

SUSTAINABLE DEVELOPMENT FROM A NETWORK THERMODYNAMIC PERSPECTIVE: LESSONS FROM THE PARADOX OF ENRICHMENT¹

The lake is an old and relatively primitive system, isolated from its surroundings. Within it matter circulates, and controls operate to produce an equilibrium comparable with that in a similar area of land. In this microcosm nothing can be fully understood until its relationship to the whole is clearly seen.

Forbes 1880

ABSTRACT

With the current struggle to "sustainably" exploit our biosphere, the "paradox of enrichment" remains an issue that is just as relevant today as it was when it was first formalised by Rosenzweig in 1971. This paradox is relevant because it predicts that attempts to sustain a population by making its food supply more abundant (*e.g.*, by nutrient enrichment) may actually have the reverse (paradoxical) effect of destabilising the network. Originally, this paradox was based upon studies of "reasonable" but quite simple predator-prey models. Here, we attempt a more "realistic" revision of the paradox that explicitly accounts for the embedded nature of the human system in a complexly interwoven set of hierarchical (spatial, temporal and organisational) relations with the rest of the ecosphere—a relationship whose exploitative nature continues to grow in intensity and extent. This revision is attempted with the aid of a combined thermodynamic and network approach. The result is that a scale-dependent asymmetry in the action of the Second Law of Thermodynamics is shown—an asymmetry that results in the creation of two antagonistic propensities: local-order and local-disorder. The point of balance between these two propensities is empirically measurable and represents a balance between processes and constraints *internal* (growth and development) and *external* (interactive and perturbing influences) to a system—a balance that may be called the most "adaptive" state (*sensu*, Conrad 1983). The use of such an index of this balance is demonstrated and is used to clarify the relevance of the paradox to more complexly organised systems. As a consequence, we conclude that the concept of "sustainable exploitation and growth" is an oxymoron.

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INTRODUCTION

Sustainable Development represents a slippery concept due to its context-specific nature. That is, the degree of success attributable to any implementation of a Sustainable Development initiative is strongly dependent upon the temporal, spatial and organisational frames of reference under which it is examined. The concept of Sustainable Development suffers from this ailment due in the main to the unforgivingly complicated and complex nature of even the simplest of natural systems.

In many ways, the current concept of Sustainable Development represents an attempt to move away from its even more reductionistically slanted precursor, the concept of Maximum Sustainable Yield. The sole focus of Maximum Sustainable Yield was a binary, predator-prey (exploited-exploiter) system of interactions that ignored all other interactions. However, to move away from such strong reductionistic underpinnings has been an arduous task as it is not at all clear how to even begin integrating such temporally, spatially and organisationally complex and interwoven systems. When the added complexities of interactions other than such “parasitic” modes are also considered (e.g., the “symbiotic” modes, *sensu* Peacock 1999), the situation becomes intractable.

One potential solution to this dilemma is to search for a scale-independent (i.e., fractal-like) phenomenon that can go across scales of time, space and organisational structure, beyond the simplistic reductionistic modes of binary interactions as predation, parasitism or symbiosis. This is the solution that we entertain. We do this by appealing to new and old developments in the study of networks and thermodynamics and using by way of example the concept of the Paradox of Enrichment. We focus upon the Paradox of Enrichment because it represents an alternate and well-known formulation of Sustainable Development that is based upon the stability characteristics of interacting systems, in contrast to the emphasis upon simple yield as in Maximum Sustainable Yield.

Fertilization for the purpose of increasing the yield available for consumption represents a widespread practice amongst humans. To have a plentiful supply of food is accepted by most as being a desirable state as it is thought to alleviate political and economic instability attributable to famine, disease and military conflicts. However, such attempts to stabilise the human population by increasing the food resources available to them were argued to be potentially disastrous, in biological terms by Rosenzweig (1971) and called the “Paradox of Enrichment” (henceforth, “Paradox”).

This Paradox represents the loss of local asymptotic steady states in predator-prey relationships that was caused by the switching of the relationship from a negative-feedback control to a positive-feedback explosion (i.e., population explosion and then implosion). Empirical evidence exists that both support (Huffaker 1958) and refute (McAllister et al. 1972, McCauley and Murdoch 1990, Murdoch et al. 1998) the presence of such Paradox-like behaviour, indicating that in reality, the situation is (as may be expected) more complicated than may be extrapolated from such simple predator-prey models.

In essence, the Paradox asks the following question: Are modifications to the carrying capacity of a system detrimental to the stability of another system that is dependent upon it, and by extension, to the stability of the whole (combined) system as well? As such, this is an important question as it has direct implications to a subset of the current notions of sustainable development/exploitation. However, the Paradox must be extended from a simple, local two-

component (binary) system to the more general case of a complex, global multi-component system, before this connection can be made more tangible. That is, the paradox must also address at the very least, the following four, related issues:

1. BIFURCATION TRAJECTORIES—Soon after Rosenzweig's initial paper, the paradox was shown to be due to the bifurcation of asymptotic steady states into globally stable limit cycles (*i.e.*, time-varying equilibria) via a so-called "Hopf bifurcation" (Gilpin 1972, May 1972a). The lesson learned was that loss of local (component-level) asymptotic stability does not necessarily mean that global (system-level) stability is also lost (*e.g.*, Gilpin 1972). However, it is nonetheless quite possible, as pointed out by Rosenzweig himself (1972), that the mere presence of "fluctuating" populations (implying more variable dynamics) may increase the potential for extreme population lows or highs, which in turn may increase the probability of local extinctions. The potential for asymptotic equilibria (henceforth "attractive sets" of points in state space) to follow a cascading sequence of bifurcations due to changes in some driving parameter (*e.g.*, such as nutrient loading, climatic change, carrying capacity) is today well appreciated (*e.g.*, Schaffer 1985, Scheffer 1991, Scheffer *et al.* 1993). However, how the presence of numerous interrelated and time-varying local attractive (and "repelling") sets may influence the dynamics and stability of an entire connected system is far from being understood. Variations in the local structure of attractive sets of component-level systems can make the attractive sets of the corresponding whole system, and therefore also the latter's dynamics, quite incomprehensible.

2. TRANSIENT DYNAMICS—Making the situation even more difficult are the rich and complex sets of "transient" (*i.e.*, non-asymptotic or "non-equilibrium") dynamics. This is especially the case for "semi-stable" attractive sets (Byers and Hansell 1992, 1996), where a dynamical system may stay in a seemingly stable configuration for a long time before eventually moving off toward its "true" attractive set, without the action of any other external influences. The concepts of bifurcation and transient dynamics go hand-in-hand as changes in a component-level system's carrying capacity changes its attractive set, and so also the system's transient behaviour. This is especially the case when the driving parameters themselves (*i.e.*, carrying capacity as in the case of the Paradox) are dynamically changing, continuously or discontinuously (Patten 1983). Thus, enormously complicated situations can be anticipated if the carrying capacities of any systems are modified.

3. SPATIAL AND TEMPORAL STRUCTURE—Spatiotemporal constraints upon resource-consumer interactions are able to modify (especially diminish) paradox-like behaviour. This has been demonstrated both empirically (Huffaker 1958) and theoretically (Holt 1984, Ballyk and Wolowicz 1995, Scheffer and De Boer 1995, Abrams and Walters 1996, Jansen 1995, Deroos *et al.* 1998), and popularised as "metapopulation" processes (Levins 1969, Hanski 1982, 1989, 1991). That is, in the presence of refuge or source populations (*e.g.*, prey) protected from strong predation pressures, system-level stability is modified (enhanced; Scheffer and De Boer 1995). However, this stabilising effect of spatiotemporal (and organisational) structure and associated constraints should not be taken for granted. It is well known that such structure can also induce instability, depending upon the specifics of flow rates and gradients of the interacting systems. Such standing-wave-like instabilities are known as "Turing instabilities" (Turing 1952, Bard and Lauder 1974). With such phenomena, the situation becomes ever more complicated when we attempt to extrapolate to larger and more global spatiotemporal scales.

4. NETWORK INDIRECT EFFECTS (ORGANISATIONAL STRUCTURE)—The strongly embedded, hierarchical/holarchical, web-like nature of ecological systems adds another layer of rather unforgiving complexity to our capacity to understand the stability characteristics of real systems (*e.g.*, see schematic in Figure 3.1). This is because "indirect effects", also known as "higher order

interactions", can become greatly pronounced when linkages are many (*i.e.*, the “n-body problem”; Poincaré 1892), as in high-dimensional, hierarchically-ordered systems (Higashi and Patten 1989). This results in nonlinear or nonlinear-like (*i.e.*, "pseudo-nonlinear"; *sensu* Patten 1983) dynamics being observed at the whole-system level—even if the components' interactions are completely linear. (Pseudo-nonlinearity, if not true nonlinearity itself, must therefore be the universally observed situation because for complex systems it is impossible to determine all the inputs that influence a given output. In fact, for this reason, the general assumption that most systems are nonlinear because their observed dynamics appear nonlinear may not be entirely true if complexity is involved in determining their behaviour.) In this, we have another factor that drastically increases the uncertainty of our capacity to understand the effects of modifications to the structure of a network (*e.g.*, changes in carrying capacity).

How can we integrate the natural complexity of these densely interwoven processes to arrive at some semblance of understanding of the relevance of the paradox? One possibility is to couple the concepts and perspectives that arise from linear thermodynamics and linear network formulations of systems (environ theory—Patten 1978, 1982, 1985. The latter expresses in a very general way, the flow-storage networks of systems and so provides a useful context for the expression of the former thermodynamic (evolutive) principles with its focus upon gradients and their breakdown. Both environ theory and thermodynamic theory build from the same dynamical equations that describe general systems. This point of conceptual commonality (reviewed in Appendix 2) is used in what follows to develop a fractal-like (scale-free) understanding of stability and its inverse concept of dynamical uncertainty. In no way do we suggest to develop a general theory that merges these two distinct theories. Rather, it is the juxtaposition of a subset of perspectives and concepts foundational to the two theories that is attempted in what follows.

GRADIENTS AND THEIR BREAKDOWN IN HOLARCHICAL NETWORKS

The focus of the Paradox is upon the influence of variations of carrying capacity upon a system. However, the focus of a thermodynamic analysis is slightly different: the influence of variations in gradients and flows. We will discuss this latter emphasis upon flows and gradients in this section and then return to the case of variations in carrying capacity in the next section.

The presence of energy or matter gradients represents an instability, in the most general sense. Such gradients cause² increased intensities of energy and matter flows (fluxes). In turn, these flows degrade the very gradients that cause their existence. “Living” systems are able to harness such gradients and flows to do work that increase their structural/functional integrity and complexity (“local-order”).

