Ecosystem homeostasis: stability in complex ecological networks

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June 25, 2025

Abstract

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Keywords – stability

1 Forward

This essay/paper is written for the non-specialist. It has been simmering for a long time. Since my doctoral work. Too long. It is offered here for the future students that wish to follow this curious path and for closure for me. There are so many paths and this is but one. But it might help you light the way forward in your endeavours.

My best wishes.

2 Introduction

Homeostatic control, or the lack thereof, represents the canonical problem in ecology. The core question is: how is the internal mileau regulated to be stable when the external environment is highly variable? Or, in the inward looking perspective: when do alterations to the internal structures and functions of a system result in the breakdown of its stability. Or, in the outward looking perspective: when do alterations in external perturbations regimes foster or reduce stability. At the organizational scale of organs and organisms, this is a well documented phenomenon (e.g., thermoregulation, ion regulation, hormone regulation). At larger organizational scales such as ecosystems, more than a century of effort has resulted in a great deal of controversies and confusion. Of course, many reasons exist for this confusion, but the two most formidable sources seem to be: (1) epistemology and (2) complexity. Before embarking upon a discussion of homeostasis, it is therefore prudent to examine these two important sources of confusion.

2.1 Epistemology

> In any formal system S, which is consistent, there can be a proposition which denies the provability of that proposition (of itself) within the system; i.e., the statement “this statement cannot be proven within S” can exist within S. Since this proposition can exist then it must be true, which denies its ‘not provable’ status, and therefore identifies an inconsistency within what is supposed to be a consistent system. Thus no formal system of propositions can be complete. (paraphrased from Gödel 193X)

Gödel’s incompleteness theorem (above) suggests that any formal system, that is, any rule-based system such as logic, mathematics, language, scientific theory, including ecological theory, can contain self-referential paradoxes. Self-referential paradoxes are statements whose truth is undecidable within the rules of that system. Or to put it another way, it is not possible to prove that the accepted body of laws and theories of a formal system of knowledge (i.e., its *rules*) are self-consistent by using the very same set of *rules*. The result is that there will always be certain core axioms or assumptions that cannot be proven to be true and so must be taken on “faith”, or at best as a consensus. In other words, circular, self-referential loops acts to bound the formal system itself!

Polite scientific society would understandably be troubled by the significant implications of Gödel’s incompleteness theorem. That their respective bullet-proof formal systems of scientific logic and reasoning can have unprovable axioms, that is, core or foundational statements, is unsettling, to say the least. Indeed, the sciences generally distinguish themselves from the non-scientific realms using this dividing line marked boldly in the sand, of whether there are inconsistencies, circular thoughts and “faith”-based core assumptions. That scientific domains may be similarly afflicted with inconsistent circularities, therefore, puts into question the very sanctity of the “Scientific Method”.

For example, the principle of *Competitive exclusion* is a central tenet of ecological thought. However, even when it was experimentally shown that competitive exclusion does not always happen (e.g., for *Drosophila* sp. by Ayala 1970), the Competitive exclusion principle was defended by Gause (1970) with the argument that the organisms tested had different niches and so did not represent a valid test. This latter statement demonstrates the intrinsic circularity or self-referential nature of the concept: If competition is not observed, it is because the organisms have different niches (Hardin 1960, McIntosh 1985:186). Thus, it is not possible to prove or disprove the importance of competition, using the formalisms/mechanisms associated with the principle of competitive exclusion. Instead, some other *external* (independent and more general) principle must be called upon to prove or disprove it; or one must have *faith* in the self-evident truth of Competitive exclusion or the niche concept.

Another such example is found in *Optimal foraging theory.* The central tenet here is that a currency relevant to lifetime reproductive success is optimized by organisms in determining behavioral choice (food selection). If the currency is found not to be optimized, it is assumed that the choice of the currency was inappropriate or incorrect. The correct currency is the one that is optimized! Another famous example of circularity of thought revolves around the most fundamental of biological principles, the concept of Natural selection. The formalism is that what is fittest will survive and reproduce. What is fittest is that which is most adaptive. And that which is most adaptive is that which is most fit to survive. Again, it is impossible to prove what is fit and what is not because fitness and survival refer to (and define) each other. To “prove” the existence of optimal foraging or natural selection, one must go beyond the confines of each formalism; or, believe in the self-evident truth of one or the other.

Another example of what may be considered such a circular concept is the very notion of ecological succession/climax: the observation that vegetational systems coherently change from some locally disturbed state (fire, storms) to some more regional stable state through a series of recognizable stages (i.e., larger spatial scales driven by climatic and evolutionary processes). Note the same difficulty: What is a climax state? A state to which a disturbed state evolves into. What is a disturbed state? A state which will change into a climax. Perhaps for obvious reasons, it has not been possible to confirm or refute the presence of ecological succession since the inception of the concept in the early 1900s (Tansley, Gleason, Wittaker), using the formal language and concepts internal to ecology. To "prove" the existence of ecological succession, one must go beyond the confines of ecological formalisms. The question being, what is this meta-formalism?

Reacting to some of the confusion caused by this intrinsic circularity of ecological ideas, some have gone so far as to suggest that they serve nothing but to confuse the real issues at hand, which should be the development of a "predictive", empirical science (e.g., Rigler 1975). However, intrinsic circularity does not mean that we must abandon all attempts at communication and comprehension; rather it means that axiomatic systems cannot be proved or disproved to be consistent within the formal logic of that system. That is, ecological concepts cannot be proved or disproved with ecological arguments. However, even though they may stand upon shaky theoretical foundations, many of these axiomatic systems function to some extent (though many may disagree), conveying information and serving a useful, albeit imperfect, function.

