

Mass and Energy Flow in Closed Ecosystems†

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The general equations of biomass and energy transfer for an n -species, closed ecosystem are written. It is demonstrated how in “ecological time” the parameters describing the dynamics of biomass transfer are related to the parameters of energy transfer, such as respiration, fixation, and energy content. This relationship is determinate for the straight-chain ecosystem, and a simple example is worked out. The results show how the density-dependent terms in population dynamics arise naturally, and how the stable system exhibits a hierarchy in energy per unit biomass. A procedure is proposed for extending the theory to include webbed systems, and the particular difficulties involved in the extension are brought before the scientific community for discussion.

“Just as the essence of food cannot be conveyed in calories; the essence of life will never be captured by even the greatest formulas.”

A. SOLZHENITSYN: *The First Circle*

1. Introduction

Models, in the words of Kac (1969), are caricatures of reality. Always simplified, sometimes distorted, they nevertheless serve to portray some of the features of the real world, to polarize thinking, and to pose sharp questions. But if the cycle of scientific activity is to be completed, they should also give some indication to the empiricist of how to minimize the requisite information to describe a system.

The bane of the ecologist is that his systems are so complex, so multi-parametered, that to treat them as a whole, even with the help of systems analysis, is a formidable task. In approaching this problem, one may choose between two approaches. One may attempt to model the system in as great detail as is possible and consistent with modern high-speed computers. With good programming the machine will then serve to model and predict the

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behavior of the system. A fine review of the benefits and problems of this approach has been made by Leigh (1968).

On the other hand, one may search for a judicious frame of reference, such that, when the system is viewed in this perspective, relationships among the various parameters become more obvious. For example, it would be very difficult to deduce the second law of thermodynamics from observations on the molecular time and space scale. Expand these scales to those of everyday observation, and the law is readily demonstrable. Information on individual molecules and their behavior is lost in the chaos, but new variables and parameters are defined which congeal into a unified theory.

Along these lines, Slobodkin (1961) has defined the concept of "ecological time" as distinct from "physiological time" and "evolutionary time". The physiological time scale ranges from the duration of some biochemical reactions up to the lifespan of the organism being studied. Of course, all of the behavioral aspects of ecology are studied within this time scale. At the other end of the spectrum, over periods of time of half a million years or more, it may be expected that significant changes in community structure and genetic make-up will occur. Between these two ranges lies the realm of ecological time, of the order of ten times the generation time of the longest-lived species involved.

Many communities (though certainly not all) achieve a steady state with respect to their physical and chemical surroundings within this time period. Also, it is important to note here that population interactions, when viewed on the scale of ecological time, may lose their explicit dependence on spatial distribution. That is, within a given community, distances separating individuals of the various species are usually traversed by these individuals or their progeny within ten generation times of the longest-lived component.

While the word population usually suggests a discrete numerical census, it has long been practice to quantify a community component in terms other than number. Particularly where individuals are small and numerous, such as with protozoa, bacteria, and fungi, or where the individual is hard to distinguish, total biomass has been a more convenient quantification of a population (A. Fredrickson *et al.*, manuscript in preparation). When viewed on a larger community scale, even the higher forms become numerous enough to be treated in this manner.

2. The Mass Balance

Thus, if a large population of a species is observed in ecological time, the biomass of the population will behave like a continuous rather than a discrete variable. Any species utilized by another as food, or whose respira-

tion by-products are assimilated by another, will give rise to what appears in this context as a continuous biomass flux from the first species to the second.

Phenomena such as these are best treated with continuous variables and differential equations. To this end, the arbitrary, simple system of Fig. 1 will serve as an initial example.

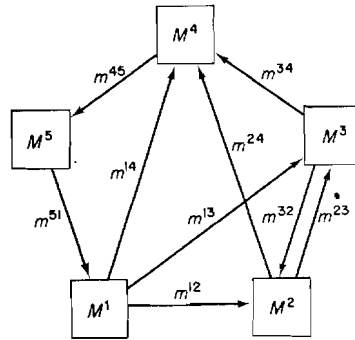


FIG. 1. Biomass fluxes in an arbitrary five-component closed ecosystem.

