



Complementarity of Ecological Goal Functions

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This paper summarizes, in the framework of *network environ analysis*, a set of analyses of energy–matter flow and storage in steady-state systems. The network perspective is used to codify and unify ten ecological orientors or extremal principles: maximum power (Lotka), maximum storage (Jørgensen–Mejer), maximum empower and emergy (Odum), maximum ascendancy (Ulanowicz), maximum dissipation (Schneider–Kay), maximum cycling (Morowitz), maximum residence time (Cheslak–Lamarra), minimum specific dissipation (Onsager, Prigogine), and minimum empower to exergy ratio (Bastianoni–Marchettini). We show that, seen in this framework, these seemingly disparate extrema are all mutually consistent, suggesting a common pattern for ecosystem development. This pattern unfolds in the network organization of systems.

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1. Ecological Organizing Principles

From classical thermodynamics two principles are firmly established for systems near equilibrium (Aoki, 1998). The first is the second law which applies to isolated systems: entropy always increases with time and approaches a maximum at equilibrium. The second is for open systems (Nicolis & Prigogine, 1977): entropy production always decreases with time and approaches a minimum at steady state. Far from equilibrium, which is where many physical systems and all living systems operate, these principles do not apply. The search for organizing principles that do apply has produced a variety of energy “orientors” (Müller & Leupelt, 1998).

The central idea of the orientor approach... refers to self-organizing processes, that are able to

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build up gradients and macroscopic structures from the microscopic “disorder” of non-structured, homogeneous element distributions in open systems, without receiving directing regulations from the outside. In such dissipative structures the self-organizing process sequences in principle generate comparable series of constellations that can be observed by certain emergent or collective features. Thus, similar changes of certain attributes can be observed in different environments. Utilizing these attributes, the development of the systems seems to be oriented toward specific points or areas in the state space. The respective state variables which are used to elucidate these dynamics, are termed *orientors*. Their technical counterparts in modeling are called *goal functions* (Müller and Fath, 1998, p. 15).

In a large part, these orientors follow from the seminal work of Odum (1969) in which he hypothesized on the trends to be expected in ecosystem development. That paper formed the basis for several of the long standing orientors

investigated herein such as biomass, cycling, internal organization, residence time, and information. More recently, Schneider & Kay (1994a), who take a thermodynamic approach, proposed seven ecosystem properties as basic orientors: exergy capture, energy flow, cycling of energy and materials, respiration and transpiration, biomass, average trophic structure, and types of organisms. Except for the last two, each of these seven properties is addressed in this paper. Additional thermodynamic goal functions have been proposed specifically in the context of ecological models. In particular, Bendoricchio & Jørgensen (1997) made the case that the primary ecosystem goal function is exergy storage. Bastianoni (1998; Bastianoni & Marchettini, 1997) suggested minimum empower to exergy ratio as the primary ecosystem goal function, and Jørgensen *et al.* (2000) suggested specific dissipation as the primary pattern observed in growth phenomena.

A few authors have investigated the subject of goal function unification. Jørgensen (1992, 1994; Jørgensen & Nielsen, 1998) found a strong correlation between several goal functions and suggested that perhaps their integration could lead to consideration of only one of them. Patten (1995), using an earlier development of network analysis, showed that many goal functions have a common basis in the path structure and associated microscopic dynamics of systems. Here, we take this a step further by demonstrating consistency of ten goal functions through a single explicit notational scheme expressing network organization. We will make these ties initially by short statements in italics at the end of each numbered section below, then amplify them later. Typically, a goal function refers to the “maximum” or “minimum” value of a particular quantity. However, because open ecosystems are self-organizing complex adaptive systems (Waldrop, 1992) responding to current environmental conditions, we view the organizing principles as “orientors” or “attractors” (Müller & Leupelt, 1998). The active descriptors “maximize” and “minimize” refer then to the directional nature of the network processes underlying the goal functions.

1. *Maximize power.* Lotka’s (1922) *maximum power principle* states that systems become organized to maximize their energy throughput. Odum

has long championed this principle in ecology, beginning with Odum & Pinkerton (1955) which argued that maximizing power produced the most energy to perform work and create order (“pump out disorder”). In networks, power is reflected in energy throughput or *total system throughflow* (TST), the sum of flows into, or alternatively out of, all compartments (Patten, 1995). Thus, in the network context, maximizing power is equivalent to maximizing total system throughflow. This affects many of the other principles to follow. *Maximizing power (throughflow) will be taken as reference condition 1.*

2. *Maximize storage.* Jørgensen & Mejer (1979, 1981) proposed a *maximum storage principle* in which energy systems maximize their distance from a thermodynamic reference point by storing usable energy (exergy). The associated accumulation of mass or energy is reflected in structure, function, gradients, order, organization, and information—all of which express in different ways departure from the reference. For entire systems, this principle asserts that *total system storage* (TSS) is maximized. For biotic systems this means maximizing biomass. *Maximizing storage will be considered as reference condition 2.*

3, 4. *Maximize empower and emergy.* Odum (1988, 1991) developed the concept of energy (embodied energy) to describe energy quality as referenced to solar radiation. As solar energy passes through a series of energy transformations, its quality increases in proportion to the amounts of original solar energy required at each step. Emergy measures this stored energy quality, and empower the associated energy flow. The accounting methods used to calculate emergy and empower reflect the total direct and indirect energy storage and throughflow in a system, respectively. *Maximizing empower (EMP) is consistent with reference condition 1 and maximizing emergy (EMG) is consistent with reference condition 2.*

5. *Maximize ascendancy.* Ulanowicz (1986, 1997) proposed a *maximum ascendancy principle*, where ascendancy quantifies network organization as the product of the total system throughflow (TST) and average mutual information (AMI). AMI involves the individual flow and a complicated expression of the logarithm of various other flow and organizational

components (Ulanowicz & Norden, 1990). Average mutual information is dimensionless and has a restricted range of values (generally between about 2.0 and 6.0). The total system throughflow, which scales this information quantity, can vary widely over the nonnegative real numbers. As a result, throughflow dominates the ascendancy measure such that power and ascendancy give strongly correlated results (Jørgensen, 1994). *Maximizing ascendancy, then, approximates reference condition 1.*

