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The Structure of Ecosystems

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Input–output theory is developed for an ecosystem in terms of production and respiration energy flows. The theory reveals a "structure" of the system by demonstrating the direct and indirect energy flow dependence of each member of the system upon the others. A method for tracing the direct and indirect element flows through the ecosystem is proposed.

The structure is determined for two examples and a perturbation technique for the energy flow is suggested.

1. Introduction

(A) GENERAL

In natural systems the currency is energy. Just as man has struggled for centuries to understand the dollar flow in his complex economic system, ecologists study the even more pervasive flow of energy in ecosystems. The interrelated flows of energy between lion, zebra, grass and sun for example are not too difficult to quantify. But what is the manner in which these truly interconnect? How dependent is the lion upon the sun? How do all the relationships change with time? When do the energy flows become steady?

There are methods which use complex systems of differential equations with energy as the dependent variable, which can roughly describe the changes in energy balance with time (Funderlic & Heath, 1971). Predator–prey and other mathematical system models have been developed (Lotka, 1956; Holling, 1966; Watt, 1968; Pielou, 1969). What seems not at all understood is the energy flow interdependence, both directly and indirectly, of each species upon the other, at any prescribed time. This I call the structure of the ecosystem, much like one refers to the structure of the economy (Leontief, 1965).

(B) DEFINITIONS

I have chosen definitions for energy flows in the system with the hope of being brief and as consistent with biological terminology as one could expect an engineer to be.

Because of the nature of the theory, I must group the energy inflows (e.g. sun) into the system with the intrasystem energy flows (e.g. grass consumed by zebras). This combination of inflows and intrasystem flows I call *production energy flow*. Thus the production system encompasses the energy sources and a prescribed number of individuals, species or trophic levels which I shall refer to as *components of the system*. Energy flows which leave the system, i.e. which have no consumer in the production system, such as component metabolism, net component growth in energy content and net energy content of exported biomass, I define collectively as *respiration energy flow*.

The term *input* is used to describe all the energy inflows to a given component. Thus inputs are exclusively production flows. *Output* describes all those energy flows which are stored in or flow from a component. A component's production and respiration energy outflows are its outputs.

The terms *direct* and *indirect energy flows* refer only to the inputs to a component. The *direct energy flow* refers to the actual energy flow through a component. *Indirect energy flow* represents those system flows, both production and respiration, that were necessary in order that the direct energy flow could occur through a given component. Thus a portion of the production and respiration energies of every component in the system is necessary so that the direct energy can occur through a specific component. The theory in this paper amounts to an allocation technique: the limit of an infinite distributing and summing process. The direct plus the indirect energy is referred to as the total energy flow.

If, during an experiment, the energy flows in an ecosystem are at the steady state condition, energy committed to net growth is negligible on the averages. Such a state of affairs allows one to ignore the energy content of the ecosystem when the major interest lies with the energy flows.

2. Theory

(A) GENERAL

Throughout this paper, matrices are in upper case boldface letters (e.g. **R**), vectors are represented by lower case boldface letters (e.g. **r**), and the matrix and vector elements are designated by lower case italic letters with the appropriate subscripts (e.g. r_i).

The production energy flows can be viewed in matrix form with each element of the matrix representing the energy output of the row (matrix) component used by the column (matrix) component for production and respiration by that column component.

Let the production matrix be **P** and its elements be p_{ij}. Let the respiration energy vector be **r** with elements r_i. Then by conservation of energy, the element of the direct energy flow vector **e**, for each component is

$$e_i = \sum_{j=1}^{n} p_{ij} + r_i, \tag{1}$$

where n is the number of system components.

Next we assume that the production energies of a species can be accurately expressed as a linear function of the direct energy flow of the consuming component for the specified instant of time. Thus,

$$p_{ij} = g_{ij} e_j, \tag{2}$$

where g_{ij} are the elements on the normalized production matrix **G**.

