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Measures of Energy Cost and Value in Ecosystems

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The physical output of ecological processes have different values even though they may be measured in the same physical units. Using linear input–output theory, we derive a set of weights based on direct and indirect energy requirements for ecosystem commodities which uniquely converts them into commensurable unit costs. Under certain conditions, these costs are equal to values or prices. Using this system, behavioral theories can be better posed for experimental verification.

Components of an ecosystem exchange physically measurable quantities with each other, in much the same way as sectors of an economy do. While these exchanges can be physically measured in a number of ways (e.g., by mass, enthalpy, or carbon content), these measures will not necessarily capture the system-wide cost of the exchange. Energy cost is defined here as a weighting factor times the physical quantity exchanged, representing the total system-wide energy required for the exchange. In economics, the relevant weighting factors are called prices and either they are determined by decentralized markets (prevalent in western economies) or they are set by a central authority (prevalent in socialist economies). The connection between unit energy cost (or energy intensity as we prefer to call it) is made later in the paper.

We can physically measure the ecosystem exchanges and the inputs of resources to a system. But what are the unit costs of exchange in an ecosystem where there are no agents to set or reveal them? In this paper we will show that a unique set of unit costs in the ecosystem can be determined by an appropriate allocation of the net input to the ecosystem through the web of system exchanges. In this process of unit cost determination, we will use an input–output description of an ecosystem and use available energy as the only net resource input (a thermodynamically closed system; one in which only energy flows across the boundary).

We will demonstrate how the two basic, alternative assumptions of modern linear input–output formalization collapse to one, yielding the basis for a unique set of energy prices for ecosystem exchanges. The development of this theoretical concept

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is important because it allows us to experimentally (e.g., using microcosms) check various behavioral hypotheses based on the value system.

I. THEORETICAL DEVELOPMENT

In this section we first review input–output economics' treatment of the joint production problem and the two alternative assumptions usually used to handle it. We then obtain two expressions for energy intensities based on these assumptions. For arbitrary commodity weightings, the two results are different, but if the weightings are proportional to the system energy intensities, we show that the two assumptions yield identical sets of energy intensities. Finally we give an example of how the energy intensities can be used to pose testable behavioral hypotheses about light-constrained ecosystems.

Theory — Standard *I–O* Economics

In previous articles [1–3], the system interchange composed of processes exchanging with other processes was described by a single matrix. This matrix, combined with a vector of total outputs of each of the processes, allowed an approximation of the direct and indirect energy cost of a unit of process output. Major problems arise because each process may produce more than one type of output and some of these outputs are also made in other processes, a situation called the production of joint commodities. The proper assignment of input costs to these joint commodities is an unresolved problem in economics. The problem can be resolved by assumption, of course, and that is the way we intend to handle it; fortunately as we shall see here, the available assumptions can be uniquely restricted.

A modern [4–7] formulation of input–output theory is designed to accomodate if not resolve the joint products problem. Production and consumption are given by two distinct matrices: one which gives the use of the n commodities by the m processes (called the "Use" matrix or $\mathbf{U}$, an $n \times m$ matrix) and the other which gives the production of commodities by the processes (called the "Make" matrix or $\mathbf{V}$, an $m \times n$ matrix). Each commodity is measured in the same units throughout $\mathbf{U}$ and $\mathbf{V}$, but the units need not be the same for all the commodities. For example, the commodity flow "algal biomass" from the process "algae" may be measured in grams but the algal oxygen flow can be measured in cubic centimeters. It is therefore always dimensionally possible to form the total commodity output vector $\boldsymbol{q}$ but not the total process output vector $\mathbf{g}$. This incommensurability problem for $\mathbf{g}$ is the basic difficulty to which this paper is devoted.

In this section we first review input–output economics' treatment of the joint production problem and the two alternative assumptions usually used to handle it. We then obtain expressions for energy intensities based on these two assumptions. For arbitrary commodity prices, the two results are different, but for the assumption that price is proportional to energy intensity, we show that the two results are identical.