As such, gradients represent increases in the capacity to do work, which in an ecological sense represents a resource of the most general kind (*e.g.*, highest biological productivities are associated with the steepest gradients: vertically (altitudinal zonation, *e.g.*, Merriam's life zones), horizontally (edges, hedgerows, corridors, ecotones, riparian and coastal zones and ergoclines) and latitudinally). The local flows of matter and energy associated/caused by these gradients represent the mechanisms by which these same gradients are eroded/destroyed. As the magnitude of the gradients is eroded with time, the magnitude of matter flows associated with the gradients also decreases with time. This tendency for the *intensity* of flows to *slow down* with time is described by the *Least specific dissipation principle* (Prigogine 1947; see Appendices 1 and 2C for more details), for energetically “open” systems (*i.e.*, where flows of energy into and out of a system exist) that are near some *local quasi-steady-state* of inputs and outputs of energy.

² “Cause” in the thermodynamic sense (phenomenologically and probabilistically).

The general (theoretical) applicability of this principle is limited due to some simplifying assumptions in its derivation, in particular, that of a *local quasi-steady state* (Appendix 2C). However, it is here assumed that the description of a system may be made at any arbitrary spatial-temporal-organisational scale such that this latter assumption can be appropriate. In other words, the dynamical equations of “motion” (*sensu* Denbigh 1951) of any non-linear system (including those that are “far-from-thermodynamic equilibrium”) can be linearised (via the application of a Taylor Series Expansion), and while the range of validity of such linearisations may be limited, they can still represent qualitatively useful indications of the state of the system when an appropriate spatial-temporal-organisation scale is used. In empirical practice, the range of applicability is known to be large in many systems and it is widely appreciated that this range can only be determined empirically (*e.g.*, see Denbigh 1951, Spanner 1964, Katchalsky and Curran 1967, Mikulecky 1985). For the sake of simplicity, this validity for ecological systems will be assumed due to the empirical evidence provided in Choi *et al.* (1999; the reader is also directed to Appendix 2C and Fath *et al.* 2001), although what follows is not entirely dependent upon this assumption.

It must be emphasised that the creation of local-order represents a gradient that is itself also subject to degradation, which in turn creates subgradients, in a hierarchically recursive manner. That is, degradation of gradients at level $x^{(0)}$ creates local gradients (local-order) in subsystem $x^{(-1)}$, which in turn creates local gradients (local-order) in sub-subsystem $x^{(-2)}$, and so on, ..., in a cascading, fractal-like sequence, as one descends the organisational holarchy/hierarchy. Simultaneously, as one ascends the holarchy/hierarchy, the flows associated with subsystem $x^{(-1)}$ act to degrade the gradients (local-disorder) that are associated with its encompassing system level $x^{(0)}$, and so on, ..., in a fractal-like manner. There is therefore, a fundamental fractal-like asymmetry in the action of the Second Law as one descends or ascends the holarchical/hierarchical scales of embedded structures (Figure 3.2). (This asymmetry was implied by Lotka 1922 and noted more explicitly by Schrödinger 1945, Prigogine 1947, Bertalanffy 1950, Odum and Pinkerton 1955, and many others. Here we have only formalised this concept in the current context to simplify the arguments that follow).

Any given system exists in a balance between these two asymmetric propensities that derive from the very same Second Law. The order-creating propensity becomes manifest as one descends organisational structure while the order-destroying propensity becomes manifest as one ascends organisational structure. The complex suite of interacting gradients and flows across numerous organisational scales that influence any given system can therefore be attributed to a quasi-local balance of local-order creating processes and local-disorder creating processes. The relative dominance of one or the other principle may be indexed by the local specific dissipation rate (*i.e.*, the ratio between boundary system free energy loss (y) and system storage (x), also known as the Respiration/Biomass ratio (or R/B) in ecological circles, dimensioned $[T^{-1}]$; Choi *et al.* 1999, Fath *et al.* 2001). By biomass, we refer to the mass of the living matter in question. By respiration, we refer to the biochemical oxidation (*i.e.*, “catabolism”) of organic molecules in plants and animals that provides biochemically useful free energy (generally in the form of high energy phosphate groups—ATP). There are many ways of estimating respiration rates, depending upon the specifics of the biochemical pathways involved. However, all methods attempt to quantify the rates of energy transformation of useful free energy to “boundary outflows” that do not return to the originating system. As such, respiration rates represent the rate of free energy lost permanently to the originating system, and the R/B ratio represents the intensity of these losses attributable to the structure (the biomass of the originating system).

Depending upon the details of the gradients and flows and their corresponding interactions propagated through the systems, a characteristic range of the specific dissipation rate (its "realised" attractive set) can be expected which indicates the relative balance between propensities for "local-order" vs. "local-disorder" for a particular system, at a particular spatial/temporal/organisational level of resolution. For example, any changes (perturbations) to a system $x^{(0)}$ via enrichment, exploitation, genetic manipulation, climatic change, *etc.*, interact to create a local alteration of flows, gradients and interactions associated with that system. The system within which $x^{(0)}$ is nested, $x^{(1)}$, as well as the system $x^{(2)}$ encompassing this, are also potentially affected. The relative influence of such changes (perturbations) upon system $x^{(0)}$ may be indexed by monitoring their effects upon the local boundary outflow (dissipation)-to-storage ratio, y/x (or R/B ratio) of the system. When there is greater environmental uncertainty, local-disorder dominates a system and R/B ratios are reduced. This means simply that when local-disorder dominates, useful free energy is lost from the system at higher intensities.

There is a second aspect of the dissipation/storage (or R/B) ratio that must be emphasised. This magnitude of the storage specific dissipation rate provides a measure of the system's deviation from thermodynamic equilibrium. That is, y/x (or R/B) measures the "effective" gradient to which the system is exposed. When modifications increase the effective gradient, this is indicative of increased deviation from the quasi-steady-state. Conversely, modifications that decrease the ratio indicate increased proximity to the quasi-steady-state (see Appendix 2C). That is, when the magnitude of R/B (the intensity of energy dissipation) is large, the assumed linear relationship between gradients and flows becomes less tenable and intrinsic nonlinearities and pseudo-nonlinearities of intersystem dynamics may be expected to become more dominant. In terms of the attractive sets of these dynamical systems, a bifurcation sequence of the attractive states a system $x_k^{(-1)}$, becomes increasingly probable as the R/B ratio increases (*i.e.*, the nonlinear terms of the "equations of motion" become more dominant; see Appendix 2C). Figure 3.3 schematically shows how the dynamical and structural uncertainty of a system increases when local-disorder dominates over local-order.

Using R/B as a universal "measuring stick", it becomes possible to study paradox-like behaviour in network-relevant thermodynamic terms. As an example, the empirical form of the relationship between specific dissipation (R/B) and the dynamic/structural variability of limnoplankton is presented in Figure 3.4. Dynamic/structural variability is expressed, after log-log transformation, as: 1 minus the coefficient of determination of the body size-abundance relationship. This has elsewhere been shown to be a practical index of dynamical/structural variability (Choi *et al.* 1999; see also Table 3.1). As Figure 3.4 depicts, the dynamical/structural variability of limnoplankton increases as storage-specific dissipation increases.

The biological implications of this observation become clearer when it is realised that near steady states, a system's turnover rate, τ_k^{-1} , approximates its specific dissipation rate:

$$\tau_k^{-1} = y_k/x_k$$

The reciprocal of this turnover rate is turnover or residence time, τ_k , with time [T] dimensions. Thus, at or near steady state, elevated dissipation rates can be expected to correspond to faster turnover rates and, reciprocally, shorter residence times. The approximation of turnover by specific dissipation (or vice versa), though less appropriate when a system deviates from steady state, remains a useful index for empirical applications. When turnover rates are larger, the rate of

return of a system to a steady state from which it has been perturbed is faster and the duration of deviation is shorter. This reflects increased "resilience", the ability to return to a steady state after deflection (Webster, et al. 1975). Such faster return rates, however, mean greater dynamic uncertainty. Within ecological circles, this is commonly referred to as an "r-adapted" system. This is because, when turnover (or specific dissipation) rates are elevated, systems are further from the quasi-steady-state which implies the existence of strong thermodynamic gradients. Matter and energy flows and gradient strength go together, the latter driving the former—the stronger the gradients the more important become the influence of true- and pseudo-nonlinearities (*e.g.*, see Figure 3.3).

With this background, the paradox of enrichment can now be interpreted in near-linear thermodynamic and environ-theoretic network terms. In particular, we can now focus upon the influence of variations in the carrying capacity of systems embedded in complex networks.

UNDERSTANDING THE PARADOX

ECOLOGICAL AND EVOLUTIONARY TIME

To see how the paradox of enrichment works in ecological networks, it is necessary to understand the manner in which specific dissipation is modified by changes in the carrying capacity of a system. As mentioned in the Introduction, a change (*e.g.*, increase) in the carrying capacity of a system represents a displacement from the attractive set prior to the change. This means that at the very least, the influence of (1) transient behaviour and (2) the form of the attractive set as a function of carrying capacity must be addressed. That is, there will exist consequences in both the short-term (*i.e.*, ecological scales) and long-term (*i.e.*, evolutionary scales).

The long-term effects are readily addressed. Let $K_k^{(-1)}$ be the carrying capacity of system $x_k^{(-1)}$ (*i.e.*, when $J_k=0$ in Appendix 2C). If the expected value of storage, $E[x_k^{(-1)}]$, can be taken as proportional to or an approximation of carrying capacity, $E[x_k^{(-1)}] \propto K_k^{(-1)}$, then it follows from the dimensionality of specific dissipation ($y_k^{(-1)}/x_k^{(-1)}$) and carrying capacity ($\approx E[x_k^{(-1)}]$) that these two quantities are inversely related. Any increase in carrying capacity, by enhancing storage, should reduce specific dissipation and turnover rates (Figure 3.5). This in turn would, because of the lowered intensity of activity implied by storage be associated with decreased dynamic variability (Figure 3.4). Thus, if transient effects are not important, the paradox of enrichment may actually be erroneous in that enrichment may result in a generally more stable, less variable system $x_k^{(-1)}$, over the long term (enhanced local-order). Of course, the cost of this local-order is a quadratically increasing local-disorder (Appendix 2C) to its encompassing system $x^{(0)}$, with associated increases to the uncertainty of the system $x^{(0)}$. If the changes in $x_k^{(-1)}$ are large (dominant), the probability of such increases in environmental uncertainty percolating back to the focal system $x_k^{(-1)}$ and all other systems of the same and lower hierarchical level increases, possibly negating or even over-powering any local gains in stability and order.

