TOWARD CANONICAL TROPHIC AGGREGATIONS

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Perhaps no other idea pervades the body of modern ecological thinking more than Lindeman's (1942) exposition of the trophic-dynamic aspect of ecology. In nearly every discussion among ecologists the terms *primary producer, herbivore,* and *carnivore* are necessary for communication. The notion of grouping organisms into categories which interact in a cascading fashion possesses a simple elegance that is difficult to resist.

The attractiveness of the trophic concept is that it was the first attempt at a holistic perspective on an ecosystem which met with any degree of success. Just as temperature, pressure, and volume allow one to characterize the incomprehensible multitude of particulate motions in a simple gas, the hope is that a small set of figures, such as trophic storages or trophic efficiencies, permit one to compare two ecosystems with overwhelmingly disparate complexities. Thus, if it were possible to demonstrate that an arbitrary network of ecosystem flows could be reduced to a trophic configuration, the aggregation process thus defined would become a key component of the evolving discipline of "macroscopic ecology" (see also Odum 1977 and Ulanowicz 1979).

Now two notions are key to a trophic representation of an ecosystem. The first of these is *level*. A trophic compartment is generally thought of as an aggregation of members, each receiving matter or energy from a source via the same integral number of population transfers. The number of transfers, or level, thus ordinates the trophic compartments. The second consideration is topological in nature—each level should receive flows only from the immediately antecedent compartment and should contribute flows only to the subsequent level. Such a linear food chain is the simplest nontrivial configuration an ecosystem can have and will be regarded as the "canonical" form. While variations on these attributes exist in the literature, any representation purported to characterize trophic structure should be clearly grouped according to level and be nearly canonical in form.

Unfortunately, trophic groupings of real populations are not always obvious. Many investigators (e.g., Hutchinson 1959; Riley 1966) are quick to point out that exchanges among species resemble complicated webs more than simple chains. Numerous populations receive energy and mass over several pathways, each with a different number of transfers. This ambiguity often confounds efforts to assign

entire populations to trophic compartments on the basis of taxonomy, function, or a combination thereof.

The idea that populations might be fractionally assigned to trophic levels was sensed by Riley (1966) who stressed the importance of developing partial feeding coefficients to properly represent predator-prey relationships within a food chain framework. Cummins et al. (1966) and notably W. M. Kemp and M. Homer (in prep.) have expanded this idea by providing numerical schemes for apportioning populations among trophic levels.

The latter studies have emphasized aggregation of species populations according to level. However, these investigators paid little attention to the network configuration of the final system. Is it, in fact, canonical? Are the laws of thermodynamics satisfied by the transformation?

Mappings and transformations are core elements of the theory of linear algebra. Therefore, in this article we choose to describe the transformation process in terms of matrices and vectors. It will be shown that level, topological form, and thermodynamic laws can all be considered within this algebraic framework. Since much of the progress to date on ecosystem structure analysis has been achieved using linear algebra, the relation of this present exercise to the larger body of literature will become immediately apparent. Finally, casting the aggregation scheme in the form of matrices and vectors readily permits the creation of computer algorithms capable of treating the most complex networks.

Before describing the grouping of species according to level, it is necessary to review the fundamental balance equations for ecosystems transfers and to state some requirements that any trophic transformation must satisfy.

THE ENERGY BALANCE

Attention from this point onward will be on energy flow through the ecosystem. While exchanges of matter and information are also necessary to define the full set of phenomena, the balance of energy flows offers a convenient starting point for considering trophic groupings and provides the most obvious manifestation of compliance with thermodynamic principles.

Most recent theoretical considerations of energy flows through ecosystems have followed the lead of Hannon (1973) and borrowed from the linear theory of economic exchanges (Leontief 1951). Hannon uses the methodology to trace direct and indirect flows through the ecosystem. Finn (1976) employs the same calculus to define such quantities as average path length, cycled flow, straight-through flow, and a cycling index of an ecosystem—all useful in discussing questions of system stability, mineral cycling strategy, and structural changes. Recently Levine (1977) started from the same balance equations and derived an extension of Levins' (1968) niche overlap index which includes indirect as well as direct flows.