To reiterate, if proof or justification of a theory (e.g., some Grand Unified Theory) is required one must look to some more superseding set of principles (which by definition nullifies the "grand-unified-ness" of the original theory), with the implication that these superseding principles are themselves also bound to the very same limitations of logical incompleteness. For example, consider the progression from the world visions of Aristotle to Copernicus to Galileo to Kepler to Newton (Classical Mechanics) to Einstein (theories of Special Relativity to General Relativity) to Quantum Mechanics to Quantum Electrodynamics to Quantum Chromodynamics to String theory, where each body of knowledge and rules attempts to go beyond the constraints of the former. However, when a degree of consistency across so many superceding (hierarchical) sets of formal systems are observed as in this example, then one may have some reason to suggest that concepts and principles are converging upon some meta-stable set of more-or-less consistent set of formalisms.

2.2 Complexity: number, type and hierarchy in space and time

> Derived from the Latin *complexus* (*complecti*), meaning to embrace or entwine, connoting an aggregation of parts, where the relationships between parts is large in number and kind as in psychology, chemistry or ecology.

Admittedly, the importance of logical circularity is perhaps partially hidden from the fore of scientific consciousness by the sheer number of bits of information streaming from the application of the Scientific Method. This decidedly reductionist program has dismantled patterns and processes to ever finer and simpler mechanisms. Through continued refinements of measurements with increasingly precise and clever instrumentation, access to ridiculously powerful computers that only a generation ago were considered an impossibility, efficient data storage and increases in storage capacity to scales previously unimagined and ever more precise variations of statistical methods to detect patterns and estimate parameters, the scientific world is now awash with information and we suffer collectively from the incapacity to synthesize all this information into a meaningful whole – *information overload*.

This is especially the case in ecological systems where the sheer *complexity* of interactions between and within the biotic and the abiotic realms remains daunting to say the least. How does one begin to rebuild any notion of ecological homeostasis from the overwhelming information about competition, predation, disease, selection, genetic variations and bottlenecks, biochemical reactions, quarks and electro-weak forces. In the classical reductionist approach, local, binary interactions between systems are studied under controlled (i.e., isolated) conditions. The object of such analyses is to qualify, quantify and classify the feedback interactions, i.e., as deviation-amplifying or deviation-reducing feedbacks. The objective being to identify the deviation-reducing (negative) feedbacks that presumably provides the homeostatic stability of the systems of interest.

The maintenance of ecosystem homeostasis is usually attributed to the dominance of these local, deviation-reducing ("negative") feedback mechanisms (e.g., density-dependent mortality, natality, immigration/emigration and behavioral factors) relative to local, positive-feedback mechanisms (e.g., sexual selection, co-evolution, mutualism; Wiener 1962, Wynne-Edwards 1966, Patten and Odum 1981). However, in natural systems, the relationships between systems are quite numerous and complexly intertwined, with coupled sets of positive and negative feedback mechanisms, all embedded in a spatially, temporally and organizationally non-uniform context. In such systems, knowledge of the idealized local binary relationships between systems is insufficient to understand the behavior of the whole system.

This intrinsic difficulty of understanding complex systems has been appreciated for a long time in the mathematical/astronomical domain, under the guise of the "three-body" problem, which relates to the difficulty of predicting the time evolution of orbital motions when there are more than two interacting systems (Poincaré 1892). How one may integrate across webs (and not simple linear chains) of hierarchically structured feedbacks: some weak, some strong, some diffuse, and others quite specific is not a simple problem. (To be fair, advances have been made in (linear) network theory making it possible to untangle some of these complex webs but such approaches are limited to idealized (static) representations of interactions when in reality these interactions are highly dynamic and spatially explicit.) While we may be quite capable of taking things apart with alarming facility, we do not know how to put the pieces back together again: to synthesize and to apply the knowledge gained.

A tangible example may be found in our personal experiences with the difficulty in moving a cup filled with water, without spilling the water. This is due to the presence of time lags between movement of water, observation of movement, response to movement and the consequent movement of water, etc. Such temporal-spatial-organizational decouplings between action and reaction can result in an amplification of over-compensations, even though the negative feedback mechanisms involved generally provide functional, deviation-reducing results under other conditions. When muscles are fatigued, over-compensation becomes stronger still. Similar effects are observed in humans that have had neural damage (e.g., cerebral palsy, muscular dystrophy) or simple muscle fatigue (e.g., trembling after holding a heavy load). The amplification of over-compensations or "overshoots" of movement, due to physiological limitations in the firing rate of neurons or contraction of muscles (i.e., spatial-temporal-organizational complexity) are thought to be responsible for the trembling response (Wiener 1962, Beuter et al. 1993).

In ecological systems, the capricious nature of complex biological interactions is better known as "indirect effects" or "higher-order effects" (e.g., Forbes 1880, Patten 1983, Smith et al. 1997). As an example, we can look at the concept of competition, one of the reductionistic explanations of the size-abundance relationship (mentioned above). Competition is a cornerstone of mainstream reductionistic ecology; it finds its origins in the works of Malthus, Darwin and Wallace and its formalization in the classic reductionistic work of Gause (1934, who paradoxically subscribed to a holistic point of view). However, its influence upon natural systems at spatial-temporal-organizational scales larger than that of two species interactions in microcosms still remains a contested subject. Criticisms focus upon the importance of other biological factors such as predation (Paine 1966, 1974), parasitism, disease, mutualism, co-operation, dispersion (Kropotkin 1902, Wynne-Edwards 1966) and perturbations such as climatic fluctuations and natural catastrophes that keep a system from reaching an internal "equilibrium" (Andrewartha and Birch 1954).