The above is relevant for the ideal case where transient behaviour is unimportant. When a system is in constant interaction with other systems, subsystems and supersystems, each itself being in somewhat of a perturbed state, transient effects and semi-stability cannot be ignored. In the short term, perturbations of any kind upon a system $x_k^{(-1)}$, including nutrient enrichment, will elevate the specific dissipation rate, $y_k^{(-1)}/x_k^{(-1)}$, and therefore also the system's dynamic and structural uncertainty, as reflected in increased turnover. Such perturbations may have cascading effects upon other systems at the same hierarchical level $x_j^{(-1)}$, which in turn would be expected to

increase their specific dissipation rates and dynamic variability. Some of the interior subsystems, $x_j^{(-1)}$, $j \neq k$, may also demonstrate the realisation of greater local-order (as lowered specific dissipation). In this case, this would have come about via local-disordering of a companion system, $x_k^{(-1)}$, at the same level of organization (see Appendix 2C). Regardless, if the gains in local-order for system $x_k^{(-1)}$ are large and increasingly dominate the flow network, the probability of destabilising the whole network $x_i^{(0)}$, increases quadratically (as mentioned above; see Appendix 2C).

Thus, the immediate effects of nutrient enrichment of a system $x_k^{(-1)}$ within a larger system $x_i^{(0)}$ may indeed be, in accordance with the paradox of enrichment, to destabilise the system and some or all of its interacting systems at the same level, and in so doing perturb the overall system as well. If the enrichment is sustained (and gradual such as on evolutionary time scales, to prevent the over-dominance of transient behaviour) and does not dominate the flow network, the long-term effects may be for the subsystems and supersystem both to return to more thermodynamically quasi-steady-states, marked by lower dynamical and structural uncertainty.

To summarise, there is indeed a paradox of enrichment that can be restated from network and thermodynamic perspectives: In the short term (ecological time scales), a sustained increase in carrying capacity at some level of organization will tend initially to increase the dynamic uncertainty of all systems, at all levels, that interact with the subject system. In the long run (evolutionary time scales), however, after an indeterminate period of uncertainty, the perturbed system and all its interrelated systems may settle back into attractive sets of greater dynamic certainty, so long as the local-ordering does not dominate the flows of the whole network.

THE PARADOX OF HUMAN SYSTEMS: THE PARADOX OF SUSTAINABLE DEVELOPMENT

The human system, x_h , more effectively than most, it seems, manipulates its environment to increase its local-order (manifested as reduced local fluctuations and uncertainty, and increased carrying capacity, $E[x_h]$). Interventions initially increase the local-disorder of other systems, x_k , $k \neq h$, sometimes driving them to avalanche-like behaviour, via cross-scale cascading effects of perturbations percolating through the complex interactive network and so also the human agent (at the $^{(+1)}$ environmental level) originally responsible for the enrichment (Bak *et al.* 1989; Choi *et al.* 1999). For example, the planetary supersystem is also currently affected, as seen in the potential global bifurcation of stable states in ambient temperatures and climate due to the influence of rapid global climate change and other large-scale perturbational phenomena.

What is somewhat unique in the human case is their attempts at an extremely active maintenance of local-order in a small subset, x_r , of companion systems which serve as “resources”. These include agriculture, silviculture, fisheries management, *etc.*, managed and manipulated by practices that include ecological engineering, biological control, nutrient enrichment, ecosystem management, ecological economics and sustainable development/exploitation. The invariably unintegrated, piecemeal, punctual and increasingly dominating nature of human interventions creates spiralling increases in local-disordering of other systems and the supersystem which are eventually received as disordering repercussions that propagates to our cultural sphere, taking various forms as human instability and strife. This is the Paradox manifested as a paradox in the most general sense: a Paradox of manipulation.

Natural selection and ecological succession have it that if one species is unable to sustain its current practices, the changes it induces will lead to its eventual replacement by other, better-

adapted species. Such change takes place on evolutionary time scales, and in the interim, the maladaptive practices can cause destabilisation and uncertainty in the whole system. The only certainty is that each system will "adaptively" tend towards a state of greatest local-order (least possible specific dissipation). If, however, mechanisms that maintain perturbational dynamics are suddenly relaxed, altered, or stopped, the change of direction necessitated by this can itself appear as a secondary perturbation. Problem-solution sequences, the essence of adaptation, can therefore in themselves cause escalating chain reactions of increasing uncertainty, marked by elevated specific dissipation and turnover rates. These kinds of adaptation-related perturbations are especially likely to be expressed when human value systems (economic, social, political, religious, ethical, aesthetic) interact in their own complex ways. This is the great danger, for when uncertainty becomes elevated, fear and irrationality take over and death, disaster and extinction become all the more probable.

This is not to say that humanity should abandon its attempts to modify or enrich its resource base and through this, itself. To do this would also be a dangerous alteration of the current network of balances. But such use should be carried out with the acute awareness that any kind of intervention to alter an established state, including attempts at sustainable development, is fraught with uncertainty. This is especially true when many interventions are attempted independently at large scales. The whole network of interacting systems must be given time to adapt. Slow, carefully monitored, graduated change can be recommended as the best policy for long-term resource management. Deforestation, overfishing and population growth at current rates represent dangerously rapid alterations to the relative balance of local and global order that can only have deleterious outcomes.

Another solution element suggested by network-thermodynamic considerations is to decrease system leakiness. When a system gets closer to a local steady state, internal cycling of energy and matter becomes an increasingly important property. Cycling increases the efficiency of energetic transactions (as specific dissipation decreases) and also the contribution of indirect flows to throughflows and storages (*i.e.*, to organization). Cycling itself is organization. Closing cycles means containing the substance and energy of a system within the system, not letting it escape to the outside (that is, dissipate). While the order represented by cycling is not completely free, increased transfer efficiencies can go a long way toward abating environmental uncertainty and achieving greatest local-order, convergent with Peacock's (1999) symbiotic mode.

Recent attempts to put economic values upon ecological structures and functions have been made in the hope that such mappings would facilitate a better accounting and management of natural resources. While laudable in focusing the attention of policy and decision-makers on their lack of consideration of ecological structures and functions, and on the notion of a sustainably integrated human society, such attempts represent quite a dangerous form of hubris when used as a mechanism for ecological management. This is because the "logic" of neoclassical economics, oriented to profit- and growth-maximising systems, does not match the "logic" of natural systems, which are oriented to adaptability-maximising systems in the face of an always-uncertain future (Conrad 1983). Such "logical" inconsistencies would introduce too many non-linearities into the management process, and so potentially greatly amplify the effects of any errors to an already uncertain science.

To summarise, human interventions of any kind may also be considered uncertainty-elevating factors, such interventions include the implementation of Sustainable Development practices. That is, Sustainable Development is an oxymoron in the deepest sense as ultimately, it is impossible to sustain that which is being altered. Peacock (1999), following upon the earlier writings of Lotka (1922) and Odum and Pinkerton (1955), has suggested that such sustainable

practices may be possible if more coherent mutualistic or synergistic modes are encouraged, rather than the exploitative, “parasitic” mode that is currently dominant. This may indeed be a useful solution to a more Sustainable Development. However, what the above analysis indicates is something quite simple and perhaps obvious in retrospect: Interventions of any kind, including parasitic or coherent synergistic modes (*sensu* Peacock 1999) are dangerous because they modify the previously negotiated balances (quasi-local steady states) of a complex network. If interventions are made, be they for reasons of management or development, they must be done so carefully and gradually to allow adaptation of the whole network and prevent the over-dominance of uncertainty enhancing transient effects. The key idea is that the rate of change of these balances caused by interventions must not exceed the adaptive capabilities of the network.

UNCERTAINTY AND ECOLOGICAL HEALTH

In the above, a scale-free, fractal-like approach to the quantification/qualification of the dynamical uncertainty of realistically complex systems was developed and used to study the concept of sustainability, using the Paradox of enrichment as a pedagogical tool. We now turn to the question of Ecosystem Health (*e.g.*, Rapport *et al.* 1999), to which we extend this perspective. For this purpose, we focus upon the intimately related concept of the adaptive capacity of complex holarchically organised systems because this latter concept is directly related to the above notion of dynamical uncertainty. It is assumed for the sake of argument, that adaptive capacity is an important indicator of Ecosystem Health.

In the face of a constantly shifting and varying network of interactions, “one must keep running to stay still” (in the game of life). Such was the wisdom of the Red Queen in the Adventures of Alice in Wonderland—the necessity of continuously adapting in the face of an ever-changing context (The Red Queen’s Hypothesis of Van Valen 1976; see also Holling 1973). There exist two main strategies in the face of such contextual heterogeneity (*e.g.*, Rosen 1967:166-169; Holling 1973). One is to respond rapidly to the various manifestations of uncertainty. The other is to resist the various manifestations of uncertainty. In the evolutionary biology literature, these are known respectively as, the “Scramble” strategy—to take advantage of available resources as much as possible because you will never see them again (*e.g.*, the dominant human mode), and the “Hedge-betting” strategy—to tide over or adsorb environmental fluctuations, waiting for a better day (*e.g.*, turtles). (Parenthetically, in the ecological literature, the former strategy has dominated over the latter as to a mechanism for the reduction of uncertainty and has even become almost synonymous with the concept of stability; DeAngelis 1980, 1992).

The first strategy (“scramble”) is embodied in the concept of “resilience”, the rate of return to some local quasi-steady state. In the previous section, we suggested that resilience may be simply and usefully measured by the R/B ratio. This was because high R/B ratios are indicative of high intensities of biological activity and faster turnover times. That is, systems of diminished local-order (*i.e.*, greater dynamical uncertainty) represent more “resilient” systems. In ecological circles, this is commonly referred to as “r-adapted” systems.

The second strategy (“hedge-betting”) is embodied in the capacity of a system to “resist” or “absorb” perturbations to state variables and driving variables and so persist in space-time-organisation (*i.e.*, an inertial characteristic) has unfortunately also been called “resilience” by some authors (*e.g.*, Holling 1973). To avoid confusion, we will refer to this concept as “resistance”. This biological inertia of a system may be quantified as the amount of biomass

simply because larger systems have a greater capacity to buffer the effects of short-term perturbations/fluctuations in energy deficits or surpluses (*e.g.*, see Choi *et al.* 1999). That is, systems of enhanced local-order represent more “resistant” systems. In ecological circles, this is commonly referred to as “K-adapted” systems.

What is immediately striking is that dimensionally, resilience and resistance are inversely related quantities/qualities (Figures 3.6a and 3.6b; similar relationships are well known at the organism level and known as allometric relationships; reviewed by Peters 1983). That is, when resilience is high, resistance is low, and vice-versa. In the face of environmental ($x^{(0)}$) uncertainty, extreme resilience is just as detrimental as extreme resistance: When resilience is too great, a system is more prone to rapid environmental fluctuations (*i.e.*, there is not enough “resistance” to environmental fluctuations), resulting in dynamical uncertainty of such systems (*e.g.*, leading to elevated rates of local extinctions and invasions). When resistance is too great, the capacity to track/follow environmental fluctuations is decreased (*i.e.*, not enough “resilience” to respond to environmental fluctuations), resulting in inadequate responsiveness to perturbations to maintain the system’s integrity (too slow, too rigid).