The present analysis proceeds from the same basic balance equations written in a slightly different form to facilitate subsequent calculations. The given system is internally divided into identifiable compartments which may exchange energy (or other flows) with each other and with the surrounding universe. At steady-state

the inputs to any one compartment must balance the outflows from the same compartment. (While storages are essential to any dynamical consideration, they do not enter into the subsequent analysis of static systems.) Inputs may be differentiated as coming from another compartment within the system or from the external universe. Outputs from a compartment can likewise flow as inputs to other compartments in the system or be exported out of the system. When energy is the flow under consideration, a further distinction can be made as to whether the export might be useful to another system in the universe, or whether it has been degraded beyond utility (respiration). This separation of respiration from export will later prove useful in defining important criteria.

Written symbolically, the balance for the ith compartment becomes:

$$\sum_{j=1}^{n} P_{ji} + e_i = \sum_{k=1}^{n} P_{ik} + x_i + r_i, \qquad i = 1, 2, ..., n, \tag{1}$$

where P_{ik} represents the flow from compartment i to compartment k within the system, e_i is the input to compartment i from outside the system, x_i is the export of usable flow to the universe, and r_i represents loss to the universe via respiration. Notice that e_j is defined differently than in Hannon (1973), where it represented all the inputs to species i.

In order to rewrite equation (1) in matrix-vector notation, square brackets will be used to enclose the symbols for matrices and parentheses will denote column vectors. Accordingly, equation (1) becomes

$$[P]^t (1) + (e) = [P] (1) + (x) + (r), \tag{2}$$

where the superscript t after a right bracket (or parenthesis) indicates matrix transportation and the column vector (1) has the value unity in each entry. Equation (2) is easily rewritten as

$$(e) = [E] (1) + (x) + (r) \tag{3}$$

by defining the exchange matrix:

$$[E] \equiv [P] - [P]^t. \tag{4}$$

The exchange matrix is antisymmetric ($E_{ij} = -E_{ji}$) by definition.

TRANSFORMATION CRITERIA

The n-dimensional energy balance defined by equation (3) is to be transformed into an m-dimensional system (usually $n > m$) which conforms to the general notions of trophic transfers. The requisite linear mapping, represented by an $m \times n$ matrix $[A]$, cannot be wholly arbitrary. It must, for example, assure that: (1) The first law of thermodynamics is preserved in the resulting network, i.e., total input, throughput, export, and respiration must be invariant under transformation; and (2) Exchanges in the transformed system obey the second law of thermodynamics, thereby requiring that the resultant respirations all be positive quantities. These criteria must hold for any transformation of energy flows. More specific to the

notion of trophic transfers is the requirement that (3) The transformed compartments form a straight chain. This means that each compartment should exchange energy only with the preceeding and subsequent members of the chain. That is to say, the resultant $m \times m$ exchange matrix should be tridiagonal ($E_{i,i+k} = 0$ for $|k| > 1$) and antisymmetric.

Now if the transformation $[A]$ is to satisfy the first law, it will be sufficient that each of the component column vectors of $[A]$ sums to unity, i.e.,

$$(1)^t [A] = (1)^t. \tag{5}$$

For example, defining the transformed respiration vector as

$$(\rho) = [A] (r), \tag{6}$$

the total transformed respiration is

$$(1)^t (\rho) = (1)^t [A] (r) = (1)^t (r), \tag{7}$$

showing that total respiration (and likewise total input and total export) are conserved under transformation.

Multiplying equation (2) by $[A]$, on the left, and using the fact (from eq. [5]) that $(1) = [A]^t(1)$ yields

$$[A] (e) = [A] [E] [A]^t (1) + [A] (x) + [A] (r). \tag{8}$$

Defining

$$(\epsilon) = [A] (e), \tag{9}$$

$$(\xi) = [A] (x), \tag{10}$$

$$[E] = [A] [E] [A]^t, \tag{11}$$

along with equation (6) allows (8) to be rewritten as

$$(\epsilon) = [E] (1) + (\xi) + (\rho). \tag{12}$$

It is easily demonstrated that $[E]$ is antisymmetric.