Even for rather simple systems, it has been shown that indirect effects are quite important relative to the direct effects between systems (Patten 1983, 1985). Further complicating the situation is the virtual impossibility of perfect information of the present, past and future states of all simultaneously occurring interactions between systems (Smith et al. 1997), which generates an uncertainty or unpredictability of cause-effect (input-output) relationships that has been termed "pseudo-nonlinearity" (Patten 1983). The spatially, temporally and organizationally varying nature of the systems and their interactions add another layer of complexity that makes any attempt to understand a whole system via the extension of binary interactions quite a formidable task.

Our attempts to use chemical pesticides as a means of controlling pests represents another rather pointed example of the distinction that needs to be made between *idealised binary feedback mechanisms* (in an ideal reductionistic world where only binary mechanisms are important) and *realised feedback effects* (in a real experiential world where indirect, nonlinear and pseudo-nonlinear effects are also expressed). After an initial period of success in controlling pest organisms, there invariably results an explosion of the abundance of the pest species. This is frequently due to the adaptive response of the pests that develop resistance and the co-incident removal of other previously co-evolved or co-developed mechanisms of biological control (e.g., predators and disease). Thus, even though the idealized binary feedback mechanism was designed to control (stabilize or diminish) a pest population, the realized feedback effect was to act as a destabilizing, deviation amplifier. The reason for this "unexpected" behavior is due to the inherent spatial-temporal-organizational complexity of real systems ("pseudo-nonlinearity", "nonlinearity", "multi-causality" (networked) and context-dependent nature of ecological interactions).

Another well-known example of the importance of the complexity of real systems and the associated indirect effects is the predation by starfish upon the invertebrates of the inter-tidal community (Paine 1966, 1974). Starfish predation upon any particular species can be devastating, however, in the presence of multiple prey species, this effect is highly modulated. Watson and Lovelock's (1983) daisy-world model represents another well-known example of the importance of complexity and indirect effects. Many other examples of the importance of complexity and indirect effects exist: the outbreaks of pest populations (e.g., spruce-budworm) and their modulation by climatic variations, food availability and predation; social, cultural, economic and environmental modulations of the expressions of complex diseases such as HIV, influenza, tuberculosis (Lewontin 1991:43), plague, Lymes disease (Barbour and Fish 1993), chronic fatigue syndrome and even stomach ulcers (Marshall and Warren 1984, NIH 1994, Hamilton 2001).

To summarize, because their relationship is not a simple one, a clear distinction must be made between idealized (local, controlled) feedback mechanisms that are identified via reductionistic analyses and the actually realized (global, integrated) feedback effects that are identified via empirical observations. In other words, it is not enough to reductionistically determine the nature and strength of pairwise feedback mechanisms if one's goal is to understand real systems because the realized ecological feedback effects can and do switch between positive and negative feedbacks in rather complex and unpredictable ways.

2.3 Dealing with information overload

Due to these two formidable challenges (circularity and complexity), the need for alternate approaches to the study of ecosystems has been identified repeatedly in the past (refs). Unfortunately, these calls to action have yet to provide a real solution to these obstacles. The progeny of these calls has been an eclectic science that has come to be known as Systems Theory (this also includes Caswell and Levins qualitative networks, etc). However, before embarking upon how Systems Theory may or may not be able to help address these issues we must take a step back and define our concepts more clearly to reduce in some measure the circularity and complexity associated with ambiguous concepts.

As a means of dealing with this information overload, some have suggested that most details can be ignored. The suggestion is that at each level of organizational complexity (hierarchy), emergent patterns exist that are not directly predictable from knowledge of the component parts and their dynamics. These "holists" argue that the whole is greater than the sum of its parts and that study of systems should focus upon these emergent patterns. The practice of the *Scientific Method* (the cycle of hypothesis proposal and verification) is decidedly dominated by the reductionistic approach. However, an understanding of the reductionistic (idealized) relationships or interactions do not help us understand how they integrate and interact to create emergent (realized) systemic patterns such as homeostasis. This incompatibility between reductionistic mechanisms and emergent patterns is a limitation that has been repeatedly expressed. Even in the most trivial of systems, unexpectedly complex spatial, temporal or structural patterns are possible (large degrees of freedom). Add to this organizational complexity, the complexity of spatial and temporal patterns and the analysis, or even basic description of ecological systems becomes epistemologically, conceptually, logistically and financially intractable.

2.4 Network theory

2.5 Thermodynamics

2.6 Holons

3 Stability and homeostasis

Stable is derived from *estable* (Old French) which had its origins from *stabilis* (Latin) meaning to stand (i.e., not move). Its current usage has similar connotations of the quality of being difficult to change or alter.

Homeostasis is derived from *homoios* (Greek) meaning same, like, resembling and *stasis* (Greek) meaning to stand.

Depending upon context, the word or concept of stability is used in ways. In behavior and sociology, there are connotations of balance or being firmly established. In physics and chemistry, isotopes that are non-radioactive are referred to being stable and has connotations of the lack of reactivity of chemical species or how much energy of activation is required to move another state. In applied mathematics, numerical stability refers to the robustness of an estimate or method of estimation of some quantity, and so has attached to it a notion of variance. In the context of differential equations, stability generally refers to the asymptotic behavior of a system near some area of interest (usually an *equilibrium* solution or "attractors").

