_n.$$

10. *Ascendency* (**AS**) – degree of network development that includes mutual network information and **TST** (Ulanowicz, 1986, 1997; Patrício et al., 2004; Ulanowicz et al., 2006):

$$\mathbf{AS} = \text{TST} \cdot \text{I},$$

where I is the degree of organization (mutual network information) with which the exchanges between compartments are processed:

$$\text{I} = k \sum \left(\frac{f_{ij}}{\text{TST}} \right) \log \left(\frac{f_{ij} x_0^2}{\text{TST} x_{0,i} x_{0,j}} \right),$$

k a constant.

11. *Development Capacity* (**DC**) – network flow organization, the upper bound of ascendancy (depending on **TST** and flow structure). It is calculated as the product of **TST** by diversity of flow structure estimated using the Shannon (1948) information formula (Ulanowicz, 1986).

5. Model parameterizations

All 31 of our empirical food webs are qualitative; they can be represented as unweighted directed graphs (digraphs; e.g., Fig. 1). Our weighting (quantification) of these to explore system dynamics is arbitrary but systematic. For the Vikno food web this means manipulating all c_F = {496 parameters} and c_Y = **Z** = {86 parameters} at a time, but in different combinations.

To check the robustness of our results over a wide range of system dynamics, the parameter values were varied over seven orders of magnitude in each EcoNet run, as follows: 0.001, 0.01, 0.1, 1, 10, 100, and 1000. The scheme of experimental manipulations is summarized and diagrammed below, going from simple to more complex combinations:

1. *Type 1 paramerizations* – one parameter set varied, the other two held constant and equal to 1.
   1.1. c_Y varied:
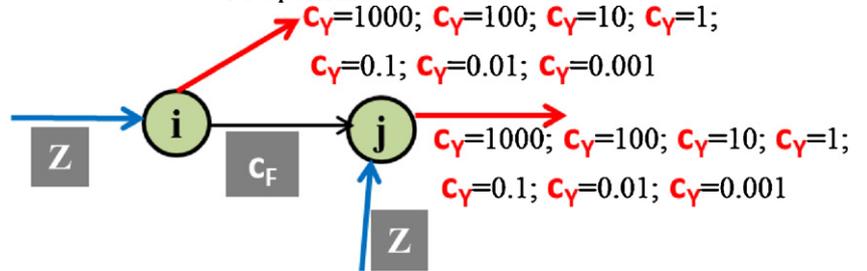
   1.2. c_F varied
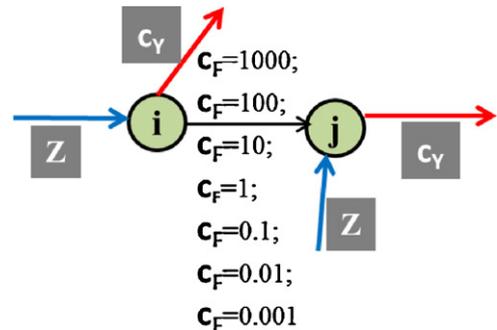
   1.3. **Z** varied
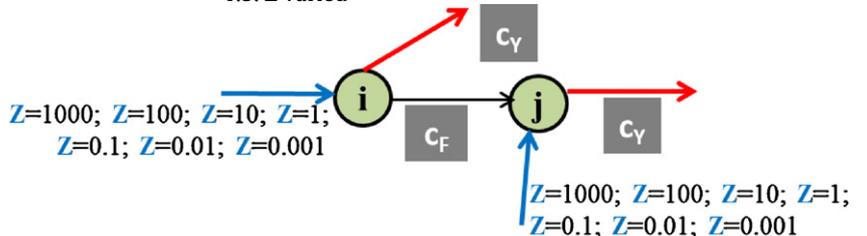
2. *Type 2 paramerizations* – two parameter sets varied, the remaining one held constant and equal to 1.