For a set of process outputs to be summable dimensionally, each output commodity must be separately weighted. These weighting factors should in some way represent the relative importance of each commodity to the system, thereby converting the various outputs to a consistent unit of measure. Let us assume for now that the weighted commodity flows are commensurate and that $\mathbf{g}$ is somehow measurable. The basic physical commodity balance equations are

$$\mathbf{q} = \mathbf{U}\mathbf{i} + \mathbf{e}, \tag{1a}$$

$$\mathbf{q} = \mathbf{V}^{\mathrm{T}}\mathbf{i}, \qquad \text{where T indicates transpose,} \tag{1b}$$

$$\mathbf{g} = \mathbf{V}\mathbf{i} \tag{1c}$$

where

$\mathbf{q}$ = commodity output vector
$\mathbf{g}$ = process output vector
$\mathbf{e}$ = net system output vector
$\mathbf{U}$ = use matrix (commodity $\times$ process)
$\mathbf{V}$ = make matrix (process $\times$ commodity) [6].

All quantities are marginal for a fixed time period. In addition, i = vector of 1's.

We want to solve for $\mathbf{q}$ as a function of $\mathbf{e}$. But to do this we must first transform the system from one with joint or multiple outputs to an equivalent system in which each sector has only one output.

We can manipulate Eqs. (1) under one of two assumptions: The process-technology or the commodity-technology assumption.

The process-technology assumption allocates inputs to joint outputs in proportion to the "market share" or proportion of total output each joint product represents [9]. This assumption requires that the outputs be in communsurable units (i.e., dollars), an assumption that does not hold for ecosystem flows measured in physical units.

The commodity-technology assumption allocates inputs to joint products based on their proportions in a "major" producing sector for each commodity [9]. These inputs in "minor" producing sectors are proportionally reassigned to the "major" producing sector to eliminate the joint product. A problem with this technique is that it can lead to "negative inputs" if the input proportions to the major and minor sectors are very different.

These two assumptions are defined more explicitly and compared in Table I.

It can be seen that the two assumptions also share this feature: a commodity requires the same direct inputs per unit of its output, regardless of what sector(s) it is produced in.

Both Eqs. (2) and (3) relate total output (say of steel) required for the economy to produce net output (say of shoes). (Steel is required indirectly, to produce shoes, if not directly.) The numerical results for $\mathbf{q}$ from Eqs. (2) and (3) will differ, depending on which technology assumption is used [9].

Theory — Energy Intensities

Energy intensities in ecosystems can be calculated in a way similar to the economic argument used so far [3].

We assume that energy "enters" in specific processes (e.g., autotrophs) and that the processes (e.g., trophic levels) exchange materials in a way describable by