AGGREGATION ACCORDING TO LEVEL

The mapping $[A]$ needs to be further defined according to some notion of what constitutes trophic levels. It is convenient to begin this search with the matrix of feeding coefficients, defined in Hannon (using the present notation) as:

$$G_{ij} \equiv \frac{P_{ij}}{\sum_{k=1}^{n} P_{kj} + e_j}. \tag{13}$$

In words, G_{ij} is the fraction of the total input to compartment j which flows directly from compartment i.

If one makes the assumption that each compartment is a nondiscriminatory processor of flows (i.e., any input flow is distributed among the various outputs in

proportion to the fraction that each output comprises of the total throughput of that compartment), then the integer powers of $[G]$ take on a particular significance. To wit, the i, jth element of $[G]^2 = [G] \, [G]$ is the fraction of the total input to compartment j which flows from compartment i along all pathways requiring two transfers (i.e., of length 2). Similarly, the i, jth component of $[G]^q$ is the fraction of the total input to the jth species flowing from the ith compartment along all pathways of length q.

The fraction of the total input to a species, i, coming from outside the system is

$$f_i = \frac{e_i}{\displaystyle\sum_{j=1}^{n} P_{ji} + e_i}. \tag{14}$$

In a trophic sense these flows are primary sources of energy to the system. The fraction of total input to species i originating from a primary input one link away (secondary flows) can be represented by the row vector

$$(a_2)^t = (f)^t \, [G]. \tag{15}$$

Likewise, tertiary flows to a compartment comprise the fractions

$$(a_3)^t = (f)^t [G]^2, \tag{16}$$

and so forth:

$$(a_k)^t = (f)^t [G]^{k-1}. \tag{17}$$

Earlier investigators, including W. M. Kemp and M. Homer (in prep.) and Cummins et al. (1966) have suggested that the attributes of a given compartment be apportioned to the mth trophic level according to the fraction of the total input it receives from external sources along pathways of length m. In the present scheme, the kth row of the transformation matrix $[A]$ would be $(a_k)^t$, i.e.,

$$A_{ij} = (a_i)^t_j. \tag{18}$$

Applying the criteria for a canonical transformation to the trophic aggregation matrix, $[A]$, one may ascertain that two of the required three criteria are satisfied. Summing any column of the $[A]$ matrix is the same as summing the fractions of the total input to the given species over all possible path lengths. Since all input to the compartment must be accounted for by this process, each column sums to unity, thereby fulfilling constraint (5) and assuring that the first law is invariant under transformation. An analytical demonstration of the fact that $[A]$ satisfies (5) is given in the Appendix.

Since the elements of (e) and $[P]$ are intrinsically positive, the chain of definitions culminating in (18) assures that all elements of $[A]$ are positive or zero. Hence, the consequent trophic inputs, exports and respirations will all be greater than or equal to zero, thereby fulfilling the second law.

The exchange matrix derived from the trophic transformation is antisymmetric. Unfortunately, it is not tridiagonal. Observation reveals that there are many jump-forward flows, i.e., flows from trophic level k to level $k+2$ or greater. While

the common notion of trophic flows could accommodate feedback, jump-forward flows contribute undesirable complications.

<div align="center">TRIDIAGONALIZATION OF THE TROPHIC EXCHANGE MATRIX</div>

There was no reason to assume a priori that the aggregation by level would yield a tridiagonal exchange matrix. There was no hint of orthogonality between the various rows of matrix $[A]$ which would indicate that some off-diagonal terms might be zero.

It is possible, however, to work with the transformed trophic compartments to eliminate the jump-forward flows beyond the next trophic level. This is accomplished by a series of two-compartment, Jacobian-like transformations.