3.1 Homeostasis – the stability of open systems

Why this interest in stability? Heraclitus would have us accept that the very essence of life revolves around change: evolution, extinction, speciation, succession. Perhaps, it is in trying to deal with this ever-changing that we become fascinated with the ever-standing? Living systems are open systems in that they exchange matter and energy with their environment. They are not stable in the static or thermodynamic sense as a crystal would be at absolute zero (i.e., a closed system). The stability of such open systems is generally associated with the concept of *homeostasis*: the maintenance of some internal dynamic balance in the face of a variable, non-stationary, external environment (i.e., a local pseudo steady-state).

Homeostasis is a *local* concept because the *global* stability of an open system is not of interest as this is generally the fixed point (asymptotic) equilibria or in the case of thermodynamic systems, maximum entropy state. It is a *steady-state* concept because the system under consideration is an open system, dynamically interacting and reacting, maintaining a balance, usually (but not always) via some negative feedback control mechanism. It is a *pseudo* steady-state because the system under consideration is part of a larger system (environment) to which it interacts or reacts. The spatial scales are physically much smaller and temporal scales are much shorter than that of the embedding system.

Well appreciated examples include the control of sugar levels in the vascular system of plants and animals, control of body temperatures in homeotherms, and ionic balance in all biota.

. . . more examples?

3.2 Characteristic space-time scales

Homeostasis emphasizes this very dynamic nature of balance (i.e., a local pseudo-steady-state): it is a balance that is variable over space and time due to various changes stemming from external perturbations (stress response) or internal modifications of activity levels such as when an animal is sleeping, resting, active, running or in a diseased state (i.e., transient dynamics). It is not limited to a fixed operating point, although some mechanisms are severely constrained to operate within a very narrow range (e.g., in redox reactions). This is in strong contrast to a static *asymptotic equilibrium* connotation of stability that is presently omni-present in mathematics, physics and chemistry (i.e., an *asymptotic* concept such as the notion of a thermodynamic equilibrium or ground state when a system ceases to change due to the (asymptotic) degradation of energy gradients via exchange with its surrounding environment; or the (asymptotic) Liapunov stability – see below). Those heavily influenced by these fields commonly refer to the possibility of having multiple steady-states as "multiple equilibria".

This difference is quite important, although it is perhaps a matter of degree. To illustrate, let us define the characteristic space-time scale, τ, of a system as being some function, G, of the dominant length scales (system size) and time scales:

$\tau \sim G(\text{length}, \text{time})$

such that high values of τ denotes larger spatial scales and longer temporal scales and small τ denotes smaller spatial scales and shorter temporal scales. For example, system dynamics (processes) occurring at the organism level (e.g., a bee) generally much larger and longer than those of the atomic scales, though of of course they include them as well ($\tau_{\text{bee}} \gg \tau_{\text{atomic}}$). The characteristic space-time scales of our observation of the system, that is a whale, (τ_{obs}) are however constrained by the resolution of our technical instruments and our innate or institutional biases in perception. Currently, this observation scale spans a wide range from molecular to scales much larger than that of the system (bee): $\tau_{\text{obs}} \gg \tau_{\text{bee}}$. This makes tractable the study of asymptotic behavior as one can wait for transient dynamics to disappear (unless perhaps the system is highly nonlinear or oscillating with a complex periodicity). As a consequence, strong stability characterizations are possible as is the possibility of controlling the dynamics of such a system.

At the organism scale, the characteristic space-times scales of the system dynamics is generally near the same order as that of the information about the system ($\tau_{\text{information}} \approx \tau_{\text{system}}$). This makes possible the meaningful description and comprehension of both transient and asymptotic dynamics as both are important. The state of an organism can be easily be modified by other factors prior to reaching asymptotic stability (if it is ever reached). In fact it is information of transient dynamics that is used in feedback control mechanisms to return a system to some operating point. For such systems, intermediate strength stability characterizations are possible. The possibility of controlling such systems is therefore possible although weaker (but to the possibility of influence from other factors during the transient stages) than for systems operating at smaller time-scales.

If the space-time scales of the system of interest is increased to the level of populations, communities and ecosystems, the characteristic time scales of the system is generally much larger than that of the information we have about the system ($\tau_{\text{information}} \ll \tau_{\text{system}}$) resulting in an increased importance of transient dynamics. The study of asymptotic solutions becomes quite intractable as one does not have enough information to know if the system behavior being observed is that of a transient or an asymptotic dynamics. In fact, one may argue that transient dynamics are of very dominant interest to us as humans as we live and evolve in such time-frames. It is perhaps more appropriate in these systems to refer to a *local* steady state, because ($\tau_{\text{information}} \ll \tau_{\text{system}}$), it makes little sense to refer to the global asymptotic steady state. For such systems, only weak stability characterizations are possible.

3.3 Control mechanisms

In engineering systems, control is generally accomplished via a small number of interacting feedback mechanisms that provide a combined negative feedback control. A well known controller is the governor in a locomotive engine or the thermostat in a heating system or the control systems of boats and aircraft to maintain an orientation or position (in the face of variations in unbalanced forces such as winds, waves, loads, etc.). For a given system A, the engineering approach relies upon having high quality information about:

- clear objective functions (well-defined operational goals or “inputs”)
- the system state (“outputs” in engineering terminology)
- the controlling forces or mechanisms, one or more of which can be altered
- transient dynamics
- asymptotic steady-state

As with physiological homeostasis, strong operational objectives can be used to engineer a control mechanism. Engineering control approaches generally deal with systems of the first two kinds:

$\tau_{\text{information}} \gg \tau_{\text{system}}$

or

$\tau_{\text{information}} \approx \tau_{\text{system}}$

as information about these systems can be brought to bear upon controlling or understanding both transients and asymptotic dynamics. The high quality information about transients and asymptotics allows for careful development and repeated testing of control strategies and understanding of the mechanistic forces. Real statistical replicates are possible via controlled experiments.