This closed system consists of five species in the general sense (i.e. biotic species or abiotic, chemical species which enter the web of life). The biomass of species i is designated by M^i (i being a superscript, not to be confused with a power index). The "flow" of biomass from species p to species q is designated m^{pq} . With this notation, the conservation of biomass of any one of the five species in the community may be written following the formula that the rate of accumulation of biomass is equal to the rate of influx of biomass minus the rate of biomass efflux. For the system illustrated, the five equations of biomass conservation would be:

$$\begin{aligned}
 \frac{dM^1}{dt} &= m^{51} - m^{12} - m^{13} - m^{14}, \\
 \frac{dM^2}{dt} &= m^{12} + m^{32} - m^{23} - m^{24}, \\
 \frac{dM^3}{dt} &= m^{13} + m^{23} - m^{32} - m^{34}, \\
 \frac{dM^4}{dt} &= m^{14} + m^{24} + m^{34} - m^{45}, \\
 \frac{dM^5}{dt} &= m^{45} - m^{51}.
 \end{aligned} \tag{1}$$

The sum of all five equations implies that the total biomass of such a closed system is a constant:

$$\frac{d}{dt}(M^1 + M^2 + M^3 + M^4 + M^5) = 0. \quad (2)$$

In order to speak of systems like (1) in a more concise fashion, and to generalize the form to a community of n species, it is helpful to make use of indicial notation and write

$$\frac{dM^i}{dt} = \sum_{p=1}^n \sum_{q=1}^n \alpha_{pq}^i m^{pq}. \quad (3)$$

Here n is the number of species in the community, and i will take on the successive values 1, 2, 3, . . . , n to represent each of the n equations. The n -cubed values of the array α_{pq}^i will take on the values +1, 0, or -1 depending on the structure of mass flows in the community, and will henceforth be designated as the structure array. The term α_{pq}^i will be +1 if m^{pq} flows into species i ; it will be -1 if m^{pq} flows out of species i ; it will be zero if m^{pq} does not directly involve species i . Thus, in the illustrated community $\alpha_{51}^1 = +1$, $\alpha_{12}^1 = -1$, $\alpha_{23}^1 = 0$, etc. To simplify further the notation, the Einstein summation convention will be employed. Briefly stated, if the same index appears twice in any term, as both a subscript and superscript, that index is to be summed over the n species. Hence, the equations in system (3) are concisely written as

$$\frac{dM^i}{dt} = \alpha_{pq}^i m^{pq}. \quad (4)$$

System (4) is a statement of the conservation of biomass for an n species community; but possessing two sets of dependent variables, biomasses and the biomass fluxes, it is of little use mathematically. In such cases one assumes a set of constitutive relations describing the biomass fluxes in terms of the biomasses, or functions thereof. For example, one may assume that the biomass flux from host species p to predator species q is proportional to the biomass of host species. This is a linear assumption often favored in systems analysis for its mathematical simplicity and the well-developed mathematical tools which can be brought to bear on linear systems. While mathematically simple, and probably applicable in certain limited cases, it is conceptually unsatisfying to think of a predator-prey relationship as always independent of one of the interacting species. This objection is removed by invoking the Lotka-Volterra hypothesis (Lotka, 1956) which states that the biomass flux between two interacting populations varies as the product of the interacting biomasses. This quadratic assumption will cause the resulting differential equations to be non-linear.

In the realm of ecology everything seems to influence everything else, and it seems somewhat restrictive to say the biomass flux between two species is dependent only on the populations of host and predator. It is easy to envision situations in which a third party, by altering the habitat of one species (such as providing cover for the host), will affect the rate of transfer of biomass between the first two species without ever directly exchanging biomass with either of them. It is easy to generalize the Lotka–Volterra hypothesis to include indirect interactions of this nature without altering the mathematical nature of the constitutive assumption. One amends the Lotka–Volterra hypothesis so that the flux of biomass between two species is a bilinear combination of the biomasses of all species in the community. Written with the help of the Einstein summation convention, this becomes

$$m^{pq} = B_{uv}^{pq} M^u M^v. \quad (5)$$

The B_{uv}^{pq} is a fourth-order array of parameters which describes all the population dynamics of the system. The reader will notice that the mathematical statement of the Lotka–Volterra hypothesis will look exactly like (5), with the exception that certain of the B 's will *a priori* be set equal to zero. Here, these parameters are not as yet specified.