6. *Maximize dissipation.* Dissipative structures far from equilibrium have been suggested to maximize entropy production (Prigogine & Stengers, 1984; Brooks & Wiley, 1986). Schneider & Kay (1990, 1994a,b, 1995, 1996) elaborated this in exergy terms, stating that systems supplied with an external exergy source will respond by all means available to degrade the received exergy. This amounts to a *maximize dissipation principle*, and systems and processes satisfying it best gain from the implied work performed. Such gains in work represent a source of selective advantage in physical and biological evolutionary systems. For biological systems dissipation includes respiration plus other usable or unusable exports. Total system export (TSE) is the sum of dissipative processes over all components. Maximizing total system export (TSE) seems counter to the maximize storage principle above. This incongruence has produced a divergence in contemporary discussion between proponents of maximizing storage (Jørgensen–Mejer) and maximizing dissipation (Schneider–Kay). The network model developed below gives a common basis for both ideas because it allows, against dissipation which must be bounded by prior energy acquisition and utilization efficiency, the indefinite development of total system storage (TSS) through increased organization. We show that *maximizing dissipation is consistent with both reference conditions 1 and 2.*

7. *Maximize cycling.* Morowitz (1968) considered that energy flow caused cycling and this produced organization:

The flow of heat from sources to sinks can lead to an internal organization of the system... The flow of heat can lead to the formation of cyclic flows of material in the intermediate system. (p. 28).

The flow of energy causes cyclic flow of matter. The cyclic flow is part of the organized behavior of the system undergoing energy flux. The converse is also true; the cyclic flow of matter such as is encountered in biology requires an energy flow in order to take place. The existence of cycles implies that feedback must be operative in the system. Therefore, the general notions of control theory and the general properties of servo networks must be characteristic of biological systems at the most fundamental level of operation. (p. 120).

Control concepts involve negative (deviation-damping) feedback (Patten & Odum, 1981), but cycling also opens the possibility for positive (deviation-amplifying) feedback. Ascendancy theory (Ulanowicz, 1986) invokes the latter in “autocatalytic loops” central to system development. Glansdorff & Prigogine (1971) and Nicolis & Prigogine (1971) hypothesized an *order-through-fluctuation principle*. These authors noted that small deviations in energy flow exist statistically in any thermodynamic system. These are generally damped out by dissipative processes, but as energy gradients (including those reflected in storage) increase, deviation amplification becomes more and more probable. Any damping fluctuations that can better dissipate the gradients became selected for and amplified over time. “This”, Odum (1983, p. 574) writes, “is probably equivalent to the principle of selection through maximizing power with pulsing”. In far-from-equilibrium thermodynamics pulsing organizations have been referred to as “dissipative structures” (Glansdorff & Prigogine, 1971; Wicken, 1980), and the significance of their oscillations is the acceleration of energy flux toward the realization of maximizing power. *Maximizing cycling contributes to both reference conditions 1 and 2, and hence is consistent with all of the foregoing principles.*

8. *Maximize residence time.* Cheslak & Lamarra (1981) proposed that ecological systems organize to maximize the residence time of energy. They demonstrated this in an experimental investigation of a simple aquatic ecosystem, showing also that the majority of the effect was due to system-level properties rather than molecular properties. The residence time of flow in a particular component, τ_i , is given by the reciprocal of the turnover rate, τ_i^{-1} . Total system residence time can be

found by summing the individual component residence times (τ_i) and is the fraction of throughflow that remains as storage (TSS/TST). *Maximizing residence time is consistent with reference condition 2.*

9. *Minimize specific dissipation.* Internal constraints, such as caused in living systems by inefficient energy transfer or limited availability of metabolites, modulate throughflow maximization and divert free energy (exergy) to storage as chemical potential. This tends to minimize dissipation per unit mass or volume, which expresses the *least specific dissipation principle* (Onsager, 1931; Prigogine, 1947, 1955). Although this least-specific dissipation principle was developed for systems near thermodynamic equilibria, we contend that even if the global system is “far from equilibrium”, sub-systems at finer spatio-temporal-organizational scales may be considered to be in some proximity to a quasi-local steady state—close enough at least for the principle to provide an understanding of “how a system should change.” A question for future research is to determine whether a system is too far or near enough for this to be valid. Choi *et al.* (1999) used the respiration/biomass ratio (TSE/TSS in our notation) of lacustrine communities as an empirical measure of least-specific dissipation at the ecosystem level. With the dimensions of reciprocal time, TSE/TSS (to be minimized) approximates how efficiently structure (TSS) can be created for a given amount of work performed (reflected in the unusable released heat portion of TSE). Minimize specific dissipation complements maximize residence time (or equivalently, minimize turnover rate) because TSE/TSS has units of reciprocal time. The two measures differ only in the proportions of throughflow (power) which is dissipated. *Minimizing specific dissipation is consistent with reference condition 2.*

10. *Minimize empower to exergy ratio.* Bastianoni & Marchettini (1997) proposed that system organization can be measured by a ratio of empower to exergy (in their paper they inadvertently label empower, a throughflow metric, as emergy, a storage metric). The empower to exergy ratio measures the total environmental cost (throughflow) required to produce a unit of organization (structure). This differs from minimizing specific dissipation in that specific

dissipation is only a fraction of TST. The metric was tested on three lagoon systems and showed that the “natural” system had the lowest empower/exergy value. Bastianoni & Marchettini (1997) concluded that it was the most efficient of the three at processing throughflow to maintain structure. In network notation this goal function is expressed as TST/TSS and has units of reciprocal time. *Minimizing empower to exergy ratio supports reference condition 2, and is consistent with maximizing residence time.* Also, note that it is not necessarily inconsistent with reference condition 1 so long as total system storage increases more rapidly than total system throughflow.