TABLE I

Comparison of Assumptions

Process-technology assumption	Commodity-technology assumption
Rewriting Eq. (1a), $$\mathbf{q} = \mathbf{U}\hat{\mathbf{g}}^{-1}\hat{\mathbf{g}}\mathbf{i} + \mathbf{e}$$ where $\hat{\mathbf{g}}$ is a diagonal matrix with the elements of g the diagonal. Substitute from Eq. (1c). $$\mathbf{q} = \mathbf{U}\hat{\mathbf{g}}^{-1}\mathbf{V}\mathbf{i} + \mathbf{e},$$ and rewriting, $$\mathbf{q} = \mathbf{U}\hat{\mathbf{g}}^{-1}\mathbf{V}\hat{\mathbf{q}}^{-1}\hat{\mathbf{q}}\mathbf{i} + \mathbf{e}.$$ Now define $\mathbf{U}\hat{\mathbf{g}}^{-1} = \mathbf{B}$ $$\mathbf{V}\hat{\mathbf{q}}^{-1} = \mathbf{D}.$$ Then $$\mathbf{q} = \mathbf{B}\mathbf{D}\mathbf{q} + \mathbf{e}$$ $$\mathbf{q} = (\mathbf{I} - \mathbf{B}\mathbf{D})^{-1}\mathbf{e} \quad (2)$$ Assuming that $\mathbf{B}$ and $\mathbf{D}$ are constant is the process-technology assumption. $\mathbf{B}$ = constant means that the inputs to each process are proportioned to its total output (assuming that the output is in commensurate units). $\mathbf{D}$ = constant is the market-shares assumption, which states that when anyone consumes 1 unit of a commodity, that unit was produced by the several processes that produce it in constant proportions.	Rewriting Eq. (1a), $$\mathbf{q} = \mathbf{U}\hat{\mathbf{g}}^{-1}\hat{\mathbf{g}}\mathbf{V}^{\mathrm{T}-1}\mathbf{V}^{\mathrm{T}}\mathbf{i} + \mathbf{e}$$ $$= \mathbf{B}(\mathbf{V}^{\mathrm{T}}\hat{\mathbf{g}}^{-1})^{-1}\mathbf{V}^{\mathrm{T}}\mathbf{i} + \mathbf{e}$$ Substitute from (1b) $$\mathbf{q} = \mathbf{B}(\mathbf{V}^{\mathrm{T}}\hat{\mathbf{g}}^{-1})^{-1}\mathbf{q} + \mathbf{e}$$ Define $\mathbf{V}^{\mathrm{T}}\hat{\mathbf{g}}^{-1} = \mathbf{C}$. Then $$\mathbf{q} = \mathbf{B}\mathbf{C}^{-1}\mathbf{q} + \mathbf{e}$$ $$\mathbf{q} = (\mathbf{I} - \mathbf{B}\mathbf{C}^{-1})^{-1}\mathbf{e}. \quad (3)$$ Assuming that $\mathbf{B}$ and $\mathbf{C}$ are constant is the commodity-technology assumption. $\mathbf{B}$ = constant means the same as before. $\mathbf{C}$ = constant is the production shares assumption, which says that when a process produces 1 unit of output (assuming that the output is in commensurate units), the various commodities produced in that process have fixed proportions.

input–output matrices as discussed above. In practice, we use this approach only as a linear approximation for small changes about an initial equilibrium condition.

Energy intensity is defined as the total system input energy necessary to facilitate production of a unit of a commodity. In this sense the intensity can be thought of as an energy cost. Most of the energy intensity of a good actually represents dissipated free energy, but here it is considered an implied property of the final good, and therefore a congenial quantity, in that, for a process:

$$\text{(energy intensities)} \times \text{(flows in)} + \text{(any directly acquired energy)}$$

$$= \text{(energy intensities)} \times \text{(flows out)}.$$

Because commodities in ecosystems are measured in different physical units (i.e., gram of biomass) the vector **g** is not necessarily calculable and the process-technology assumption is not directly applicable. However, it is indirectly applicable by

TABLE II

Comparison of Assumptions for Ecosystems

Process-technology assumption

The derivation of energy intensities here is not as simple as for the economic case, because we first have to obtain a *process* energy intensity vector $\mathbf{E}^p$, (using the process technology assumption) and then convert it to a commodity energy intensity (without changing the assumption).

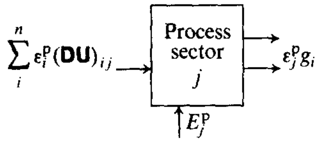

FIG. 2. A graphic representation of the process-technology assumption and energy balance across a typical process.

Figure 2 represents the conservation of embodied energy across process j. It is necessary to use the market shares assumption ($\mathbf{D}$ is constant) to "connect" process outputs to commodity inputs in the term $\mathbf{DU}$. We have assumed for the moment that g is self-consistent. $\boldsymbol{\varepsilon}^p j$ is the energy intensity of the *process* output. Solving, as before:

$$\boldsymbol{\varepsilon}^p = \mathbf{E}^p \hat{\mathbf{g}}^{-1}(\mathbf{I} - \mathbf{DB})^{-1}. \qquad (6)$$