Substitution of (5) into (4) gives the equations of population dynamics:

$$\frac{dM^i}{dt} = \alpha_{pq}^i B_{uv}^{pq} M^u M^v. \quad (6)$$

It is a system of first-order, ordinary, quadratic differential equations. There is, as yet, no analytical solution for a general set of such equations, but that is not to say that information about system behavior cannot be derived from such equations without their explicit solution.

Other investigators who have brought the computer to bear on simplified sets of equations such as (6) have run into several interesting difficulties. Foremost among these problems is finding a set of parameters which will yield stable and meaningful behavior. In an interesting series of articles, Garfinkel (1962, 1967) and Garfinkel & Sack (1964) found that not long after the commencement of a numerical analogue for such systems, some of the populations would become negative or begin to increase without bound. Curiously, he found that orthodox behavior of the system could be prolonged by the addition of quadratic “density-dependent” terms. That is, the time rate of change of a given population is proportional to, among other things, the negative square of the population itself.

But rather than guessing at the proper configuration of population dynamics constants, a systematic way of arriving at a set of constants which yields stable behavior is necessary. Hopefully, such a system would pose

another point of view in the controversy over ecological stability, as well as show necessary relationships between parameters so that input information may be reduced—as alluded to previously.

Odum & Odum (1959) state that the first order of population control is the energy flow-physical factor complex. While certain elements of the physical factor complex are outside the scope of this model, the energy flow can be handled in much the same way that biomass was treated. Hopefully, the energy balance will shed at least partial light on the problem of community stability.

3. The Energy Balance

For a population in an isobaric, isothermal environment, it is sufficient to consider the fate of the bound chemical or internal energy possessed by the population. The pathways over which energy may travel in the arbitrary five component system previously considered are illustrated in Fig. 2. Biomass fluxes into and out of any one population carry energy along with them. The chemical energy carried from species p to species q is labeled e^{pq} . But the community is not closed with respect to energy, as it is to mass. Indeed, there is continual degradation of chemical energy into heat via metabolic respiration. The second law of thermodynamics applied to each population requires that an amount of energy, say R^i , be lost in this manner.

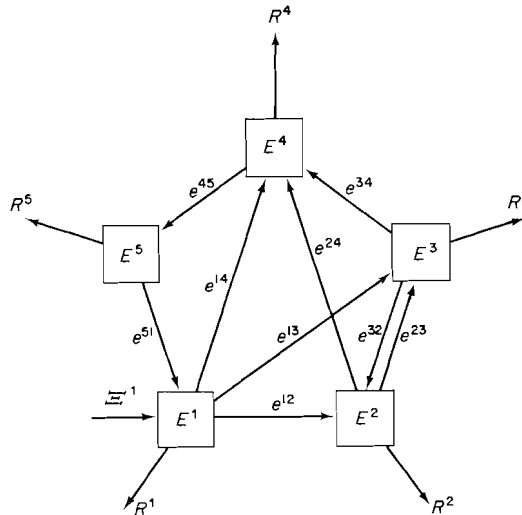


FIG. 2. Energy fluxes in an arbitrary five-component closed ecosystem.