The above dimensional relationship leads directly to the following observation: only at some intermediate level of resilience and resistance can a system be said to be optimally adapted to the predominant environmental fluctuations to which it is subject. There is no way to determine, *apriori*, the exact nature of this optimally adapted state—it can only be known empirically. The significance of this optimally adapted (or “adjusted”) state cannot be emphasised enough as its relationship to the current concepts of ecological integrity and health are striking. What is extremely clear is that the dynamical uncertainty (the balance between local-order and local-disorder) at the environmental ($x^{(0)}$) level has a direct effect upon the dynamical uncertainty of the focal system $x_k^{(-1)}$. Any activities of $x_k^{(-1)}$ that alters the local-balance of the containing system $x^{(0)}$ has a direct influence upon the short- and long-term adaptive capacity (and ecological health) of the focal system $x_k^{(-1)}$. In other words, human interventions of any kind are uncertainty elevating factors that not only modify the short- and long-term sustainability of a system but also the short- and long-term health or adaptability of the system.

A probability level may be assigned to a specific location in the attractive region as a function of the distance from the expected state of system (Figure 3.6a). Those systems that exist in an increasingly more improbable state relative to such a system-specific attractive regions may thus be expected to be more prone to strong/rapid ecological change (*e.g.*, invasions, cataclysmic extinctions, variable population dynamics, strong/rapid evolutionary change—*i.e.*, an “unstable” system; Figure 3.6a: systems 2a and 2b).

Attempts to maintain a system in a precarious, unadapted (unadjusted) situation (*e.g.*, the practice of monocultures) would require enormous expenditures of energy. Such a situation may appropriately be labelled an “unsustainable” system or a system that has lost its global “integrity” or “health”. For example, the current human system modifies enormously its environment to increase material and energy flows available for its use via fertilisation, genetic modification, monocultures, pesticides, and other forms of environmental and biological manipulations. As the yield of plants and animals matter is being aggressively increased, the total metabolic flows (*i.e.*, respiration rates) are also being elevated while the total system storage (standing biomass) of all organisms is being depleted. The creation of such a persistently diminished local-order system (high R/B system), will lead to less resistant, more resilient ecosystems.

There exists one final layer of complexity in these matters that must be here addressed: the interaction between local and global stability (Figure 3.6a). Influences that are locally stabilising

can be globally destabilising. This is because the unique historical and compositional nature of an isolated system may exist in a locally stable or semi-stable state (*sensu* Byers and Hansell 1992) but simultaneously in a globally unstable state. There is a decoupling between how variations in the state variables influence the global and local stability of systems. The potential for locally stabilising influences to be antagonistic to global stability (*e.g.*, consider the attempt to maintain boreal forests even though climate changes to another climatic regime) and vice versa (*e.g.*, see Figures 3.6a, 3.6b) represents a particularly important issue in the management context and as such great care must be taken in any attempts at remediation.

The determination of these relationships and breakpoints at both local (ecological) and global (evolutionary) scales would be the critical task that needs to be addressed. Any attempts to ameliorate the sustainability or integrity of systems must make explicit reference to the locally and globally “expected” state of such systems. We must therefore focus our efforts at delineating acceptable distances from, or ranges in the locally and globally expected states, such that the adaptive capacity of the system is compatible with our own tolerances for environmental uncertainty. We must be critically aware of the biota and environment that can catalytically modulate these state variables (*i.e.*, “keystone” species) and appreciate the delicate nature of any tenuous balance within which we exist, as we continue to grapple with the health of our environment and our selves.

ACKNOWLEDGEMENTS

The many insightful thoughts of Nathalie Saint-Jacques, Roger I.C. Hansell, Henry Regier, James J. Kay, Pierre Legendre, L. Van Valen, Brian Fath and an anonymous reviewer were sincerely appreciated. This work is dedicated to three special children whose lives were lost all too early, but whose loving memory will continue to inspire.

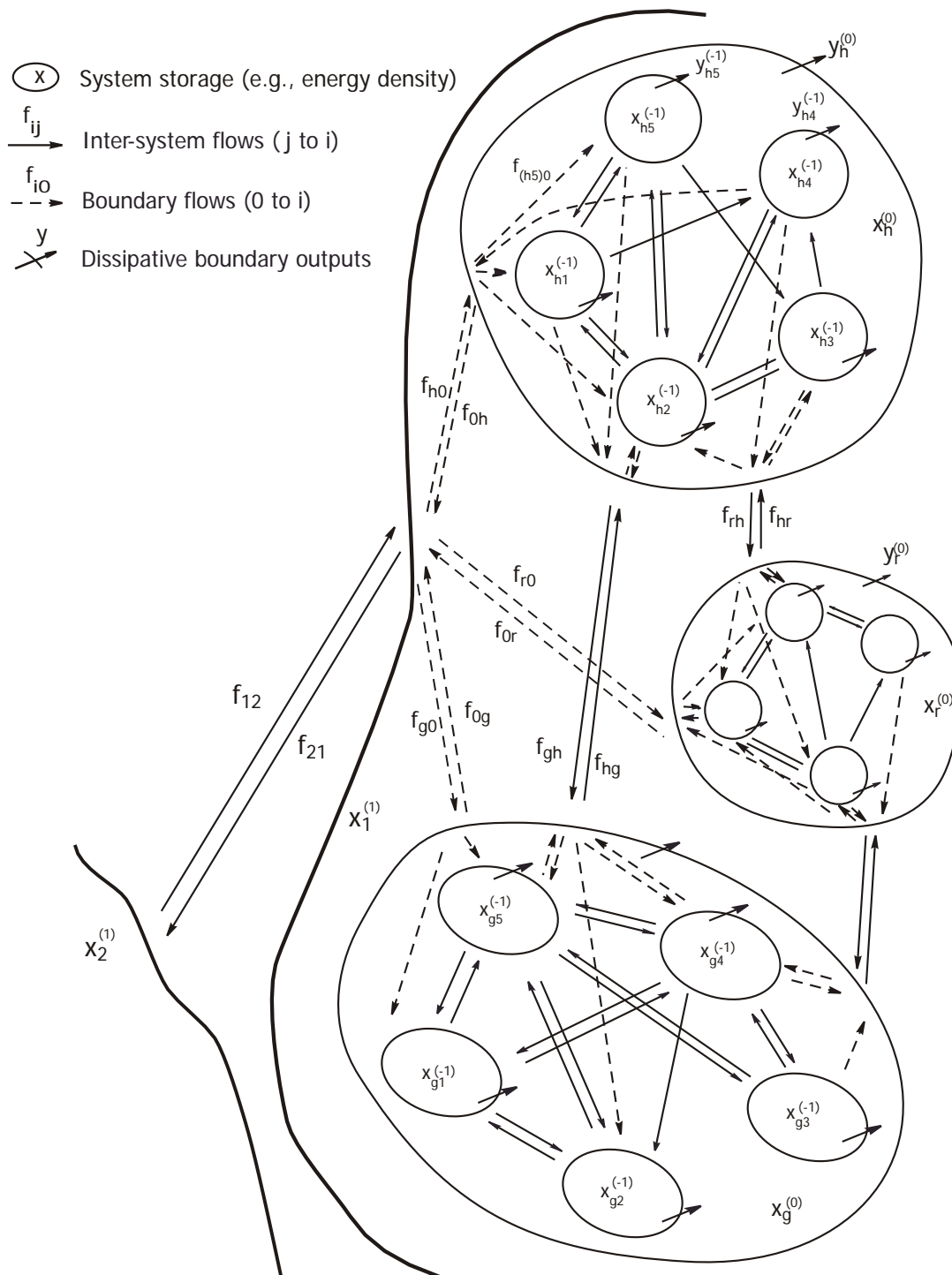


Figure 3.1. Conceptual schematic depicting the storage and flows between systems of various hierarchical levels. Subscripts identify systems and superscripts identify hierarchical level. Boundary outputs are represented by, y ; system storage by, x .

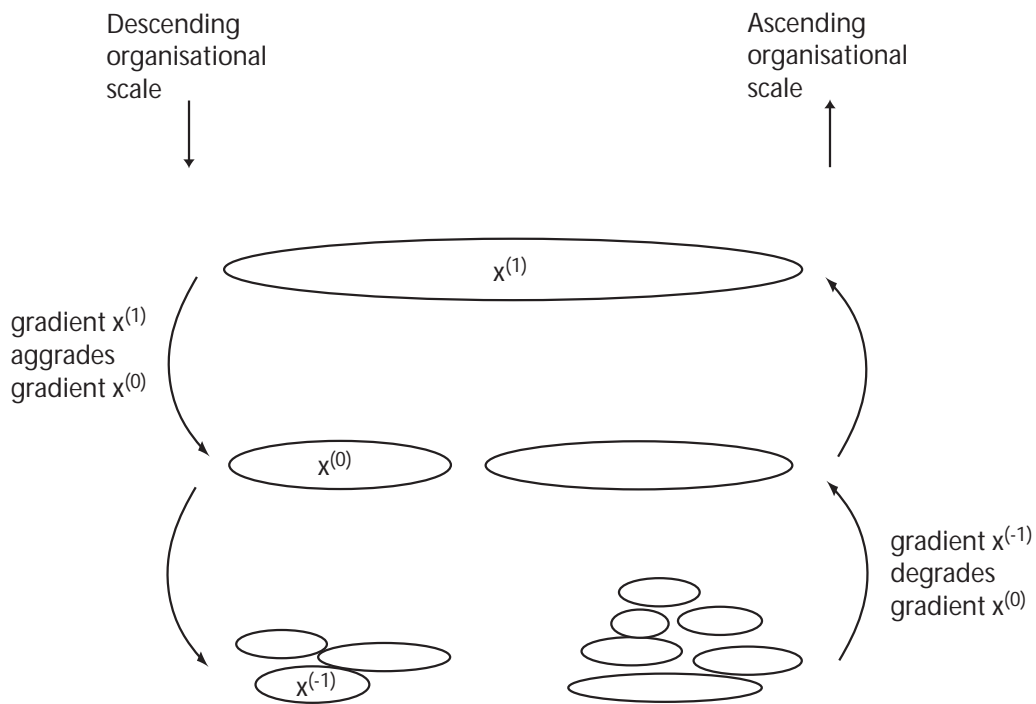


Figure 3.2. A schematic showing the fractal-like, asymmetrical influence of the Second Law of Thermodynamics as one ascends or descends spatial-temporal-organisational scales. The existence of a gradient at the super-system level $x^{(1)}$ creates and aggrades the gradients of system $x^{(0)}$ which in turn creates and aggrades gradients of its sub-system $x^{(-1)}$. This cascading sequence as one descends the holarchical/hierarchical scale may be termed the propensity for "local-order"—that gradients from the nesting system $x^{(1)}$ help to increase the structure (storage) and function (flows) of the focal system $x^{(0)}$. As one ascends spatial-temporal-organisational scales, the gradients and associated flows of sub-system $x^{(-1)}$ act to degrade the gradients $x^{(0)}$ that cause them which in turn act to degrade the gradient $x^{(1)}$. This process of gradient degradation may be termed the propensity for "local-disorder". Any system $x^{(0)}$ exists in a dynamic interplay between local-ordering and local-disordering processes. This characteristic balance is quantifiable and related to other structural and dynamical properties of the system. See text for more details. Lateral and cross-holarchical interactions are ignored for simplicity but similarly influence the balance between local-order and local-disorder.

