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Natural ecosystem design and control imperatives for sustainable ecosystem services

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ABSTRACT

Sustainability of ecosystem services to humanity will depend on knowledge of how ecosystems work in their natural states, which can then be carried over to managed states. The *objective* of this paper is to describe four properties of ecosystems taken as natural conditions to be maintained under exploitation. Three of these are design properties: near-steady-state or extremal dynamics, dominance of indirect effects, and positive utility in network organization. One is a regulatory property: distributed multivariable control. The *methodology* of the paper is mathematical modeling. The design properties are drawn from the inherent formalism in models. The control property is demonstrated by manipulating model parameters to achieve a management goal. The *results* show that: (1) natural ecosystems operate near, but not at, steady states or extrema, and ecosystems exploited for human purposes should be similarly maintained (near-steady-state imperative); (2) indirect effects are dominant in natural ecosystem networks, and should be taken into account in managing ecosystems for human benefits (nonlocal imperative); (3) natural ecosystems enhance positive relationships among their constituents, and ecosystems maintained for human services should be managed to maximize their expression of mutualistic and synergistic network properties (nonzero imperative); and (4) natural ecosystems are regulated by checks and balances distributed across many control variables in interactive networks, so that obtaining human services from ecosystems should similarly be through coordinated use of many, not few, control variables (multifactorial control imperative). The *conclusion* from these results is that ecosystems under natural conditions evidence organizational properties evolved over evolutionary time, and management for sustainable extraction of ecosystem services should seek to preserve and emulate these properties in the new exploited states.

1. Introduction

The United Nations' Millenium Ecosystem Assessment (2005) comprehensively reviewed the status and change of *Supporting Services* such as nutrient cycling, soil formation, and primary production provided to humankind by the natural world. Ecosystem services were classified into three categories. *Provisioning Services* refer to the supply of resources—food, fiber, water, fuel, and other needed materials and energy. *Regulation Services* are associated with climate, floods, disease, water quality, and other factors involved in control of provisioning. *Cultural Services* include aesthetic, spiritual, educational, and recreational aspects of ecosystems. These three categories – material, cybernetic, and virtual, respectively – are all very different, and thus pose a challenge for unification within a single theory. Of course, it is not given that theory is absolutely necessary for an applied Ecosystem Services science to be successful. Yet, such theory is already manifested, implicitly, in the elements of geosphere, atmosphere, hydrosphere, biosphere, and noosphere woven together in the world's ecosystems. The premise has to be that the acquisition of Ecosystem Services will be more correct and powerful to the extent it follows from theoretical understanding of some of the deeper principles involved in man–nature coupling. This paper attempts a preliminary sketch of several facets of such a theory from the perspective and methodology of ecological network analysis.

Sustaining the flow of goods and services from ecosystems to humanity will benefit from knowledge of how ecosystems function under unexploited conditions. As products of evolutionary selection, the structure and function of natural ecosystems are well tested and should be understood and carried over into exploited states. Ecosystems under exploitation should have the same design (McHarg, 1995; Shu-Yang et al., 2004) and control (Redfield, 1958; Shan-Yu, 1986; Lovelock, 1979, 1990) characteristics as their unexploited counterparts. The purpose of this paper is to describe four such properties derived from the study of ecosystem network models. The first three are design principles, and the fourth a control principle:

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1. *Near-steady-state imperative*. Natural ecosystems operate near, but not at, steady states or extrema; exploited systems should have similar dynamics.
2. *Nonlocal imperative*. Indirect effects dominate causality in natural ecosystems; exploitation should be based on understanding the systemic holism this implies.
3. *Nonzero imperative*. Natural ecosystems promote positive relationships among their constituents; exploited systems should be managed to maximize these relationships.
4. *Multifactorial control imperative*. Natural ecosystems are regulated by diffuse checks and balances distributed in networks involving many control variables; ecosystem services should be obtained by the coordinated use of many, rather than one or a few, control variables.

These four properties are next described for natural ecosystems, followed by inferences about their exploited counterparts.

2. How natural ecosystems work

2.1. Near-steady-state imperative

In the late 19th Century, ecologists began asking questions about the organization and dynamics of natural systems (e.g., Forbes, 1887). Throughout the 20th Century, in studies of succession and population dynamics, the persistent question about whether ecological systems achieve and maintain steady states (often referred to as "equilibria") was pursued (e.g., Clements, 1936; Gleason, 1926; Watt, 1947; Odum, 1969; May, 1973; DeAngelis and Waterhouse, 1987). In recent times, the question still persists, in theory and methodology, without definitive resolution. For example, Likens and Bormann (1979) saw, in a biomass accumulation model of exploited forest dynamics, four stages of recovery following clear-cutting—reorganization, aggradation, transition, and steady state. Lugo and Brown (1986) challenged a widely held proposition in biogeochemical cycling that mature landscapes are in carbon balance with the atmosphere. Jørgensen et al. (2000) recognized three forms of growth in ecosystem development, all tending to steady-state endpoints. Allesina and Bondavalli (2003) sought to bring ecosystem flow models to steady state for analytical purposes. And recently, in a proposition reminiscent of Schödinger's (1974) *What is Life?* prescription, Ulanowicz (2009) envisioned in ecosystems an ongoing autocatalytic process, balanced against second-law energy degradation at points of maximum evolutionary potential.

One has to ask, in the long history of planetary evolution, can anything ever remain in balance for more than a brief instant in time? Ecosystems are complex and multifaceted, and seeming steady states with respect to one set of criteria (e.g., metabolic) may co-occur with simultaneous changes in others (e.g., biodiversity). Thus, in general, the problem of existence of steady states in ecosystems seems academic, though perhaps this is the wrong question. A more fruitful line of inquiry might be not whether steady states are achieved and maintained, but rather, are there self-organizing "orientors" (Müller and Leupelt, 1998) that steer systems persistently in such directions? Existence of the tendency may be more important for understanding ecosystems than the attainment and holding of rigid endpoints.

In physics, ideal gases and frictionless resistances do not exist in reality, but such abstractions are useful in exploring and explaining how nature works. Idealization gives points of reference against which to compare. A spinning top is stable so long as it keeps spinning, and the explanatory knowledge that spinning is the stabilizing force is different from, and more instructive than, the descriptive knowledge that the top is or is not spinning. The useful steady-state question, then, is not about whether such states are achieved in ecosystems, but rather, is there a steady-state directing tendency that organizes the succession process, whether the endpoint is realized or not?

That is the question of this section—do ecosystems possess an innate tendency to develop and maintain steady states with respect to many criteria and many time scales, even though in reality they are often out of balance with respect to many criteria and over many time scales? The structure of descriptive mathematical models is examined for the possibility of deeper explanation.