Of course, there are situations in ecosystems such as host-parasite mass flows and detritus-decomposer fluxes, where the constants of proportionality between biomass flux and bioenergy flux will not be identical to those in (8). Thus, it may be necessary to define another diagonal array, λ_j^i , whose diagonal elements are equal to λ_j^i when the biomass flux is from prey to predator, but are otherwise not identical. The general proportionality between biomass fluxes and bioenergy flows would then be

$$e^{pq} = \lambda_i^{p'} m^{iq}. \quad (10)$$

Utilization of (5) in (10) gives

$$e^{pq} = \lambda_i^{p'} B_{uv}^{iq} M^u M^v. \quad (11)$$

Substitution of (8) and (11) into (7) yields

$$\lambda_j^i \frac{dM^j}{dt} = \alpha_{pq}^i \lambda_i^{p'} B_{uv}^{iq} M^u M^v - R^i + \Xi^i. \quad (12)$$

The set of equations (12) bears marked similarity to (6) but with the additional terms for respiration and fixation. The question of how these may be related to the biomasses should then be pursued.

Using an argument analogous to the one leading up to the statement of (8), it may be hypothesized that the rate of energy lost through the respiration of a population is proportional to the biomass of that population. The constants of proportionality, or the specific respiration coefficients, may likewise be represented as a diagonal array, ρ_j^i , so that

$$R^i = \rho_j^i M^j. \quad (13)$$

Likewise, in an environment with a constant light source, the rate of fixation is proportional to biomass of the primary producer:

$$\Xi^i = \psi_j^i M^j, \quad (14)$$

where the diagonal element of ψ_j^i is zero when species i is heterotrophic.

With these assumptions, equation (12) now reads,

$$\lambda_j^i \frac{dM^j}{dt} = \alpha_{pq}^i \lambda_i^{p'} B_{uv}^{iq} M^u M^v - \rho_j^i M^j + \psi_j^i M^j. \quad (15)$$

Still, the right-hand side of (15) contains two linear terms, unlike (6). However, in a closed ecosystem this poses no particular difficulty (Aris, 1964). For example, in the five species arbitrary system one may integrate the equation of total mass conservation (2) to get

$$M^1 + M^2 + M^3 + M^4 + M^5 = \phi, \text{ a constant} \quad (16)$$

Each of the linear terms in (15) may be multiplied by unity in the form $(M^1 + M^2 + M^3 + M^4 + M^5)/\phi$ to yield a series of bilinear terms. Thus,

The system does not run down, however, because certain members of the community are continually fixing an amount of energy, Ξ^i , from a light source. The term Ξ^i is zero if the population i is not a primary producer.

An energy balance for the population i may now be written. In words, the time rate of change of energy of a population is equal to the rate of biomass energy flux into the population, minus the rate of biomass energy flux out of the population, minus the rate of energy loss through respiration, plus the rate of fixation energy, if the species is autotrophic in nature. As an equation:

$$\frac{dE^i}{dt} = \alpha_{pq}^i e^{pq} - R^i + \Xi^i. \quad (7)$$

The structure array α is identical to that defined in the mass balance.

One may rightfully ask whether a population with biomass M^i and total energy E^i possesses a constant energy per unit biomass, A^i . To assess this question, it is necessary to regard the structure of a population. If a population consisted of perfectly identical individuals never changing over their lifespan, A^i would certainly be constant. But populations possess a structure, i.e. a distribution of age, morphology, lifespan, etc. (This structure is not to be confused with community structure as defined by the structure array α .) Since population structure is time dependent, it would follow that A^i is a function of time. The perspective here, however, is over ecological time where these variations appear as rapid fluctuations about some mean quantity. This mean quantity, in turn, would be a characteristic of the species itself, expected to change only when the species itself changes, i.e. evolves over the evolutionary time scale. The observer in ecological time, with his eyes too blurred to perceive the fluctuations on the physiological time scale, perceives a constant A^i . Henceforth in this argument, it will be assumed that the "energy content" or energy per unit biomass of a species, is a constant property of the population.