Substitution into equation (1) yields,

$$e_i = \sum_{j=1}^{n} g_{ij} e_j + r_i. \tag{3}$$

Equation (3) can be restated in matrix form and solved for **e**:

$$\mathbf{e} = \mathbf{G}\mathbf{e} + \mathbf{r} = (\mathbf{I} - \mathbf{G})^{-1}\mathbf{r}, \tag{4}$$

where **I** is the identity matrix. Equation (4) in element form is

$$e_i = \sum_{j=1}^{n} (I-G)_{ij}^{-1} r_j. \tag{5}$$

The physical conditions which assure that $(\mathbf{I}-\mathbf{G})^{-1}$ exists are important. Each irreducible block diagonal submatrix of **G**, defined as $\hat{\mathbf{G}}$ with elements $\hat{g}_{ij}$, must meet the following criterion: $\sum_i \hat{g}_{ij} \leq 1$ with the inequality holding for at least one j (Ortega, 1972). If the sun is included in the production matrix and with the recognition that every component in the system must have at least one non-zero input, always less than or equal to one, the conditions for the existence of $(\mathbf{I}-\mathbf{G})^{-1}$ are met. Inclusion of the sun as a production component guarantees that **G** is reducible to a block diagonal matrix with the primary producer column sum less than one. The presence of at least one non-zero element in all other columns provides the condition of irreducibility.

The $(I-G)_{ij}^{-1}$ are called the structural elements of the ecosystem since **r** can be varied to produce changes in **e** without changing $(\mathbf{I}-\mathbf{G})^{-1}$. Each element represents the total energy flow both directly and indirectly from the ith to the jth component per unit of respiration of the jth component. These elements are the key to understanding the interdependence of each component on the other.

Since the sun is included in the energy flow system as a separate component (which provides energy without respiring), it is possible to determine the direct and indirect demands on the sun by each component.

(B) ENERGY FLOW MATRIX

It is possible to make special interpretations of **r**. First, I can diagonalize the r_i to form a matrix **R**. Thus

$$\mathbf{E} = (\mathbf{I}-\mathbf{G})^{-1}\mathbf{R}. \tag{6}$$

Here **E** is a special total energy matrix in which each element e_{ij} is the total (direct and indirect) energy demand from the ith component by the jth component so that the jth component can respire at the necessary rate (see Table 5). The sum $\sum_i^n e_{ij}$ is defined as the total energy flow (direct and indirect) for the component j.

The formation of the **E** matrix allows the illustration of the total energy flow concept. The column sums of the **E** matrix represent the total energy flow as defined earlier. Such a scheme actually counts certain units of energy more than once. Such multiple counting reflects the importance to the system of some units of energy relative to others. For example, a unit of the sun's energy is depended upon by the system more when it is passing through the producer level than when passing through the decomposers.

I define the quantity $\sum_i^n \sum_j^n e_{ij}$ as the total system output. Stability of this output over long periods of time for the same system seems to be a practical definition of system equilibrium. This concept indicates that even though the energy demands of certain components of a system may decrease, others will increase to maintain the total output, if the system is in equilibrium. Thus steady-state conditions may not have to exist at the component level for the system to be in equilibrium.

(C) ACTIVITIES MATRIX

The second special interpretation of **r** is to realize that it can be formed by the multiplication of an "activities" matrix **R′** by an "activities" vector **r′**. The liberation of heat energy through metabolism, the net system loss of energy via the importing and exporting of biomass, and the energy content of the net growth of certain system components are three examples of respiratory activities. Accordingly, **r** becomes a matrix **R′**, composed of three column vectors, one for metabolism, another for net export energy and the third for net energy accumulation. The three vectors are normalized with respect to their column sum. These sums become the three components of the vector **r′**. Each of these vectors of **R′** can be diagonalized separately as in equation (6), producing a particular subset of the special energy matrix, **E′**. In this manner, the direct and indirect effects of system maintenance (metabolism) can be distinguished from growth (net storages) and from loss (net exports).

Note that the net storage is similar to the net capital formation of an economic system. Decomposers, a component of living systems, handle the energy flow associated with the "depreciation of capital".

(D) PERTURBATION

The control of net exports is the normal manner in which we crop the ecosystem for our own use. Readjustment of the production flows following an imposed respiration flow change can be approximated by a perturbation procedure.