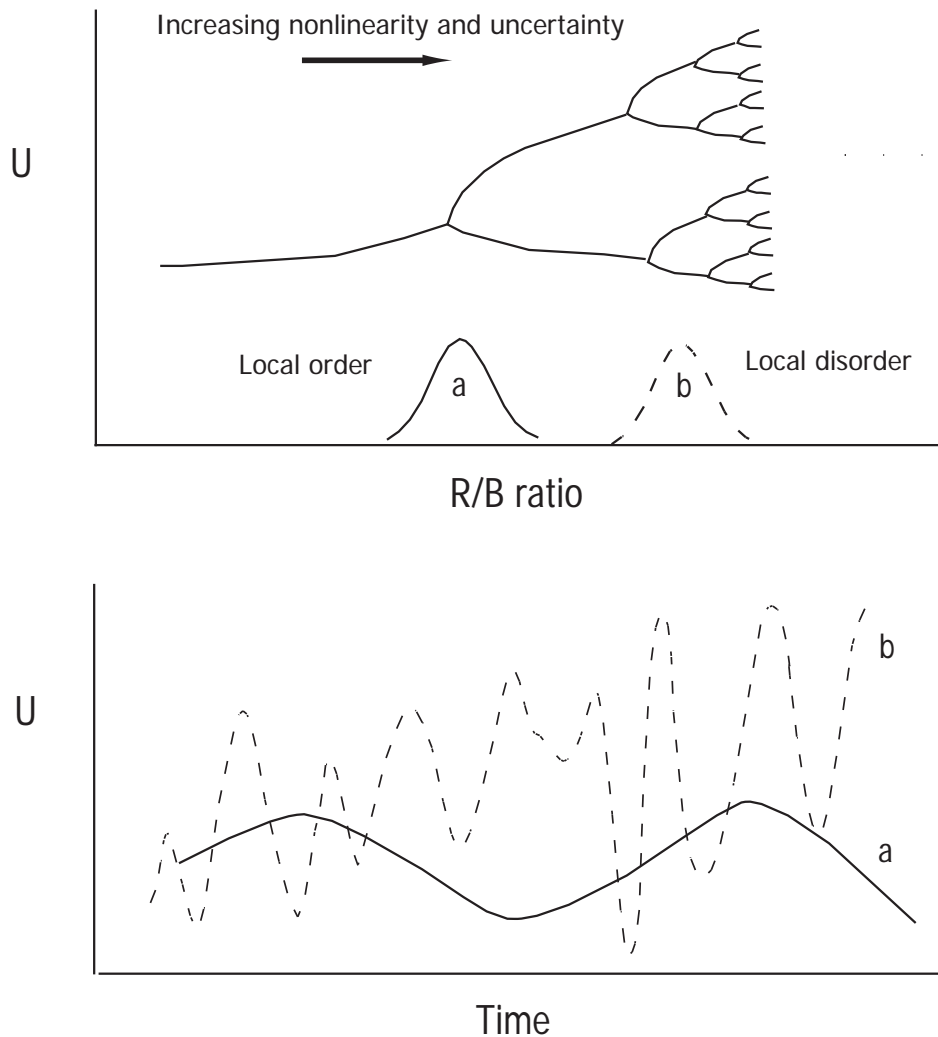


Figure 3.3. A bifurcation sequence is shown in the top panel. The state variable "U" (*e.g.*, biomass or storage, respiration rate, numerical abundance) of a given system as a function of the R/B ratio. As the magnitude of the intensity of energy dissipation (R/B) increases, the linear approximation of the gradients and flows breaks down and nonlinear dynamics become important. Increasing complexity of the attractive region is heuristically represented as this classical bifurcation sequence. Increased R/B ratios (*e.g.*, system b, reflecting increased local-disorder due to perturbing interactions with other systems of all hierarchical levels) increases system uncertainty (the attractive set is more complex—the Boltzmann entropy increases). Such a sequence is diagrammed in the time domain in the bottom panel. Modified from Choi *et al.* (1999).

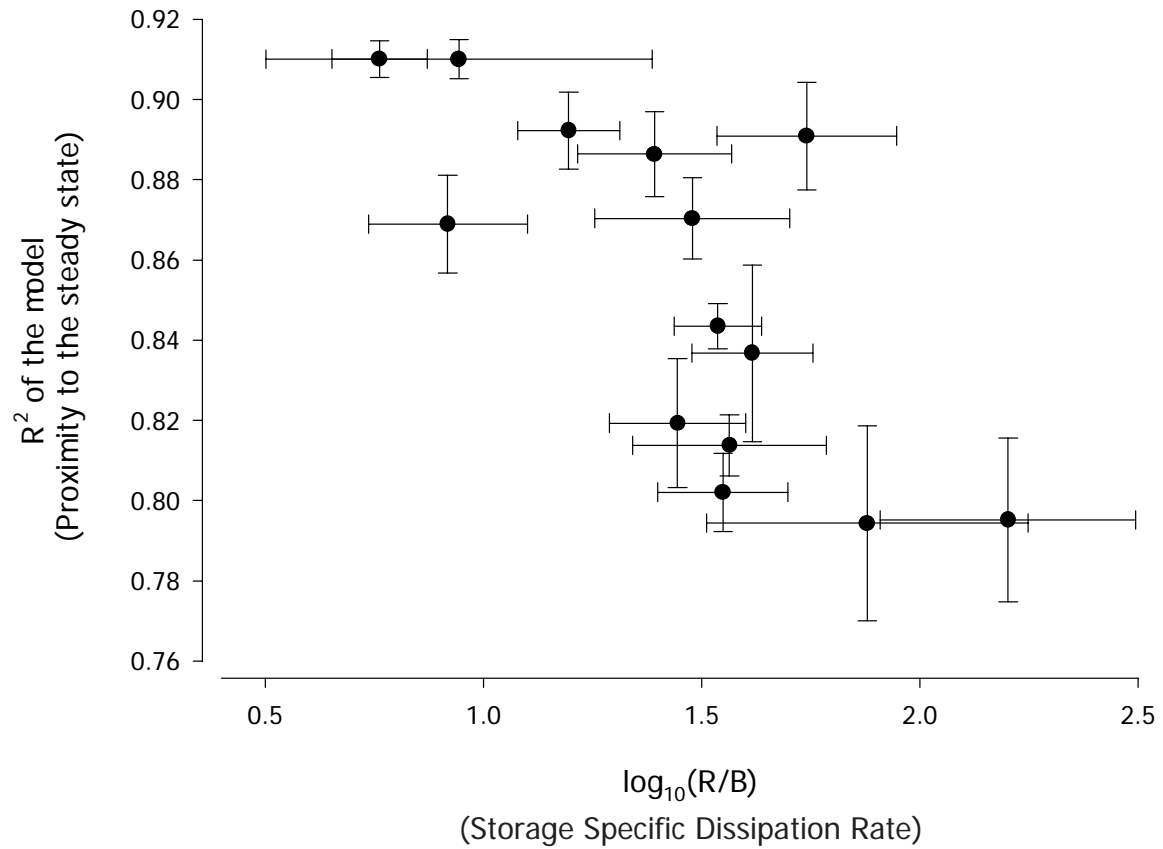


Figure 3.4. Dynamical/structural determination of a system (the R^2 of the size-abundance relationship, after log-log transformation) as a function of the specific dissipation rate of limnoplankton (units of yr^{-1}). ($1-R^2$) thus represents the degree of non-determination (variability), or more simply the degree of perturbation of the size-abundance relationship. Note the statistically significant negative correlation ($R^2_{\text{Pearson}} = 0.541$, $n=14$, $p=0.002$). Modified from Choi *et al.* (1999).

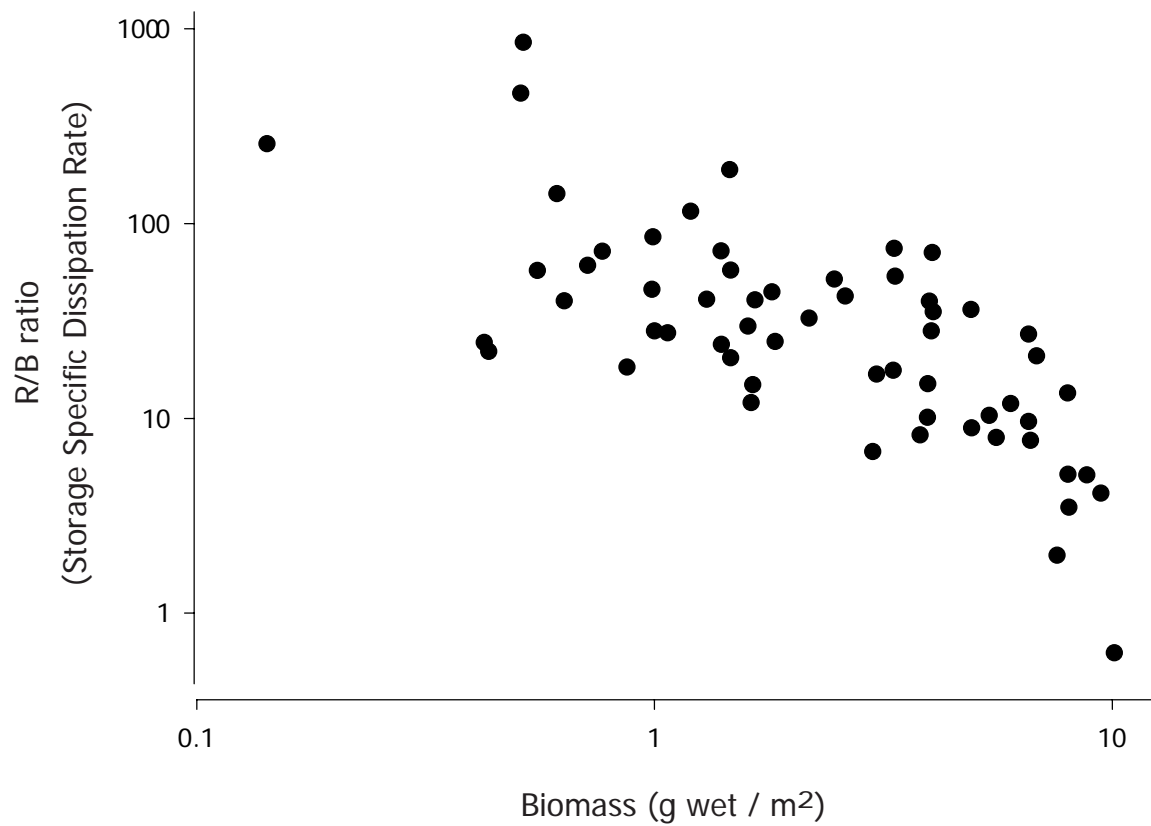


Figure 3.5. Respiration to biomass ratio (R/B ; units of yr^{-1}) as a function of the standing biomass (\sim carrying capacity) of limnoplankton. Increases in the carrying capacity should dimensionally reduce the storage-specific dissipation, which in turn indicates a decrease in long-term dynamical variability of the system. Data from a subset of Canadian Shield lakes, modified from Choi *et al.* (1999).