At this point, it would be a waste to abandon the summation convention which has served so well. Thus, in order to write the last assumption, it is necessary to define a two-dimensional array λ_j^i such that when $i = j$, $\lambda_j^i = A^i$, and when $i \neq j$, $\lambda_j^i = 0$. Then the proportionality between biomass and energy may be written as

$$E^i = \lambda_j^i M^j. \quad (8)$$

To be consistent with the preceding assumption, the energy flows associated with predator-prey relationships should be proportional to biomass flow, with the constant of proportionality being the specific energy content of the host population. This may be written as

$$e^{pq} = \lambda_p^q m^{lq}. \quad (9)$$

the respiration of species 1 may be written:

$$\begin{aligned}
 R^1 &= \rho_1^1 M^1 \\
 &= \frac{\rho_1^1}{\phi} M^1 (M^1 + M^2 + M^3 + M^4 + M^5) \\
 &= \frac{\rho_1^1}{\phi} (M^1)^2 + \frac{\rho_1^1}{\phi} M^1 M^2 + \frac{\rho_1^1}{\phi} M^1 M^3 + \frac{\rho_1^1}{\phi} M^1 M^4 + \frac{\rho_1^1}{\phi} M^1 M^5.
 \end{aligned} \tag{17}$$

Proceeding in this manner, one may generate a third order array, r_{uv}^i , such that

$$R^i = r_{uv}^i M^u M^v, \tag{18}$$

and the elements of the degenerate array r_{uv}^i are related to the respiration coefficients and the total biomass of the system.

In exactly similar manner, one may define an even more degenerate third order array for the fixation terms so that:

$$\Sigma^i = \sigma_{uv}^i M^u M^v. \tag{19}$$

Now that the respiration and fixation terms appear in bilinear form, the energy balance (12) appears in the same form as the mass balance (6)

$$\begin{aligned}
 \lambda_j^i \frac{dM^j}{dt} &= \alpha_{pq}^i \lambda_l^{p'} B_{uv}^{lq} M^u M^v - r_{uv}^i M^u M^v + \sigma_{uv}^i M^u M^v \\
 &= (\alpha_{pq}^i \lambda_l^{p'} B_{uv}^{lq} - r_{uv}^i + \sigma_{uv}^i) M^u M^v.
 \end{aligned} \tag{20}$$

This isomorphism of the mass and energy balance implies a relationship between the population dynamics coefficients and the energy parameters. To state these constraints more explicitly, it is advantageous to use equation (6) to eliminate the derivative in (20)

$$\lambda_j^i \alpha_{pq}^j B_{uv}^{pq} M^u M^v = (\alpha_{pq}^i \lambda_l^{p'} B_{uv}^{lq} - r_{uv}^i + \sigma_{uv}^i) M^u M^v, \tag{21}$$

or, upon rearranging,

$$(\lambda_j^i \alpha_{pq}^j B_{uv}^{pq} - \alpha_{pq}^i \lambda_l^{p'} B_{uv}^{lq} + r_{uv}^i - \sigma_{uv}^i) M^u M^v = 0. \tag{22}$$

(Matrix multiplication is a non-commutative group operation, and the reader should verify that the first two terms in parentheses will not cancel, even if the λ and λ' arrays are identical.) For the sake of abbreviation, the constant arrays in parentheses may be relabeled as one single third-order array:

$$\Omega_{uv}^i M^u M^v = 0, \tag{23}$$

where

$$\Omega_{uv}^i = \lambda_j^i \alpha_{pq}^j B_{uv}^{pq} - \alpha_{pq}^i \lambda_l^{p'} B_{uv}^{lq} + r_{uv}^i - \sigma_{uv}^i. \tag{23a}$$

System (23) is a set of quadratic homogeneous equations which must be valid for any arbitrary positive apportionment of biomass among the M^i . This will hold if and only if Ω is antisymmetric in the lower indices, i.e.

$$\Omega_{uv}^i = -\Omega_{vu}^i. \tag{24}$$

Equations (24) now explicitly relate the energy parameters to the parameters of population dynamics, once the structure of the community has been determined. The relationship is not always deterministic, however, since there are usually more B 's to be determined than there are equations in (24). To be exact, there are $\frac{1}{2}mn(n+1)$ independent B 's, where m is the number of mass flows in the system, and the factor $\frac{1}{2}$ comes from the fact that the B 's are symmetrical in their lower indices by definition. There are $\frac{1}{2}n^2(n-1)$ constraints in (24). the number of mass flows in a community is bounded from below by the number of species present, and from above by the number of flows in a system which each species transfers mass with every other species reciprocally, i.e.

$$n \leq m \leq n(n-1). \quad (25)$$

The system, then, is usually indeterminate with $\frac{1}{2}(m-n)(n^2+n)$ degrees of freedom.