We want the energy intensity of commodities, and therefore must convert process output to commodity output. We cannot assume $\mathbf{C}$ = constant here since we have already assumed $\mathbf{D}$ = constant (assuming both $\mathbf{C}$ and $\mathbf{D}$ to be constants is inadmissably restrictive). Then

$$\varepsilon_j^c = \frac{\partial E}{\partial q_j} = \sum_{i=1}^{h} \frac{\partial E}{\partial q_i}\frac{\partial q_i}{\partial q_j}$$

$$= \sum_{i=1}^{n} \varepsilon_i^p D_{ij} = (\boldsymbol{\varepsilon}^p \mathbf{D})_j$$

or

$$\boldsymbol{\varepsilon}^c = \boldsymbol{\varepsilon}^p \mathbf{D}, \quad \text{and}$$

$$\boldsymbol{\varepsilon}^c = \mathbf{E}^p \hat{\mathbf{g}}^{-1}\mathbf{D}(\mathbf{I} - \mathbf{BD})^{-1}. \qquad (7)$$

Commodity-technology assumption

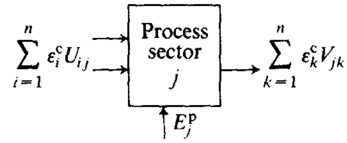

FIG. 1. Graphic representation of the commodity-technology assumption and energy balance across a typical process.

Figure 1 represents graphically the conservation of embodied energy, i.e., of energy intensities times flows across process j.

Matrices $\mathbf{U}$ and $\mathbf{V}$ are the "use" and "make" matrices mentioned previously. ε_j^c is the energy intensity under the commodity technology assumption (measured in calories/unit). E_j is the energy input to sector j from outside the system (in a fixed time period). In the figure, ε_k^c is assumed to be independent of j; this is the commodity technology assumption.

The balance equation implied by Fig. 1 is

$$\boldsymbol{\varepsilon}^c(\mathbf{V}^T - \mathbf{U}) = \mathbf{E}^p.$$

Post multiplying by $\hat{\mathbf{g}}^{-1}$ (assuming g makes sense dimensionally) yields

$$\boldsymbol{\varepsilon}^c(\mathbf{V}^T\hat{\mathbf{g}}^{-1} - \mathbf{U}\hat{\mathbf{g}}^{-1}) = \mathbf{E}^p\hat{\mathbf{g}}^{-1} \qquad (4)$$

or

$$\boldsymbol{\varepsilon}^c(\mathbf{C} - \mathbf{B}) = \mathbf{E}^p\hat{\mathbf{g}}^{-1}.$$

Thus

$$\boldsymbol{\varepsilon}^c = \mathbf{E}^p\hat{\mathbf{g}}^{-1}\mathbf{C}^{-1}(\mathbf{I} - \mathbf{BC}^{-1})^{-1}. \qquad (5)$$

Equation (5) should be compared with its economic counterpart, Eq. (2). Note that in Eq. (4), $\mathbf{E}^p$ is the counterpart of other process inputs in $\mathbf{U}$ with two differences: $\mathbf{E}^p$ comes from outside the system and hence there is no counterpart in $\mathbf{V}$ (in energy terms). By definition the energy intensity associated with $\mathbf{E}^p$ is one.

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assuming a set of weights to allow the formation of g and then investigating the properties of these weights. We describe more explicitly and compare the process- and commodity-technology assumptions for ecosystems in Table II.

Since Eqs. (5) and (7) describe commodity energy intensities for different technology assumptions, we need to use more complete notation.

The commodity energy intensities we wish to calculate, under the two technology assumptions, are

$$\text{commodity technology:} \quad \boldsymbol{\varepsilon}(c,c) = \mathbf{E}^{\mathrm{P}}\hat{\mathbf{g}}^{-1}\mathbf{C}^{-1}(\mathbf{I}-\mathbf{B}\mathbf{C}^{-1})^{-1} \tag{8}$$

$$\text{process technology:} \quad \boldsymbol{\varepsilon}(c,p) = \mathbf{E}^{\mathrm{P}}\hat{\mathbf{g}}^{-1}\mathbf{D}(\mathbf{I}-\mathbf{B}\mathbf{D})^{-1} \tag{9}$$

where for example, the notation $\boldsymbol{\varepsilon}(c,p)$ means commodity base, process technology. Conditions for invertibility can be derived in a way similar to that of Hawkins and Simon [8].