We first assume that the **e** vector which describes the direct energy flow for the initial system condition remains constant. Next we specify a new respiration vector

$$\mathbf{r}'' = \mathbf{r}+\Delta\mathbf{r}. \tag{7}$$

$\Delta\mathbf{r}$ might be chosen to duplicate the effects of water or air pollution or of component cropping, for example. With equations (4) and (7) we calculate Δg_{ij} from

$$\Delta g_{ij} = \frac{\Delta p_{ij}}{e_j}, \tag{8}$$

where Δp_{ij} is derived from experimental knowledge of the relation between Δp_i and Δr_i and the distribution of Δp_{ij} for changes in Δp_i. From equation (8) we can derive $\Delta\mathbf{G}$ and

$$\mathbf{G}'' = \mathbf{G}+\Delta\mathbf{G}. \tag{9}$$

Equation (9) leads to

$$\mathbf{e}'' = (\mathbf{I}-\mathbf{G}'')^{-1}\mathbf{r}''. \tag{10}$$

We can now compare **e″** with **e** to determine the magnitude of the impact of the specified change, $\Delta\mathbf{r}$.

(E) CARBON FLOWS

An interesting possibility arises if we wish to predict the distribution of carbon flows between the components of the system. Let **c** be the carbon flow (row) vector and c_i be the direct carbon flow from the ith component. Assume that c_i is proportional to e_i, the direct energy flow from the ith component. Then,

$$c_{ij} = \frac{c_i}{e_i}(I-G)^{-1}_{ij}, \tag{11}$$

where c_{ij} is the total (direct and indirect) carbon flow the ith to the jth component per unit of respiration energy of the jth component. Further, the total (direct and indirect) carbon flow into the jth component is

$$c'_j = \sum_{i=1}^{n} \frac{c_i}{e_i}(I-G)^{-1}_{ij}\, e_j, \tag{12}$$

where n is the number of components of the system.

An immediate question arises with regard to the flow of energy from the sun. The sun can be treated as a force whose energy drives the carbon from the air, water or soil such that the carbon flow into the producer component is proportional to the sun's *direct and indirect* energy flow. From each component of the system, carbon is returned to the air, water or soil at a rate proportional to the respiration energy flow (excluding storage) for that component. I can only speculate that carbon is stored at a rate proportional to the rate at which energy is stored. The quotient c'_i/c_i is defined as the efficiency of carbon flow for the ith component.

Hopefully, similar arguments for the determination of the flow of other elements through the system can be made.

Equations (5), (11) and (12) provide a basis for determining changes in elemental flow caused by induced changes in the respiration flows.

3. Application

(A) GENERAL

The following data were gathered from Silver Springs, Florida (Odum, H., 1956, 1957), and are used here to illustrate the application of some of the foregoing theory.

In Table 1, the total energy content of the five system components at the time of the experiment is given and the components are defined.

TABLE 1

Component description and energy content, Silver Springs, Florida, food web (Odum, H., 1957)

Component description	Symbol	Average annual energy content (kcal/m²)
Producers	X_1	3421
Herbivores	X_2	213
Carnivores	X_3	62
Top carnivores	X_4	9
Decomposers	X_5	24

The system energy inputs were 20,810 kilocalories per square meter per year (kcal/m²/yr) from the sun and 486 kcal/m²/yr of bread fed to X_2 by tourists.

The input–output matrix of production energy flows (p_{ij}) is given in Table 2 (see equation (1)). The inputs to a given component are listed in the column for that component. The outputs are listed along the row for that component.

To form the production matrix **G** (Table 3), each matrix element is divided by its column sum. Thus **G** can be thought of as a normalized production matrix. Although the sun makes an input through wheat to bread, I neglect this term as it is difficult to determine and adds nothing to the example.

TABLE 2

Input–output energy matrix display for production matrix **P** *and respiration vector* **r** *for Silver Springs, Florida ecosystem* (*values are kcal/m²/yr*) (Odum, H., 1957)

	X_1	X_2	X_3	X_4	X_5	Bread	Sun	Respiration vector, **r**
X_1	0	2874	0	0	3455	0	0	14,481†‡
X_2	0	0	382	0	1095	0	0	1891
X_3	0	0	0	21	46	0	0	315‡
X_4	0	0	0	0	6	0	0	15‡
X_5	0	0	0	0	460	0	0	4602‡
Bread	0	494‡	0	0	0	0	0	0
Sun	20,810	0	0	0	0	0	0	0

† 2498 kcal/m²/yr was lost to downstream areas, and is combined with the respiration energy of X_1 here.