Employing ecologically oriented variables, these ten extremal principles can be estimated by a set of metrics to be optimized: power and empower by total system throughflow, max(TST); storage and emergy by total system storage, max(TSS); ascendancy by the product of total system throughflow an average mutual information, max(ASC); dissipation by total system export, max(TSE); cycling by total system cycling, max(TSC); residence time by the ratio of total storage to throughflow, max(TSS/TST); specific dissipation by the ratio of total system export and total system storage, min(TSE/TSS); and empower to exergy ratio by the ratio of total system throughflow to total system storage, min(TST/TSS). We employ established notation for total system throughflow (TST) and introduce TSS, TSC, and TSE as total system storage, cycling, and export, respectively. Note, at steady state the complement of total system export, total system import (TSI), also follows from this derivation. The extremal principles apply to system-wide properties, whereas most basic network metrics address pair-wise interactions between system compartments. We describe below how pair-wise interactions are summed to determine whole system contributions that are comparable to the ecological interpretations. Basic network fundamentals are sketched below so that the ten extremal principles can be described in network notation. For a more complete treatment of network environ analysis see Patten (1978, 1981, 1982, 1985), Higashi & Patten (1989), Higashi *et al.* (1993), and Fath & Patten (1999).

2. The Environ Model: Setup

Environ (Patten, 1978, 1982; see Fig. 1) are afferent and efferent networks leading to and away from open systems that are components of systems at higher scales. Both the systems and their components are “holons” (Koestler, 1967). Given a mathematical description of the system in terms of its components, the latter’s *input* and *output environs* bounded within the system can also be described. With this, it is possible to partition the interior conservative (energy or matter) flows and storages of an n -th-order dynamical system with a differential or difference equation description into n input environs or n output environs, where n is the number of components whose storages x_i , $i = 1, \dots, n$, serve as *state variables*. A system with n such storage components, or *compartments*, will have $2n$ environs running within it, half of them *input environs* traceable backward in time to boundary inputs, z_j , from boundary outputs, y_i , and the other half *output environs* driving forward in time from boundary inputs, z_j , to boundary outputs, y_i . The set of input environs forms one partition of the storages and flows, and the set of output environs another (Patten, 1978).

**3. Functional Analyses:
For Throughflows and Storages**

To identify the direct and indirect contributions of flow and storage, taking account of all

$$\boxed{
 \begin{array}{l}
 N = \underbrace{I}_{\text{integral}} + \underbrace{G}_{\text{initial}} + \underbrace{G^2 + G^3 + \dots + G^m + \dots}_{\text{direct}} = (I - G)^{-1}. \quad (1) \\
 \text{integral} = \text{initial} + \text{direct} + \text{indirect}
 \end{array}
 }$$

possible pathways, several variants of input-output analysis as originated by Leontief (1936, 1966) and introduced into ecology by Hannon (1973) are employed. These methodological extensions were developed to implement the environ concept as a quantitative system theory of the environment. The objective here is to demonstrate how flow components of storage and throughflows can be partitioned into five distinct stages or modes: boundary input (mode 0), first-passage (mode 1), cycled (mode 2), componentwise dissipative (mode 3), and systemwise dissipative boundary output (mode 4). These

modes are described in more detail below. This explicit network accounting is used to show consistency and complementarity of the goal functions described in Section 1.

3.1. FLOW COMPONENTS OF THROUGHFLOW—LEONTIEF MODEL

Network flow analysis is predicated upon dimensional flow information for the system under investigation. Here, f_{ij} are elements of a square matrix F denoting flows *from column elements j to row elements i* and $T_j = \sum_{i=0}^n f_{ij}$ where f_{ij} represents boundary outflow. The motivation for flow partitioning begins with nondimensional flow intensities (that is, throughflow-specific flows) which result when flows are divided by throughflows of *originating* compartments: $g_{ij} = f_{ij}/T_j$. [Note that the original Leontief (1966) approach normalized the flows by the throughflows of the receiving compartments. The flow-forward orientation used here was independently introduced by Augustinovic (1970) and Finn (1976)]. The elements of matrix $G = (g_{ij})$ give the transfer efficiencies corresponding to each direct flow, f_{ij} . Powers G^m of this matrix give the indirect flow intensities associated with paths of lengths $m = 2, 3, \dots$. Due to dissipation these flows tend to zero as $m \rightarrow \infty$ so that the power series $\sum_{m=0}^{\infty} G^m$ representing the sum of the initial, direct, and indirect flows converges to an integral flow intensity matrix, N :

N maps the steady-state input vector z into the steady-state system throughflow vector (Patten *et al.*, 1990):

$$T = Nz = (I + G + G^2 + G^3 + \dots + G^m + \dots)z. \quad (2)$$

Term by term, flow intensities G^m of different orders m are propagated over paths of different lengths m . These paths can be enumerated by powers of the corresponding adjacency matrix (Patten, 1985). The first term $G^0 = I$ brings the input vector z across the system boundary as