Equations (8) and (9) yield different values for the energy intensities. Both sets of intensities can be shown to satisfy energy closure, i.e., that energy coming into the system equals embodied energy leaving it embodied in net system output). That is,

$$E^T = \sum_{i=1}^{n} E_i^P = \sum_{i=1}^{n} \varepsilon_i e_i = \text{total energy into the system.} \tag{10}$$

When Are the Intensities Calculated by Both Methods Equal?

We will show that Eqs. (8) and (9) yield the same values when specific weightings are used for the flows in $\mathbf{U}$ and $\mathbf{V}$. In order to address this, we first derive general expressions for the effects of changing weights. Assume that the use and make matrices change thus (primes denote the new values):

$$\mathbf{U}' = \hat{\mathbf{p}}\mathbf{U}$$
$$\mathbf{V}' = \mathbf{V}\hat{\mathbf{p}},$$

where $\hat{\mathbf{p}}$ is a diagonal matrix containing the (commodity) weights. Then it follows that

$$\mathbf{g}' = \mathbf{V}\mathbf{p}$$
$$\mathbf{q}' = \hat{\mathbf{p}}\mathbf{q}$$
$$\mathbf{B}' = \hat{\mathbf{p}}\mathbf{U}\widehat{(\mathbf{V}\mathbf{p})}^{-1}$$
$$\mathbf{D}' = \mathbf{V}\hat{\mathbf{p}}\widehat{(\hat{\mathbf{p}}\mathbf{q})}^{-1} = \mathbf{V}\hat{\mathbf{p}}\hat{\mathbf{p}}^{-1}\hat{\mathbf{q}}^{-1} = \mathbf{V}\hat{\mathbf{q}}^{-1} = \mathbf{D}$$
$$\mathbf{C}' = \hat{\mathbf{p}}\mathbf{V}^T\widehat{(\mathbf{V}\mathbf{p})}^{-1}.$$

We substitute these primed values into (8) and (9) to produce expressions involving the $\mathbf{p}$ which have the relation to the desired energy intensities, $\varepsilon = \boldsymbol{\varepsilon}'\hat{\mathbf{p}}$. Note that since $E_i \geq 0$ for all i, for physical reality, $p_i > 0$ for all i.

We find that the commodity-technology energy intensity $\boldsymbol{\varepsilon}(c,c)$ (Eq. (8)) is unchanged. This seems reasonable when we note that it is not *necessary* to specify a process output g in the derivation of $\boldsymbol{\varepsilon}(c,c)$. On the other hand, the expression for the process-technology energy intensities does change:

$$\boldsymbol{\varepsilon}(c,p) = \mathbf{E}^{\mathrm{P}}\widehat{(\mathbf{V}\mathbf{p})}^{-1}\mathbf{D}\left(\mathbf{I} - \hat{\mathbf{p}}\mathbf{U}\widehat{(\mathbf{V}\mathbf{p})}^{-1}\mathbf{D}\right)^{-1}\hat{\mathbf{P}}. \tag{11}$$

Equation (11) is the general expression for the process technology energy intensity when commodity flows are given new weightings $\mathbf{p}$. It reduces to Eq. (9), as it should, when $\mathbf{p} = \mathbf{i}$.

In economic systems an alternative set of weights inherently exists: the monetary commodity prices $\mathbf{p}^c$. In earlier work [2, 5] we used this combined system with $\mathbf{g} = \mathbf{V}\mathbf{p}^c$ in Eqs. (8) and (9) to calculate the commodity-based process technology energy intensities $\boldsymbol{\varepsilon}^c$. We did this because in the economy the physical flows are generally not measured and reported, only the already priced dollar flows are, and because the commodity-technology assumption yielded some negative $\boldsymbol{\varepsilon}^c$ values. We now realize that such negative values are mainly a result of flaws in the original data acquisition and aggregation and can be eliminated by judicious further aggregation,[1] or by better data [16].

To summarize, Eqs. (8) and (10) give different values for energy intensities. For a particular choice of weightings $\mathbf{p}$, Eq. (10) becomes identical to Eq. (8). The choice that accomplishes this is the equality of weighting to the energy intensity itself, i.e., in Eq. (10), let $\mathbf{p} = \boldsymbol{\varepsilon}$.