A scalar ordinary differential equation (ODE) describing the storage (x_i), interior flow (f_{ij}), and boundary exchange (z_i, y_i) of conservative substance in an open, dissipative (Glansdorf and Prigogine, 1971) system of $i, j = 1, 2, \ldots, n$ compartments is:

$$\begin{aligned}\frac{dx_i}{dt} &= \text{inflow} - \text{outflow}\\ &= (z_i + f_{i1} + f_{i2} + \ldots + f_{in}) - (y_i + f_{1i} + f_{2i} + \ldots + f_{ni}).\end{aligned} \qquad (1)$$

This can be separated into *input-driven*, or exogenous flows, z_i, and remaining *state-driven*, or endogenous terms:

$$\frac{dx_i}{dt} = z_i + [(f_{i1} + f_{i2} + \ldots + f_{in}) - (y_i + f_{1i} + f_{2i} + \ldots + f_{ni})]. \qquad (2)$$

Fig. 1 depicts a generalized $n = 3$ compartment ecosystem model so described. A corresponding matrix ODE is:

$$\frac{d\mathbf{x}}{dt_{n\times 1}} = \mathbf{z}_{n\times 1} + \mathbf{F}_{n\times n} \cdot \mathbf{1}_{n\times 1}. \qquad (3)$$

The subscripts $n \times 1$ and $n \times n$ denote column vectors and a square matrix, respectively. The i'th row of $\mathbf{F}$, except the diagonal element f_{ii}, consists of the interior inflow terms of (1) and (2): $f_{i1}, f_{i2}, \ldots, f_{in}$; the outflow terms are summed to form the principal diagonal entries: $f_{ii} = -(y_i + f_{1i} + f_{2i} + \ldots + f_{ni})$. The state of the system is expressed as standing stocks, $\mathbf{x} = (x_i)$, which are given by the equation solution. The first time derivative of the stocks is $d\mathbf{x}/dt$; $\mathbf{z} = (z_i)$ are boundary inputs; and $\mathbf{y} = (y_i)$ are boundary outputs, embedded in the f_{ii} terms of $\mathbf{F}$, and representing the dissipation property; $\mathbf{1}$ is a vector of ones that, when pre-multiplied by $\mathbf{F}$, yields the corresponding scalar equations (1) and (2) for each i'th compartment.

The flows in Eq. (3) are often represented as functions of the standing stocks, for example $\mathbf{F}\cdot\mathbf{1} = \mathbf{C}\cdot\mathbf{x}$, whereupon (3) becomes:

$$\frac{d\mathbf{x}}{dt_{n\times 1}} = \mathbf{z}_{n\times 1} + \mathbf{C}_{n\times n} \cdot \mathbf{x}_{n\times 1}. \qquad (4)$$

$\mathbf{C}$ is a matrix of stock-specific coefficients; a comparable matrix in population ecology is called the "community matrix" (e.g., May, 1973). If $\mathbf{C}$ is constant (the most common usage) or a function of time, system (2) is linear; if a function of state $\mathbf{x}$, or both state and time, it is nonlinear. The transfer function or operator form of (4) is:

$$\mathbf{x}_{n\times 1} = -\mathbf{C}^{-1}_{n\times n} \cdot \left[\mathbf{z}_{n\times 1} - \frac{d\mathbf{x}}{dt_{n\times 1}}\right]. \qquad (5)$$

The inverse matrix maps boundary input, $\mathbf{z}$, and internal change, $d\mathbf{x}/dt$, into a resultant standing stock, $\mathbf{x}$. The elements of $\mathbf{z}$ are always positive or zero, whereas those of $d\mathbf{x}/dt$ may be positive, negative or zero. It is the changing relationships in time between these driving quantities that provide the argument for the near-steady-state imperative—that systems describable by ODE's tend to operate in small neighborhoods around steady or extremal states, so-defined when $d\mathbf{x}/dt = 0$.

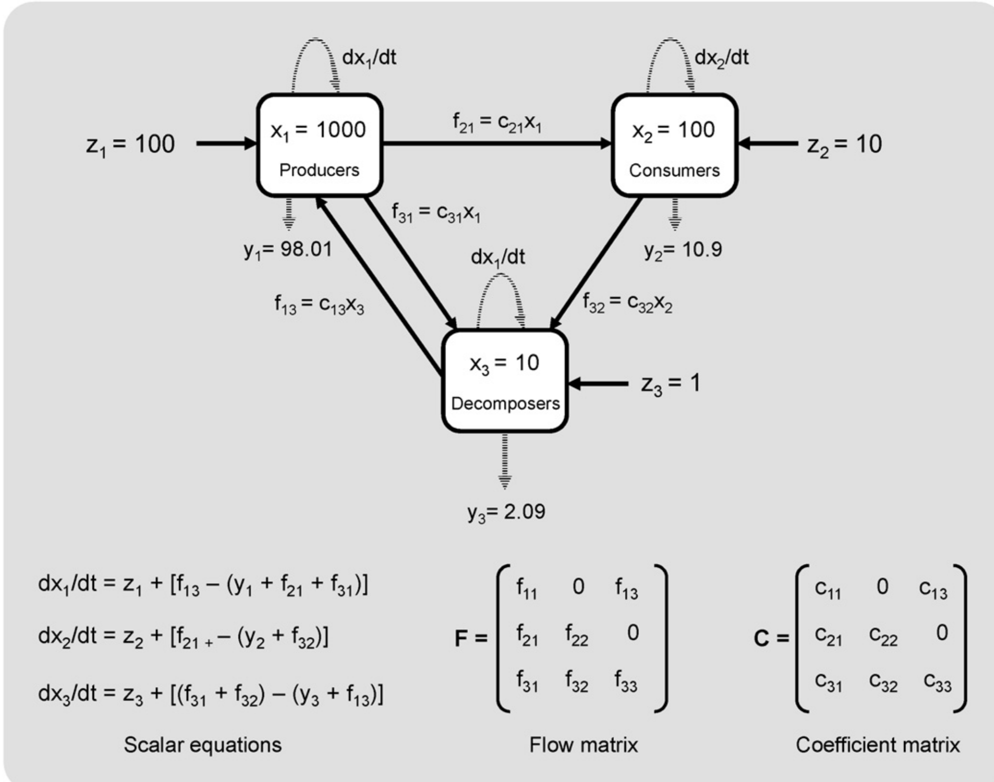

Fig. 1. Generalized steady-state ecosystem compartment model and corresponding scalar equations (2). Inputs balance outputs, for the individual compartments and the system as a whole. The numerical data are hypothetical.