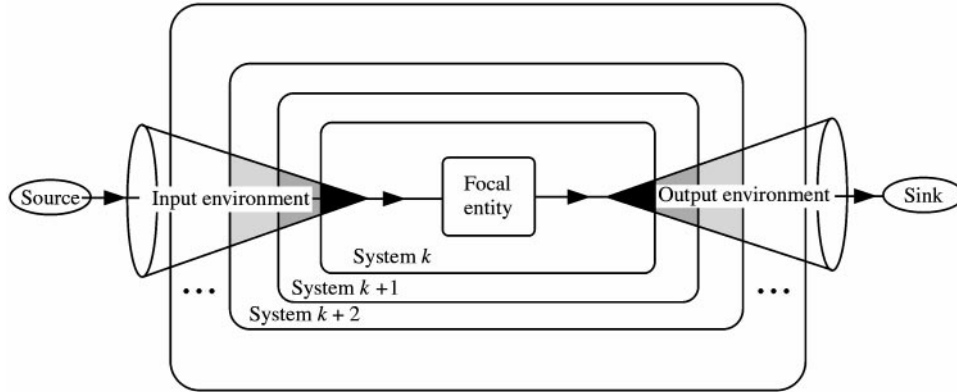


FIG. 1. Depiction of the environment of any focal entity at any level of organization, including (left to right): (a) afferent input environment from an ultimate source, partitioned successively into (b) input environs defined within k -th, $k + 1$ -th, etc. level systems in which the focal entity is a compartment, (c) internal state-defining milieu (not shown) of the focal entity, (d) efferent output environs defined within k -th, $k + 1$ -th, etc. level systems of focal-entity membership, and (e) efferent output environment extending to an ultimate sink. The input and output environments are shown as light cones, which bound (because nothing moves faster than light) possible cause and effects, respectively, that can influence and be influenced by the focal entity at any given moment. The environs are restrictions of the light cones to within scaled systems (levels $k, k + 1, \dots$) of definition. Environs, as partition elements of described systems, have quantitative descriptions available; environments external to described systems have no such descriptions, and cannot be specified. (■) k -th level environs; (▣) $k + 1$ -th level environs; (▤) $k + 2$ -th level environs.

input z_j to each initiating compartment, j . The second term, G , produces the first-order ($m = 1$) direct transfers from each j to each i in the system. The remaining terms where $m > 1$ define m -th order indirect flows associated with length m paths. As stated before, these go to zero in the limit as $m \rightarrow \infty$, which is necessary for series convergence. In the above developments F , T , and z represent matter or energy fluxes, and G and N are dimensionless intensive flows.

A heuristic point to be made from eqn (2) is that the steady-state (far-from-equilibrium) throughflow consists of flow contributions arriving at each terminal compartment i after originating at various source compartments j and being transferred over all paths of all kinds (acyclic or cyclic in different permutations) and lengths (m). In other words, the steady-state throughflows are distributed quantities, not only with respect to the flows that add directly to them, but also in relation to the shorter or longer, direct and indirect, histories of these flows back to their points of introduction into the system. What are called and appear in digraphs as “direct flows” f_{ij} in environ analysis, are really not direct at all. They are actually fractions of antecedent through-flows T_j , $f_{ij} = g_{ij}T_j$, distributed to

different destinations:

$$T_j \equiv T_j^{(\text{out})} = \sum_{i(\neq j)=0}^n T_{ij}, \quad (3)$$

where each distribution element, T_{ij} , is derived historically [eqn (4)] from boundary inputs z_j :

$$T_{ij} = n_{ij}z_j = \sum_{m=0}^{\infty} g_{ij}^{(m)} z_j. \quad (4)$$

T_{ij} , as the i -th component of the j -th element of T , shares the same direct and indirect decomposition elements as given in eqn (2) for T :

$$T_{ij} = \underbrace{(g_{ij}^{(0)})}_{\text{initial}} + \underbrace{(g_{ij}^{(1)})}_{\text{direct}} + \underbrace{(g_{ij}^{(2)} + g_{ij}^{(3)} + \dots + g_{ij}^{(m)} + \dots)}_{\text{indirect}} z_j. \quad (5)$$

From eqns (4) and (5) it follows that

$$f_{ij} = g_{ij} \left[\sum_{i(\neq j)=0}^n \sum_{m=0}^{\infty} g_{ij}^{(m)} z_j \right]. \quad (6)$$

This demonstrates that each “direct” flow f_{ij} at steady state is actually composed of flow elements of all orders, $m = 1, 2, \dots$, and is, therefore, a doubly distributed quantity (reflected in the double sum) derived from a large number set of direct and indirect paths leading from the originating inputs, z_j . This is no real surprise if one thinks about it. When a herbivore i in an ecosystem eats a primary producer j to generate a direct food flow f_{ij} , clearly the energy and matter embodied in this flow have had different histories within the encompassing ecosystem since the

the indirectness involved, C must first be non-dimensionalized. This is accomplished in discrete time: $P = I + C\Delta t$, where Δt is selected so that $0 \leq p_{ij} < 1, \forall i, j$. Specifically, the diagonal elements become $p_{ii} = 1 + c_{ii}\Delta t = 1 - \tau_i^{-1} \Delta t$, thus making P a one-step Markovian transition matrix (Barber, 1978). $P = (p_{ij})$ defines dimensionless storage-specific flow intensities representing the probability that substance in j at time t will be in i at time $t + \Delta t$. The different orders m of flow contributions to storage can then be expressed, analogously to eqn (1), as

$$Q = \underbrace{I}_{\text{integral}} + \underbrace{P}_{\text{initial}} + \underbrace{P^2 + P^3 + \dots + P^m + \dots}_{\text{direct}} + \dots = (I - P)^{-1}. \quad (8)$$

energy was originally photosynthetically fixed at different times at the boundary as z_j . These different histories imply different pathways, and thus different degrees of indirectness, even though the bulk food flow is “direct”. The formulation points, in fact, to little real “directness” at all in the flow phenomenology of steady-state connected systems, and leads to the conclusion that nature is organized more around dominant indirect effects (Higashi & Patten, 1989) and holistic determination (Patten, 2001) than around direct causes and their immediate effects.

The series in eqn (8) converges so long as column sums of P are less than one (Matis & Patten, 1981). Since the systems in question are energetically and materially open, the convergence condition can be realized by making the time step, Δt , sufficiently small. And, corresponding to eqn (2), this series maps steady-state boundary inputs, z , in discrete time Δt , into a steady-state internal storage vector:

$$x = Q(z\Delta t) = (I + P + P^2 + P^3 + \dots + P^m + \dots)z\Delta t. \quad (9)$$

3.2. FLOW COMPONENTS OF STORAGE—MARKOV MODEL

Identifying direct and indirect contributions to storage follows the same basic logic as for throughflows. In storage analysis, flows are normalized by steady-state storage values of the donating compartments, x_j , giving $c_{ij} = f_{ij}/x_j$, with

$$c_{ii} = - \sum_{k(\neq i)=0}^n c_{ki} = - \tau_i^{-1}. \quad (7)$$

Here, τ_i^{-1} is the *turnover rate* of storage at i and τ_i is the *turnover time*. $C = (c_{ij})$ is the Jacobian matrix in the standard linear system formulation of the input-driven form. The state vector $x = (x_j)$ is a storage, and C contains flow rates. To obtain an input–output power series formulation comparable to eqns (1) and (2), which explicitly shows