THEOREM. *A sufficient condition for the equality of energy intensities calculated using the commodity-technology assumption (Eq.* (8)) *and the process-technology assumption (Eq.* (10)) *is that the commodity weightings in the process-technology assumption are the energy intensities, i.e.,* $\mathbf{p} = \boldsymbol{\varepsilon}$.

Proof. Rewriting Eq. (11),

$$\boldsymbol{\varepsilon}\left[\hat{\mathbf{p}}^{-1}\mathbf{D}^{-1}\widehat{\mathbf{V}\mathbf{p}} - \mathbf{U}\right] = \mathbf{E}^{\mathrm{P}}, \tag{12}$$

and reducing the commodity-technology equation for $\mathbf{E}^{\mathrm{P}}$ (Eq. (8)) gives

$$\boldsymbol{\varepsilon}[\mathbf{V}^{\mathrm{T}} - \mathbf{U}] = \mathbf{E}^{\mathrm{P}}. \tag{13}$$

These two equations are identical if

$$\boldsymbol{\varepsilon}\mathbf{V}^{\mathrm{T}} = \boldsymbol{\varepsilon}\hat{\mathbf{p}}^{-1}\mathbf{D}^{-1}\mathbf{V}\mathbf{p}. \tag{14}$$

The RHS of this equation reduces to $\boldsymbol{\varepsilon}\mathbf{V}^{\mathrm{T}}$ if $\mathbf{p} = \boldsymbol{\varepsilon}$ (sufficiency), thus

$$\begin{aligned}
\boldsymbol{\varepsilon}\hat{\mathbf{p}}^{-1}\mathbf{D}^{-1}\widehat{\mathbf{V}\mathbf{p}} &= \boldsymbol{\varepsilon}\hat{\boldsymbol{\varepsilon}}^{-1}\mathbf{D}^{-1}\widehat{\mathbf{V}\boldsymbol{\varepsilon}} && \text{assuming } \mathbf{p} = \boldsymbol{\varepsilon},\\
&= \mathbf{i}\mathbf{D}^{-1}\widehat{\mathbf{V}\boldsymbol{\varepsilon}},\\
&= \boldsymbol{\varepsilon}\mathbf{V}^{\mathrm{T}}\widehat{\mathbf{i}\mathbf{D}^{-1}},\\
&= \boldsymbol{\varepsilon}\mathbf{V}^{\mathrm{T}} && \text{since } \mathbf{i}\mathbf{D}^{-1} = \mathbf{i}\hat{\mathbf{q}}\mathbf{V}^{-1} = \mathbf{q}\mathbf{V}^{-1} = \mathbf{i}\mathbf{V}\mathbf{V}^{-1} = \mathbf{i}.
\end{aligned}$$

But does Eq. (14) hold for any other $\mathbf{p}$? We can easily show by many 3×3 counterexamples that other $\mathbf{p}$ also exist. In each case, however, at least one element of each of the additional $\mathbf{p}$ was negative. Thus we suspect that the only "real" solution (i.e., all $p_i > 0$) is $\mathbf{p} = \boldsymbol{\varepsilon}$, but we are unable to complete the proof. Of course in a system with multiple inputs of non-produced commodities (the usual way in which an economy is viewed) we have several possible vectors of positive definite prices, one for each non-produced input.

In other words, if we choose to weight the commodity outputs by their energy intensities to form a process output value, we find the difference in the energy

[1] For example, the radio and TV broadcasting sector consumed all of its own product according to the 1972 I–O tables. This was one of 3 obvious data lapses that explained the negative energy intensities obtained via the commodity-technology assumption. Stone [9] has a detailed explanation for the occurrence of negative elements.

intensities provided by the two principle assumptions of I–O analysis disappear: the simpler result from the commodity-technology assumption suffices.

What significance does this have for ecosystem modeling? We have shown that using weightings which are equal to energy intensities results in only one method (Eq. (8)) for computing those energy intensities.[2] There is certainly something suggestive and attractive about the notion of commodity weighting in an ecosystem being proportional to energy intensity. It allows use of embodied energy as the "fundamental" unit of transaction between components of ecosystems in a manner analogous to the way dollar values are used to track exchanges in economic systems. This analogy does not hold for "raw" calorie energy content.