‡ Small data adjustments for balance.

TABLE 3

Normalized production matrix **G** *and energy vectors for Silver Springs, Florida, ecosystem* (*vector values are in kcal/m²/yr*)

	X_1	X_2	X_3	X_4	X_5	Bread	Sun	Production vector, **p**	Direct energy vector, **e**
X_1	0	0·853	0	0	0·683	0	0	6329	20,810
X_2	0	0	1·000	0	0·216	0	0	1477	3368
X_3	0	0	0	1·000	0·009	0	0	67	382
X_4	0	0	0	0	0·001	0	0	6	21
X_5	0	0	0	0	0·091	0	0	460	5062
Bread	0	0·147	0	0	0	0	0	494	494
Sun	1·000	0	0	0	0	0	0	20,810	20,810

TABLE 4

The structure matrix for the Silver Springs ecosystem

	X_1	X_2	X_3	X_4	X_5	Bread	Sun
X_1	1·000	0·853	0·853	0·853	0·963	0	0
X_2	0	1·000	1·000	1·000	0·249	0	0
X_3	0	0	1·000	1·000	0·011	0	0
X_4	0	0	0	1·000	0·001	0	0
X_5	0	0	0	0	1·100	0	0
Bread	0	0·147	0·147	0·147	0·037	1·000	0
Sun	1·000	0·853	0·853	0·853	0·963	0	1·000

Carrying out the inversion $(\mathbf{I}-\mathbf{G})^{-1}$ produces Table 4 (see equation (5)). Each element of the inverse matrix is the (direct and indirect) total energy flow consumed by the (row) component i for the column component j per unit of respiration energy of component j. These numbers represent the structure of the Silver Springs ecosystem. Note that $(I-G)^{-1}_{55}$ is not unity since X_5 consumes some of its own production.

The last two rows of the structure matrix in Table 4 give the distribution of the energy of the sun and bread to each of the components, directly and indirectly. Multiplying each component's coefficients by the direct energy flow from that component produces Table 5. Such a table reveals the relative dependence of each component on the two energy sources.

TABLE 5

The distribution of the system input energy over the system components of the Silver Springs ecosystem (values are kcal/m²/yr²)

	X_1	X_2	X_3	X_4	X_5
Sun	20,810	2873	326	18	4875
Bread	0	495	56	3	187
Total	20,810	3368	382	21	5062

(B) ENERGY FLOW MATRIX

Multiplying the inverse matrix in Table 4 by the respiration matrix (see equation (6)) produces the special energy matrix, $\mathbf{E}$, in Table 6.

Each entry of the special flow matrix, e_{ij}, can be interpreted as the total direct and indirect energy consumed by the ith component so that the component can carry out its respiration at the given rate. For example, in

TABLE 6

The special energy flow matrix (direct and indirect) with component respiration efficiencies (matrix and vector values are kcal/m²/yr)

	X_1	X_2	X_3	X_4	X_5	Bread	Sun	Direct energy vector (row sum)
X_1	14,481	1613	270	13	4433	0	0	20,810
X_2	0	1891	315	15	1147	0	0	3368
X_3	0	0	315	15	52	0	0	382
X_4	0	0	0	15	6	0	0	21
X_5	0	0	0	0	5062	0	0	5062
Bread	0	276	47	1	168	0	0	494
Sun	14,481	1613	270	13	4433	0	0	20,810
Total energy vector (column sum)	*28,962*	*5393*	*1217*	*72*	*15,302*	*0*	*0*	*50,947*
Component efficiency, % (respiration/total energy)	*50·0*	*35·1*	*25·9*	*20·8*	*30·1*			

Table 6, X_4 used 21 units of energy directly, but 72 units directly and indirectly. Therefore, the indirect energy demanded by X_4 is 51 units, some of which are counted into other components also, as I explained above. The sun contributed 13 units to X_4 and bread gave 1. X_1, X_2 and X_3 gave 13, 15 and 15 units respectively, and X_4 gave 15 units to itself for respiration.