In the following description of these relationships, inferences drawn from the logical structure of ODE's were verified by study of the Fig. 1 compartment model. There are four cases to consider:

Case 1: $\mathbf{z}$ *positive,* $\mathrm{d}\mathbf{x}/\mathrm{d}t$ *negative, and* $\mathbf{z} > |\mathrm{d}\mathbf{x}/\mathrm{d}t|$. For elements of $\mathrm{d}\mathbf{x}/\mathrm{d}t$ to have negative derivatives their inflows must be less than outflows. More outflow than inflow indicates net loss of standing stock. If stocks decrease, $\mathrm{d}\mathbf{x}/\mathrm{d}t < 0$ then both endogenous ($-\mathrm{d}\mathbf{x}/\mathrm{d}t > 0$) and exogenous ($\mathbf{z} > 0$) drivers are positive, making $[\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t]$ positive also. Operation on positive quantities by $-\mathbf{C}^{-1}$, Eq. (5), causes stocks to increase, reflected in $\mathrm{d}\mathbf{x}/\mathrm{d}t$ becoming positive. The initially negative derivative, $\mathrm{d}\mathbf{x}/\mathrm{d}t < 0$, becomes sign-reversed, $\mathrm{d}\mathbf{x}/\mathrm{d}t > 0$, indicating the system shifts from decreasing its standing stock to increasing it. Runs with the Fig. 1 model showed this. Progressive reduction in the magnitude, $|\mathrm{d}\mathbf{x}/\mathrm{d}t|$, of $\mathrm{d}\mathbf{x}/\mathrm{d}t < \mathbf{0}$, reducing the force of the $[\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t]$ driver, slowly and monotonically decreased the resultant stocks. Progressive increase, however, amplifying $[\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t]$, caused rapid growth in proportion to the increase. Thus, initially negative stock derivatives were turned positive at the end of the Eq. (5) mapping operation, setting up for a situation (completed in the remaining cases) where stocks tend spontaneously to alternate between substance gains and losses. These results are summarized in the Case 1 row of Table 1; the different shaded shapes (ovals in this case) identify initial and final derivative pairs where alternation of signs occurs.

Case 2: $\mathbf{z}$ *positive,* $\mathrm{d}\mathbf{x}/\mathrm{d}t$ *positive, and* $\mathbf{z} > \mathrm{d}\mathbf{x}/\mathrm{d}t$. If $\mathrm{d}\mathbf{x}/\mathrm{d}t$ is positive, then $-\mathrm{d}\mathbf{x}/\mathrm{d}t$ is negative and becomes a diminishing force in the $[\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t]$ driver. However, as $\mathbf{z}$ is always positive and greater than $\mathrm{d}\mathbf{x}/\mathrm{d}t$, $[\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t]$ always remains positive and the Eq. (5) mapping will tend to increase the standing stock, $\mathbf{x}$. Model runs showed that as $\mathrm{d}\mathbf{x}/\mathrm{d}t$ is reduced to smaller and smaller fractions of $\mathbf{z}$, stocks drop precipitously to very low levels and then only slowly recover slightly as further reductions in $\mathrm{d}\mathbf{x}/\mathrm{d}t$ values continue. The shift in derivative signs observed in Case 1 is repeated here even more dramatically. Table 1 summarizes the results.

Case 3: $\mathbf{z}$ *positive,* $\mathrm{d}\mathbf{x}/\mathrm{d}t$ *negative, and* $\mathbf{z} < |\mathrm{d}\mathbf{x}/\mathrm{d}t|$. Here, input is less than the absolute value of the driving stock derivative, which being negative, contributes positively ($-\mathrm{d}\mathbf{x}/\mathrm{d}t > 0$) and dominantly (since $|-\mathrm{d}\mathbf{x}/\mathrm{d}t| > \mathbf{z}$) to the driving function, $[\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t]$. The latter, being positive as in the two preceding cases, contributes by Eq. (5) to further stock accumulation. In the Fig. 1 model, stocks fell immediately to low levels when the negative $\mathrm{d}\mathbf{x}/\mathrm{d}t$ values were further reduced ($-\mathrm{d}\mathbf{x}/\mathrm{d}t$ driver values increasing accordingly), then increased rapidly in proportion to further derivative increases in absolute values. The net stock increases reflect positive final derivatives, $\mathrm{d}\mathbf{x}/\mathrm{d}t > 0$, reversed in sign from their initially negative values, $\mathrm{d}\mathbf{x}/\mathrm{d}t < 0$ (Table 1).

Case 4: $\mathbf{z}$ *positive,* $\mathrm{d}\mathbf{x}/\mathrm{d}t$ *positive, and* $\mathbf{z} < \mathrm{d}\mathbf{x}/\mathrm{d}t$. Although this case preserves derivative sign switching as observed above, it is unrealistic because the driver $[\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t]$ is always negative. Input $\mathbf{z}$ is positive, but with $\mathrm{d}\mathbf{x}/\mathrm{d}t$ also positive and greater than $\mathbf{z}$, negatively valued $-\mathrm{d}\mathbf{x}/\mathrm{d}t$ always dominates $[\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t]$. Model runs showed in all cases that negative standing stocks were produced. Thus, the switch from initially positive to finally negative stock derivatives is preserved in all four cases investigated. Case 4 results are summarized with the others in Table 1.

The crux of these relationships lies in the negative sign of the stock derivative in the $[\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t]$ driving function, and whether this derivative is greater or smaller in magnitude than $\mathbf{z}$. If standing stock decreases, initial $\mathrm{d}\mathbf{x}/\mathrm{d}t < 0$, this immediately causes the sign-reversed derivative to increase $-\mathrm{d}\mathbf{x}/\mathrm{d}t > 0$, which becomes a positive force for growth in the $[\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t]$ driver. Application of Eq. (5) to this increases the stock, final $\mathrm{d}\mathbf{x}/\mathrm{d}t > 0$. The feedback is immediate. Reciprocally, if stocks increase, initial $\mathrm{d}\mathbf{x}/\mathrm{d}t > 0$, this positive derivative

Table 1
Relations between **z** and d**x**/d*t* in keeping systems near steady state. Key to symbols: + = >, − = < , ↑ = increase, ↓ = decrease). Description in text.