This series shows explicitly the direct and indirect flow contributions to storage, and makes apparent the basis for dominant indirectness in the flow–storage phenomenology. Just as throughflow and flows are distributed quantities, [eqns (3)–(6)], so is storage:

$$x_j = \sum_{i(\neq j)=0}^n x_{ij}, \quad (10)$$

where

$$x_{ij} = q_{ij}(z_j\Delta t) = \sum_{m=0}^{\infty} p_{ij}^{(m)} z_j\Delta t \quad (11)$$

so that

$$x_{ij} = p_{ij} \left[\sum_{i(\neq j)=0}^n \sum_{m=0}^{\infty} p_{ij}^{(m)} z_j\Delta t \right]. \quad (12)$$

As eqn (6) does for flows, this shows steady-state storages are doubly distributed quantities also,

the resultant of inputs from all sources (first summation) being subsequently distributed to compartments over all paths of all lengths m (second summation).

3.3. FLOW AND STORAGE PARTITIONING INTO MODES

As stated earlier, flow and storage contributions can be partitioned into five modes (0, 1, 2, 3, and 4) using network analysis (based on an earlier two- and three-mode partitioning presented, respectively, by Higashi *et al.*, 1993; Patten & Fath, 1998). This partitioning is key to demonstrating consistency of the orientors in Section 1. Mode 0 is the boundary input into the system. Mode 1 accounts for all flow in which substance moves from node j to a terminal node i for the first time only. Mode 2 is flow cycled at terminal nodes i of each (i, j) pair. Mode 3 is componentwise dissipative flow in the sense that it exits from node i never to return again. Mode 4 is the boundary output from i constituting systemically dissipative flows exiting the system. Gallopin (1981) independently proposed a similar, but non-mathematical, classification in which within-system flow is partitioned into three categories: strictly influenced (1), both influencing and influenced (2), and strictly influencing (3). These categories encompass and are conceptually equivalent to modes 1–3 as indicated

parenthetically. The five modes can be quantified and notated for both flow and storage contributions for each (i, j) pair using the equations in Table 1, where superscripts refer to the modes. System-wide mode contributions are obtained by summing all pair-wise combinations. Notations without subscripts ($f^{(k)}$, $x^{(k)}$, for $k = 0, \dots, 4$) represent single- (for boundary flows) or double-summed (for internal flows and storages) system-wide quantities.

Note from Table 1 that just as boundary inputs, $f^{(0)}$, and outputs, $f^{(4)}$, are equal at steady state, mode 3 is numerically equal to mode 1 for both flow and storage: $f^{(1)} = f^{(3)}$ and $x^{(1)} = x^{(3)}$. These equivalences are implicit in the first law of thermodynamics and mass conservation since any matter or energy which crosses a system or compartment boundary for the first time must also be dissipated from that system or compartment regardless, in the compartment case, of how many nodes it passes through en route to its final destined exit.

Total flow into i derived from j , T_{ij} for $j = 0, \dots, n$, is the sum of modes 0, 1, and 2, $T_{ij} = f_{ij}^{(0)} + f_{ij}^{(1)} + f_{ij}^{(2)}$, as is node storage, $x_{ij} = x_{ij}^{(0)} + x_{ij}^{(1)} + x_{ij}^{(2)}$. Because of mode 0–mode 4 and mode 1–mode 3, equivalences, these relations can also be written as, $T_{ij} = f_{ij}^{(2)} + f_{ij}^{(3)} + f_{ij}^{(4)}$ and $x_{ij} = x_{ij}^{(2)} + x_{ij}^{(3)} + x_{ij}^{(4)}$. These relations can

TABLE 1

Network representation of flow and storage partitioning into five modes for any (i, j) pair in a system

	Flow		Storage	
	Equation (pair-wise interactions)	Notation (system-wide contribution)	Equation (pair-wise interactions)	Notation (system-wide contribution)
Mode 0 (boundary input)	$f_{j0}^{(0)} = z_j$	$f^{(0)} = \sum f_{j0}^{(0)}$	$x_{j0}^{(0)} = z_j \Delta t$	$x^{(0)} = \sum x_{j0}^{(0)}$
Mode 1 (first-passage)	$f_{ij}^{(1)} = \left(\frac{n_{ij}}{n_{ii}} - \delta_{ij}^* \right) z_j$	$f^{(1)} = \sum \sum f_{ij}^{(1)}$	$x_{ij}^{(1)} = \left(\frac{q_{ij}}{q_{ii}} - \delta_{ij} \right) z_j \Delta t$	$x^{(1)} = \sum \sum x_{ij}^{(1)}$
Mode 2 (cyclic)	$f_{ij}^{(2)} = \frac{n_{ij}}{n_{ii}} (n_{ii} - 1) z_j$	$f^{(2)} = \sum \sum f_{ij}^{(2)}$	$x_{ij}^{(2)} = \frac{q_{ij}}{q_{ii}} (q_{ii} - 1) z_j \Delta t$	$x^{(2)} = \sum \sum x_{ij}^{(2)}$
Mode 3 (compartment-wise dissipative)	$f_{ij}^{(3)} = \left(\frac{n_{ij}}{n_{ii}} - \delta_{ij} \right) z_j$	$f^{(3)} = \sum \sum f_{ij}^{(3)}$	$x_{ij}^{(3)} = \left(\frac{q_{ij}}{q_{ii}} - \delta_{ij} \right) z_j \Delta t$	$x^{(3)} = \sum \sum x_{ij}^{(3)}$
Mode 4 (boundary output)	$f_{0i}^{(4)} = y_i$	$f^{(4)} = \sum f_{0i}^{(4)}$	$x_{0i}^{(4)} = y_i \Delta t$	$x^{(4)} = \sum x_{0i}^{(4)}$