2.1. c_Y and c_F varied:
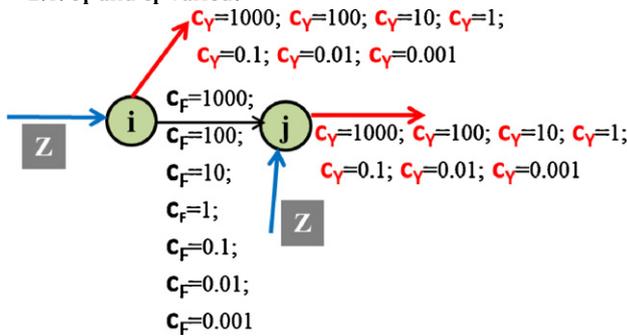
2.2. c_Y and Z varied:
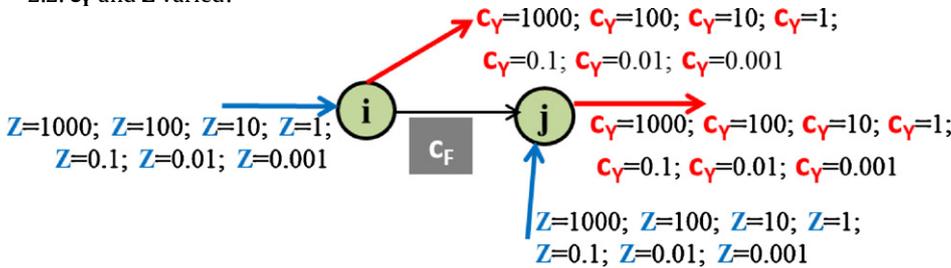
2.3. c_F and Z varied:
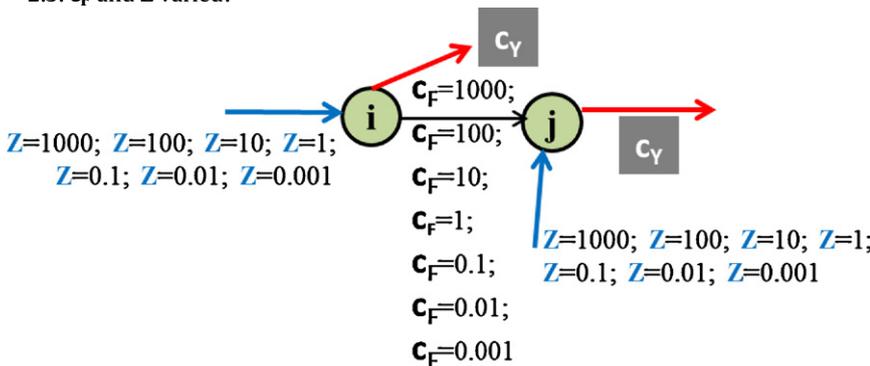
3. *Type 3 paramerizations* – all three parameter sets, c_Y, c_F and Z, varied.
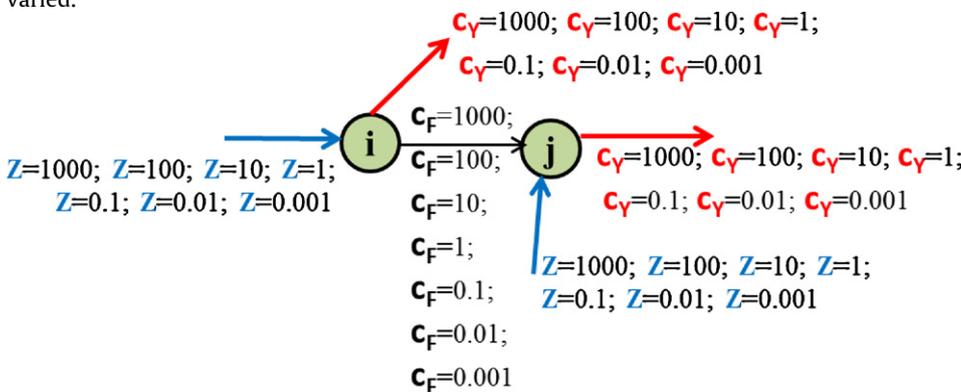
6. Results

6.1. Type 1 parameterization (endogenous)

EcoNet run Types 1.1 (c_Y varied; Table 1) and 1.2 (c_F varied; Table 2) showed unchanging system-wide properties at steady state, but in the two cases the magnitude relations associated with the different c_F/c_Y ratios (upper panels) are reversed. As the Z values are fixed, the observed results are determined by these ratios.