Case	**z**	d**x**/d*t* (initial)	**z**/|d**x**/d*t*|	[**z** − d**x**/d*t*] driver	Δ**x**	d**x**/d*t* (final)
1	+	−	>1	+	↑	+
2	+	+	>1	+	↓	−
3	+	−	<1	+	↑	+
4	+	+	<1	−	↓	−

becomes a negative force in the [$\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t$] driver, $-\mathrm{d}\mathbf{x}/\mathrm{d}t < 0$, which when operated upon by Eq. (5) reduces the stock, final $\mathrm{d}\mathbf{x}/\mathrm{d}t < 0$. Again, the feedback is immediate. Because alternation of d**x**/d*t* between positive and negative values requires passing through extrema, $\mathrm{d}\mathbf{x}/\mathrm{d}t = 0$, the resultant oscillatory steady-state seeking behavior must be restricted to neighborhoods around these values. This is the near-steady-state imperative.

It is important to realize that systems cannot remain at steady states, only near them. This is because when they are at an extremum, $\mathrm{d}\mathbf{x}/\mathrm{d}t = 0$, boundary input alone becomes the driver:

$$\mathbf{x}_{n\times 1} = -\mathbf{C}_{n\times n}^{-1} \cdot [\mathbf{z}_{n\times 1}]. \qquad (6a)$$

When input is null, $\mathbf{z} = 0$, the system becomes self-driven on its own interior dynamics:

$$\mathbf{x}_{n\times 1} = -\mathbf{C}_{n\times n}^{-1} \cdot \left[\frac{-\mathrm{d}x}{\mathrm{d}t_{n\times 1}}\right]; \qquad (6b)$$

this ultimately is limited by the dissipation property. Investigating these two extremes in Fig. 1 model, Eq. (6a) accounted for less than 10% and (6b) for more than 90% of the generated stock vectors. These are model-specific results, of little general interest because real systems must surely run the gamut of all possibilities. They do give a sense of the relative weight in ODE dynamics of input-driven (6a) vs. state-driven (6b) components. In steady-state analyses, the most common, the former get the most attention and the latter are, by comparison, little represented.

There is more to these relationships than described above (e.g., Patten, in preparation), but the development given is sufficient to establish that all ODE-defined systems are constrained to operate near, though not at, steady states or extrema. Ecological and other dynamical systems must accordingly become viewed as steady-state seeking, and studied in light of this property. The cause?—very simply, the negative sign associated with state changes in the driving function, [$\mathbf{z} - \mathrm{d}\mathbf{x}/\mathrm{d}t$], which turns negative change into a force for growth and positive change into one for decline, the

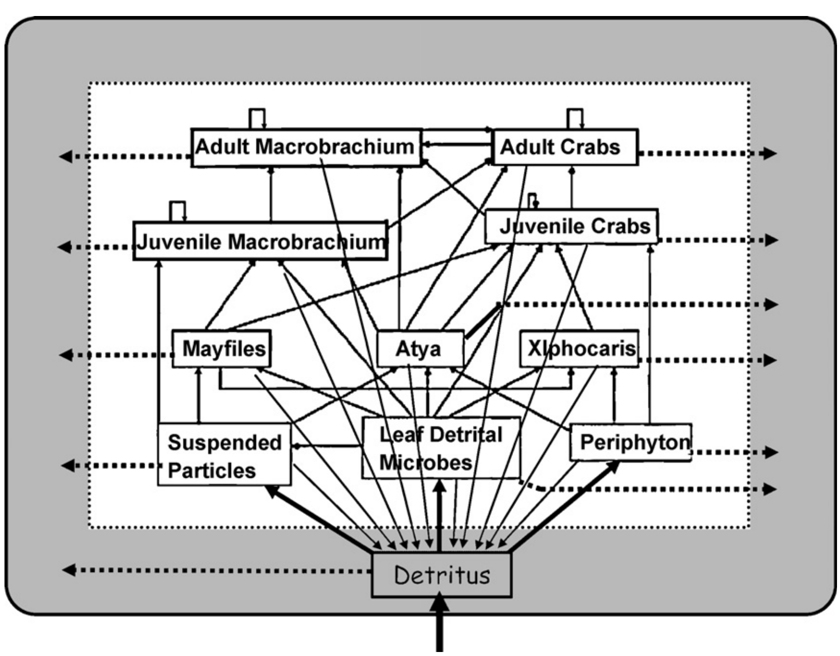

Fig. 2. Food-web model of a tropical stream community at the Luquillo, Puerto Rico LTER site, after Brokaw et al. (in press) except Detritus added for greater realism.

quintessence of a cybernetic system (Patten, 1959; Patten and Odum, 1981).

2.2. Nonlocal imperative

Fig. 2 is a food-web model for a tropical stream community at the Luquillo, Puerto Rico LTER site (US National Science Foundation, *L*ong *T*erm *E*cological *R*esearch program), slightly modified after Brokaw et al. (in press). The model contains 10 stocks, 30 adjacent links, and is 30% connected. Nonlocality refers to dominance of network-generated indirect effects in a connected network (e.g., Patten, 1984; Higashi and Patten, 1989). Quantifying this model by estimating realistic parameter values (g/m^2 dry biomass), it generally fit the observed pattern in well-connected systems, that indirect effects exceed adjacent ones. Only 0.6% of the aggregate standing stock was attributable to direct flows between the compartments; the remaining 99.4% was due to indirect flows. This model, like most others investigated in this way, evidenced dominant nonlocality in its propagated causal relationships.

From many such studies (e.g., Patten, 1984, 1991; Higashi and Patten, 1989, and others), it is evident that causality in ecosystems is mainly expressed through indirect effects.

2.3. Nonzero imperative

Ecological network analysis begins with the physics and works towards biology. Of physics' four forces – strong and weak nuclear, gravitation, electromagnetic – the first three serve as implicit background with respect to ecosystem services. Electromagnetic is of explicit concern. Electromagnetic force is transferred between any two foci by binary *transactions*; these are zero–sum because the energy and matter directly exchanged are conservative—what is lost from one pole is exactly gained by the other. Transactions give rise secondarily to binary *relations*; these are non-conservative, from which follows nonzero–sumness—what one pole gives up may be less or more than the other receives. Also, in the relational domain, subjectivity enters. Beyond the basic requirements for life, "ecosystem services" are to a great extent in the eye of the beholder—that is, human needs have both objective and subjective elements. Sustainably entraining human change to global change, accessing evolving patterns of ecosystem services and the changing requirements and perceptions of human needs, requires continually transforming transactional zero–sumness – the physics – into relational nonzero–sumness – the biology. This "nonzero imperative" of network organization may be a property of life-and-environment coevolution on a par with overcoming the second law of thermodynamics. Designing human organizations, values, economies, fashions, and behaviors in the "search for nonzero" (Wright, 2000, 2007) is the ongoing work of each human generation. Possessing certain knowledge of the scientific principles involved, emergent from a comprehensive unified theory, can only help.