ENERGY COSTS AND VALUE

Finally, under what conditions can we think of the energy intensities (which are actually "costs") as "prices" or "unit values" in exchange in an ecosystem? Both Sraffa [10] and Samuelson [11] have shown that unless the *present* cost of historic capital (biomass in our case) formation is included in the calculation of the cost, then they cannot say that the costs equal value in exchange (price) in an economic system. These authors calculate the present value of historic costs in economic systems by enlarging these historic costs, depending on their age, by an "interest" rate (the time cost of capital), and adding them on to the current cost. So, they argue, that cost is price in economic systems only if they add to the costs calculated from current inputs, those historic capital costs of capital items used up in the current period, weighted by their age using an interest rate [12]. But the present-day value of capital created several periods ago is influenced by two other phenomena: first the physical, irreparable damage suffered by the capital item over time and second, the existence of a new, more efficient capital item which accomplishes the same end result as the older capital. For value balance to occur at the end of each period, the interest or appreciation rate suggested by Sraffa and Samuelson should just overcome the loss of value of the capital item due to these two effects. Thus the present value of historic capital is its present replacement value. In the case of our ecosystem, that value is the direct and indirect energy cost of producing the biomass *in the present period*. Thus, if we include in the energy inputs to the system the energy required for the present period's production of replacement biomass, we should have satisfied the capital-aging problem.

In the most general equilibrium solution described in economics, both the levels of demand and of supply are functions of the price and the quantity involved in exchange. The intersection of these two functions determines the equilibrium price (and quantity). This price represents the lowest possible direct and indirect energy per unit output achievable in the system. We have defined our system so that the solution to this problem is simplified, although this procedure might restrict the utility of our approach.

Another theorem [10] from economics allows prices to be calculated in the absence of knowledge of consumer preferences. These conditions are: (1) a known distribution among the processes of a single input factor (energy in our case); (2) constant, linear production coefficients (Eqs. (8) or (9) with constant $\mathbf{B}$, and $\mathbf{C}$ or

[2] We also note that this means that we must define $\mathbf{U}$ and $\mathbf{V}$ as square matrices, i.e., the number of commodities and of processes must be equal.

D)[3]; and (3) the absence of joint production of commodities (the result of applying the process-technology or commodity-technology assumption).

Such a set of assumptions allows the formation of new biomass considered as a net output (a "profit") and disconnects demand from the determination of price or unit value in the system. Cost is linearly proportional to total production and production technique *alone* determines price. The quantity produced is determined only by the collective demand for the various commodities.

This set of assumptions allows the price (ε) of the various system commodities to be determined by the normalized coefficients of the use and production matrices. The columns in the $\mathbf{BD}$ and $\mathbf{BC}^{-1}$ matrices are said to be "technological" descriptors of the production processes of their respective commodities. As long as none of these technologies change (or change little) the prices in the ecosystem are constant (or nearly constant). But under the assumptions given above this means that each set of normalized production process inputs is independent of the level of production (no economics of scale) and it means that each species (and perhaps even each different age cohort in each species) should be defined as a separate process. Otherwise the technological descriptors will change simply due to shifts in the population balance between various species (e.g., algae) collected into the same process. This is a definitional or aggregational problem and it requires more data (on each subspecies) to allow separate process definition.

Prices in the ecosystem can be viewed in terms of the opportunity costs for the components (processes). While ecosystems do not have the level of "consciousness" and choice apparently available in economic systems, and exchanges are not tracked with an easily observable common currency, the concepts of cost, benefit, and "choice" are still important in an evolutionary sense. Any ecosystem faces a scarcity of primary resource (solar energy) in the long run and intermediate resources (nutrients, water, etc.) in the short run. Competition requires an optimal allocation of these resources and a balancing of costs (measured in the units of E^{T}) and benefits (in the same units). These measures of embodied energy can be used to quantify and summarize the complex trade-offs between foraging and predator avoidance faced by organisms in ecosystems. In the ecosystem, natural "unconscious" natural selection chooses the optimal allocation. Humans seem capable of improving (though some would argue just speeding up) this unconscious process by applying conscious modeling and forethought. The completely "rational" consumer is, however, only an idealization and "choice" via natural selection seems to play an important role in both ecological and economic systems. The energy prices we define are merely a convenient index of the results of this process that may be useful in understanding ecosystem and economic system behavior.