As shown in Fig. 2, steady states increase with increasing c_F/c_Y ratios under unit inputs, Z.

6.2. Type 2 parameterization

Results for a Type 2.1 run are shown in Table 3 and Fig. 3. Both c_F and c_Y were manipulated, but in such a way that their ratio always remained the same, $c_F/c_Y = 1$. Under these conditions, all the system-wide properties (Table 3) and the resultant steady

Table 1
System-wide properties at steady state under Type 1.1 parameterization (c_Y varied).

Parameterization details							
Ratio c_F/c_Y	0.001	0.01	0.1	1	10	100	1000
c_F per c_Y	1/1000	1/100	1/10	1/1	1/0.1	1/0.01	1/0.001
$Z = 1$, $c_F = 1$	$c_Y = 1000$	$c_Y = 100$	$c_Y = 10$	$c_Y = 1$	$c_Y = 0.1$	$c_Y = 0.01$	$c_Y = 0.001$
Structural properties							
LD	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744
C	0.0670633	0.0670633	0.06706	0.06706	0.06706	0.06706	0.06706
Intensive/non-dimensional properties							
FCI	2.11E−07	2.22E−05	0.00262	0.08611	0.26219	0.30918	0.31468
IEI	0.0036678	0.0362087	0.31693	1.85894	5.01298	6.1953	6.3476
AI	1.00573	1.05406	1.40222	3.34185	9.00885	12.0452	12.488
SI	178.424	17.454	3.04961	1.80404	1.65613	1.63774	1.63583
MI	0.714816	0.698278	0.81008	0.80655	0.78303	0.78777	0.78045
HI	0.407337	0.427637	0.59473	1.31849	1.62723	1.63312	1.63302
Extensive/dimensional properties							
TST	86.4925	90.649	120.591	287.4	774.761	1035.89	1073.97
AS	117.855	116.5	156.627	432.08	1121.67	1501.84	1563.74
DC	504.826	525.866	665.014	1251.67	2573.04	3226.03	3319.9

Table 2
System-wide properties at steady state under Type 1.2 parameterization (c_F varied).

Parameterization details							
Ratio $c_F/c_{Y=}$	0.001	0.01	0.1	1	10	100	1000
c_F per c_Y	0.001/1	0.01/1	0.1/1	1/1	10/1	100/1	1000/1
$Z = 1$, $c_Y = 1$	$c_F = 0.001$	$c_F = 0.01$	$c_F = 0.1$	$c_F = 1$	$c_F = 10$	$c_F = 100$	$c_F = 1000$
Structural properties							
LD	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744
C	0.0670633	0.0670633	0.06706	0.06706	0.06706	0.06706	0.0670633
Intensive/non-dimensional properties							
FCI	2.11E−07	2.22E−05	0.00262	0.08611	0.26219	0.30918	0.314678
IEI	0.003667	0.0362087	0.31693	1.85894	5.01298	6.1953	6.3476
AI	1.00573	1.05406	1.40222	3.34185	9.00885	12.0452	12.488
SI	178.424	17.454	3.04961	1.80404	1.65613	1.63774	1.63583
MI	0.714816	0.698278	0.81008	0.80655	0.78303	0.78777	0.780453
HI	0.407337	0.427637	0.59473	1.31849	1.62723	1.63312	1.63302
Extensive/dimensional properties							
TST	86.4925	90.649	120.591	287.4	774.761	1035.89	1073.97
AS	117.855	116.5	156.627	432.08	1121.67	1501.84	1563.74
DC	504.826	525.866	665.014	1251.67	2573.04	3226.03	3319.9

state (Fig. 3) remained invariant but the time to reach the steady state increased in proportion to the coefficienct magnitudes. The unchanging steady state is the kind of result that, as described in the Introduction, first puzzled us and led us to pursue this research. It takes longer to reach steady state with decreasing coefficient values because the system operates more slowly as these are reduced.