In the transactional–relational scheme of network organization, information is relational, as are ecological interactions such as competition and mutualism that involve no transactional connections between interrelated compartment pairs (i, j). When a conservative quantity, f_{ij}, is transferred in a coupled system, i gains the quantity ($+f_{ij}$) and j loses it exactly ($-f_{ij}$). All transactions are thus zero–sum $(+f_{ij}) + (-f_{ij}) \equiv 0$, as demanded by mass–energy conservation.

Wright (2000, 2007) argued that nonzero–sum interactions are the basis for emergent positive relationships in nature and humanity. The basis for this can be seen in transactional network organization, wherein indirect pairwise relations generated at higher orders give rise to dominant indirect effects, as discussed in the previous section. As the domain of interactions shifts from transactional (adjacent) to higher order relational (indirect), the conservative zero–sum property is lost and non-conservative nonzero–sumness comes to be expressed as positive relations between directly as well as indirectly interacting (i, j) compartment pairs. The mathematics of ecological utility theory (Patten, 1991; Patten and Whipple, 2007a), developed as part of the broader theory of input–output environ analysis (Patten et al., 1976; Patten, 1978, 1981, 1982; Fath and Patten, 1999), formalizes and extends the "nonzero" vision enunciated by Wright (op. cit.).

The following example from Patten (1991) shows this. A compartmental food-web model for a marshland in Okefenokee Swamp, USA, was analyzed by the utility methodology. The model had 24 compartments distributed among seven sectors (Organic Matter, Microinvertebrates, Nutrients, Macroinvertebrates, Decomposers, and Vertebrates). It was 21% connected by 116 of 552 possible adjacent links (i, j), discounting self-loops ($i \neq j$). A simple path in a network is a path without repeated nodes, that is, an acyclic pathway; paths with embedded cycles are compound. The model in question had 44,025,553 simple paths whose maximum and mean lengths were 21 and 15.52 links, respectively. It also had 3,953,202 simple cycles (paths beginning and ending at the same compartment) with maximum and mean lengths of 20 and 14.81 links, respectively. Given this amount of cycling, the numbers of compound paths and repeating cycles would be enormously more than the simple ones. The purpose of this numerical accounting is to underscore that ecological networks, even for small models, are replete with large numbers of pathways over which such network properties as nonlocality and nonzero–sumness are manifested. These kinds of ecological properties could never be revealed by empirical observations alone; they have to come from models, and these in turn from theory.

Environ utility analysis enables two kinds of network measurements (Patten, 1991), both adjacent (proximate) and distributed (nonlocal, or ultimate). The first is specification of interaction types for every directly and indirectly interacting (i, j) pair. Table 2 shows the nine ecological interaction types defined by ordered pairs of the three signs +, −, and 0. Three of these, shown in the middle three columns of the figure, are adjacent and therefore zero–sum. These and six others (left column), nonadjacent, are nonzero–sum. The last row shows the number of adjacent interactions of each kind, and the last column shows the number of nonadjacent ones. Remember that the former are the result of direct mainly feeding transactions, f_{ij}, in the model, while the latter are feeding-based relations manifested over millions and millions of simple and compound relational pathways.

As shown in Table 2, the zero–sum interactions include 51 predations, 44 altruisms and 205 neutralisms. None of these are ultimately expressed, however (first three rows of right-hand column). The next three entries in the right-hand column show no ultimate competitive or dissipative interactions, and 64 amensalisms. The latter is in fact the only example of a negative relation remaining in the model once all pathway transactions have played out and the introduced substance (dry biomass) is completely dissipated to the surroundings. The remaining 236 interactions (shaded) are all positively signed—49 commensalisms, 106 aggradations (Patten and Fath, 1998; Fath and Patten, 2001a), and 81 mutualisms. This model expresses Wright's nonzero hypothesis in very strong terms. In environ theory this network-induced shift to positive nonlocal interaction types is referred to as *network mutualism* (Patten, 1991; Patten and Whipple, 2007b).

The second utility property is *network synergism* (Patten, 1995; Fath and Patten, 1998a,b)—the emergence through indirect network relationships of excess benefits (positive utility) over costs (negative utility). The lower panel in Table 3 summarizes

Table 2
Proximate to ultimate ecological interaction-type transitions between nine types defined by ordered pairs of three signs, +, −, and 0, in a 24-compartment food-web model for Okefenokee Swamp, USA. Three hundred proximate and 300 ultimate pairwise interactions (*i*, *j*) are resolved in the large-number-pathway network. These are computed as follows: (*i*, *j*) pairs = 24 × 24 (576); less 24 to temporarily exclude self interactions, $i \neq j$ (552); divide by 2 to get the number of $i \neq j$ pairs (276); finally, add back the 24 removed as self-interactions (*i*, *i*).

Utility values near zero set equal to zero		Predation (+,–)	Neutralism (0,0)	Altruism (–,+)	Ultimate (nonzero-sum)
Predation	(+,–)	0	0	0	0
Neutralism	(0,0)	0	0	0	0
Altruism	(–,+)	0	0	0	0
Dissipation	(–, 0)	0	0	0	0
Competition	(–,–)	0	0	0	0
Amensalism	(0,–)	3	51	10	64
Commensalism	(0,+)	0	23	6	49
Aggradation	(+,0)	45	58	3	106
Mutualism	(+,+)	3	73	5	81
Adjacent (zero-sum)		51	205	44	300

Table 3
Summary of network mutualism (upper panel) and synergism (lower panel) expressed in the Okefenokee Swamp food-web model.

Interaction signs	Adjacent signs	Ultimate signs
Number of +	95	317
Number of −	95	64
+/− ratio	1.00	4.95
Utility summary	**Adjacent utiles**	**Ultimate utiles**
Sum of + utilities	+4914	+15721
Sum of − utilities	−4914	−3789
|Benefit(+)/cost(−)| ratio	1.00	4.15

these utility relationships for the Okefenokee food-web model. The adjacent utilities are zero–sum (±4914 utiles), and thus their ratio in absolute value is 1.00. The utilities expressed at the end of the long chains of higher order network relationships are, however, nonzero–sum (Patten, 1995; Fath and Patten, 2001b; Patten and Whipple, 2007a,b). The excess of positive (+15,721) vs. negative (−3789) ultimate utilities generated over the large-number interactive pathways of this model gives a |benefit/cost| ratio of 4.15. This expresses network synergism, which is universally positive (Fath, 1998; Fath and Patten, 1998a) in compartmental systems engaged in storage and transfer of conservative quantities. The upper panel of Table 3 illustrates the network mutualism property in summary form. A simple count of the positive and negative signs of the computed utilities shows a +/− sign ratio of 1.00 for the zero–sum proximate utilities, and 4.95 for the ultimate ones. Network mutualism is not quite universal, as it goes unexpressed in a few simple, and ecologically unrealistic, cases of digraph topology (Fath, 1998).