Consider, for example, a nonzero flow from trophic level $r-1$ to trophic level s, where $s \geq r+1$ and $r>1$. The strategy will be to transfer a portion of compartment s to compartment r so that the flow will be completely shunted into r. This can be achieved by using an $m \times m$ transformation matrix $[B]$ which differs from the $m \times m$ identity matrix in only four elements—B_{rr}, B_{rs}, B_{sr}, and B_{ss}.

To assure conservation of energy under transformation $[B]$ it is sufficient that

$$B_{rr} + B_{sr} = 1 \tag{19}$$

and

$$B_{rs} + B_{ss} = 1. \tag{20}$$

A complete shunt of the flow away from compartment s implies that the $r-1, s$th component of $[B] [E] [B]^t$ is zero, i.e.,

$$B_{sr} E_{r-1,r} + B_{ss} E_{r-1,s} = 0. \tag{21}$$

Finally, the constituent row vectors of $[B]$ should be mutually orthogonal to avoid interfering with flows other than those involving trophic compartments $r-1, r$, and s. For a matrix as simple as $[B]$ the single component equation

$$B_{rr} B_{sr} + B_{ss} B_{rs} = 0 \tag{22}$$

will guarantee mutual orthogonality.

Equations (19) through (22) may be solved for the four components to give

$$B_{rr} = E_{r-1,r} \frac{E_{r-1,r} + E_{r-1,s}}{D}, \tag{23}$$

$$B_{rs} = E_{r-1,s} \frac{E_{r-1,r} + E_{r-1,s}}{D}, \tag{24}$$

$$B_{sr} = E_{r-1,s} \frac{E_{r-1,s} - E_{r-1,r}}{D}, \tag{25}$$

$$B_{ss} = E_{r-1,r} \frac{E_{r-1,r} - E_{r-1,s}}{D}, \tag{26}$$

where

$$D = E_{r-1,r}^2 + E_{r-1,s}^2. \tag{27}$$

Successive application of this formula for each nonzero flow outside of the tridiagnoals will result in a transformed system satisfying the third criterion.

AN ILLUSTRATIVE EXAMPLE

Examples of total ecosystems for which the web of energy exchanges between the species has been quantified are rare. There are, however, numerous examples of estimated steady-state energy exchanges between aggregated compartments of an ecosystem. A convenient food web based on the main groups of organisms in the North Sea has been quantitatively estimated by Steele (1974). In this instance species have already been aggregated according to both function and habitat. Nevertheless, the resulting web is still not in canonical form and will serve as a useful illustration of the described aggregation schemes. The flow estimates in parentheses (fig. 1) were not provided by Steele and are our guesses. The respirations were calculated by the difference between inputs and outputs.

Figure 2 presents the trophic aggregations effected by the transform defined in equation (18). There are eight trophic compartments in view of the fact that the longest path length in the hypothesized web was eight steps. Arrows pointing away from the chain represent the apportionment of the yields to man from the various trophic levels. The presence of net jump-forward flows implies that the transformed system is not canonical as defined by the third criterion. Curiously, the transformation of the production matrix

$$[\Pi] = [A] [P] [A]^t \tag{28}$$

possesses the symmetry

$$\Pi_{i(j+1)} = \Pi_{j(i+1)}, \tag{29}$$

which is not apparent from diagramming the net exchanges as in figure 2.

A sequence of nine rotations as described in equations (23)–(27) culminates in the decoupled food chain exhibited in figure 3. The effect of the decoupling has primarily been to increase the lower trophic flows at the expense of the higher levels. The initial aggregation, therefore, tends to overestimate higher-level phenomena.

The values for the flows depicted on figures 2 and 3 are indicated only by a few digits to show their relative magnitudes. Some compartments appear not to balance perfectly, but would do so if enough significant figures were provided.

As stated earlier, the flows depicted in figure 3 can be used to characterize the ecosystem for the purposes of comparison with, say, a desert biome. In addition, if one is willing to make two key assumptions, one can use the canonical representation to generate possible strategies for management of the North Seas fishery. Suppose, for example, one wishes to increase the total yield of the system to man while at the same time ensuring the integrity of the ecosystem.