Results for a Type 2.1 run with variable c_F/c_Y ratios are shown in Table 4 and Fig. 4. The c_F/c_Y ratios were varied over four orders or magnitude, 0.1, 1.0, 10, and 100 (Table 4, upper panel; ratio 1.0 in Table 3). In each case the system-wide properties are fixed within a ratio but variable between them. This is highlighted in Table 4 by the shaded or unshaded blocks of columns. Correspondingly, the steady states and dynamic rates of approach to them as a function

Table 3
System-wide properties at steady state under Type 2.1 parameterization in which c_F and c_Y were varied in fixed ratio, $c_F/c_Y = 1$.

Parameterization details								
	Ratio $c_F/c_Y = 1$							
$Z = 1$, $c_F = c_Y =$	1000	100	10	1	0.1	0.01	0.001	0.0001
Structural properties								
LD	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744
C	0.06706	0.06706	0.06706	0.06706	0.06706	0.06706	0.06706	0.06706
Intensive/non-dimensional properties								
FCI	0.08611	0.08611	0.08611	0.08611	0.08611	0.08611	0.08611	0.08611
IEI	1.85894	1.85894	1.85894	1.85894	1.85894	1.85894	1.85894	1.85894
AI	3.34185	3.34185	3.34185	3.34185	3.34185	3.34185	3.34185	3.34185
SI	1.80404	1.80404	1.80404	1.80404	1.80404	1.80404	1.80404	1.80404
MI	0.80655	0.80655	0.80655	0.80655	0.80655	0.80655	0.80655	0.80655
HI	1.31849	1.31849	1.31849	1.31849	1.31849	1.31849	1.31849	1.31849
Extensive/dimensional properties								
TST	287.4	287.4	287.4	287.4	287.4	287.4	287.4	287.4
AS	432.08	432.08	432.08	432.08	432.08	432.08	432.08	432.08
DC	1251.67	1251.67	1251.67	1251.67	1251.67	1251.67	1251.67	1251.67

Table 4
System-wide properties at steady state under Type 2.1 parameterization in which c_F and c_Y were varied in variable ratios c_F/c_Y spanning four orders of magnitude.

Parameterization details									
	0.1			10			100		
$c_F/c_Y =$	0.1	10	100						
c_F per c_Y	0.001/0.01	0.01/0.1	0.1/1	1/0.1	0.1/0.01	0.01/0.001	10/0.1	1/0.01	0.1/0.001
Structural properties									
LD	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744
C	0.0670633	0.06706	0.06706	0.06706	0.06706	0.0670633	0.06706	0.06706	0.067063
Intensive/non-dimensional properties									
FCI	0.0026198	0.00262	0.00262	0.26219	0.26219	0.26219	0.30918	0.30918	0.309183
IEI	0.316932	0.31693	0.31693	5.01298	5.01298	5.01298	6.1953	6.1953	6.1953
AI	1.40222	1.40222	1.40222	9.00885	9.00885	9.00885	12.0452	12.0452	12.0452
SI	3.04961	3.04961	3.04961	1.65613	1.65613	1.65613	1.63774	1.63774	1.63774
MI	0.810083	0.81008	0.81008	0.78303	0.78303	0.783028	0.78777	0.78777	0.787769
HI	0.594728	0.59473	0.59473	1.62723	1.62723	1.62723	1.63312	1.63312	1.63312
Extensive/dimensional properties									
TST	120.591	120.591	120.591	774.761	774.761	774.761	1035.89	1035.89	1035.89
AS	156.627	156.627	156.627	1121.67	1121.67	1121.67	1501.84	1501.84	1501.84
DC	665.014	665.014	665.014	2573.04	2573.04	2573.04	3226.03	3226.03	3226.03

of the coefficient magnitudes vary also (Fig. 4). These results hold across all 42 possible combinations of values within the current parameterization framework, as follows:

$$7Xc_F \times 7Xc_Y - 7Xc_F = c_Y = 42,$$
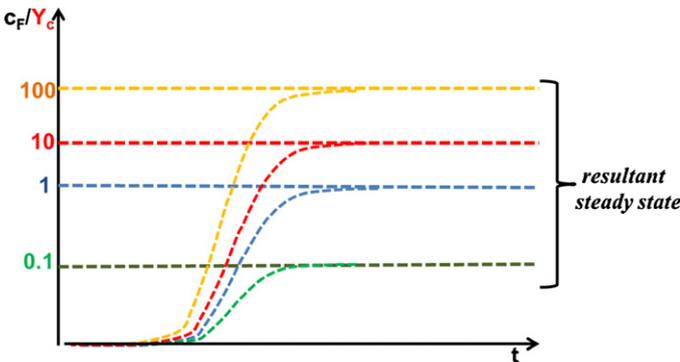
Fig. 2. Different system steady states produced by different c_F/c_Y ratios under fixed unit boundary inputs, **Z**. As interior flow coefficients c_F increase relative to boundary output coefficients c_Y, the steady states increase.
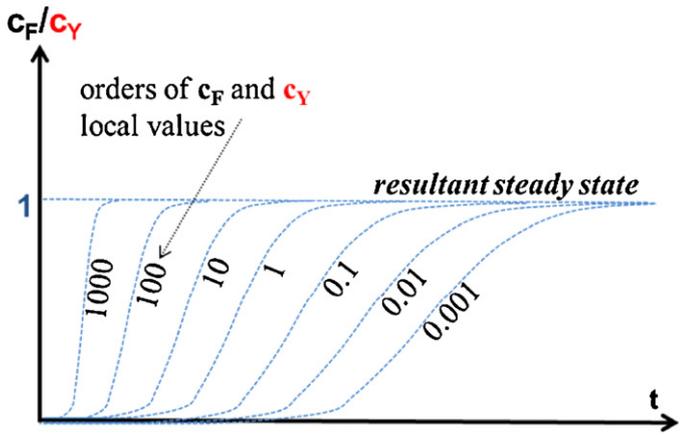
Fig. 3. Illustration of approaches to steady state under fixed inputs **Z** when values of both c_F and c_Y are changed over seven orders of magnitude, but in fixed ratio, $c_F/c_Y = 1$. Such changes make no difference in the system-wide properties (Table 3), thus the resultant steady-state magnitude is invariant, but the time required to reach it decreases as the c_F and c_Y values decrease.

where Xc_F are orders of magnitudes (0.001, 0.01, 0.1, 1, 10, 100, 1000) for c_F values, Xc_Y are orders of magnitudes (0.001, 0.01, 0.1, 1, 10, 100, 1000) for c_Y values, and $Xc_F = c_Y$ are orders of magnitudes (0.001, 0.01, 0.1, 1, 10, 100, 1000) for $c_F = c_Y$ when $c_F/c_Y = 1$.

The conclusion is that the ratios of internal flows to boundary outputs, not their individual magnitudes, determine the quantitative system-wide properties at steady state, but the magnitudes determine the time of development to steady state.

6.3. Type 1 parameterization (exogenous)

Internal flows and outputs are endogenous variables in system dynamics. Inputs are exogenous and it is of interest to also assess the role of these in the relationships under study. To approach this we fixed the internal flows (c_F) and environmental outputs (c_Y), and the c_F/c_Y ratio, to unit values and varied the inputs (**Z**). Table 5 shows the inputs have no effect on the intensive/non-dimensional properties (again, the kind of puzzling result that led to this study), but they do indeed determine extensive/dimensional properties (bottom panel). The changes are proportional to the magnitudes of the **Z** values. These same kinds of proportional changes extend to both the numerators and denominators of the intensive/non-dimensional set of properties with the result that these are invariant under input changes. Fig. 5 shows what at
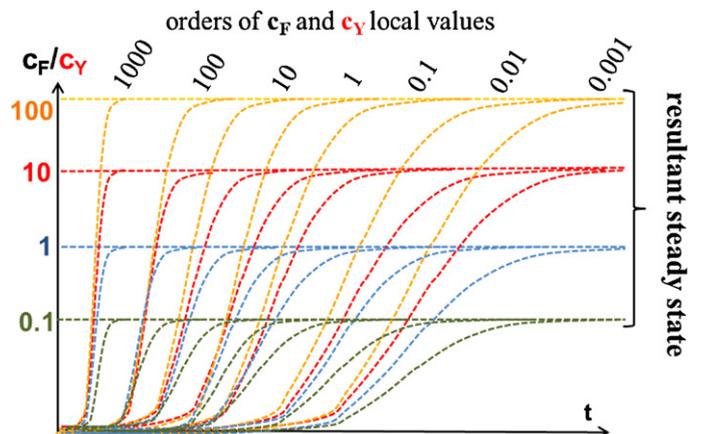
Fig. 4. Steady states produced by fixed unit inputs (**Z**) and variable c_F/c_Y ratios spanning four orders of magnitude. The c_F/c_Y ratios determine the magnitudes of the system-wide properties at each steady state, while the flows generated by c_F and c_Y values determine the development time to steady state.