Utilizing the Energy Prices

The ultimate quest of this exercise is to provide a value base for ecosystem exchanges so that the behavior pattern of the components can be modeled. When such behavior is understood, the future course of ecosystem development may be

[3] It is possibly that the full production potential is not reached by every component at all times. The marginal energy costs can be determined empirically by Eq. (8) or (12), by letting the $\mathbf{V}^{\mathrm{T}}$, $\mathbf{U}$, and $\mathbf{E}^{\mathrm{P}}$ be the matrices and vector of *change* in their respective elements between two consecutive time periods [13].

better predicted when the system is subjected to predetermined changes in the basic inputs or outputs.

We can proceed with the above set of assumptions regarding the connection between cost and price. We can, for example, posit a behavioral hypothesis such as the following:

Define the net output vector **e**, in a given time period, to be composed of three independent vectors:

(1) The vector of commodity depreciation. The depreciation rates of the "closed system" commodities are exactly countered at the steady state by the input of energy to the system. The depreciation rates can be determined experimentally by suddenly removing the energy input and observing the initial rates of change of the commodity stocks. As experience is gained from such observations, theoretical descriptions of the depreciation rates can be made (such as, these being equal to a constant times the stock level). These depreciation rates may also be thought of as the "basal" or "resting" metabolism rates of each of the processes. These rates would be represented by the commodity flows required in the ecosystem which would occur if the system's components were producing only enough to satisfy their minimum needs (i.e., no flows for predators, for predation, or for reproduction).

(2) The vector of total new additions of each of the commodities.

(3) The vector of commodity net exports from the system. These would be commodity exports less the imports of the same commodities.

Note that we define the commodities as organized substances produced (ordered) by the system. The only non-produced commodity used by the system is light energy. We note that an ecosystem cannot long have commodity net exports. Therefore, let us assume that our system is thermodynamically closed, i.e., our system has light as its only input and heat and light as its only net outputs. We can then perform controlled experiments on this ecosystem to see if it is, for example, maximizing Q, where $Q = \boldsymbol{\varepsilon}(\mathbf{e}^2 - \mathbf{e}^1)$, where $\mathbf{e}^2$ is the vector of the change in net biomass formation rate and $\mathbf{e}^1$ is the vector of change in the depreciation rates and $\boldsymbol{\varepsilon}$ is derived from Eq. (13) for the initial state. The maximizing procedure is constrained by the given amount of light increase, the temperature of the environment surrounding the system, and a series of equations which set the maximum flow rate for each commodity as determined from the physical aspects of the given system (e.g., niche size). The change in the net system output $\mathbf{e}^1$ and $\mathbf{e}^2$ can also be experimentally determined. Their difference vector can be compared to the same vector determined from the optimization program. This procedure allows for changes in the output of each of the commodities (Eq. (3)).

We note that this specification of an optimizing program is such that if it is an accurate predictor of the resulting net output, then the concept of $\boldsymbol{\varepsilon}$ as a measure of ecosystem exchange value is upheld.

We might also specify columns and rows of U and V respectively for a large number of possible processes in an ecosystem and let the optimizing program select the appropriate mix of components as it tries to maximize $\boldsymbol{\varepsilon}\mathbf{e}$. This is similar to the linear programming approach suggested by Costanza and Neil [14]. Other behavior patterns in economics are demonstrated by Simon [15].

We have recently begun the construction of small (1000 ml) aquatic ecosystems in which all exchanges can either be directly measured or imputed from direct measurement. We will be able to control all of the system inputs and outputs. We should then be able to measure the energy costs and test for behavioral strategies using an actual system. It is this blend of system theory and real experiments on living systems which we believe will be fruitful for ecological and, perhaps, economic understanding.

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