The universal and near-universal occurrence in models of benefits reflected in network synergism and mutualism, respectively, argues that these are general properties to be found also in natural ecosystems.

This concludes the treatment of the three ecosystem design imperatives of this paper, which turns now to the question of control.

2.4. Multifactorial control imperative

There are no discrete controllers in ecosystems, such as the engine governors, autopilots, and thermostats of man-made systems. Control, to the extent it exists, is decentralized and inherent in non-discrete, distributed, mechanisms. These are the "checks and balances" known for complex economies and governments. Fig. 3 shows the scheme for ecosystem services developed by the Millenium Ecosystem Assessment (2005) program displayed as a negative-feedback control system. The control objectives, "Constituents of Well-being", are introduced into the generating system for "Ecosystem Services" via a comparator, or controller (the circle). Output from the Ecosystem Services sector is shown as the trajectory to the right, representing the changing states of the various identified services. The goal is sustainability—keeping the services coming by maintaining them near, but not at, steady state (first design imperative, above). In the diagram, this can be taken to mean managing service dynamics to remain within a "safe" zone (shaded). The patterned areas indicate zones of "danger", and the white areas in between represent "caution" zones. Deviations from the shaded zone are fed back to the controller, signaling the need for corrective action.

Provisioning is one of the service categories shown in Fig. 3. In the control segment of the next section, a provisioning example from wildlife management will develop a prescription for complex systems control based on knowledge gained in controlling a man-made machine—an aircraft under instrument flight conditions.

3. Husbanding for ecosystem services

There are, of course, many more properties of natural systems than the four discussed above from which management lessons can be drawn. As examples, let us examine how the four under consideration relate to ecosystem services objectives.

3.1. Near-steady-state imperative

Sustainability – keeping ecosystems as they are or little changed for future generations – implies near-steady-state dynamics. Good conservation practices are "good" probably

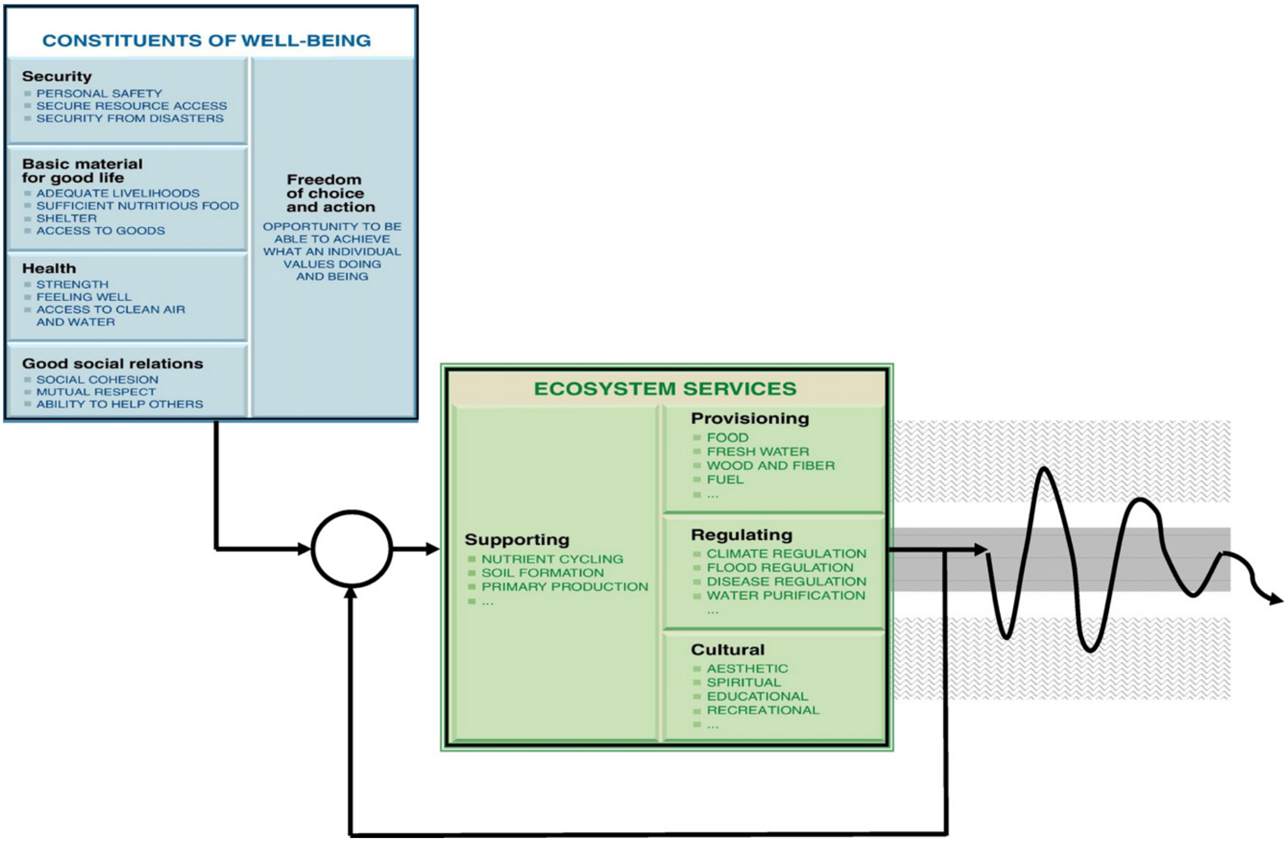

Fig. 3. The Millenium Ecosystem Assessment (2005) categories of ecosystem services and goals, schematized as a negative-feedback control system.

because they promote such dynamics, marked by sustainability-enhancing characteristics such as:

Linear dynamics	Low disturbance susceptibility
Well behavedness	High resistance stability
Gradually changing behavior	High resilience stability
Low exogenous subsidies	High predictability
Low maintenance	High reliability
Low incidence of surprise	High biodiversity

and so on. Examples include organic farming (Phelan, 2004), integrated farming (Titi and Ipach, 1989), stem-based and shelterwood forestry (Marquis, 1979), ecosystem mimicking (Lefroy et al., 1999) and management (Christensen et al., 1996; McLeod and Leslie, 2009), and integrated pest management (Kogan, 1998).