The assumption is made that the larger the flows at higher trophic levels, the more desirable is the state of the ecosystem. This statement is equivalent to the commonly held subjective belief that more diverse, more complex (i.e., highly connected) ecosystems represent more mature and, therefore, more desirable ecological assemblages. M. Homer and W. M. Kemp (in prep.) have data which
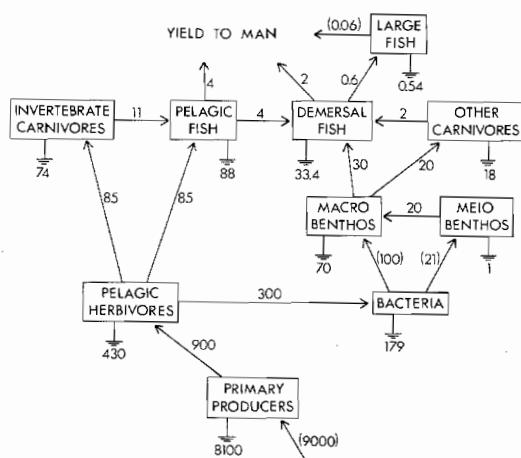
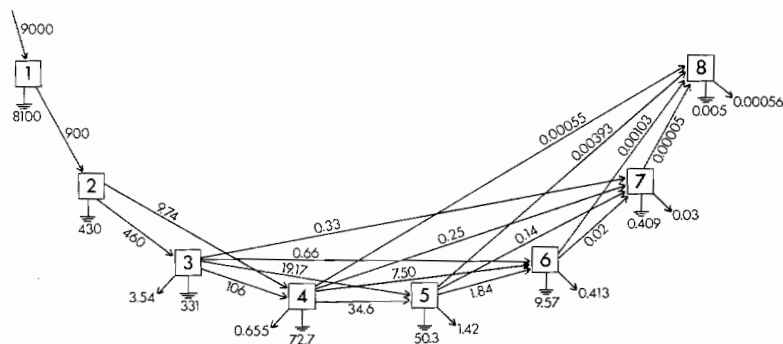FIG. 1.—Estimated flows (kcal/m² · yr) through the North Sea Food Web (after Steele 1974).

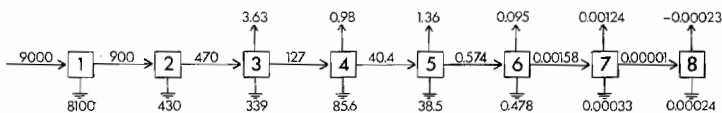FIG. 2.—North Sea food web as transformed according to equation (18) (flows in kcal/m² · yr).

FIG. 3.—North Sea canonical trophic food chain (flows in kcal/m² · yr).

purport to show that the effect of thermally stressing a marsh community is to drastically reduce the aggregated flows at higher trophic levels while having little effect upon transfers between lower compartments.

In order to maintain or augment the flows at higher trophic levels, one may use the truism that a chain is only as strong as its weakest link. Trophic efficiencies ($[\epsilon_i - \rho_i]/\epsilon_i$) in the North Sea chain go through a minimum of 4.8% in compartment 5. One may view level 5 as a bottleneck impeding the flow to the higher levels. Furthermore, 71.3% of the total production from this aggregate is har-

vested by man, in contrast to the 2.8% and 2.4% withdrawals from levels 3 and 4, respectively. Assuming that a decrease in the harvest at a given level will result in an increase in the transfer to the next higher level (and vice versa), the desirable strategy would be to increase the catch from levels 3 and 4 while cutting back on the take from level 5.

The transformation matrix defining the canonical heirarchy shows that pelagic fish are apportioned to ranks 3 and 4 in almost a 90%/10% split, whereas demersal fish are assigned 27% to stage 4 and 70% to stage 5. It should be possible, therefore, to increase the take of pelagic fish considerably, cut back on the catch of demersal fish by a moderate amount, and still transmit more energy to levels 6, 7, and 8!