* δ_{ij} is the Kronecker delta defined by $\delta_{ij} = 1$ for $i = j$ and $\delta_{ij} = 0$ for $i \neq j$.

further be written using the system-level notation as $TST = f^{(0)} + f^{(1)} + f^{(2)} = f^{(2)} + f^{(3)} + f^{(4)}$ and $TSS = x^{(0)} + x^{(1)} + x^{(2)} = x^{(2)} + x^{(3)} + x^{(4)}$, where the left-hand sums in each case represent afferent relations and the right-hand sums efferent relations. The network mapping $T_{ij} = n_{ij}z_j$ [eqn (2)] and $TST = \sum \sum n_{ij}z_j$ verify the mode partitioning for throughflows as follows:

$$\begin{aligned} T_{ij} &= f_{ij}^{(0)} + f_{ij}^{(1)} + f_{ij}^{(2)} \\ &= z_j \delta_{ij} + \left(\frac{n_{ij}}{n_{ii}} - \delta_{ij} \right) z_j + \frac{n_{ij}}{n_{ii}} (n_{ii} - 1) z_j \\ &= \left(\delta_{ij} + \frac{n_{ij}}{n_{ii}} - \delta_{ij} + n_{ij} - \frac{n_{ij}}{n_{ii}} \right) z_j = n_{ij} z_j \end{aligned} \quad (13)$$

and similarly for storages:

$$\begin{aligned} x_{ij} &= x_{ij}^{(0)} + x_{ij}^{(1)} + x_{ij}^{(2)} \\ &= z_j \Delta t \delta_{ij} + \left(\frac{q_{ij}}{q_{ii}} - \delta_{ij} \right) z_j \Delta t + \frac{q_{ij}}{q_{ii}} (q_{ii} - 1) z_j \Delta t \\ &= \left(\delta_{ij} + \frac{q_{ij}}{q_{ii}} - \delta_{ij} + q_{ij} - \frac{q_{ij}}{q_{ii}} \right) z_j \Delta t \\ &= q_{ij} z_j \Delta t. \end{aligned} \quad (14)$$

It is the recognition that internal flows and storages are comprised of input, first-passage, cyclic, locally dissipative, output portions, that makes possible the demonstration of goal function complementarity. Notational conventions across scales are summarized in Box 1.

4. Goal Function Unification

At the end of Section 1 the ten extremal principles power, storage, empower, emergy, ascendancy, dissipation, cycling, residence time, specific dissipation, and empower/exergy ratio were listed using simple ecological notation. Network parameter equivalents of these principles are given in Table 2, including the formulation used to generate the parameters. The mode partitioning in Table 1 is for a specific (i, j) pair. Therefore, a double sum over all (i, j) pairs is needed to convert Table 1 quantities to the total system-wide properties of Section 1. In Table 2 the definition of turnover time as storage divided by throughflow (Higashi *et al.*, 1993) is used to map throughflows and inputs into storages: $x_{ij} = \tau_i T_i = \tau_i n_{ij} z_j$. The objective is to use the network understanding and explicit notation to show that

Box 1. Clarification of notation for the three levels for each flow and storage:

- (1) Pair-wise interactions—the contribution to any i from any j ($i, j = 0, 1, \dots, n$);
- (2) Compartmental level—the total contribution to i from all j ($i, j = 0, 1, \dots, n$); and
- (3) Total system level contribution to all i from all j ($i, j = 0, 1, \dots, n$)

We assume that these levels are additive, $T_i = \sum T_{ij}$ and $TST = \sum T_i$, and $x_i = \sum x_{ij}$ and $TSS = \sum x_i$, leading to doubly distributed throughflows and storages: $TST = \sum T_i = \sum \sum T_{ij}$ and $TSS = \sum x_i = \sum \sum x_{ij}$. The mode distinction indicates that total flow and storage are partitioned into input (vector), first-passage (matrix) and cycled (matrix) portions. Table B1 presents the notation incorporated herein.

Table B1. Notation representing various hierarchical levels of flow and storage in the environs of (i, j) pairs using network analysis

Level	Flow	Storage
(1) Contribution to any i from any j plus boundary input (pair-wise)	$T_{ij} = f_{i0}^{(0)} + f_{ij}^{(1)} + f_{ij}^{(2)}$	$x_{ij} = x_{i0}^{(0)} + x_{ij}^{(1)} + x_{ij}^{(2)}$
(2) Contribution to i from all j plus boundary input (compartmental)	$T_i = f_{i0}^{(0)} + \sum_{j=1}^n (f_{ij}^{(1)} + f_{ij}^{(2)})$	$x_i = x_{i0}^{(0)} + \sum_{j=1}^n (x_{ij}^{(1)} + x_{ij}^{(2)})$
(3) Total system level—the contribution to all i from all j plus boundary input (system-wide)	$TST = \sum_{i=1}^n f_{i0}^{(0)} + \sum_{i=1}^n \sum_{j=1}^n (f_{ij}^{(1)} + f_{ij}^{(2)})$	$TSS = \sum_{i=1}^n x_{i0}^{(0)} + \sum_{i=1}^n \sum_{j=1}^n (x_{ij}^{(1)} + x_{ij}^{(2)})$

TABLE 2

Energy organizing extremal principles with associated network formulations. Superscripts denote modes. These are system-wide properties so the appropriate notation is used (Box 1): TST = total system throughflow, TSS = total system storage, TSE = total system export, TSC = total system cycling, EMP = empower, EMG = emergy, ASC = ascendancy, AMI = average mutual information. The term n_{ij}^ used in the emergy and empower formulations denotes network transformities which convert energy flow and storage to empower and emergy and differs from the n_{ij}^* of eqn (1) is the extent that transformities do not account for cyclic feedback.*