In contrast, production-intensive practices are probably "less good" because they deflect systems away from steady-state neighborhoods and discourage sustainability:

Nonlinear dynamics	High disturbance susceptibility
Poorly behaved dynamics	Low resistance stability
Abruptly changing behavior	Low resilience stability
High exogenous subsidies	Uncertainty and unpredictability
High maintenance	Low reliability
High surprise incidence	Low biodiversity

etc. Examples include "industrial" approaches to natural capital (Jansson et al., 1994), agriculture (Kimbrell, 2002), forestry (Devall, 1993; Orton, 1998), fisheries (Gillette, 2007), whaling (Dolin, 2007), and maximum sustained yield (MSY)-based management of living resources (Larkin, 1977; Sissenwine, 1978; Mace, 2001).

This first imperative – to maintain exploited ecosystems near, but not at, steady states – can be considered the touchstone of sustainable management for all four categories (Fig. 3) of ecosystem services. The new reference steady states will, of course, differ from those of their unmanaged counterparts.

3.2. Nonlocality imperative

Environ analysis literature establishes not only that indirect effects exceed adjacent ones in well-connected networks, which all ecological networks are, but also that they tend to increase in proportion to six network properties (Higashi et al., 1993). These are: number of compartments, density of adjacent connections, non-feedback cycling, feedback cycling, compartment standing stocks, and strength of adjacent linkages.

In natural systems these properties tend to increase with development and maturity, but in management situations it is not always clear that indirect effects are desirable. Unwanted consequences, for example, are in the category of undesirable indirect effects. Assuming management for sustainable ecosystem services is enhanced through mimicking nature, network non-locality is then to be a goal of management protocols. This means increasing the number of compartments, which for living compartments means enhancing biodiversity and population numbers. Increased connectivity could follow because all organisms and species must occupy their supporting ecosystems successfully, which means being coupled into the established resource networks and niches. Increase in adjacent linkages would engender combinatorial explosion of indirect relations, such as seen in the Okefenokee model (24 compartments, 44-million simple paths). Increased connectivity would also result in increased storage as well as both non-feedback and feedback cycling. Storage is the limiting case of cycling, i.e., "cycling" over pathways of lengths ≤ 1. Feedback is the basis of control (e.g., Figs. 3 and 4), which in ecosystem networks is distributed control

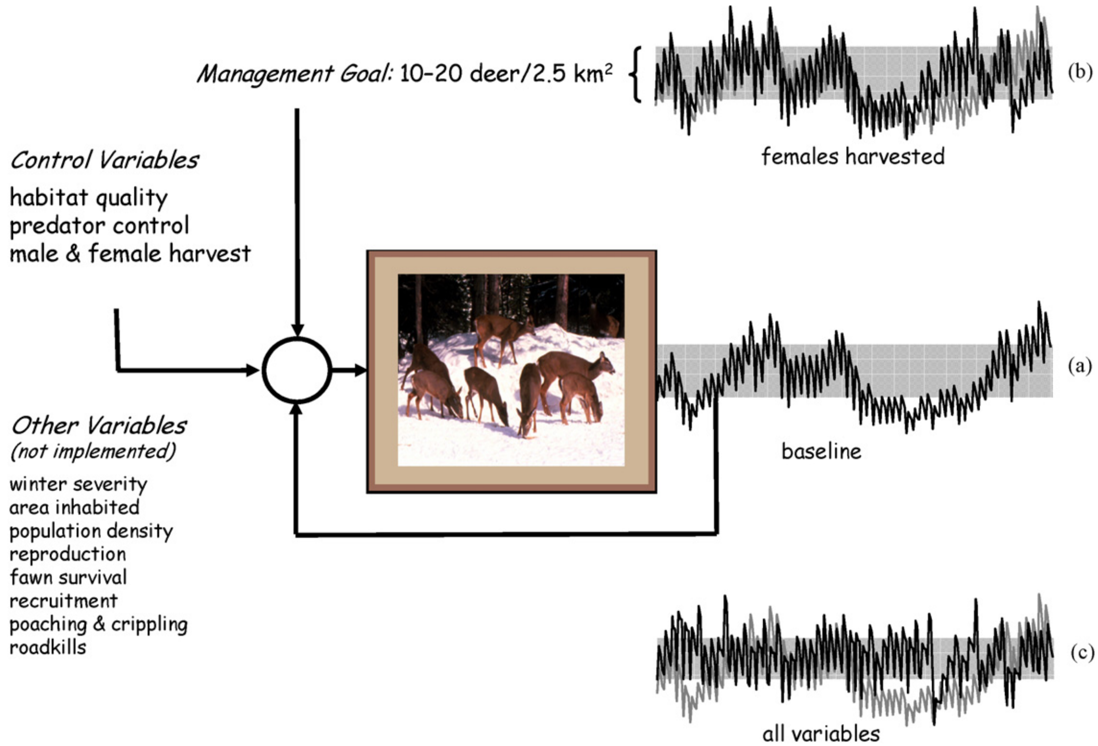

Fig. 4. Multifactorial control applied to a deer management example. A goal is set (10–20 animals/2.5 km^2) and several variables manipulated to return the population to the desired range (shaded area) whenever it drifts above or below this range. Negative feedback (error correction, deviation damping) is the basis of this form of control—"closed-loop" control.

made up of checks-and-balances. Finally, as adjacent transactions strengthen, associated nonadjacent relations increase faster with increasing path length. Therefore, strengthening adjacent interactions increases indirect ones even more.

If a situation called for the reverse prescription – unsustainablility, as in industrial intensive-production enterprises – this same set of properties would be redirected in opposite ways to those ends.

3.3. Nonzero imperative

Managing ecosystem networks for near-steady-state and nonlocal imperatives tends to increase nonzero–sumness as well. That is, positive outcomes from the first two are expected to correlate with increased network synergism and mutualism in the utility domain. This is a surmise at this point, as environ utility analysis has not found use yet in the ecosystem management and services domains. When better studied, however, how complex networks enhance positive interactions and benefit/cost relationships may become clearer. Experience suggests that when good management practices are followed, benefits will accrue from many directions. Those deriving from nonzero–sumness may be well hidden in the underlying networks, but are manifestly real nevertheless.

3.4. Multifactorial control imperative

A lesson in multivariate control of resource systems for useful purposes can be taken from instrument flight. In flying an aircraft when the physical horizon cannot be seen, control is achieved by reference to indications from the flight instruments. All the instruments are important, and the student instrument pilot learns that fixation on any one of them to the exclusion of the others will result in loss of control. This is because an aircraft can maintain a constant altitude, attitude, or airspeed by monitoring the primary instrument presenting that information and manipulating the aircraft controls to correct deviations. The problem is the aircraft can go out of control in terms of other variables if only one is held constant. All flight variables must be given attention together, and the student instrument pilot learns how to scan all the flight instruments in a continuous coordinated way and make small corrections to observed deviations. Flying an aircraft on instruments is thus an exercise in multivariable control. Since management of a complex system is involved, the principle would appear to extend to resource systems designed to deliver ecosystem services as well.