Of course it is possible that a more detailed analysis of the dynamics of the original system or a study of the life histories of the individual species involved will prove this strategy to be folly. No one should advance a steady-state analysis as the sole determinant of a management decision. The canonical trophic analysis should function, nonetheless, as a rational generator of working management hypotheses.

REMARKS ON THE GENERALITY OF THE TRANSFORMATION SEQUENCE

It would be extremely satisfying to be able to present the two-step transform as a general method for reducing food webs to canonical trophic form. At present such an assertion is premature at best. A clue to possible difficulties is the negative sign on the export from the eighth compartment in figure 3. While one might be able to rearrange exchanges and exports in such a case to make all flows appear positive, it is another matter if one of the rotation transformations results in a negative respiration. In fact, there is no intrinsic mathematical reason (as there is in the initial aggregation) why negative respirations cannot result from rotation. Calculations with arbitrary food webs show that while the rotations tridiagonalize the exchange matrix, they do not, in general, preserve the second law.

Experience shows that violations of the second criterion occur routinely when there is significant external input to a species feeding at a higher level. It is possible to circumvent this situation, however, by decomposing the given network with several inputs to separate networks, each with one of the given inputs as the sole source. This is readily accomplished by employing Hannon's (1973) method to calculate the fraction of any given flow attributable to a specific input. The separate networks can subsequently be transformed in turn with much less probability of the second law being violated.

As long as the exchanges and respirations vary independently, however, there remains the possibility that a negative respiration may appear. Studying equations (23)–(26) reveals that this will happen whenever

$$B_{sr}\rho_r + B_{ss}\rho_s < 0, \tag{30}$$

or, equivalently, when

$$\left| \frac{\rho_s}{\rho_r} - 1 \right| > \left| \frac{E_{r-1,s}}{E_{r-1,r}} - 1 \right|. \tag{31}$$

As mentioned, the example trophic chain possesses eight components—a dimension commensurate with the longest path length in the food web. In this instance the sequence of row vectors calculated by (17) automatically truncates after eight rows. Should there be a feedback loop imbedded within the starting web, however, the sequence of calculating row vectors will go on indefinitely. W. M. Kemp and M. Homer (in prep.) show how, in most instances, these loops may be obviated by dividing the troublesome populations into age-class compartments. In the remaining cases one must decide how to treat the residuals. Since the columns of the transformation vector always sum to unity, the magnitude of any residuals can always be calculated. One may, therefore, continue creating trophic compartments until the residuals fall below some specified level, or one may calculate a predetermined number of rows (say $n - 1$) and lump all the residuals (higher-order transfers) into the final compartment.

It is worth noting that total systems throughput (see Finn 1976) is conserved under both transformations. This will not be apparent when studying the transformed exchange matrix as in equation (11). Questions concerning total systems throughput are best addressed with the aid of the transformed productivity matrix, $[\Pi]$, as defined by equation (28). The diagonal elements of $[\Pi]$ are generally nonzero indicating the transformations give rise to "internal circulations" within trophic compartments.

Finally, Odum (1971) has pointed out that most ecosystems exhibit two major food chains—a grazing chain and a detritus chain. For comparison it is often helpful to describe both chains rather than lumping them together and masking certain functional properties of the ecosystem's populations. This is easily accomplished under the general methods outlined in this paper. One simply amends the boundary between system and universe to excise both autotrophs and detritus from the system. Their contributions to the various species now appear as external inputs and the web may be separated according to Hannon's scheme into two webs, one having only autotrophic inputs and another having only detrital inputs. The distinct networks are subsequently transformed via the methods outlined previously into two parallel trophic chains.