The particular case where the system is determinate ($m = n$) represents the straight chain ecosystem. In spite of the fact that most actual systems resemble webs more than a closed straight chain, much of ecological conceptualization is done in terms of trophic levels with the implication of straight chains. For this reason, an example of how the parameters are related in a simple straight chain should prove to be an informative exercise.

4. A Simple Example

The system illustrated in Fig. 3 will now be considered. The energy per unit biomass of each species will be designated by λ_1 , λ_2 , and λ_3 , respectively, and the respirations per unit biomass per unit time by r_1 , r_2 , and r_3 . The rate of fixation of energy per unit biomass of the single producer, say species 1, is represented by σ . The total biomass will be ϕ , and it will be further assumed that $\lambda_j' = \lambda_j^i$.

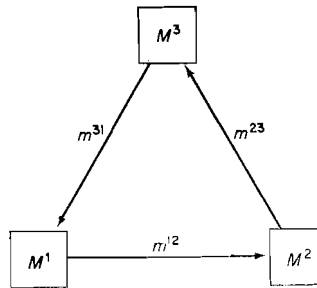


FIG. 3. A simple three-component straight-chain ecosystem.

The structure array will have the following entries:

$$\begin{aligned}\alpha_{31}^1 &= \alpha_{12}^2 = \alpha_{23}^3 = +1, \\ \alpha_{12}^1 &= \alpha_{23}^2 = \alpha_{31}^3 = -1, \\ \text{all other } \alpha^i &= 0.\end{aligned}$$

The energy content array will have as its entries:

$$\lambda_1^1 = \lambda_1, \quad \lambda_2^2 = \lambda_2, \quad \lambda_3^3 = \lambda_3,$$

with all the non-diagonal elements being zero.

As explained above, the pseudo-third-order arrays for respiration and fixation can be generated and are as follows:

$$\begin{aligned}r_{11}^1 &= r_1/\phi, \\ r_{21}^1 &= r_{12}^1 = r_{31}^1 = r_{13}^1 = r_1/2\phi, \\ r_{12}^2 &= r_{21}^2 = r_{32}^2 = r_{23}^2 = r_2/2\phi, \\ r_{22}^2 &= r_2/\phi, \\ r_{23}^3 &= r_{32}^3 = r_{13}^3 = r_{31}^3 = r_3/2\phi, \\ r_{33}^3 &= r_3/\phi, \\ \text{all other } r_{uv}^i &= 0, \\ \sigma_{11}^1 &= \sigma/\phi, \\ \sigma_{12}^1 &= \sigma_{21}^1 = \sigma_{13}^1 = \sigma_{31}^1 = \sigma/2\phi, \\ \text{all other } \sigma_{uv}^i &= 0.\end{aligned}$$

The only variables without assigned values are the B 's and these are determined by substitution of the above into (24) and solving. When the 18 independent B 's are solved for, they in turn can be substituted into (6) and the population equations will be written directly with the energy parameters as follows:

$$\begin{aligned}\frac{dM^1}{dt} &= \frac{\sigma - r_1}{\phi(\lambda_1 - \lambda_3)} (M^1)^2 + \left[\frac{\sigma - r_1}{\phi(\lambda_1 - \lambda_3)} - \frac{r_2}{\phi(\lambda_1 - \lambda_2)} \right] M^1 M^2 + \\ &\quad + \frac{\sigma - r_1}{\phi(\lambda_1 - \lambda_3)} M^1 M^3 - \frac{r_2}{\phi(\lambda_1 - \lambda_2)} M^2 M^3 - \frac{r_2}{\phi(\lambda_1 - \lambda_2)} (M^2)^2, \quad (26)\end{aligned}$$