In ecological systems, $\tau_{\text{information}} \ll \tau_{\text{system}}$ and so an information intensive approach to control is likely to be intractable. Information about all of the above is either entirely missing or at best, poorly understood. Real replicates are seldom attainable as not all sources of error can be controlled. Finally, whether ecological systems are guided by or optimizing some goal function is not known. While one may hear of the balance of nature, what this really means is far from being clear.

3.4 Objective or goal functions

Following from the introductory remarks upon the limits of axiomatic systems, one may expect that the concept of homeostasis may be difficult to rationalize based upon purely physiological axioms: What is physiological homeostasis? The maintenance of a stable internal mileu to allow optimal physiological function. Why optimal function?

If one accepts the neo-Darwinian principal of Natural Selection, the raison d'être of *homeostasis* for an organism would be quite simple: evolutionary fitness of individuals is enhanced with greater homeostatic capacity. It would seem plausible to conclude that individuals able to maintain a steady internal balance (i.e., "healthy") relative to those that are not (i.e., "sick", distressed or mal-adapted) would be reproductively more successful and produce more offspring that would survive to reproduce again reinforcing the selection for the homeostatic trait. Therefore healthy people should make more children that survive to reproduce than those that are not. Is this really the case?

Let us ignore for the moment the lower reproductive rates of region X, renowned for their healthy populations in contrast to the majority of people from the region Y that live in conditions rife with poverty, disease and poor health. Instead, let us begin with the more fundamental problem of whether or not it is possible to prove or disprove that *homeostasis* confers some evolutionary (fitness) advantage? Fundamental to the formalism of natural selection is the following well-known tautaulogy:

1. Those that are fit are those that survive and reproduce.
2. Those that survive and reproduce are fit.

That is, fitness and survival are self-referential (circular) concepts. This self-referential nature of concepts is a characteristic that the principle of natural selection shares with other axiomatic systems: logically unprovable statements will exist is any rational conceptual system. How does one proceed to explain the evolution of homeostasis when it is not possible to definitively prove or disprove that homeostasis provides an evolutionary fitness advantage? Perhaps the people of region X are being selected for another trait that dominates over the selection for homeostasis? Perhaps the prevalence of homeostasis is sufficient to indicate that it does provide an evolutionary advantage?

Perhaps.

Ultimately, the point is that the seeming clarity of the goal function in physiological homeostasis is not as clear as might have been initially assumed. The distinction between physiological and the ecological usage of the concept of homeostasis thus becomes less definitive. The definite advantage that physiological studies have over ecological studies is that the quality and quantity of information about physiological systems are order or magnitudes better as are the nature of the processes and forces controlling homeostatic behavior (transients and asymptotics).

Lovelock has argued that homeostasis may also be observed at a planetary scale (the Gaia hypothesis). In fact, he inverted the argument to say that any observation of planetary scale balance (homeostatic dampening of variations) will be indicative of a biotic system. (Of course there are problems with this kind of logical inversion as balance and dampening can occur through other mechanisms other than via biota? : Passive homeorhesis ? .. is this the case: .). To support his claim, he developed the Daisy-world model: a simple control mechanism where the relative abundance of dark and light daisies was able to regulate global temperatures due to their differing capacities to absorb or reflect solar radiation and habitat preferences. Note that the Daisy-world control mechanism is a passive control mechanisms and not an active (goal oriented). However to being understanding this to be the case, the time scales of the information describing the earth would need to be similar to that of the planetary dynamics or more ($\tau_{\text{planet}} \leq \tau_{\text{information}}$); i.e., stratigraphic evidence would be the most useful in elucidating homeostatic tendencies at planetary scales.

3.5 Ecological homeostasis

In ecology, the word *stability* has come to have so many different connotations that its utility in any technical sense is highly problematic. The large number of variations of the stability concept is confusing but directly related to the level of importance it has upon ecological thought. To make any such usage less ambiguous, it is useful to algebraically define these connotations at the outset:

To describe the stability, θ, of a system, S, after some perturbation, P (internal or external), let us define the following key quantities and symbols:

s_0 the reference state of S with which we are comparing

s_t the state of S at time t, where $t = 0$ is the onset of a perturbation and is positive definite

p the strength (magnitude, frequency) of a perturbing influence P

$\Delta s_t^p = s_t^p - s_0^p$ the magnitude of the effect upon the system due to a perturbation of size p after time t

Using the above notation, the primarily encountered connotations of stability (mostly after Pimm 19XX, Connell and Sousa 1983, Harrison 1979) can be heuristically defined as follows. The probability or likelihood of an event is expressed as $Pr(\cdot)$:

Liapunov (local) stability : $Pr(\Delta s^{p}_{t\to\infty} = 0)$

That is, will a system return to the reference state after a perturbation, asymptotically with time. In the standard analysis of stability of physical and model systems, the asymptotic Liapunov stability criterion is frequently used. The dynamical behavior near some reference point (s^R) after some small perturbation (Δs, where $s^R \gg |\Delta st|$). In the case where the reference point ($\mathbf{s}^{\boldsymbol{R}}$) is an (asymptotic) equilibrium point in ordinary differential equations and the deviation from the reference point decreases with time (i.e., $\boldsymbol{\Delta st} \to 0$ as $t \to \infty$), the system is said to be (asymptotically) Liapunov stable. Evaluation of stability is generally based upon the sign of the largest eigenvalue of the Jacobian matrix evaluated at an equilibrium point. Note that this approach exist in the time-domain: the spatial dimensions are completely ignored. The spatial distribution of a species or community or ecotype is very important, both in terms of total area covered as well as their connectivity and spatial structure. This requires explicit knowledge of s^{R} . Note also that what is meant by a “small” perturbation is ambiguous in real complex, multidimensional systems, especially when nonlinearities exist in functional relationships.

Amplitude : $\max(\ \Delta s[\Delta st = 0 \ \text{ as } \ t \to \infty\ ])$

The distance that can be moved and still return (to the reference state). This is therefore a re-statement of the Liapunov stability condition in terms of the magnitude of the perturbation to a system. This requires explicit knowledge of s^R.

Elasticity : $t^R[\Delta st = 0]$ or $\Delta st = 0$

The time required to return (to some reference state). This can be seen as a variant of the Resilience concept but formulated in terms of time. This requires explicit knowledge of s^R. This concept was defined as “resilience” by Pimm (1984).

Resilience : $\Delta s/\Delta t$ or max(Eig(M))

The rate of return to some reference state. In model systems of community dynamics, the largest eigenvalue of a community matrix M. This is a local concept (first derivative) that does not require explicit knowledge of s^R nor s^P. Classical usage in ecology is ... DeAngelis. In a more general systems theoretic approach, resilience can be considered an analogue of turnover rates or the ratio of boundary inputs (or outputs) to system size (e.g., Choi et al. used Respiration/Biomass).

Sensitivity to a perturbation : $(s^R - s_{t=0}p)/p$

Closely related to the “resistance” concept, the sensitivity to a pulse or press perturbation is a measure of the degree to which s changes, relative to the magnitude of the perturbation p.

Resistance :

The opposition to a change in system (as in a dissipative or frictional force). In electrical systems, it is the force opposing the flow of charge. In mechanical systems, the force opposing movement (as in frictional air resistance). As the notion of an ecological force is highly controversial, we may focus upon an index of the outcome of resistance: total dissipative energy loss (q; i.e., waste heat production) as a result of the perturbation (i.e., for the interval of initial perturbation t=0, to complete recovery t=t^R).

Robustness or hyper-stability : p[sr → sp]

The amount of perturbation a system can absorb before changing state. This refers the likelihood of the system not changing in the face of “normal” sized (generally encountered) perturbations and is quite akin to the notion of hyper-stability. This is therefore a variant of “Persistance” and “Inertia” where the focus is upon both the system and the perturbation (s and p). Implicit is the notion of alternate basins of attraction and external perturbations as a forcing function. This can only be known a-posteriori (when a system has already transitioned to an alternate state). This requires explicit knowledge of both the external forcing functions (p; e.g. nutrient loading) and the internal state (s). This concept has been championed as “Ecological resilience” by Holling and colleagues (e.g., Holling 1996 and to which he attributes to Walker et al. 1969). Further, in another terminological twist, Holling refers to Resilience ($\Delta s/\Delta t$ or max(Eig(M)) as defined above) as “Engineering Resilience”. Implicit in Holling’s “Ecological Resilience” and Robustness (p[sr $\rightarrow$ sp]) in general is the assumption that the basins of attraction of the complex dynamical systems are well-behaved semi-static basins (“regimes”) where the choice between one or a small number of alternate system “regimes” is determined by external perturbations that modify the internal functional diversity of the system and therefore the structure and control mechanisms of the system. Due to the presence of multiple equilibria implicit in Holling’s formulation, he considers systems to be “far from any equilibrium steady-state” such that “instabilities can flip a system into another regime of behavior (another stability domain)”. This concept is claimed to be derived from “inductive theory formation” obtained through the medium of intimate experience with the impacts of large-scale management disturbances (in contrast to the a narrow deductive mathematical tradition).

Persistence : t [s>0] or Pr(s>0)

The time a system exists (i.e., not extinct). It may also be a probability measure. Pimm (1984) suggests that the inverse of this time (1/t [s>0]) may be considered a measure of turnover. This concept is frequently associated with the invasability of a system and also the “sustainability” of a system (e.g., Costanza 1996 in the book Engineering within ecological constraints).

Constancy : f (var (s)) or f (CV (s))

The lack of change (i.e., changeability of a state measure, e.g. some function of variance). Intrinsic variability can occur (e.g., due to chaotic dynamics in even very simple systems of equations) and so the system even though being “stable” in terms of the governing parameters and dynamics can result in a large temporal variance. As a result, its relevance in determining the stability of the system is poor. It is however relevant for an external system that interacts with the system S. Some have suggested that this connotation does not refer/require the presence of perturbations (e.g., in nonlinear systems) but this is misleading as in all but the most contrived examples external and internal perturbations impinge upon the dynamics of an open system. Indeed the notion of stability is meaningless without perturbation.