DISCUSSION

The development of a systematic trophic aggregation scheme has both applied and theoretical implications. W. M. Kemp and M. Homer (in prep.) have already dwelt at length on the utility of their aggregations to the comparative ecologist. It is no small advantage that the transform is unambiguous and results in a system which "makes biological sense." It is of great help in reducing the dimension of the system to be considered. For example, it is possible, in concept at least, to condense a complicated ecosystem with hundreds of species into five or 10 compartments. The comparison of two many-specied communities is thereby enabled. Even the troublesome jump-forward flows could provide useful keys with which to contrast the underlying dynamics of the two systems.

The fact that the initial transformation does not yield a "canonical" trophic

food chain provides some interesting questions for both theoreticians and empiricists. In this paper only one of an undetermined number of possible secondary transforms has been explored. It remains to either discover an aggregation formula satisfying all three criteria, or to prove conclusively that no such transform is possible.

Even if it can be deduced that a canonical transform necessarily satisfying the laws of thermodynamics does not exist, several ecological questions remain. For instance, it may be possible that a given type of canonical transform is sufficient to treat real ecosystems. Supposing, for the sake of argument, that the joint transformations described in this article always yielded well-behaved canonical trophic analogs when applied to real data. Then the inequality (31) would be "prohibited" by weight of empirical evidence. Physical science is replete with instances where mathematical possibilities are not realized by the real system (e.g., forbidden transitions in quantum mechanics).

Certainly, ecology would benefit by more theoretical-empirical interplay such as has advanced the science of physics. Unfortunately for ecology, the scope of precision necessary in experiments which would test many current hypotheses greatly diminishes the opportunity for feedback. Nonetheless, this exercise has been advanced in the hope of stimulating such interaction.

SUMMARY

Steady-state input-output analysis of energy flows in an ecosystem conveniently delineates the discrete steps of energy processing in a given ecosystem. The fraction of a specific flow between species which results from a given input via any integral number of transfers can be calculated. The portions of all flows which are the same number of steps from any external input may, therefore, be aggregated. Furthermore, the mapping which creates these groupings preserves the first and second laws of thermodynamics.

The aggregated compartments are "trophic" in the sense that they are ordered according to the number of transfers from an external input. They do not, however, represent a sequential chain of energy flow in the strict sense. Transfers between compartments which are not nearest neighbors in the chain are still present.

A secondary transformation which decouples the exchanges between non-neighboring compartments can be effected. In the resultant chain of flows more energy appears to be dissipated in the lower trophic levels. There is no a priori reason why the second law of thermodynamics should be preserved under the second transformation.

APPENDIX

It is to be demonstrated that the column vectors of the initial trophic transformation always sum to unity, i.e.,

$$\sum_{i=1}^{\infty} A_{ij} = 1, \quad j = 1, 2, \ldots, n, \tag{A1}$$

where (A1) can be expressed in matrix-vector format, using (17) and (18), as

$$(f)^t \left\{ \sum_{i=1}^{\infty} [G]^{i-1} \right\} = (1)^t. \tag{A2}$$

Now the infinite series of matrices enclosed in braces converges to the limit $\{[I] - [G]\}^{-1}$ (Yan 1969), so that

$$(f)^t \{[I] - [G]\}^{-1} = (1)^t. \tag{A3}$$

Where $[I]$ is the $n \times n$ identity matrix. Since the term in braces is generally nonsingular, matrix multiplication from the right by the inverse is permitted, giving

$$(f)^t = (1)^t \{[I] - [G]\} \tag{A4}$$

or

$$(1)^t = (f)^t + (1)^t [G]. \tag{A5}$$

Equation (A5) is the vector transpose of

$$(1) = (f) + [G]^t (1), \tag{A6}$$

which may be written in component form with the aid of (13) and (14) as

$$1 = \frac{e_i}{\sum_{k=1}^{n} P_{ki} + e_i} + \frac{\sum_{j=1}^{n} P_{ji}}{\sum_{k=1}^{n} P_{ki} + e_i}, \tag{A7}$$

for $i = 1, 2, \ldots, n$. Since k and j are dummy indices, (A7) is immediately recognized as an identity for each i and the demonstration is complete.

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