Principle	Extremal principle	Network parameter (system level)	Network analysis formulation
Maximize power	max(TST)	$TST = f^{(0)} + f^{(1)} + f^{(2)}$	$TST = \sum \sum (n_{ij})z_j$
Maximize storage	max(TSS)	$TSS = x^{(0)} + x^{(1)} + x^{(2)}$	$TSS = \sum \sum \tau_i(n_{ij})z_j$
Maximize empower	max(EMP)	$EMP = f^{(0)} + f^{(1)} + f^{(2)}$	$EMP = \sum \sum (n_{ij}^*)z_j$
Maximize emergy	max(EMG)	$EMG = x^{(0)} + x^{(1)} + x^{(2)}$	$EMG = \sum \sum \tau_i(n_{ij}^*)z_j$
Maximize ascendancy	max(ASC)	$ASC = AMI*[f^{(0)} + f^{(1)} + f^{(2)}]$	$ASC = AMI*\sum \sum (n_{ij})z_j$
Maximize dissipation	max(TSE)	$TSE = f^{(4)}$	$TSE = \sum \sum \varepsilon_i(n_{ij})z_j$
Maximize cycling	max(TSC)	$TSC = f^{(2)}$	$TSC = \sum \sum (n_{ij}/n_{ii})(n_{ii} - 1)z_j$
Maximize residence time	max(TSS/TST)	$TSS/TST = \tau$	$TSS/TST = \sum \sum \tau_i(n_{ij})z_j/(n_{ij})z_j = \sum \tau_i$
Minimize specific dissipation	min(TSE/TSS)	$TSE/TSS = f^{(4)}/(x^{(0)} + x^{(1)} + x^{(2)})$	$TSE/TSS = \frac{\sum \sum \varepsilon_i(n_{ij})z_j/\tau_i(n_{ij})z_j}{\sum \sum \varepsilon_i/\tau_i}$
Minimize empower to exergy ratio	min(TST/TSS)	$TST/TSS = 1/\tau$	$TSS/TST = \frac{\sum \sum (n_{ij}^*)z_j/\tau_i(n_{ij})z_j}{\sum \sum (n_{ij}^*)/\tau_i(n_{ij})}$

these extremal principles are internally consistent and complementary.

Much debate and confusion have centered on the appropriateness of these various goal functions because, at first glance, the simultaneous realization of max(TST), max(TSS), max(EMP), max(EMR), max(ASC), max(TSE), max(TSC), max(TSS/TST), min(TSE/TSS), and min(TST/TSS) seems contradictory. Further inspection, however, shows that all these goal functions are in fact mutually consistent. They are all generated by network processes and they give complementary perspectives on the spontaneous directions of ecological growth and development.

Maximize power has been taken as the first reference condition against which to evaluate the others. Maximize power, as represented by total system throughflow using network parameters ($TST = f^{(0)} + f^{(1)} + f^{(2)}$), is a combination of input, $f^{(0)}$, first-passage flow, $f^{(1)}$, and cycling, $f^{(2)}$. Each of these three basic building blocks contribute to overall throughflow. Using the network derivation as described in eqn (2) and Table 2, TST is composed of the products of integral flow intensities, n_{ij} , and inputs, z_j . Maximize power

appears to be the primary orientor and foundation for the complementarity of ecological goal functions because the combination $n_{ij}z_j$ figures in the network formulation of all the others (as seen in the last column of Table 2). However, a closer look reveals a more subtle situation in which there are tradeoffs between the goal functions particularly regarding the rate at which they occur.

Maximize storage, $TSS = x^{(0)} + x^{(1)} + x^{(2)}$, is the second reference condition and it also combines input, first-passage, and cyclic contributions. In the network formulation, $x_{ij} = \tau_i n_{ij} z_j$, storage is directly proportional to power by the factor of the turnover time, τ_i , at each compartment. Storage is a measure of flow impedance, therefore, greater flow and higher capacitance (in an analogous sense to electrical networks) result in greater storage. Maximizing power supports the maximize storage principle and maximizing storage reinforces the maximize residence time principle.

Maximize empower (EMP) and emergy (EMG), consider total system throughflow and storage as expressed in terms of the source energy, $EMP = f^{(0)} + f^{(1)} + f^{(2)} = n_{ij}^* z_j$ and

$EMG = x^{(0)} + x^{(1)} + x^{(2)} = \tau_i(n_{ij}^*)z_j$, where n_{ij}^* is a network-based transformity which converts energy (in joules) to emergy (in emjoules). [For a thorough treatment comparing network and emergy analyses see Brown & Herendeen, 1996.] These principles are conceptually equivalent to maximizing total system throughflow and total system storage, but within the context of the process transformations from the initial source. These goal functions are consistent with reference conditions 1 and 2.

Maximize ascendancy is the product of total system throughflow (TST) and average mutual information (AMI), $ASC = AMI*[f^{(0)} + f^{(1)} + f^{(2)}] = AMI*n_{ij}z_j$. The AMI scales TST according to the system organization, but the measure is primarily dominated by the throughflow because the contribution of average mutual information is usually small in relation to that of throughflow. Thus, this goal function is consistent and highly correlated with the first reference condition (Jørgensen, 1994).

Maximize dissipation, $TSE = f^{(4)}$, is to increase the total boundary flow exiting the system. Dissipation is expressed here as compartment-specific fractions, ε_i , of throughflows at i derived from each source input z_j : $TSE = \sum \varepsilon_i T_i = \sum \sum \varepsilon_i n_{ij} z_j$; since at steady state, total system export equals total system import ($f^{(4)} = f^{(0)}$). Therefore, maximizing dissipation is equivalent to maximizing input which is one component of total system throughflow. Maximizing input contributes to maximizing power.