metabolic rates (Peters 1983). Due to this constraint, high resilience systems (*e.g.*, system 1—with a high R/B ratio) are also low resistance systems (low biomass); and low resilience systems (*e.g.*, system 3—with a low R/B ratio) are also more resistant systems (high biomass). Any local deviations from this pattern (*e.g.*, system 4) represents a globally unstable situation and a return towards the global pattern becomes more probable. Within each system, local deviations from the system-specific expected behaviour represents a more ecologically unstable situation. As can be seen, ecologically (local) and evolutionarily (global) favoured directions for change can be antagonistic or mutualistic, depending upon the specific configuration of the system concerned. In the Bottom panel, systems marked with an asterisk (*) represent order of magnitude estimates; italicised systems indicate the relative magnitude of the net primary production (NPP) of representative systems and so serves to approximately delineate the lower bound of community respiration rates for each representative system. The codes are structured as follows: [ecological type].[climatic region].[ID number]. Climatic regions: Te=temperate; Tr=tropical; Ar=arctic; Bo=boreal. Ecological types: E=estuary/brackish water; L=whole lake; P=freshwater pelagic; Lit=littoral; M=marine pelagic; Sh=continental shelf; CR=coral reef; R=river; Tu=tundra; Gr=grassland; Cul=culture; and F=forest.

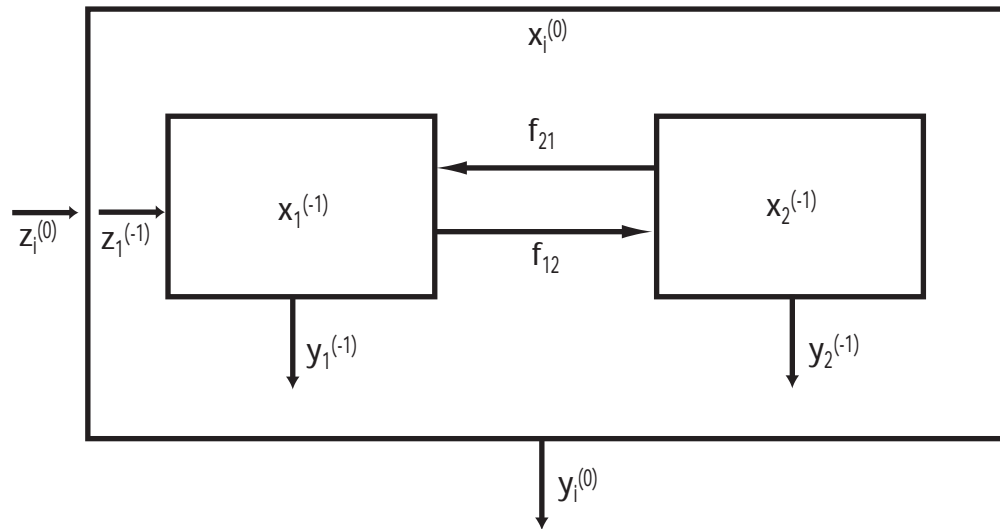


Figure 3.7. A simple system with two subsystems. See Appendix 2 for discussion.

Table 3.1. Linear regression parameters of the relationship between \log_{10} (numerical abundance) vs. \log_{10} (organism size). Data were obtained from the literature (details in Choi *et al.* 1999), and ranked in order of R^2 , the coefficient of determination of the relationship. Deviations from the log-linear state have been shown to be representative of systems that are perturbed (Choi *et al.* 1999). When the deviations are large, this is generally due to large fluctuations in the abundance of organisms, which indicates a system that is dynamically and structurally more variable. Thus, the relative placement of each ecosystem type along the sequence is an index of the relative degree of perturbation of that system. All relationships are statistically significant ($p < 0.0001$).

	INTERCEPT	SLOPE	R^2	N
MARINE PELAGIC	-0.278	-1.053	0.971	44
GREAT LAKES	-0.289	-1.006	0.965	182
BENTHIC SYSTEMS	0.339	-0.899	0.930	159
CANADIAN SHIELD LAKES	-0.832	-0.991	0.898	288
EUTROPHIC/SHALLOW LAKES	-1.621	-0.975	0.755	308
INTERTIDAL	1.831	-0.782	0.520	50

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LEAST SPECIFIC DISSIPATION

The Least specific dissipation principle is a thermodynamic criterion of evolution. It applies to systems that experience a weak and continuous energy gradient. Developed by Onsager (1931a,b), Prigogine (1955), Glansdorff and Prigogine (1971), Prigogine and Nicolis (1971), the principle specifies that any general energy dissipating system, in the face of a small but continued energy gradient, will tend towards a state of least specific energy dissipation. The proof of this principle is as follows:

The mass-specific rate of entropy change in a system (ds/dt) may be partitioned into two terms: the mass-specific rate of entropy production due to irreversible processes inside the system (i); and the mass-specific rate of entropy flow due to an exchange between the system and the external environment (e):

$$(1) \quad ds/dt = d_i s/dt + d_e s/dt$$

The entropy production ($d_i s/dt$) cannot be directly measured, but it is constrained to be larger than 0, due to the Second Law of thermodynamics. There are no such constraints for the entropy flow ($d_e s/dt$) but it may be approximated by heat calorimetry as specific heat dissipation or simply as the ratio of community respiration to biomass (R/B ratio; see footnote 11 in Appendix 2C). The general observation that increased order is found in living systems may be attributed to the dominance of the entropy transferred to the environment over the entropy production inside the system (*i.e.*, $|d_e s/dt| > |d_i s/dt|$). This is found to be generally true except perhaps under extremely rapid periods of biological activity (Lurié and Wagensberg 1979; *e.g.*, the earliest stages of embryonic activity, or immediately after a large-scale perturbation) when $d_i s/dt$ can also be large due to intensive growth and differentiation. As one approaches some quasi-stationary (steady) state ($ds/dt \approx 0$), the entropy production may be approximated with greater validity by the entropy flow ($d_i s/dt \approx -d_e s/dt$; *i.e.*, the R/B ratio).

The specific entropy production ($d_i s/dt$) can be represented as the sum of the product of flows (J) and forces (X) for all irreversible biological processes (k):

$$(2) \quad d_i s/dt = \sum_k (J_k / X_k)$$

The power series expansion of these flows (J) with respects to the forces (X) near some local steady state is given by:

$$(3) \quad J_k(\{X_m\}) = J_k(0) + \sum_m (\partial J_k / \partial X_m)_0 X_m \\ + \frac{1}{2} \sum_{mn} (\partial^2 J_k / \partial X_m \partial X_n)_0 X_m X_n \\ + \text{higher order terms} \dots$$

which when linearised becomes:

$$(4) \quad J_k = \sum_m L_{km} X_m$$

where, $L_{km} = (\partial J_k / \partial X_m)_0$ are the so-called “phenomenological coefficients”. In the steady state with respect to variations in the forces (X), the cross coefficient are equal ($L_{km} = L_{mk}$) due to the so-called “Onsager reciprocal relations” (Onsager 1931a,b). The entropy production term of equation 2 thus becomes simplified to:

$$(5) \quad d_i s / dt = \sum_{km} (L_{km} X_k X_m)$$

In the case of k=2 irreversible processes, equation 5 becomes:

$$(6) \quad d_i s / dt = L_{11} X_1^2 + 2 L_{12} X_1 X_2 + L_{22} X_2^2 \geq 0$$

where $L_{12} = L_{21}$ due to the Onsager relation. The inequality $d_i s / dt > 0$ is due to the Second Law of thermodynamics. The derivative of the entropy production with respects to the force X_2 is:

$$(7) \quad \partial (d_i s / dt) / \partial X_2 = 2 (L_{21} X_1 + L_{22} X_2) = 2 J_2$$

Since the system is near a steady state, $J_2 = 0$ and as $d_i s / dt \geq 0$, $d_i s / dt$ has an extremum which is a minimum. This means that the thermodynamic steady state of a system in the presence of a weak energy gradient is characterised by a local minimum in the specific rate of entropy production.