Naturally, the used output energy of the sun is identical to that of X_1 as the sun's only connection to this ecosystem is through X_1. Just as naturally, the distribution of bread energy is proportional to the energy distributed from X_2 again since X_2 is the system connection for bread.

What cannot be anticipated, however, is the distribution of energy inputs or more accurately, energy demands, shown in the column below each component. In general, the demands of each component are rather uniformly distributed over the other components, except for X_5, where the variation is more than two orders of magnitude.

Much more detail would be preferred so that energy feedback loops could be observed. Feedback conditions allow this theory to demonstrate the dependence of a component upon itself. Interspecies energy flows as opposed to interlevel flows would display the relative dependence of certain detailed components upon others. Then rather than the triangular distribution of Table 6, which is indicative of a strict hierarchy of feeding, we could expect a more revealing distribution of the numbers. Perhaps radiographic tracer experiments (Odum, E., 1963) will lead to such detail.

The efficiencies calculated in Table 6 are unusual. They are found by dividing the respiration energy by the total direct and indirect energy demand. This is more of a system efficiency than the usual output divided by the direct energy input. It may be thought of as a measure of the fit of the component in the entire system.

The direct energy column total (50,947 kcal/m^2/yr) is defined as the "total system output" and when divided by the system energy content (Table 1) provides a measure of the system productivity as compared to other time frames or other systems. If this product remains steady with time, it is hypothesized that the system is in equilibrium.

No data on carbon flows for the Silver Springs ecosystem were found. Nor could I find sufficient additional information to carry out the perturbation concepts of equations (7) to (10). Likewise only one data point exists for r_i' other than the metabolism data and the concept of the activities matrix and vector cannot be demonstrated satisfactorily.

(c) Application to other studies

Other examples of such empirical data as Odum's are rare. A study of an old-field ecosystem food chain (Golley, 1960) produced data which led to the following special energy flow matrix (Table 7).

TABLE 7

Special energy flow matrix for an old field ecosystem food chain with component respiration efficiencies (vector values kcal/hectare/yr) (Golley, 1960)

	Vegetation	Microtus	Mustela	Direct energy
Vegetation	8760	170	5·4	8935
Microtus	0	171	5·5	177
Mustela	0	0	5·7	6
Sun	8760	170	5·4	8935
Total energy	17,520	511	22	18,053
Respiration efficiency, %	50·0	33·3	24·5	

Similar results are obtained with the Golley data, although they lack the detail of the Odum (1957) study. The Golley data do not include decomposer respiration or the matrix could be increased by one row and column.

The original study of ecosystem energy flows in Cedar Lake Bog (Lindeman, 1942) produced slightly less detail than the Golley study and is not included here.

4. Conclusion

It is possible, given the condition of linearity on the distribution of production energy flows, to determine the total energy flows which directly and indirectly connect an ecosystem component to the remainder of the ecosystem. If carbon flows (or any element) are proportional to the direct energy flows then a component's direct and indirect connection to the rest of the ecosystem can be expressed in terms of carbon flows.

With additional information on the relationship between production and respiration energy for each component and on the sensitivity of the distribution of a component's output, the system equations can be perturbed to determine the system response. The system effects of air or water pollution or of small exports (cropping) could be estimated.

It seems likely that dollar economic systems could benefit from the definition of input–output analysis given here. Ecologists are those few people who actually see systems which achieve the results of overgrowth and equilibrium.

The primary difference between the view of ecosystems demonstrated in this paper and the standard input–output view of the economic system is that here the respiration of all levels of activities are grouped into one vector. In the economic input–output system the counterpart dollar values of maintenance and overhead are considered part of the production costs and consequently growth and real depreciation flows are difficult to distinguish. In addition, the production process of a human society is directed toward the needs of a single system component, man. Such an arrangement makes it difficult to perceive the conditions of equilibrium.

The speculative view is that an improved economy would be based more on energy than on dollars.

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