Table 5
System-wide properties at steady state under Type 1.3 parameterization in which c_F, c_Y, and c_F/c_Y were set at unit values and Z was varied.

Parameterization details Ratio $c_F/c_Y = 1$							
$c_F = 1$, $c_Y = 1$	$Z = 1000$	$Z = 100$	$Z = 10$	$Z = 1$	$Z = 0.1$	$Z = 0.01$	$Z = 0.001$
Structural properties							
LD	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744	5.76744
C	0.067063	0.06706	0.06706	0.06706	0.06706	0.06706	0.06706
Intensive/non-dimensional properties							
FCI	0.086112	0.08611	0.08611	0.08611	0.08611	0.08611	0.08611
IEI	1.85894	1.85894	1.85894	1.85894	1.85894	1.85894	1.85894
AI	3.34185	3.34185	3.34185	3.34185	3.34185	3.34185	3.34185
SI	1.80404	1.80404	1.80404	1.80404	1.80404	1.80404	1.80404
MI	0.806546	0.80655	0.80655	0.80655	0.80655	0.80655	0.80655
HI	1.31849	1.31849	1.31849	1.31849	1.31849	1.31849	1.31849
Extensive/dimensional properties							
TST	287,400	28,740	2874	287.4	28.74	2.874	0.2874
AS	432,080	43,208	4320.8	432.08	43.208	4.3208	0.43208
DC	1.25E+06	125,167	12,516.7	1251.67	125.167	12.5167	1.25167
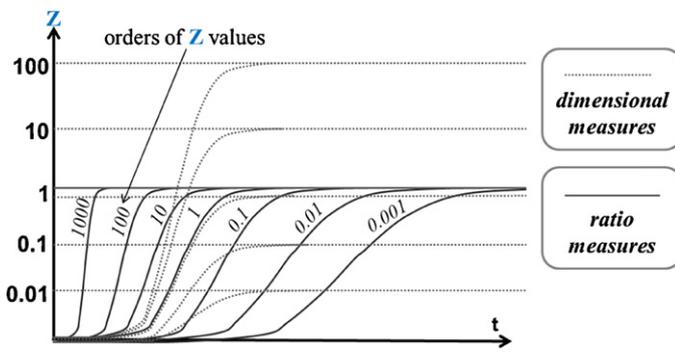
Fig. 5. Behavior patterns of dimensional vs. ratio system measures based upon changes in environmental inputs, Z. Increased inputs drive the dimensional system-wide properties to proportionally higher steady states, while ratio measures remain constant. The rates of reaching the steady states are proportional to the input magnitudes in all cases.

this point can be expected for the steady states. They hold constant for the ratio properties but change proportionally with the dimensional ones, and in both cases the rates of approach vary directly with the input magnitudes. This is expected on the basis that processing time is proportional to the quantity of substance introduced.

6.4. Type 3 parameterization

Finally, we checked the robustness of the foregoing results by systematically exploring the 343 possible combinations of values for the three parameter sets, c_F, c_Y, and Z, changing the orders of magnitudes of their values as follows:

$$7Xc_F \times 7Xc_Y \times 7X_Z = 343,$$

where Xc_F are orders of magnitudes (0.001, 0.01, 0.1, 1, 10, 100, 1000) for c_F values, Xc_Y are orders of magnitudes (0.001, 0.01, 0.1, 1, 10, 100, 1000) for c_Y values, and X_Z are orders of magnitudes (0.001, 0.01, 0.1, 1, 10, 100, 1000) for Z values.