Inertia : s

The resistance an object has to a change in its state of motion. This is a physical principle as in Newton’s First Law of Motion. The closely related concept of inertial mass is often used in physical systems: measuring the degree of resistance to changes in its velocity relative to its inertial frame of reference, *MASS=FORCE / ACCELERATION*. In ecology, MacArthur and Wilson’s theory of Island Biogeography considered the size of an island (system size) as a index of the likelihood of species extinction simply due to the inertial stability of larger systems with more biomass, habitat space, etc. Choi et al. (2001) used this inertial concept with the size of lakes in a thermodynamic context. For example, the removal of an individual in a system composed of individuals is much more influential than removing an individual from a system composed of 10^6 individuals – the latter system exhibits greater inertial stability.

There are many other variations and parameterizations possible, however these are the main concepts discussed in the literature. Each of these stability concepts focus upon a subset of the elements required for any discussion of stability: $\{s,\ p,\ t,\ sR\}$. In tabular form, the dependencies upon these core elements make the relationships between the various connotations clearer.

Table 1. A comparison of stability concepts.

From the above, two classes of stability connotations are evident. The first four connotations (Liapunov, amplitude, elasticity and resilience) relate to the system having been *already perturbed* in some manner and describes the manner in which the system *returns to* the reference state. The last six connotations (sensitivity, resistance, robustness, persistence, constancy and inertia) relate to a system that is *being challenged* in some fashion and describes the ability of the system *to hold on* and not change. Amongst the first class, heavy information requirements are evident for all but the concept of resilience which is more of a local concept of the rate of return to some reference state. Amongst the second class of stability concepts, heavy information requirements also exist for all but the last three (persistence, constancy and inertia).

By heavy information requirements, I am mostly referring to the need for a well defined reference state (sR) which is all but intractable except in modelled systems or the requirement for measures of the strength the perturbation p (in the case of robustness). Recall that ecological systems are generally characterized by the constraint: $\tau_{\text{information}} \ll \tau_{\text{system}}$. That is, one does not have enough information to know if the observed system behavior is that of a transient or an asymptotic. The reference state is changing with time in step with predatory, competitive, synergistic associations at space-time scales of ecological, evolutionary, climatic, biogeochemical and even planetary phenomena. This of course has accelerated during various epochs due to strong changes in inter-specific interactions (runaway evolutionary change e.g., sexual selection) and strong environmental fluctuations (e.g., ice ages) in various stages in the past; including the currently alarming rapid changes associated with the increasing dominance of humans in the last 10,000 years. The definition of the reference state is a-priori a difficult (impossible?) task. Just how far back in time should one go to find a reference state. In ecological systems the concept of a *quasi-local* steady state is much more relevant than that of the global asymptotic steady state(s): the choice of a very narrow window of time as a measuring stick allows the local consideration of stability characteristics.

Even if some reference time period could be identified, it is not clear how even the system state s is to be quantified. Simplistic approaches consider only the basic state variables: biomass, number per unit surface area or volume. However, ecological interactions being numerous and complex, network topology and structural and functional redundancies/capabilities are significant contributors the system state. Methods of multivariate data simplification exist but even these are simple approximations to a highly multidimensional, nonlinear and complex system state, s. So how to proceed?

4 Perturbation

To throw into confusion or disorder; agitation from an orderly or peaceful state; interference or noise to communication or wave pattern

Two ideas are germane:

1. order; and
2. degree of displacement from that order (i.e., disorder)

Tab. 1: *Stability definitions and proposed indices. The dependencies of the definitions to the core descriptive elements of stability are indicated. These are: measures of the state of a system* s*, the strength of a perturbation* p*, the time since the perturbation* t *and some reference state* s^R*.*

Stability concept	Proposed index	Dependencies				Description
		s	p	t	s^R	
Lianpunov	$Pr(\triangle s_t = 0\ [t \rightarrow \infty])$	x		x	x	Will a system *return to* the reference state after a small perturbation?
Amplitude	$max(\triangle s\ [\triangle s_t = 0\ as\ t \rightarrow \infty])$	x		x	x	The distance that the system can be moved and still *return to* the reference state.
Elasticity	$t^R\ [\triangle s_t = 0]$ or $\triangle s_t = 0$	x		x	x	The time required to *return to* some reference state.
Resilience	$\triangle s / \triangle t$	x		x		The rate of return to some reference state (no explicit need for s^R or s^P).
Sensitivity	$(s^R - s^P_{t=0})/p$	x	x	x	x	The degree to which the system changes, relative to the magnitude of the perturbation.
Resistance	$\sum_{t=0}^{t^R} q$	x		x	x	The opposition to a change in the system, measured as the dissipative heat loss resulting from the perturbation.
Robustness	$p[s^r \rightarrow s^p]$	x	x		x	The amount of perturbation a system can absorb before changing state.
Persistence	$t\ [s > 0]$	x		x		The time a system continues to exist (i.e., and not go extinct).
Constancy	$f(var(s_t))$ or $f(CV(s_t))$	x				The lack of change in state, some function of system variability (e.g., variance, or coefficient of variation).
Inertia	s	x				The degree of resistance to changes in the system's "velocity", relative to its intertial frame of reference.

That is, some measurable index of the degree of order/disorder must be explicitly defined. There are two approaches to this:

1. global
2. local

The global approach is untenable as it is very easy to define a ground state but relative change from the ground state is highly uninformative.

1. A perturbation is identifiable if it has a measurable change in effect (physical, biological or ecological). For example an object moving through space will continue to move unless it interacts with another object (i.e., some force associated with object B). This previously unexpected interaction (A-B) brought about by the sudden appearance of object B into the universe of A, modifies the kinetic and potential energies of A. This modification is a perturbation. Many measures of this perturbation is possible: a change in kinetic energy of A, a change in potential energy of A, some combination of changes in kinetic and potential energy, a change in trajectory of A, a change in the internal structure of A, a change in the internal processes in A, etc.
2. The important points are:

- There are many possible measures of change, internal to A … which is the correct one?