Maximize cycling, $f^{(2)}$, occurs when the mode 2 portion of total system throughflow increases. Cycled flow contributes to TST separately from input or first-passage flow. The diagonal elements n_{ii} of N give the total number of times a resource will exit a particular compartment. When the cycled portion, $n_{ii} - 1$, is weighted by the first passage flow, $(n_{ij}/n_{ii})z_j$, this gives the total system cycling. (Note, total system cycling (TSC) is an absolute measure of the amount of cycled flow in the system. Finn (1976) developed a cycling index which calculates the portion of system flow that is cycled). There is a seeming discrepancy between maximizing cycling and maximizing dissipation because it appears dissipation is limited by cycling. If TST were fixed, i.e. zero-sum, then there would be a tradeoff among

mode 4 (boundary dissipation), mode 2 (cycling), and mode 1 (first-passage flow). However, TST is not fixed but is itself being maximized. Maximizing cycling is, therefore, consistent with the first reference condition since TST is comprised of both dissipation and cycling.

Maximize residence time, $\tau = TSS/TST$, is a single parameter goal function that is clearly consistent with the maximize storage goal function as previously discussed. Unlike the previous energy organizing principles, this one is independent of the input z_j . Maximizing residence time is also foundational to the two following goal functions minimizing specific dissipation and minimizing empower to exergy ratio as discussed above.

Minimize specific dissipation, $f^{(4)}/(x^{(0)} + x^{(1)} + x^{(2)})$, states that the ratio of total system export to total system storage decreases. In network notation, this simplifies to ε_i/τ_i , which has units of reciprocal time. There is an important distinction here because the throughflow term $T_i = n_{ij}z_j$ is not present. Minimizing specific dissipation is dependent on turnover time τ_i and the fraction of throughflow that is exported, ε_i . Turnover time is generated from the internal storage transfer efficiencies [eqn (7)] and fractional dissipation from boundary input. Therefore, this principle captures two basic systems properties and to optimize it residence time should increase.

Minimize empower to exergy ratio, notated as TST/TSS , simplifies to minimizing the turnover rate which is equivalent to maximizing residence time. This goal function combines both reference conditions and measures the system efficiency at maintaining structure. To the extent that the transformity, N^* , approaches the integral flow matrix, N , this ratio approximates the maximize residence time principle. The implicative loop appears to be close around three fundamental properties—throughflow, storage, and residence time.

The two principles that seem most contradictory are *maximize dissipation* ($\max(f^{(4)})$) and *minimize specific dissipation* ($\min(f^{(4)}/(x^{(0)} + x^{(1)} + x^{(2)}))$). However, both can co-occur if total system storage increases faster than total system export. That is, if $f^{(4)}$ is maximized, then the ratio, $f^{(4)}/(x^{(0)} + x^{(1)} + x^{(2)})$, can still be minimized if total system storage, $(x^{(0)} + x^{(1)} + x^{(2)})$, maximizes more rapidly. Minimizing specific dissipation combines output (and by equivalence, input)

and storage into one organizing principle such that both dissipation and structure are maximizing while at the same time their ratio is minimizing. Jørgensen *et al.* (2000) have argued that this is in fact the pattern observed in all growth phenomena. System dissipation rises rapidly to near-theoretical maxima in early growth, but storage continues to increase indefinitely throughout middle and late developmental stages. In biological systems, the tendency of storage to increase faster than dissipation is well known in the power scaling of respiration rates to organism size, $R \approx B^{3/4}$ (von Bertalanffy, 1957). It has been speculated by various authors that this may be simply due to dimensional constraints (e.g. Stahl, 1962; Economos, 1979; Platt & Silvert, 1981; Barenblatt & Monin, 1983; Patterson, 1992). The present analysis adds thermodynamic and organizational constraints as well.

5. Conclusion

The consistency of the goal functions investigated here by network methods is more than just the sharing of several notated variables— z_j , n_{ij} , and τ_i . Only those pertaining to empower, emerge, and ascendancy were originally conceived in an explicit network context, yet it is global systemic organization that is behind the similarities inherent in all the studied goal functions. The implication is that the network perspective is fundamental, and somehow the originators of different orientors managed to capture this intuitively in their concepts.

At steady state all ten energy organizing principles are founded on increasing boundary flow (import or export since $f^{(0)} = f^{(4)}$), and three primary internal properties: first-passage flow ($f^{(1)}$), cycling ($f^{(2)}$), and residence time (τ_i). Boundary flow along with first-passage and cycling flows all contribute to increasing total system throughflow and give a complete picture of flow partitioning. Boundary flow follows from exogenous inputs (z_j and $z_j \Delta t$) and first-passage flow from endogenous transfer efficiencies ($n_{ij}/n_{ii} - \delta_{ij}$ and $q_{ij}/q_{ii} - \delta_{ij}$). In addition to the inputs and transfer efficiencies, cycling is also a function of system connectivity and organization. Retention time depends on cycling and system structure because cycling retains and stores flow, thus increasing

the turnover time. Cycling at one scale is structural storage at another. The primary boundary and internal properties that are common to these organizing principles can be summed up in the following maxim: Get as much as you can (maximize input and first-passage flow), hold on to it for as long as you can (maximize retention time), and if you must let it go, then try to get it back (maximize cycling).

The ten energy organizing extremal principles are all consistent with these properties. Not only are all these orientors mutually consistent, but they are interdependent for fulfillment. Maximizing boundary dissipation and maximizing cycling both contribute to maximizing throughflow. Maximizing throughflow contributes to maximizing storage, subject to turnover considerations. The intuition of Jørgensen, Bendoricchio, and Patten to show consistency of the goal functions was correct. However, contrary to Bendoricchio & Jørgensen (1997), but in agreement with Jørgensen *et al.* (2000), we find that specific dissipation rather than storage *per se* is the primary goal function. Minimizing specific dissipation is most encompassing because it captures all three properties above and is dependent on maximizing storage faster than maximizing dissipation, which is empirically observed. In conclusion, we support the use of a plurality of goal functions because each organizing principle reflects a slightly different aspect of overall system function. In fact, it is probably their complementarity and interdependency that has made the identification of a single universal extremal principle difficult.

Dedication

The prior work of Masahiko Higashi, who perished with four other ecologists in the field during late March 2000, runs all through this paper and much of our previous investigations. With sadness and fond remembrance we dedicate this small increment of new knowledge in the conviction that his “indirect effects” will continue to propagate into the long future of ecology, wherever networks become its objects of study.

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