The above results and general conclusions drawn from them were verified.

7. Discussion and conclusions

Linearity is an important property operating in ecological systems (Patten, 1975, 1983, 1998). In the Introduction we called attention to its basis in superposition, and the role of this defining property in creating well-behaved system dynamics. The latter

were clearly on display in our experimental parameter manipulations. We conducted many more of these than are described here, and the sum of them reinforced the results we have reported. The second point in the Introduction was the fact that linear systems too can be complex; superposition is not a prescription for simplicity, only for well-behavedness, and this does not necessarily mean simple.

The Vikno pasture food web is clearly a complex network structure (Fig. 1), and when parameterized to produce linear flows (Eq. (2)) this does not change. The linearity is expressed *through* the complexity. Its 86 compartments and 496 links translate (from knowledge of other models) into hundreds, perhaps thousands (we have not assessed this), of simple paths and cycles. Simple paths have no repeated nodes and simple cycles mean to first closure. Cycles enable pathways to extend and generate millions and millions of compound pathways (e.g., Patten, 1985). These are invisible in Fig. 1, and although individually, and increasingly, insignificant as they get longer, collectively these extended pathways are typically responsible for indirect effects being dominant features of ecological networks (e.g., Patten, 1984; Higashi and Patten, 1989).

All these characteristics were operating in the background of our exploration of the Vikno pasture food web. Our experimental parameterization trials were systematic, and superposition expressed through the known-to-be large-number network structure allowed behavioral results to be generated systematically as well. Real nature does not operate in such lock-step fashion, however. The result is complex system behavior that cannot be analyzed beyond empirical measurement is interpreted as nonlinear dynamics.

At this point, it remains only to summarize our results. We do so below, following each summary statement with a parenthetical comment about our expectations based on prior understanding:

1. The values of interior (**F**) and boundary output (**Y**) flow coefficients, c_F and c_Y, have no effect on the magnitudes of attained steady states (Fig. 3) or associated system-wide properties (Table 3). (This was unexpected; it is counterintuitive.)
2. It is ratios between interior and output flow-coefficients, c_F/c_Y, that determine, proportionally, the magnitudes of the resultant steady states (Fig. 2) and system-wide properties (Tables 1 and 2). (This was uncertain because interior flows are zero-sum, therefore gain/loss neutral, whereas outputs entail only loss.)
3. Under fixed unit inputs (**Z**), the values of interior and output flow coefficients, c_F and c_Y, determine the time of system development to steady state (Figs. 3–5). (This was expected from system dynamics considerations.)

4. The relationship of time of development to the c_F and c_Y coefficient magnitudes is direct (Figs. 3–5); higher coefficients generate faster dynamics, therefore shorter times to reach steady states. (This was expected from system dynamics considerations.)

5. With c_F/c_Y ratios fixed to unit values, inputs **Z** proportionally determined the magnitudes of steady states (Fig. 5) and extensive or dimensional system-wide properties at steady state (Table 5, bottom panel). (These results were expected).

6. However, with fixed unit values of c_F/c_Y ratios, inputs **Z** had no effect on values of the intensive or non-dimensional system-wide properties (Table 5, largest panel). (This was counterintuitive, but understandable after the fact because both numerators and denominators of the ratio indexes are equally affected).

7. In the two preceding cases the rates of approach to steady states varied directly with the **Z** magnitudes (Fig. 5). (This was expected because processing time should take longer if there is introduced more material to process).

These results show that linear models of empirical food webs can harbor considerable dynamic and relational complexity, which can be expected to complicate further study.

In continuing investigations we plan similar analyses to those reported here for several common formulations of nonlinear dynamics – Lotka–Volterra and Michaelis–Menten. Then, with the insights gained, we will endeavor to quantify our 31 food webs by link-tracking and compare their network properties across the pastoral landscapes of the Ukrainian Chernivtsi region.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2012.02.024.

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