$$\begin{aligned}\frac{dM^2}{dt} &= \frac{r^2}{\phi(\lambda_1 - \lambda_1)} (M^2)^2 + \frac{r_2}{\phi(\lambda_1 - \lambda_2)} M^1 M^2 - \frac{r^3}{\phi(\lambda_2 - \lambda_3)} M^1 M^3 + \\ &\quad + \left[\frac{r_2}{\phi(\lambda_1 - \lambda_2)} - \frac{r_3}{\phi(\lambda_2 - \lambda_3)} \right] M^2 M^3 - \frac{r_3}{\phi(\lambda_2 - \lambda_3)} (M^3)^2, \quad (27)\end{aligned}$$

$$\begin{aligned} \frac{dM^3}{dt} = & \frac{r_3}{\phi(\lambda_2 - \lambda_3)} (M^3)^2 - \frac{(\sigma - r_1)}{\phi(\lambda_1 - \lambda_3)} M^1 M^2 + \\ & + \left[\frac{r_3}{\phi(\lambda_2 - \lambda_3)} - \frac{(\sigma - r_1)}{\phi(\lambda_1 - \lambda_3)} \right] M^1 M^3 + \\ & + \frac{r_3}{\phi(\lambda_2 - \lambda_3)} M^2 M^3 - \frac{(\sigma - r_1)}{\phi(\lambda_1 - \lambda_3)} (M^1)^2. \end{aligned} \quad (28)$$

One notices the presence of density-dependent terms [such as the first term on the right-hand side of (26)] which arise naturally in this derivation. In fact, if the B 's connected with these terms had *a priori* been set equal to zero, it can be shown with the help of (24) that this leads to a contradiction of the second law of thermodynamics in at least one of the species. One may question the sign of these density dependent terms and how they affect the behavior of the system. Indeed, one might better inquire of the conditions on the parameters for which the system as a whole behaves acceptably.

I am unable to give necessary and sufficient conditions for stable behavior at this time; however, the direction in which one might seek these conditions is discussed later. One is able, nevertheless, to state a set of sufficient (but not necessary) conditions which will always insure that the biomasses remain positive (Wei, 1965). For example, in (26) the independent variable does not appear explicitly on the right hand side of the equation. If one chooses parameters such that the limit of the right hand side as M^1 approaches zero is always positive, then this implies that if M^1 ever gets close enough to extinction, it must begin to increase again, i.e. it never goes negative. One can impose this same condition on (27) and (28) so that the entire system can never misbehave. In mathematical notation the conditions are:

$$\lim_{M^1 \rightarrow 0} \frac{dM^1}{dt} > 0, \quad (29)$$

$$\lim_{M^2 \rightarrow 0} \frac{dM^2}{dt} > 0, \quad (30)$$

$$\lim_{M^3 \rightarrow 0} \frac{dM^3}{dt} > 0. \quad (31)$$

Applying these restrictions to (26), (27), and (28) yields respectively:

$$-r_2/\phi(\lambda_1 - \lambda_2) > 0, \quad (32)$$

$$-r_3/\phi(\lambda_2 - \lambda_3) > 0, \quad (33)$$

$$-(\sigma - r_1)/\phi(\lambda_1 - \lambda_3) > 0. \quad (34)$$

Now the total biomass ϕ is always positive, and the respiration coefficients, fixation coefficient, and specific energies are all defined as intrinsically

positive. Therefore, (32) and (33) yield the inequalities

$$\lambda_3 > \lambda_2 > \lambda_1. \quad (35)$$

In turn, (34) and (35) give

$$\sigma > r_1. \quad (36)$$

That specific fixation must on the average exceed specific respiration in the primary producer, as in (36), agrees well with intuition. That specific energies should increase as one ascends the trophic ladder seems less intuitive. The fact that animal fats and proteins have generally higher caloric values than plant proteins and carbohydrates does not argue against the result, however (White, Handler, Smith & Stetten, 1959). Interestingly enough, if the equations of population dynamics are compared with a community entropy balance in the same manner as was done above with the energy, the analogue of (35) would state that the specific entropy would decrease as one ascends the trophic levels, in agreement with intuition.