- There are many external measures of the perturbing influence B … what is the correct influence that *must be measured? Is there a correct measure?*

- There are many internal measures

Local order vs local disorder – the transformation of matter and energy being always inefficient, any creation of order (biomass, structured/organized flows) results in entropy production. The amount of entropy produced increases more rapidly than any order created. Thus the total entropy production rate is maximized (in + out). This is line with the MEPP.

4.1 Parameter

: (1) factor that defines a system and determines (or limits) its performance; (2) invariable constant

4.2 Attractor

Definition of state space .. funny diagrams of hill : what is the potential function? (A state variable?)

4.3 Basins of attraction

In the Holling school, resilience is seen as the robustness of a basin of attraction. A basin of attraction is the I.e., a system exists in a large definable state measured by it's hyper-area. The magnitude of the scale of parameter change/unit time » magnitude of system dynamics .. such that external parameters are slow changing or assumed constant. However, by the very nature of hierarchical organization, all system characteristics are in dynamic flux at all scales .. this is not necessarily a reasonable assumption. The result is that the form and size of the basins of attraction can change rapidly relative to the characteristic time scales of the within-system dynamics. This is especially the case when some keystone or dominant species is rapidly removed/replaced (I.e., over-fishing of groundfish, nutrient subsidized-agriculture). In such cases the characteristic time-scales of system internal dynamics and system external dynamics become comparable. The simple semi-stable basin analogy does not work.

The likelihood of systemic catastrophic (sensu Thom) change is increased when previously slowly changing externalities become fast-changing (i.e., when the whole fitness-landscape undergoes rapid fluctuations), relative to the internal dynamics of the system. Take for example the idea of climate change. Climate change is a fact of life: it has changed from the beginning of the formation of the earth and will continue to do so into the foreseeable future. What is currently at stake is the rapidity of this change, *relative to the characteristic time-scales of humans and other biota.* This relative rapidity of change is causing problems of adaptation. Rapid adaptive change does occur but there are organizational (i.e., structural and functional) constraints. This results in information overload. This in turn leaded to greater expressed complexity and expressed nonlinearity. The likelihood of systemic changes increases as new solutions are rapidly expressed and rejected until sustained solutions are found. Cusp-catastrophe changes result (e.g., a trophic cascade, or succession replacement) which seems orderly after-the-fact, leading to the observer to the perspective that only one of a few possible states are available to a system (i.e., with large basins of attraction, sensu Holling) where externalities can still be treated as a constant.

Thus what is really meant by resilience in the Holling school is that both the external parameters are relatively fixed (the characteristic time scales of system dynamics « that of externalities) and that the number of viable attractive basins are few in number and semi-stable. But when a major component of an ecosystem goes missing, does the structural parameters (governing dynamical forces) of the system remain the same. Perhaps so in a game where rules are fixed by some external body, but does it in a evolutionary game where the presence of a new set of genes (e.g., those associated with photosynthetic capacity) can dramatically catalyze changes to the whole evolutionary landscape and associated "external" parameters.

That is, there is a general lack of attention to the existence of a feedback loop between so-called external "parameters" and internal system state changes. Changes to one change the other. No scientist would argue for example that metabolic efficiency is a fixed parameter that itself does not evolve with time or even with ambient conditions (e.g., type of food ingested, prior state of health of organisms, genetic history, temperature variations, environmental stress from predation intensity or food scarcity, environmental toxicity from anoxia, redox potential changes).

Due however to the constant state of perturbation in ecological systems and their complexity, it has been argued by the Holling school that this is inappropriate as a measure of resilience. Instead, resilience represents in such more "ecological" sciences the likelihood of staying within the prior (multidimensional) basin of attraction and not moving to another. This is to be noted by looking at changes in the relative abundance of some keystone ("indicator") species.

Resilience has a clear quantifiable meaning as the return to some previous state. This definition is irrespective of whether the stable point is fixed or a more complex set of basins of attraction. This has been layered upon by Holling to mean many other things. This is unfortunate. The real trick is to identify and quantify this multidimensional previous state and some characteristic of this return (if any). In most of "non-ecological" sciences this has come to be measured by the characteristic time scale of the rate of return to the unperturbed state.

4.4 Relationship to SOC and network structure

small networks and critical behavior

Thermodynamic theory is conceptually and methodologically suited to the study of complex systems.

Its principles allow the study of the behavior of general systems with respects to how it may be EXPECTED to change. This time directionality is lacking in all other physical laws. The focal variable that describes this time sense is the irreversible loss of energy from a system (degradation of free energy into entropy).

When applied to systems open to the flow of matter and energy, a local, linearised formulation of the second law has been found to provide a similar directionality to change that guarantees the local stability of any given steady-state. Any form of creation of order (e.g. creation of structured flows, biomass) results in at the very least, a quadratic increase in entropy production For some, these factors are quite general (ref) while for others, these factors are system-specific and ungeneralisable (ref). The *systems* approach views such factors in the former manner.

Key ideas:

- general overview of what is meant by stability and associated terms
- intrinsic-extrinsic: measuring or defining externally determined (apriori) perturbations is ecologically meaningless. (A reaction to Kostolev's project on benthic mapping based upon temperature, depth and flow fields)
- other applications

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