ENVIRONS AND NETWORKS

A. DYNAMIC MODEL

Conservative (energy or matter) flows and storages within an n^{th} order dynamical system can be decomposed via differential or difference equation descriptions into n input environs or n output environs, where n is the number of intrasystem components whose storages (*e.g.*, biomass or energy density), x_k , $k = 1, \dots, n$, serve as state variables. An n -component system has $2n$ environs within it. Half of these are output environs, propagating forward in time from boundary inputs (\mathbf{z}) to boundary outputs:

$$(1a) \quad d\mathbf{x}/dt = \mathbf{F} \mathbf{w} + \mathbf{z} = \mathbf{0} \quad (\text{at steady state})$$

The other half are input environs, traceable backward in time to boundary inputs from boundary outputs (\mathbf{y}):

$$(1b) \quad d\mathbf{x}/dt = -\mathbf{F}^T \mathbf{w} - \mathbf{y} = \mathbf{0} \quad (\text{at steady state})$$

By boundary flows, we refer to the flows that do not go to other systems of the same hierarchical level but rather to environmental sources and sinks that represent the next larger hierarchical level of organisation (see Figure 3.1). A useful perspective is that boundary inputs originate output environs (1a) and boundary outputs are terminals of input environs (1b). Boldfaced symbols indicate matrices or vectors. The state vector is $\mathbf{x}_{nx1}^{(0)} = (x_k^{(-1)})$, with energy dimensions $[\text{ML}^2\text{T}^{-2}]$. Parenthesised superscripts will, when used, denote hierarchical level. For example, $\mathbf{x}^{(0)}$ above applies to the focal, whole-system level and $x_k^{(-1)}$ refers to this system's k 'th component; a $^{(+1)}$ superscript would refer to the $\mathbf{x}^{(0)}$ -system's environment. The first time derivative is $d\mathbf{x}/dt$, dimensioned $[\text{ML}^2\text{T}^{-3}]$; these dimensions denote power. $\mathbf{F}_{n \times n} = (f_{kj})$ is a matrix of conservative energy flows $[\text{ML}^2\text{T}^{-3}]$ from components j to k , where $j, k = 1, \dots, n$; the principal diagonal elements are corresponding total flows, or throughflows, through each component k : $f_{kk} = -T_k = -\sum_{j(\neq k)=1}^n f_{kj}$. $\mathbf{w}_{nx1} = (1_k)$ is a vector of ones [dimensionless, 1], and $\mathbf{0}_{nx1} = (0_k)$ a vector of zeros (with power dimensions). $\mathbf{z}_{nx1} = (z_k)$ is a vector of boundary inputs, with dimensions of power $[\text{ML}^2\text{T}^{-3}]$. $\mathbf{y}_{nx1} = (y_k)$ is a vector of boundary outputs, also dimensioned $[\text{ML}^2\text{T}^{-3}]$.

B. ENVIRON THEORY

In the theory of environs, which defines environments as interactive networks, every open system at any level of organization has associated with it two environments, one afferent (input environment, derived from equation 1b) and the other efferent (output environment, derived from equation 1a). These two environments together with their defining system are, at any given moment, partition elements (*i.e.*, identifiers) of physical reality. This means that in the input

environment of a system, at some present (or usually initial) time, resides an infinite regress of events and interactions receding backward to the beginning of time. These events and interactions are uniquely associated at that time with that system and none other. On the output side, a unique future of events and interactions is uniquely generated by the system moment by moment. These have their origins at that time with that system and none other. Thus, unique portions of both pasts and futures in the universe come to a focus on each existent open system, and the three units together are inseparable, as given by the sufficient conditions of openness (for matter) and nonisolation (for energy).

The environments of component-level systems, say $x_k^{(-1)}$ (see Figure 3.7, where $k = \{1, 2\}$), can be traced within the boundaries of the focal-level systems, say $x_i^{(0)}$, in which they are members because it is these that are fully described by dynamical equations like (1a), and less frequently, (1b). In other words, the infinite regresses to past and future inherent in the concept of system-defined environments are truncated at the boundaries of the next-higher-level systems; the indefinite environments of $x_k^{(-1)}$, say, are cut off at the border of the encompassing system, $x_i^{(0)}$, and because this system is fully described (*e.g.*, equations 1a, b) so can be (as truncated "environs") its $k = 1, \dots, n$ components' n input and n output environments, giving $2n$ environs in all. The sets of input environs of all the component parts within the entire system comprise a partition of the whole into n nonoverlapping units. Similarly, the set of output environs forms a second such partition.

Environs are explicit networks that carry energy and matter around the established circuits of ecosystems. Output environ analysis concerns the mapping of boundary inputs generated outside the whole-system level, $z_i^{(0)}$, into throughflows, $T_k^{(-1)}$, and storages, $x_k^{(-1)}$, associated with component-level systems. Input environ analysis backtraces boundary outputs, $y_i^{(0)}$, to their throughflows, $T_k^{(-1)}$, and storages, $x_k^{(-1)}$, of origins. In both cases it is the tracing over direct and indirect pathways in the intrasystem⁽⁰⁾ network that is of interest because it reveals the importance of network indirect effects, as discussed in the Introduction.

For throughflow analysis, equations (1) are converted to the forms:

$$\begin{aligned} (2a) \quad d\mathbf{x}/dt &= (\mathbf{G} - \mathbf{I}) \mathbf{T} + \mathbf{z} = \mathbf{0} & (\text{at steady state}) \\ (2b) \quad d\mathbf{x}/dt &= -(\mathbf{G}' - \mathbf{I}) \mathbf{T} - \mathbf{y} = \mathbf{0} & (\text{at steady state}) \end{aligned}$$

where, $\mathbf{G}_{n \times n} = (g_{kj}) = (f_{kj}/T_j)$, $\mathbf{G}'_{n \times n} = (g_{kj}') = (f_{kj}/T_k)$, and $\mathbf{T}_{n \times 1} = (T_k)$ is the vector of throughflows; \mathbf{I} is the identity matrix; $g_{kk} = g_{kk}' = 0$. Letting $\mathbf{N}_{n \times n} = (\mathbf{I} - \mathbf{G})^{-1}$ and $\mathbf{N}'_{n \times n} = (\mathbf{I} - \mathbf{G}')^{-1}$, the forward- and back-mappings of inputs and outputs, respectively, to throughflows are given by:

$$\begin{aligned} (3a) \quad \mathbf{T} &= (\mathbf{I} + \mathbf{G} + \mathbf{G}^2 + \dots + \mathbf{G}^m + \dots) \mathbf{z} = \mathbf{Nz} \\ (3b) \quad \mathbf{T} &= (\mathbf{I} + \mathbf{G}' + \mathbf{G}'^2 + \dots + \mathbf{G}'^m + \dots) \mathbf{y} = \mathbf{N}'\mathbf{y} \end{aligned}$$

boundary	direct	indirect
inputs	flows	flows
($m = 0$)	($m = 1$)	($m > 1$)

In both cases, in environs with well-developed networks, the sums of terms with powers $m = 2$ usually significantly exceed the direct-flow term, where $m = 1$. Throughflow-specific output environs are computed from \mathbf{N} , and input environs from \mathbf{N}' .

For storage analysis, equations (1) are converted to the forms:

$$\begin{aligned} (4a) \quad d\mathbf{x}/dt &= \mathbf{C}\mathbf{x} + \mathbf{z} = \mathbf{0} && \text{(at steady state)} \\ (4b) \quad d\mathbf{x}/dt &= -\mathbf{C}'\mathbf{x} - \mathbf{y} = \mathbf{0} && \text{(at steady state)} \end{aligned}$$

where $\mathbf{C}_{n \times n} = (c_{kj}) = (f_{kj}/x_j)$, $\mathbf{C}'_{n \times n} = (c'_{kj}) = (f_{kj}/x_k)$, and $\mathbf{x}_{n \times 1} = (x_k)$ is the vector of storages; $c_{kk} = c'_{kk} = -\tau_k^{-1}$, the turnover rate of the k 'th subsystem. Letting $\mathbf{Q}_{n \times n} = -\mathbf{C}^{-1}$ and $\mathbf{Q}'_{n \times n} = -\mathbf{C}'^{-1}$, the forward- and back-mappings of inputs and outputs, respectively, to throughflows are given by:

$$\begin{aligned} (5a) \quad \mathbf{x} &= -\mathbf{C}^{-1} \mathbf{z} \\ (5b) \quad \mathbf{x} &= -\mathbf{C}'^{-1} \mathbf{y} \end{aligned}$$

Because \mathbf{C} and \mathbf{C}' are dimensional, $[T^{-1}]$, power series like (3a, b) cannot be formed. To achieve these, nondimensional coefficients are constructed as $\mathbf{P} = \mathbf{I} + \mathbf{C}\Delta t$ and $\mathbf{P}' = \mathbf{I} + \mathbf{C}'\Delta t$, where Δt is a discrete-time interval. Then, the (5a, b) mappings of inputs and outputs, respectively, into storages can be written:

$$\begin{aligned} (6a) \quad \mathbf{x} &= (\mathbf{I} + \mathbf{P} + \mathbf{P}^2 + \dots + \mathbf{P}^m + \dots) \mathbf{z} = (\mathbf{Q}\Delta t) \mathbf{z} \\ (6b) \quad \mathbf{x} &= (\mathbf{I} + \mathbf{P}' + \mathbf{P}'^2 + \dots + \mathbf{P}'^m + \dots) \mathbf{y} = (\mathbf{Q}'\Delta t) \mathbf{y} \end{aligned}$$

boundary	direct	indirect
inputs	flows	flows
($m = 0$)	($m = 1$)	($m > 1$)

As with throughflows, in environs with well-developed networks the sums of terms with powers $m = 2$ usually greatly exceed the direct-flow term, where $m = 1$. Storage-specific output environs are computed from \mathbf{Q} , and input environs from \mathbf{Q}' .

C. LINEARISED THERMODYNAMICS OF HEIRARCHICAL NETWORKS

To better understand the relevance of the Second Law to dynamical system networks, an algebra of needed concepts is presented below. Due to generality of the environ formalism, we will deviate from the standard thermodynamic approach by making no reference, suggestion, or assumption as to the reductionistic form of the transport and reaction processes involved (e. g., diffusion, heat flow, temperature change, electron or ion transport, *etc.*). We treat each system at any level as a complex set of reaction processes that are phenomenologically summarised in terms of their associated flows and gradients (also known as "forces"), and these relate to the dynamical equations. This amounts to a simple application of nonequilibrium, near-linear thermodynamics as developed and elaborated by Onsager 1931(a,b), De Donder and Van Rysselberghe 1936, Prigogine 1947, Spanner 1964, Katchalsky and Curran 1967, and Glansdorff and Prigogine 1971, among others.

Let S be the entropy of a system $x_i^{(0)}$, and dS/dt its rate of change. The storage-specific rate of change can be partitioned into two terms: entropy production by internal irreversible processes, $d_{\text{int}}S$, and boundary exchange of entropy between the system and its external environment, $d_{\text{ext}}S$:

$$(7) \quad dS/dt = d_{\text{int}}S/dt + d_{\text{ext}}S/dt$$

The storage-specific rate of entropy production, $d_{\text{int}}S/dt \equiv d_{\text{int}}s/dt$, cannot be measured directly, but it is constrained by the Second Law of Thermodynamics to be > 0 . No such constraint exists for the specific rate of entropy flow, $d_{\text{ext}}S/dt \equiv d_{\text{ext}}s/dt$. However, this quantity can be

approximated by calorimetry³ as storage-specific heat dissipation, $\sum_{k=1}^n y_k^{(-1)} / \sum_{k=1}^n x_k^{(-1)}$. For living

systems, this latter quantity is conveniently measured as the ratio of respiration to biomass (R/B ratio; Choi *et al.* 1999).