The density-dependent terms for the stable situation do turn out to be negative, which is consistent with Garfinkel's results.

The reader may have noticed that the bilinear right-hand sides of equations (26) through (28) can be rearranged into linear form. This simplification seems to be due to the simple straight-chain system, and is not to be expected of more complicated food webs.

5. Extending the Theory

The preceding analysis is incomplete in two respects. First, there remains the question of the "degrees of freedom" in the general case. Are these true degrees of freedom, always changing; or does the system usually tend towards, or oscillate about, a steady state? If there is a steady state, how are the remaining population parameters determined? Second, there is a need for necessary and sufficient conditions which will assure the proper behavior of any system, once the structure has been determined.

The student of irreversible thermodynamics will immediately recognize that these two issues are not unrelated. In the theory of near-equilibrium thermodynamics, the criterion for a stable steady state is that the entropy production be at a minimum. Written out:

$$d\left(\sum_i J_i X_i\right) = 0, \quad (37)$$

where the J_i are the generalized thermodynamic fluxes in the system, and the X_i are the generalized thermodynamic forces. Examples of thermodynamic fluxes are the rates of chemical reactions, the mass diffusion flux, and a conductive heat flux. Their respective thermodynamic forces are the affinity

of a chemical reaction, the chemical potential gradient (for isothermal systems), and the temperature gradient.

Besides assuring stability, a theory such as that of minimum entropy production can be used to fix certain relations between parameters in the absence of other determining factors. For example, in a non-straight chain ecosystem, $\frac{1}{2}n^2 (n+1)$ population parameters could be eliminated with the help of (24). The entropy could then be written in terms of the energy parameters and the remaining B 's. Finally, with the help of variational calculus, the remaining $\frac{1}{2}(m-n)(n^2+n)$ population parameters could be chosen so that the entropy production was at a minimum. In this proposed procedure the importance of the constraints (24) should not be underemphasized. If one were to attempt to write the entropy production in terms of the B 's alone, the minimization procedure would result in thermodynamic equilibrium, or the total death of the system. By using (24), one introduces the energy fixation and respiration rates which set the lower and upper bounds, so to speak, of the scale of mass cycling. In mathematical terms, one is minimizing with respect to a set of constraints, which precludes the trivial solution.

In the above outline, minimization of the entropy production was said to determine the stable steady state. Entropy production is a concept for which many have, to some greater or lesser extent, an intuitive feel, and was employed for that reason. Actually, the hypothesis of minimum entropy production is valid only in the near-equilibrium domain. While this domain cannot be excluded from ecological interest, it is more likely that ecosystems operate far from thermodynamic equilibrium.

Fortunately, Prigogine (1967) has advanced a minimization principle valid over the whole range of thermodynamics. This new principle states that at a steady state

$$\sum_i J_i dX_i = 0. \quad (38)$$

In the last reference Prigogine shows how (38) reduces to (37) in the near-equilibrium range.

With the procedure thus outlined for treating webbed ecosystems, one may next inquire as to the identity of the fluxes and forces. The fluxes, quite obviously, are the biomass fluxes between the species. The forces pose another problem; in fact, they elude me at the present time. What is needed is the biological analogue of the affinity function. The principle which allows the definition of the affinity function in chemical systems is the law of definite proportions, or stoichiometry. There appears to be no analogue to the law of definite proportions which acts on a macrobiological scale. A force which is dimensionally consistent with the biomass flux, and at the same time makes good biological sense, is needed. I am presently working to

evaluate alternative hypotheses for the thermodynamic force behind the biomass flows.

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Note added in proof: Since this paper went to press, I have discovered that a few of the ideas presented in the introduction and statement of the generalized Lotka-Volterra hypothesis agree closely with some previously published by Kerner (1969), but unknown to me at the time of writing [see KERNER, E. H. (1969) in *Towards a Theoretical Biology*, Vol. II. (C. H. Waddington, ed.) p. 129. Edinburgh: University of Edinburgh Press.]