Consider the following example. Referring to Fig. 4, suppose it is desired to manage a deer population within a specified range of 10–20 animals per 2.5 km^2. Sage et al. (2003a,b) investigated this problem using a 60-year (1941–2001), 240-season data set for the Adirondack (New York, USA) White-tailed Deer (*Odocoileus virginianus*). They selected a set of control variables from a broader available set (listed in Fig. 4), and proceeded in a Stella simulation environment to assess the power of these, applied singly and in various combinations of 2, 3, etc., to all at a time to try to achieve the control objective. They verified the teaching from instrument flight—if multiple variables are available to control a complex dynamic process, all of these that can be used should be used.

Of the set of variables investigated, female hunting (which is almost never done because it can quickly decimate a population) was the strongest. Yet, used by itself in tens of simulation trials, it was powerless to keep the population within the desired range. This is shown for a typical simulation run in Fig. 4b (dark trace), superimposed on the lighter baseline trace taken from Fig. 4a, established for intermediate values of the control variable set. None of the other (weaker) control variables could achieve the desired management objective either, singly or in combination with the others. The best control was achieved when all the available variables were utilized to make deviation corrections as they occurred. One such all-variable trial is illustrated in Fig. 4c (dark trace), again superimposed on the lighter Fig. 4a baseline curve. The dark trajectory remains within the desired zone much more of the time. Even here, though, the control achieved is far from perfect as several crashes and explosions outside the desired range are experienced. Presumably, if some of the other variables listed in Fig. 4 had also been manipulated, this would give further improvement.

That multiple variables whose networks reach into the interiors of their systems are needed to achieve control reflects the diffuse "checks-and-balances" concept of distributed control. Aircraft in clouds cannot be controlled by adjusting their airspeed, altitude, or attitude alone, and wildlife, fisheries, agriculture, and other provisioning services cannot be managed by attention to harvest, habitat quality, or other variables taken by themselves. Multivariable control is necessary to gain surest regulation when systems become at least as complex as an aircraft navigating through physical three-space.

4. Summary and conclusions

This paper has explored, from the perspective of ecological networks, three design and one control imperative relating to sustainable delivery of ecosystem services. Although the "ecosystem" concept is well established in lay and scientific usage, too little is known beyond basic description that is applicable to the ecosystem services topic. In this applied domain, all four of the properties investigated must be considered speculative and premature. They are put forward to point the way toward a future science where practice can be guided by theory founded in first principles—in particular, the principles of network organization.

Considering the first imperative, sustainability almost by definition implies that a system evidence neighborhood dynamics near steady states. Wide swings in state space would not be conducive to, or reflective of, the sustainability property. Ecosystems from which human services are derived should not be allowed to slip far from recoverable states, and nearness implies they be maintained dynamically close to $d\mathbf{x}/dt = 0$. The steady-state seeking dynamic hidden in ODE models (Eqs. (4) and (5)) would seem to ensure this at some fundamental level.

It is often observed in network models (e.g., Figs. 1 and 2) that indirect effects are more than those associated with adjacent linkages; this is the second imperative. It is not known whether this property is generally favorable or inimical to ecosystem services. What can be inferred is the property is expressed naturally in direct proportion to the growth status of an ecosystem—the more highly developed the latter, the fuller the network, and the greater the indirect effects (Jørgensen et al., 2000). As deriving some categories of ecosystem services (Fig. 3) must perturb normal states, sustained provisioning and other activities can be expected to set systems back in successional time, and thus reduce their network indirect effects. It is probable, as ecology's "intermediate disturbance hypothesis" (Grime, 1973; Horn, 1975; Connell, 1978; Wilkinson, 1999) suggests by implication (it nominally concerns biodiversity), that optimal states for ecosystem services lie somewhere between successional extremes.

The third property, network nonzero–sumness, is related to the last. Environ utility studies of ODE models indicate that network synergism (utility benefit/cost ratios >1) and mutualism (utility +/− sign ratios >1) (Table 3) are enhanced by the same properties that increase indirect effects—more compartments, connections, feedback and non-feedback cycling, storage, and strength of adjacent linkages. Thus, ecosystems with richer, more diverse, and more interconnected components and processes are expected to express the nonzero imperative more strongly, enabling delivery of higher quality goods and services than otherwise.

The fourth imperative is multivariable control. There are no discrete controllers in ecosystems, so if control occurs distributed control manifested as network checks-and-balances must be the mechanism. Ecosystems with more diverse components and linkages will have more cycling, thus more possibilities for negative feedback control (Figs. 3 and 4). In ecological network theory, input and output environs are sub-networks of opposite temporal orientation (past and future, respectively) leading backward in time from outputs and forward from inputs. Patten (2006) used these opposing orientations to develop a network perspective on ecological "indicators" vs. "actuators" that bears on distributed control.

An *indicator* is a system output signaling some internal, usually alarm, condition of which an external observer wishes to be made aware. Traced backward through time and the system network from the output event, an indicator traverses the causal chains and pathways that led to it. This sub-network is the input environ defined by and specific to that indicator. It is a diffuse historical construct, a web of energy–matter transfers and transformations, leading to the output. In a similar manner, an *actuator* is an external control variable exerted as input, which generates in future time a whole interior output environ of network direct and indirect effects.

Undistributed multivariable control (e.g., Fig. 4) is complicated by the need to assess deviational trends and exert reversing control actions. The distributed case is harder because of inherent diffuseness. In this, each control variable specifies an output environ in future time wherein the consequences of control actions propagate and become more and more dispersed and dampened with time. Applied to the problem of sustaining extraction of goods and services from ecosystem networks, one can see enormous impediments to progress—multiple control variables, whose effects propagate through different portions of complex networks by different processes and at different rates starting from their points of actuation, are to be manipulated and coordinated in ways to maintain near-steady-state dynamics and deliver nonzero–sum benefits $>$ costs in nonlocal environments where indirect effects are dominant.

This is work for strong science—well-developed ecological network science, in the conception of this paper, science still to be built. Or, limitation by carrying capacity can supply the control, as it does with other organisms, which operate by evolutionary "cut-and-try." Husbanding ecosystem services optimally, and sustainably, in a constantly changing world will present a strong challenge to the development of a correspondingly strong science.

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