Increased order in living systems is generally attributed to the dominance of entropy transferred to the environment over internal entropy production, $|d_{\text{ext}}S/dt| > |d_{\text{int}}S/dt|$. This is generally true except under periods of rapid biological activity (*e.g.*, early stages of embryonic development, or immediately after a strong perturbation; Lurié and Wagensberg 1979). Then, $d_{\text{int}}S/dt$ can also be large due to intensive growth and differentiation. The closer the approach to some local steady state, $dS/dt = 0$, such that from equation (7), $d_{\text{int}}S/dt = -d_{\text{ext}}S/dt$, the closer can specific entropy production due to irreversible processes within the system ($d_{\text{int}}s/dt$) be approximated by the specific rate of entropy flow to the exterior ($-d_{\text{ext}}s/dt$). (We emphasise that we are focussing upon a local (quasi) steady state, relevant to the characteristic space, time and organisational scales of the system being treated).

For each component-level (local) system, say $x_k^{(-1)}$ within a focal (global) system $x_i^{(0)}$, the net storage specific flow through the local system, J_k dimensioned $[T^{-1}]$, can be expressed as the sum of a function, F , of all the $j = 1, \dots, n$ gradients, X_j , with which x_k directly or indirectly interacts (*e.g.*, see Figure 3.7). That is:

$$(8a) \quad J_k = \sum_{j=1}^n F(X_j)$$

which, when linearised near some local steady state, gives:

$$(8b) \quad J_k = L_{k1}X_1 + L_{k2}X_2 + L_{k3}X_3 + \dots + L_{kk}X_k + \dots + L_{kn}X_n$$

³ Fundamentally, the relationship between entropy production (dS) and heat transfer (dQ) is: $dS = dQ * 1/T$; where T is temperature (Kelvin). Because of the influence of temperature, the measurement of metabolic waste heat production as index of entropy production ("dissipation", sensu Prigogine 1955; "irreversibilities", sensu Professor J.J. Kay, pers. comm., University of Waterloo) is truly valid when temperature is constant. In the range of application of the freshwater lakes studied in the thesis, temperatures ranged from about 10 to about 22 degrees Celsius at the surface. The maximum "error" attributable to these temperature variations represents an error of $1/(273+10) = 0.0035$ to $1/(273+22) = 0.0034$, or about 3% to 4% error. Relative to the methodological errors in the determination of respiration rates and field sampling errors (*e.g.*, Appendix 3), this amounts to a negligible effect. What this means is that for most biological applications, the waste heat measured represents a pragmatic and easily measured index of entropy production rates ("irreversibility", sensu Kay).

or more compactly,

$$(8c) \quad J_k = \sum_{j=1}^n L_{kj} X_j$$

The L_{kj} parameters, termed phenomenological coefficients, represent empirically determined constants of proportionality for the relative influence of the gradients $X_j^{(-1)}$, for all $j=1, \dots, n$ component-systems upon the flow $J_k^{(-1)}$ through component-system $x_k^{(-1)}$.

The gradients $X_j^{(-1)}$ may be represented as a function of their storage $x_j^{(-1)}$, which when linearised near the steady state, gives:

$$(9) \quad X_j = k_j x_j$$

where k_j is a proportionality constant. Thus, when linearity assumptions are appropriate, the gradients X_j may be considered proportional to the storage x_j of a component-level system.

Using these quantities, the irreversible storage-specific dissipation rate, $d_{\text{int}} s^{(0)}/dt$, of the focal system $x_i^{(0)}$ may be represented as the sum of products of storage specific through flows, J_k , and gradients, X_k , for all $k = 1, \dots, n$ sets of irreversible processes making up the interior of the focal system:

$$(10a) \quad d_{\text{int}} s^{(0)}/dt = \sum_{k=1}^n J_k X_k$$

Or, represented alternatively as a function of the gradients using equation (8c), the storage-specific dissipation rate of the overall system becomes the sum of products of the internal gradients, $(X_k X_j)$, and their cross-couplings (L_{kj}):

$$(10b) \quad d_{\text{int}} s^{(0)}/dt = L_{11} X_1^2 + L_{12} X_1 X_2 + L_{13} X_1 X_3 + \dots + L_{1n} X_1 X_n \\ + L_{21} X_2 X_1 + L_{22} X_2^2 + L_{23} X_2 X_3 + \dots + L_{2n} X_2 X_n \\ + L_{31} X_3 X_1 + L_{32} X_3 X_2 + L_{33} X_3^2 + \dots + L_{3n} X_3 X_n \\ \dots \\ + L_{n1} X_n X_1 + L_{n2} X_n X_2 + L_{n3} X_n X_3 + \dots + L_{nn} X_n^2$$

In the neighbourhood of linear relations between the flows (J_k) and gradients (X_k), and given the applicability of Onsager's reciprocal relations, $L_{kj} = L_{jk} \forall j, k$, this simplifies to:

$$(10c) \quad d_{\text{int}} s^{(0)}/dt = L_{11} X_1^2 + 2 L_{12} X_1 X_2 + 2 L_{13} X_1 X_3 + \dots + 2 L_{1n} X_1 X_n \\ + L_{22} X_2^2 + 2 L_{23} X_2 X_3 + \dots + 2 L_{2n} X_2 X_n \\ + L_{33} X_3^2 + \dots + 2 L_{3n} X_3 X_n \\ \dots \\ + L_{nn} X_n^2$$

or more compactly:

$$(10d) \quad d_{\text{int}} s^{(0)}/dt = \sum_{k=1}^n \sum_{j=1}^n L_{kj} X_k X_j, \quad \text{where } L_{kj} = L_{jk} \forall j, k$$

Alternately, by substitution with equation (9), we obtain an expression of the specific dissipation rate of the focal system in terms of the storage of the component-systems:

$$(10e) \quad d_{\text{int}} s^{(0)}/dt = \sum_{k=1}^n \sum_{j=1}^n L_{kj}^* x_k x_j$$

where $L_{kj}^* = L_{kj} x_j$ and $L_{kj}^* = L_{jk}^* \forall j, k$. These phenomenological coefficients L_{kj}^* are therefore analogous to the community (interaction) matrix of ecological communities in that they indicate the relative influence of one system upon another. The only difference being that the state variables, x , are represented as the storage (biomass) of systems and not the numerical abundance of species.

Because $d_{\text{int}} s^{(0)}/dt$ is constrained by the Second Law to be > 0 , the following algebraic constraints upon the phenomenological coefficients may be recognised (*e.g.*, see Katchalsky and Curran 1967, p. 91):

1. $L_{kk}^* x_k^2 > 0$; all L_{kk} (interpreted as "conductivities", or "permeabilities") are positive-valued since any x_j can be made to vanish.
2. $L_{kk}^* L_{jj}^* > L_{kj}^2$; the magnitudes of cross-coupling coefficients, L_{kj}^* ($k \neq j$), are limited by the magnitudes of the conjugate coefficients, L_{kk}^* and L_{jj}^* . This is because the determinant of the matrix, $\mathbf{L}^* = (L_{kj}^*)$, of phenomenological coefficients must be greater than or equal to 0, $\det \mathbf{L}^* \geq 0$.

Consider, for example (Figure 3.7), a two-system interaction within a focal system $x_i^{(0)}$, where there is a continuous flow through the primary subsystem ($x_1^{(-1)}$), and the other ($x_2^{(-1)}$) is at steady state: $J_2 = 0$; $X_2 = k_2 x_2 = 0$. The specific dissipation rate for the whole system becomes (from equation 10a):

$$(11a) \quad d_{\text{int}} s^{(0)}/dt = J_1 X_1; \quad (\text{because } J_2 = 0)$$

or, in terms of storage:

$$(11b) \quad d_{\text{int}} s^{(0)}/dt = J_1 k_1 x_1$$

and gradient X_2 becomes a simple function of gradient X_1 because of the coupling of the two systems expressed by the phenomenological coefficients L_{21} and L_{22} of the output environ of $x_1^{(-1)}$ to the input environ of $x_2^{(-1)}$:

$$(12a) \quad J_2 = L_{22} X_2 + L_{21} X_1 = 0 \Rightarrow X_2 = -(L_{21}/L_{22}) X_1$$

or, in terms of storage,

$$(12b) \quad J_2 = L_{22}^* x_2 + L_{21}^* x_1 = 0 \Rightarrow x_2 = -(L_{21}^*/L_{22}^*) x_1$$

This result is important in that it shows how the primary gradient, the storage x_1 , "actively" displaces the secondary gradient x_2 away from the steady state (*i.e.*, "creates" storage) via the interaction coefficient L_{21}^* . This displacement is directly (and linearly) proportional to the magnitude of the primary gradient x_1 , and consequently causes an "active" flow ($J_2 = 0 \Rightarrow J_2 \neq 0$) through system x_2 . Indeed, what is especially interesting from the biological point of view is exactly when such "active" interactions moves a system to an ever increasing gradient (potential; *i.e.*, "aggradation"; Schrödinger 1945, Bertalanffy 1950, Spanner 1964, p. 261).

Due to the interaction between the two systems, the flow (J_1) is in turn reduced by an amount, $(L_{21}^* L_{12}^* / L_{22}^*) x_1$, where $L_{11}^* \geq L_{21}^* L_{12}^* / L_{22}^*$ (property 2, above):

$$(13) \quad J_1 = L_{11}^* x_1 + L_{12}^* x_2 = [L_{11}^* - (L_{21}^* L_{12}^* / L_{22}^*)] x_1$$

but the total dissipation of the whole system actually increases by a factor x_1 :

$$(14) \quad d_{\text{int}} S^{(0)} / dt = [L_{11}^* - (L_{21}^* L_{12}^* / L_{22}^*)] x_1^2$$

This means that interactions with other component-systems can alter a system's local flow (J_2) and as a consequence, the global entropy production. Any useful (or "ordering") effect of such interactions increases as a linear function of the primary gradient (x_1 ; equation 13), while the total rate of energy dissipation of the focal system, $x_1^{(0)}$, increases as the square of the primary gradient (x_1^2 ; equation 14) rather than simply as a linear function (equation 11b). Thus, any linear increase of the "local-order" of a system $x_k^{(-1)}$ will be associated with a quadratically increasing "cost" in the dissipation of gradients of the global system $x_i^{(0)}$ (that is, "global-Disorder"). This means that the creation and maintenance of local-order can be considered a thermodynamic mechanism by which global gradients are dissipated in accordance with the Second Law.

However, this "local-order" is also subject to Second-Law degradation, in a hierarchically recursive manner: Second Law dissipation at level $x_i^{(0)}$ creates local gradients in $x_k^{(-1)}$ while simultaneously being subject to the Second-Law degradation of the gradient in $x_k^{(-1)}$, which in turn creates local gradients in $x_l^{(-2)}$, and so on, ..., in a cascading sequence. There is therefore, a fundamental and cascading **asymmetry in the action of the Second Law** at different hierarchical levels.